ISSN 1881-9109
National Museum of Nature and Science Monographs No. 55

PALEOGENE MAMMALS FROM EUROPE: A Collection at the National Museum of Nature and Science

Edited by
Yukimitsu Tomida
Yuri Kimura

National Museum of Nature and Science, Tokyo
March, 2025

National Museum of Nature and Science Monographs

No. 55

Cover illustration:
Plagiolophus (*Paloplotherium*) *annectens* (Owen, 1848) from Baby.
(NMNS-PV 21432, incomplete skull, ventral view; see page 122 for further information)

PALEOGENE MAMMALS FROM EUROPE: A Collection at the National Museum of Nature and Science

Edited by

Yukimitsu Tomida

Yuri Kimura

National Museum of Nature and Science, Tokyo

March, 2025

National Museum of Nature and Science
Ueno Park, Tokyo 110–8718
Japan

Published on 25 March 2025
Printed by Kokusai Bunken Insatsusha Co., Ltd., Tokyo
ISSN 1881-9109
ISBN 978-4-87803-051-2

CONTENTS

CONTRIBUTORS

Naoko EGI

Department of Anthropology, National Museum of Nature and Science, Tsukuba, Ibaraki 305–0005, Japan. (e-mail: egicyon@gmail.com)

Yuri KIMURA

Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Ibaraki 305–0005, Japan. (e-mail: ykimira.research@gmail.com)

Kazunori MIYATA

Fukui Prefectural Dinosaur Museum, Katsuyama, Fukui 911–8601, Japan. (e-mail: k-miyata@dinosaur.pref.fukui.jp)

Yukimitsu TOMIDA

Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Ibaraki 305–0005, Japan. (e-mail: aztlanolagus@yahoo.co.jp)

Takehisa TSUBAMOTO

Earth Sciences, Graduate School of Science and Engineeing, Ehime University, Matsuyma, Ehime 790–8577, Japan. (e-mail: tsubamoto.takehisa.yt@ehime-u.ac.jp)

National Museum of Nature and Science Monographs, No. 55, pp. 1–2, 2025

INTRODUCTION

Yukimitsu Tomida

Department of Geology and Paleontology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: aztlanolagus@yahoo.co.jp)

National Museum of Nature and Science (previously National Science Museum) obtained a collection of Paleogene mammalian fossils of European localities from Mr. Nicolas Tourment of France in 1996 (called Tourment Collection hereafter). On the other hand, only several isolated fragmentary mammalian fossils have been known from the Paleogene sediments in Japan up to the early 1990s. Discoveries of the early/middle Eocene and late Eocene mammalian faunas started one after another in Kumamoto and Hyogo prefectures in the early to late 1990s (Miyata and Tomida, 1998a, b; Miyata *et al.*, 2011, and references in it; Tsubamoto *et al.*, 2007; Saegusa and Tanaka, 2010, and references in it). They include rather well preserved mammalian fossils of perissodactyls, artiodactyls, tillodonts, primates, and rodents, etc. Also, some research groups from Japan recently started working on the Paleogene mammals in Myanmar and other countries. However, virtually no comparative material (especially original specimens) was available in Japan. Thus, the National Museum of Nature and Science decided to publish the Tourment Collection as a reference of original comparative material in 2024.

The Tourment Collection consists of the mammalian fossils from rather well known localities in Europe, covering from the Paleocene to Oligocene (plus just a few specimens from Miocene), and the majority is the Eocene perissodactyls and artiodactyls. Some marsupials, primates, creodonts, carnivorans, "condylarths", and rodents are also included. Therefore, four authors divided the Tourment Collection into five groups: perissodactyls (Miyata), artiodactyls (Tsubamoto), primates+carnivores (Egi), and marsupials, "insectivorans", chiropterans, and rodents (Tomida), with the "condylarths" (Tomida and Egi). All authors studied and identified the specimens with not only published literatures but also direct comparisons with the original specimens stored in the museums and universities in France and England, in addition to the discussions with researchers in those institutions (see acknowledgement of each chapter). Each specimen was identified at the most recent taxonomic status, measured, illustrated with photos, and given some comments. Thus, this volume can be a good reference to identify and to understand most recent status of the Paleogene mammals from Europe.

The manuscripts of all chapters in this monograph were almost completed by January 2011, but the publication was delayed due to various reasons. Although the publication was finally accepted by the museum as mentioned above, time was not enough to update the manuscripts. Thus, each chapter does not include the references published after 2011.

Mr. Nicolas Tourment who collected the specimens included in this volume was bone in 1963 and was interested in fossils since he was only 6 or 7 years old. Since he was 18, he started collecting Eocene mammalian fossils mainly from southern France. This is why the Tourment Collection consists mainly of fossils from the localities there. He is rather serious fossil collector. For example, he has donated and/or lent some of his collections to museums for research and exhibits, including some Oligocene bird fossils from southern France (Louchart *et al.*, 2007, 2010).

All specimens of the Tourment Collection were cataloged before the museum name in English

was changed, and they are numbered with the acronym NSM-PV (e.g. Fig. 4 of Chap.7 and Fig. 15 of Chap. 8), which stands for the National Science Museum, Paleontology, Vertebrates. However, we use "NMNS-PV" on the catalog numbers in this volume, because it is the official acronym now.

Special thanks go to Ms. Hiroko Nagaoka and Ms. Sonoko Suzuki (both National Museum of Nature and Science), and Ms. Emma Dangerfield (University of Tsukuba) for inputting all the specimen data of the Tourment Collection into the Collection Database of Specimens and Materials of the National Museum of Nature and Science.

Literatures Cited

Louchart, A., N. Tourment, J. Carrier, T. Roux, and C. Mourer-Chauviré, 2007. Hummingbird with modern feathering: an exceptionally well-preserved Oligocene fossil from southern France. Naturwissenschaften, DOI 10.1007/s00114-007-0309-0

Louchart, A, N. Tourment, and J. Carrier, 2010. The earliest known pelican reveals 30 million years of evolutionary stasis in beak morphology. Jour. Ornithol., DOI 10.1007/s10336-010-0537-5

Miyata, K. and Y. Tomida, 1998a. A new tillodont from the early Middle Eocene of Japan and its implication to the subfamily Trogosinae (Tillodontia: Mammalia). Paleontogical Research, **2**(1): 53–66.

Miyata, K. and Y. Tomida, 1998b. *Trogosus*-like tillodont (Tillodontia, Mammalia) from the early Middle Eocene of Japan. Paleontogical Research, **2**(3): 193–198.

Miyata, K., Y. Tomida, K. C. Beard, G. F. Gunnell, H. Ugai, and K. Hirose, 2011. Eocene mammals from the Akasaki and Nakakoshiki formations, western Kyushu, Japan: preliminary work and correlation with Asian land mammal ages. Vertetrata PalAsiatica, **49**(1): 53–68.

Saegusa, H. and S. Tanaka, 2010. Preliminary notes on mammalian fossils of the Yokawa Formation of the Kobe Group and the sedimentary facies at the excavation sites. Journal of Fossil Research, **42**(2): 83–94 (in Japanese).

Tsubamoto, T., T. Matsubara, S. Tanaka, and H. Saegusa, 2007. Geological age of the Yokawa Formation of the Kobe Group (Japan) on the basis of terrestrial mammalian fossils. Island Arc, **16**: 479–492.

National Museum of Nature and Science Monographs, No. 55, pp. 3–7, 2025

Chapter 1

LOCARITY INFORMATION

Yukimitsu Tomida[1)], Naoko Egi[2)], and Yuri Kimura[3)]

[1)] Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: aztlanolagus@yahoo.co.jp)
[2)] Department of Anthropology, National Museum of Nature and Science, Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: egicyon@gmail.com)
[3)] Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: ykimira.research@gmail.com)

Each of mammalian fossil localities in Europe is identified in general by its own name (or nick name), so that it is fairly easy to recognize a specific locality (or site) by its name, at least for specialists of fossil mammals. The Tourment Collection consists of the mammalian fossils from 13 localities, 10 of which are in France, two are in England, and one in Germany (Fig. 1). Except for one in Germany, other 12 localities are rather famous ones, and some of them such as Berru, Aumelas, Robiac, Le Bretou, and Baby are listed as standard levels of MP (European Paleogene land mammal) zones or reference localities of each zone by Schmidt-Kittler (1987).

Name of the locality, administrative unit, stratigraphy, geologic age, latitude and longitude, and some geologic information of each locality are listed below. Order of the localities is based on the geologic age (MP numbers), from the oldest to the youngest. The latitude and longitude coordinates of each locality are approximate, which were indicated in the Paleobiology Database (Alroy *et al.*, 2001; http://paleodb.org; the data downloaded in February 2011) and Hooker *et al.* (2009).

We understand that three localities in France, Aumelas, Robiac, and La Débruge, are currently protected as geological parks and that paleontological resources from these localities have been preserved since the protection law went into effect. Thus, we requested Mr. Francois Escuillie, an expert of fossil mammal collecting in France, to examine the Tourment Collection in December 2022. He confirmed that Mr. Nicholas Tourment had collected fossils from each locality before the protection law became effective. For example, he was certain that Mr. Tourment collected fossils between 1980 and 1984 from La Débruge, which has been protected since 1987. Based on the information given by Mr. Escuillie, Dr. Philippe Guillet (former vice-chairman of the French section of ICOM and vice-chairman of the International Natural History Committee of ICOM) sent us a statement that our acquisition of Mr. Tourment's fossil collection is perfectly legal (pers. comm., May 24, 2023).

1. Berru

Administrative unit: Reims, Marne, Champagne-Ardenne, France. See Savage and Russell (1983, p. 35) for a map.

Stratigraphy: Cernay Formation. For the stratigraphic profile of Berru and Cernay, see Savage and Russell (1983, p. 32).

Age: late Paleocene (Thanetian). European mammal zone MP 6 (Schmidt-Kittler, 1987).

Latitude and longitude: 49.3°N, 4.2°E.

Environment and lithology: fluvial; conglomerate.

Primary reference: D. E. Russell, 1981. Un primate nouveau du Paléocène supérieur de France.

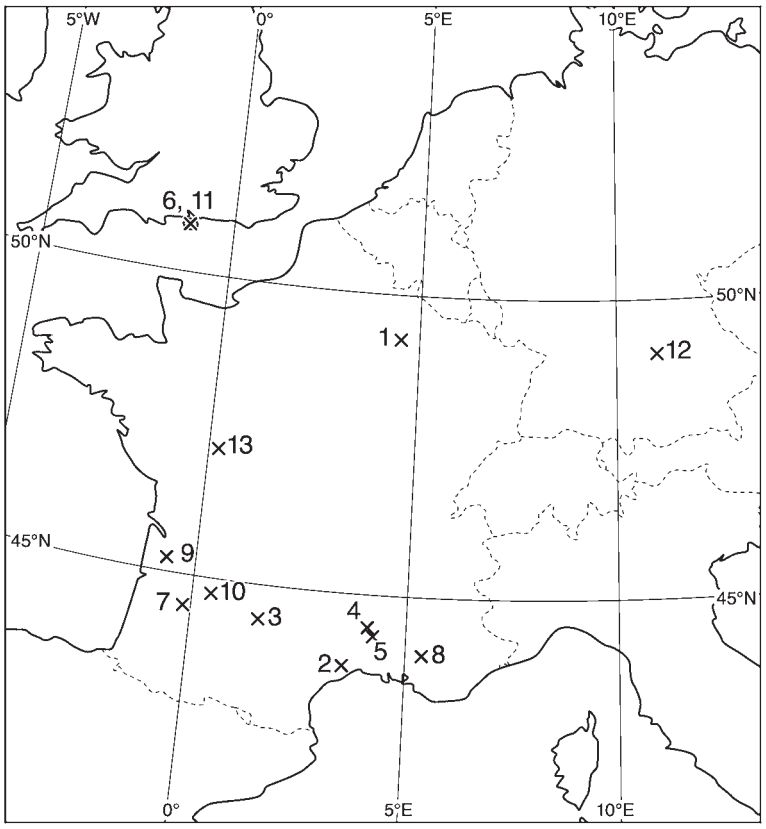

Figure 1. Map showing the localities from which the mammalian fossils of Tourment Collection were collected. 1. Berru, 2. Aumelas, 3. Le Bretou, 4. Robiac, 5. Euzet les Bains, 6. Headon Hill, 7. Baby, 8. La Débruge, 9. Civrac de Blaye, 10. St. Capraise d'Eymet, 11. Hamstead Beds, 12. Name unknown, 13. Faluns de Touraine.

Geobios, 14(3): 399–405.

2. Aumelas

Administrative unit: Hérault, Montpellier, Languedoc-Roussillon, France.

Age: middle Eocene (Lutetian). European mammal zone MP 13 (Schmidt-Kittler, 1987).

Latitude and longitude: 43.6°N, 3.6°E.

Environment/lithology: lacustrine, lithified limestone.

Primary reference: J.-L. Hartenberger, B. Sigé, and J. Sudre, 1969. Les gisements de vertebres de la region montpellieraine; 1. Gisements eocenes. Bulletin du B.R.G.M. (Bureau de recherche Geologique et Miniere), 1(1): 7–18.

3. Le Bretou

Administrative unit: Tarn-et-Garonne, Midi-Pyrenees, France.

Stratigraphy: a part of Phosphorites du Quercy.

Age: late middle Eocene (Bartonian). European mammal zone MP 16, Robiac standard zone (Schmidt-Kittler, 1987).

Latitude and longitude: 44.2°N, 1.7°E.

Environment/lithology: karst; phosphorite. Fossils are indicative of a dense, equatorial forest envi-

ronment and a warm and moist climate.

Primary reference: J.-Y. Crochet, J.-L. Hartenberger, J.-C. Rage, J. A. Remy, B. Sigé, J. Sudre, and M. Vianey-Liaud, 1981. Les nouvelles faunes de vertebres anterieurs a la "Grande Coupure" decouvertes dans les phosphorites du Quercy. Bulletin du Museum national d'Histoire Naturelle de Paris, 3(3): 245–266.

4. Robiac

Administrative unit: Bessèges, Alès, Gard, Languedoc-Roussillon, France.

Age: late middle Eocene (Bartonian). European mammal zone MP 16, Robiac standard zone (Schmidt-Kittler, 1987).

Latitude and longitude: 44.3°N, 4.1°E.

Environment: terrestrial.

Primary reference: P. Louis and J. Sudre, 1975. Nouvelles donnees sur les primates de l'Eocene superieur europeen. Colloque international CNRS, Problemes actuels de paleontologie - evolution des vertebres, (218): 805–828.

5. Euzet les Bains

Administrative unit: Vézénobres, Alès, Gard, Languedoc-Roussillon, France.

Age: late Eocene (Priabonian). European mammal zone MP 17 (Schmidt-Kittler, 1987).

Latitude and longitude: 44.1°N, 4.2°E.

Environment: terrestrial.

Primary reference: P. Louis and J. Sudre. 1975. Nouvelles donnees sur les primates de l'Eocene superieur europeen. Colloque international CNRS, Problemes actuels de paleontologie - evolution des vertebres, (218): 805–828.

6. Headon Hill

Administrative unit: West end, Isle of Wight, England.

Stratigraphy: just under the How Ledge, Totland Bay Member, Headon Hill Formation, Salent Group.

Age: late Eocene (Priabonian). European mammal zone MP 17; polarity chron C16n-2r, ca. 36.4 Ma (Hooker *et al.*, 2009, figs. 3-4).

Latitude and longitude: 50°40′ N, 1°34′ W.

Environment: terrestrial.

Primary reference: J. J. Hooker, S. T. Grimes, D. P. Mattey, M. E. Collinson, N. D. Sheldon, 2009. Refined correlation of the UK Late Eocene—Eraly Oligocene Solent Group and timing of its climate history. Geol. Soc. America, Spec. Pap., 452: 179–195.

7. Baby

Administrative unit: Sainte-Foy-la-Grande, Libourne, Gironde, Aquitaine, France.

Age: late Eocene (Priabonian). European mammal zone MP 17 or MP 20 (Schmidt-Kittler, 1987). There are two localities at Baby, Baby 1 and Baby 2, each of which is correlated to MP 17 and MP 20, respectively (Schmidt-Kittler, 1987). Although locality data of the Tourment Collection do not specify which locality, based on the fossil taxon from this locality, it is more likely the Baby 1, which is correlated to MP 17 (see *Plagiolophus* (*Paloplotherium*) *annectens* section in chapter 6).

Latitude and longitude: 44.4°N, 0.2°W.

Environment: terrestrial.

Primary reference: J. Sudre, 1978. Les artiodactyles de l'Eocene moyen et superieur d'Europe

occidentale; systematique et evolution. Memoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Etudes, 7: 1–229.

8. La Débruge

Administrative unit: Apt, Vaucluse, Alpes-Côte d'Azur, France.

Age: late Eocene (Priabonian). European mammal zone MP 18 (Schmidt-Kittler, 1987).

Latitude and longitude: 43.9°N, 5.4°E.

Environment/lithology: mire or swamp; black, sandy marl.

Primary reference: L. de Bonis, 1964. Etude de quelques mammiferes du Ludien de la Debruge (Vaucluse). Annales de Paleontologie (Vertebres), 50(2): 121–154.

9. Civrac de Blaye

Administrative unit: Saint-Savin, Blaye, Gironde, Aquitaine, France.

Age: late Eocene (Priabonian); European mammal zone MP 18 (Schmidt-Kittler, 1987).

Latitude and longitude: 45.1°N, 0.7°W.

Primary reference: M. Richard, 1946. Contribution a l'étude du basin d'Aquitaine, Les Gisements de Mammiferes Tertiares. Memoires de la Societe Geologique de France, Nouvelle Serie, 24(52): 1–380.

10. St. Capraise d'Eymet

Locality: Eymet, Bergerac, Dordogne, Aquitaine, France.

Age: late Eocene (Priabonian). European mammal zone MP 20 (Schmidt-Kittler, 1987).

Latitude and longitude: 44.7°N, 0.4°E.

Primary reference: M. Brunet, 1977. Les mammifères et le problème de la limite Eocène-Oligocène en Europe. Géobios, Mém. spécial 1: 11–27.

11. Hamstead Beds

Administrative unit: Northwest shoreline, Isle of Wight, England.

Stratigraphy: lower part of Upper Hamstead Member, Bouldnor Formation, Salent Group.

Age: early Oligocene (Ruperian). European mammal zone MP 21; polarity chron C13n–C12r; ca 33.2 Ma (Hooker *et al.*, 2009, figs. 3–4).

Latitude and longitude: 50°43′ N, 1°26′ W.

Environment: terrestrial.

Primary reference: J. J. Hooker, S. T. Grimes, D. P. Mattey, M. E. Collinson, N. D. Sheldon, 2009. Refined correlation of the UK Late Eocene—Eraly Oligocene Solent Group and timing of its climate history. Geol. Soc. America, Spec. Pap., 452: 179–195.

12. Locality name unknown

Administrative unit: Pappenheim?, Mittelfranken, Bayern Province, Germany.

Age: early Oligocene (Rupelian).

Latitude and longitude: 49°N, 11°E.

13. Faluns de Touraine

Administrative unit: Sainte-Maure-de-Touraine, Chinon, Indre-et-Loire, Centre, France.

Age: basal part of middle Miocene (Langhian). European mammal zone MN 5 (Steininger *et al.*, 1996).

Latitude and longitude: 47.1°N, 0.2°E.

Primary reference: L. Ginsburg and P. Janvier, 1975. Les mammiferes marins des faluns de la Touraine et de l'Anjou: faune, gisements et paleobiologie. Bulletin Society E. sci. Anjou, N. S., 9: 73–96.

Literature Cited

Alroy, J., C. R. Marshall, R. K. Bambach, K. Bezusko, M. Foote, F. T. Fürsich, T. A. Hansen, S. M. Holland, L. C. Ivany, D. Jablonski, D. K. Jacobs, D. C. Jones, M. A. Kosnik, S. Lidgard, S. Low, A. I. Miller, P. M. Novack-Gottshall, T. D. Olszewski, M. E. Patzkowsky, D. M. Raup, K. Roy, J. J. Sepkoski, Jr., M. G. Sommers, P. J. Wagner, and A. Webber, 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. *Proceedings of the National Academy of Sciences*, 98: 6261–6266.

Hooker, J. J., S. T. Grimes, D. P. Mattey, M. E. Collinson, and N. D. Sheldon, 2009. Refined correlation of the UK Late Eocene—Eraly Oligocene Solent Group and timing of its climate history. *Geol. Soc. America, Spec. Pap.*, 452: 179–195.

Savage, D. E. and S. E. Russell, 1983. *Mammalian paleofaunas of the world.* Addison-Wesley Publ. Co., London, 432 pp.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A* , 10: 1–312.

Steininger, F. F., W. B. Berggren, D. V. Kent, R. L. Bernor, S. Sen, and J. Agusti, 1996. Circum Mediterranean Neogene (Miocene and Pliocene) marine-continental chronologic correlations of European mammal units and zones. *In* Bernor, R. L., V. Fahlbusch, and H. W. Mittmann (eds.), *The evolution of western Eurasian Neogene mammal faunas*, Columbia Univ. Pr., New York, p. 7–46.

National Museum of Nature and Science Monographs, No. 55, pp. 9–17, 2025

Chapter 2

MARSUPIALIA, “INSECTIVORA”, AND CHIROPTERA

Yukimitsu Tomida

Department of Geology and Paleontology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: aztlanolagus@yahoo.co.jp)

Introduction

Marsupial, “insectivore” and chiropteran material treated in this chapter consists of six species from Le Bretou and Robiac in France. Majority of the specimens from Le Bretou are in situ on the dentary (exceptions are two upper molars), while those from Robiac are all isolated teeth.

Measurements of the specimens are shown in Tables 1 and 2.

Abbreviations: R, right; L, left; P/p, upper/lower premolar; M/m, upper/lower molar; 1/2, 1 or 2.

Systematic Paleontology

Supercohort Marsupialia Illiger, 1811
Cohort Ameridelphia Szaley, 1982
Order Didelphimorpha Gill, 1872
Family Didelphidae Gray, 1821
Subfamily Herpetotheriinae Trouessart, 1879
Genus *Amphiperatherium* Filhol, 1879

Amphiperatherium bourdellense Crochet, 1979

(Fig. 1; Table 1)

Material: NMNS-PV 21146, right M2; NMNS-PV 21145, left dentary w/ m3-4; NMNS-PV 21147, left dentary w/ m1-3; NMNS-PV 21150, right dentary w/ m3-4.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France).

Table 1. Measurements of marsupial specimens from Le Bretou and Robiac (in mm)

Specimen number	Tooth identification	Length	Width	Specimen number	Tooth identification	Length	Width
Amphiperatherium bourdellense							
NMNS-PV 21145	L m3	—	0.92	NMNS-PV 21147	L m2	1.44	0.86
	L m4	1.72	0.92		L m3	—	—
NMNS-PV 21146	R M2	1.68	2.04	NMNS-PV 21150	R m3	1.44	0.82
NMNS-PV 21147	L m1	1.48	0.86		R m4	1.42	0.74
Peratherium sudrei							
NMNS-PV 21207	R m2?	1.76	0.82	NMNS-PV21212	L m1?	1.42	0.78
NMNS-PV 21208	L m2?	1.68	0.90	NMNS-PV 21213	R p2?	1.30	0.66
NMNS-PV 21209	R m2?	1.64	0.88	NMNS-PV 21214	L M2	1.64	2.08
NMNS-PV 21210	L m1/2	1.56	0.90	NMNS-PV 21215	L M2	1.60	2.04
NMNS-PV 21211	L m1/2	1.60	0.86	NMNS-PV 21216	L dP3	1.20	0.96

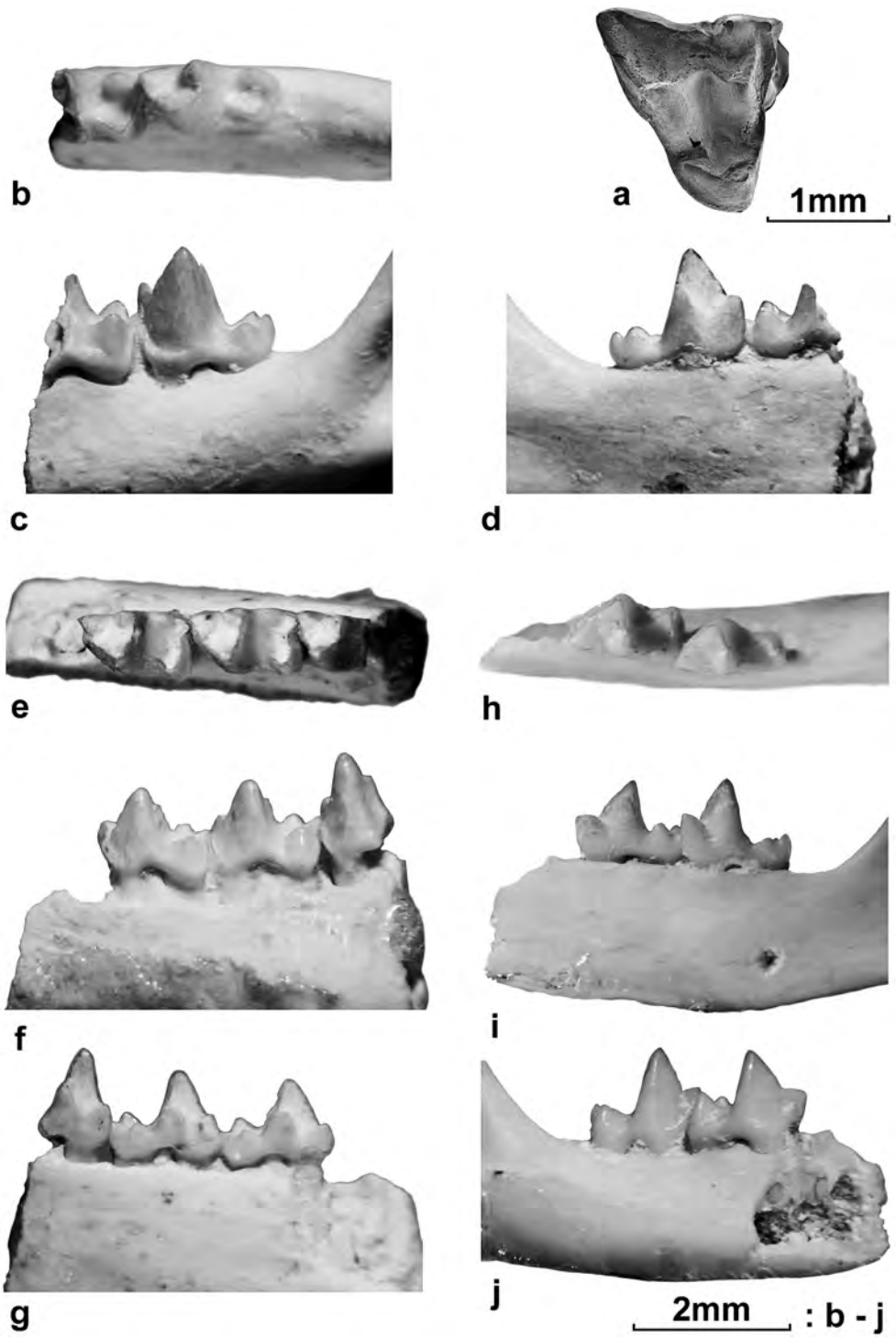

Fig. 1. *Amphiperatherium bourdellense* from Le Bretou
(a) NMNS-PV 21146, R M2; (b–d) PV-21145, L dent. w/ m3-4; (e–g) NMNS-PV 21147, L dent. w/ m1-3; (h–j) NMNS-PV 21150, R dent. w/ m3-4. a, b, e, h, occlusal views; c, f, j, buccal views; d, g, i, lingual views.

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Total of 12 species of the genus have been known in Europe since 1846, and it is not easy to identify based on the lower teeth. However, the M2 is characterized by the stylar cusp B well developed, other stylar cusps poorly developed, and a small gap is present between stylar cusps B and C, all of which and the size are indicative that the M2 belongs *A. bourdellense* (Crochet, 1979). This species was described based only on the specimens from Le Bretou (Crochet, 1979), thus all the dentaries are also included int this species, although NMNS-PV 21147 and 21150 are somewhat smaller than 21145.

Genus *Peratherium* Aymard, 1850

***Peratherium sudrei* Crochet, 1979**
(Fig. 2, Table 1)

Material: NMNS-PV 21207 to NMNS-PV 21216, 10 isolated cheek teeth. For the correspondence between the specimen number and the tooth identification, see table X.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Main cusps of the upper and lower molars are slenderly tall. On the upper molars, the buccal slopes of the paracone and metacone are not flat but possess shallow concavity, the metacone is quite higher than the paracone, the stylar cusp B is conspicuous, while C is poorly developed and seems like a ridge following B. The entoconid of the lower molars is conical (Crochet, 1980). These characteristics are indicative of the genus *Peratherium*. *Peratherium sudrei* is one of the smallest species of the genus known in Europe, and characterized by 1) the stylar cusp C poorly developed, and 2) the paraconid is tallest, metaconid is taller than protoconid, etc. (Crochet, 1980). The type specimen and the hypodigm of this species are from the Robiac south locality.

Supercohort Placentalia Owen, 1837
"Insectivora"
Family Nyctitheriidae Simpson, 1928
Subfamily Nyctitheriinae Simpson, 1928
Genus *Saturninia* Stehlin, 1941

***Saturninia mamertensis* Sigé, 1976**
(Fig. 3, Table 2)

Material: NMNS-PV 21217 and 21218, both right m1 or m2; NMNS-PV 21219, left m3.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Possibility of NMNS-PV 21217 and 21218 to be p4 is much less than that to be m1 or m2, because the paraconid is located posteriorly compared to m1 and m2. NMNS-PV 21219 is interpreted to be m3, because width of the tooth is narrower and especially the talonid is clearly narrower than the trigonid.

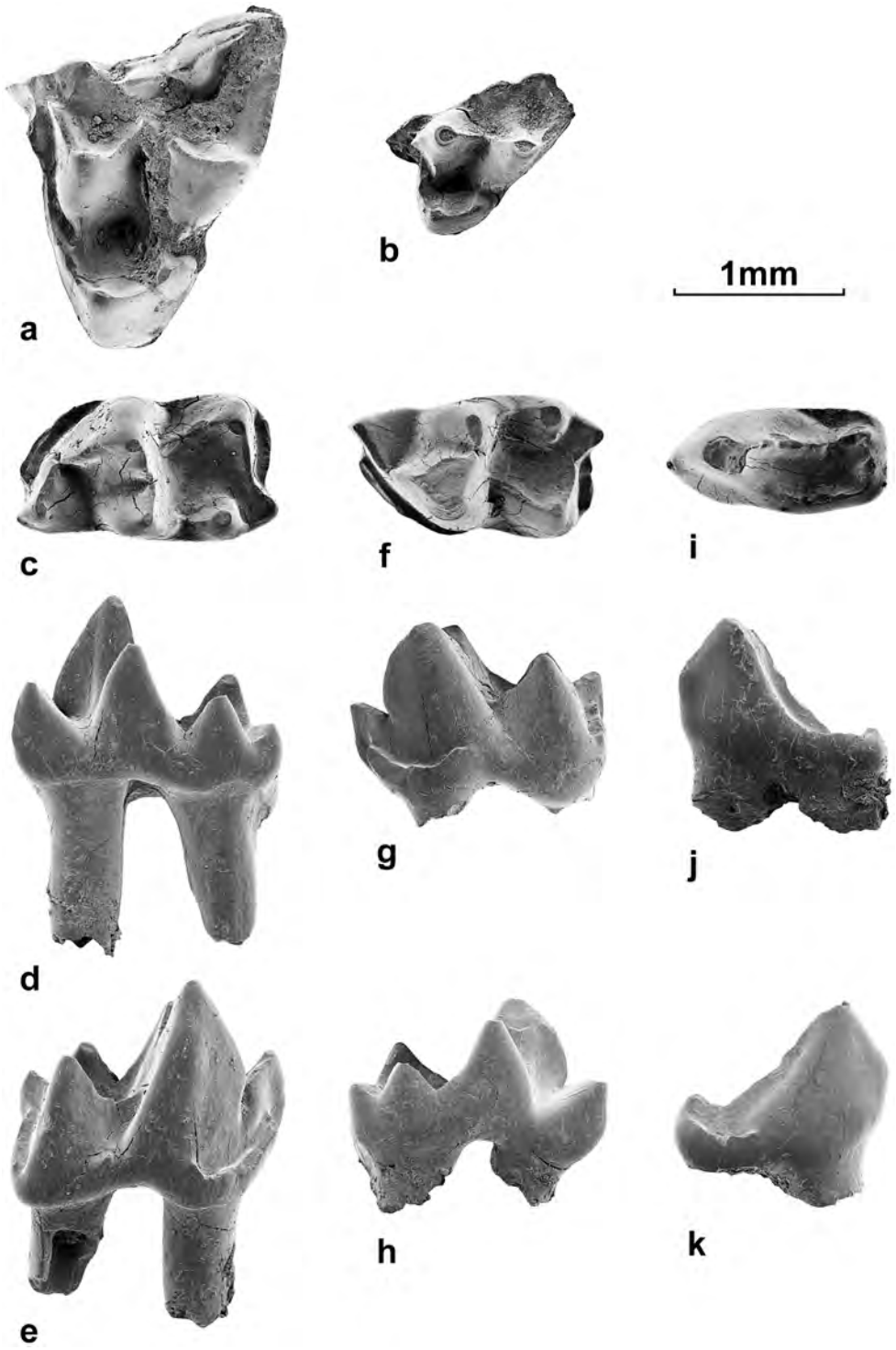

Fig. 2. *Peratherium sudrei* from Robiac
(a) NMNS-PV 21215, L M2; (b) NMNS-PV 21216, dP3; (c–d) NMNS-PV 21209, R m2; (f–h) NMNS-PV 21211, m1/2; (i–k) NMNS-PV 21213, R p2?. a, b, c, f, i, occlusal views; d, h, j, lingual views; e, g, k, buccal views.

Fig. 3. *Saturninia mamertensis* from Robiac
(a–c) NMNS-PV 21218, R m1/2. a, occlusal, b, buccal, and c, lingual views.

Table 2. Measurements of Nyctytheriidae specimens from Robiac and Chroptera specimens from Le Bretou (in mm)

Specimen number	Tooth identification	Length	Width	Specimen number	Tooth identification	Length	Width
Saturninia mamertensis							
NMNS-PV 21217	R m1/2	—	—	NMNS-PV 21219	L m3	1.00	0.60
NMNS-PV 21218	R m1/3	1.06	0.60				
Cryptotopos hartenbergeri							
NMNS-PV 21220	L m1?	1.62	1.06	NMNS-PV 21225	L P4	1.56	—
NMNS-PV 21221	L m2?	1.40	1.10	NMNS-PV 21226	L P4	1.64	—
NMNS-PV 21222	L p4	1.32	0.74	NMNS-PV 21227	R M1/2	1.48	1.96
NMNS-PV 21223	L p4	1.40	0.78	NMNS-PV 21235	R p3	1.20	0.62
NMNS-PV 21224	L p4	1.46	0.80				
Vespertiliavus sp. cf. *V. schlosseri*							
NMNS-PV 21144	R p4	2.06	1.08	NMNS-PV 21144	R m3	2.04	1.48
NMNS-PV 21144	R m1	2.36	1.52	NMNS-PV 21144	R m1~3	8.5	
NMNS-PV 21144	R m2	2.28	1.56	NMNS-PV 21148	L M2	2.24	3.02
Cf. *Hipposideros trassounius*							
NMNS-PV 21149	R m2	1.08	0.72	NMNS-PV21149	R m3	0.98	0.66

Genus *Cryptotopos* Crochet, 1974

***Cryptotopos hartenbergeri* (Sigé, 1976)**
(Fig. 4, Table 2)

Material: NMNS-PV 21220, left m1?; NMNS-PV 21221, left m2?; NMNS-PV 21222 ~ 21224, 3 left p4s; NMNS-PV 21225 and 21226, 2 left P4s; NMNS-PV 21227, right M1/2; NMNS-PV 21235, right p3.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: This species was originally described as a new species of the genus *Saturninia* by Sigé

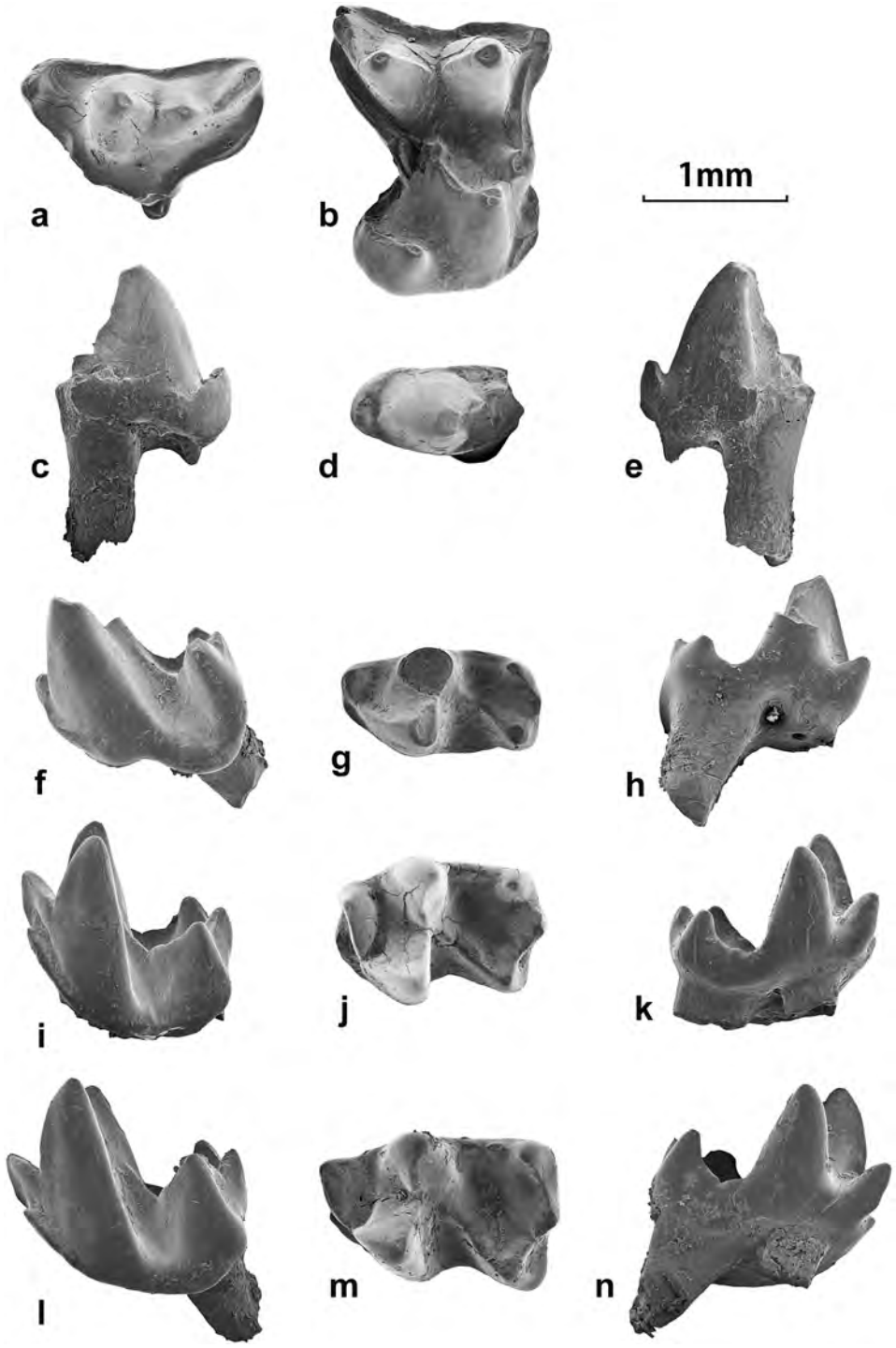

Fig. 4. *Cryptotopos hartenbergeri* from Robiac
(a) NMNS-PV 21226, L P4 frag.; (b) NMNS-PV 21227, R m1/2; (c–e) NMNS-PV 21235, R p3; (f–h) NMNS-PV 21222, L p4; (i–k) NMNS-PV 21221, L m1/2; (l–n) NMNS-PV 21220, L m1/2. a, b, d, g, j, m, occlusal views; c, f, i, l, buccal views; e, h, k, n, lingual views.

(1976), but Hooker and Weidmann moved this species to the genus *Cryptotopos* as a new combination (Hooker and Weidmann, 2000), and here I follow him. On the lower molars, the trigonid stands nearly vertically, and the hypoconulid is located medially. M1 or M2 (NMNS-PV 21227) possesses clear paraconule and metaconule. NMNS-PV 21225 and 21226 are fragmentally P4s, both missing approx. lingual half. Robiac is the type locality of this species.

Order Chiroptera Blumenbach, 1779
Suborder Microchiroptera Dobson, 1875
Family Emballonuridae Dobson, 1875
Genus *Vespertiliavus* Schlosser, 1887

***Vespertiliavus* sp. cf. *V. schlosseri* Revilliod, 1920**
(Fig. 5, Table 2)

Material: NMNS-PV 21144, right dentary with p4 m1-3; NMNS-PV 21148, left M2.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: NMNS-PV 21144 is very similar to this species in both the morphology (especially p4) and size (Sigé, 1988). Although the size of some teeth is within the known range of this species, it is closer to the smaller end, and the size of some other teeth is slightly less than the known range (Sigé, 1988). NMNS-PV 21148 (M2) is about 11-13 % smaller than the only specimen of M2 by Sigé (1988, p. 87), but NMNS-PV 21144 is also near the smaller end, NMNS-PV 21148 can be included in this species.

Family Hipposideridae Miller, 1907
Genus *Hipposideros* Gray, 1831

Cf. *Hipposideros trassounius* Sigé, 1988
(Fig. 5; Table 2)

Material: NMNS-PV 21149, right dentary fragment with m2-3.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Total of eight species of Chiropteran fossils are known from Le Bretou (Sigé, 1988). Among them, *H. trassounius* is the smallest species. The holotype possesses p4-m1 while NMNS-PV 21149 possesses m2-3, thus the direct comparison is not possible. All the referred specimens (except a single m1/2 = BRE2-748; Sigé, 1988) are somewhat larger than NMNS-PV 21149, but BRE2-748 (length, 1.10; width 0.69) is almost the same size of m2 (1.08 and 0.72) of NMNS-PV 21149. Based on the general morphology and the size (near the smallest end), NMNS-PV 21149 is likely referred to *H. trassounius*.

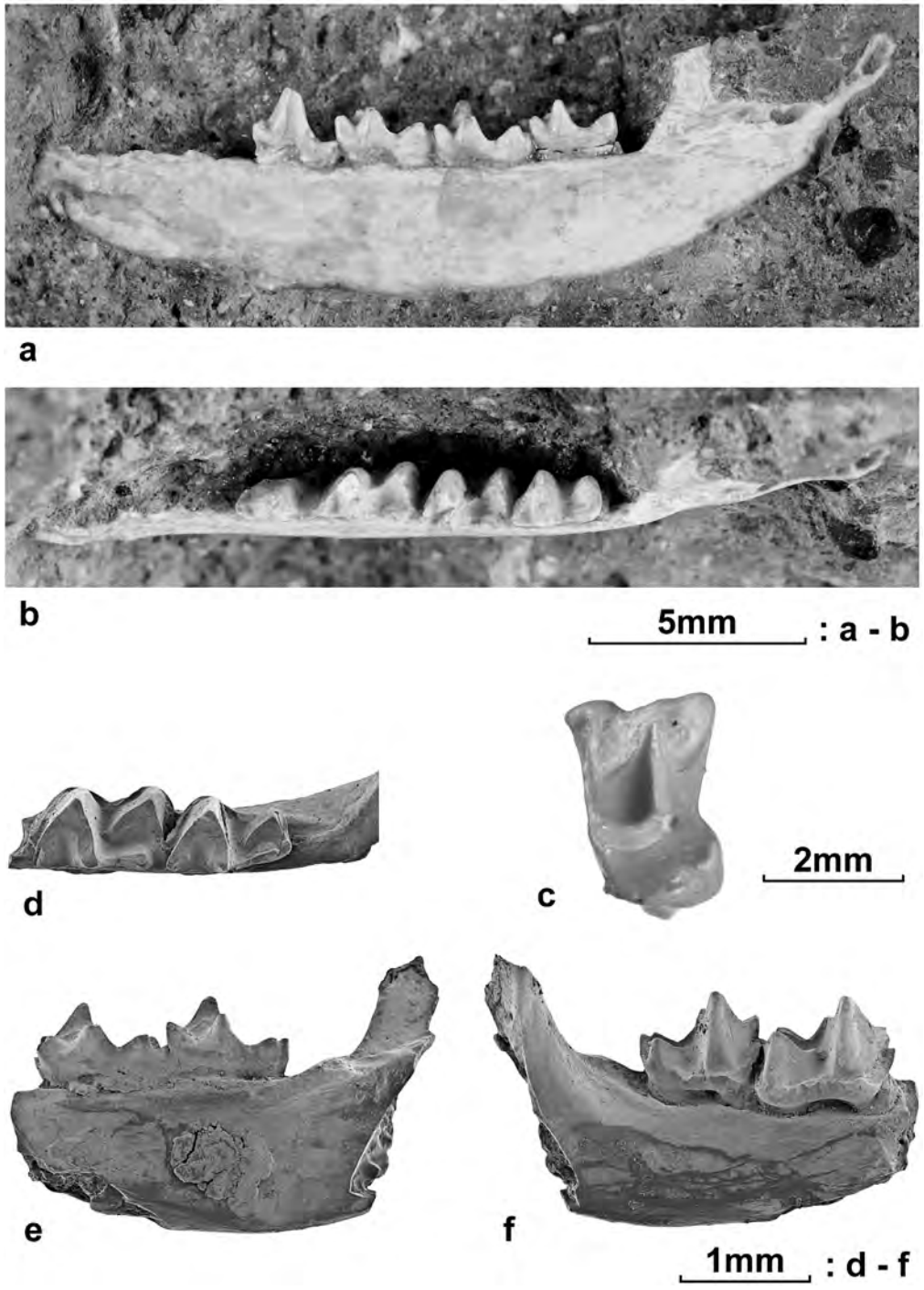

Fig. 5. Chiroptera from Le Bretou
Vespertiliavus sp. cf. *V. schlosseri*, (a, b) NMNS-PV 21144, R dentary frag. w/ p4 m1-3; (c) NMNS-PV 21148, L M2. Cf. *Hipposideros trassounius*, (d–f) NMNS-PV 21149, R dentary frag. w/ m2-3. a, e, lingual views; b-d, occlusal views; f, buccal view.

Acknowledgments

I thank Dr. Christine Argot of Muséum national d'Histoire naturelle, Paris for her great help and access of the comparative specimens.

Literature Cited

Crochet, J.-Y., 1979. Diversité systématique des Didelphidae (Masupialia) européens tertiaries. Géobios, **12**(3): 365–378.

Crochet, J.-Y., 1980. Les Marsupiaux du Tertiaire d'Europe. Ed. Fondation Singer-Polignac, Paris, 279 pp.

Hooker, J. J. and M. Weidmann, 2000. The Eocene mammal faunas of Mormont, Switzerland. Systematic revision and resolution of dating problems. Schweizerische Paläontologische Abhandlungen, **120**: 1–141.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A* , **10**: 1–312.

Sigé, B., 1976. Insectivores primitifs de l'Éocène supérieur et Oligocène inférieur d'Europe occidentale. Nyctithériidés. Mem. Mus. natl. d'Hist. nat. Paris, Ser. C, **34**: 1–140.

Sigé, B., 1988. Le Gisement du Bretou (Phosphorites du Quercy, Tarn-et- Garonne, France) et sa faune de vertebres de l'Eocene superieur. IV. Insectivores et Chiropteres. Palaeontograhica Abt. A, **205**: 69–102.

National Museum of Nature and Science Monographs, No. 55, pp. 19–27, 2025

Chapter 3

PRIMATES

Naoko Egi

Department of Anthropology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: egicyon@gmail.com)

Introduction

The taxa included in this chapter are divided into the Plesiadapiformes Simons and Tattersall, 1972 (cited in Simons 1972) and the Euprimates Hoffstetter, 1977. Living primates consists of the Strepsirrhini É. Geoffroy Saint-Hilaire, 1812 and the Haplorhini Pocock, 1918. The Euprimates includes the crown group that is defined by the Strepsirrhini and Haplorhini and a few fossil taxa that are closely related to the crown group (Rose, 2006). The Plesiadapiformes is a paraphyletic group, and is a sister group of the Euprimates (Silcox *et al.*, 2005). Ranks for some taxonomic groups within the order Primates may vary between researchers. The ranks used in this study follow those in Rose (2006, table 10.2).

The eight plesiadapiform specimens catalogued in this paper are *Plesiadapis tricuspidens* and are from the late Paleocene of France. Forty-two specimens are from two late middle Eocene (MP16) localities in France. These include adapids (*Adapis* and cf. *Leptadapis*) and omomyids (*Necrolemur* and *Pseudoloris*). The remaining one specimen is from the basal part of the Middle Miocene of France, and is identified as *Pliopithecus piveteaui*. The Pliopithecidae is a family in the Catarrhine Geoffroy Saint-Hilaire 1812, but its systematic position has been controversial (Begun, 2002).

Measurements of each specimen are shown in Table 1.

Abbreviations: P/p, upper/lower premolar; M/m, upper/lower molar.

Systematic Paleontology

Suborder Plesiadpiformes Simons and Tattersall, 1972
Family Plesiadapidae Trouessart, 1897
Genus *Plesiadapis* Gervais, 1877

Plesiadapis tricuspidens Gervais, 1877

(Fig. 1)

Material: NMNS-PV 21112, left mandibular fragment with p4-m3; NMNS-PV 21113, incisor; NMNS-PV 21114, right p3; NMNS-PV 21115, left m2; NMNS-PV 21116, left P4; NMNS-PV 21117, left P3; NMNS-PV 21118, right m2; NMNS-PV 21119, left M3.

Locality: Berru (Reims, Marne, Champagne-Ardenne, France).

Age: late Paleocene (Thantian). European mammal zone MP6 (Schmidt-Kittler, 1987).

Comments: The occurrence of *Plesiadapis tricuspidens* is limited to the MP6 level (Godinot, 1987). NMNS-PV 21113 to 21115 and NMNS-PV 21116 to 21119 may be associated.

Table 1. Measurements (in mm) of plesiadpiform and primate specimens.

Plesiadapis tricuspidens
NMNS-PV 21112: mandibular D below m1 = 9.6;
p4 L = 3.2, W = 3.6, H = 4.2;
m1 L = 4.3, W = 3.7;
m2 L = 4.9, W = 4.4;
m3 L = 7.4, W = 4.4.
NMNS-PV 21113: incisor L = 2.2, W = 2.6, H > 6.9 .
NMNS-PV 21114: p3 L = 3.5, W = 3.4, H > 4.1.
NMNS-PV 21115: m2 L = 5.2, W = 4.3.
NMNS-PV 21116: P4 L = 2.7, W = 4.2.
NMNS-PV 21117: P3 L = 2.9, W = 3.7.
NMNS-PV 21118: m2 L = 5.3, W = 4.8.
NMNS-PV 21119: M3 L = 4.1, W = 5.4.
Adapis sudrei
NMNS-PV 21242: mandibular D below m1 = 9.1;
p4 L = 4.9, W = 2.7;
m1 L = 4.0, W = 3.0;
m2 L = 5.1, W = 3.2;
m3 L = 6.2, W = 3.2.
NMNS-PV 21243: P2 L = 4.5*;
P3 L = 4.5, W = 3.7;
P4 L = 4.3, W = 4.4;
M1 L = 4.5, W = 5.4;
M2 L = 5.2, W = 5.9.
NMNS-PV 21245: M2 L = 5.3, W = 6.3.
NMNS-PV 21246: m1 L = 4.5, W = 3.1.
NMNS-PV 21247: p1 L = 2.9, W = 1.6, H = 3.1.
NMNS-PV 21249: p1 L = 4.2, W = 2.0, H = 3.8.
NMNS-PV 21250: P3 L = 3.7, W = 4.9.
NMNS-PV 21252: M1 or 2 L = 4.4, W = 5.4.
NMNS-PV 21253: p3 or 2 L = 4.4, W = 2.5, H > 3.0.
NMNS-PV 21254: p2 or 3 L = 4.7, W = 2.8.
NMNS-PV 21255: m1 or 2 L = 5.1*, W = 3.4*.
NMNS-PV 21256: m1 or 2 L = 5.0, W = 3.5.
NMNS-PV 21257: m1 or 2 W = 3.3*.
NMNS-PV 21258: m1 or 2 L = 4.1, W = 2.5.
NMNS-PV 21259: m3 L = 6.6, W = 2.8.
Cf. *Leptadapis* sp.
NMNS-PV 21263: p4 L = 6.8, W = 4.0.
Necrolemur sp. cf. *N. antiquus*
NMNS-PV 21151: right. mandibular D below m2 = 3.4;
m2 L = 2.5, W = 1.9;
m3 L = 2.5, W = 1.7.
NMNS-PV 21236: lower canine L = 1.5, crown L = 2.3, W = 1.3, H = 1.2.
NMNS-PV 21237: p3 L = 1.8, W = 1.4.
NMNS-PV 21264: p4 L = 3.5, W = 2.0.
NMNS-PV 21265: m2 L = 2.8, W = 2.2.
NMNS-PV 21266: m1 L = 2.5, W = 2.1.
NMNS-PV 1267: m1 or 2 L = 2.9, W = 2.1.
NMNS-PV 21268: M2 L = 2.2, W = 2.9.
NMNS-PV 21269: M3 L = 1.7, W = 2.3.
NMNS-PV 21270: M1 L = 2.5, W = 2.6.
NMNS-PV 21271: m3 L = 2.9, W = 2.0.
NMNS-PV 21272: m3 L = 2.4, W = 1.7.
NMNS-PV 21275: M3 L = 1.6, W = 2.3.
NMNS-PV 21280: m3 L = 2.3, W = 1.7.
NMNS-PV 21281: m3 L = 2.5, W = 1.7.
NMNS-PV 21282: m3 L = 2.6, W = 1.9.
NMNS-PV 21283: m3 L = 2.5, W = 1.6.
NMNS-PV 21300: P4 L = 2.0, W = 2.6.
Pseudoloris parvulus
NMNS-PV 21153: mandibular D below m1 = 1.8;
p3 L = 1.1, W = 0.7;
p4 L = 1.1, W = 0.8;
m1 L = 1.5, W = 1.0;
m2 L = 1.5, W = 1.1;
m3 L = 1.6, W = 1.0.
NMNS-PV 21152: mandibular D = 2.0;
p2? L = 0.9, W = 0.6;
p3? L = 1.2, W = 0.6.
Pliopithecus piveteaui
NMNS-PV 21664: M3 L = 6.6, W = 8.1.

Abbreviations: L = length, W = width, H = height, D = depth. *, estimate.

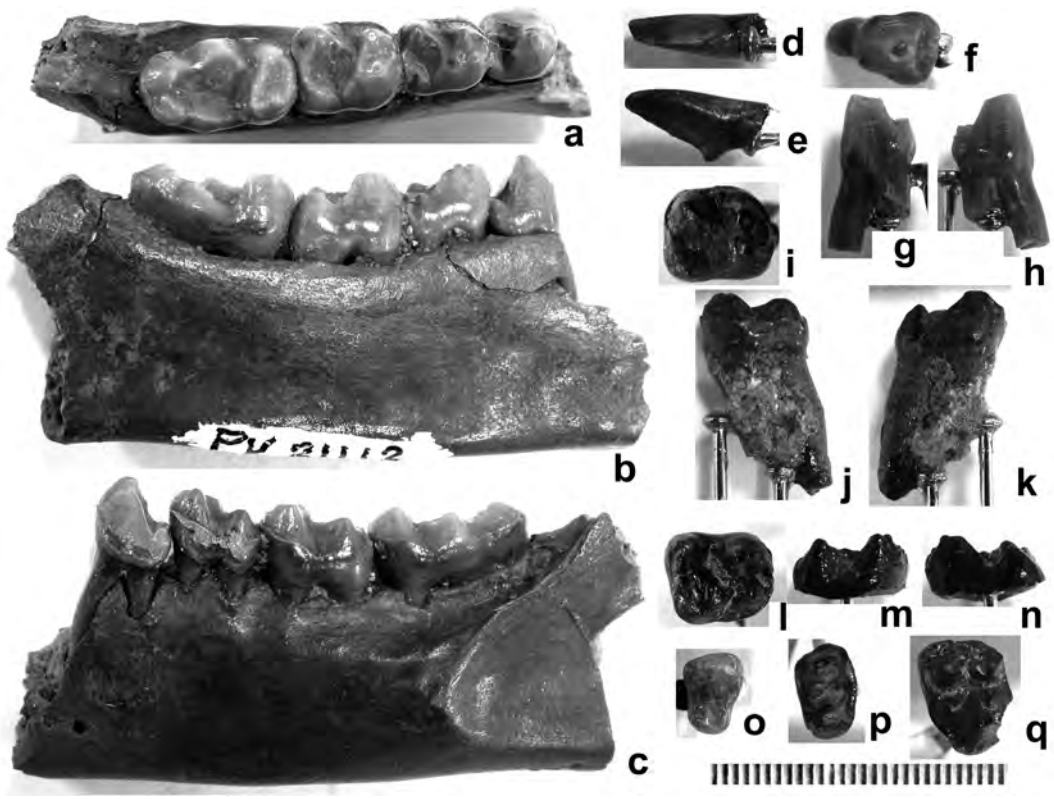

Fig. 1. *Plesiadapis tricuspidens* Gervais, 1877. NMNS-PV 21112, left mandibular fragment with p4-m3 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21113, incisor in labial (d) and lateral (e) views. NMNS-PV 21114, right p3 in occlusal (f), buccal (g), and lingual (h) views. NMNS-PV 21115, left m2 in occlusal (i), buccal (j), and lingual (k) views. NMNS-PV 21118, right m2 in occlusal (l), buccal (m), and lingual (n) views. NMNS-PV 21117, left P3 in occlusal view (o). NMNS-PV 21116, left P4 in occlusal view (p). NMNS-PV 21119, left M3 in occlusal view (q). One division of scale equals 0.5 mm.

Suborder Euprimates Hoffstetter, 1977
Infraorder Strepsirrhini É. Geoffroy Saint-Hilaire, 1812
Superfamily Adapoidea Hoffstetter, 1977
Family Adapidae Trouessart, 1879
Genus *Adapis* G. Cuvier, 1821

***Adapis sudrei* Gingerich, 1977**
(Fig. 2)

Material: NMNS-PV 21242, right mandibular fragment with p4-m3; NMNS-PV 21243, right maxillary frgament with P3-M2; NMNS-PV 21244, half of an upper molar; NMNS-PV 21245, heavily worn right M2; NMNS-PV 21246, left mandibular fragment with m1; NMNS-PV 21247, left p1; NMNS-PV 21248, half of upper premolar; NMNS-PV 21249, right p1; NMNS-PV 21250, right P3; NMNS-PV 21251, left M1 or M2; NMNS-PV 21252, left M1 or M2; NMNS-PV 21253, right p3 or p2; NMNS-PV 21254, right p2 or p3; NMNS-PV 21255, left m1 or m2; NMNS-PV 21256, right m1 or m2; NMNS-PV 21257, left m1 or m2; NMNS-PV 21258, left m1 or m2; NMNS-PV 21259, right

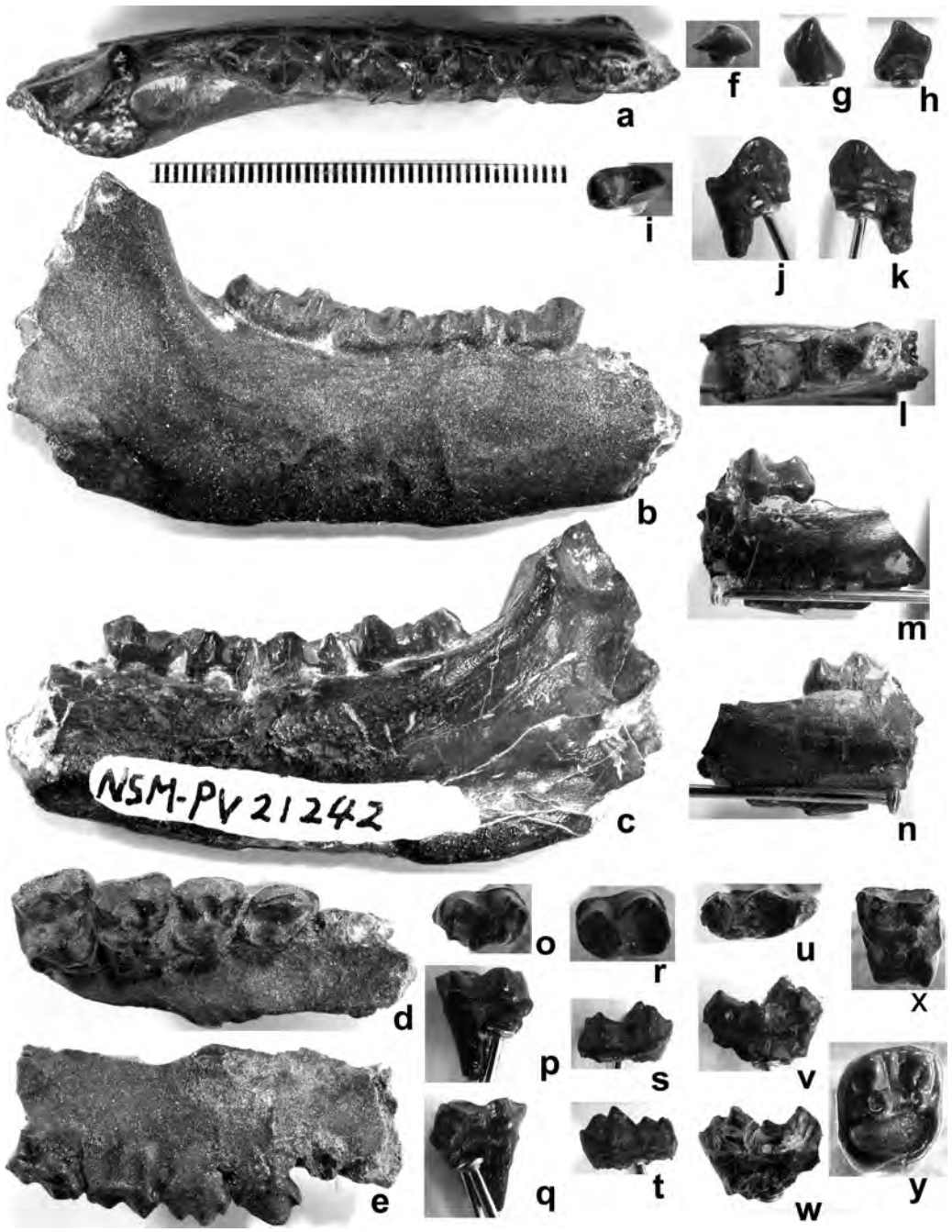

Fig. 2. *Adapis sudrei* Gingerich, 1977. NMNS-PV 21242, right mandibular fragment with p4-m3 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21243, right maxillary frgament with P3-M2 in occlusal (d) and buccal (e) views. NMNS-PV 21247, left p1 in occlusal (f), buccal (g), and lingual (h) views. NMNS-PV 21253, right p3 or p2 in occlusal (i), buccal (j), and lingual (k) views. NMNS-PV 21246, left mandibular fragment with m1 in occlusal (l), buccal (m), and lingual (n) views. NMNS-PV 21255, left m1 or m2 in occlusal (o), buccal (p), and lingual (q) views. NMNS-PV 21256, right m1 or m2 in occlusal (r), buccal (s), and lingual (t) views. NMNS-PV 21259, right m3 in occlusal (u), buccal (v), and lingual (w) views. NMNS-PV 21252, left M1 or M2 in occlusal view (x). NMNS-PV 21245, heavily worn right M2 in occlusal view (y). One division of each scale equals 0.5 mm.

m3; NMNS-PV 21260, dental (m3?) fragment; NMNS-PV 21261, dental fragment (right m3?); NMNS-PV 21262, mandibular fragment with 3 roots.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: *Adapis sudrei* is the only species that occurs in the MP16 level (Hooker, 1987).

Cf. *Leptadapis* sp.
(Fig. 3)

Material: NMNS-PV 21263, left p4.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: NMNS-PV 21263 is apparently larger than the above listed *Adapis* specimens. *Leptadapis* has been the name for the large European adapids, and is also used in this paper. However, Godinot & Couette (2008) classified large-sized European adapids into three species of *Leptadapis* Gervais, 1876 and four species of *Magnadapis* Godinot & Couette, 2008 based on cranial morphology. Stratigraphic ranges of some of these species are not known because the materials are from the Old Quercy collection without stratigraphic level information. NMNS-PV 21263 is an isolated tooth, and cannot be assigned to any species under the classification by Godinot & Couette (2008).

Fig. 3. Cf. *Leptadapis* sp. NMNS-PV 21263, left p4 in occlusal (a), buccal (b), and lingual (c) views. One division of scale equals 0.5 mm.

Infraorder Haplorhini Pocock, 1918
Family Omomyidae Trouessart, 1879
Subfamily Microchoerinae (Lydekker, 1887)
Genus *Necrolemur* Filhol, 1873

***Necrolemur* sp. cf. *N. antiquus* Filhol, 1873**
(Fig. 4)

Material: NMNS-PV 21151, right mandibular fragment with m2-3; NMNS-PV 21236, left c; NMNS-PV 21237, left p3; NMNS-PV 21264, right p4; NMNS-PV 21265, right m2; NMNS-PV 21266, right m1; NMNS-PV 21267, right m1 or m2; NMNS-PV 21268, right M2; NMNS-PV 21269, right M3; NMNS-PV 21270, right M1; NMNS-PV 21271, left m3; NMNS-PV 21272, left m3; NMNS-PV 21275, right M3; NMNS-PV 21280, left m3; NMNS-PV 21281, right m3; NMNS-PV 21282, left m3; NMNS-PV 21283, left m3; NMNS-PV 21300, right P4.

Locality: NMNS-PV 21151 is from Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France), which is a part of Phosphorites du Quercy. The others (NMNS-PV 21264-21271, 21300) are from Robiac

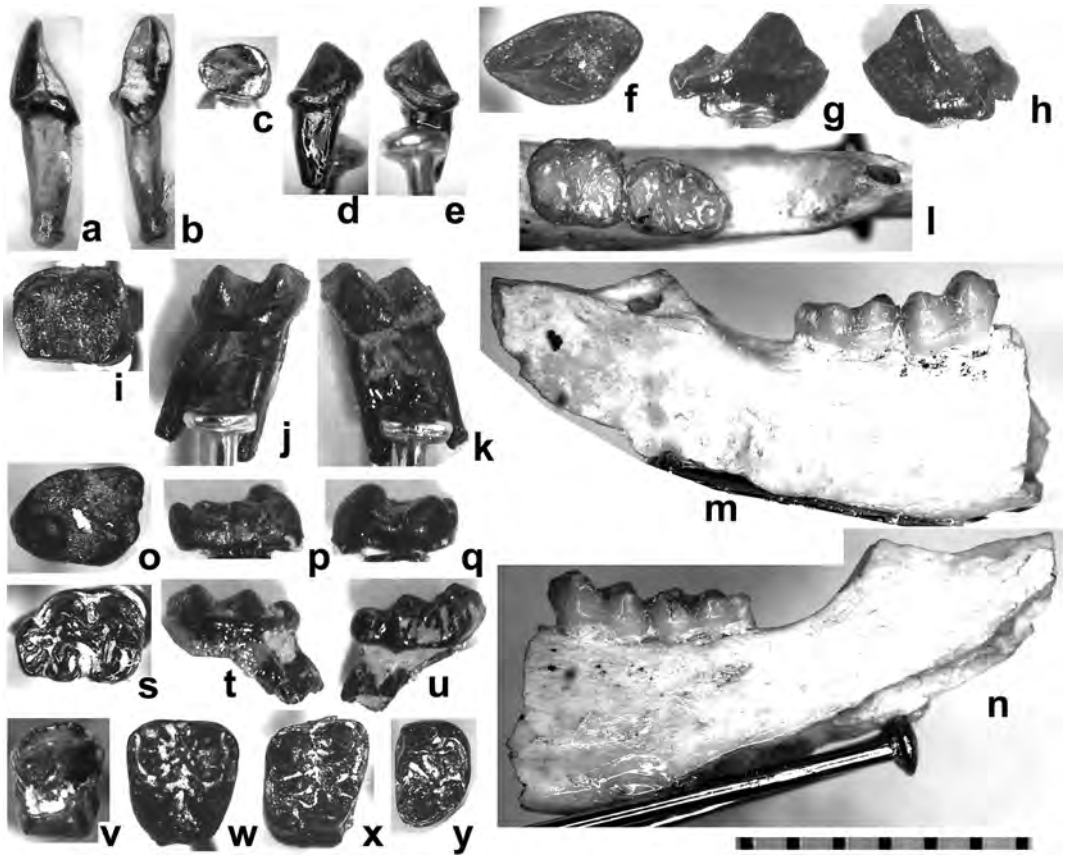

Fig. 4. *Necrolemur* sp. cf. *N. antiquus* Filhol, 1873. NMNS-PV 21237, left lower canine in lateral (a) and posterior (b) views. NMNS-PV 21237, left p3 in occlusal (c), buccal (d), and lingual (e) views. NMNS-PV 21264, right p4 in occlusal (f), buccal (g), and lingual (h) views. NMNS-PV 21266, right m1 in occlusal (i), buccal (j), and lingual (k) views. NMNS-PV 21151, right mandibular fragment with m2-3 in occlusal (l), buccal (m), and lingual (n) views. NMNS-PV 21265, right m2 in occlusal (o), buccal (p), and lingual (q) views. NMNS-PV 21271, left m3 in occlusal (r), buccal (s), and lingual (t) views. NMNS-PV 21300, right P4 in occlusal view (u). NMNS-PV 21270, right M1 in occlusal view (v). NMNS-PV 21268, right M2 in occlusal view (w). NMNS-PV 21269, right M3 in occlusal view (x). One division of each scale equals 1 mm.

(Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The occurrence of *Necrolemur* cf. *antiquus* is limited to the MP16 level (Hooker, 1987). Godinot (2003) studied variation within a large number of *Necrolemur* specimens collected from one locality, and pointed out a considerably large variation within the population and an absence of threshold that distinguishes large forms from smaller forms, resulting in the assignment of all specimens into *Necrolemur* cf. *antiquus*.

Genus *Pseudoloris* Stehlin, 1916

***Pseudoloris parvulus* (Filhol, 1889–90)**
(Fig. 5)

Material: NMNS-PV 21152, mandibular fragment with 2 premolars. NMNS-PV 21153, right mandibular fragment with p3-m3.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France). A part of Phosphorites du Quercy.

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: *Pseudoloris parvulus* appeared in MP16 and existed until MP19 (Hooker, 1987; Legendre, 1987).

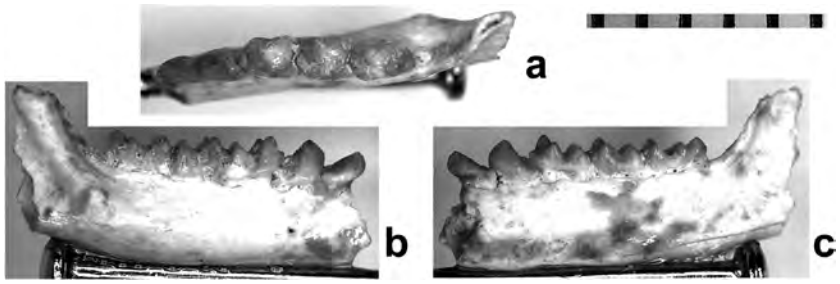

Fig. 5. *Pseudoloris parvulus* (Filhol, 1889–90). NMNS-PV 21153, right mandibular fragment with p3-m3 in occlusal (a), buccal (b), and lingual (c) views. One division of each scale equals 1 mm.

Parvorder Anthropoidea Mivart, 1864
(unnamed rank) Catarrhini Geoffroy Saint-Hilaire 1812
Family Pliopithecidae Zapfe, 1961
Genus *Pliopithecus* Gervais, 1849

***Pliopithecus piveteaui* Hürzeler, 1954**
(Fig. 6)

Material: NMNS-PV 21664, right M3.

Locality: Faluns de Touraine, (Sainte-Maure-de-Touraine, Chinon, Indre-et-Loire, Centre, France).

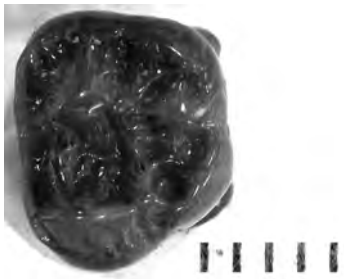

Fig. 6. *Pliopithecus piveteaui* Hürzeler, 1954. NMNS-PV 21664, right M3 in occlusal view. One division of scale equals 1 mm.

Age: Basal part of middle Miocene (Langhian). European mammal zone MN5 (Steininger *et al.*, 1996).

Comments: *Pliopithecus* first appeared in MN5 (Begun, 2002). *Pliopithecus piveteaui* is known from some other MN5 localities (Mein, 1989), and an occurrence of this species from Faluns de Touraine has been reported previously (Ginsburg, 1992).

Acknowledgments

I thank the following personnels for access of the comparative specimens: Drs. B. Marandat, L. Marivaux, J.-Y. Crochet, and J.-J. Jaeger (Université Montpellier II, Montpellier), and C. Argot, P. Tassy, C. Sagne, M. Pickford, B. Senut (Muséum national d'Histoire naturelle, Paris). I also thank Dr. M. Godinot (Muséum national d'Histoire naturelle, Paris) for his helpful comments.

Literature Cited

Begun, D., 2002. The Pliopithecoidea. *In*: W. C. Hartwig (ed.), *The primate fossil record*. Cambridge University Press, Cambridge. p. 221–240.

Cuvier, G., 1821. *Discours sur la théorie de la terre, servant d'introduction aux recherches sur les ossements fossiles*. G. Dufour et E.d'Ocagne, Paris. 174pp.+6pls.

Filhol, H., 1873. Sur un nouveau genre de lémurien fossile, récemment découvert dans les gisements de phosphate de chaux du Quercy. *Comptes rendus de l'Académie des sciences, Paris,* **77**: 1111–1112.

Filhol, H., 1889-1890. Description d'une nouvelle espèce de Lémurien fossile (*Necrolemur parvulus*). *Bulletin du Musee d'Histoire Naturelle de Paris,* **1**: 39–40.

Gervais, P., 1849. Note sur une nouvelle espèce de singe fossile. *Comptes rendus hebdomadaires des séances de l'Académie des sciences,* **28**: 699–700.

Gervais, P., 1876. *Zoologie et paléontologie générales*. Bertrand, Paris.

Gervais, P., 1877. Enumération de quelques ossements d'animaux vertébrés recueillis aux environs de Reims par M. Lemoine. II. *Journal de Zoologie,* Paris, **6**: 74–79.

Geoffroy Saint Hilaire, É., 1812. Tableau des Quadrumanes, 1. Ord. Quadrumanes. *Annales du Muséum national d'Histoire naturelle, Paris,* **19**: 85–122.

Gingerich, P. D., 1977. New species of Eocene primates and the phylogeny of European Adapidae. *Folia Primatologica,* **28**: 60–80.

Ginsburg, L., 1992. The *Pliopithecus* species of the Faluns of Touraine and Anjou (France). *Folia Primatologica,* **58**: 169–170.

Godinot, M., 1987. Mammalian reference levels MP 1-10. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A,* **10**: 21–23.

Godinot, M., 2003. Variabilité morphologique et évolution des *Necrolemur* (Primates, Omomyiformes) des niveaux-repères MP 17 à MP 20 du sud de la France. *Coloquios de Paleontologia,* **Ext.1**: 203–235.

Godinot, M. and S. Couette, 2008. Morphological diversity in the skulls of large adapines (Primates, Adapiformes) and its systematic implications. *In*: E. L. Sargis and M. Dagosto, M. (eds.), *Mammalian evolutionary morphology: a tributte to Frederick S. Szalay*. Springer Science+Business Media B.V., Dordrecht. p. 285–313.

Hoffstetter, R., 1977. Philogénie des Primates. Confrontation des résultats obtenus par les diverses voies d'approche du probléme. *Bulletins et mémoires de la Société d'anthropologie de Paris. Sér. 13*, **4**: 327–346.

Hooker, J. J., 1987. Mammalian reference levels MP 14–16. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A,* **10**: 26–27.

Hürzeler, J., 1954. Contribution à l'odontologie et à la phylogénèse du genre *Pliopithecus* Gervais. *Annales de Paléontologie,* **40**: 1–63.

Legendre, S., 1987. Mammalian reference levels MP 17–20. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A,* **10**: 28–29.

Linnaeus, C., 1758: *Systema Naturae. 10th edition*. Laurentii Salvii, Holmiae. 823pp.

Lydekker, R., 1887. *Catalogue of the fossil Mammalia in the British Museum. Part V. Containing the group Tillodontia, the orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata, and Supplement*. British Museum (Natural History), London. 345pp.

McKenna, M. C. and S. K. Bell, 1997. *Classification of mammals above the species level.* Columbia University Press, New York. 631pp.

Mein, P., 1989. Updating of MN zones. *In*: E. H. Lindsay, V. Fahlbusch, and P. Mein (eds.), *European Neogene Mammmal Chronology*. Plenum Press, New York. p. 73-90.

Mivart, St. G., 1864. Notes on the crania and dentition of the Lemuridae. *Proceedings of the Zoological Society of London,* **1864**: 611–648.

Pocock, R. I., 1918. On the external characters of the lemurs and *Tarsius*. *Proceedings of the Zoological Society of London,* **1918**: 19–53.

Rose, K. D., 2006. *The beginning of the age of mammals*. The Johns Hopkins University Press, Baltimore. 428pp.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A* , 10: 1–312.

Silcox, M., J. I. Bloch, E. J. Sargis, and D. M. Boyer, 2005. Euarchonta (Dermoptera, Scandentia, Primates). *In*: K. D. Rose and J. D. Archibald (eds.), *The rise of placental mammals: origins and relationships of the major extant clades*. The Johns Hopkins University Press, Baltimore. p. 127–144.

Simons, E., 1972. *Primate evolution: an introduction to man's place in nature*. Macmillan, New York. 322pp.

Stehlin, H. G., 1916. Die Säugetiere des schweizerischen Eocaens. Critischer Catalog der Materialien. *Abhandlungen Schweizerische Paläontologische,* **41**: 1297–1552.

Steininger, F. F., W. A. Berggren, D. V. Kent, R. L. Bernor, S. Sen, and J. Agusti, 1996. Circum-Mediterranean Neogene (Miocene and Pliocene) marine–continental chronologic correlations of European Mammal Units. *In*: R. L. Bernor, V. Fahlbusch, and H.-W. Mittmann (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York. p. 7–46.

Trouessart, É.-L., 1879. Catalogue des mammifères vivants et fossiles. *Revue et Magasin de Zoologie, Paris,* **7**: 223–230.

Trouessart, É.-L., 1897. *Catalogus Mammalium tam viventium quam fossilium, vol.1*. R. Friedlander und Sohn, Berlin. 664pp.

Zapfe, H., 1961. Ein Primatenfund aus der miozänen Molasse von Oberösterreich. *Zeitschrift für Morphologie und Anthropologie,* **51**: 247–267.

National Museum of Nature and Science Monographs, No. 55, pp. 29–41, 2025

Chapter 4

RODENTIA

Yukimitsu Tomida

Department of Geology and Paleontology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: aztlanolagus@yahoo.co.jp)

Rodent material treated in this chapter consists of eight species from Le Bretou and Robiac in France and two localities in Isle of Wight in England. Specimens from Le Bretou are all in situ on the maxilla or dentary, while those from Robiac are all isolated teeth.

Three taxa from Isle of Wight were most likely collected by R. L. E. Ford because his name was written on the labels together with the formation, geologic age, and locality information, and also Mr. Tourment has never been in Isle of Wight (pers. comm. Jan. 2011). Mr. Ford is a rather well known fossil collector, as his name is crowned on two species out of three from Isle of Wight reported in this chapter, and he donated numerous rodent specimens from Isle of Wight to the Natural History Museum in London, with which I could compare directly the specimens treated in this chapter.

Thalerimys fordi is from "under How Ledge, Lower Headon Beds, Headon Hill, I.O.W." How Ledge is the locally well known ledge of limestone bed, which is part of the Totland Bay Member of Headon Hill Formation, Solent Group in western Isle of Wight (Hooker *et al.*, 2009; Hooker, pers. comm., Oct. 7, 2009).

Isoptychus margaritae and *Glamys fordi* are from "Hamstead Beds, I.O.W.", which sounds rather vague stratigraphically. But, *I. margaritae* is known, in Isle of Wight, only from the lower part of the Upper Hamstead Member of Bouldnor Formation, and the upper most locality level of the Hamstead Member in figure 1 of Hooker *et al.* (2004) is known as Ford's locality (Hooker, pers. comm., Oct. 7, 2009). Therefore, the stratigraphic level of the specimens of those two species is precisely known.

Classification of the order Rodentia above the family level by McKenna and Bell (1997) is drastically changed recently, at least on the living taxa, based mainly on the molecular phylogenetic analyses (e.g. Janis *et al.*, 2008; Honeycutt, 2009). But, on the other hand, it is extremely difficult to classify the extinct groups (including Theridomyidae) within such a scheme of the molecular phylogeny, and united classification of the order Rodentia is currently unavailable. Thus, I hesitate to use higher taxa above the family level in the following systematics.

Measurements of the specimens are shown in Tables 1 and 2.

Abbreviations: R, right; L, left; P/p, upper/lower premolar; M/m, upper/lower molar; DP/dp, upper/lower deciduous premolar; 1/2, 1 or 2; w/, with; frag., fragment.

Systematic Paleontology

Order Rodentia Bowdich, 1821
Family Gliridae Thomas, 1897
Subfamily Gliravinae Schaub, 1958
Genus *Gliravus* Stehlin et Schaub, 1951

Gliravus sp. aff. *G. robiacensis* Hartenberger, 1965

(Fig. 1-b; Table 1)

Material: NMNS-PV 21159 (left maxillary fragment with P4-M2)

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France)

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: *G. robiacensis* was originally described from Robiac by Hartenberger (1965) and was described in detail by Hartenberger (1971). A dentary with p4-m1 similar to *G. robiacensis* was reported from Le Bretou as *G.* cf. *robiacensis*, mainly because it was old individual and the cusps were well worn. NMNS-PV 21159 is the only specimen known from Le Bretou in our collection, and it is obviously (approximately 15~20%) larger than *G. robiacensis* from Robiac (compare with Hartenberger, 1971, p. 116–117).

Table 1. Measurements of rodent specimens from Le Bretou and Robiac (in mm)

Specimen number	Tooth identification	Length	Width	Specimen number	Tooth identification	Length	Width
Gliravus sp. aff. *G. robiacensis*							
NMNS-PV 21159	R P4	0.92	1.02	NMNS-PV 21159	L M2	1.10	1.24
NMNS-PV 21159	R M1	1.04	1.20				
Sciuroides romani							
NMNS-PV 21154	R P4	2.32	2.16	NMNS-PV 21154	R M3	2.28	2.44
NMNS-PV 21154	R M1	2.36	2.40	NMNS-PV 21278	R M1/2	2.44	2.44
NMNS-PV 21154	R M2	2.40	2.36				
Paradelomys sp. cf. *P. crusafonti*							
NMNS-PV 21155	L m1	1.60	1.28	NMNS-PV 21157	R m2	1.64	1.52
NMNS-PV 21155	L m2	1.64	1.36	NMNS-PV 21157	R m3	1.72	1.34
NMNS-PV 21155	L m3	1.64	1.32	NMNS-PV 21158	R m1	1.60	1.36
NMNS-PV 21156	R m1	1.64	1.48	NMNS-PV 21158	R m2	1.56	1.44
NMNS-PV 21156	R m2	1.72	1.56	NMNS-PV 21273	R M1/2	1.68	1.68
NMNS-PV 21157	R m1	1.60	1.32	NMNS-PV 21276	R m3	1.96	1.48
Elfomys tobieni							
NMNS-PV 21279	R m1/2	1.32	1.16				
"*Protadelomys*"? sp.							
NMNS-PV 21277	L M3	—	1.92				

Table 2. Measurements of rodent specimens from IOW

Specimen number	Tooth identification	Length	Width	Specimen number	Tooth identification	Length	Width
Glamys fordi							
NMNS-PV 21617	R DP4	0.86	1.08	NMNS-PV 21636	R p4	1.04	1.04
NMNS-PV 21618	R DP4	0.84	1.04	NMNS-PV 21637	R m3	1.12	1.14
NMNS-PV 21619	R DP4	1.00	1.10	NMNS-PV 21638	R m3	1.18	1.18
NMNS-PV 21620	R DP4	1.02	1.12	NMNS-PV 21639	L m3	1.18	—
NMNS-PV 21621	R M3 frag.	1.00	—	NMNS-PV 21640	L m2	1.22	1.30
NMNS-PV 21622	R M3	1.02	1.28	NMNS-PV 21641	R m2	1.20	1.24
NMNS-PV 21623	L M1/2	1.06	1.44	NMNS-PV 21642	L m2	1.24	1.32
NMNS-PV 21624	R P4	1.06	1.40	NMNS-PV 21643	L m1	1.26	1.24
NMNS-PV 21625	L P4	1.06	1.42	NMNS-PV 21644	L m1	1.26	1.22
NMNS-PV 21626	L M2	1.24	1.56	NMNS-PV 21645	L DP4	1.04	1.02
NMNS-PV 21627	R M1/2	1.08	1.42	NMNS-PV 21646	R P4	1.10	1.40
NMNS-PV 21628	R M1/2	1.16	1.50	NMNS-PV 21647	R M1	1.02	1.24
NMNS-PV 21629	L M3	1.02	1.20	NMNS-PV 21648	L M2	1.12	1.32
NMNS-PV 21630	L M1/2	1.00	1.20	NMNS-PV 21649	L M3	0.94	1.16
NMNS-PV 21631	R P4?	0.96	1.18	NMNS-PV 21651	L p4	1.04	0.92
NMNS-PV 21632	R dp4	0.94	0.92	NMNS-PV 21652	L m1	1.22	1.20
NMNS-PV 21633	L p4	1.08	0.98	NMNS-PV 21653	L m2	1.24	1.26
NMNS-PV 21634	L p4	1.06	1.08	NMNS-PV 21654	R m3	1.24	1.26
NMNS-PV 21635	R p4	1.08	1.04				
Thalerimys fordi							
NMNS-PV 21598	R P4	2.36	2.96	NMNS-PV 21603	L M1/2	2.52	2.64
NMNS-PV 21599	L M1/2	2.40	2.52	NMNS-PV 21604	L M1/2	2.60	2.72
NMNS-PV 21600	L M1/2	2.52	2.64	NMNS-PV 21605	L M1/2	2.32	2.40
NMNS-PV 21601	L M1/2	2.48	2.72	NMNS-PV 21606	L P4	2.36	2.60
NMNS-PV 21602	L P4	2.36	2.92				
Isoptychus margaritae							
NMNS-PV 21559	L i1	1.95	1.30	NMNS-PV 21584	R M1/2	1.84	2.08
NMNS-PV 21560	R M1/2	1.88	2.00	NMNS-PV 21585	L m1/2	1.96	1.72
NMNS-PV 21561	R M1/2	1.80	2.24	NMNS-PV 21586	L M1/2?	—	—
NMNS-PV 21562	R m1/2	1.96	2.04	NMNS-PV 21587	R P4?	2.20	2.32
NMNS-PV 21563	L m1/2	1.92	1.88	NMNS-PV 21588	L m1/2	—	1.68
NMNS-PV 21564	L p4	2.68	1.76	NMNS-PV 21589	R m1/2	2.04	2.00
NMNS-PV 21565	R M1/2	1.84	2.20	NMNS-PV 21590	R M1/2	1.92	2.08
NMNS-PV 21566	R M1/2	1.64	1.76	NMNS-PV 21591	L M3	1.76	2.36
NMNS-PV 21567	R m1/2	2.00	1.96	NMNS-PV 21592	L m3	2.04	1.76
NMNS-PV 21568	R M1/2	2.08	2.36	NMNS-PV 21593	L m1/2	1.96	1.96
NMNS-PV 21569	R dp4	—	1.36	NMNS-PV 21594	R m1/2	1.84	2.04
NMNS-PV 21570	R M1/2	1.84	2.04	NMNS-PV 21595	R m1/2	1.80	2.04
NMNS-PV 21571	L DP4	2.16	1.52	NMNS-PV 21596	R m1/2	2.08	1.88
NMNS-PV 21572	L m3	2.20	1.96	NMNS-PV 21597	R M1/2	1.92	1.96
NMNS-PV 21573	R M1/2	1.92	2.20	NMNS-PV 21607	L m1/2	2.08	1.92
NMNS-PV 21574	R m1/2	1.92	1.96	NMNS-PV 21608	L m1/2	2.20	1.88
NMNS-PV 21575	R m1/2	2.12	1.84	NMNS-PV 21609	L P4	2.08	2.04
NMNS-PV 21576	R m3	1.96	1.80	NMNS-PV 21610	R M1/2	2.00	2.00
NMNS-PV 21577	L m1/2	1.92	2.04	NMNS-PV 21611	L m1/2	2.00	2.04
NMNS-PV 21578	R m1/2	2.04	1.92	NMNS-PV 21612	L m1/2	1.88	1.92
NMNS-PV 21579	L M1/2	1.84	1.84	NMNS-PV 21613	R DP4	2.20	1.80
NMNS-PV 21580	L M1/2	1.72	2.28	NMNS-PV 21614	R p4	—	1.96
NMNS-PV 21581	R M1/2	1.92	2.08	NMNS-PV 21615	R m3	2.12	—
NMNS-PV 21582	L M1/2	2.00	2.04	NMNS-PV 21616	L dp4	2.96	1.52
NMNS-PV 21583	R M1/2	1.84	2.04				

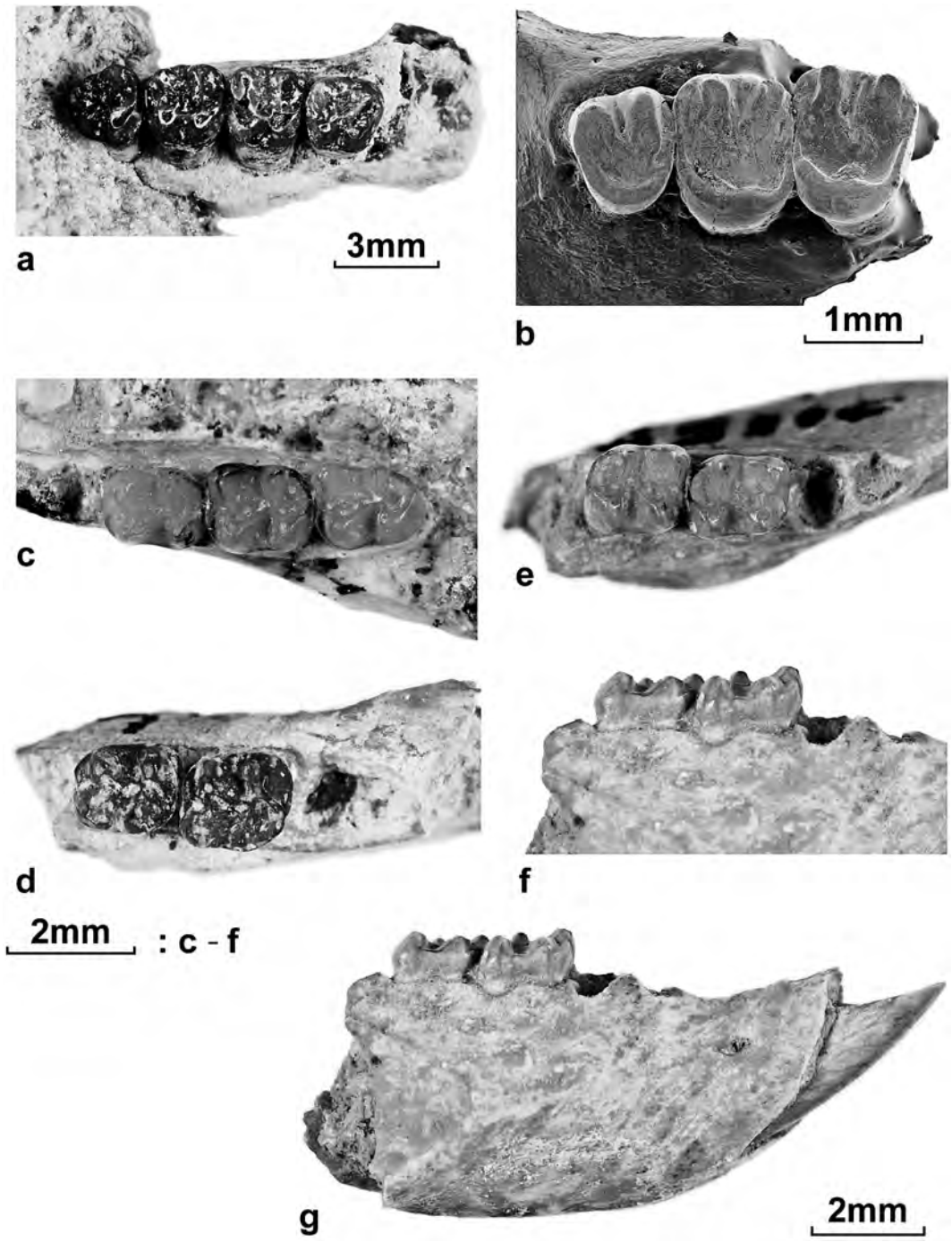

Fig. 1. Rodents from Le Bretou
(a) *Sciuroides romani*, NMNS-PV 21154 (R P4-M3). (b) *Gliravus* sp. aff. *G. robiacensis*, NMNS-PV 21159 (maxillary frag. w/P4-M2). (c–g) *Paradelomys* sp. cf. *P. crusafonti*; c, NMNS-PV 21155 (L dentary frag. w/ m1-3); d, NMNS-PV 21156 (R dentary frag. w/m1-2); e–g, NMNS-PV 21158 (R dentary frag. w/i1+m1-2). a–e, occlusal views; f, g, buccal views.

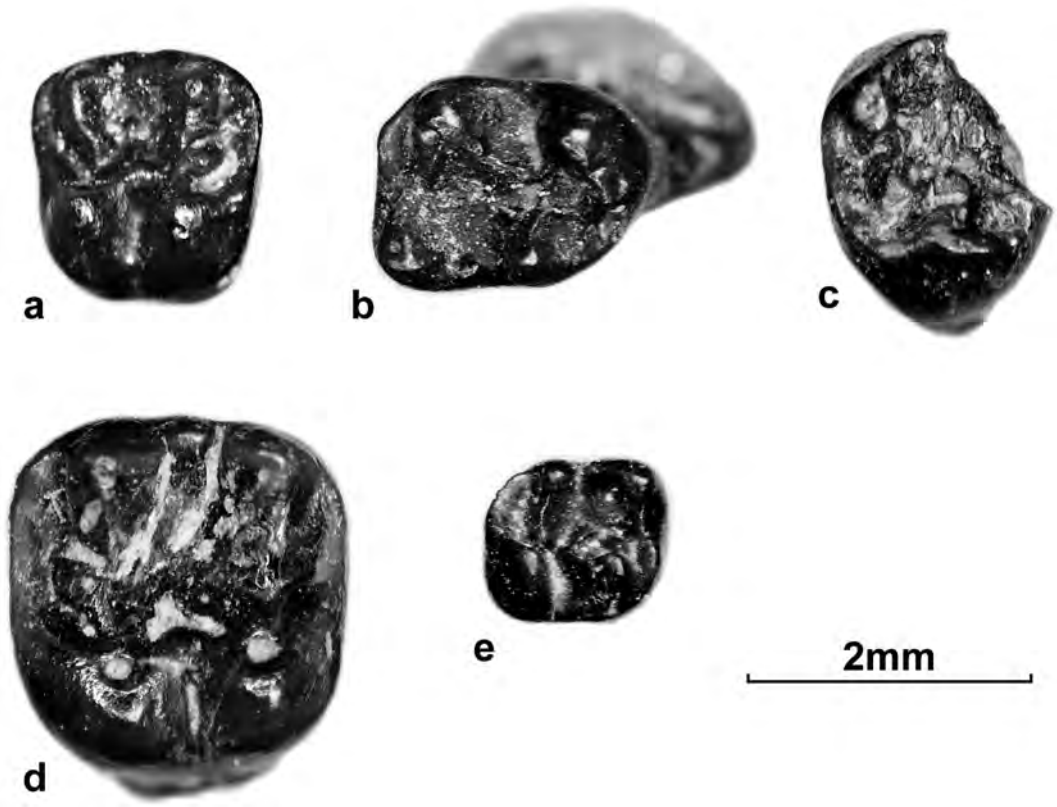

Fig. 2. Rodents from Robiac
(a, b) *Paradelomys* sp. cf. *P. crusafonti*; a, NMNS-PV 21273 (R M1/2); b, NMNS-PV 21276 (R m3). (c) "*Protadelomys*"? sp., NMNS-PV 21277 (L M3 fragment). (d) *Sciuroides romani*, NMNS-PV 21278 (L M1/2). (e) *Elfomys tobieni*, NMNS-PV 21279 (R m1/2). All occlusal views.

Subfamily Glamyinae Vianey-Liaud, 1994
Genus *Glamys* Vianey-Liaud, 1989a

***Glamys fordi* (Bosma et de Bruijn, 1979)**
(Figs. 3-4; Table 2)

Material: NMNS-PV 21617 to 21649 and NMNS-PV 21651 to 21654, all isolated teeth. For the identification of tooth position of each specimen, see table 2.

Locality: Hamstead Bed, Isle of Wight, England; lower part of the Upper Hamstead Member, Bouldnor Formation, Salent Group.

Age: early Oligocene (Ruperian). European mammal zone MP 21 (Hooker *et al.*, 2009).

Comments: This species was originally described under the genus *Gliravus* (Bosma and de Bruijn, 1979). The genus *Gliravus* was defined based mainly on the dental characters by Stehlin and Schaub (1951), because only a fragmentary skull of the type species, other than teeth, was known. At least 11 species had been described in the genus, when Vianey-Liaud (1989a) established the genus *Glamys* based mainly on the differences in morphology of the zygomatic plate, infra-orbital foramen, and cor-

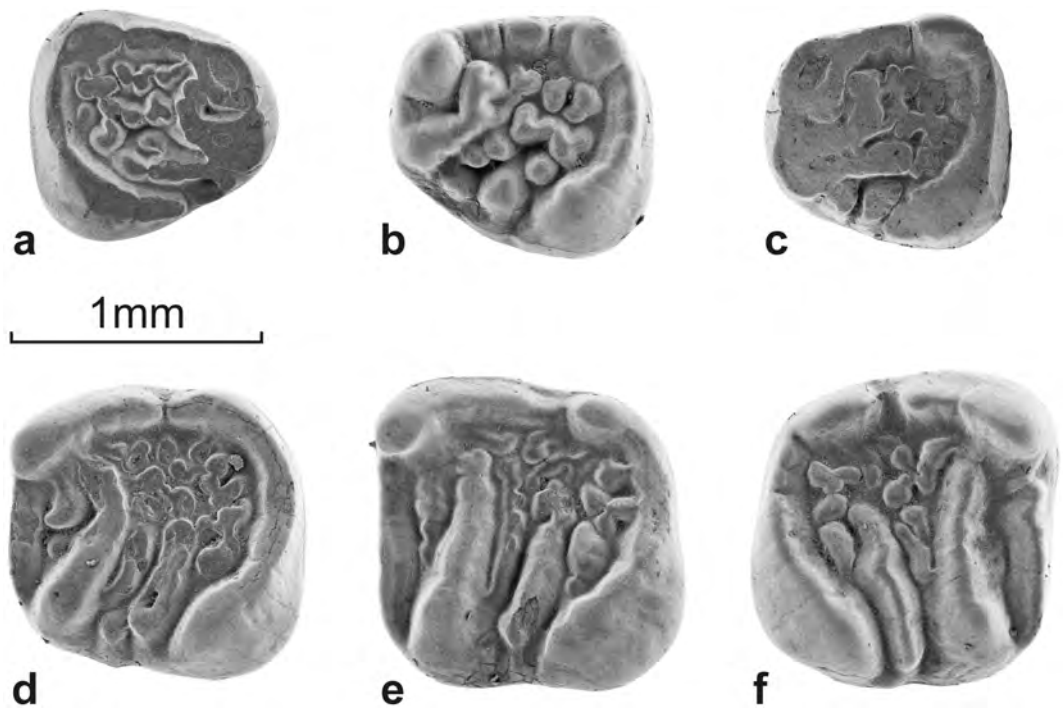

Fig. 3. *Glamys fordi* from Hamstead Bed, I.O.W., lower teeth.
(a) NMNS-PV 21632, R dp4; (b) NMNS-PV 21651, L p4; (c) NMNS-PV 21633, L p4; (d) NMNS-PV 21652, Lm1; (e) NMNS-PV 21653, Lm2; (f) NMNS-PV 21654, R m3. All occlusal views.

onoid process, plus some dental characters. She removed "*Gliravus*" *priscus* to *Glamys* as the type species, but "*G.*" *fordi* was remained. Vianey-Liaud (1994) reviewed the glirid taxa from the late Eocene through Oligocene in West Europe with abundant dental specimens and re-diagnosed three known genera (*Glamys*, *Gliravus*, *Bransatoglis*) based not only on the morphology of the infra-orbital foramen and presence/absence of P3, but also on dental characters as well. In species of the genus *Glamys*, cheek teeth have salient tubercles, and the trigon of upper molars forms an asymmetric V shape, while it looks more like a U shape in species of *Gliravus* and *Bransatoglis* (Vianey-Liaud, 1994, p. 121). She attributed four species (*G. priscus*, *G. robiacensis*, *G. devoogdi*, *G. fordi*) in the genus *Glamys*, and re-described the first three species. I follow her classification here.

Superfamily Theridomyoidea Alston, 1876
Family Pseudosciuridae Zittel, 1893
Genus *Sciuroides* Major, 1873

***Sciuroides romani* (Hartenberger, 1973)**
(Figs. 1-a, 2-d; Table 1)

Material: NMNS-PV 21154, right max. frag. with P4M1-3; NMNS-PV 21278, left M1/2.

Locality: NMNS-PV 21154 is from Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France), and NMNS-PV 21278 is from Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

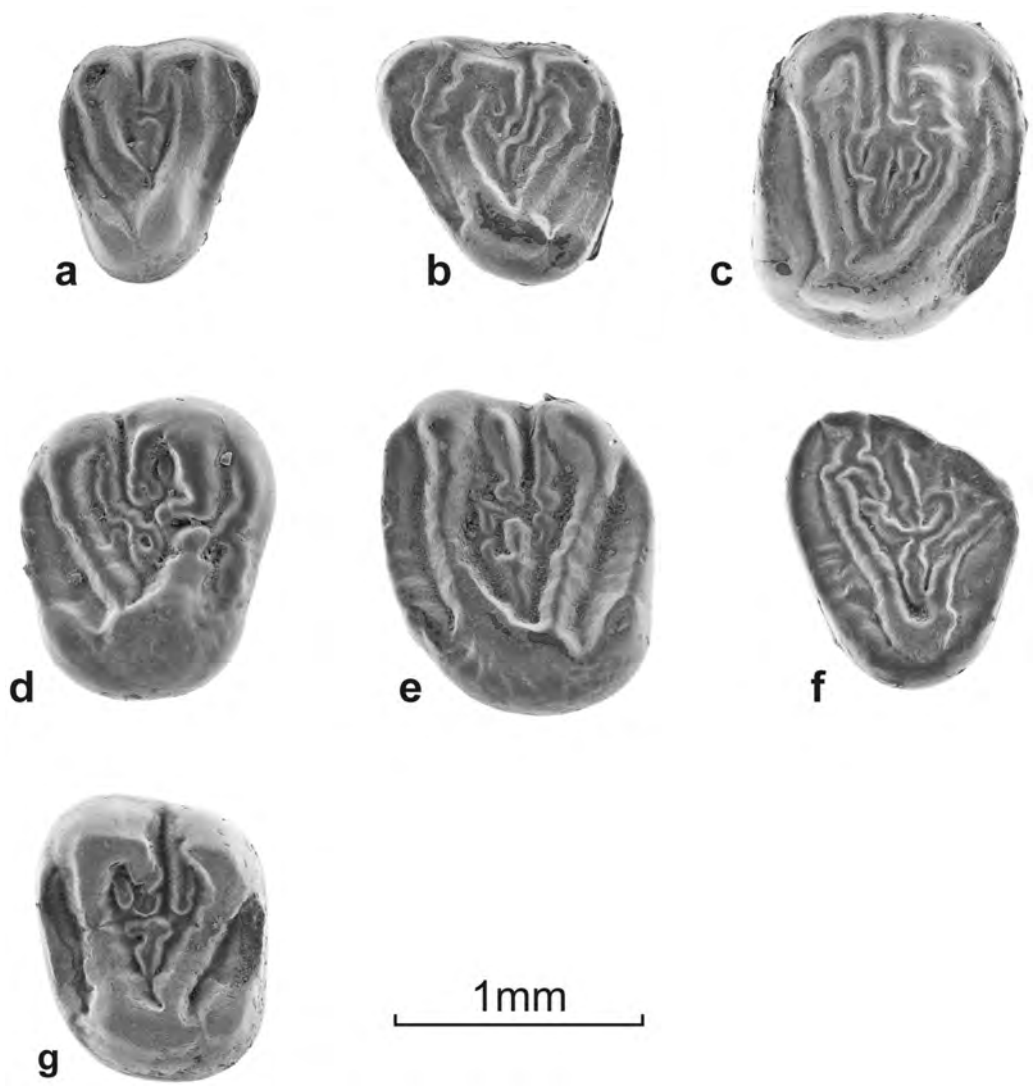

Fig. 4. *Glamys fordi* from Hamstead Bed, I.O.W., upper teeth.
(a) NMNS-PV 21617, R DP4; (b) NMNS-PV 21645, L DP4; (c) NMNS-PV 21646, R P4; (d) NMNS-PV 21647, R M1; (e) NMNS-PV 21648, L M2; (f) NMNS-PV 21649, L M3; (g) NMNS-PV 21630, L M1/2. All occlusal views.

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: A species closely related to *Sciuroides siderolithicus* (type species) has been recorded from Robiac and Le Bretaou localities under the name *Suevosciurus romani* Hartenberger, 1973. Hooker (1986) synonymized *Suevosciurus romani* with *Sciuroides siderolithicus*, but Hartenberger (1988) reinstated *S. romani* within the genus *Suevosciurus*. Hooker and Weidmann (2000, p. 27) discussed this problem and proposed a new combination, *Sciuroides romani* (Hartenberger, 1973). Here, I follow Hooker and Weidmann (2000).

The size of both specimens (NMNS-PV 21154 and 21278) well fits within the previously known range of the species, *Sciuroides romani*, from both localities (see Hooker and Weidmann, 2000, fig. 19).

Family Theridomyidae Alston, 1876
Subfamily Columbomyinae Thaler, 1966
Genus *Paradelomys* Thaler, 1966

***Paradelomys* sp. cf. *P. crusafonti* Thaler, 1966**
(Figs. 1-c-g, and 2-a, b; Table 1)

Material: NMNS-PV 21155, left mandibular frag. with m1-3; NMNS-PV 21156, right mandibular frag. with m1-2; NMNS-PV 21157, right mandibular frag. with m1-3; NMNS-PV 21158, right mandibular frag. with m1-2; NMNS-PV 21273, right M1/2; NMNS-PV 21276, right m3.

Locality: NMNS-PV 21154 to 21158 are from Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France), and NMNS-PV 21273 and 21276 is from Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The type locality of this species is Sosis, Spain, and three other localities are listed as distribution area (Euzet, Fons 4, and Malperie) (Hartenberger, 1973). Hartenberger (1973) identified the specimens from Robiac Nord and Le Bretou as *P*. cf. *crusafonti* based only on slight differences, although he listed them in the table 5 and plate 4 as *C. crusafonti*. Probably those specimens from all

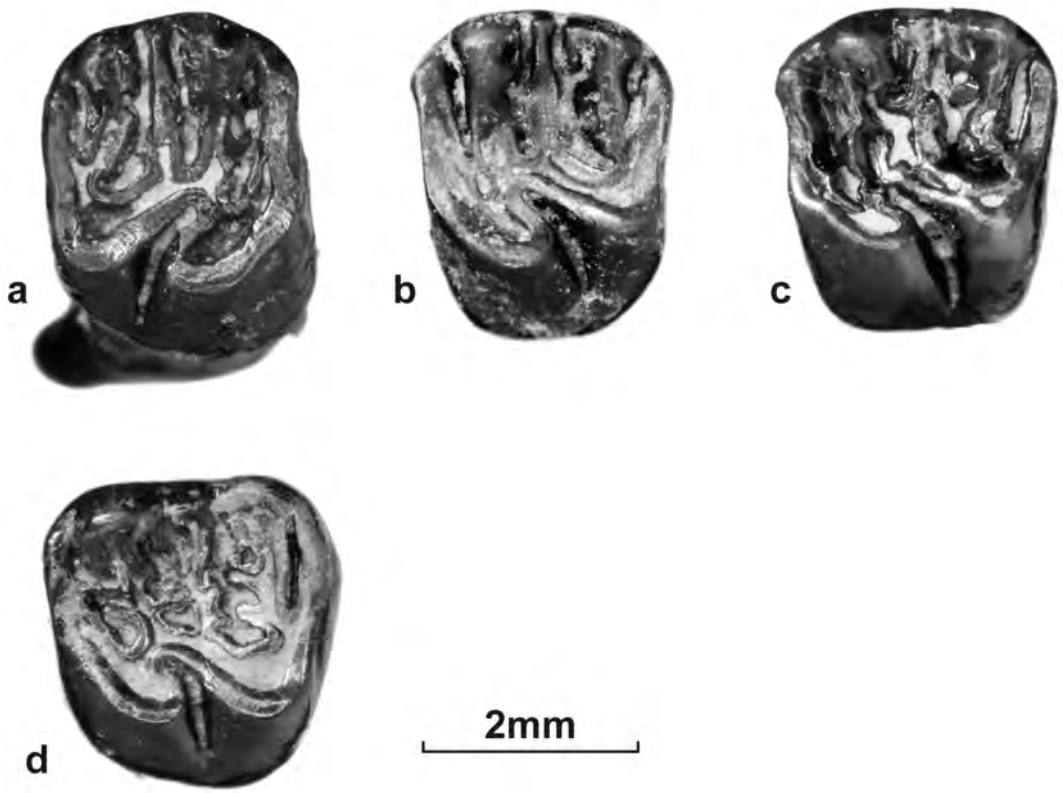

Fig. 5. *Thalerimys fordi* from Headon Hill, I.O.W.
(a) NMNS-PV 21598, R P4; (b) NMNS-PV 21600, L M1/2; (c) NMNS-PV 21602, L P4; (d) NMNS-PV 21604, L M1/2. All occlusal views.

six localities belong to the same species, but I just follow him to use "cf.". A single m3 specimen from Robiac (NMNS-PV 21276) is larger than NMNS-PV 21155 and 21157 from Le Bretou in size (Table xx), but it just fits the size range of *C. crusafonti* from Robiac listed in Hartenberger (1973, table 5). On the other hand, a single M1/2 (NMNS-PV 21273) from Robiac is larger than those from Robiac listed in Hartenberger (1973), but it is within the size range (but close to the largest end) of the *S. crusafonti* (Table 5 of Hartenberger, 1973).

Subfamily Issiodoromyinae Schlosser, 1884
Genus *Elfomy* Hatenberger, 1971
***Elfomys tobieni* (Thaler, 1966)**
(Fig. 2-e; Table1)

Material: NMNS-PV 21279, right M1/2.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: This is one of the smallest species of the rodents known from Robiac. It was described based on only two teeth (type locality is Robiac) originally, but later many specimens were found from

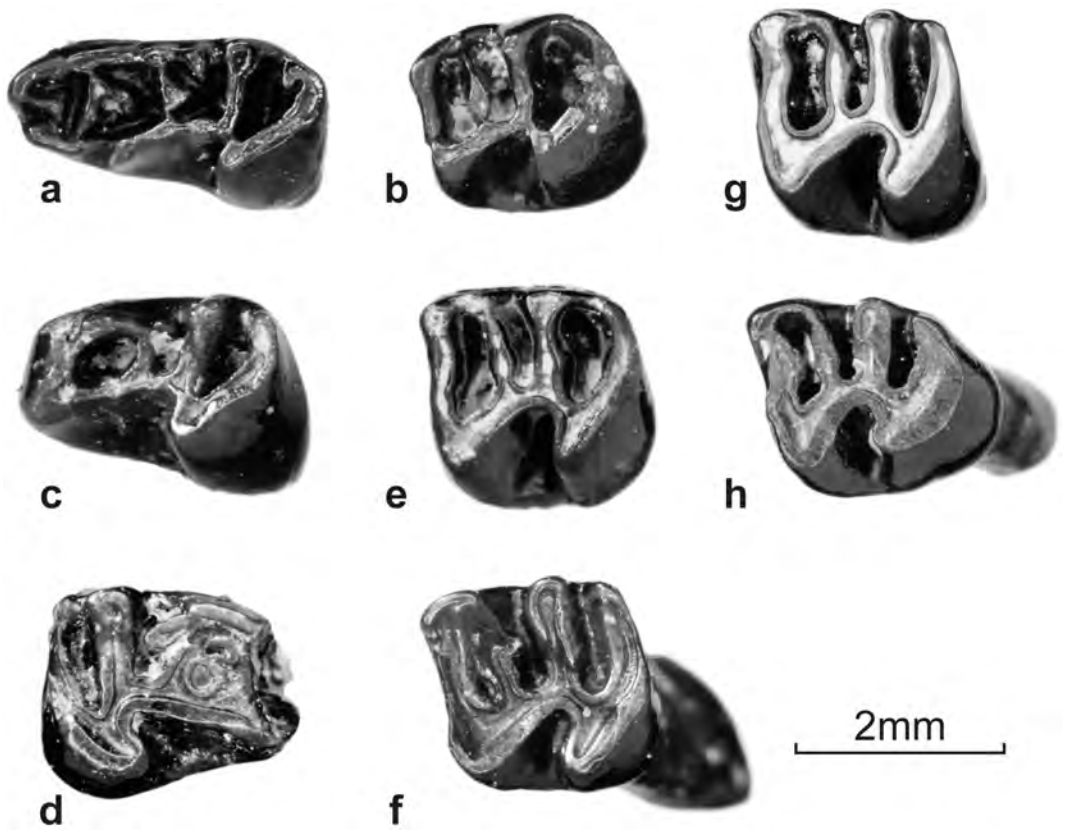

Fig. 6. *Isoptychus margaritae* from Hamstead Bed, I.O.W., lower teeth
(a) NMNS-PV 21616, L dp4; (b) NMNS-PV 21585, L m1/2; (c) NMNS-PV 21564, L p4; (d) NMNS-PV 21614, R p4; (e) NMNS-PV 21607, L m1/2; (f) NMNS-PV 21611, L m1/2; (g) NMNS-PV 21577, L m1/2; (h) NMNS-PV 21572, L m3. All occlusal views.

Robiac and other localities. NMNS-PV 21279 is brachydont, and the mesolophid is imcomplete. The size of NMNS-PV 21279 fits almost the central point of the size range of this species (fig. 13 in Hartenberger, 1973).

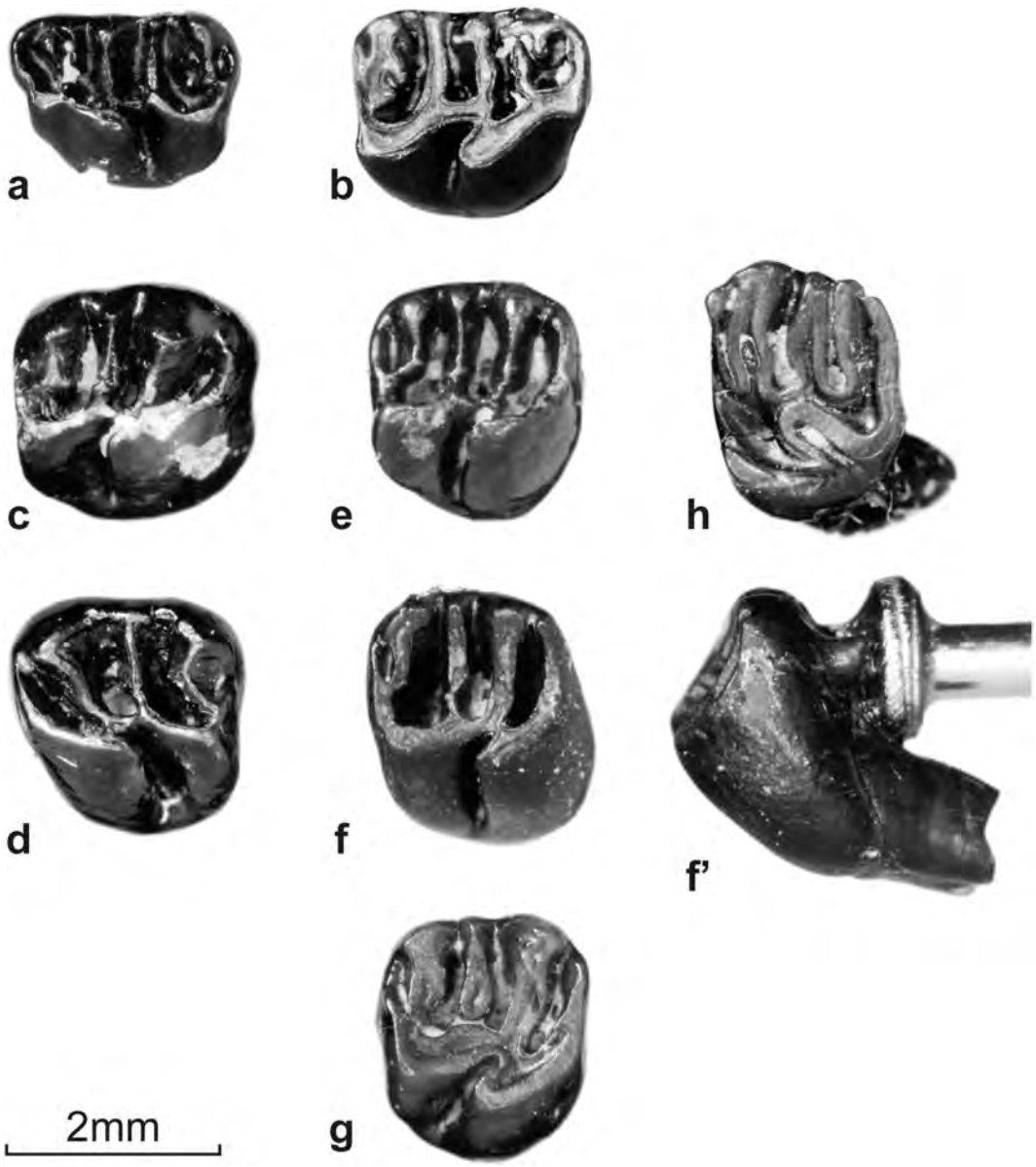

Fig. 7. *Isoptychus margaritae* from Hamstead Bed, I.O.W., upper teeth
(a) NMNS-PV 21571, L DP4; (b) NMNS-PV 21613, R DP4; (c) NMNS-PV 21587, R P4?; (d) NMNS-PV 21609, L P4; (e) NMNS-PV 21610, R M1/2; (f, f') NMNS-PV 21581, R M1/2; (g) NMNS-PV 21565, R M1/2; (h) NMNS-PV 21591, L M3. All (except f') occlusal views; f', anterior view.

Subfamily uncertain
Genus *Protadelomys* Hartenberger, 1969

"*Protadelomys*"? sp.
(Fig. 2-c; Table1)

Material: NMNS-PV 21277, left M3 fragment.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late Middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Identification of the genus is uncertain, but NMNS-PV 21277 is somewhat similar to the same tooth known from the middle Bartonian locality of Switzerland (Hooker and Weidmann, 2007), although the former is obviously smaller in size. NMNS-PV 21277 is slightly larger than M3 of *P. alsaticus* (Hartenberger, 1969, plate 2), but the enamel structure of occlusal surface is more complicated than the latter.

Subfamily Theridomyinae Alston, 1876
Genus *Thalerimys* Tobien, 1972

***Thalerimys fordi* (Bosma et Insole, 1972)**
(Fig. 5; Table 2)

Material: NMNS-PV 21598, R P4; NMNS-PV 21599–21601, three L M1/2s; NMNS-PV 21602, L P4; NMNS-PV 21603–21605, three L M1/2; NMNS-PV 21606, L P4; all isolated teeth.

Locality: Headon Hill, west end of Isle of Wight, Englnad; just under the How Ledge, Totland Bay Member, Headon Hill Formation, Salent Group.

Age: late Eocene (Priabonian). European mammal zone MP 17 (Hooker *et al*., 2009).

Comments: This species was originally described under the genus *Isoptychus* (Bosma and Insole, 1972), and in the same year, the genus *Thalerimys* was established by Tobien (1972) to include "*I.*" *fordi* as the type species. Major differences between *Thalerimys* and *Isoptychus* (and *Theridomys*) are more complicated dental pattern, including many additional cuspules and crests, and the double metalophid (anterior and posterior branches) in the lower molars in *Thalerimys* (see Tobien, 1972 for more detail). Also, the teeth of *Thalerimys* are clearly larger than those of *Isoptychus* and *Theridomys* species in general. Status of the genus *Thalerimys* is rather stable since its establishment.

Genus *Isoptychus* Pomel, 1853

***Isoptychus margaritae* (Vianey-Liaud, 1989b)**
(Figs. 6, 7; Table 2)

Material: NMNS-PV 21559 to 21597 and NMNS-PV 21607 to 21616, all isolated teeth. For the identification of tooth position of each specimen, see table 2.

Locality: Hamstead Bed, Isle of Wight, England; lower part of Upper Hamstead Member, Bouldnor Formation, Salent Group.

Age: early Oligocene (Ruperian). European mammal zone MP 21 (Hooker *et al*., 2009).

Comments: This taxon was originally described under the genus *Theridomys* by Vianey-Liaud (1989b). The genera *Theridomys* and *Isoptychus* have been used interchangeably (e.g. Mayo, 1987;

Vianey-Liaud, 1989b), or the latter is synonymized with the former (Hooker and Weidmann, 2000, p. 49). There has been much discussion on the phylogenetic relationships among these two genera and *Blainvillimys* (see Hooker and Weidmann, 2000, p. 49), but it is beyond the scope of this paper to repeat such discussion. I follow Hooker and Weidmann (2000) and use the genus *Isoptychus* to house this species.

In addition to the problem at generic level mentioned above, some problems at specific level were also present; that is, certain specimens recently identified as traditional species may not be correct. For example, Vianey-Liaud (1989b) distinguished the specimens identified as "*Theridomys*" *aquatilis* by Misonne (1957) and Vianey-Liaud (1972) from the real "*T*" *aquatilis* and described a new species ("*T*" *margaritae*) to house them, which was diagnosed mainly by the characters on the maxilla and mandible (Vianey-Liaud, 1989b, p. 206-207).

The specimens treated here were originally identified as *I. pseudosiderolithicus* by R. L. E. Ford, but this species is restricted, within Isle of Wight, to the Lower Hamstead "Beds" (Lower Hamstead Member of Bouldnor Formation) and older beds (Bosma, 1974), or to the Bembridge Marls Member of Bouldnor Formation and older beds (Hooker *et al.*, 2004), which are correlated to the European mammal zones MP 17–20. The specimens treated here are from the Upper Hamstead Member of Bouldnor Formation, which is right after the Grande Coupure and is correlated to the European mammal zones MP 21, and they are identified as *I. margaritae* in Hooker *et al.* (2004), which is followed here. They also match with the size of *I. margaritae* given in Vianey-Liaud (1989b).

Acknowledgments

I wish to express my gratitude to Dr. Jeremy J. Hooker (Department of Palaeontology, Natural History Museum, London) for his kind and great help on access of the comparative specimens and providing published literatures and unpublished information on Mr. R. L. E. Ford's locality and collection. I also thank Dr. Christine Argot of Muséum national d'Histoire naturelle, Paris for her great help and access of the comparative specimens.

Literatures Cited

Bosma, A. A., 1974. Rodent biostratigraphy of the Eocene-Oligocene transitional strata of the Isle of Wight. Utrecht Micropaleontological Bulletins, Sp. Pub., **1**: 1–126.

Bosma, A. A. and H. de Bruijn, 1979. Eocene and Oligocene Gliridae (Rodentia, Mammalia) from the Isle of Wight, England. Proceedings Koninkl. Nederl. Akademie van Wetenschappen, (B), **82**: 367–384.

Bosma, A. A. and A. N. Insole, 1972. Theridomyidae (Rodentia, Mammalia) from the Osborne Beds (Late Eocene), Isle of Wight, England. Proceedings Koninkl. Nederl. Akademie van Wetenschappen, (B), **75**(2): 133–144.

Hartenberger, J.-L., 1965. *Gliravus robiacensis* n.sp., nouveau Rongeur (Gliridae) de l'Eocene superieur de Languedoc. C. R. somm. Soc. geol. Fr., **1965**: 326–327.

Hartenberger, J.-L., 1969. Les Pseudosciuridae (Mammalia, Rodentia) de l'Éocène moyen de Bouxwiller Lissieu, Egerkingen. Palaeovertebrata, **3**(2): 27–61.

Hartenberger, J.-L., 1971. La systématique des Theridomyoidea (Rodentia). C. R. Acad. Paris, **273**(D): 1917–1920.

Hartenberger, J.-L., 1973. Étude systématique des Theridomyoidea (Rodentia) de l'Éocène supérieur. Mém. Soc. Géol. de France, N. S., Tome 52, Mem. 117, p. 1–76, pl. 1–8.

Hartenberger, J.-L., 1988. Le gisement du Bretou (phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertebres de l'Eocene superieur. Palaeontographica Abt. A, **205**: 103–112.

Honeycutt, R., 2009. Rodetns (Rodentia). *In* Hedges, S. and S. Kumar (eds.), 2009. The timetree of life. Oxford Univ. Pr., p. 490–494.

Hooker, J. J., 1986. Mammals from the Bartonian (middle/late Eocene) of the Mampshisre Basin, southern England. Bull. Br. Mus. nat. Hist. (Geol.), **39**(4): 191–478.

Hooker, J. J., M. E. Collinson, and N. P. Sille, 2004. Eocene-Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event. Jour. Geol. Soc. London, 161: 161: 172.

Hooker, J. J., S. T. Grimes, D. P. Mattey, M. E. Collinson, and N. D. Sheldon, 2009. Refined correlation of the UK Late Eocene–Eraly Oligocene Solent Group and timing of its climate history. *Geol. Soc. America, Spec. Pap.*, **452**: 179–195.

Hooker, J. J. and M. Weidmann, 2000. The Eocene mammal faunas of Mormont, Switzerland. Systematic revision and resolution of dating problems. Schweizerische Paläontologische Abhandlungen, 120: 1–141.

Hooker, J. J. and M. Weidmann, 2007. A diverse rodent fauna from the middle Bartonian (Eocene) of Les Alleveys, Switzerland: snapshot of the early theridomyid radiation. Swiss j. geosci., 100: 469–493.

Janis, C.. M., M. R. Dawson, and L. J. Flynn, 2008. Glires summery. *In* C. M. Janis, G. E. Gunnell, & M. D. Uhen (eds.), Evolution of Tertiary mammals of North America vol. II: small mammals, xenarthrans, and marine mammals. Cambridge U. Pr., p. 263–292.

Mayo, N. A., 1987. The development of the Theridomyidae in the Oligocene of the Molasse of Switzerland and Savoy. Münchner Geowiss. Abh., (A), 10: 159–168.

McKenna, M. C. and S. K. Bell, 1997. Classification of mammals above the species level. Columbia Univ. Pr., New York, 631 pp.

Misonne, X., 1957. Mammiferes oligocenes de Hoogbutsel et Hoeleden: 1 Rongeurs et Ongules. Bull. Inst. r. Sci. nat. Belgique, **33**: 1–61.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene–Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 1–312.

Stehlin, H. G. and S. Schaub, 1951. Die Trignodontie der Simplicidentaten Nager. Schweizerische Palaeont. Abh., **67**: 1–385.

Tobien, H., 1972. Mikromammalier aus dem alttertiären Melanienton von Nordhessen. Teil 2: Rodentia, Biostratigraphie, Biostratonomie. Sonderdruch aus dem Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden, **100**: 7–40.

Vianey-Liaud, M., 1972. L'évolustion de genre *Theridomys* à l'Oligocène moyen. Intérèt biostratigraphique. Bull. Mus. Nat. Hist. Nat., Paris, 98, Sc. Terre, **18**: 295–372.

Vianey-Liaud, M., 1989a. Parallelism among Gliridae (Rodentia): the genus *Gliravus* Stehlin and Schaub. Historical Biology, **2**: 213–226.

Vianey-Liaud, M., 1989b. Parallélisme chez les Theridomyinae (Rodentia) de l'Oligocène: etude de deux nouveles espèces des genres *Theridomys* et *Blainvillimys*. N. Jb. Geol. Paläont. Abh., **178**(2): 203–241.

Vianey-Liaud, M., 1994. La radiation des Gliridae (Rodentia) à l'Eocène supérieur en Europe Occidentale, et sa descendance Oligocène. Münchner Geowiss. Abh., (A), **26**: 117–160.

National Museum of Nature and Science Monographs, No. 55, pp. 43–63, 2025

Chapter 5

CREODONTA AND CARNIVORA

Naoko Egi

Department of Anthropology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: egicyon@gmail.com)

Introduction

Canivorous mammals catalogued in this paper consist of creodonts and carnivorans. All specimens except one were collected from French Eocene localities. Twenty-seven specimens are hyaenodontid creodonts, including four genera (*Allopterodon*, *Paracynohyaenodon*, *Pterodon*, and *Hyaenodon*). Ten specimens are Eocene carnivorans, including miacids (*Paramiacis* and *Quercygale*), amphicyonids (*Cynodictis* and *Simamphicyon*), an ursid (cf. *Cephalogale*), and a nimravid (cf. *Nimravus*). The number of creodont specimen exceeds to that of carnivorans in the studied French Eocene collection. This likely corresponds to the fact that creodonts dominated the mammalian predator niche over carnivorans in the number of individuals and in the number of species during the Eocene of Europe (Agusti and Anton, 2005). The remaining one specimen is an isolated canine of a large carnivoran from the Miocene of France.

The order Creodonta has been traditionally considered as the sister group of the order Carnivora; however, relationships of the Creodonta to other orders and relationships within the order Creodonta are poorly solved. We follow the framework proposed by Polly (1993) for the subfamilial divisions within the Hyaenodontidae. Wesley-Hunt and Flynn (2005; Wyss and Flynn, 1993) suggested that the Carnivora should be limited to the crown group defined by the Feliformia and Caniformia and proposed the Carnivoramorpha for the group including the Miacidae and the crown group. The usage of the Carnivora in this paper follows the traditional classification (e.g., McKenna and Bell, 1997); i.e., the Miacidae is included in the Carnivora. However, the traditional placement of the Miacidae in the Caniformia do not agree with the morphological evidences (Wesley-Hunt and Flynn, 2005) as well as the molecular data that suggests 53.5 Ma for the divergence time of Caniformia and Feliformia (Springer *et al.*, 2003). Thus, the Miacidae were here placed to the outside of the crown carnivorans, following Wesley-Hunt and Flynn (2005).

The list of the creodont and carnivoran taxa reported in this paper is shown in Table 1. Measurements on the specimens are shown in Table 2.

Abbreviations: I/i, upper/lower incisor; C/c, upper/lower canine; P/p, upper/lower premolar; M/m, upper/lower molar; DP/dp, upper/lower deciduous premolar.

Table 1. List of creodont and carnivoran taxa reported in this paper.

- Creodonta Cope, 1875
  - Hyaenodontidae Leidy, 1869
    - Proviverrinae Matthew, 1909
      - *Allopterodon* Ginsburg, 1977
        - *Allopterodon* sp. cf. *A. bulbousus* Lange-Badré, 1979
      - *Paracynohyaenodon* Martin, 1906
        - *Paracynohyaenodon magnus* Crochet, 1988
        - *Paracynohyaenodon schlosseri* Martin, 1906
      - Proviverrinae gen. et sp. indet.
    - Hyaenaelurinae Pilgrim, 1932
      - *Pterodon* de Blainville, 1839
        - *Pterodon dasyuroides* de Blainville, 1839
    - Hyaenodontinae Leidy, 1869
      - *Hyaenodon* Laizer and Parieu, 1838
        - *Hyaenodon brachyrhynchus* Dujardin, 1840
        - *Hyaenodon minor* Gervais, 1848–52
        - *Hyaenodon requieni* Gervais, 1846
        - *Hyaenodon* sp. cf. *H. cayluxi* Filhol, 1876
        - *Hyaenodon* sp. cf. *H. rossignoli* Lange-Badré, 1979
- Carnivora Bowdich, 1821
  - Miacidae Cope, 1880
    - *Paramiacis* Mathis, 1985
      - *Paramiacis exilis* (Filhol, 1876)
    - *Quercygale* Kretzoi, 1945
      - *Quercygale angustidens* (Filhol, 1872)
  - Caniformia Kretzoi, 1943
    - Amphicyonidae Haeckel, 1866
      - *Cynodictis* Bravard and Pomel, 1850
        - *Cynodictis lacustris* (Gervais, 1848)
      - *Simamphicyon* Viret, 1942
        - *Simamphicyon helvecticus* (Pictet and Humbert, 1869)
    - Arctoidea Flower, 1869
      - Ursidae (Fischer von Waldheim, 1817)
        - Hemicyoninae Frick, 1926
          - *Cephalogale* Jourdan, 1862
            - Cf. *Cephalogale* sp.
    - Caniformia fam. gen. et sp indet.
  - Feliformia Kretzoi, 1943
    - Nimravidae Cope, 1880
      - *Nimravus* Cope, 1879
        - Cf. *Nimravus* sp.

Table 2. Measurements (in mm) of creodont and carnivoran specimens.

Allopterodon sp. cf. *A. bulbousus*
NMNS-PV 21135: M1 L = 7.6, W = 11.6, metastyle L = 3.3.
NMNS-PV 21137: p4 L = 7.4, W = 3.8, H = 5.6.
Paracynohyaenodon magnus
NMNS-PV 21132: I3 L = 4.9, W = 3.0, H = 8.8.
NMNS-PV 21133: P3 L = 7.1, W = 6.5, H = 4.3.
NMNS-PV 21134: P3 L = 7.1, H = 4.5.
NMNS-PV 21136: M3 L = 5.8.
NMNS-PV 21138: p4 L = 7.6*, W = 4.5, H > 5.5.
NMNS-PV 21139: m2 L = 9.3, trigonid L = 7.0, trigonid W = 5.2, talonid W = 4.1.
NMNS-PV 21140: m3 L = 9.0, trigonid L = 7.2, trigonid W = 5.8, talonid W = 3.2, H = 9.1.
NMNS-PV 21141: dP4 L = 5.6, W = 4.4.
Paracynohyaenodon schlosseri
NMNS-PV 21201: p3 L = 6.7, W = 4.0, H > 5.6.
Proviverrinae indet.
NMNS-PV 21142: IVth metacarpal L = 30.0;
mid-shaft dorsopalmar diameter = 3.1, mediolateral diameter = 3.5;
proximal articulation dorsopalmar L = 6.3, mediolateral W = 4.4;
distal articulation dorsopalmar L = 5.1, mediolateral W = 4.5.
Pterodon dasyuroides
NMNS-PV 21446: mandibular D below m2 = 33.2;
m2 L = 15.4, trigonid L = 12.2, trigonid W = 8.5, talonid W = 5.7;
m3 L = 18.6, trigonid L = 15.4, trigonid W = 10.6, talonid W = 6.3.
NMNS-PV 21447: mandibular D below m1 = 30.0;
p1 L = 9.1*;
p2 L = 11.8*;
p3 L = 13.5, W = 6.1, H > 8.8;
p4 L = 15.1, W = 7.4, H > 14.5;
m1 L = 12.6, trigonid L = 9.4, trigonid W = 5.9, talonid W = 5.2;
m2 L = 17.1, trigonid L = 12.9, trigonid W = 8.2, talonid W = 6.5, H > 13.4;
m3 L = 17.9, trigonid L = 14.7, trigonid W = 10.0, talonid W = 4.0, H > 15.2.
NMNS-PV 21522: mandibular D below m1 = 40.8*;
p2 L = 13.4, W = 6.8;
p3 L = 14.4, W = 8.5;
p4 L = 17.2, W = 10.5;
m1 L = 14.6*;
m2 L = 20.9, trigonid L = 15.1, trigonid W = 10.8, talonid W = 7.4;
m3 L = 24.4, trigonid L = 19.3, trigonid W = 13.6, talonid W = 8.7, H > 20.2.
Hyaenodon brachyrhynchus
NMNS-PV 21362: P4 L = 13.2, W = 10.4.
NMNS-PV 21381: P4 L = 12.9, H =9.5*.
NMNS-PV 21521: lower canine L = 11.1, W = 7.4.
Hyaenodon minor
NMNS-PV 21380: mandibular D below m1 (left) = 20.2*; symphyseal length = 34.6;
right c L = 9.4, W = 6.7, H > 18.5;
right p2 L = 8.6*, W = 4.1; left p2 L = 8.1*, W = 4.1;
right p3 L = 9.4*, W = 4.9; left p3 L = 9.4, W = 4.7;
right p4 L = 10.1, W = 5.1; left p4 L = 9.8, W = 5.2;
left m1 L = 7.9*;
right m2 L = 9.1, trigonid L = 7.4, trigonid W = 4.9, talonid W = 3.3;
left m2 trigonid L = 7.6, trigonid W = 4.8.
Hyaenodon requieni
NMNS-PV 21383: mandibular D below m1 (juvenile) = 29.7;
dp3 L = 11.7, W = 5.3*, H > 7.9;
dp4 L = 11.7, W = 6.0, H > 8.1;
p2 W = 7.1*, H = 10.3;
p3 H = 16.6;
m3 paraconid H > 13.8.
NMNS-PV 21441: P3 L = 14.8, W = 8.2, H = 14.1;
M1 L = 15.1, W = 9.7, metastyle L = 8.3, H > 11.0;
M2 L = 21.7, W = 13.2, metastyle L = 12.3, H > 15.9.

Table 2. Continued

NMNS-PV 21442: P4 L = 14.5, W = 12.9.
NMNS-PV 21443: upper canine L = 15.1, W = 10.8.
NMNS-PV 21444: P2 L = 13.8, W = 9.0, H = 16.2.
NMNS-PV 21445: p1 L =9.2, W = 5.4.

Hyaenodon sp. cf. *H. cayluxi*
NMNS-PV 21440: p3 L = 10.5, W = 4.5, H = 8.9.

Hyaenodon sp. cf. *H. rossignoli*
NMNS-PV 21382: upper canine L = 7.0, H > 14.9;
lower canine L = 7.3, H > 11.8.

Paramiacis exilis
NMNS-PV 21143: m1 L = 4.7, trigonid L = 2.7, trigonid W = 2.6, talonid W = 2.6, H = 4.1.

Quercygale angustidens
NMNS-PV 21202: p4 L = 9.7, W = 5.6, H = 7.4.
NMNS-PV 21203: P4 L = 12.3, W = 7.7, metastyle L = 4.6;
M1 L = 11.1, W = 6.2, metastyle L = 4.0.

Cynodictis lacustris
NMNS-PV 21448: mandibular D below m1 = 15.5*;
c L = 5.8*;
p3 L = 8.4*, W = 3.5*, H > 4.5;
p4 L = 8.5*;
m1 L = 10.8, trigonid L = 7.2, trigonid W = 5.7, talonid W = 5.5, H > 8.5;
m2 L = 6.3, trigonid L = 3.2, trigonid W = 4.0, talonid W = 3.7.

Simamphicyon helvecticus
NMNS-PV 21204: P4 L = 18.2, metastyle L = 7.0, H > 11.0;
M1 L = 14.4*, W =18.8*;
M2 L = 13.0*, W = 15.3*.
NMNS-PV 21205: m2 L = 12.5, trigonid L = 8.5, trigonid W = 8.2, talonid W = 6.7.

Cf. *Cephalogale* sp.
NMNS-PV 21523: lower canine L = 9.8, W= 6.9, H > 17.0.
NMNS-PV 21524: P4 L = 14.2, W = 7.8, metastyle L = 5.2, H > 8.2.

Caniformia indet.
NMNS-PV 21663: upper canine L = 25.1, W= 17.2, H = 47.5.

Carnivora indet.
NMNS-PV 21421: femoral L (preserved part only) = 84.1;
shaft mediolateral diameter = 19.1;
proximal width = 40.0;
femoral head anteroposterior diameter = 17.1, superoinferior diameter = 19.4, mediolateral depth = 11.3.

Abbreviations: L = length, W = width, H = height, D = depth, tr = trigonid, tl = talonid. *, estimate.

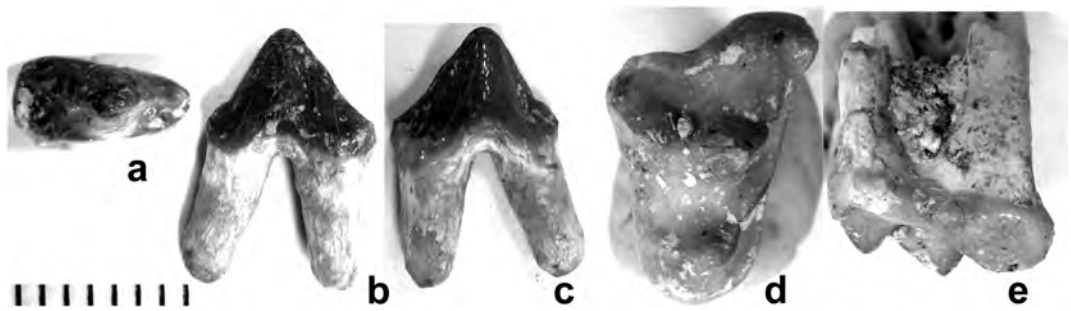

Fig. 1. *Allopterodon* sp. cf. *A. bulbosus* Lange-Badré, 1979. NMNS-PV 21137, left p4 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21135, left M1 in occlusal (d) and buccal (e) views. One division of scale equals 1 mm.

Systematic Paleontology

Order Creodonta Cope, 1875
Family Hyaenodontidae Leidy, 1869
Subfamily Proviverrinae Matthew, 1909
Genus *Allopterodon* Ginsburg, 1977

Allopterodon sp. cf. *A. bulbousus* Lange-Badré, 1979
(Fig. 1)

Material: NMNS-PV 21135, left M1; NMNS-PV 21137, left p4.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France). A part of Phosphorites du Quercy.

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The genus *Allopterodon* was revised by Polly and Lange-Badré (1993). They included only one species, *A. torvidus* (Van Valen, 1965), in the genus, but the later authors kept assigning other two French species, *A. minor* (Filhol, 1877) and *A. bulbosus* (Lange-Badré, 1979), to the genera (Morlo & Habersetzer, 1999). Cf. *Prototomus*? *minor* has been reported from the Le Bretou locality (Crochet, 1988), and the materials were introduced as *Allopterodon minor* in Morlo & Habersetzer (1999). These materials are likely the same species as the present materials. *Allopterodon bulbosus* is a relatively larger form in the genus, and is known from Robiac (MP16), Perriere (MP17b), and the old Quercy collection (unknown stratigraphic level) (Morlo & Habersetzer, 1999).

The two specimens have smooth dental enamel, thereby being distinguished from the materials of co-occurring *Paracynohyaenodon*. The posterior part of the premolar (NMNS-PV 21137) is wide and flat; thus, the premolar was identified as a p4. In the M1 (NMNS-PV 21235), the parastyle is not well-developed, and the anterobuccal corner of the paracone is directly in contact with a weakly developed cingulum. The paraconule is absent. The upper first molar (NMNS-PV 21235) indicates a characteristics of *A. bulbosus*; that is, the metacone is clearly higher than the paracone in M1 (Morlo & Habersetzer, 1999). However, both of the teeth are larger than the size of *A. bulbosus* as well as other *Allopterodon* species in the previous studies (Lange-Badré, 1979; Morlo & Habersetzer, 1999). The premolar (NMNS-PV 21137) is pointed; the form is similar to those of *A. minor* than the broad and clumpy premolars of *A. bulbosus*. It seems difficult to settle taxonomic assignment of the materials from Le Bretou without data on variation within *A. bulbosus* and among *Allopterodon* species.

Genus *Paracynohyaenodon* Martin, 1906

Paracynohyaenodon magnus Crochet, 1988
(Fig. 2)

Material: NMNS-PV 21132, left I3; NMNS-PV 21133, left P3; NMNS-PV 21134, right P3; NMNS-PV 21136, right M3 fragment; NMNS-PV 21138, left p4 fragment; NMNS-PV 21139, right m2; NMNS-PV 21140, right m3; NMNS-PV 21141, right DP4.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France). A part of Phosphorites du Quercy.

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Occurrences of *Paracynohyaenodon magnus* from Le Bretou have been reported by Crochet (1988). Lange-Badré and Mathis (1992) considered *P. magnus* as a synonym of *P. schlosseri*, the type species of the genus. However, the present materials support the size differences between the

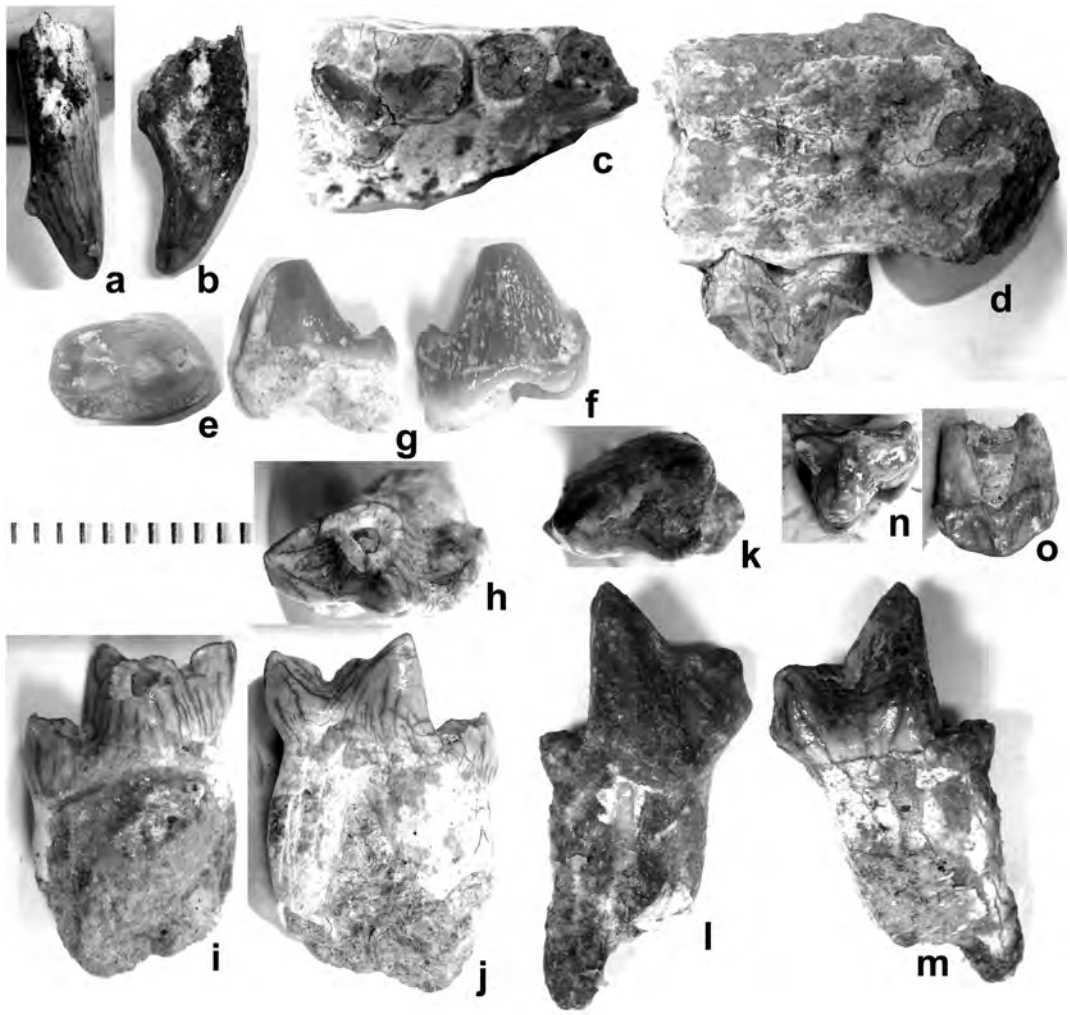

Fig. 2. *Paracynohyaenodon magnus* Crochet, 1988. NMNS-PV 21132, I3 in labial (a) and medial (b) views. NMNS-PV 21133, left P3 in occlusal (c) and buccal (d) views. NMNS-PV 21138, left p4 in occlusal (e), buccal (f), and lingual (g) views. NMNS-PV 21139, right m2 in occlusal (h), buccal (i), and lingual (j) views. NMNS-PV 21140, right m3 in occlusal (k), buccal (l), and lingual (m) views. NMNS-PV 21141, right DP4 in occlusal (n) and buccal (o) views. One division of scale equals 1 mm.

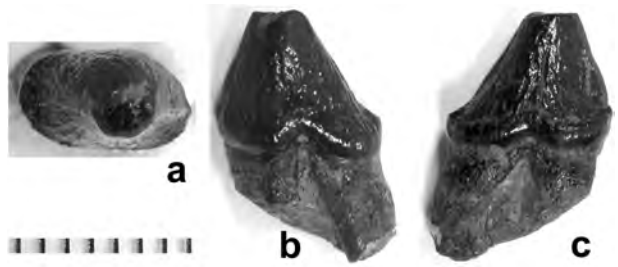

Fig. 3. *Paracynohyaenodon schlosseri* Martin, 1906. NMNS-PV 21201, left p3 in occlusal (a), buccal (b), and lingual (c) views. One division of each scale equals 1 mm.

Fig. 4. Proviverrinae gen. et sp. indet. NMNS-PV 21142, left metacarpal IV in proximal (a), medial (b), dorsal (c), and distal (d) views. One division of each scale equals 1 mm.

two species suggested by Crochet (1988). Therefore, the present materials are placed in *P. magnus*, following the classification by Crochet (1988). The eight teeth presented in this paper may be associated.

***Paracynohyaenodon schlosseri* Martin, 1906**

(Fig. 3)

Material: NMNS-PV 21201, left p3.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The material is smaller than the above described *P. magnus*. Occurrences of *Paracynohyaenodon schlosseri* from Robiac have been reported (Hooker, 1987).

Proviverrinae gen. et sp. indet.

(Fig. 4)

Material: NMNS-PV 21142, left metacarpal IV.

Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France). A part of Phosphorites du Quercy.

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The shaft curvature is weak, suggesting a digitigrade tendency for the posture of the animal. The overall size indicates that this metacarpal belonged to an animal smaller than a red fox (*Vulpes vulpes*) and larger than a fenec (*V. zerda*) (Egi, pers. observ.). The carnivrans found from this locality belong to plantigrade families, and their body sizes are too small (*Paramiacis*) or too large (*Quercygale*, *Simamphicyon*) for this metacarpal (NMNS-PV 21142). *Hyaenodon* is a digitigrade carnivore, but it has been reported that the genus is absent in this locality (Crochet, 1988) and that *Hyaenodon* appeared at the MP17 level (Lange-Badré, 1979; Legendre, 1987). Some species of proviverrine hyaenodontids have been reconstructed in a semi-digitigrade posture (Matthew, 1909). At present, NMNS-PV 21142 belongs most likely to one of the above mentioned proviverrines, *Allopterodon* and *Paracynohyaenodon*.

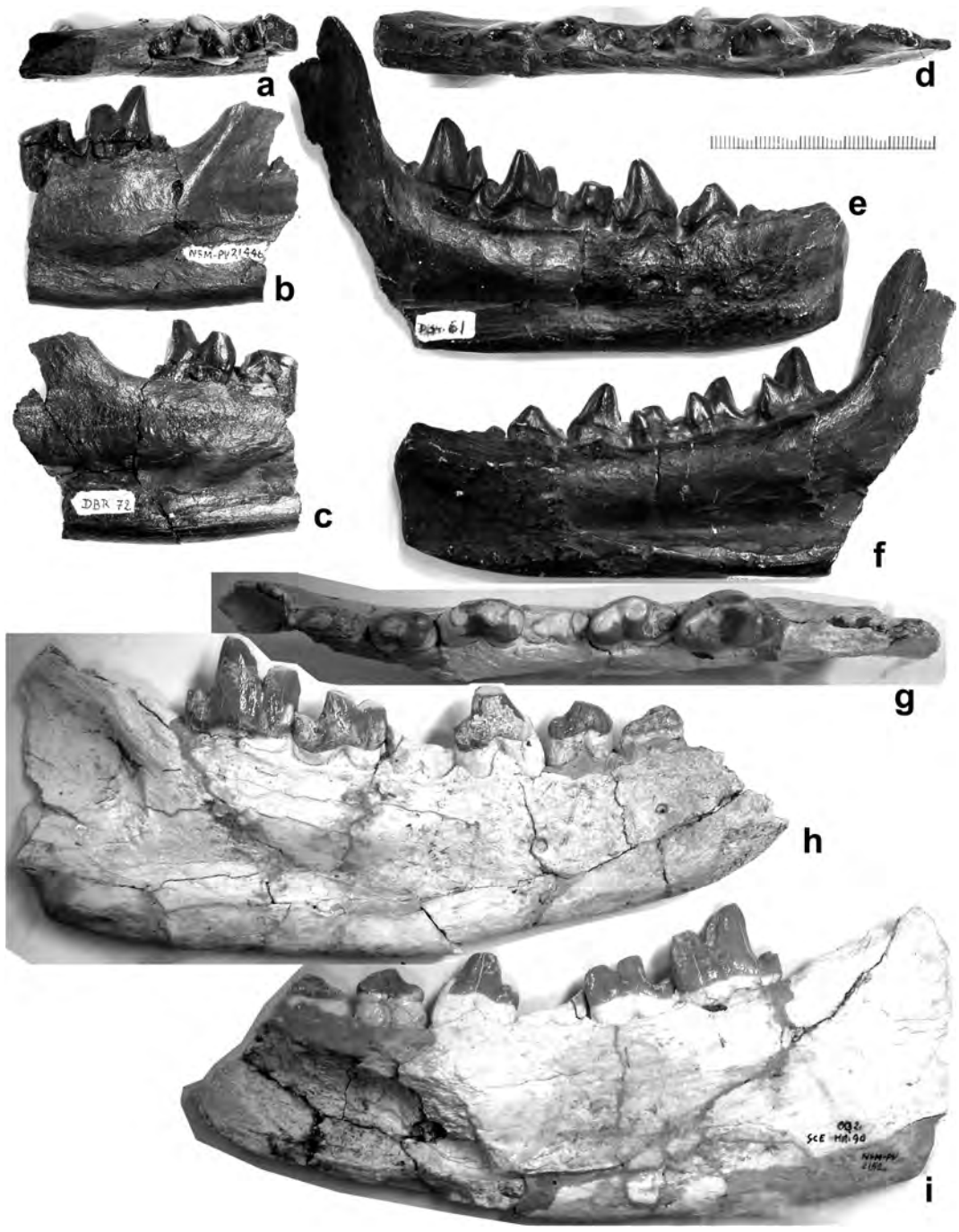

Fig. 5. *Pterodon dasyuroides* de Blainville, 1839. NMNS-PV 21446, left mandibular fragment with m2-3 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21447, right mandible with p3-m3 in occlusal (d), buccal (e), and lingual (f) views. NMNS-PV 21522, right mandible with p2-4 and m2-3 in occlusal (g), buccal (h), and lingual (i) views. One division of scale equals 1 mm.

Subfamily Hyaenaelurinae Pilgrim, 1932
Genus *Pterodon* de Blainville, 1839

***Pterodon dasyuroides* de Blainville, 1839**
(Fig. 5)

Material: NMNS-PV 21446, left mandibular fragment with m2-3; NMNS-PV 21447, cast of right mandible with p3-m3; NMNS-PV 21522, right mandible with p2-4 and m2-3.

Locality: NMNS-PV 21446 and 21447 are from La Débruge (Apt, Vaucluse, Alpes-Côte d'Azur, France). NMNS-PV 21522 is from St. Capraise d'Eymet (Eymet, Bergerac, Dordogne, Aquitaine, France).

Age: late Eocene (Priabonian). European mammal zone MP18 (La Débruge) and MP20 (St. Capraise d'Eymet) (Schmidt-Kittler, 1987).

Comments: A taxonomic revision on the genus *Pterodon* was conducted by Holroyd (1999). The genus consists of a European species, *P. dasyuroides*, and three African species. *P. dasyuroides* has been known many localities in France, England, Germany, and Switzerland (Lange-Badré, 1979). NMNS-PV 21522 is approximately one and a quarter larger than the other two specimens. This size difference corresponds with the previous comparison between specimens from St. Capraise d'Eymet and those from La Débruge (Lange-Badré, 1979) and is considered as an intraspecific variation in *P. dasyuroides*.

Subfamily Hyaenodontinae Leidy, 1869
Genus *Hyaenodon* Laizer and Parieu, 1838

***Hyaenodon brachyrhynchus* Dujardin, 1840**
(Fig. 6)

Material: NMNS-PV 21362, right P4; NMNS-PV 21381, left P4 in matrix; NMNS-PV 21521, heavily worn lower canine.

Locality: NMNS-PV 21362 is from Civrac de Blaye (Saint-Savin, Blaye, Gironde, Aquitaine, France). NMNS-PV 21381 is from Euzet les Bains, (Vézénobres, Alès, Gard, Languedoc-Roussillon, France). NMNS-PV 21521 is from St. Capraise d'Eymet (Eymet, Bergerac, Dordogne, Aquitaine, France).

Age: late Eocene (Priabonian); European mammal zone MP17 (Euzet les Bains), MP18 (Civrac de Blaye), and MP20 (St. Capraise d'Eymet) (Schmidt-Kittler, 1987**).**

Fig. 6. *Hyaenodon brachyrhynchus* Dujardin, 1840. NMNS-PV 21362, right P4 in occlusal (a) and buccal (b) views. One division of scale equals 1 mm.

Comments: This paper follows Lange-Badré (1979) for the classification of *Hyaenodon* species. Six species of the European species listed in Lange-Badré (1979) occur in the late Eocene. Additionally, two other European species are from the Old Quercy collection of unknown stratigraphic level. According to the measurements provided by Lange-Badré (1979), *H. brachyrhynchus* is a medium-sized species, being larger than *H. minor* and smaller than *H. requieni*. *H. brachyrhynchus* first appeared in MP17 and existed until the Oligocene (Lange-Badré, 1979; Legendre, 1987). Biochrom'97 (1997) provided the appearence timing of the species more specifically as MP17b. The occurrence of H. *brachyrhynchus* from Euzet les Bains (MP 17a according to Biochrom'97 (1997)) is a little older than the previously reported stratigraphic level.

***Hyaenodon minor* Gervais, 1848–52**

(Fig. 7)

Material: NMNS-PV 21380, right and left mandibles with right c, p2-4, m2 and left p2-4, m1 fragment, m2.

Locality: Euzet les Bains (Vézénobres, Alès, Gard, Languedoc-Roussillon, France).

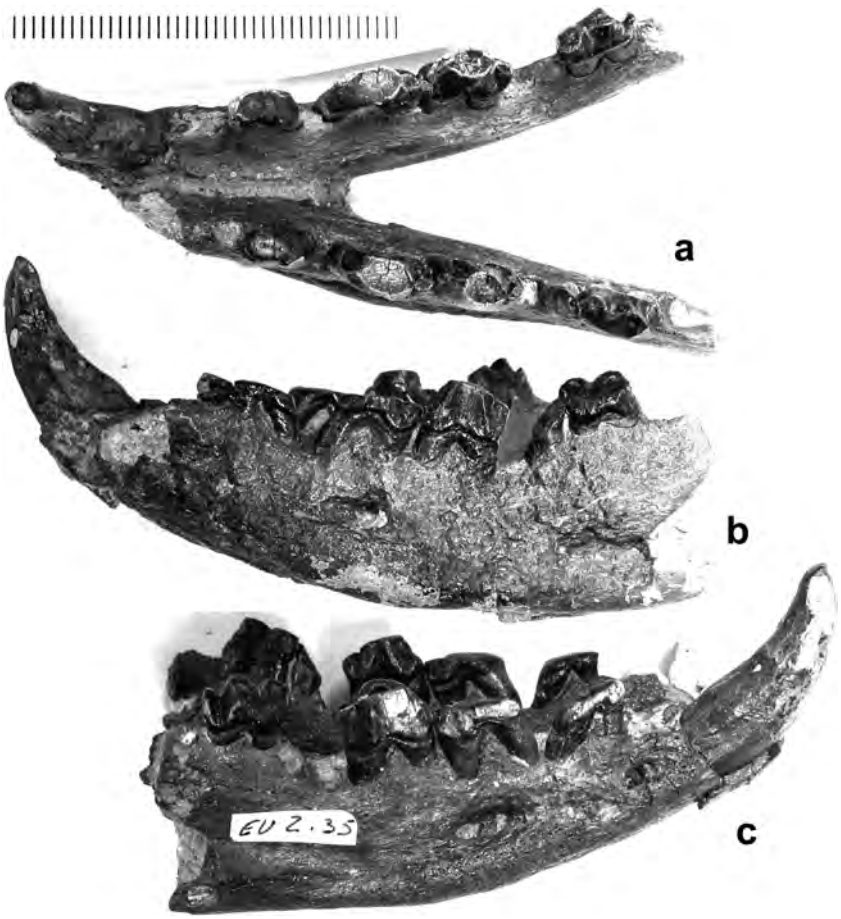

Fig. 7. *Hyaenodon minor* Gervais, 1848-52. NMNS-PV 21380, right and left mandibles with right c, p2-4, m2 and left p2-4, m2 in occlusal (a), left (b), and right (c) views. One division of each scale equals 1 mm.

Age: late Eocene (Priabonian). European mammal zone MP17 (Schmidt-Kittler, 1987).

Comments: *Hyaenodon minor* is a small *Hyaenodon* species known from MP17 and 18 (Lange-Badré, 1979). The measurements of the present materials are within the range presented by Lange-Badré (1979).

***Hyaenodon requieni* Gervais, 1846**

(Fig. 8)

Material: NMNS-PV 21383, right mandibular fragment with dp3-4 and errupting c, p2-3, and paraconid of m2 in the mandibular body; NMNS-PV 21441, right maxillary fragment with C (erruptting), P3, M1-2, part of skull roof; NMNS-PV 21442, right P4; NMNS-PV 21443, C; NMNS-PV 21444, right P2; NMNS-PV 21445, p1.

Locality: NMNS-PV 21383 is from Euzet les Bains (Vézénobres, Alès, Gard, Languedoc-Roussillon, France). The others (NMNS-PV 21441–21445) are from La Débruge (Apt, Vaucluse, Alpes-Côte d'Azur, France).

Age: late Eocene (Priabonian). European mammal zone MP17 (Euzet les Bains) and MP18 (La Débruge) (Schmidt-Kittler, 1987).

Comments: *Hyaenodon requieni* is known from MP17 and 18 (Lange-Badré, 1979). It is relatively larger than the other French *Hyaenodon* species from the same stratigraphic levels. The present materials exceed the size range of *H. brachyrhynchus*, thereby likely belong to *H. requieni*. For the specimens from La Débruge, *H. heberti* Filhol, 1876, may be the other possiblity because *H. heberti* is reported to be a relatively large species.

NMNS-PV 21383 contains a paraconid of a permanent second molar in the mandibular ramus. The m1 seems to have already errupted, but only the alveoli are preserved. There are considerebale size differences between deciduous premolars and permanent one. The specimen is at the erruption stage of the second premolar, and the elongation of the mandible is much greater below p1-2 than below dp3-4.

***Hyaenodon* sp. cf. *H. cayluxi* Filhol, 1876**

(Fig. 9)

Material: NMNS-PV 21440, left p3.

Locality: La Débruge (Apt, Vaucluse, Alpes-Côte d'Azur, France).

Age: late Eocene (Priabonian). European mammal zone MP18 (Schmidt-Kittler, 1987).

Comments: The crown length is in the ranges of *Hyaenodon minor* and *H. cayluxi* (the data for *H. minor* is from Lange-Badré (1979); the data for *H. cayluxi* is based on Egi (pers. observ.)). The premolar is too narrow for that of *Hyaenodon minor*.

***Hyaenodon* sp. cf. *H. rossignoli* Lange-Badré, 1979**

(Fig. 10)

Material: NMNS-PV 21382, left C and c in matrix.

Locality: Euzet les Bains (Vézénobres, Alès, Gard, Languedoc-Roussillon, France).

Age: late Eocene (Priabonian). European mammal zone MP17 (Schmidt-Kittler, 1987).

Comments: This specimen is smaller than the above mentioned material (NMNS-PV 21380) of *H. minor*, but it is not small enough to be *H. filholi* Schlosser, 1887. Thus, this specimen is likely to be *H. rossignoli* Lange- Badré, 1979, which is slightly smaller than *H. minor*.

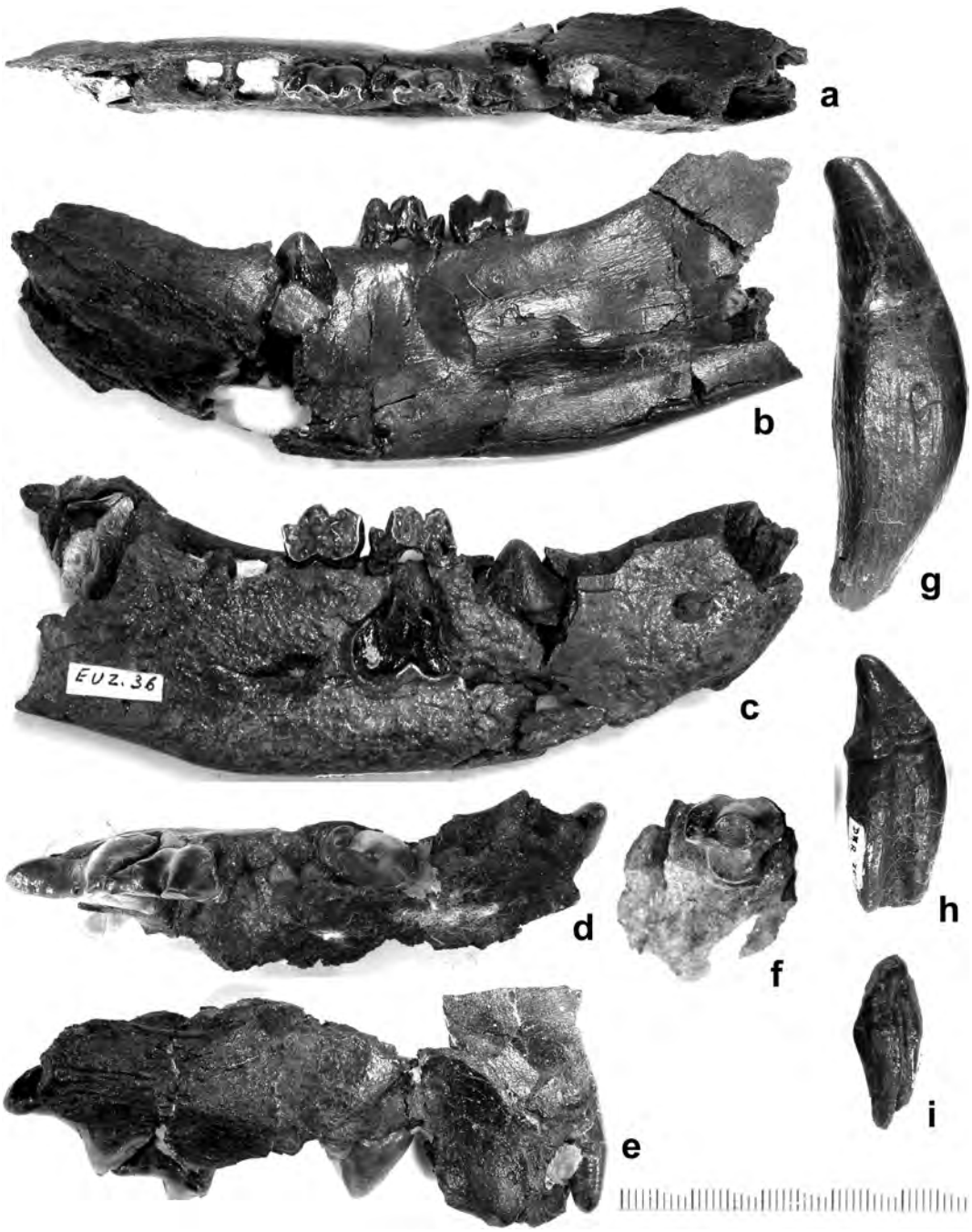

Fig. 8. *Hyaenodon requieni* Gervais, 1846. NMNS-PV 21383, right mandibular fragment with dp2-3, c, p1-2, half of m1 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21441, right maxillary fragment with C, P3, M1-2, part of skull roof in occlusal (d) and buccal (e) views. NMNS-PV 21442, right P4 in occlusal view (f). NMNS-PV 21443, upper canine (g). NMNS-PV 21444, right P2 in lingual view (h). NMNS-PV 21445, p1 (i). One division of scale equals 1 mm.

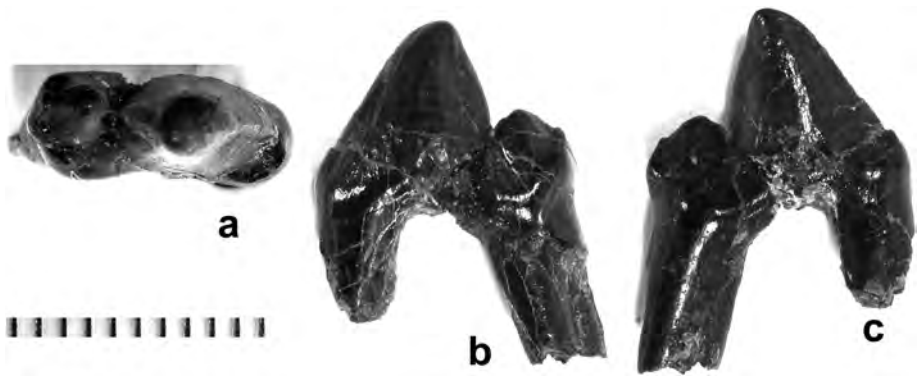

Fig. 9. *Hyaenodon* sp. cf. *H. cayluxi* Filhol, 1876. NMNS-PV 21440, left p3 in occlusal (a), buccal (b), and lingual (c) views. One division of each scale equals 1 mm.

Fig. 10. *Hyaenodon* sp. cf. *H. rossignoli* Lange-Badré, 1979. NMNS-PV 21382, left upper and lower canines in medial view. One division of each scale equals 1 mm.

Order Carnivora Bowdich, 1821
Family Miacidae Cope, 1880
Genus *Paramiacis* Mathis, 1985

***Paramiacis exilis* (Filhol, 1876)**
(Fig. 11)

Material: NMNS-PV 21143, left m1.
Locality: Le Bretou (Tarn-et-Garonne, Midi-Pyrenees. France). A part of Phosphorites du Quercy.
Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

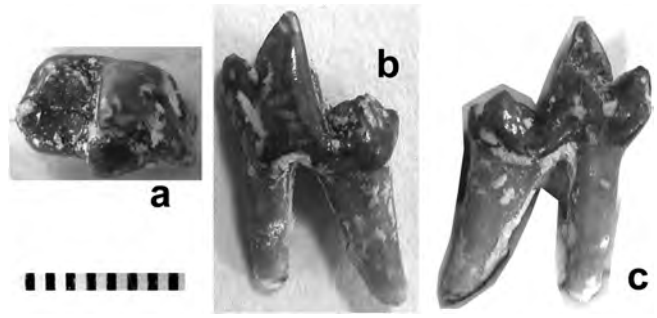

Fig. 11. *Paramiacis exilis* (Filhol, 1876). NMNS-PV 21143, left m1 in occlusal (a), buccal (b), and lingual (c) views. One division of each scale equals 0.5 mm.

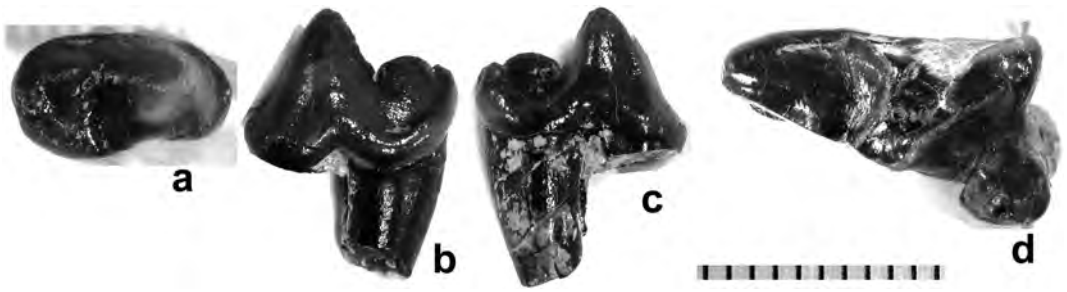

Fig. 12. *Quercygale angustidens* (Filhol, 1872). NMNS-PV 21202, left p4 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21203, right P4 in occlusal view (d). One division of each scale equals 1 mm.

Comments: The type locality for *Paramiacis exilis* is Robiac, a MP16 locality in France (Mathis, 1985). This species occurs in MP16 and 17 localities (Hooker, 1987; Legendre, 1987).

Genus *Quercygale* Kretzoi, 1945

***Quercygale angustidens* (Filhol, 1872)**
(Fig. 12)

Material: NMNS-PV 21202, left p4; NMNS-PV 21203, right P4.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: *Quercygale* appeared in the MP16 level and existed until the MP18 level (Hooker, 1987; Legendre, 1987). Systematic position of the genus has been controversial. This paper follows the classification by Wesley-Hunt and Flynn (2005), placing the genus in the Miacidae.

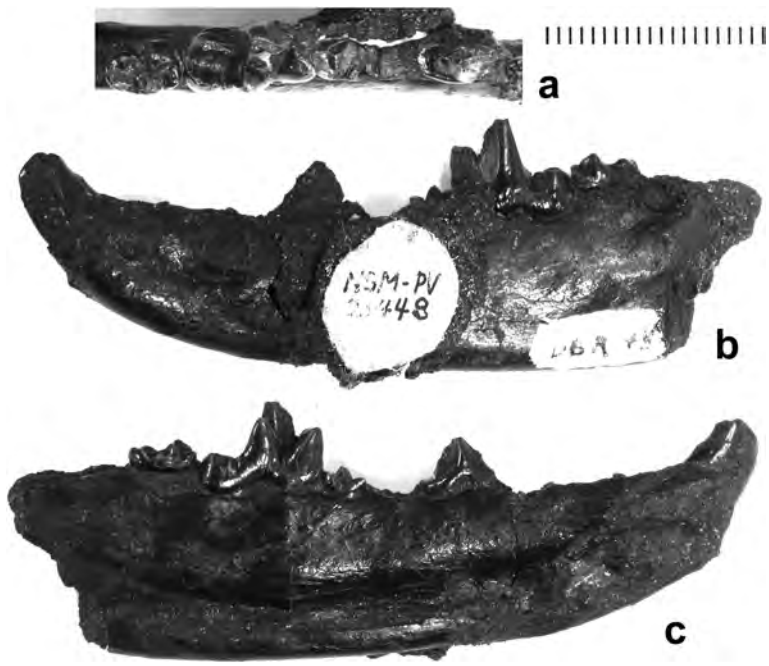

Fig. 13. *Cynodictis lacustris* (Gervais, 1848). NMNS-PV 21448, left mandibular fragment with c, p3, a half of p4, m1, m2 in occlusal (a), buccal (b), and lingual (c) views. One division of each scale equals 1 mm.

Suborder Caniformia Kretzoi, 1943
Family Amphicyonidae Haeckel, 1866
Genus *Cynodictis* Bravard and Pomel, 1850

***Cynodictis lacustris* (Gervais, 1848)**
(Fig. 13)

Material: NMNS-PV 21448, left mandibular fragment with c, p3, a half of p4, m1, m2.

Locality: La Débruge (Apt, Vaucluse, Alpes-Côte d'Azur, France).

Age: late Eocene (Priabonian). European mammal zone MP18 (Schmidt-Kittler, 1987).

Comments: Kostakis (1980) revised the taxonomy of *Cynodictis* and regarded only six of the species, all from Europe, as *Cynodictis*. Many species were considered as subspecies of *C. lacustris* in this revision. La Débruge is the type locality for the *C. lacustris*. Legendre (1987) listed the range of occurrence of *C. lacustris* as MP18 and 19.

Genus *Simamphicyon* Viret, 1942

***Simamphicyon helvecticus* (Pictet and Humbert, 1869)**
(Fig. 14)

Material: NMNS-PV 21204, right maxillary fragment with P4, alveoli of M1-2; NMNS-PV 21205, right m2; NMNS-PV 21206, C without root, dental fragments.

Locality: Robiac (Bessèges, Alès, Gard, Languedoc-Roussillon, France).

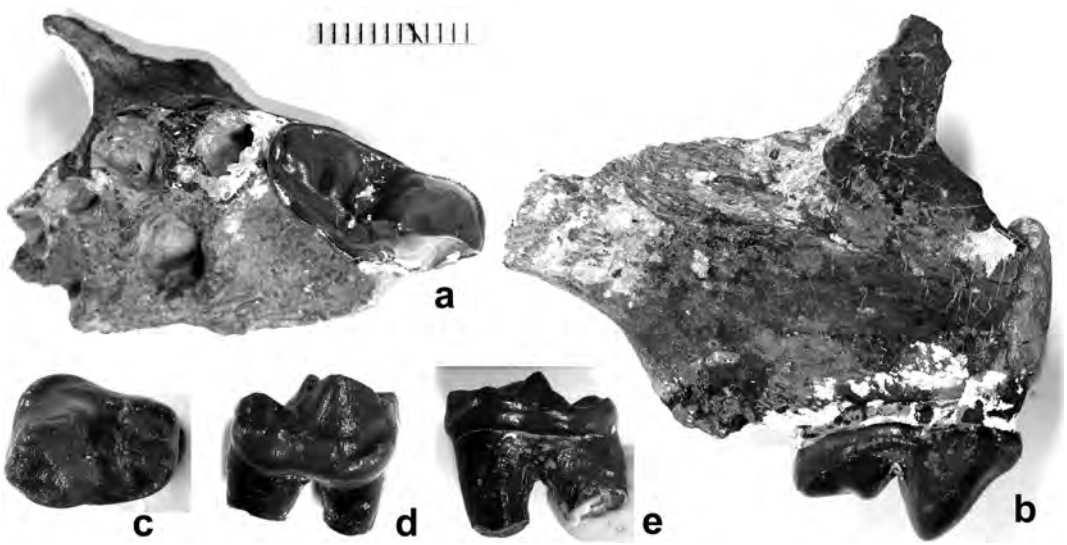

Fig. 14. *Simamphicyon helvecticus* (Pictet and Humbert, 1869). NMNS-PV 21204, right maxillary fragment with P4 in occlusal (a) and buccal (b) views. NMNS-PV 21205, a right m2 in occlusal (c) and buccal (d) views. One division of scale equals 1 mm.

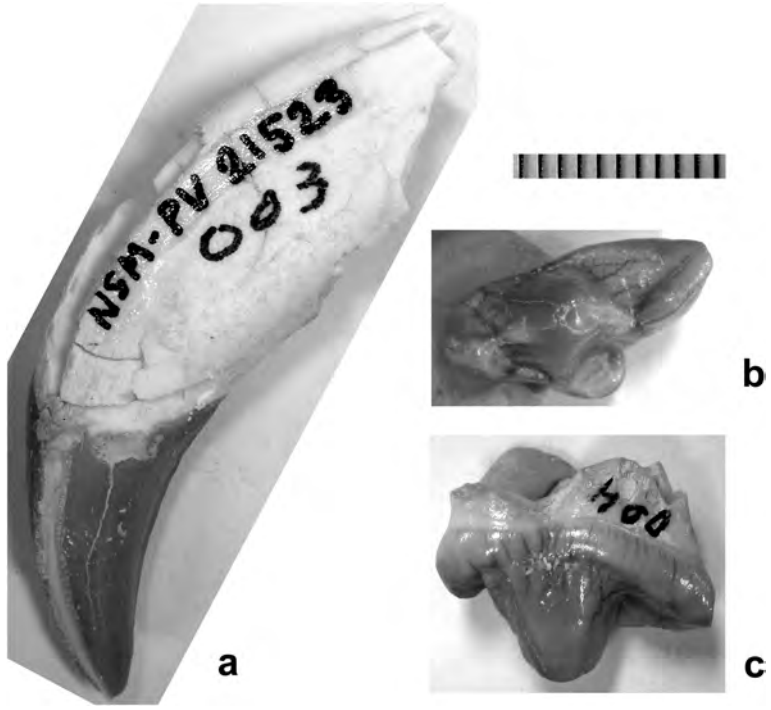

Fig. 15. Cf. *Cephalogale* sp. NMNS-PV 21523, canine (a). NMNS-PV 21524, left P4 in occlusal (b) and buccal (c) views. One division of each scale equals 1 mm.

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The genus *Symamphicyon* has been known from Robiac and Le Bretou. Both localities are MP16, and the genus occurs only from this level (Sudre, 1969; Hooker, 1987; Crochet, 1988). This taxon is one of the earliest fossil records among the Amphicyonidae, but its morphology is specialized. Springhorn (1977) placed this genus in the Tribe Haplocyonini Ginsburg (1966).

Infraorder Arctoidea Flower, 1869
Family Ursidae (Fischer von Waldheim, 1817)
Subamily Hemicyoninae Frick, 1926

Cf. *Cephalogale* sp.
(Fig. 15)

Material: NMNS-PV 21523, canine; NMNS-PV 21524, left P4.

Locality: St. Capraise d'Eymet (Eymet, Bergerac, Dordogne, Aquitaine, France).

Age: late Eocene (Priabonian). European mammal zone MP20 (Schmidt-Kittler, 1987).

Comments: Occurrences of *Cephalogale* Jourdan, 1862 from the Phosphorites of Quercy was reported by de Beaumont (1965), but the stratigraphic levels of these Quercy materials are not clear. *Cephalogale* is included in the faunal list of the late Eocene Naduo fauna in southern China (Tang & Qiu, 1979). All other fossil records of *Cephalogale* are from the Oligocene or early Miocene (e.g., Kuss, 1962; Gabounia, 1966; BiochromM'97, 1997; Ginsburg and Morales, 1998; Wang *et al.*, 2005). NMNS-PV 21523 and 21524 may be considered to be important materials because they indicate an existence of *Cephalogale* in the MP 20, the latest Eocene, of Europe.

Systematics of bear affinities vary between researchers. The ranks used in this study follow the ones in Ginsburg (1999) and Hunt (1998).

Caniformia fam., gen et sp. indet.
(Fig. 16)

Material: NMNS-PV 21663, left C.

Locality: Faluns de Touraine, (Sainte-Maure-de-Touraine, Chinon, Indre-et-Loire, Centre, France).

Age: Basal part of middle Miocene (Langhian). European mammal zone MN5 (Steininger *et al.*, 1996).

Comments: There are some large carnivorous mammals in this stratigraphic level of Europe (Gins-

Fig. 16. Caniformia fam., gen. et sp. indet. NMNS-PV 21663, left upper canine. One division of each scale equals 1 mm.

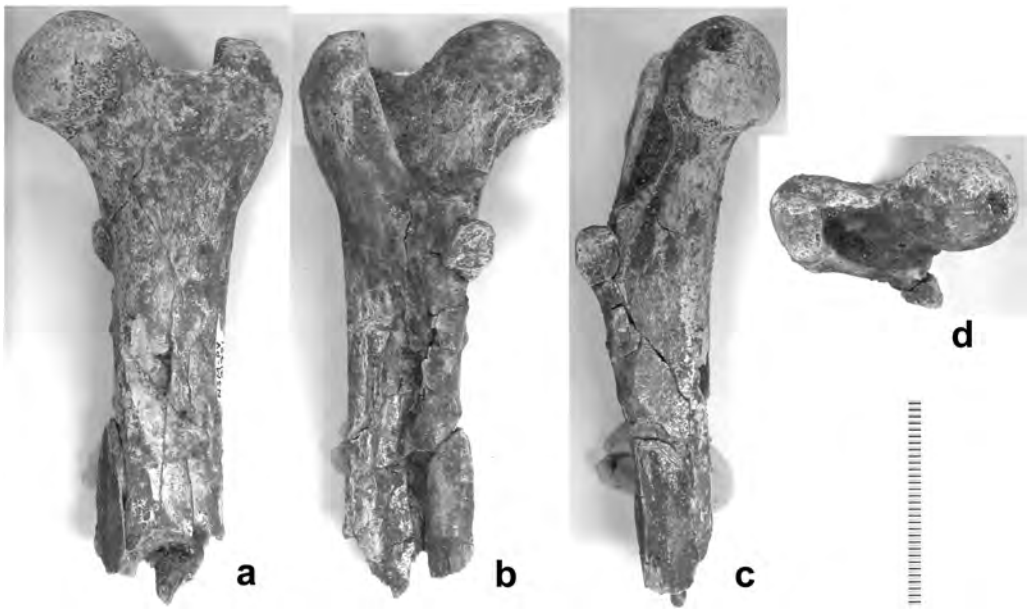

Fig. 17. Cf. *Nimravus* sp. NMNS-PV 21421, left proximal femur in anterior (a), posterior (b), medial (c), and proximal (d) views. One division of each scale equals 1 mm.

burg, 1999a, 1999b). A creodont, *Hyainailouros sulzeri*, is too big for the canine. Nimravids and felids have flatter canines, while NMNS-PV 21663 is rather conical. The overall size indicates that the canine belonged to a large hemicyonid or an amphicyonid.

Suborder Feliformia Kretzoi, 1943
Family Nimravidae Cope, 1880
Genus *Nimravus* Cope 1879

Cf. *Nimravus* sp.
(Fig. 17)

Material: NMNS-PV 21421, left proximal femur.

Locality: Baby, (Sainte-Foy-la-Grande, Libourne, Gironde, Aquitaine, France)

Age: late Eocene (Priabonian). European mammal zone MP17 or MP20 (Schmidt-Kittler, 1987).

Comments: The size of the femur fit to perissodactyls, artiodactyls, creodonts, and carnivorans of the age. Perissodactyls have the third trochanter. The femoral shaft of creodonts has lateral curvature around the third trochanter. In artiodactyls, the greater trochanter is high, the femoral head is rather flat, and the lesser trochanter projects posteriorly. NMNS-PV 21421 lacks these characters and belongs likely to a carnivoran rather than to other mammals. Body mass of approximately 20 kg is estimated based on the femoral head dimension (using the equation in Egi, 2001), indicating that the animal was a relatively large carnivoran, an amphicyonid or a nimravid. The shaft of NMNS-PV 21421 is rather straight, although the posterior surface is broken; thus, the femur is more likely to be that of a nimravid. The stratigraphic level may be too early for *Eusmilus*, which first appeared in MP21 (Brunet & Vianey-Liaud, 1987). Although the basal border of the confirmed stratigraphic range for *Nimravus* in Europe is MP22 (Peigné, 2003), this genus existed in the late Eocene of Asia and has

been known in the old Quercy collection of unknown stratigraphic level (Peigné, 2003). NMNS-PV 21421 seems to have belonged to a *Nimravus* individual based on the morphology, size, and the stratigraphic level.

Acknowledgments

I thank the following personnels for access of the comparative specimens: Drs. B. Marandat, L. Marivaux, J.-Y. Crochet, and J.-J. Jaeger (Université Montpellier II, Montpellier), C. Argot, P. Tassy, C. Sagne, M. Pickford, B. Senut (Muséum national d'Histoire naturelle, Paris), J. Hooker (Natural History Museum, London), Meng Jin (American Museum of Natural History, New York), and L. Gordon (United States National Museum of Natural History, Washington, D.C.).

Literature Cited

Agusti, J. and M. Anton, 2005. *Mammoths, sabertooths, and hominids: 65 million years of mammalian evolution in Europe*. Columbia University Press, New York. 328 pp.

BiochroM'97, 1997. Syntheses and correlation tables. *In*: J.-P. Aguilar, S. Legendre, and J. Michaux (Eds.), Actes du congrès BiochroM'97, *Mémoires et Travaux de l'École Pratique des Hautes Études, Institut de Montpellier* **21**: 769–805.

Bowdich, T. E., 1821. *An analysis of the natural classifications of Mammalia for the use of students and travellers*. J. Smith, Paris. 115 pp.

Bravard, A. and A. Pomel, 1850. *Notice sur les ossements fossiles de la Débruge, près Apt*. Paris. 8 pp.

Brunet, M. and M. Vianey-Liaud, 1987. Mammalian reference levels MP 21-30. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene–Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 30–31.

Cope, E. D., 1875. On the supposed Carnivora of the Eocene of Rocky Mountains. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **27**: 444–448.

Cope, E. D., 1879. On the genera of Felidae and Canidae. *Proceedings of the Academy of Natural Sciences, Philadelphia*, **31**: 168–194.

Cope, E. D., 1880a. On the genera of the Creodonta. *Proceedings of the American Philosophical Society*, **19**: 76–82.

Cope, E. D., 1880b. On the extinct cats of America. *American Naturalist*, **14**: 833–858.

Crochet, J.-Y., 1988. The Bretou locality (Quercy phosphorites, Tran-et-Garonne, France) and its late Eocene vertebrate fauna III. Marsupialia, Creodonta and Fissipeda. *Palaeontographica Abteilung A*, **205**: 51–67.

De Beaumont, G., 1965. Contribution a l'étude du genre *Cephalogale* Jourdan (Carnivora). *Mémoires suisses de Paléontologie*, **82**: 1–34.

De Blainville, H. M. D., 1839. Sur l'*Hyaenodon leptorhynchus* (de Laizer) nouveau genre de carnassiers fossiles d'Auvergne. *Annales français et étrange d'Anatomie et Physiologie*, **3**: 17–31.

Dujardin, F. 1840. Note sur une tête fossile d'*Hyaenodon* trouvée au bord du Tarn, près de Rabasteins. *Comptes rendus de l'Académie des sciences, Paris*, **10**: 134–135.

Egi, N., 2001. Body mass estimates in extinct mammals from limb bone dimensions: the case of North American hyaenodontids. *Palaeontology*, **44**: 497–528.

Filhol, H., 1872. Recherches sur les mammifères fossiles des dépots de phos—phate de chaux dans les départements du Lot, du Tarn et de Tarn—et—Garonne. *Annales des Sciences Géologiques*, **3**: 1–31.

Filhol, H., 1876a. Mammiferes fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **82**: 288–289.

Filhol, H. 1876b. Recherches sur les phosphorites du Quercy. Étude des fossiles qu'on y rencontre et spécialement des mammifères. *Annales des Sciences géologiques*, **7**: 1–220.

Filhol, H. 1877. Recherches sur les phosphorites du Quercy. *Annales des sciences géologiques*, **8**: 1–340.

Fischer de Waldheim, G. W., 1817. Adversaria Zoologica. *Memoir Societie Naturelle, Moscow*, **5**: 368–428.

Flower, W. H., 1869. On the values of the characters of the base of the cranium in the classification of the Order Carnivora, and on the systematic position of *Bassaris* and other disputed forms. *Proceedings of the Zoological Society of London*, 1869: 4–37.

Frick, C., 1926. The Hemicyoninae and an American Tertiary bear. *Bulletin of the American Museum of Natural History*, **56**:

1–119.

Gabuniia, L. K., 1966. Sur les mammifères oligocènes du Caucase. *Bulletin de la Société de la France*, **8**: 857–869.

Gervais, P., 1848–1852. *Zoologie et Paléontologie françaises (animaux vertébrés) ou Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France*. Arthus Bertrand, Paris. 271 pp.

Ginsburg, L., 1966: Les amphicyons des Phosphorites du Quercy. *Annales de Paléontologie (Vertébrés)*, **52**: 23–64.

Ginsburg, L., 1999a. Order Creodonta. *In*: G. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München. p. 105–108.

Ginsburg, L., 1999b. Order Carnivora. *In*: G. Rössner and K. Heissig (eds.), *The Miocene Land Mammals of Europe*. Verlag Dr. Friedrich Pfeil, München. p. 109–148.

Ginsburg, L., J. Arques, F. de Broin, Y. le Calvez, J. Mouton, D. Obert, C. Privé-Gill, and J. P. Roucan, 1977. Découverte d'une faune de Mammifères dans le Lutétien supérieur de La Défense à Puteaux près Paris (Hauts-de-Seine). *Comptes rendus sommaire des séances de la Société géologique de France*, **6**: 311–313.

Ginsburg, L. and J. Morales, 1998. Les Hemicyoninae (Ursidae, Carnivora, Mammalia) et les formes apparentées du Miocène inférieur et moyen d'Europe occidentale, *Annales de Paléontologie*, **84**: 71–123.

Haeckel, E., 1866. *Generale Morphologie der Organismen*. Verlag von Georg Reimer, Berlin.

Holroyd, P. A., 1999. New Pterodontinae (Creodonta: Hyaenodontidae) from the late Eocene-early Oligocene Jebel Qatrani Formation, Fayum province, Egypt. *PaleoBios*, **19**: 1–18.

Hooker, J. J., 1987. Mammalian reference levels MP 14–16. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 26–27.

Hunt, R. M. Jr., 1998. Ursidae. *In*, C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary mammals of North America. Volume 1*. Cambridge University Press, Cambridge. p. 174–195.

Jourdan, C., 1862. Description de restes fossiles de grands mammifères. *Revue des Société Savantes*, **1**: 126–130.

Kotsakis, T., 1980. Rivisione sistematica e distribuzione stratigrafica e geografica del genere *Cynodictis* Bravard and Pomel (Carnivora, Mammalia). *Bolletino della Società Paleontologica Italiana*, **19**: 259–273.

Kretzoi, M., 1943. *Kochictis centennii* n. g. n. sp., ein altertümlicher Creodonte aus dem Oberoligozän Siebenbürgens. *Földtani Közlöny*, **73**: 190–195.

Kretzoi, M., 1945. Bemerkungen über das Raubtiersystem. *Annales Historico Naturale, Museum Nationale Hungaricum*, **38**: 59–83.

Kuss, S. E., 1962. Deux nouveau canidés (Carnivora) du Stampien de Toulouse. *Bulletin de la Société d'histoire naturelle de Toulouse*, **97**: 330–344.

Laizer, L. d. and Parieu, d., 1838 Description et détermination d'une mâchoire fossile appartenant à un mammifère jusqu'à présent inconnu, *Hyaenodon leptorhynchus*. *Comptes Rendus de l'Académie des Sciences Paris*, **7**: 442.

Lange-Badré, B., 1979. Les Créodontes (Mammalia) d'Europe occidentale de l'Éocéne supérieur a l'Oligocene supérieur. *Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre*, **42**: 1–249.

Lange-Badré, B. and C. Mathis, 1992. Données nouvelles sur les Créodontes Proviverrinés des zones MP16 et MP17 des Phosphorites de Quercy. *Bulletin du Muséum national d'histoire naturelle. 4e série. Sect. C, Sciences de la terre, paléontologie, géologie, minéralogie*, **14**: 161–184.

Legendre, S., 1987. Mammalian reference levels MP 17–20. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 28–29.

Leidy, J., 1869. The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences of Philadelphia (Ser. 2)*, **7**: 1–472.

Martin, R., 1906. Revision der obereocänen und unteroligocänen Creodonten Europas. *Revue suisse de Zoologie*, 14: 405–600.

Mathis, C., 1985. Contribution à la connaissance des Mammifères de Robiac (Éocène supérieur): Creodonta et Carnivora. *Bulletin du Muséum national d'histoire naturelle. 4e série. Sect. C, Sciences de la terre, paléontologie, géologie, minéralogie*, **7**: 305–326.

Matthew, W. D., 1909. The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. *Memoirs of the American Museum of Natural History*, **4**: 291–567.

McKenna, M. C. and S. K. Bell, 1997. *Classification of mammals above the species level.* Columbia University Press, New York. 631 pp.

Morlo, M. and J. Habersetzer, 1999. The Hyaenodontidae (Creodonta, Mammalia) from the lower middle Eocene (MP11) of Messel (Germany) with special remarks on new x-ray methods. *Courier Forschungsinstitut Senckenberg*, **216**: 31–73.

Peigné, S., 2003. Systematic review of European Nimravinae (Mammalia, Carnivora, Nimravidae) and the phylogenetic relationships of Palaeogene Nimravidae. *Zoologica Scripta*, **32**: 199–229.

Pictet, J. F. and A. Humbert, 1869. Mémoire sur les animaux vertébrés trouvés dans le terrain sidérolithique du Canton de Vaud et appartenant à la faune éocène. Supplément. *Matériaux Paléontologie Suisse*, **5**: 121–197.

Pilgrim, G. E., 1932. The fossil Carnivora of India. *Palaeontologia Indica, n.s.*, **18**: 1–232.

Polly, P. D., 1993. *Hyaenodontidae (Creodonta, Mammalia) and the position of systematics in evolutionary biology*. Ph.D. dissertation, University of California, Berkeley. 283 pp.

Polly, P. D. and B. Lange-Badré, 1993. A new genus *Eurotherium* (Mammalia, Creodonta) in reference to taxonomic problems with some Eocene Hyaenodontids from Eurasia. *Comptes Rendus de l'Académie des Sciences, Paris. Série II*, **317**: 991–996.

Schlosser, M., 1887. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupialier, Creodonten und Carnivoren des europäischen Tertiärs und deren Beziehungen zu ihren lebenden und fossilen aus europäischen Verwandten. *Beiträge Palaeontologie Oesterreich-Ungarns und des Orients (Mojsisovics und Neumayr)*, **4**: 1–227.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 1–312.

Springer, M. S., W. J. Murphy, E. Rizirik, and S. J. O'Brien, 2005. Molecular evidence for major placental clades. *In*: K. D. Rose and J. D. Archibald (eds.), *The rise of placental mammals: origins and relationships of the major extant clades*. The Johns Hopkins University Press, Baltimore. p. 37–49.

Springhorn, R., 1977. Revision der Alttertiaren Europaischen Amphicyonidae (Carnivora, Mammalia). *Palaeontographica Abteilung A*, **158**: 26–113.

Steininger, F. F., W. A. Berggren, D. V. Kent, R. L. Bernor, S. Sen, and J. Agusti, 1996. Circum-Mediterranean Neogene (Miocene and Pliocene) marine–continental chronologic correlations of European Mammal Units. *In*: R. L. Bernor, V. Fahlbusch, and H.-W. Mittmann (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas*. Columbia University Press, New York. p. 7–46.

Sudre, J., 1969. Les gisements de Robiac (Eocène supérieur) et leurs faunes de Mammifères. *Palaeovertebrata*, **2**: 95–156.

Tang, Y. J. and Z. D. Qiu. 1979. Vertebrate faunas of Baise, Guangxi. *In*: Academia Sinica, Institute of Vertebrate Paleontology and Paleoanthropology and Nanking Institute of Geology and Paleontology (eds), *Mesozoic and Cenozoic red beds of south China*. Science Press, Beijing. p. 407–415.

Van Valen, L., 1965. Some European Proviverrini (Mammalia, Deltatheridia). *Palaeontology*, **8**: 638–665.

Viret, J., 1942. Observations sur les canides du genre *Pseudamphicyon*. *Annales de l'Université de Lyon. Sect. C, Sciences naturelles*, **3**: 85–98.

Wang, X., M. C. McKenna, and D. Dashzeveg, 2005. *Amphicticeps* and *Amphicyonodon* (Arctoidea, Carnivora) from Hsanda Gol Formation, central Mongolia and phylogeny of basal arctoids with comments on zoogeography. *American Museum Novitates*, **3483**: 1–57.

Wesley-Hunt, G. D. and J. J. Flynn, 2005. Phylogeny of the Carnivora: basal relationships among the carnivoramorphans, and assessment of the position of "Miacoidea" relative to Carnivora. *Journal of Systematic Palaeontology*, **3**: 1–28.

Wesley-Hunt, G. D. and L. Werdelin, 2005. Basicranial morphology and phylogenetic position of the upper Eocene carnivoramorphan *Quercygale*. *Acta Palaeontologica Polonica*, **50**: 837–846.

Wyss, A. R. and J. J. Flynn, 1993. A phylogenetic analysis and definition of the Carnivora. *In*: F. S. Szalay, M. J. Novacek, and M. C. McKenna (eds.), *Mammal phylogeny: placentals, volume 2*. Springer-Verlag, New York. p. 32–52.

National Museum of Nature and Science Monographs, No. 55, pp. 65–70, 2025

Chapter 6

"CONDYLARTHRA"

Yukimitsu Tomida[1] and Naoko Egi[2]

[1] Department of Geology and Paleontology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305–0005, Japan.
(e-mail: aztlanolagus@yahoo.co.jp)
[2] Department of Anthropology, National Museum of Nature and Science,
Tsukuba, Ibaraki 305-0005, Japan.
(e-mail: egicyon@gmail.com)

Introduction

Order Condylarthra once included number of archaic ungulate taxa as if it was a taxonomic waste-basket, but cladistic analyses on morphology during 1980's and 1990's re-organized the families and genera in the order, and the order name itself disappeared (Archibald, 1998), or some families were removed from the order, including Arctocyonidae (+ Oxyclaenidae) and Mesonichidae (McKenna and Bell, 1997). But, recent development of the molecular phylogenetic analyses (e.g. Murphy *et al.*, 2001) rejects some of the phylogenetic relationships based solely on the morphological cladistics. This tendency seems resurrect the order "Condylarthra" (e.g. Kielan-Jaworowska *et al.*, 2004; Rose, 2006), and we here follow them but maintain inside quotation marks, designating a probable non-monophyletic taxon (Archibald, 1998; Ladeveze *et al.*, 2010).

"Condylarth" families included in this chapter are Arctocyonidae and Pleuraspidotheriidae. Arctocyonid specimens reported in this chapter consist of one species, *Arctocyon primaevus*. The Arctocyonidae is a group of archaic mammals of Paleocene and early Eocene (Rose, 2006). The fossil records are known mainly from Europe and North America. The group has been placed in various orders such as the Condylarthra (Romer, 1966; Rose, 2006), the Procreodi (Matthew, 1915; McKenna and Bell, 1997), and an independent order, the Arctocyonia (Van Valen, 1969).

Pleuraspidotheriid specimens reported in this chapter consist of one species, *Pleuraspidotherium aumonieri*. The genus *Pleuraspidotherium* has been thought to be related to or placed in various groups, such as perissodactyl *Palaeotherium*, lemurs, some carnivorans, stem-perissodactyl, insectivoran, condylarth related to meniscotheriids, and finally condylarth family Pleuraspidotheriidae (Ladevese *et al.*, 2010). Even after that, it was classified in Meniscotheriidae (Russell, 1964; Romer, 1966) or Mioclaenidae (McKenna and Bell, 1997) within the order Condylarthra. The family Pleuraspidotheriidae is fairly abundant mammals in the late Paleocene in Europe (France), and a recent new member (*Hilalia*) extended the range to the Middle Eocene of Turkey, but is least understood in systematic point of view (Ladevese *et al.*, 2010).

Abbreviations: C/c, upper/lower canine; P/p, upper/lower premolar; M/m, upper/lower molar.

Systematic Paleontology

Order "Condylarthra" Cope, 1881
Family Arctocyonidae Giebel, 1855
Genus *Arctocyon* de Blainville, 1841

Arctocyon primaevus de Blainville, 1841
(Fig. 1)

Material: NMNS-PV 21120, almost complete right mandible with c, p2-m2; NMNS-PV 21121, left maxillary fragment with P3-M3.

Locality: Berru (Reims, Marne, Champagne-Ardenne, France).

Age: late Paleocene (Thanetian). European mammal zone MP 6 (Schmidt-Kittler, 1987).

Comments: Measurements are shown in Table 1. NMNS-PV 21120 is an almost complete hemimandible of which condyle and ascending ramus are preserved. *Arctocyon primaevus* is known only from the MP 6 level (Godinot, 1987). Many dental and postcranial specimens have been collected from Berru and Cernay localities. This species has been reconstructed as a small bear-like animal with omnivorous and ambulatory scansorial behaviors (Russell, 1964).

Family Pleuraspidotheriidae Zittel, 1892
Genus *Pleuraspidotherium* Lemoine, 1878

Pleuraspidotherium aumonieri Lemoine, 1878
(Fig. 2)

Material: NMNS-PV 21122, fragmentary right mandible with p3-4; NMNS-PV 21123, fragmentary right mandible with m3; NMNS-PV 21124, isolated right m1 or m2 (probably m2).

Table 1. Measurements (in mm) of *Arctocyon primaevus* and *Pleuraspidotherium aumonieri* specimens.

Arctocyon primaevus	
NMNS-PV 21120:	Mandibular symphysis - condyle L = 140, D below m1 = 28.3;
	Mandibular ascending ramus H = 67*;
	c L = 14.9, W = 7.3, H = 32.1;
	p2 L = 5.7, W = 3.2, H = 3.4;
	p3 L = 9.6, W = 5.4, H = 6.9;
	p4 L = 13.1, W = 7.7, H = 11.4;
	m1 L = 11.6, trigonid L = 6.3, trigonid W = 8.6, talonid W = 9.7;
	m2 L = 12.8, trigonid L = 7.0, trigonid W = 12.0, talonid W = 11.2
	m3 L = 13.9*.
NMNS-PV 21121:	P3 L = 10.2, W = 6.8, H = 7.8;
	P4 L = 10.8, W = 10.3, H = 9.4;
	M1 L = 10.4, W = 12.6;
	M2 L = 11.3, W = 15.5;
	M3 L = 9.4, W = 10.8.
Pleuraspidotherium aumonieri	
NMNS-PV 21122:	p3 L = 6.42, W = 4.25
	p4 L = 7.50, W = 5.08
NMNS-PV 21123:	m3 L = 8.58, W = 5.25
NMNS-PV 21124:	likely m2 L = 8.08, W = 5.00

Abbreviations: L = length, W = width, H = height, D = depth. *, estimated.

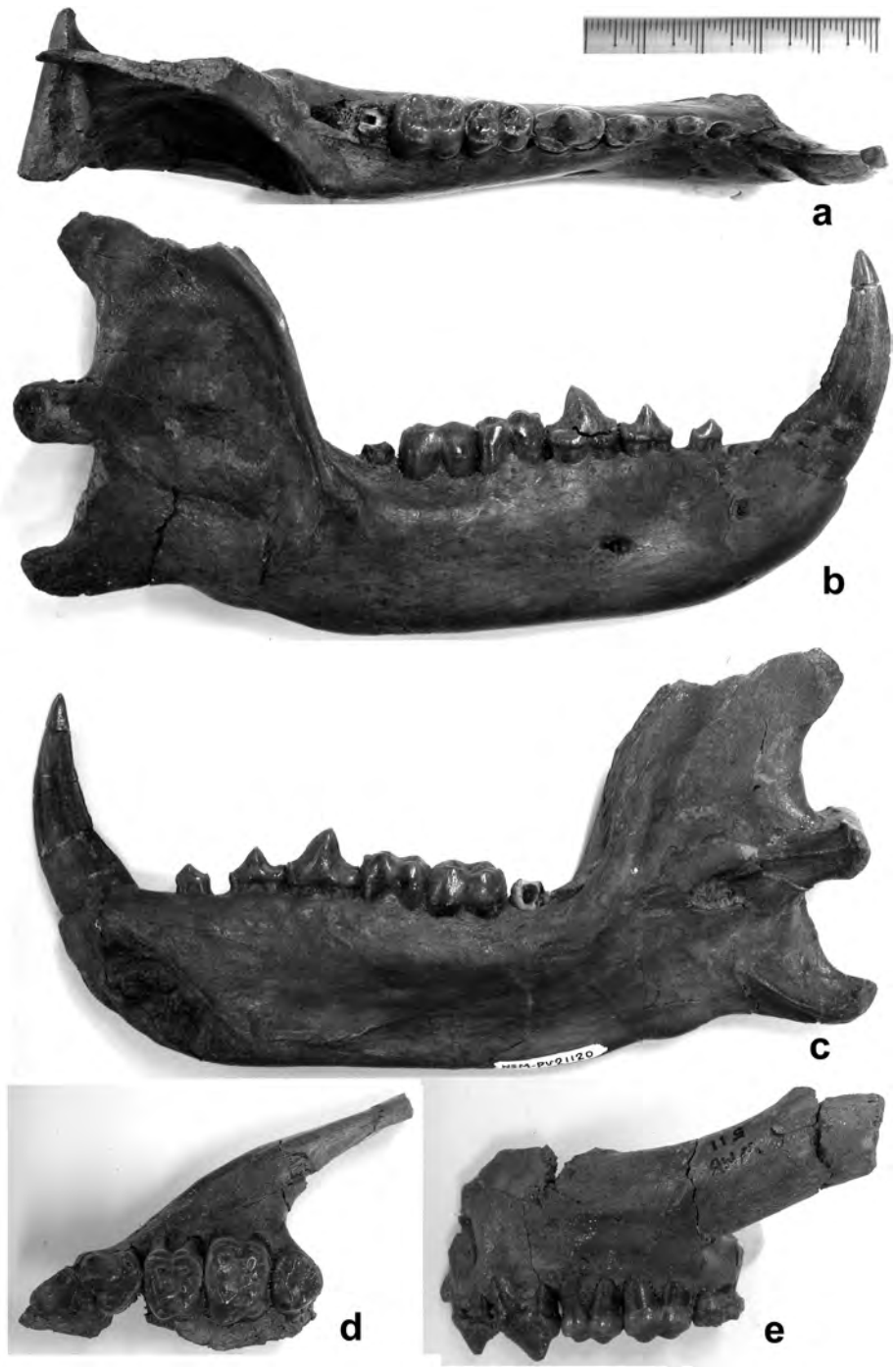

Fig. 1. *Arctocyon primaevus* de Blainville, 1841. NMNS-PV 21120, almost complete right mandible with c, p2-m2 in occlusal (a), buccal (b), and lingual (c) views. NMNS-PV 21121, left maxillary fragment with P3-M3 in occlusal (d) and buccal (e) views. One division of each scale equals 1 mm.

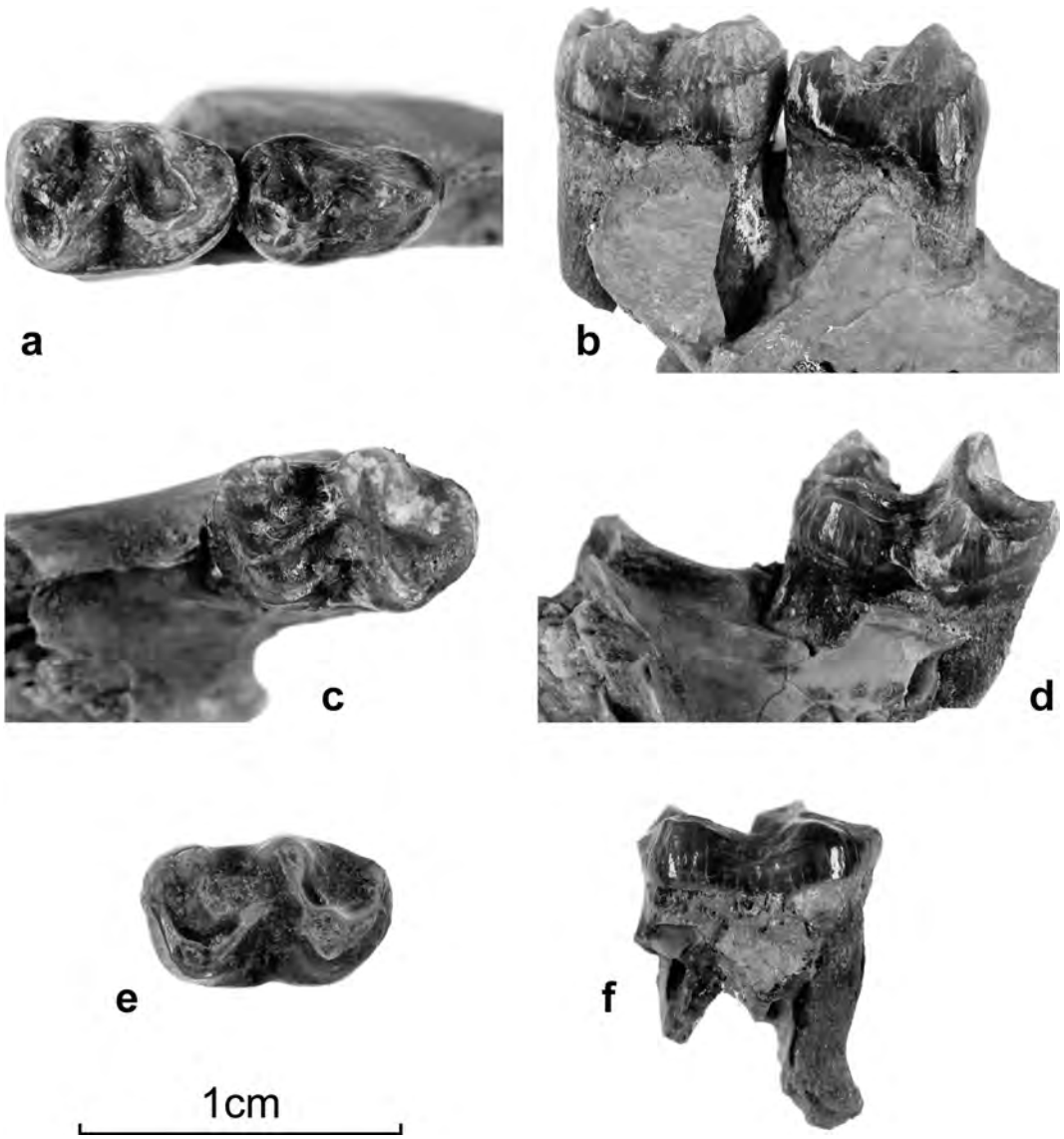

Fig. 2. *Pleuraspidotherium aumonier* Lemoine, 1878. NMNS-PV 21122, fragmentary right mandible with p3-4 in occlusal (a) and buccal (b) views. NMNS-PV 21123, fragmentary right mandible with m3 in occlusal (c) and buccal (d) views. NMNS-PV 21124, isolated right m1 or m2 (probably m2) in occlusal (e) and buccal (f) views.

Locality: Berru (Reims, Marne, Champagne-Ardenne, France).

Age: late Paleocene (Thanetian). European mammal zone MP 6 (Schmidt-Kittler, 1987).

Comments: Measurements are shown in Table 1. Based on the direct comparisons with the specimens from Cerney (R 627, 636, 641, 647, 648, 654, 668) and Berru (BR 1039, 12511, 12516), the molar morphology is almost identical, and molar size is near the largest end. The premolars are also very similar in morphology, but their width is somewhat wider than those we compared. Russell (1964, p. 313) shows the observed range of tooth measurements, of which the range of p4 length (50–52) is misprint, and it should be 50–82. Compared with this corrected table, the width of p3 is the only

measurement slightly outside of the range, but all others are within the range.

Another species, *P. remense*, was named by Lemoine (1891), but the holotype is supposed be an aberrant form of *P. aumonieri* according to Russell (1964 p. 249). Thus, the genus includes its type species, *P. aumonieri*, only. In this context, the faunal list of the type Cernaysian (including *P. remense* Lemoine, 1878 [*sic*]) is misleading (Savage and Russell, 1983).

Orthaspidotherium edwardsi is another taxon of the same family and known from the same localities, but it is about 2/3 of *P. aumonieri* in size, and it is easy to distinguish both taxa by their size.

In conclusion, all three NMNS specimens are among the largest specimens of the species, and their measurements are within the known range (Russell, 1964, p. 313), with a slight exception of the width of p3. But, we conclude that all three specimens should be identified as *P. aumonieri*, because p3 and p4 belong to the same individual.

Acknowledgments

We thank following persons for access of the comparative specimens: C. Argot, P. Tassy, C. Sagne, M. Pickford, and B. Senut (Muséum national d'Histoire naturelle, Paris).

Literature Cited

Archibald, J. D., 1998. Archaic ungulates ("Condylarthra"). *In* C. M. Janis, K. M. Scott, and L. L. Jacobs (eds.), *Evolution of Tertiary mammals of North America, Volume 1: Terrestrial carnivores, ungulates, and ungulatelike mammals.* Cambridge University Press, p. 292–331.

Cope, E. D., 1881. A new type of Perissodactyla. *American Naturalist*, 15: 1017–1018.

de Blainville, H. M. D., 1841. *Ostéographie ou description iconographique comparée du squeoette et du système dentaire des mammifères récents et fossiles pour servir de base a la zoologie et a la géologie. Tome 2: Secundatès*. J. B. Baillière et Fils, Paris.

Giebel, C. G., 1855. *Odontographie: Vergleichende Darstellung des Zahnsystemes der lebenden und fossilen Wirbelthiere*. A. Abel, Leipzig. 129 pp.+52 pls.

Godinot, M., 1987. Mammalian reference levels MP 1–10. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 21–23.

Kielan-Jaworowska, Z., R. L. Cifelli, and Z.-X. Luo, 2004. *Mammals from the age of dinosaurs: origins, evolution, and structure*. Columbia Univ. Press, New York, 630 pp.

Ladevese, S., P. Missiaen, and T. Smith, 2010. First skull of *Orthaspidotherium edwardsi* (Mammalia, "Condylarthra") from the Late Paleocene of Berru (France) and phylogenetic affinities of the enigmatic European family Pleuraspidotheriidae. Journal of Vertebrate Paleotology, 30(5): 1559–1578.

Lemoine, V., 1878. Recherches sur les Ossements fossiles des terrains tertiaires inf ' erieurs des environs de Reims. *Annales de Sciences naturelles*, **8**(1): 1–56.

Lemoine, V., 1891. E'tude d'ensemble sur les dents des mammifères fossiles des environs de Reims. *Bulletin de la Société géologique de France*, 19:263–290.

Matthew, W. D., 1915. A revision of the Lower Eocene Wasatch and Wind River Faunas. Part I. Order Ferae (Carnivora). Suborder Creodonta. *Bulletin of the American Museum of Natural History*, **34**: 4-103.

McKenna, M. C. and S. K. Bell, 1997. *Classification of mammals above the species level.* Columbia University Press, New York. 631 pp.

Murphy, W. J., E. Eizirik, S. J. O'Brien, O. Madsen, M. Scaily, *et al.*, 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. *Science*, **294**: 2348–2351.

Romer, A. S., 1966. *Vertebrate Paleontology*, 3rd edition. The University of Chicago Press, Chicago, 468 pp.

Rose, K. D., 2006. *The beginning of the age of mammals*. The Johns Hopkins University Press, Baltimore. 428 pp.

Russell, D. E., 1964. Les mammifères paléocènes d'Europe. *Mémoires du Muséum National d'Histoire Naturelle*, série C. **13**: 1–324.

Savage, D. E. and D. E. Russell, 1983. *Mammalian paleofaunas of the world*. Addison-Wesley Publ. Co., London, 432 pp.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene – Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 1–312.

Van Valen, L. M., 1969. The multiple origins of the placental carnivores. *Evolution*, **23**: 118–130.

Zittel, K. A. v. 1892. *Handbuch der Paläontologie. 1 Abteilung. Palaeozologie, Band 4*, Vertebrata. Druck Und Verlag Von R. Oldenburg, München and Leipzig.

National Museum of Nature and Science Monographs, No. 55, pp. 71–177, 2025

Chapter 7

PERISSODACTYLA

Kazunori Miyata

Fukui Prefectural Dinosaur Museum, Katsuyama, Fukui 911–8601, Japan.
(e-mail: k-miyata@dinosaur.pref.fukui.jp)

Introduction

The total number of perissodactyl specimens cataloged here is 194, which represents approximately half of the collection. Most of the perissodactyl specimens are derived from eight Eocene localities in France (Aumelas, Baby, Civrac de Blaye, Euzèt les Bains, La Débruge, Le Bretou, Robiac, and St. Capraise d'Eymet), while three specimens from the Miocene locality of Faluns de Touraine are also included. The European mammal reference levels of the Eocene localities extend from MP 13 to 20, the early Middle to Late Eocene (= Lutetian to Priabonian; Luterbacher et al., 2004). Eight Eocene perissodactyl genera are identified here with approximately 80% being remains of palaeotheriids, the great majority of which are *Palaeotherium* and *Plagiolophus*. For the convenience of the reader, the section on Miocene perissodactyls is mentioned as the last part of this chapter.

Taxonomy of perissodactyls has varied greatly in recent decades, although the close relationship between Tapiroidea and Rhinocerotoidea in Ceratomorpha is unanimous (Hooker, 2005). The classifications of perissodactyl families related to the Eocene taxa in this chapter (Lophiodontidae, Pachynolophidae, and Palaeotheriidae) are controversial among researchers and not yet resolved well (Hooker, 1986; Franzen, 1989; Prothero and Schoch, 1989; Schoch, 1989; Cuesta, 1994a, b; Cuesta, 1996; Froehlich, 1999, 2002; Remy, 2004; Holbrook, 2009). Following the systematic arrangement by Remy (1976), the Palaeotheriidae is supposed to include all of the Eocene taxa in this chapter except *Lophiodon*, since Pachynolophinae or Pachynolophidae, considered as an independent group by other workers, is affiliated in the Palaeotheriidae. Hooker (1989, 1994) proposed that the Pachynolophidae consists of *Anchilophus*, *Pachynolophus*, and their ancestor, and *Paranchilophus* is also likely a member of Pachynolophidae (Casanovas and Santafé, 1989). However, Cuesta (1994a) suggested that Pachynolophidae further includes *Leptolophus*, *Lophiotherium*, *Plagiolophus*, and *Propalaeotherium*. Meanwhile, McKenna and Bell (1997) established the family Anchilophidae consisting of *Anchilophus*, *Lophiotherium*, and *Paranchilophus*. The subject of perissodactyl classification is beyond the scope of this monograph, and no attempt is made here to review the classification comprehensively.

This chapter follows the systematic arrangement of the perissodactyl families by Hooker (2005, table 13.1) and his higher-rank classification, which affiliates Lophiodontidae in Ancylopoda. The arrangements for Palaeotheriidae and Pachynolophidae are based mainly on Prothero and Schoch (1989) and Hooker (1989, 1994). The genera *Leptolophus*, *Lophiotherium*, *Palaeotherium*, *Plagiolophus* and *Propalaeotherium* are considered as members of the Palaeotheriidae, while *Anchilophus* and *Pachynolophus* are placed in Pachynolophidae here.

Table 1 lists the perissodactyl taxa included in this chapter. Appendix 1 provides measurements of specimens. The measurement positions of cheek teeth and astragali largely follow those of Franzen (1968) and Abusch-Siewert (1983). Tooth length (anteroposterior or mesiodistal maximum length) listed

in the Appendix 1 is measured on the labial side of the crown, to make comparison with the dimensions from the previous literature.

Abbreviations for tooth classes, as mentioned in other chapters: I/i, upper/lower incisors; C/c, upper/lower canine; P/p, upper/lower premolar; M/m, upper/lower molar; DP/dp, upper/lower deciduous premolar. PMI means the ratio (percentage) of premolar series length/molar series length; in case of *Palaeotherium*, P2–4/M1–3 length ratio at maxilla and p2–4/m1–3 length ratio at mandible are available (Franzen, 1968). MN and MP are abbreviations for the European mammal Neogene and Paleogene reference levels, respectively.

Systematic Paleontology
(Eocene Perissodactyls)

Order Perissodactyla Owen, 1848a
Suborder Hippomorpha Wood, 1937
Superfamily Equoidea Gray, 1821
Family Palaeotheriidae Bonaparte, 1850, sensu (Hooker, 1989, 1994)

Genus *Propalaeotherium* Gervais, 1849

Type species: *Propalaeotherium isselanum* (Cuvier, 1824).

Comments: *Propalaeotherium* is a well-documented genus among Eocene perissodactyl taxa in Europe, and seven or eight species of the genus have been recognized as valid (Savage et al., 1965; Franzen and Haubold, 1986; Hooker, 1986; see also synonym lists in Franzen, 2006). The classification of *Propalaeotherium* in this chapter largely follows that of Savage et al. (1965), but Franzen (2006) assigned "*P.*" *parvulum* (Laurillard, 1849) and "*P.*" *messelense* (Haupt, 1925) to the genus *Eurohippus*.

***Propalaeotherium* sp. cf. *P. isselanum* (Cuvier, 1824)**
(Fig. 1)

Localities and Materials: Aumelas: NMNS-PV 21128, right maxillary fragment with M2–3.

Comments: *Propalaeotherium isselanum* is a large species of the genus (Savage et al., 1965), and is known only from MP 12 and 13 (Franzen, 1987; Luterbacher et al., 2004). However, the previously referred specimens of *P.* "*isselanum*" from the Geiseltal localities, Germany, (MP 12, Untere Mittelkohle; MP 13, Obere Mittelkohle) seem not to be assignable to *P. isselanum* (Remy, 2001).

The maxillary fragment from Aumelas (MP 13) preserves M2–3 which clearly show the characteristic cusp pattern of *Propalaeotherium*, despite the breakage of the anterolingual surface of the M3 protocone (Fig. 1); the para- and metastyles are distinct and form the stylar shelves with labial cingula, and the salient M2 mesostyle connecting to the ectoloph is positioned anterolabial to the metacone. However, the M3 mesostyle exhibits a small enamel swelling on the labial cingulum. The molars of NMNS-PV 2112 are smaller than those of *P.* "*isselanum*" from the Geiseltal localities and *P. argentonicum* Gervais, 1859 but larger than that of *P. voigti* (Matthes, 1977) (Appendix 1; see also Savage et al., 1965; Franzen and Haubold, 1986; Remy, 2001). Except for the weak M3 mesostyle, NMNS-PV 21128 could be referred to *P. isselanum*.

Table 1. List of perissodactyl taxa reported in this chapter. Asterisks (*) mean the Miocene taxa.

- Perissodactyla Owen, 1848a
  - Hippomorpha Wood, 1937
    - Equoidea Gray, 1821
      - Equidae Gray, 1821
        - *Anchitherium* Meyer, 1844
          - *Anchitherium aurelianense* (Cuvier, 1825)*
      - Palaeotheriidae Bonaparte, 1850
        - *Propalaeotherium* Gervais, 1849
          - *Propalaeotherium* sp. cf. *P. isselanum* (Cuvier, 1824)
        - *Lophiotherium* Gervais, 1859
          - *Lophiotherium cervulum* Gervais, 1859
        - *Palaeotherium* Cuvier, 1804
          - *Palaeotherium castrense* Noulet, 1863
            - *Palaeotherium castrense robiacense* Franzen, 1968
          - *Palaeotherium curtum* Cuvier, 1812
            - *Palaeotherium curtum frohnstettense* Franzen, 1968
            - *Palaeotherium curtum villerealense* Franzen, 1968
          - *Palaeotherium* sp. cf. *P. curtum* Cuvier, 1812
          - *Palaeotherium lautricense* Stehlin, 1904a
          - *Palaeotherium magnum* Cuvier, 1804
            - *Palaeotherium magnum girondicum* Blainville, 1846
          - *Palaeotherium medium* Cuvier, 1804
            - *Palaeotherium medium euzetense* (Depéret, 1917)
            - *Palaeotherium medium perrealense* (Stehlin, 1904b)
          - *Palaeotherium* sp. cf. *P. medium* Cuvier, 1804
          - *Palaeotherium muehlbergi* Stehlin, 1904b
            - *Palaeotherium muehlbergi thaleri* Remy, 1985
          - *Palaeotherium* sp.
          - Cf. *Palaeotherium* sp.
        - *Plagiolophus* Pomel, 1847a
          - *Paloplotherium* Owen, 1848b
            - *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b)
            - *Plagiolophus* (*Paloplotherium*) *major* (Brunet and Jehenne, 1989)
            - *Plagiolophus* (*Paloplotherium*) *oweni* Depéret, 1917
          - *Plagiolophus* Pomel, 1847a
            - *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804)
            - *Plagiolophus* sp.
            - Cf. *Plagiolophus* sp.
        - *Leptolophus* Remy, 1965
          - *Leptolophus* sp.
  - Tapiromorpha Haeckel, 1866
    - Pachynolophidae Pavlow, 1888
      - *Pachynolophus* Pomel, 1847b
        - *Pachynolophus bretovensis* Remy, 1988
        - *Pachynolophus* sp. cf. *P. bretovensis* Remy, 1988
        - *Pachynolophus duvali* Pomel, 1847b
      - *Anchilophus* Gervais, 1852
        - *Anchilophus* sp. cf. *A. desmaresti* Gervais, 1852
        - *Anchilophus dumasi* (Gervais, 1852)
        - *Anchilophus* sp. cf. *A. gaudini* Pictet and Humbert, 1869
        - Cf. *Anchilophus* sp.
    - Ancylopoda Cope, 1889
      - Lophiodontidae Gill, 1872
        - *Lophiodon* Cuvier, 1822
          - *Lophiodon lautricense* Noulet, 1851
          - *Lophiodon* sp.
    - Ceratomorpha Wood, 1937
      - Rhinocerotoidea Gray, 1821
        - Rhinocerotidae Gray, 1821
          - Gen. et sp. indet. 1*
          - Gen. et sp. indet. 2*

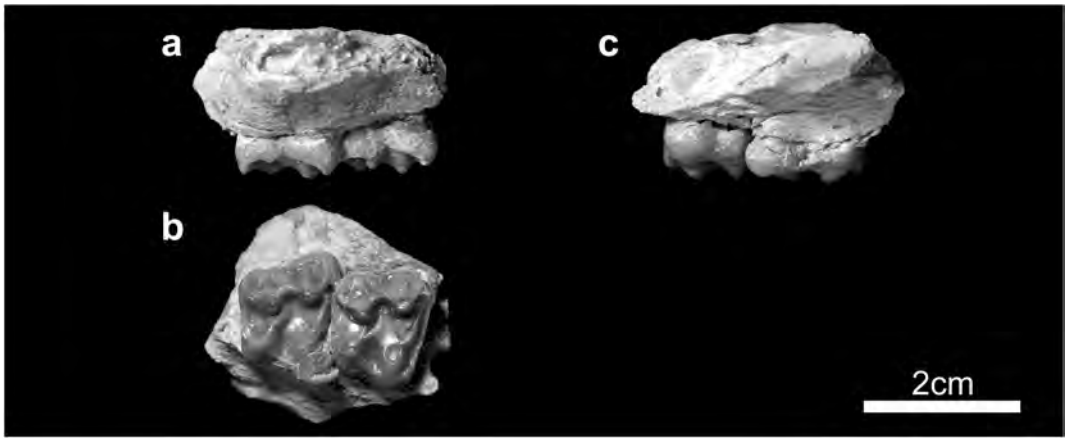

Fig. 1. *Propalaeotherium* sp. cf. *P. isselanum* (Cuvier, 1824) from Aumelas. NMNS-PV 21128, right maxillary fragment with M2–3 in labial (a), occlusal (b), and lingual (c) views.

Genus *Lophiotherium* Gervais, 1859

Type species: *Lophiotherium cervulum* Gervais, 1859.

Comments: Hooker (1986) recognized three species in the genus as valid: *Lophiotherium cervulum*, *L. pygmaeum* (Depéret, 1901), and *L. siderolithicum* (Pictet, 1857). Later, Franzen (1999) erected an earlier species, *L. sondaari*, from the early Middle Eocene (upper MP 11) in Geiseltal, Germany. This chapter basically follows this taxonomic concept. Furthermore, Hooker (1986) stated that *Lophiotherium robiacense* Depéret, 1917 was a synonym of *L. siderolithicum*, and Franzen and Haubold (1986) suggested that other species (*L. magnum*, *L. geiseltalensis*, and *L. voigti*) erected by Matthes (1977) were synonymous with existing species of *Propalaeotherium*.

Lophiotherium is a genus consisting of small-sized species and is widely distributed in Europe (Germany, Switzerland, England, France, and Spain; Savage et al., 1965; Hooker, 1986; Franzen, 1999). The occurrence of *Lophiotherium* extends from early Middle to late Middle Eocene (MP 11–17A; Franzen, 1999; Luterbacher et al., 2004). According to Franzen (1987) and Hooker (1987), *L. pygmaeum* has been recorded from MP 13 to 14, whereas *L. siderolithicum* and *L. cervulum* are known from MP 16 and 17, respectively. The *Lophiotherium* specimens cataloged here were collected from the type locality of *L. cervulum*, or Euzèt les Bains.

***Lophiotherium cervulum* Gervais, 1859**

(Figs. 2–7)

Localities and Materials: Euzèt les Bains: NMNS-PV 21388, left maxillary fragment with P3–M3; 21389, left maxillary fragment with DP3–4 and M1–3 (M3 is not erupted); 21390, left mandible with c1, p2–m3, and right symphysial part with broken c1; 21391, left mandibular fragment with possible p3–m2 (or dp3–4 and m1–2); 21392, right mandibular fragment with p2–m3; 21393, left maxillary fragment with possible M1 root and M2–3 (or P4 root and M1–2).

Comments: The Euzèt specimens show the typical dental features of *L. cervulum*. The two maxillary fragments, NMNS-PV 21388 and 21389, preserve the molariform premolars and upper molars

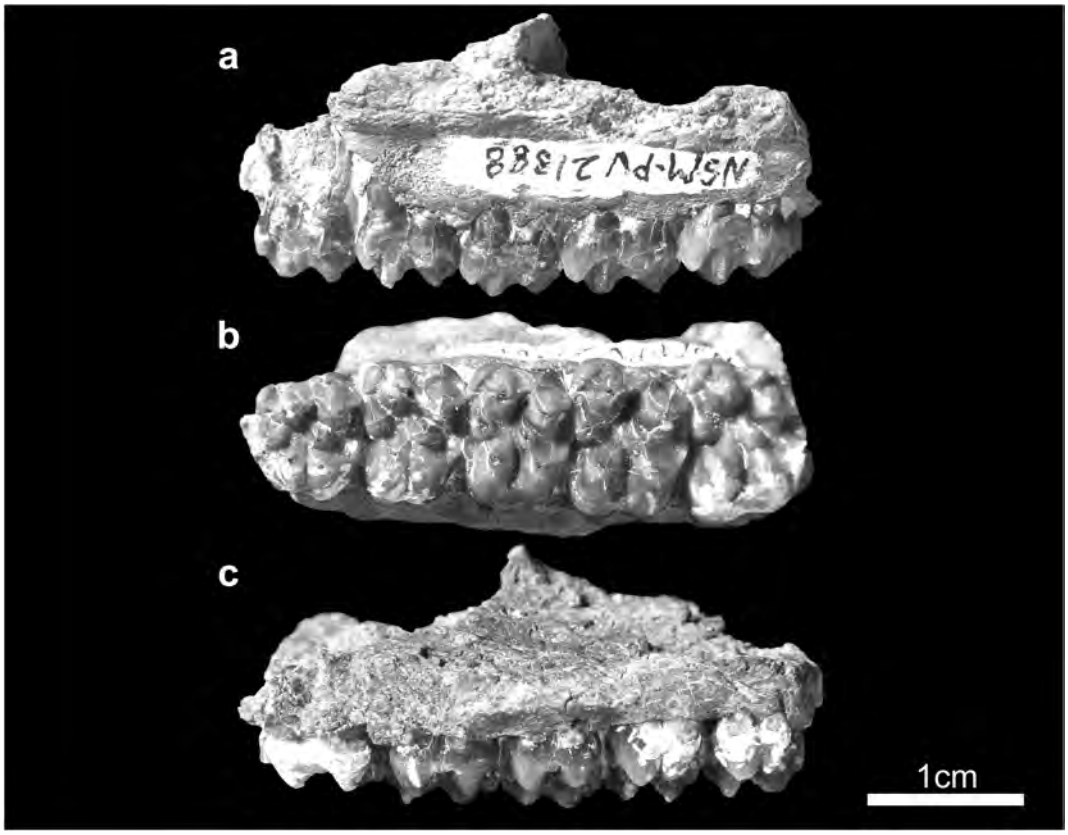

Fig. 2. *Lophiotherium cervulum* Gervais, 1859 from Euzèt les Bains. NMNS-PV 21388, left maxillary fragment with P3–M3 in labial (a), occlusal (b), and lingual (c) views.

with developed para- and metaconules and strong mesostyles (Figs. 2 and 3). The deciduous premolars (DP3–4) in NMNS-PV 21389 resemble the permanent ones in NMNS-PV 21388, but they are slightly narrower transversely (Figs. 2b and 3b). The premolars of NMNS-PV 21388 are more molariform than in *L. siderolithicum*, but the degree of molarization of premolars is variable in *Lophiotherium* species (see Depéret, 1917).

The undamaged molariform teeth in NMNS-PV 21393 are most likely M2 and M3 based on the position of maxillary swelling connecting to the jugal. The molars, with distinct mesostyles, are slightly larger than those of NMNS-PV 21388 and 21389 (Appendix 1), and the maxilla is more robust (Fig. 7). The dental dimensions of NMNS-PV 21393 are rather close to those of *Eurohippus parvulus* (Laurillard, 1849), but the molars of NMNS-PV 21393 are less lophodont unlike in *Eurohippus* and have more developed para- and metaconules, supporting assignment to this species.

The three mandibles (Figs. 4–6; NMNS-PV 21390–21392) also beautifully preserve the cheek tooth series, although the horizontal ramus in NMNS-PV 21391 is damaged. The best-preserved mandible (Fig. 4, NMNS-PV 21390) shows a long post-canine diastema, which is one of the characteristics of *Lophiotherium.*

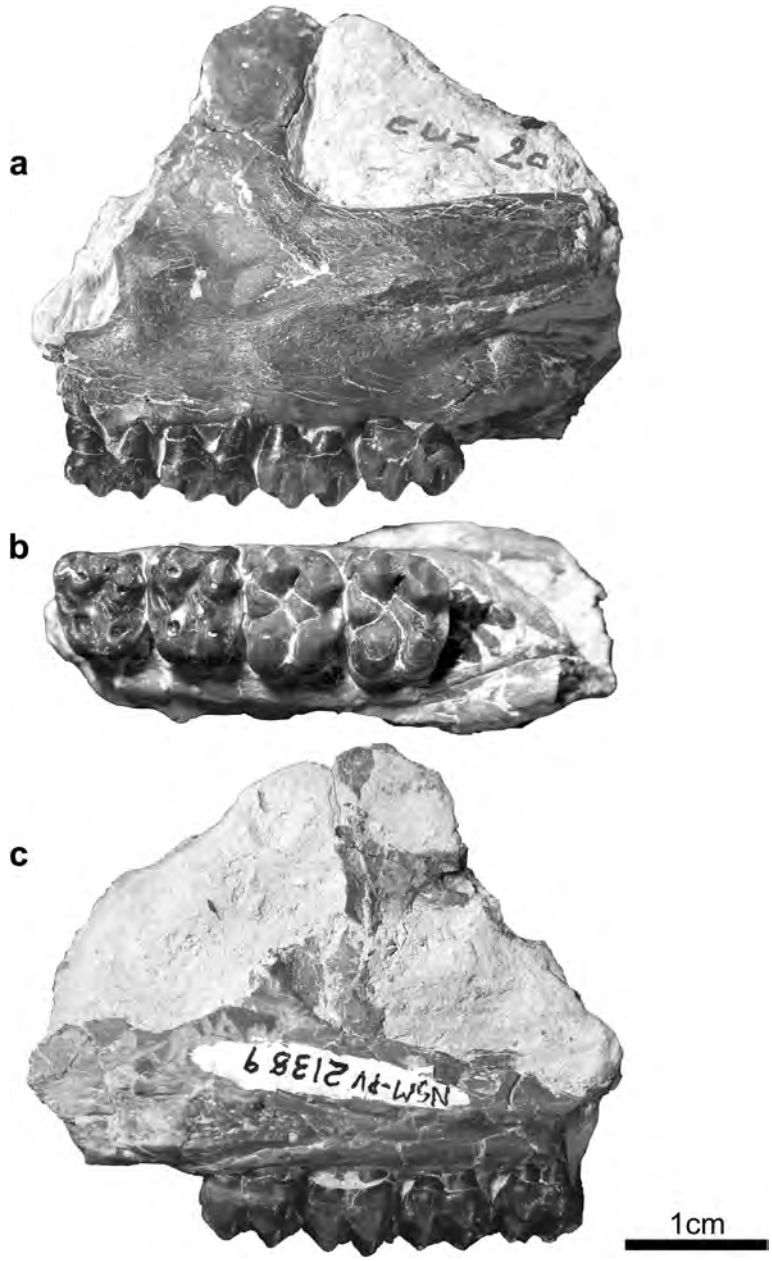

Fig. 3. *Lophiotherium cervulum* Gervais, 1859 from Euzèt les Bains. NMNS-PV 21389, left maxillary fragment with DP3–4 and M1–3 (M3 is not erupted) in labial (a), occlusal (b), and lingual (c) views.

Genus *Palaeotherium* Cuvier, 1804

Type species: *Palaeotherium magnum* Cuvier, 1804.

Comments: The representative genus of palaeotheres, *Palaeotherium*, has been recorded from the middle Eocene to the earliest Oligocene (MP 13–21) in Europe (Schmidt-Kittler, 1987; Cuesta, 1993; Luterbacher et al., 2004). The classification of *Palaeotherium* in this chapter mainly follows Franzen (1968).

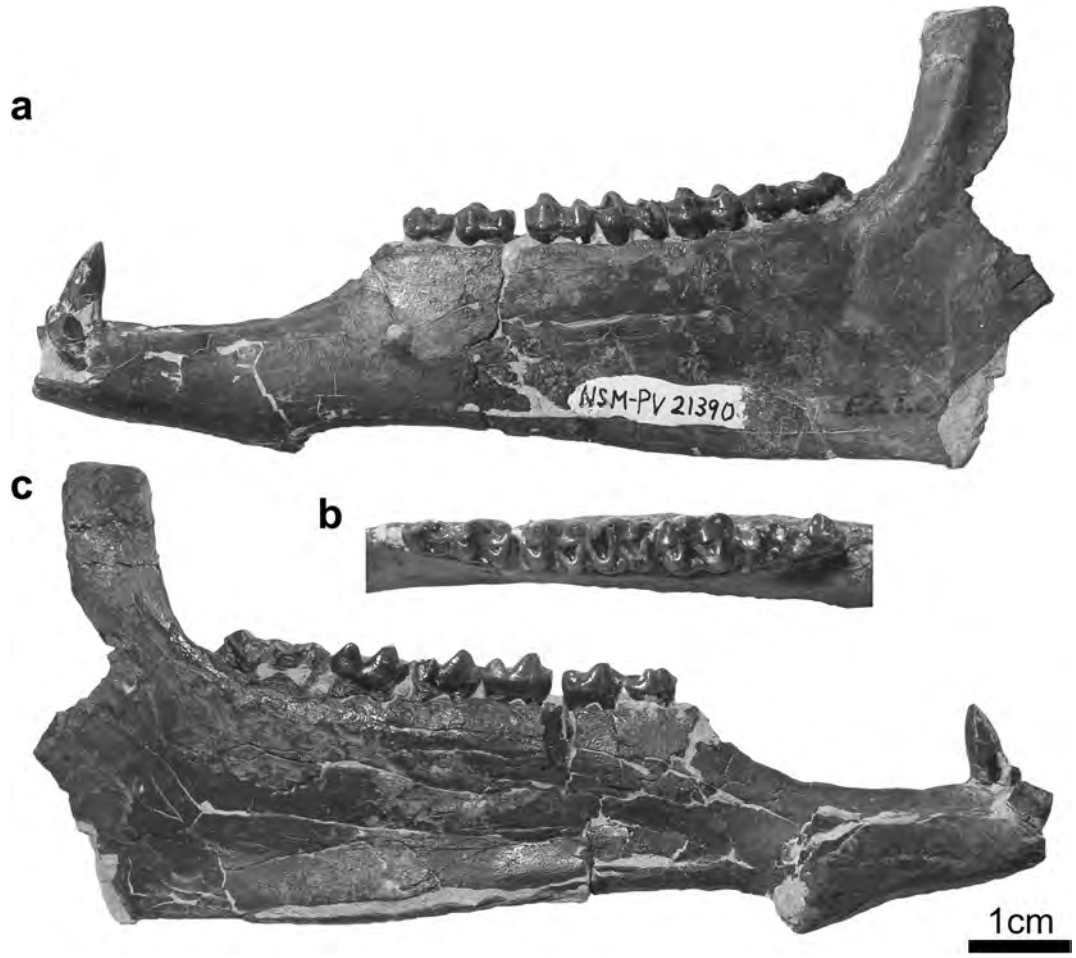

Fig. 4. *Lophiotherium cervulum* Gervais, 1859 from Euzèt les Bains. NMNS-PV 21390, left mandible with c1, p2–m3, and right symphysial part with broken c1 in left lateral (a), occlusal (p2–m3 only) (b), and lingual (c) views.

A comprehensive systematic review and revision of the genus *Palaeotherium* was carried out by Franzen (1968), who recognized 13 species: *P. castrense* Noulet, 1863; *P. crassum* Cuvier, 1805; *P. curtum* Cuvier, 1812; *P. duvali* Pomel, 1853; *P. eocaenum* Gervais, 1875; *P. lautricense* Stehlin, 1904a; *P. magnum* Cuvier, 1804; *P. medium* Cuvier, 1804; *P. muehlbergi* Stehlin, 1904b; *P. pomeli* Franzen, 1968; *P. renevieri* Stehlin, 1904b; *P. ruetimeyeri* Stehlin, 1904b; and *P. siderolithicum* (Pictet and Humbert, 1869). Many workers have followed Franzen's (1968) classification, which applies subspecies rank in the systematics of *Palaeotherium* species (e.g., Casanovas and Santafé, 1980; Remy, 1985, 1992; Cuesta, 1993). After the systematic review of Franzen (1968), three or four species from the Iberian Peninsula (*P. crusafonti* Casanovas, 1975; "*P. franzeni*" Casanovas and Santafé, 1980; *P. giganteum* Cuesta, 1993; and *P. llamaquiquense* Casanovas and Santafé, 1989 (see also Casanovas and Santafé, 1991) and one subspecies (*P. muehlbergi thaleri* Remy, 1985) were subsequently established. Meanwhile, some workers considered *P. llamaquiquense* as a synonym with *P. magnum* (e.g., Pulgar et al., 1999), and *P. renevieri* was allocated as a subspecies of *P. crassum* (*P. crassum renevieri*; Remy, 1992). Remy (1992) further proposed the establishment of subgeneric rank based on skull morphology; he erected two subgenera:

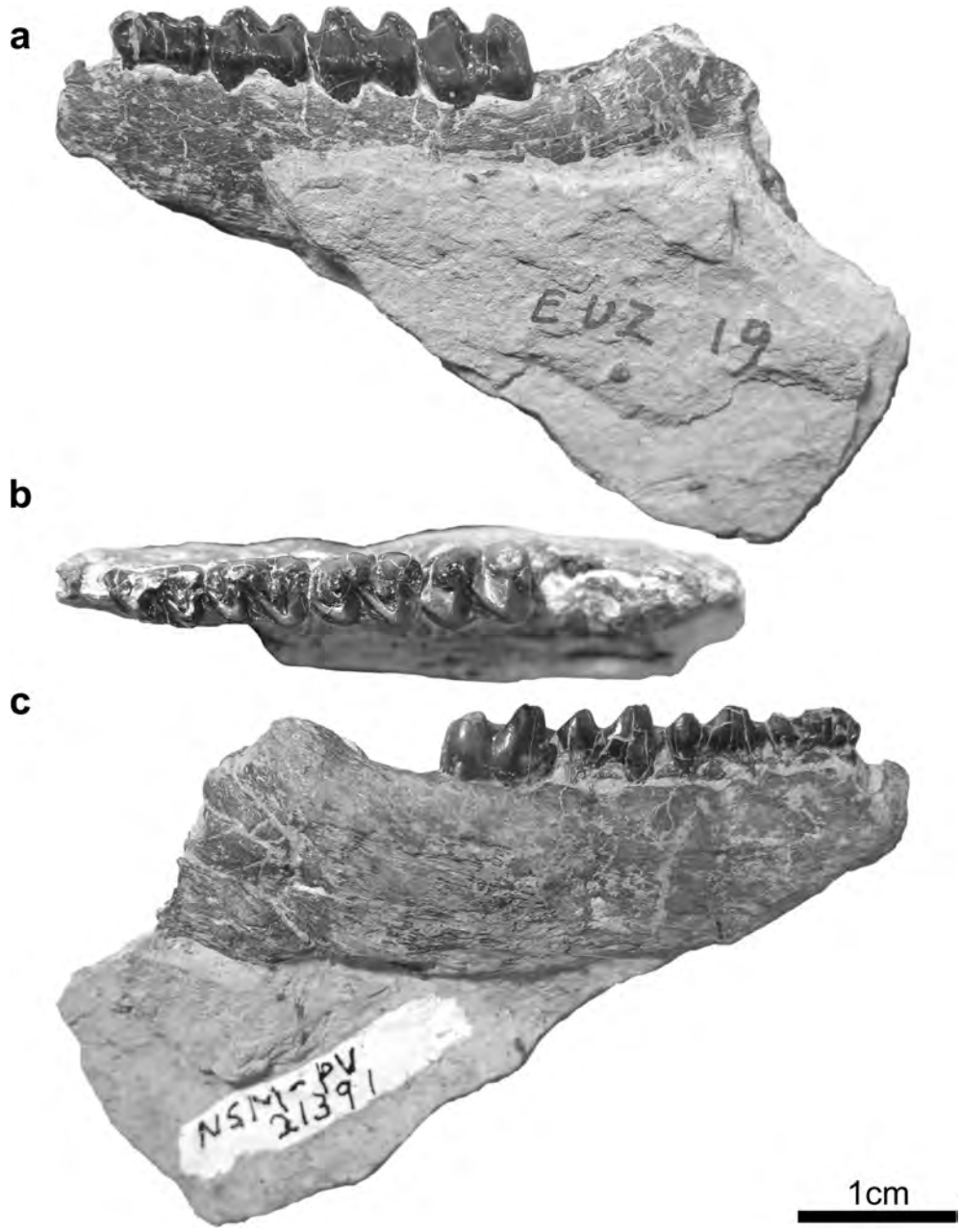

Fig. 5. *Lophiotherium cervulum* Gervais, 1859 from Euzèt les Bains. NMNS-PV 21391, left mandibular fragment with possible p3–m2 (or dp3–4 and m1–2) in labial (a), occlusal (b), and lingual (c) views.

Palaeotherium and *Franzenitherium* Remy, 1992. The former subgenus includes seven species (*P. castrense*, *P. crassum*, *P. curtum*, *P. magnum*, *P. medium*, *P. muehlbergi*, and *P. siderolithicum*), and the latter consists of *P. duvali* and *P. lautricense* (Remy, 1992). Other species are not allocated in either subgenus because of the lack of cranial information.

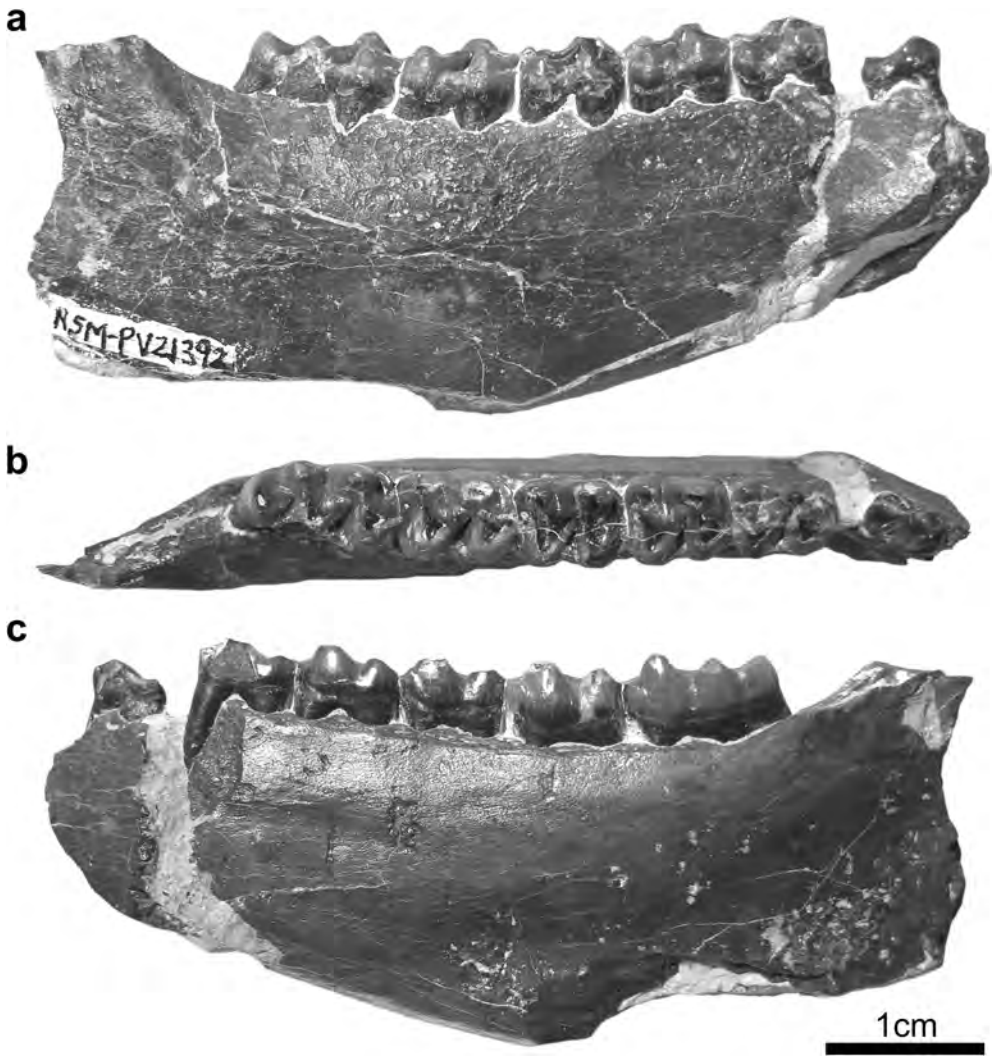

Fig. 6. *Lophiotherium cervulum* Gervais, 1859 from Euzèt les Bains. NMNS-PV 21392, right mandibular fragment with p2–m3 in labial (a), occlusal (b), and lingual (c) views.

Palaeotherium castrense Noulet, 1863

Comments: Franzen (1968) diagnosed *Palaeotherium castrense* as the largest species in the Bartonian (= MP 16; Luterbacher et al., 2004), with long cheek teeth (the maximum lengths of P2–M3 and p2–m3 reach ca. 155.0 mm and ca. 159.0 mm, respectively) and low PMI (maximum 64.5 at maxilla, 58.7–59.5 at mandible). Franzen established two subspecies (*P. castrense castrense* Noulet, 1863 and *P. castrense robiacense* Franzen, 1968). Moreover, the skull of *P. castrense* is characterized by having a nasomaxillary groove extending to the level of the P4 paracone, a short maxilla, and an infraorbital foramen placed above the P4 paracone (Franzen, 1968).

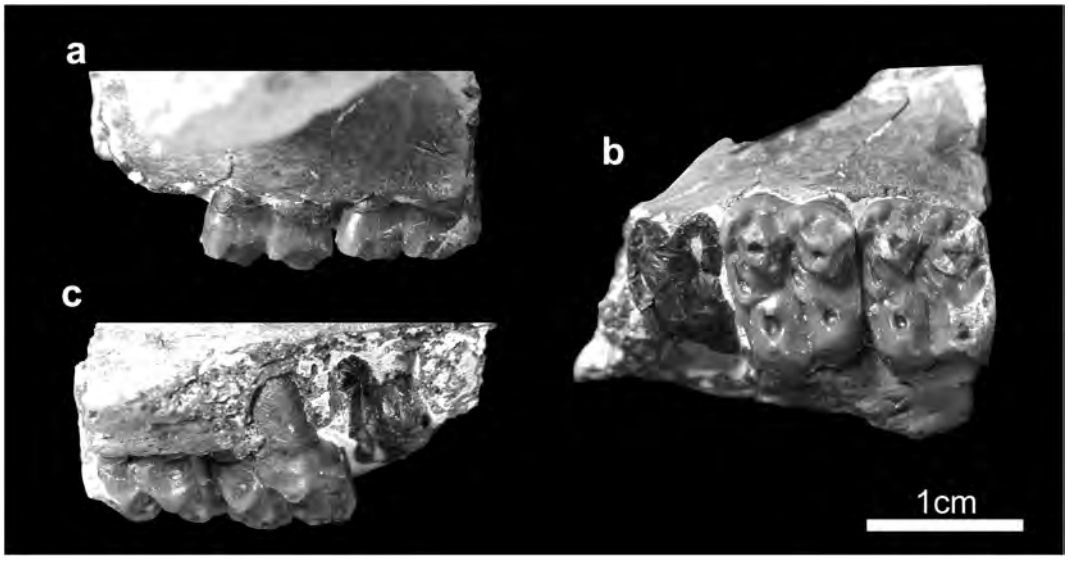

Fig. 7. *Lophiotherium cervulum* Gervais, 1859 from Euzèt les Bains. NMNS-PV 21393, left maxillary fragment with possible M1 root and M2–3 (or P4 root and M1–2) in labial (a), occlusal (b), and lingual (c) views.

Palaeotherium castrense robiacense **Franzen, 1968**

(Fig. 8)

Localities and Materials: Robiac: NMNS-PV 21332, right M3 in matrix; 21333, left P3; 21334, two left lower molariform teeth, possible p3–4; 21335, right P2–4.

Comments: *P. castrense robiacense* is a larger subspecies (59.9–62.4 mm in P2–4 length, 100.2–106.4 mm in m1–3 length; Franzen, 1968) than *P. castrense castrense. P. castrense robiacense* is known only from the type locality, Robiac (Franzen, 1968; Hooker, 1987; Remy, 1992).

Part of the specimens in the collection are isolated cheek teeth (Fig. 8), but they are referable to *P. castrense robiacense* based on size and morphology. The occlusal outlines of the upper premolars (Fig. 8d–f, j–l; NMNS-PV 21333 and 21335) are sub-rectangular with U-shaped lingual walls and flattened labial walls. The M3 (Fig. 8a–c, NMNS-PV 21332) is hypsodont, although it appears to be narrow transversely because of breakage. The paraconids of the lower premolars (Fig. 8 g–i, NMNS-PV 21334) are relatively stout. These are diagnostic features of *P. castrense robiacense* (Franzen, 1968).

Palaeotherium curtum Cuvier, 1812

Comments: *P. curtum* is a medium-sized species (108.3–123.0 mm in P2–M3 length, 122.1–ca. 132 mm in p2–m3 length) with a moderate or relatively low PMI (68.7–71.1 at maxilla, 65.1–66.2 at mandible) (Franzen, 1968). Franzen (1968) listed many diagnostic cranial and dental characters of *P. curtum* and identified three subspecies: *P. curtum curtum* Cuvier, 1812; *P. curtum frohnstettense* Franzen, 1968; and *P. curtum villerealense* Franzen, 1968. The earliest subspecies *P. curtum villerealense* is known from MP 17 and 18, whereas *P. curtum curtum* and *P. curtum frohnstettense* are recorded only from MP 19 and 20, respectively (Legendre, 1987). The collection includes 10 specimens of *P. curtum* consisting of maxillary and mandibular fragments with cheek teeth derived from three localities: Civrac de Blaye (MP 18), La Débruge (MP 18), and St. Capraise d'Eymet (MP 20).

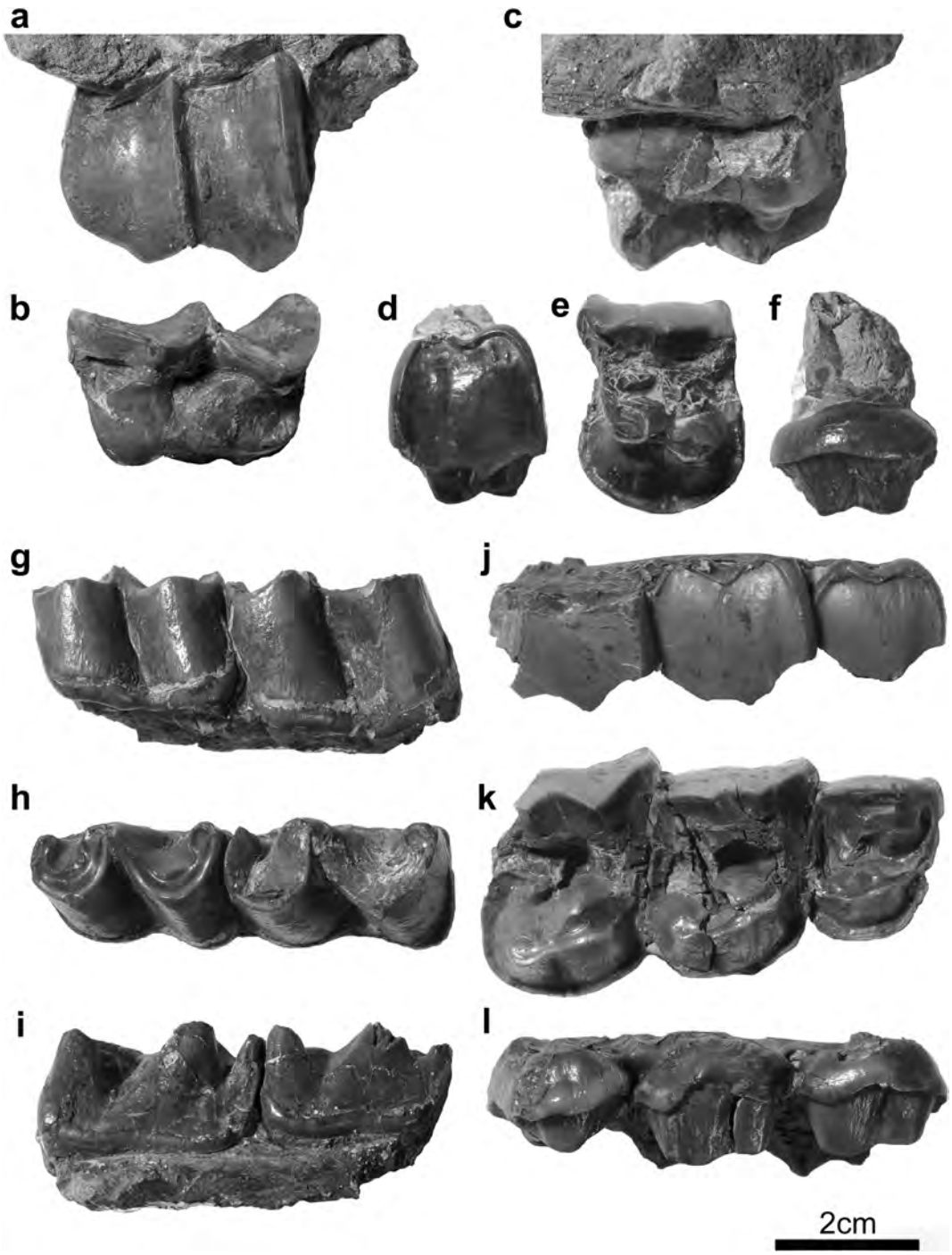

Fig. 8. *Palaeotherium castrense robiacense* Franzen, 1968 from Robiac. NMNS-PV 21332, right M3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21333, left P3 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21334, two left lower molariform teeth, possible p3–4 in labial (g), occlusal (h), and lingual (i) views. NMNS-PV 21335, right P2–4 in labial (j), occlusal (k), and lingual (l) views.

Palaeotherium curtum frohnstettense Franzen, 1968
(Fig. 9)

Localities and Materials: St. Capraise d'Eymet: NMNS-PV 21543, cranial fragment with broken right M2, M3, broken left M1, and M2–3.

Comments: Franzen (1968) established *P. curtum frohnstettense* based mainly on dental characters. *P. curtum frohnstettense* is generally larger than other *P. curtum* subspecies and the upper premolars possess some diagnostic characters including distinct mesostyles on P3–4 (Franzen, 1968). Although Franzen (1968) did not note any cranial characters of *P. curtum frohnstettense*, Remy (1992) described unique characters of a skull of this subspecies from St. Capraise d'Eymet (FPO Sec-18, housed in the University of Poitiers, France).

The upper molars in NMNS-PV 21543 (Fig. 9) are relatively large; the dimensions are comparable to those of *P. curtum frohnstettense* provided by Franzen (1968). Although NMNS-PV 21543 is not fully prepared and is compressed dorsoventrally, the specimen shows a relatively small orbit and stout jugal (Fig. 9b, ca. 29 mm in dorsoventral thickness). A large infraorbital foramen (ca. 15 mm in diameter) is positioned above the midline of M2; the position of the foramen is more posterior than in other *Palaeotherium* species, and its canal is very short (ca. 11 mm). These cranial features are similar to those found in FPO Sec-18 described by Remy (1992), supporting the taxonomic assignment. However, Remy (1992) concluded that some cranial characters of *P. curtum frohnstettense*, including orbital position, make it questionable as to whether it should be allocated to the *P. curtum* lineage.

Palaeotherium curtum villerealense Franzen, 1968
(Figs. 10–16)

Localities and Materials: Civrac de Blaye: NMNS-PV 21366, incomplete left mandible with p2 root and p3–m3; 21367, right maxillary fragment with P2 root and P3–M3; 21368, right maxillary fragment with P2–M2; 21369, right mandibular fragment with m2 talonid root and m3; 21370, incomplete left mandible with p3–m3 (the ramus and m2–3 are partially restored); 21376, right maxillary fragment with P3–M1.

La Débruge: NMNS-PV 21468, right mandibular fragment with p3–4; 21469, right mandibular fragment with p1–4; 21490, right mandibular fragment with p2–3 on matrix.

Comments: Although the maxillary specimens from Civrac de Blaye (Figs. 11, 12, and 15; NMNS-PV 21367, 21368, and 21376) preserve incomplete cheek tooth series, all of them are similar in dental size (Appendix 1). Based on the lengths of the tooth series and the alveolus positions, both NMNS-PV 21367 and 21368 have relatively low maxillary PMI (ca. 67.7), which is comparable to the PMI ranges of *P. curtum villerealense* in previous studies (66.2–70.2; Remy, 1985). *P. curtum*, known from MP 17 and 18, normally has a mesostyle developed on the cheek teeth (Franzen, 1968; Remy, 1985). However, NMNS-PV 21367 lacks distinct mesostyles on the premolars (Fig. 11a, b), while other specimens (NMNS-PV 21368 and 21376) display the diagnostic development of the external styles and their connection to the labial cingulum (Figs. 12a, b and 15a, b). NMNS-PV 21367 represents a robust individual with an infraorbital foramen opening above the M1 paracone, whereas the foramen in NMNS-PV 21368 is smaller and is positioned above the midline of P4. Although these differences imply that the assignment of NMNS-PV 21367 should be questionable, the maxillary specimens cataloged here are most likely referable to *P. curtum villerealense* in having a low PMI and rectangular premolars with short anteroposterior lengths, distinct labial and lingual cingula, and well

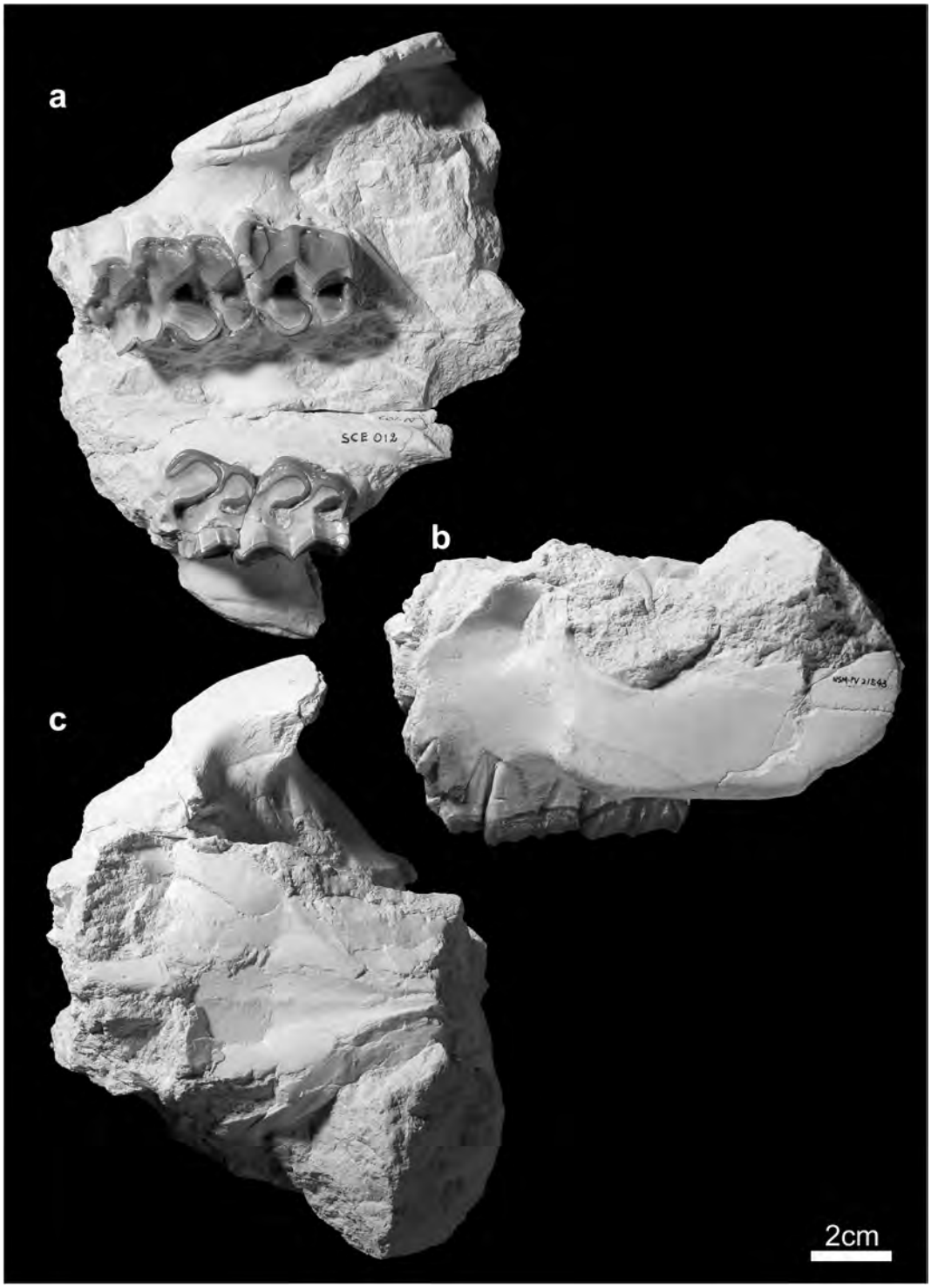

Fig. 9. *Palaeotherium curtum frohnstettense* Franzen, 1968 from St. Capraise d'Eymet. NMNS-PV 21543, cranial fragment with broken right M2, M3, broken left M1, and M2–3 in ventral (a), left lateral (b), and dorsal (c) views.

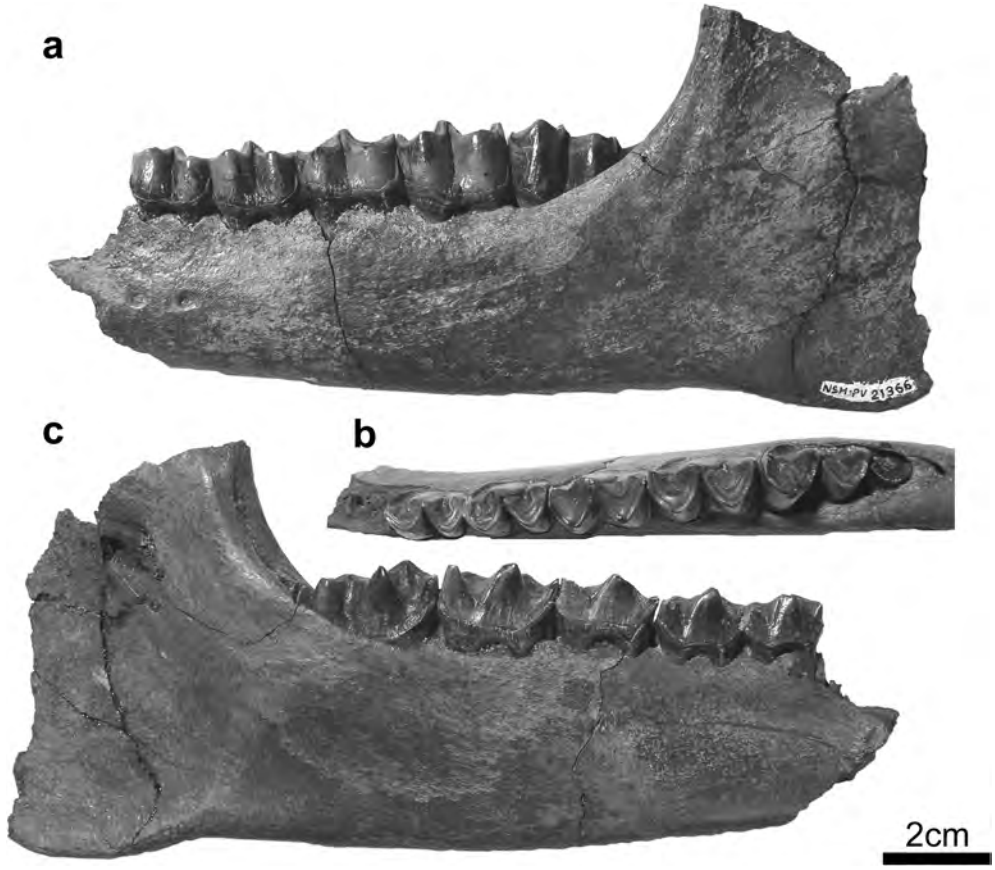

Fig. 10. *Palaeotherium curtum villerealense* Franzen, 1968 from Civrac de Blaye. NMNS-PV 21366, incomplete left mandible with p2 root and p3–m3 in labial (a), occlusal (p3–m3 only) (b), and lingual (c) views.

developed mesostyles (except for NMNS-PV 21367).

Mandibular specimens from Civrac de Blaye (Figs. 10, 13, and 14; NMNS-PV 21366, 21369, and 21370) incompletely preserve the cheek tooth series, with m2 and m3 in NMNS-PV 21370 having been restored (plaster casts). The PMI in both NMNS-PV 21366 and 21370 can be estimated at about 66.8, which is rather high compared to the PMI range of *P. curtum* (65.1–66.2 in Franzen, 1968). The labial and lingual cingula on the cheek teeth are distinct in NMNS-PV 21366 and 21370. NMNS-PV 21370 preserves a mental foramen under the p3 talonid (Fig. 14a); whereas NMNS-PV 21366 shows multiple mental foramina under the p3 trigonid, p3 talonid, and m2 talonid (Fig. 10a). NMNS-PV 21369 and 21370 possess vertical ascending rami with rectangular coronoid processes (Figs. 13 and 14). These are general features of *P. curtum villerealense.*

The specimens from La Débruge (Fig. 16; NMNS-PV 21468, 21469, and 21490) are fragmentary mandibles with almost unworn or barely worn premolars, which also show general features of the subspecies. The mandibles are shallow, and the premolars bear continuous lingual cingula. The labial walls of trigonid and talonid in p3 are U-shaped unlike *P. medium* from the same locality (La Débruge). NMNS-PV 21469 has three mental foramina placed under the p2 trigonid, p2 talonid, and the midline of p3 (Fig. 16d).

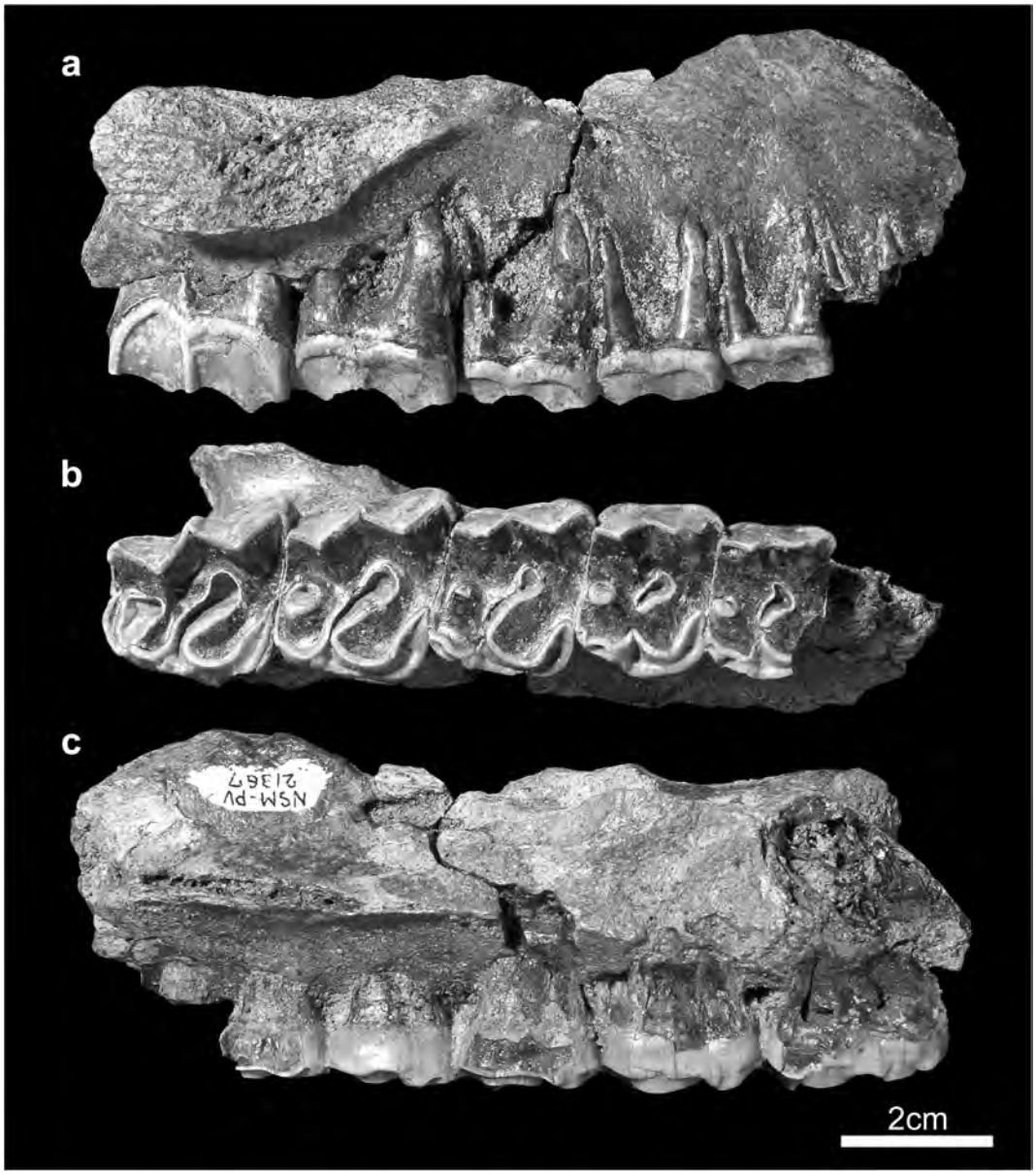

Fig. 11. *Palaeotherium curtum villerealense* Franzen, 1968 from Civrac de Blaye. NMNS-PV 21367, right maxillary fragment with P2 root and P3–M3 in labial (a), occlusal (b), and lingual (c) views.

***Palaeotherium* sp. cf. *P. curtum* Cuvier, 1812**

(Fig. 17)

Localities and Materials: La Débruge: NMNS-PV 21470, possible right p3 or p4.

St. Capraise d'Eymet: NMNS-PV 21540, possible right P2; 21541, possible left P2; 21542, labial fragment of possible upper premolar.

Comments: NMNS-PV 21470 (Fig. 17a, b) resembles a posterior premolar (p3 or p4) of *P. curtum*

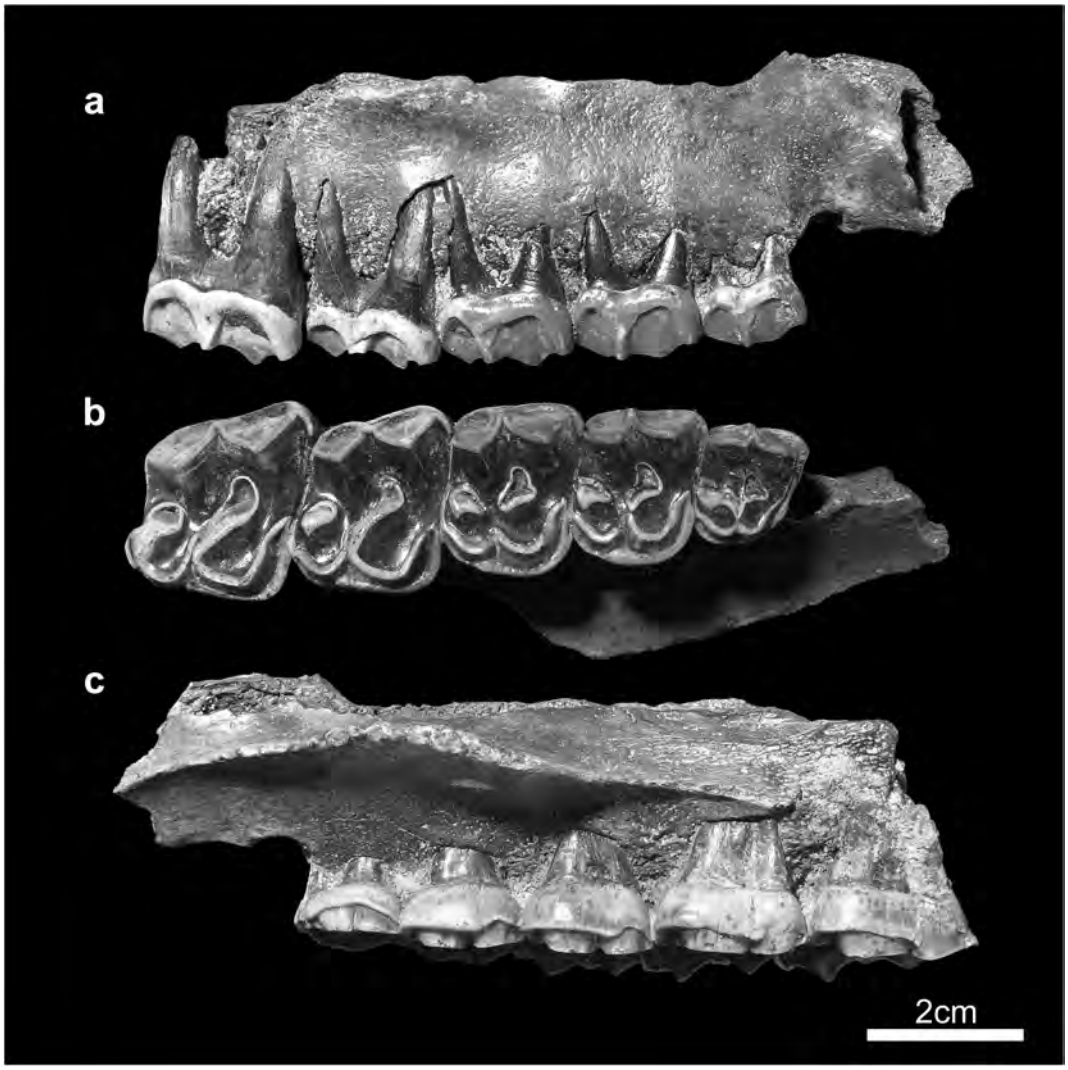

Fig. 12. *Palaeotherium curtum villerealense* Franzen, 1968 from Civrac de Blaye. NMNS-PV 21368, right maxillary fragment with P2–M2 in labial (a), occlusal (b), and lingual (c) views.

villerealense from the same locality (La Débruge, see also previous section) in having a U-shaped labial trigonid wall. The P2s and a fragment of an upper premolar from St. Capraise d'Eymet (Fig. 17c–g; NMNS-PV 21540–21542) are probably referable to *P. curtum frohnstettense* or *P. muehlbergi muehlbergi* in being labiolingually wide with well developed hypocones and are rather similar to those of the former in displaying weak labial cingula and lingual cingula interrupted at hypocones. However, the weak mesostyle on the premolars as seen in the specimens is generally unusual in *P. curtum*, although some morphological variation is known in the species (Franzen, 1968).

***Palaeotherium lautricense* Stehlin, 1904a**

(Figs. 18–20)

Localities and Materials: Robiac: NMNS-PV 21336, left mandibular fragment with p3–m2 and

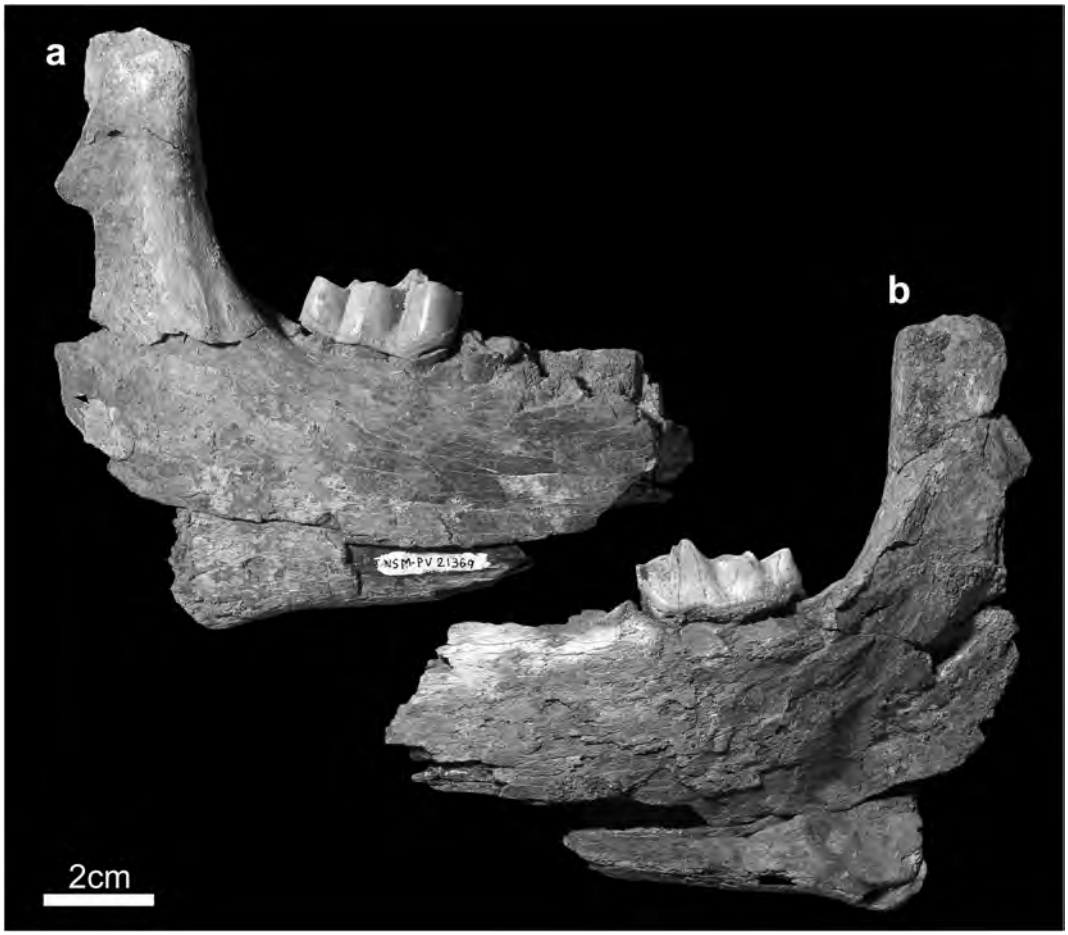

Fig. 13. *Palaeotherium curtum villerealense* Franzen, 1968 from Civrac de Blaye. NMNS-PV 21369, right mandibular fragment with m2 talonid root and m3 in labial (a) and lingual (b) views.

broken m3; 21337, left lower molariform tooth in matrix, possible p4 or m1; 21338, left mandibular fragments with p3–m3; 21339, right mandibular fragment with broken m1 and m2–3 on matrix; 21340, right p3; 21341, right p3; 21344, left maxillary fragment with M3.

Comments: *Palaeotherium lautricense* is the smallest species of the genus (66.1 mm in P2–M3 length, 35.8 mm in M1–3 length; Franzen, 1968). *P. lautricense* is known only from MP 16 (Hooker, 1987; Remy, 1992). The skull of *P. lautricense* possesses many diagnostic characters including orbit mid-positioned anteroposteriorly, distinctly short post-canine diastema, and short nasomaxillary groove extending alongside of P3 (Franzen, 1968; Remy, 1992).

The specimens cataloged here do not preserve any cranial characters. However, the small dental and mandibular sizes from Robiac, even the isolated cheek teeth (Fig. 20d–i, NMNS-PV 21340 and 21341), suggest that all of them are assignable to *P. lautricense*. The lower cheek teeth have distinct lingual cingulids making them readily distinguishable from those of *Plagiolophus* from the same locality. NMNS-PV 21339 (Fig. 20a–c) has a slightly deeper mandible than NMNS-PV 21338 (Fig. 19, Appendix 1); the minor difference can be viewed as a variation within *P. lautricense*.

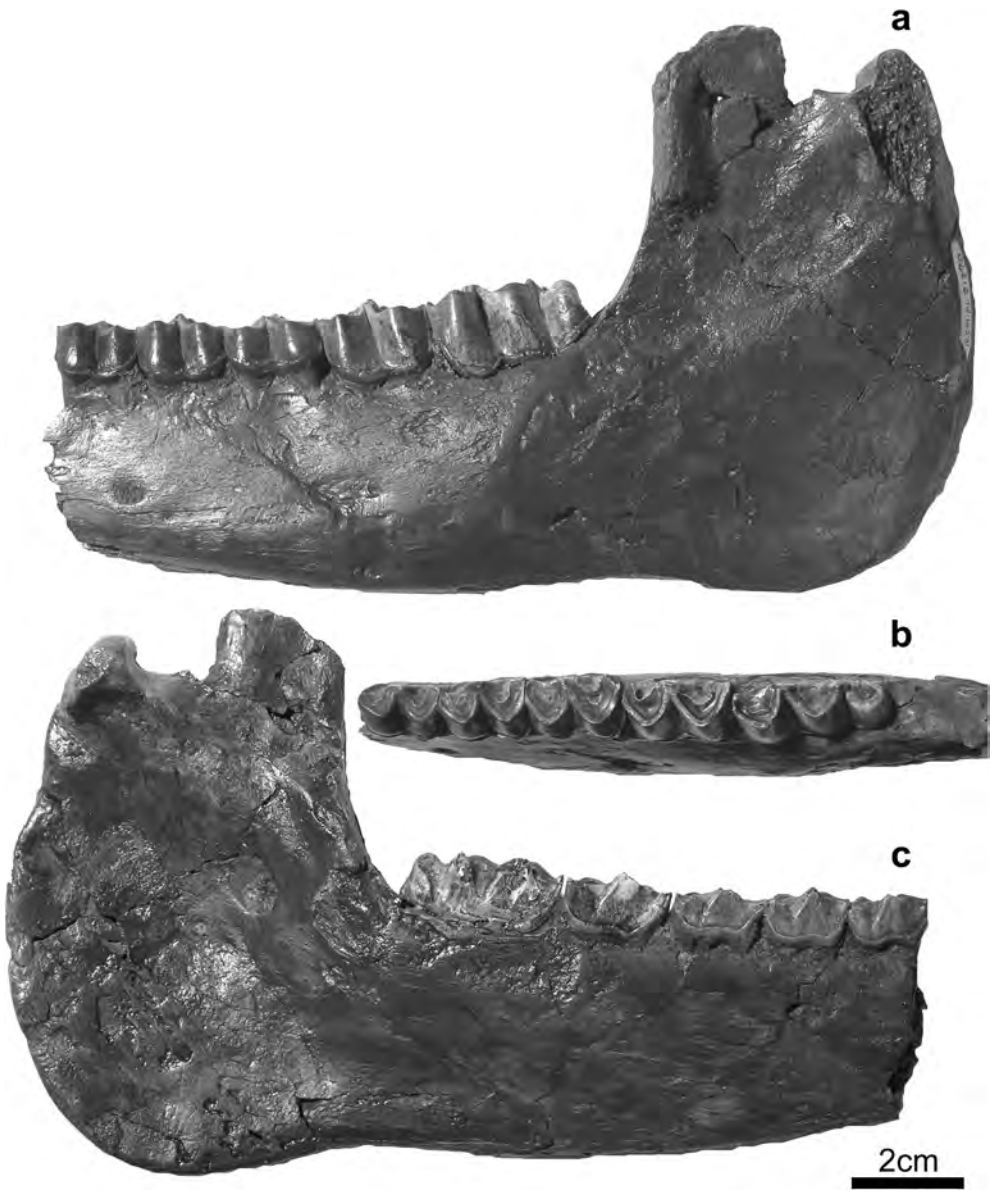

Fig. 14. *Palaeotherium curtum villerealense* Franzen, 1968 from Civrac de Blaye. NMNS-PV 21370, incomplete left mandible with p3–m3 (the ramus and m2–3 are partially restored) in labial (a), occlusal (p3–m3 only) (b), and lingual (c) views.

Palaeotherium magnum Cuvier, 1804

Comments: *Palaeotherium magnum* is the largest species of the genus (P2–M3 length: 160.6–208.6 mm); even the smallest subspecies, *P. magnum stehlini* Depéret, 1917, has a longer cheek tooth series (67.2–74.8 mm in P2–4 length) than in other *Palaeotherium* species (Franzen, 1968). Franzen discriminated three subspecies: *P. magnum girondicum* Blainville, 1846; *P. magnum magnum* Cuvier, 1804; and *P. magnum stehlini*. *P. magnum stehlini* and *P. magnum girondicum* are respectively known

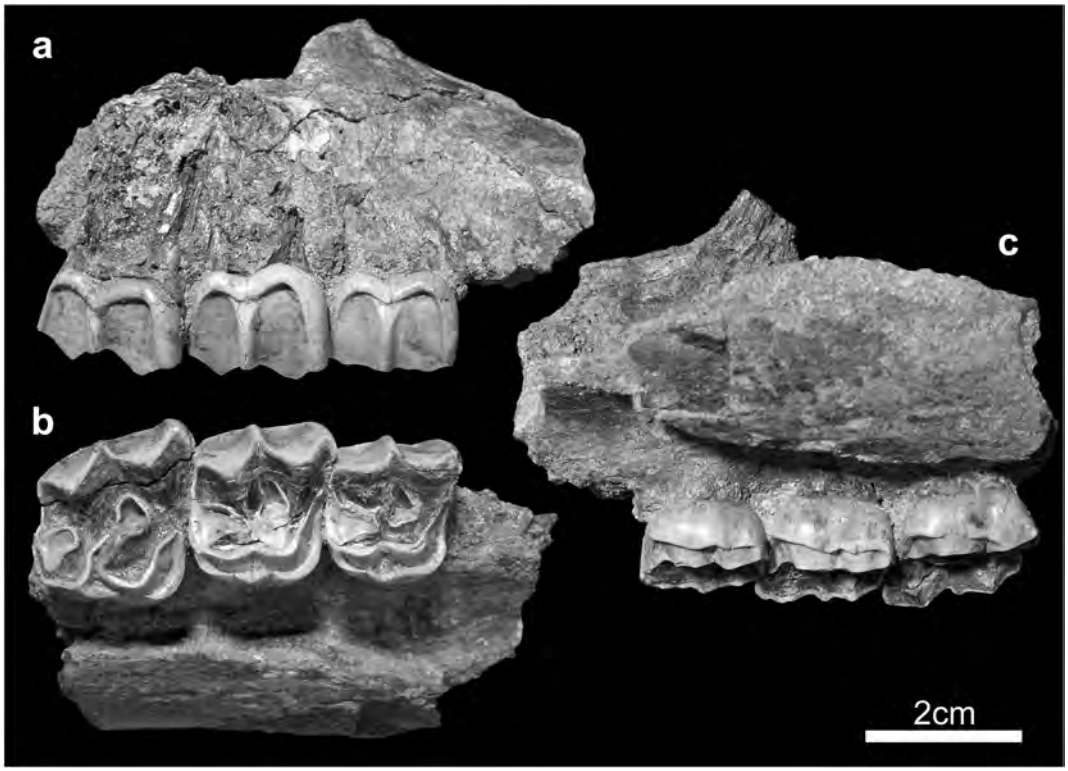

Fig. 15. *Palaeotherium curtum villerealense* Franzen, 1968 from Civrac de Blaye. NMNS-PV 21376, right maxillary fragment with P3–M1 in labial (a), occlusal (b), and lingual (c) views.

only from MP 17 and 18, whereas the largest subspecies *P. magnum magnum* extends from MP 19 to 20 (Legendre, 1987). The PMI in *P. magnum* is high (70.8–79.2 at maxilla, 70.0–73.9 at mandible in *P. magnum girondicum* and *P. magnum magnum*; Franzen, 1968). The 13 specimens here referred to *P. magnum* were collected from Civrac de Blaye and La Débruge.

***Palaeotherium magnum girondicum* Blainville, 1846**

(Figs. 21–27)

Localities and Materials: Civrac de Blaye: NMNS-PV 21365, possible left M2; 21371, incomplete right mandible with p2–m3; 21372, right maxillary fragment with P2–M3; 21373, left maxillary fragment with M2 and broken M3; 21374, possible right I2 or left i2; 21375, possible right C1 or left c1.

La Débruge: NMNS-PV 21471, left maxillary fragment with broken P3–4 and M1–3 (M3 labial half is artificial); 21472, right maxillary fragment with P4 and M1 on matrix; 21473, right p2; 21474, left p2; 21475, talonid of right anterior premolar; 21476, possible left P4 or M1 on matrix; 21477, left upper or right lower anterior incisor; 21478, right upper or left lower anterior incisor; 21479, right C1.

Comments: *Palaeotherium magnum girondicum* is generally larger than *P. magnum stehlini* and smaller than *P. magnum magnum* (Franzen, 1968). The large *Palaeotherium* species from Civrac de Blaye, assigned to *P. magnum girondicum* here, is known from nearly complete upper and lower dentitions (Figs. 21d–f and 22; NMNS-PV 21371 and 21372). Both of these specimens have been partially

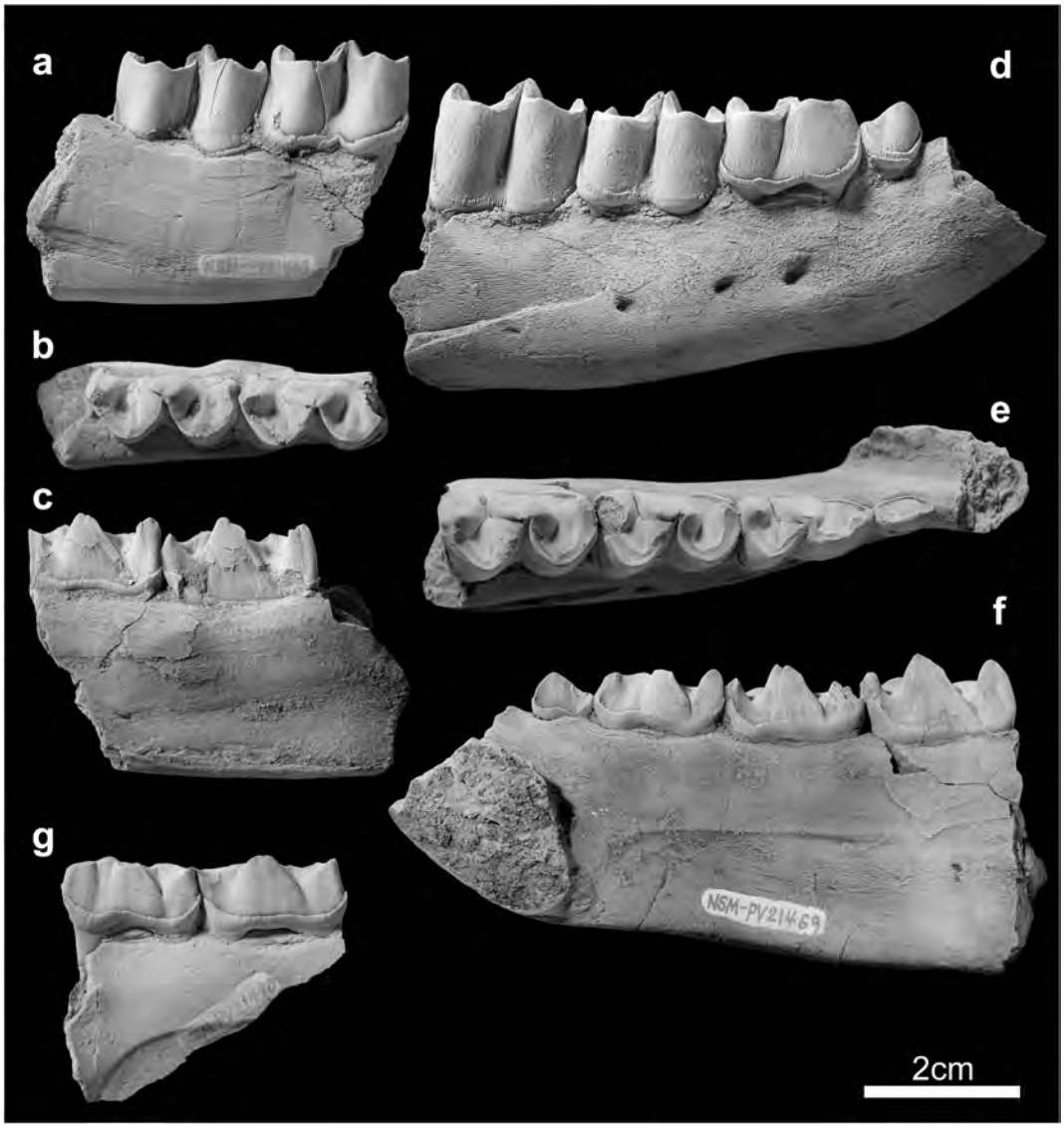

Fig. 16. *Palaeotherium curtum villerealense* Franzen, 1968 from La Débruge. NMNS-PV 21468, right mandibular fragment with p3–4 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21469, right mandibular fragment with p1–4 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21490, right mandibular fragment with p2–3 (g) in lingual view.

reconstructed using plaster. The mental foramen in NMNS-PV 21371 and the infraorbital foramen in NMNS-PV 21372 are not preserved. The Civrac specimens have large dental sizes typical of *P. magnum*; the cheek tooth length in NMNS-PV 21372 (187.2 mm in P2–M3 length, 81.3 mm in P2–4 length) is greater than that of *P. magnum stehlini* (160.6 mm in P2–M3 length, 67.2–74.8 mm in P2–4 length; Franzen, 1968), supporting the taxonomic identification. The PMI in NMNS-PV 21371 and 21372 (76.4 at mandible and 75.5 at maxilla, respectively) are relatively high like in *P. magnum girondicum* described by Franzen (1968) and Remy (1985). However, all the dental materials from Civrac are slightly smaller than *P. magnum girondicum* known from other localities including La

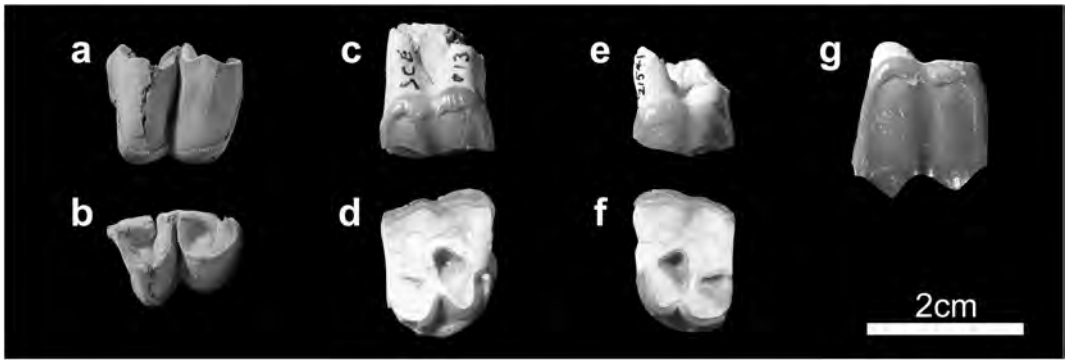

Fig. 17. *Palaeotherium* sp. cf. *P. curtum* Cuvier, 1812 from La Débruge (NMNS-PV 21470) and St. Capraise d'Eymet (NMNS-PV 21540–21542). NMNS-PV 21470, possible right p3 or p4 in labial (a) and occlusal (b) views. NMNS-PV 21540, possible right P2 in labial (c) and occlusal (d) views. NMNS-PV 21541, possible left P2 in labial (e) and occlusal (f) views. NMNS-PV 21542, labial fragment of possible upper premolar (g) in labial view.

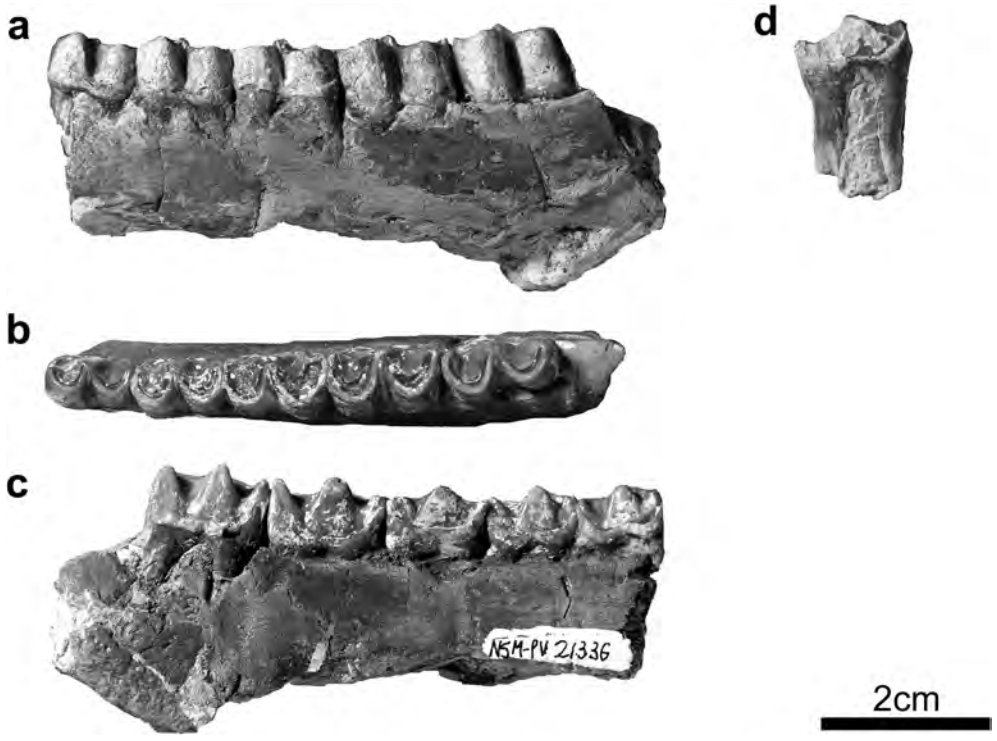

Fig. 18. *Palaeotherium lautricense* Stehlin, 1904a from Robiac. NMNS-PV 21336, left mandibular fragment with p3–m2 and broken m3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21337, left lower molariform tooth, possible p4 or m1 (d) in lingual view.

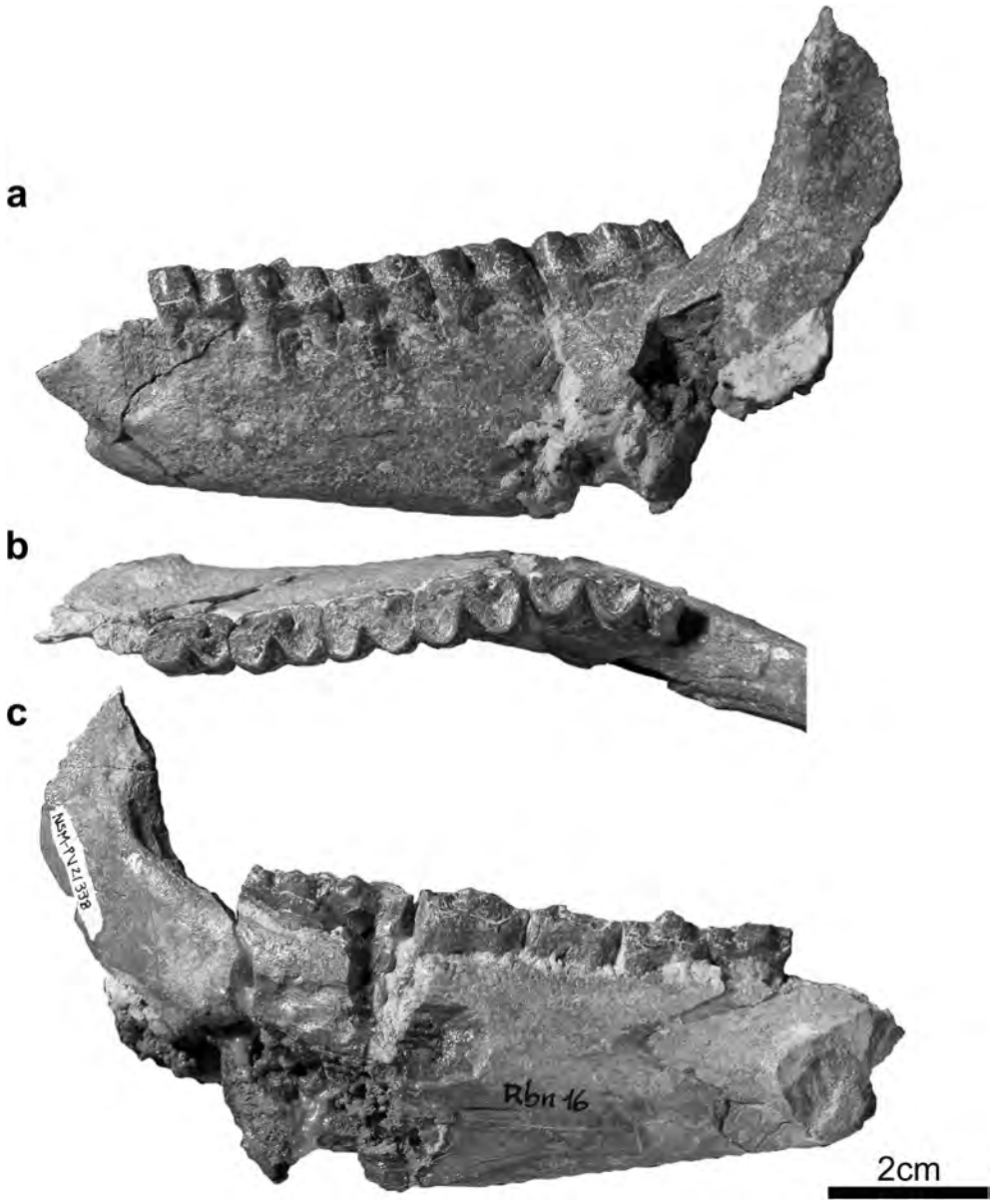

Fig. 19. *Palaeotherium lautricense* Stehlin, 1904a from Robiac. NMNS-PV 21338, left mandibular fragment with p3–m3 in labial (a), occlusal (b), and lingual (c) views.

Débruge and Sainte-Croix-de-Brignon (the Célas sandstones) (Appendix 1; cf. the dimensions in Franzen, 1968 and Remy, 1985). Moreover, the p2 in NMNS-PV 21371 has a narrow trigonid (not forming a trigonid basin) with a posterolabial ridge running down from a high protoconid (Fig. 21d–f), unlike *P. magnum* from La Débruge. Although these characteristics are different compared to *P. magnum girondicum* from other localities, the large *Palaeotherium* species from Civrac is most likely referable to *P. magnum girondicum* based on tooth dimensions and geological age.

The specimens from La Débruge are poorly preserved, but their tooth dimensions are of similar

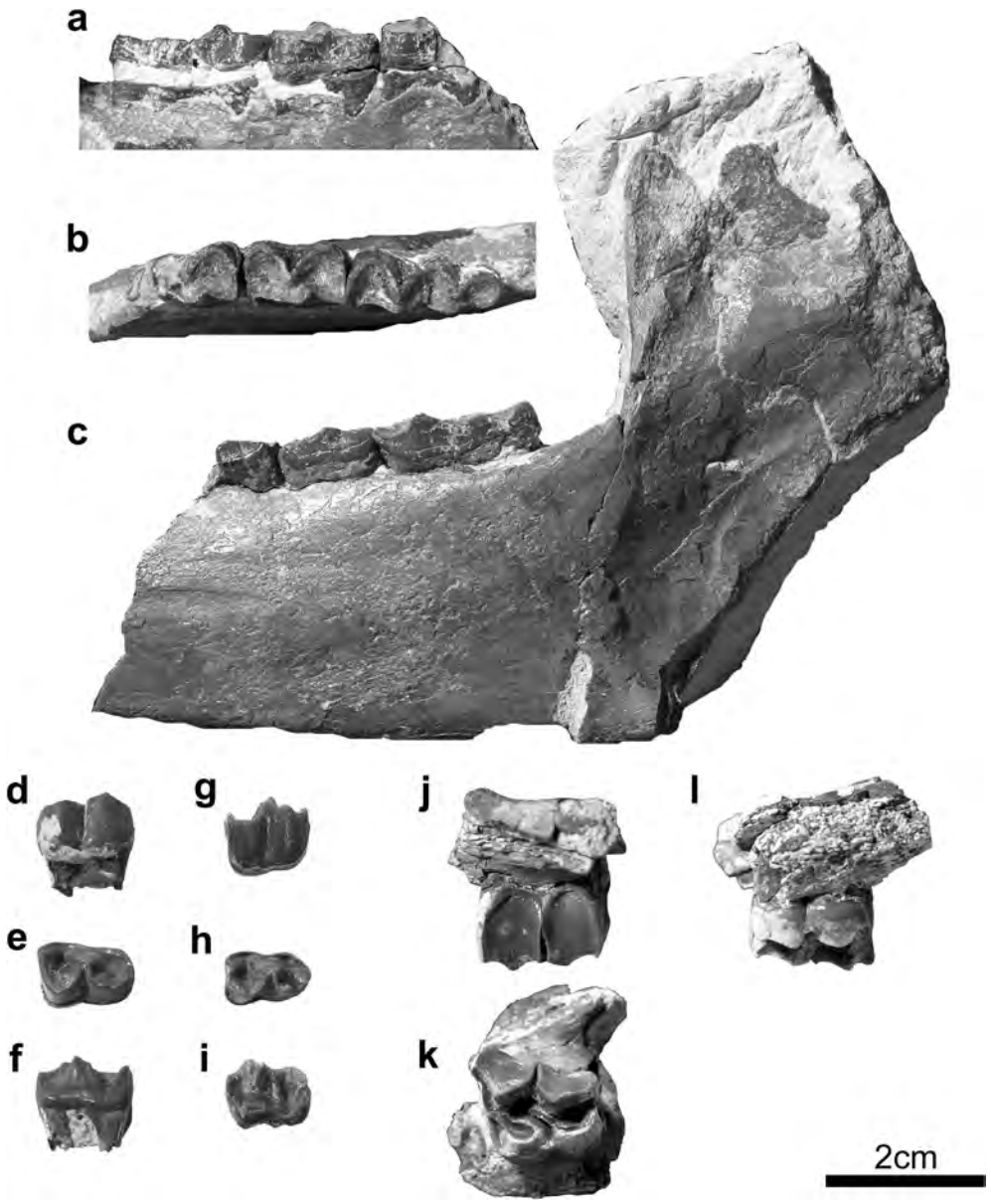

Fig. 20. *Palaeotherium lautricense* Stehlin, 1904a from Robiac. NMNS-PV 21339, right mandibular fragment with broken m1 and m2–3; the lower molars in labial (a) and occlusal (b) views, and the mandibular fragment (c) in lingual view. NMNS-PV 21340, right p3 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21341, right p3 in labial (g), occlusal (h), and lingual (i) views. NMNS-PV 21344, left maxillary fragment with M3 in labial (j), occlusal (k), and lingual (l) views.

large size with *P. magnum girondicum* (Appendix 1). NMNS-PV 21471 (Fig. 25), the best-preserved specimen from La Débruge, shows a diagnostic large infraorbital foramen positioned above the posterior margin of P4. The labial and lingual cingula on the upper cheek teeth are sharp and continuous (Figs. 25 and 26a, b, h, i; NMNS-PV 21471 (note that the M3 labial half is artificial), 21472, and

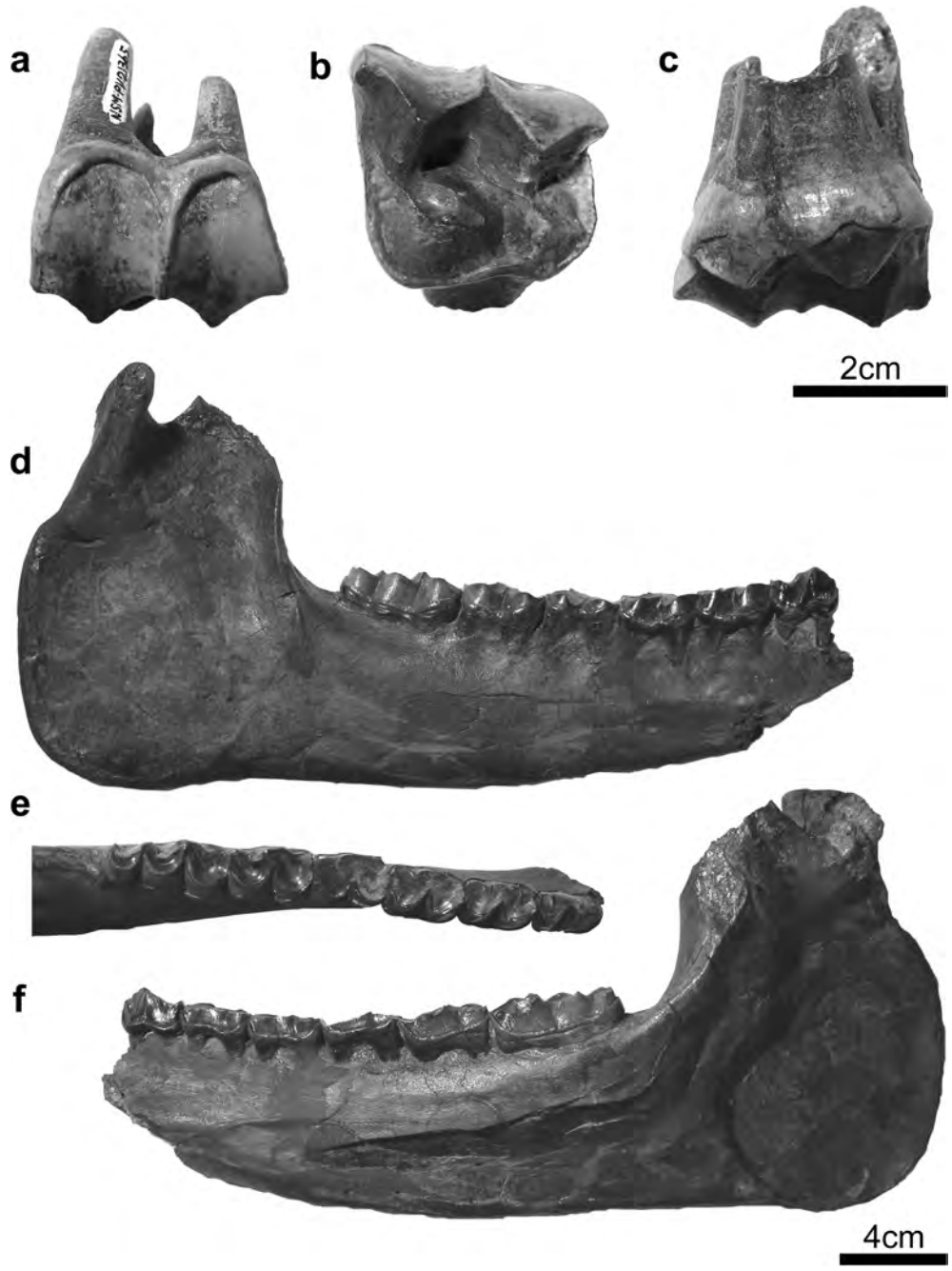

Fig. 21. *Palaeotherium magnum girondicum* Blainville, 1846 from Civrac de Blaye. NMNS-PV 21365, possible left M2 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21371, incomplete right mandible with p2–m3 in labial (d), occlusal (e, p2–m3 only), and lingual (f) views. Scale bar for d–f is shown at bottom right.

21476). The p2s are molariform with narrow trigonid basins (Fig. 26c–f; NMNS-PV 21473 and 21474). The large incisors and canine from La Débruge (Fig. 27; NMNS-PV 21477–21479) can also be assigned to *P. magnum girondicum*.

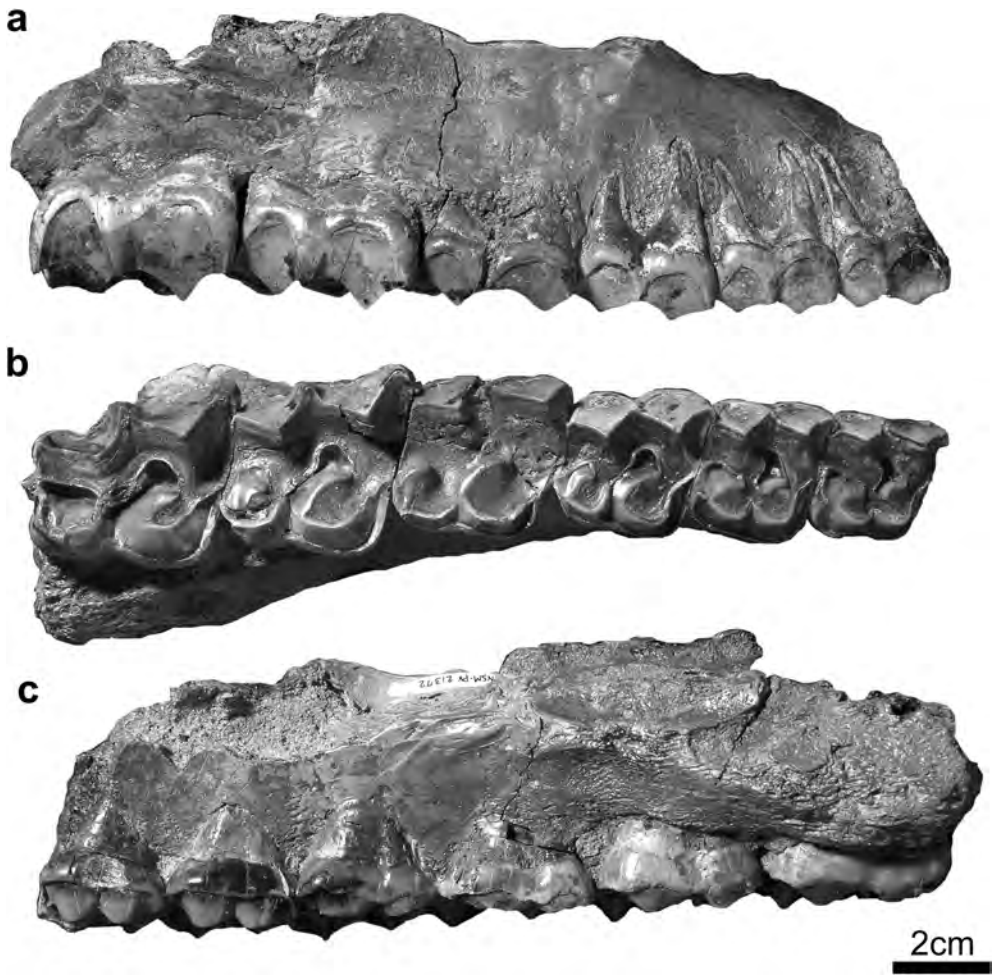

Fig. 22. *Palaeotherium magnum girondicum* Blainville, 1846 from Civrac de Blaye. NMNS-PV 21372, right maxillary fragment with P2–M3 in labial (a), occlusal (b), and lingual (c) views.

Palaeotherium medium Cuvier, 1804

Comments: *P. medium* is a moderate-sized species (103.6–ca. 138.7 mm in P2–M3 length, 111.4–ca. 139.7 mm in p2–m3 length) with a relatively high PMI (73.3–85.5 at maxilla, 69.5–76.2 at mandible) (Franzen, 1968). Franzen (1968) recognized four subspecies: *P. medium euzetense* (Depéret, 1917); *P. medium perrealense* (Stehlin, 1904b); *P. medium medium* Cuvier, 1804; and *P. medium suevicum* Fraas, 1869. Based on Legendre (1987), the first three subspecies are known from MP 17, 18, and 19, respectively. *P. medium suevicum* has been described from MP 20 and 21 (Franzen, 1968; Legendre, 1987).

***Palaeotherium medium euzetense* (Depéret, 1917)**
(Figs. 28–30)

Localities and Materials: Euzèt les Bains: NMNS-PV 21394, left mandible and right symphysial

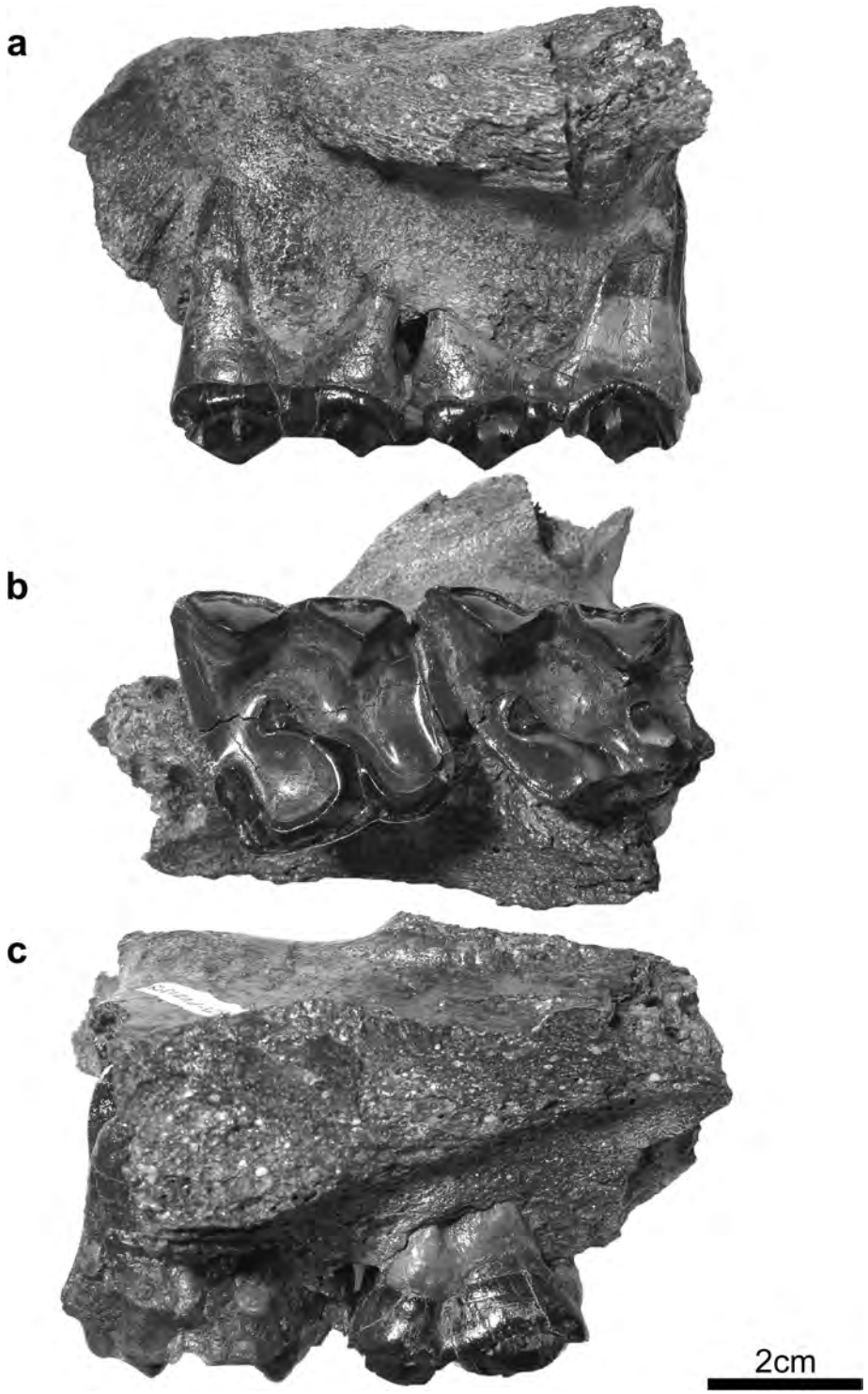

Fig. 23. *Palaeotherium magnum girondicum* Blainville, 1846 from Civrac de Blaye. NMNS-PV 21373, left maxillary fragment with M2 and broken M3 in labial (a), occlusal (b), and lingual (c) views.

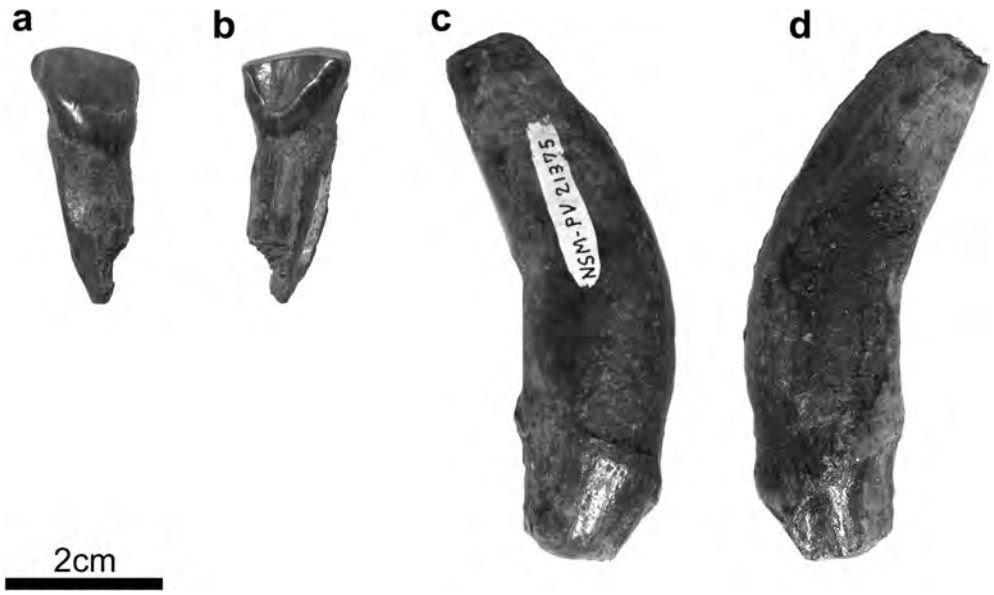

Fig. 24. *Palaeotherium magnum girondicum* Blainville, 1846 from Civrac de Blaye. NMNS-PV 21374, possible right I2 or left i2 in labial (a) and lingual (b) views. NMNS-PV 21375, a possible right C1 or left c1 in labial (c) and lingual (d) views.

part with right c1, p2–3, left c1, and p1–m3; 21395, left mandibular fragment with broken p3 and p4–m3; 21396, right M2; 21398, left mandibular fragment with m2–3.

Comments: *P. medium euzetense* is the earliest subspecies of *P. medium* with a diagnostic spoon-shaped nasal projection ("löffelförmig" in Franzen, 1968) and a relatively low PMI among *P. medium* subspecies (Franzen, 1968). *P. medium euzetense* has been described from Euzèt (the type locality) and Roc de Santa, Spain (Casanovas et al., 1992). The Euzèt specimens cataloged here do not include any cranial material but represent a moderate-sized species referable to *P. medium euzetense* based on the dental characters mentioned below.

The best-preserved specimen from Euzèt, NMNS-PV 21394 (Fig. 28), shows a nearly complete lower cheek tooth row including p1 with a PMI of 77.2, which is greater than that of *P. curtum*. The p2 trigonid is less compressed labiolingually (broader) than those of *P. medium medium* and *P. medium suevicum* (Fig. 28b). The p2–m3 length (106.7 mm, Appendix 1) and the PMI of NMNS-PV 21394 are slightly shorter and greater than those of *P. medium euzetense* (111.4–124.3 mm in p2–m3 length, PMI: 69.5–75.4 at mandible) described by Franzen (1968), respectively. However, the dental dimensions indicate the differences from other contemporaneous *Palaeotherium* species (i.e. species known from MP 17): *P. curtum villerealense* Franzen, 1968; *P. duvali priscum* Franzen, 1968; *P. magnum stehlini* Depéret, 1917; and *P. muehlbergi praecursum* Franzen, 1968. Two other mandibular fragments (Figs. 29 and 30d–f, NMNS-PV 21395 and 21398) preserve slightly longer cheek teeth than those of NMNS-PV 21394 (Appendix 1); but these are neither assignable to *P. muehlbergi praecursum*, which is larger, nor to *P. duvali priscum*, which is smaller. The m3 talonids in NMNS-PV 21395 and 21398 bear sharp hypoconulid crests, which are typical for *P. medium* and form a hook shape in occlusal view (Figs. 29b and 30e). An upper molar (Fig. 30a–c, NMNS-PV 21396) displays a mesostyle that becomes weaker where it joins the labial cingulum.

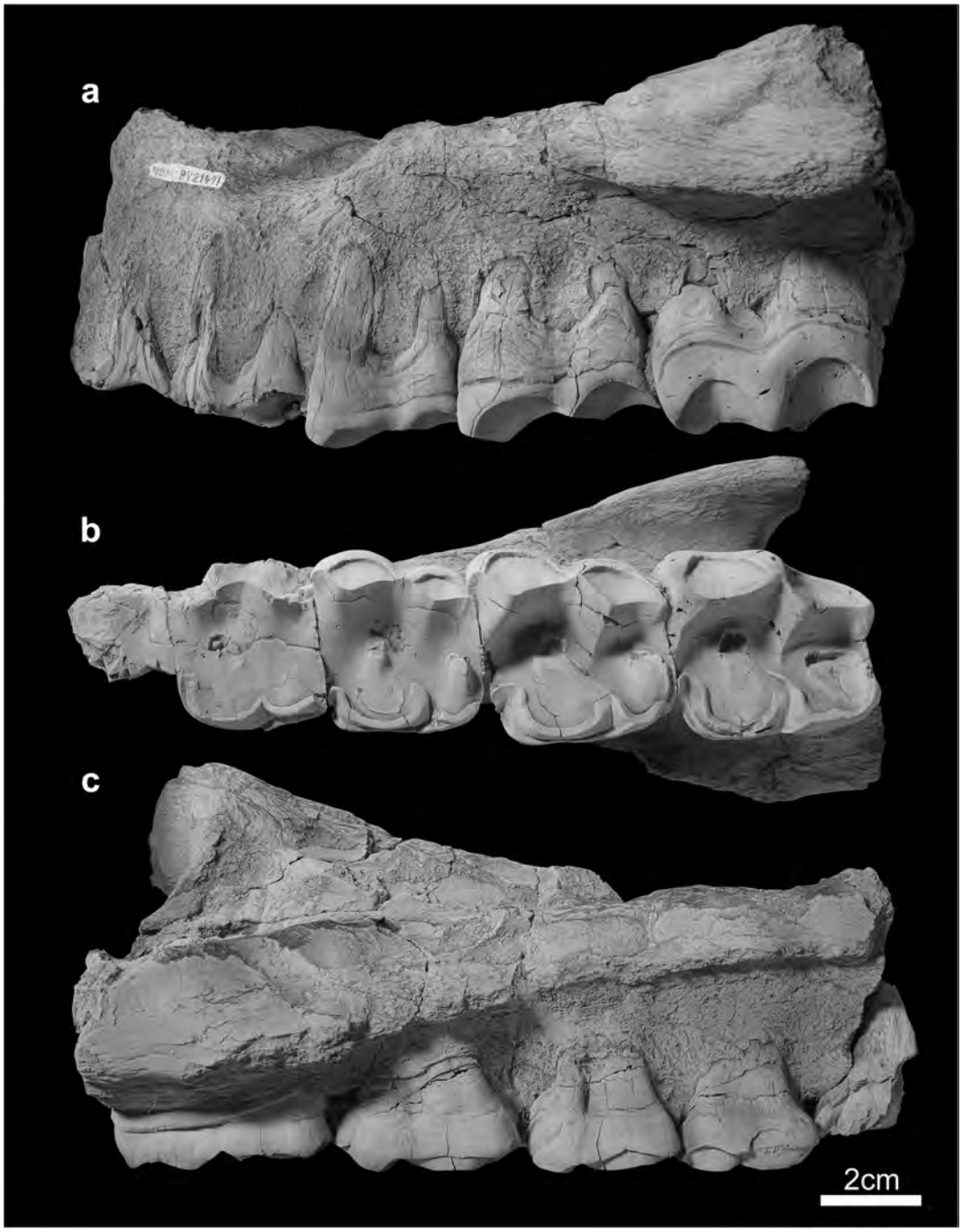

Fig. 25. *Palaeotherium magnum girondicum* Blainville, 1846 from La Débruge. NMNS-PV 21471, left maxillary fragment with broken P3–4 and M1–3 (note that M3 labial half is artificial) in labial (a), occlusal (b), and lingual (c) views.

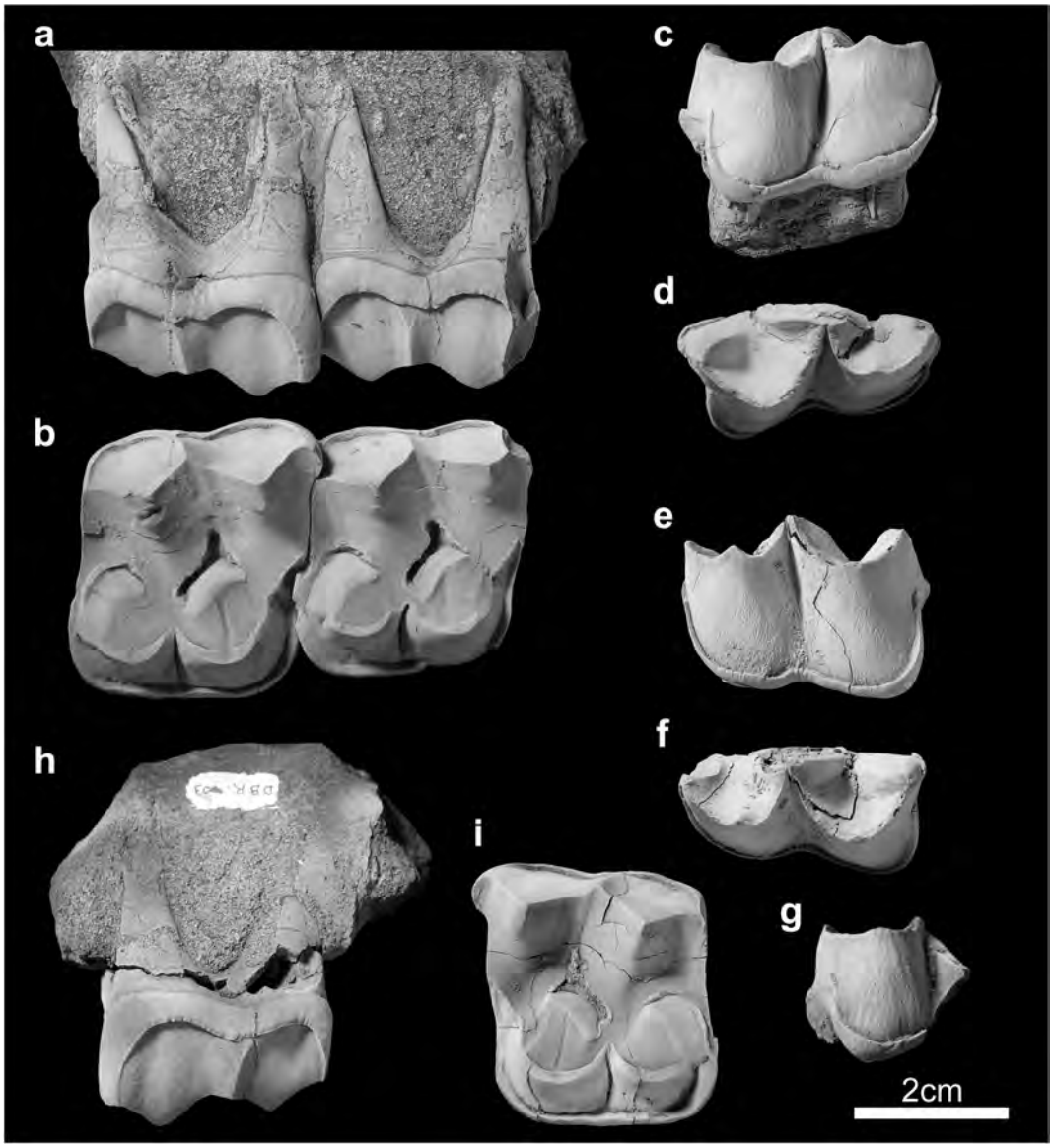

Fig. 26. *Palaeotherium magnum girondicum* Blainville, 1846 from La Débruge. NMNS-PV 21472, right maxillary fragment with P4 and M1 on matrix in labial (a) and occlusal (b) views. NMNS-PV 21473, right p2 in labial (c) and occlusal (d) views. NMNS-PV 21474, left p2 in labial (e) and occlusal (f) views. NMNS-PV 21475, talonid of right anterior premolar (g) in labial view. NMNS-PV 21476, possible left P4 or M1 on matrix in labial (h) and occlusal (i) views.

***Palaeotherium medium perrealense* (Stehlin, 1904b)**

(Figs. 31–34)

Localities and Materials: La Débruge: NMNS-PV 21480, left maxillary fragment with broken P3 and P4–M3; 21481, right maxillary fragment with M3; 21482, right maxillary fragment with DP3–4; 21483, left maxillary fragment with P3–4; 21485, possible right P3; 21486, left mandibular fragment

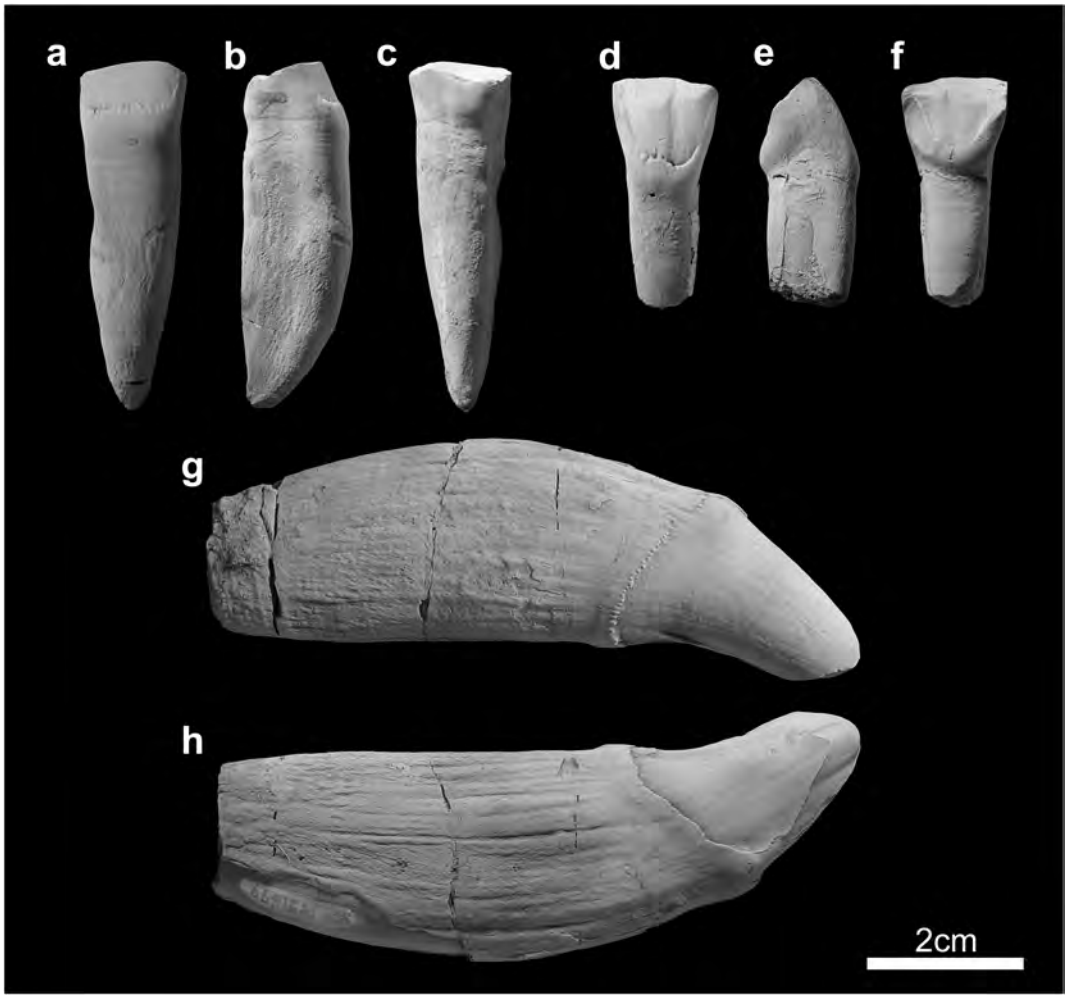

Fig. 27. *Palaeotherium magnum girondicum* Blainville, 1846 from La Débruge. NMNS-PV 21477, left upper or right lower anterior incisor in labial (a), distal (b) and lingual (c) views. NMNS-PV 21478, right upper or left lower anterior incisor in labial (d), mesial (e) and lingual (f) views. NMNS-PV 21479, right C1 in labial (g) and lingual (h) views.

with p4–m3; 21487, right mandibular fragment with p3–m3; 21489, right maxillary fragment with broken P2–3 and P4 root.

Comments: *P. medium perrealense* is distinguished from *P. medium euzetense* in having a more posteriorly positioned infraorbital foramen (usually between P4 and M1), narrower p2, and slightly greater PMI (79.7–85.5 at maxilla) (Franzen, 1968). La Débruge is the type locality of *P. medium perrealense*, which is recorded only from MP 18 (Legendre, 1987).

The *P. medium* specimens from La Débruge include maxillary fragments (Figs. 31 and 32j, k; NMNS-PV 21480, 21489) preserving the infraorbital foramen positioned above the midline of P4 and accessory foramen. The length of P2–M3 in NMNS-PV 21480 estimated from the alveolus position (ca. 110.0 mm, Appendix 1) is within the observed range of *P. medium perrealense* (103.6–121.8 mm; Franzen, 1968). Although the PMI in NMNS-PV 21480 (ca. 78.8) seems to be rather low among *P. medium* subspecies, the dental dimensions of NMNS-PV 21480 are distinguishable from other *Palaeotherium* species known from MP 18: *P. crassum robustum* Franzen, 1968; *P. curtum villerealense* Franzen, 1968;

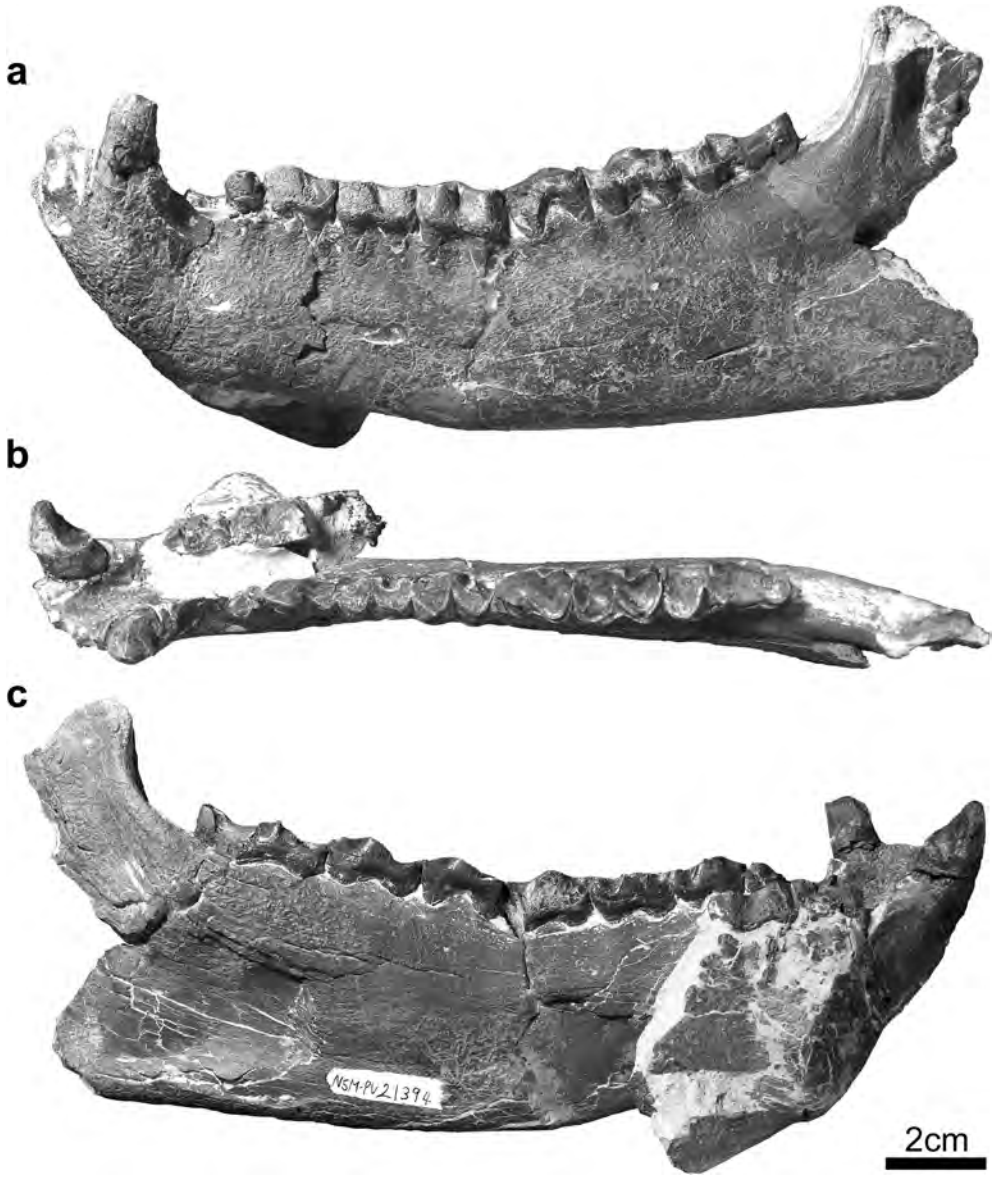

Fig. 28. *Palaeotherium medium euzetense* (Depéret, 1917) from Euzèt les Bains. NMNS-PV 21394, left mandible and a right symphysial part with right c1, p2–3, left c1, and p1–m3 in left lateral (a), occlusal (b), and left lingual (c) views.

P. duvali duvali Pomel, 1853; *P. magnum girondicum* Blainville, 1846; *P. muehlbergi muehlbergi* Stehlin, 1904b; and *P. muehlbergi thaleri* Remy, 1985. The other upper dental specimens cataloged here are identical to NMNS-PV 21480 in size (Appendix 1). The upper premolars (Figs. 31b and 32 g, i, k; NMNS-PV 21480, 21483, 21485, and 21489) exhibit sub-quadratic outlines in occlusal view. The labial surfaces of premolars are flattened with faint or no mesostyle ribs, and the labial and lingual cingula on the premolars are sharp and continuous. The mesostyles in M1 and M2 (NMNS-PV 21480) are also weak, but the mesostyle in M3 (NMNS-PV 21480 and 21481) is stronger. Unworn DP3 and DP4 (Fig.

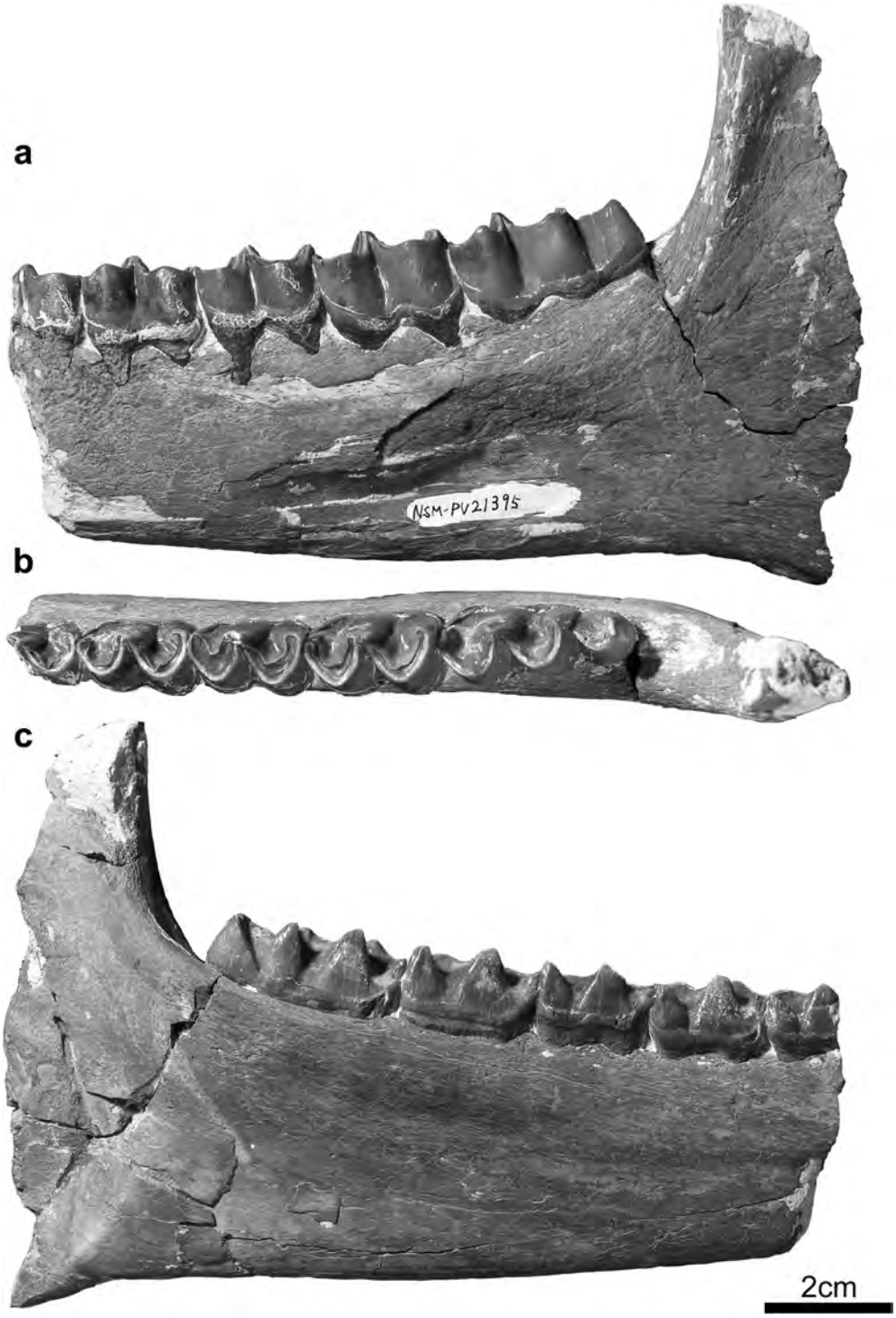

Fig. 29. *Palaeotherium medium euzetense* (Depéret, 1917) from Euzèt les Bains. NMNS-PV 21395, left mandibular fragment with broken p3 and p4–m3 in labial (a), occlusal (b), and lingual (c) views.

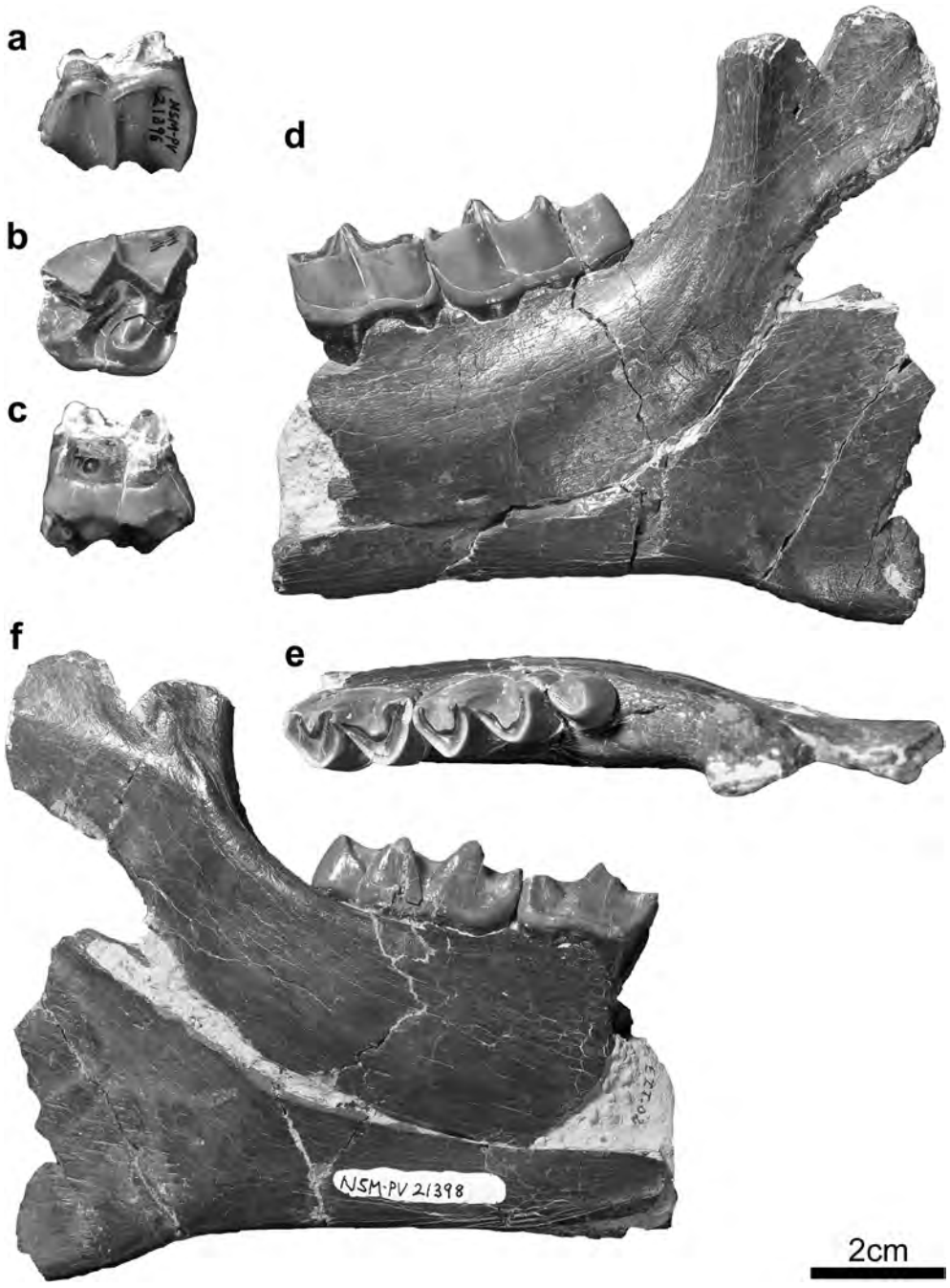

Fig. 30. *Palaeotherium medium euzetense* (Depéret, 1917) from Euzèt les Bains. NMNS-PV 21396, right M2 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21398, left mandibular fragment with m2–3 in labial (d), occlusal (e), and lingual (f) views.

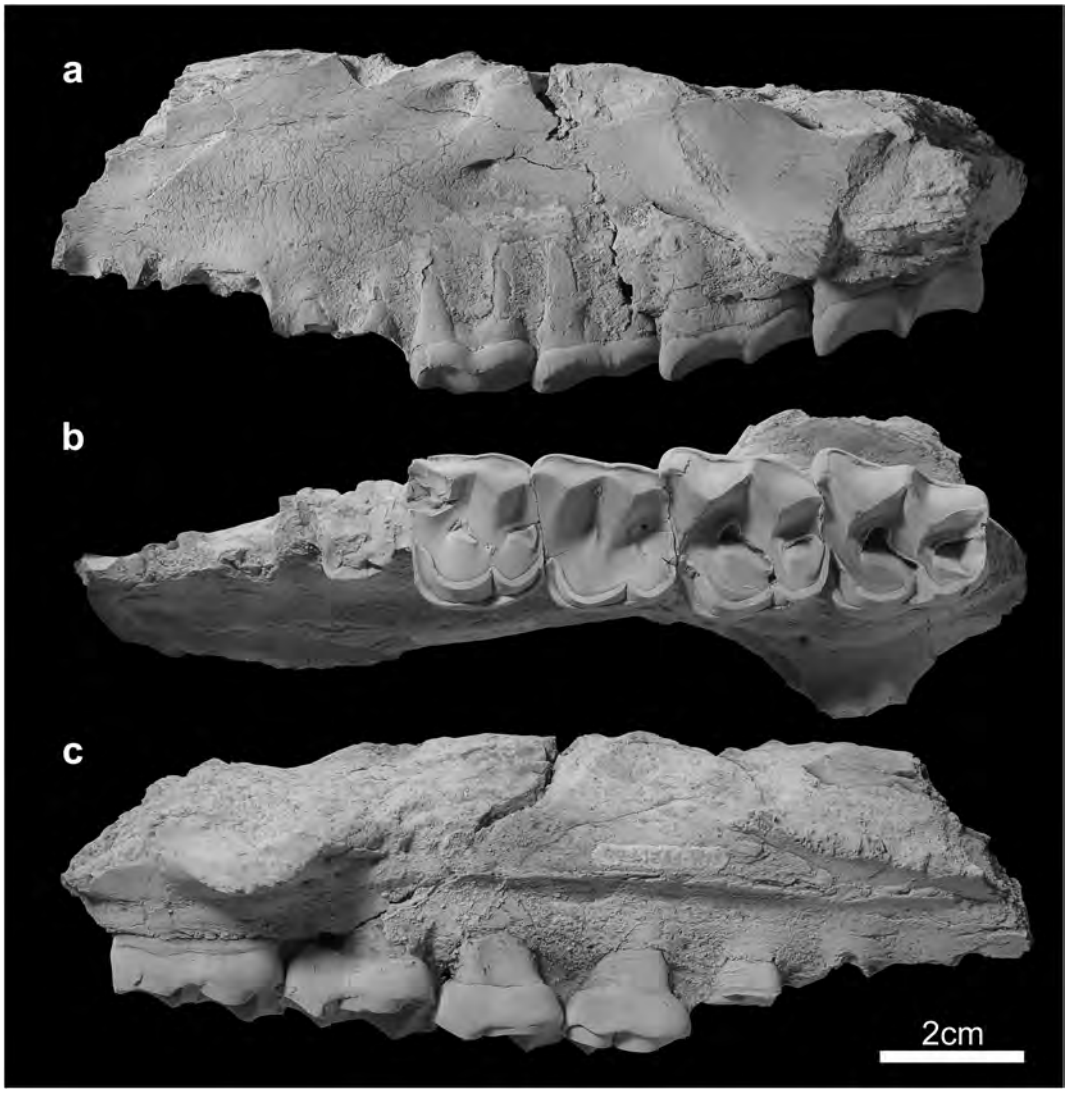

Fig. 31. *Palaeotherium medium perrealense* (Stehlin, 1904b) from La Débruge. NMNS-PV 21480, left maxillary fragment with broken P3 and P4–M3 in labial (a), occlusal (b), and lingual (c) views.

32c–e, NMNS-PV 21482) have distinct cingula running on the anterior and lingual margins of protocones.

Despite being fragmentary, two mandibular fragments with cheek teeth (Figs. 33 and 34, NMNS-PV 21486 and 21487) are also referable to *P. medium perrealense* based on size and morphology. The labial and lingual cingula on the cheek teeth are sharp, and the m3 hypoconulids exhibit hook-shaped crests in occlusal view. The length of the preserved tooth row in NMNS-PV 21487 implies a relatively higher PMI (at least 69.0) than in other contemporary *P. curtum* and *P. muehlbergi.* The labial wall of p3 is less expanded externally unlike in *P. curtum villerealense* from La Débruge.

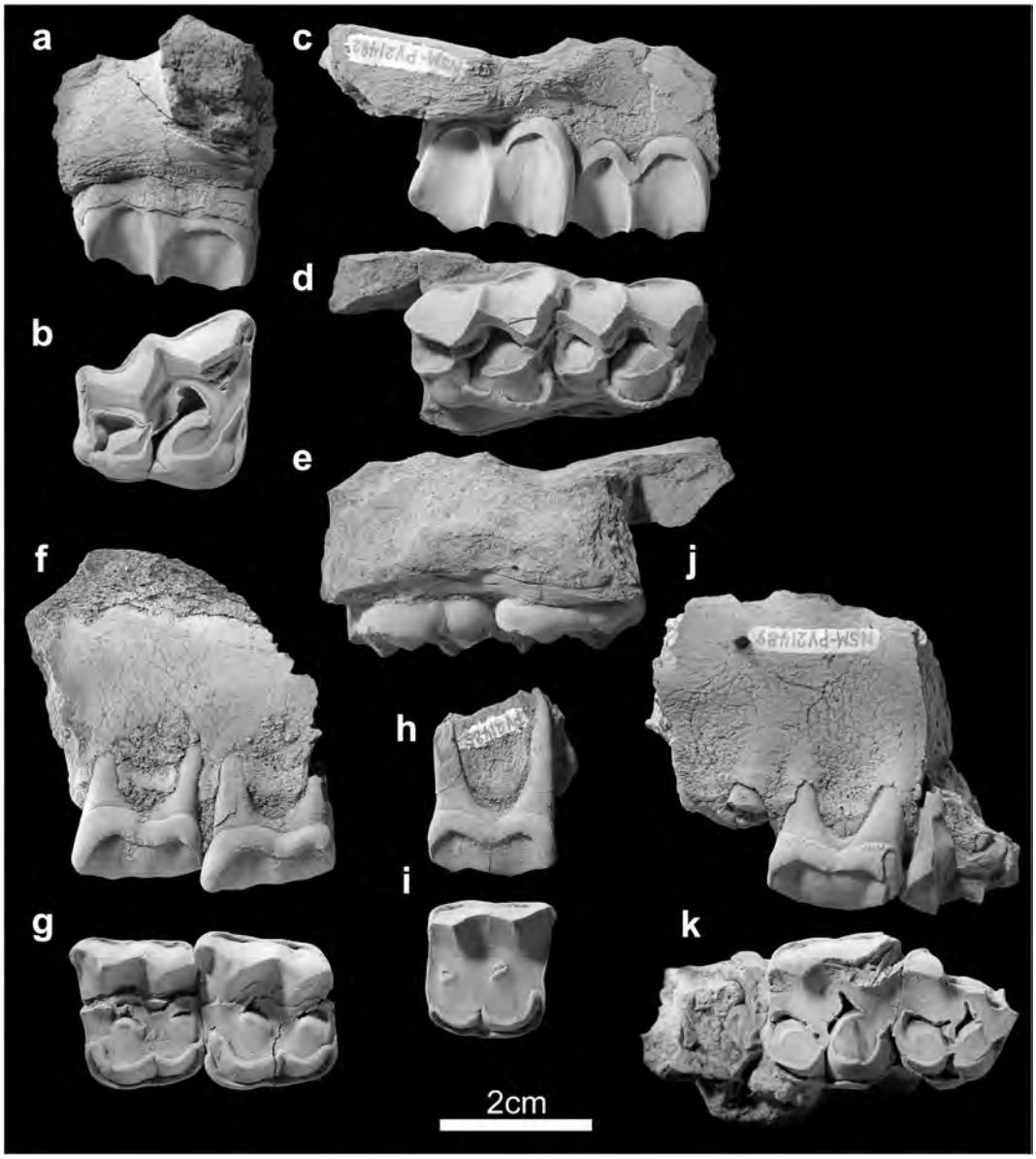

Fig. 32. *Palaeotherium medium perrealense* (Stehlin, 1904b) from La Débruge. NMNS-PV 21481, a right maxillary fragment with M3 in labial (a) and occlusal (b) views. NMNS-PV 21482, right maxillary fragment with DP3–4 in labial (c), occlusal (d), and lingual (e) views. NMNS-PV 21483, left maxillary fragment with P3–4 in labial (f) and occlusal (g) views. NMNS-PV 21485, possible right P3 in labial (h) and occlusal (i) views. NMNS-PV 21489, right maxillary fragment with broken P2–3 and P4 root in labial (j) and occlusal (k) views.

***Palaeotherium* sp. cf. *P. medium* Cuvier, 1804**
(Fig. 35)

Localities and Materials: La Débruge: NMNS-PV 21484, right mandibular fragment with possible p4 or m1; 21491, left mandibular fragment with m1–2; 21493, labial part of right M3.

Comments: The La Débruge specimens cataloged here represent a medium-sized *Palaeotherium*

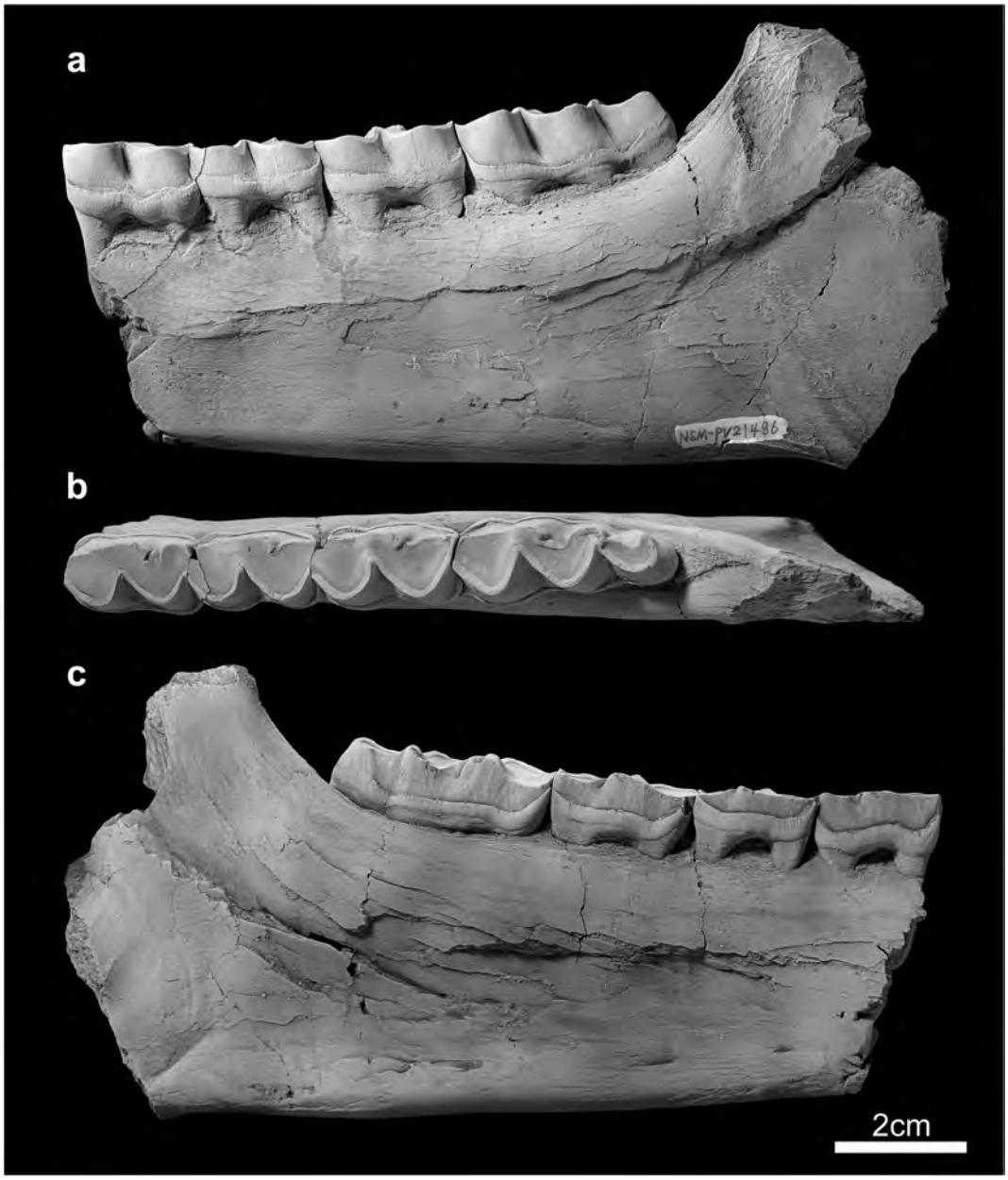

Fig. 33. *Palaeotherium medium perrealense* (Stehlin, 1904b) from La Débruge. NMNS-PV 21486, left mandibular fragment with p4–m3 in labial (a), occlusal (b), and lingual (c) views.

species; the dental sizes are close to those of *P. medium perrealense* from the same locality (Appendix 1, see also the previous section). However, all of the specimens lack definitive characters of *P. medium*, and the labial and lingual cingulids of lower cheek teeth are rather weak unlike in *P. medium*. Considering the hypsodonty of lower teeth and the strength of M3 mesostyle, all of them might be assignable to a contemporaneous *P. crassum robustum*. NMNS-PV 21491 (Fig. 35d–f) is a mandibular fragment from a juvenile individual.

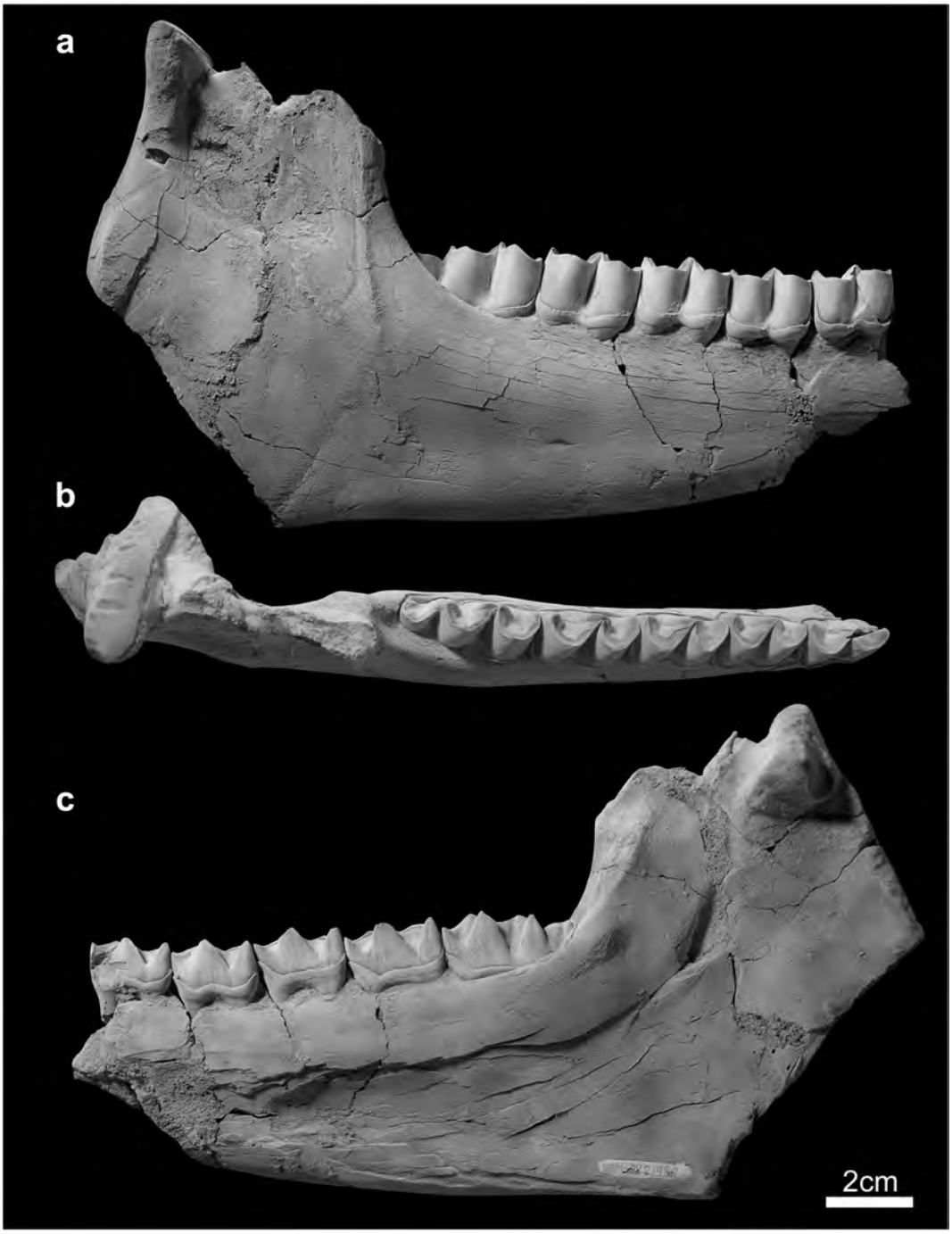

Fig. 34. *Palaeotherium medium perrealense* (Stehlin, 1904b) from La Débruge. NMNS-PV 21487, right mandibular fragment with p3–m3 in labial (a), occlusal (b), and lingual (c) views.

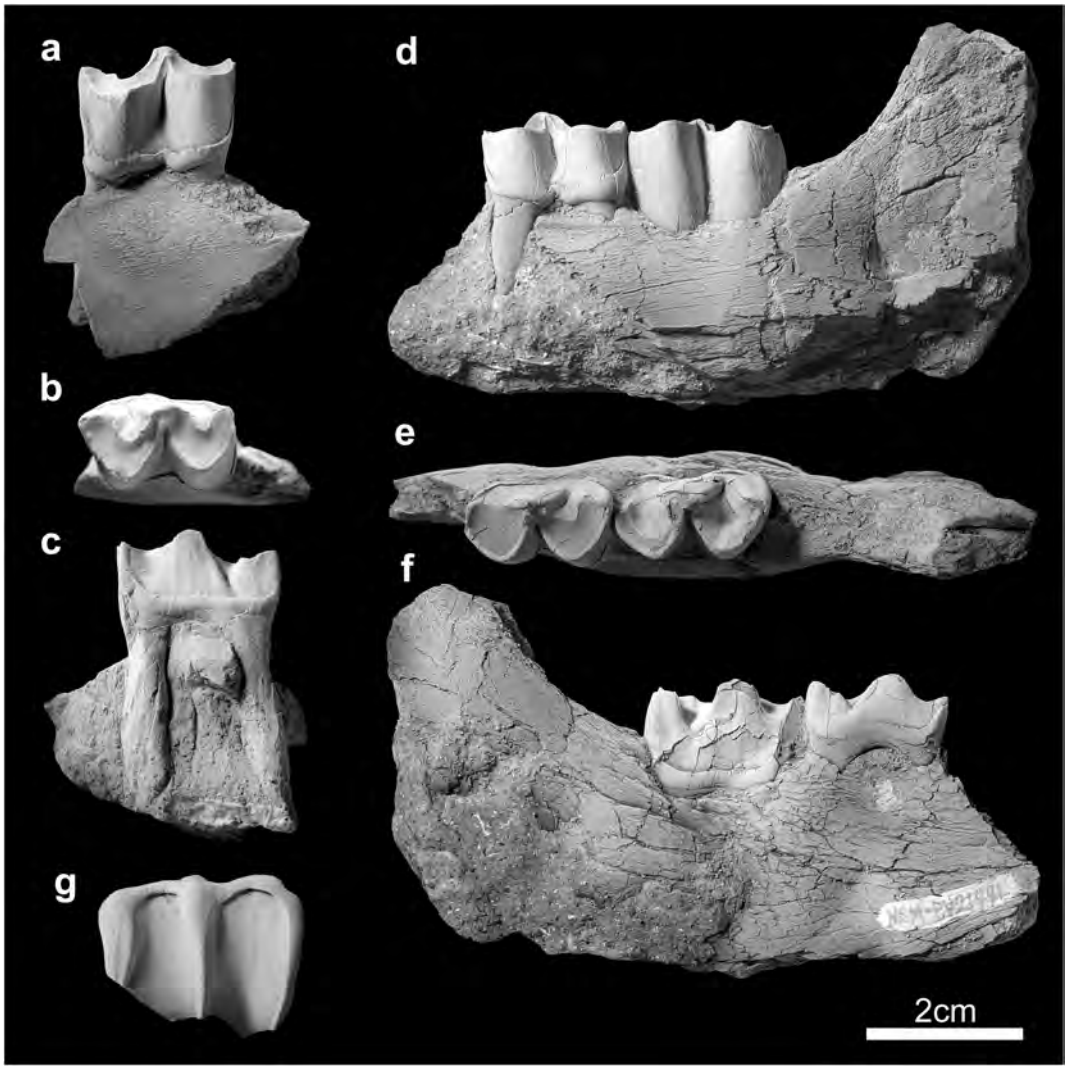

Fig. 35. *Palaeotherium* sp. cf. *P. medium* Cuvier, 1804 from La Débruge. NMNS-PV 21484, right mandibular fragment with possible p4 or m1 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21491, left mandibular fragment with m1–2 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21493, labial part of right M3 (g) in labial view.

Palaeotherium muehlbergi Stehlin, 1904b

Comments: *Palaeotherium muehlbergi* is a medium-sized species, and three subspecies (*P. muehlbergi muehlbergi* Stehlin, 1904b; *P. muehlbergi praecursum* Franzen, 1968; and *P. muehlbergi thaleri* Remy, 1985) have been discriminated (Franzen, 1968; Remy, 1985). *P. muehlbergi praecursum* and *P. muehlbergi thaleri* are from MP 17 and 18, respectively, and *P. muehlbergi muehlbergi* is known from MP 18 to MP 20 (e.g., Frohnstetten in Germany) (Franzen, 1968; Legendre, 1987). *P. muehlbergi thaleri* is found at La Débruge; Remy (1985) reassigned specimens of *P. muehlbergi muehlbergi* described by Franzen (1968) from La Débruge to *P. muehlbergi thaleri*.

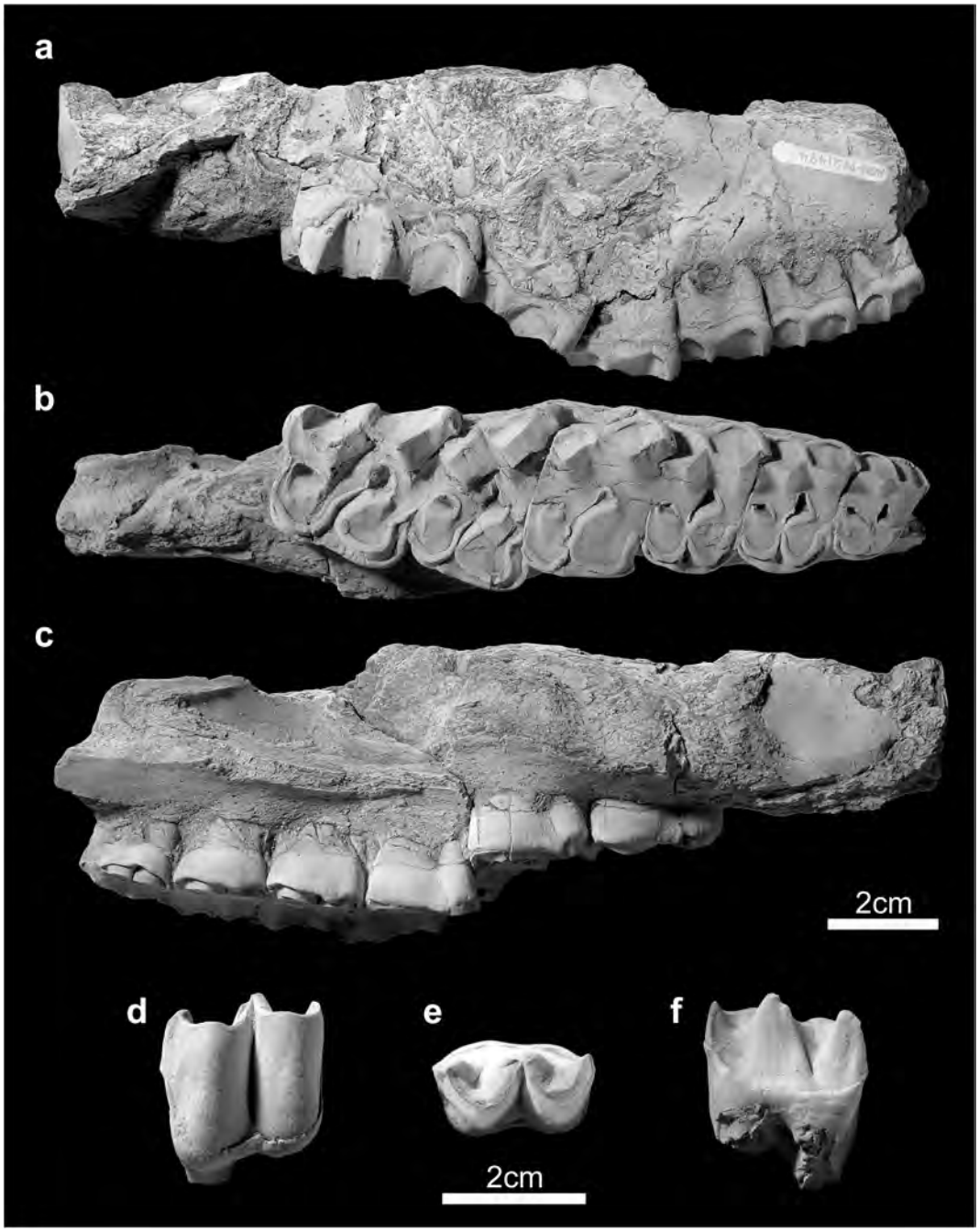

Fig. 36. *Palaeotherium muehlbergi thaleri* Remy, 1985 from La Débruge. NMNS-PV 21494, right maxillary fragment with P2–M3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21495, right m1 or m2, in labial (d), occlusal (e), and lingual (f) views. Scale bar for d–f is shown at bottom.

Palaeotherium muehlbergi thaleri Remy, 1985
(Fig. 36)

Localities and Materials: La Débruge: NMNS-PV 21494, right maxillary fragment with P2–M3; 21495, right m1 or m2.

Comments: NMNS-PV 21494 (Fig. 36a–c) shows a diagnostic dental character of *Palaeotherium muehlbergi*, although the labial half of M2 is deformed. The upper cheek teeth are compressed anteroposteriorly or expanded labiolingually (the width is greater than the length in each tooth except the M3).

The maxillary fragment of NMNS-PV 21494, partially repaired by plaster, preserves a hint of the mental foramen positioned above the M1. The length of P2–M3 in NMNS-PV 21494 (ca. 113.7 mm) is comparable to those of *P. muehlbergi thaleri*, although the PMI in NMNS-PV 21494 (ca. 72.7) slightly exceeds the range of *P. muehlbergi thaleri* (68.8–70.9; Remy, 1985). These characters differ from those of *P. muehlbergi praecursum*, suggesting the taxonomic assignment to *P. muehlbergi thaleri*. The mesostyles on the premolars are not as strong as in the type specimen of *P. muehlbergi thaleri* (SEO 2, collection of the Université des Sciences et Techniques du Languedoc, Montpellier) described by Remy (1985), but the minor difference can be considered as a variation within this subspecies. The right lower molar (Fig. 36d–f, NMNS-PV 21495) is more hypsodont than in *P. medium* and *P. curtum* from La Débruge and has a weak lingual cingulid, supporting an assignment to *P. muehlbergi thaleri*.

Palaeotherium sp.
(Figs. 37 and 38)

Localities and Materials: Euzèt les Bains: NMNS-PV 21397, left C1; 21399, right lower or left upper incisor.

Baby: NMNS-PV 21422, right c1; 21423, right tibia; 21424, trigonid of left lower molar; 21425, talonid of possible left m2; 21429, fragment of right upper molar; 21430, fragment of left P2.

Civrac de Blaye: NMNS-PV 21364, right C1.

La Débruge: NMNS-PV 21492, right mandibular fragment with p3.

Comments: The *Palaeotherium* specimens from Euzèt (Fig. 37a–e) represent a medium-sized species, which is comparable in size to *P. medium euzetense* or *P. curtum villerealense* from the same locality (Euzèt les Bains). The specimens from Baby are poorly preserved (Fig. 37f–n), but the large canine and tibia imply the presence of a large species in the locality. The tibia is stout with a developed medial condyle and medial malleolus, but it is heavily compressed and partially damaged (Fig. 37h, i).

The canine from Civrac de Blaye (NMNS-PV 21364) bears a flat lingual surface and a sharp cingulum encompassing the base of the crown (Fig. 38a, b). The mandibular fragment from La Débruge (Fig. 38c–e, NMNS-PV 21492) preserves a worn p3 and alveoli for double-rooted p2 and belongs to a moderate-sized *Palaeotherium* species. The anterior wall of p3 shows a strong indentation for the p2. The tooth identification in NMNS-PV 21492 is reasonable with the positions of the multiple mental foramina: the anterior two are located above the p2, and a single foramen is positioned above the p3 talonid (Fig. 38c). NMNS-PV 21492 has no p1 and a less developed mandibular symphysis extending to the midline of p2, and the mandible is shallower than in *P. medium perrealense*. These features of NMNS-PV 21492 indicate the differences from *P. curtum villerealense* from the same locality (La Débruge; see also Fig. 16d–f, NMNS-PV 21469).

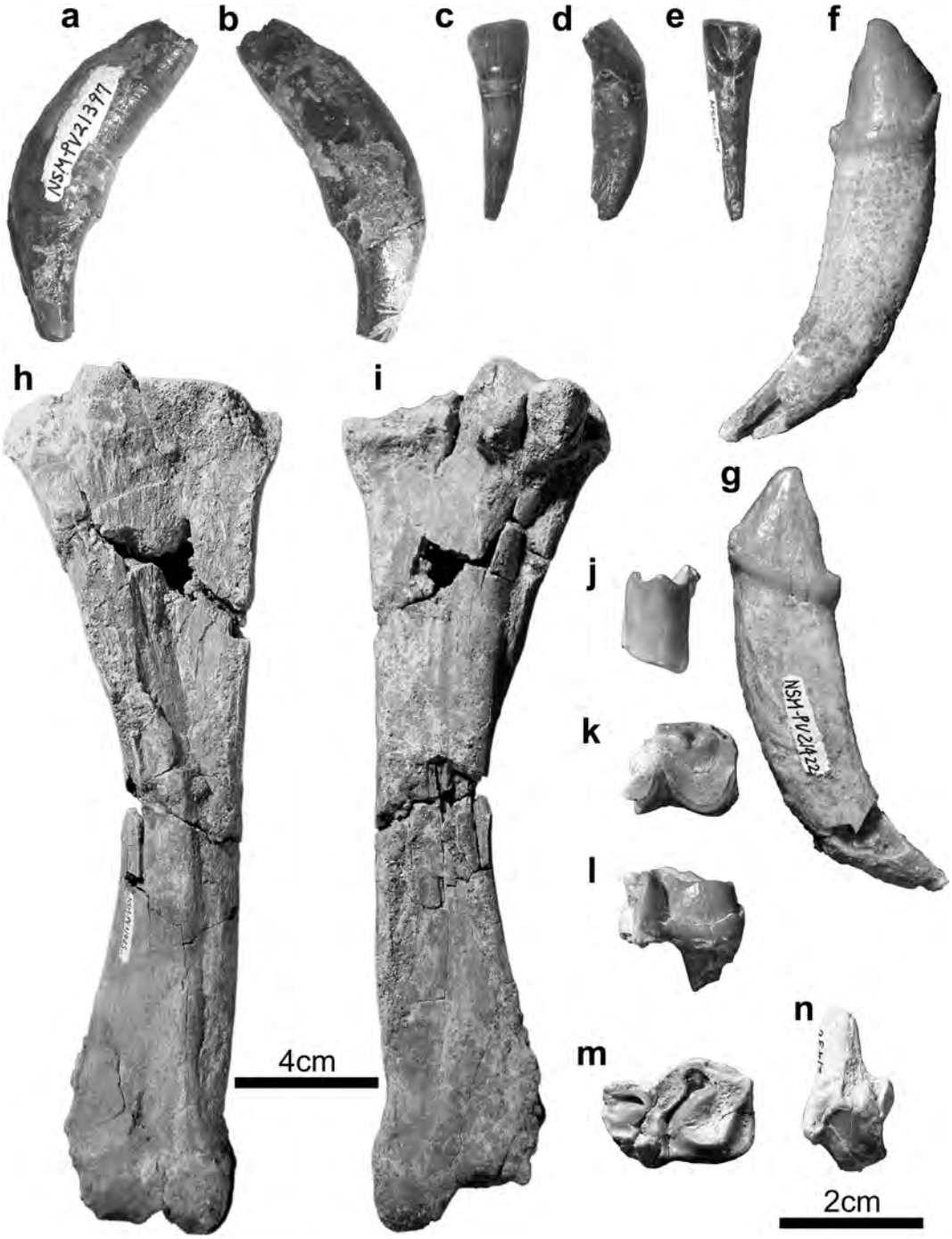

Fig. 37. *Palaeotherium* sp. from Euzèt les Bains (NMNS-PV 21397 and 21399) and Baby (NMNS-PV 21422–21425, 21429, and 21430). NMNS-PV 21397, left C1 in labial (a) and lingual (b) views. NMNS-PV 21399, right lower or left upper incisor in labial (c), distal (d), and lingual (e) views. NMNS-PV 21422, right c1 in labial (f) and lingual (g) views. NMNS-PV 21423, right tibia in anterior (h) and posterior (i) views. NMNS-PV 21424, trigonid of left lower molar (j) in labial view. NMNS-PV 21425, talonid of possible left m2 in occlusal (k) and labial (l) views. NMNS-PV 21429, fragment of right upper molar (m) in occlusal view. NMNS-PV 21430, fragment of left P2 (n) in labial view. Scale bar for h and i is shown between the two.

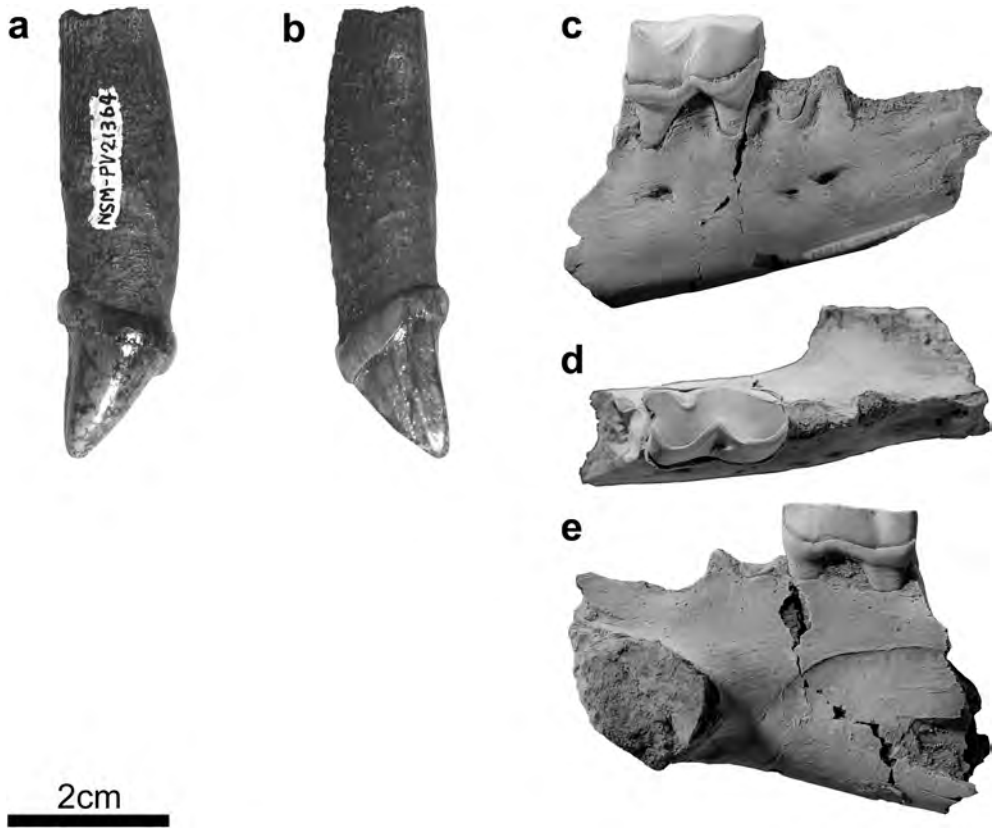

Fig. 38. *Palaeotherium* sp. from Civrac de Blaye (NMNS-PV 21364), and La Débruge (NMNS-PV 21492). NMNS-PV 21364, right C1 in labial (a) and lingual (b) views. NMNS-PV 21492, right mandibular fragment with p3 in labial (c), occlusal (d), and lingual (e) views.

Cf. *Palaeotherium* sp.
(Fig. 39)

Localities and Materials: Baby: NMNS-PV 21426, thoracic vertebra; 21427, possible fibular shaft and unidentifiable fragment; 21428, right proximal femur.

Civrac de Blaye: NMNS-PV 21377, occipital condyles

La Débruge: NMNS-PV 21488, lumbar vertebra

Comments: These postcranial remains are presumably referable to *Palaeotherium* based on size and morphology. However, because of the incompleteness, there is no definitive feature clarifying the generic assignment.

Genus *Plagiolophus* Pomel, 1847a

Type species: *Plagiolophus minor* (Cuvier, 1804).

Comments: The genus *Plagiolophus* has been traditionally included in the family Palaeotheriidae (Remy, 2004), but some workers have allocated it to the family Pachynolophidae Pavlow, 1888 (Cuesta, 1994a, b; Badiola et al., 2005). *Plagiolophus* has been described from the middle Eocene to early Late

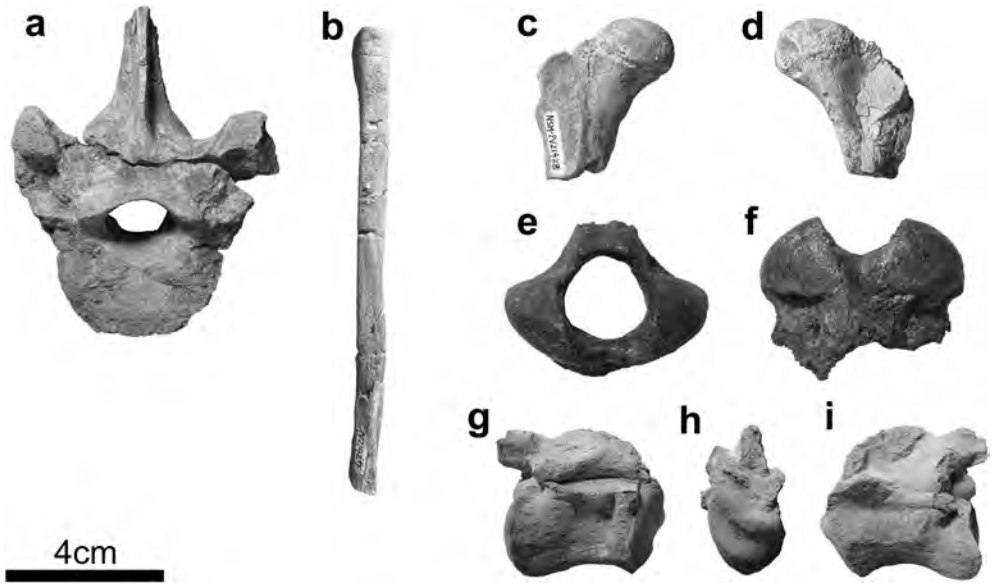

Fig. 39. Cf. *Palaeotherium* sp. from Baby (NMNS-PV 21426–21428), Civrac de Blaye (NMNS-PV 21377), and La Débruge (NMNS-PV 21488). NMNS-PV 21426, thoracic vertebra (a) in anterior view. NMNS-PV 21427, possible fibular shaft (b). NMNS-PV 21428, right proximal femur in anterior (c) and posterior (d) views. NMNS-PV 21377, occipital condyles in posterior (e) and ventral (f) views. NMNS-PV 21488, lumber vertebra in right lateral (g), anterior (h), and left lateral (i) views.

Oligocene in Europe (MP 12–25, Luterbacher et al., 2004). The genus flourished during the late Eocene and early Oligocene (Remy, 2004). Remy recognized 17 species belonging to three subgenera: *Fraasiolophus* Remy, 2004; *Paloplotherium* Owen, 1848b; and *Plagiolophus* Pomel, 1847a. The genus *Paloplotherium* is considered a junior synonym of *Plagiolophus* (e.g. Hooker, 1986; Remy, 2004), while Brunet and Jehenne (1989) separated the genus *Paloplotherium* from *Plagiolophus* following a revision of *Plagiolophus*. The systematic concept of the genus *Plagiolophus* in this chapter follows Remy (2004), who provides the most recent systematic revision of the genus with the comprehensive reviews.

Subgenus *Paloplotherium* Owen, 1848b
***Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b)**
(Figs. 40–49)

Localities and Materials: Robiac: NMNS-PV 21342, left maxillary fragment with M2–3; 21343, right maxillary fragment with M1–3; 21347, broken right M3.

Euzèt les Bains: NMNS-PV 21400, right and left mandibles with c1s and p2–m3s; 21401, right and left mandibles with right p2–m3, left c1, p2 root, and p3–m1; 21402, right and left maxillae with broken right P2, P3–M3, broken left I3, and incomplete P2–M3; 21403, left mandible with c1, p3 root, and p4–m3 and right symphysial part with broken c1; 21404, right m1; 21405, right mandibular fragment with p2–m3 on matrix; 21406, proximal half of left radius; 21407, broken left calcaneum; 21408, right astragalus; 21409, broken left M2; 21410, broken right M3; 21412, right M2; 21413, broken left P4; 21414, left p4; 21415, right mandibular fragment with m3; 21416, left maxillary fragment with DP3–4 and broken M1; 21417, right DP3.

Baby: NMNS-PV 21431, incomplete skull with right P3–M3, broken left P4, M1–3, and left man-

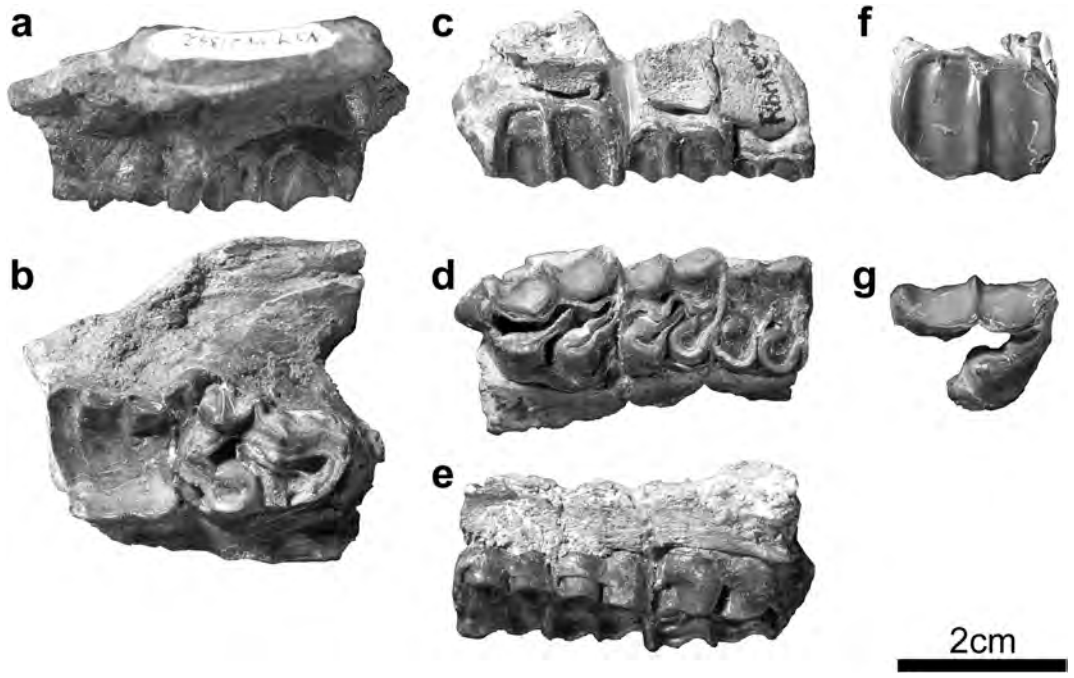

Fig. 40. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Robiac. NMNS-PV 21342, left maxillary fragment with M2–3 in labial (a) and occlusal (b) views. NMNS-PV 21343, right maxillary fragment with M1–3 in labial (c), occlusal (d), and lingual (e) views. NMNS-PV 21347, broken right M3 in labial (f) and occlusal (g) views.

dibular fragment with m1–3 (artificial parts: nasals, left premaxilla, anterior part of left maxilla, left P2–3, left mandible anterior to m1, and vertical ramus of left mandible); 21432, incomplete skull with right and left P2–M3s; 21433, left mandibular fragment with p2 roots and p3–m3; 21434, left C1; 21437, broken right M3.

Comments: *Plagiolophus annectens* was originally established as the type species of *Paloplotherium* Owen, 1848b, which was considered a subgenus by Remy (2004). The subgenus *Paloplotherium* is characterized by having a deep nasal incision extending posterior to P2; no preorbital fossa and no extended post-canine diastema; relatively massive skull and mandible; rather primitive dental characters including less hypsodont molars and sometimes absent coronal dental cementum (Remy, 2004). According to Remy (2004), *Plagiolophus annectens* is a larger species than *P. minor*; the length of P2–M3 ranges from 76 to 87 mm. The post-canine diastema (between C1 and P2, c1 and p2) in *P. annectens* is relatively short, but the ratio for the cheek tooth length (length of P2–M3, p2–m3) varies from 19 to 32% at maxilla and from 26 to 37% at mandible (Remy, 2004). The upper molars of *P. annectens* are hypsodont compared to those of *P. cartieri* Stehlin, 1904b and are less anteroposteriorly compressed unlike in *P. minor* (Remy, 2004). Remy (2004) mentioned that *P. annectens* basically has a complete series of premolars (P1 seems to be lost early) and relatively high cheek tooth variation.

The specimens of *P. annectens* cataloged here are derived from Robiac, Euzèt les Bains, and Baby. *P. annectens* has been described only from MP 16 and 17 in Robiac and Euzèt les Bains (Remy, 2004). The presence of *P. annectens* in the assemblage from Baby suggests that it is most likely associated with an equivalent biochronologic range, presumably with Baby 1 (MP 17) in Schmidt-Kittler (1987).

The Robiac maxillary specimens (Fig. 40a–e, NMNS-PV 21342 and 21343) display a labiolingually narrower M2 than M3, unlike in the *P. annectens* specimens from Euzèt les Bains and Baby. Remy (2004) documented some Robiac specimens that are smaller than *P. annectens* specimens known from

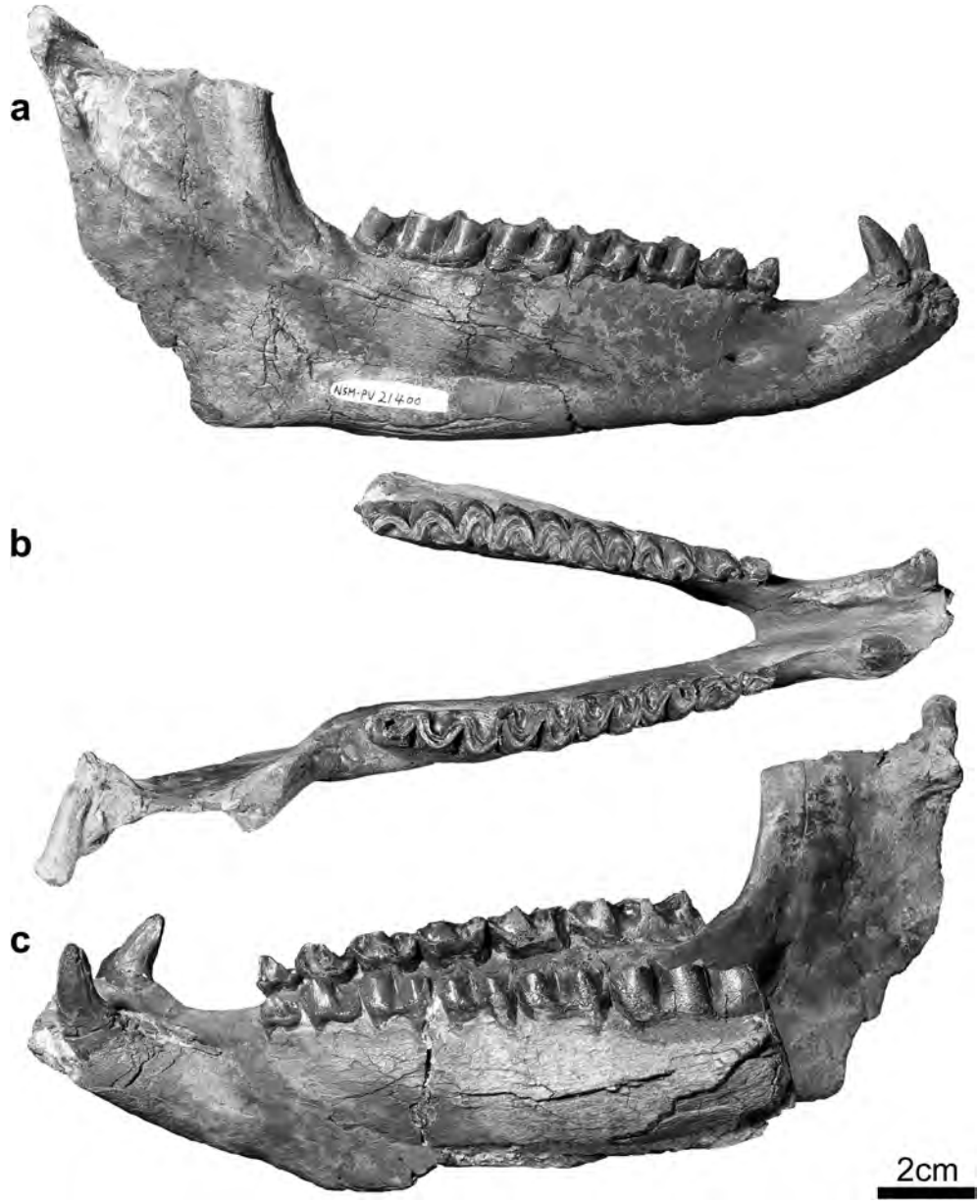

Fig. 41. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Euzèt les Bains. NMNS-PV 21400, right and left mandibles with c1s and p2–m3s in right lateral (a), occlusal (b), and left lateral (c) views.

other localities. A size difference can be observed between NMNS-PV 21342 and 21343 which respectively represent large and small individuals (Appendix 1), although the molars of NMNS-PV 21343 are roughly as small as those of *P. minor*. *P. annectens* from Robiac can be distinguished from larger Robiac species, *Plagiolophus cartailhaci* Stehlin, 1904a and *P. mamertensis* Remy, 2004: *P. cartailhaci* has a prominent mesostyle on M1, and *P. mamertensis* is more robust and hypsodont (Remy, 2004).

More than half of the *P. annectens* specimens in the collection are derived from Euzèt les Bains. Most of the mandibles represent adult individuals (Figs. 41, 42, and 44a–c, g; NMNS-PV 21400,

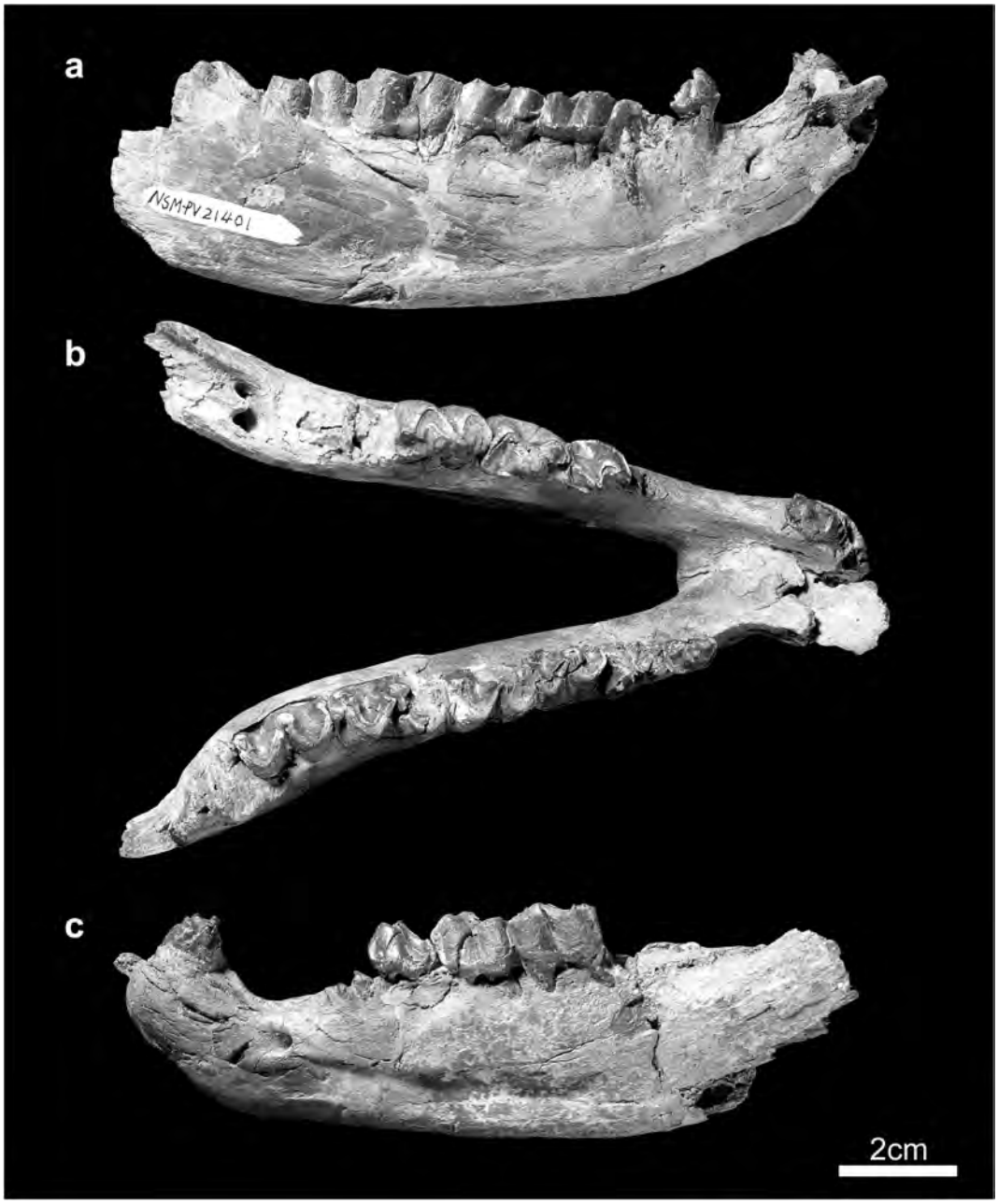

Fig. 42. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Euzèt les Bains. NMNS-PV 21401, right and left mandibles with right p2–m3, left c1, p2 root, and p3–m1 in right lateral (a), occlusal (b), and left lateral (c) views.

21401, 21403, and 21405) that preserve moderately long molar lengths (55.3–56.4 mm in m1–3 length) within the range observed at Euzèt (Remy, 2004). NMNS-PV 21401 has a relatively short mandible with an unerupted m3 representing a younger individual (Fig. 42). NMNS-PV 21403 seems to have a relatively long post-canine diastema, but the mandible is restored at p2–3; thus, its exact length is unknown because of the breakage. Almost all of the lower cheek teeth are identical in size

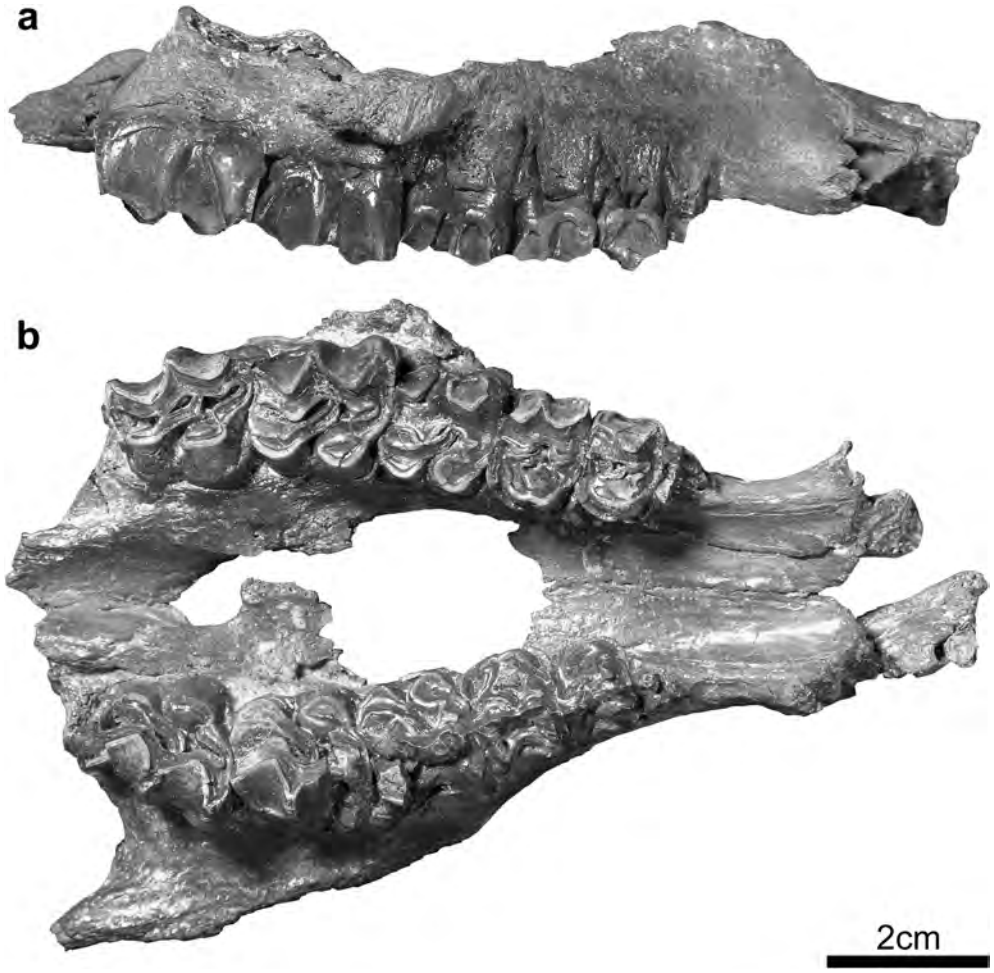

Fig. 43. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Euzèt les Bains. NMNS-PV 21402, right and left maxillae with broken right P2, P3–M3, broken left I3, and incomplete P2–M3 in right lateral (a) and occlusal (b) views.

and morphology. NMNS-PV 21415 is tentatively referred to *P. annectens* based on size, but it has a strong labial cingulid on the m3 hypoconulid lobe (Fig. 46n, o).

Based on the specimen lists provided by the collector, NMNS-PV 21405 appears to be associated with some postcranial material from the same locality (Fig. 45, NMNS-PV 21406–21408). Although the left calcaneum (NMNS-PV 21407) is poorly preserved, these postcrania belong presumably to the same individual. Therefore, all of them are assigned to the same species in here.

NMNS-PV 21402 (Fig. 43) documents the upper dental morphology of a relatively small individual of the Euzèt *P. annectens*. The taxonomic assignments for isolated upper cheek teeth from Euzèt les Bains (Fig. 46a–j; NMNS-PV 21409, 21410, 21412, and 21413) are based on the similarity with NMNS-PV 21402. The Euzèt specimens include deciduous upper premolars of *P. annectens* (Fig. 46q–v; NMNS-PV 21416 and 21417), which are labially broad with strong parastyles and developed lingual cingula.

Baby is listed as locality yielding *P. annectens* (Remy, 2004). Skull morphology of *P. annectens* is preserved in specimens from Baby (Figs. 47 and 48; NMNS-PV 21431 and 21432), but various parts

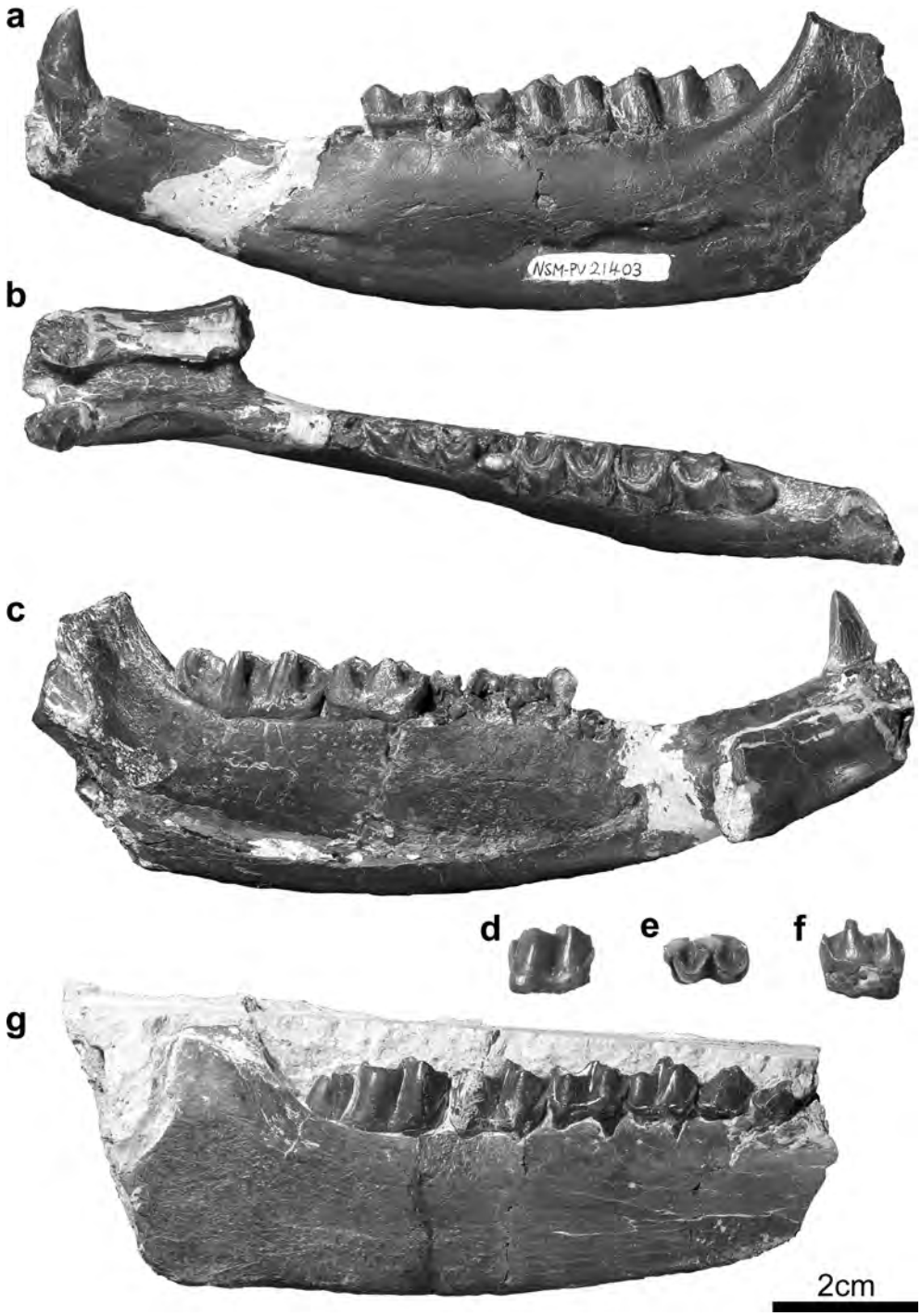

Fig. 44. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Euzèt les Bains. NMNS-PV 21403, left mandible with c1, p3 root, p4–m3, and right symphysial part with broken c1 in left labial (a), occlusal (b), and left lingual (c) views. NMNS-PV 21404, right m1 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21405, right mandibular fragment with p2–m3 on matrix (g) in labial view.

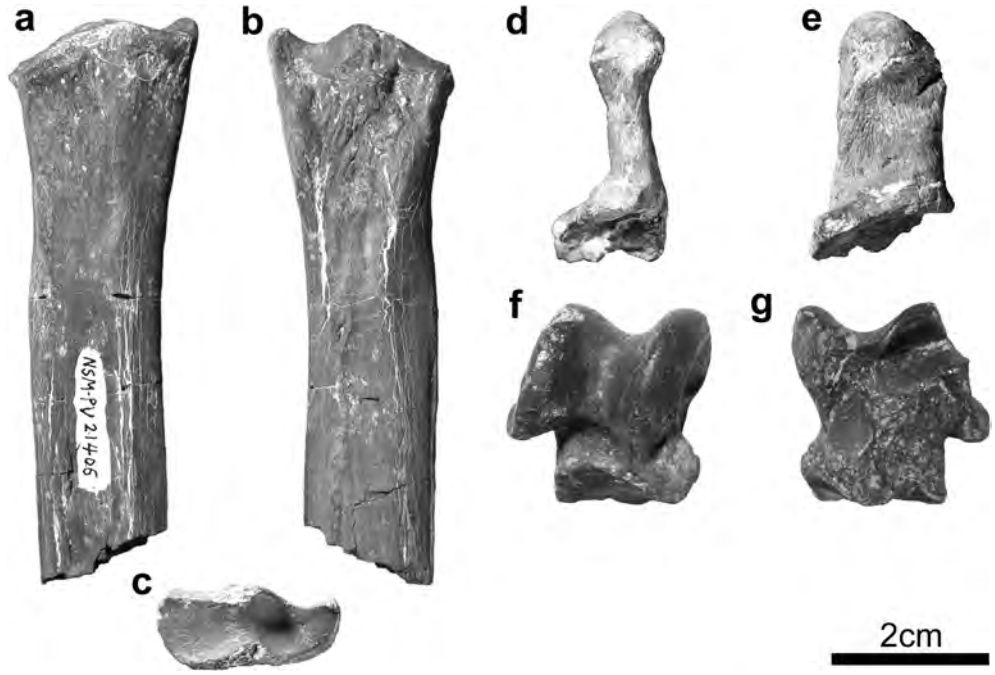

Fig. 45. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Euzèt les Bains. NMNS-PV 21406, proximal half of left radius in anterior (a), posterior (b), and proximal (c) views. NMNS-PV 21407, broken left calcaneum in dorsal (d) and medial (e) views. NMNS-PV 21408, right astragalus in dorsal (f) and plantar (g) views.

are roughly restored in NMNS-PV 21431 (the nasals, left premaxilla, anterior part of left maxilla, and left P2–3). Dental size and morphology are identical between NMNS-PV 21431 and 21432. However, the anterior orbital rim in NMNS-PV 21431 is positioned above the anterior part of M3, whereas the orbital rim in NMNS-PV 21432 is more anteriorly positioned above the anterior part of M2. The difference of the orbital position can be considered as an ontogenetic development of *P. annectens* (see also Remy, 2000; the ontogenetic changes of skull in *Plagiolophus huerzeleri*). The mandible of NMNS-PV 21431 is largely restored (Fig. 47a, the part anterior to m1 and vertical ramus are artificial), but it preserves the lower molars. Lower dental size in both NMNS-PV 21431 and 21433 (Fig. 49a–c) is in the range of *P. annectens* (Appendix 1; Remy, 2004). The isolated upper canine (Fig. 49d, e; NMNS-PV 21434) bears a wear facet on the anterior edge of crown.

***Plagiolophus* (*Paloplotherium*) *major* (Brunet and Jehenne, 1989)**

(Figs. 50 and 51)

Localities and Materials: St. Capraise d'Eymet: NMNS-PV 21544, right maxillary and premaxillary fragments with I2–3, C1, DP2–4, and M1.

Comments: *Plagiolophus major* is the largest species of the subgenus *Paloplotherium* and is significantly larger than *P. fraasi* Meyer, 1852 (Remy, 2004). According to the diagnosis of *P. major* emended by Remy (2004), the species possesses a robust and massive mandible, a short post-canine diastema, and posteriorly positioned infraorbital foramen and orbit. In addition, the teeth are hypsodont, the PMI is relatively low, the premolars are small but molariform, the M3 is relatively larger than in *P. fraasi*, and thick coronary cementum is present (Remy, 2004).

St. Capraise d'Eymet is the type locality of *P. major* (Remy, 2004). NMNS-PV 21544 from St.

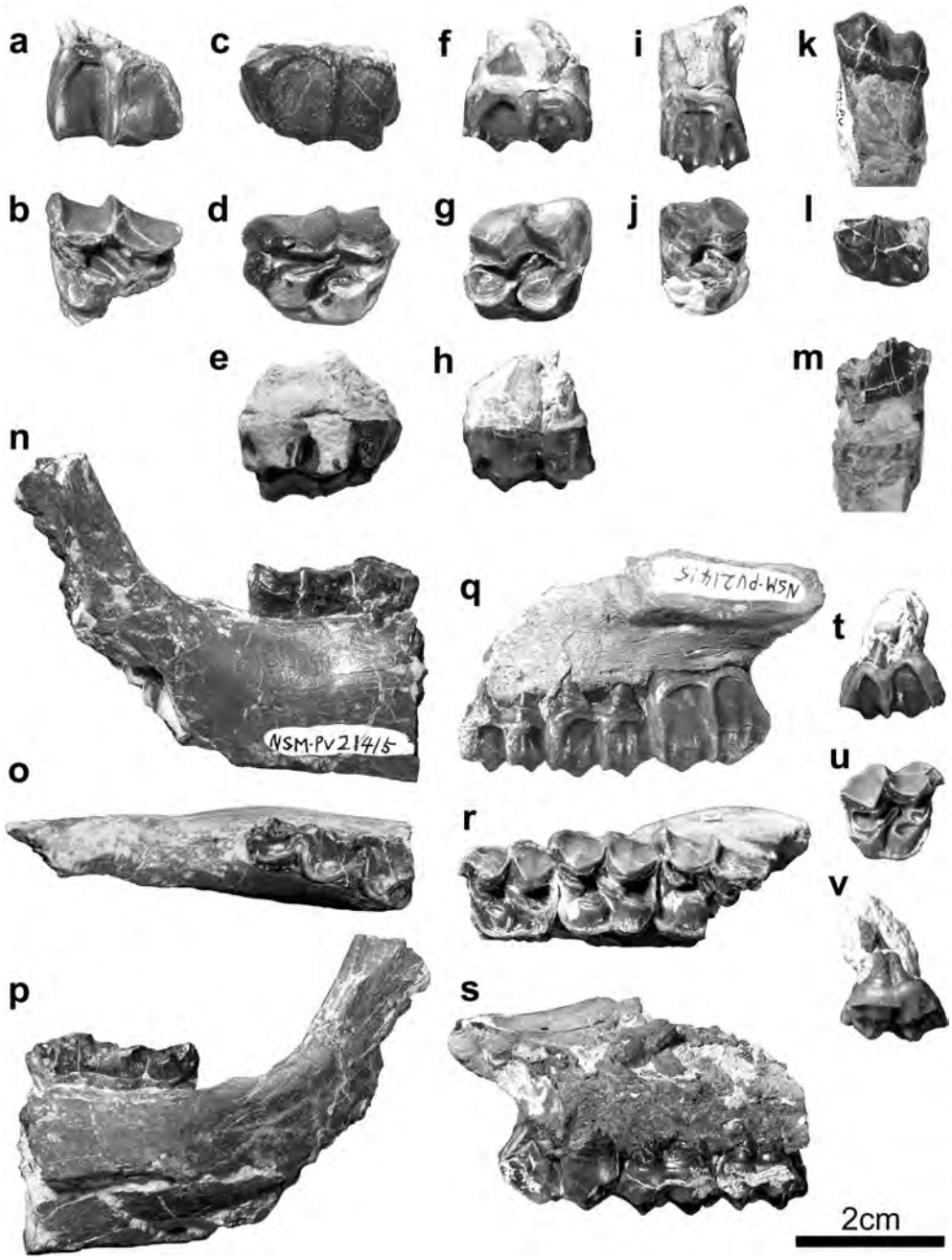

Fig. 46. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Euzèt les Bains. NMNS-PV 21409, broken left M2 in labial (a) and occlusal (b) views. NMNS-PV 21410, broken right M3 in labial (c), occlusal (d), and lingual (e) views. NMNS-PV 21412, right M2 in labial (f), occlusal (g), and lingual (h) views. NMNS-PV 21413, broken left P4 in labial (i) and occlusal (j) views. NMNS-PV 21414, left p4 in labial (k), occlusal (l), and lingual (m) views. NMNS-PV 21415, right mandibular fragment with m3 in labial (n), occlusal (o), and lingual (p) views. NMNS-PV 21416, left maxillary fragment with DP3–4, and broken M1 in labial (q), occlusal (r), and lingual (s) views. NMNS-PV 21417, right DP3 in labial (t), occlusal (u), and lingual (v) views.

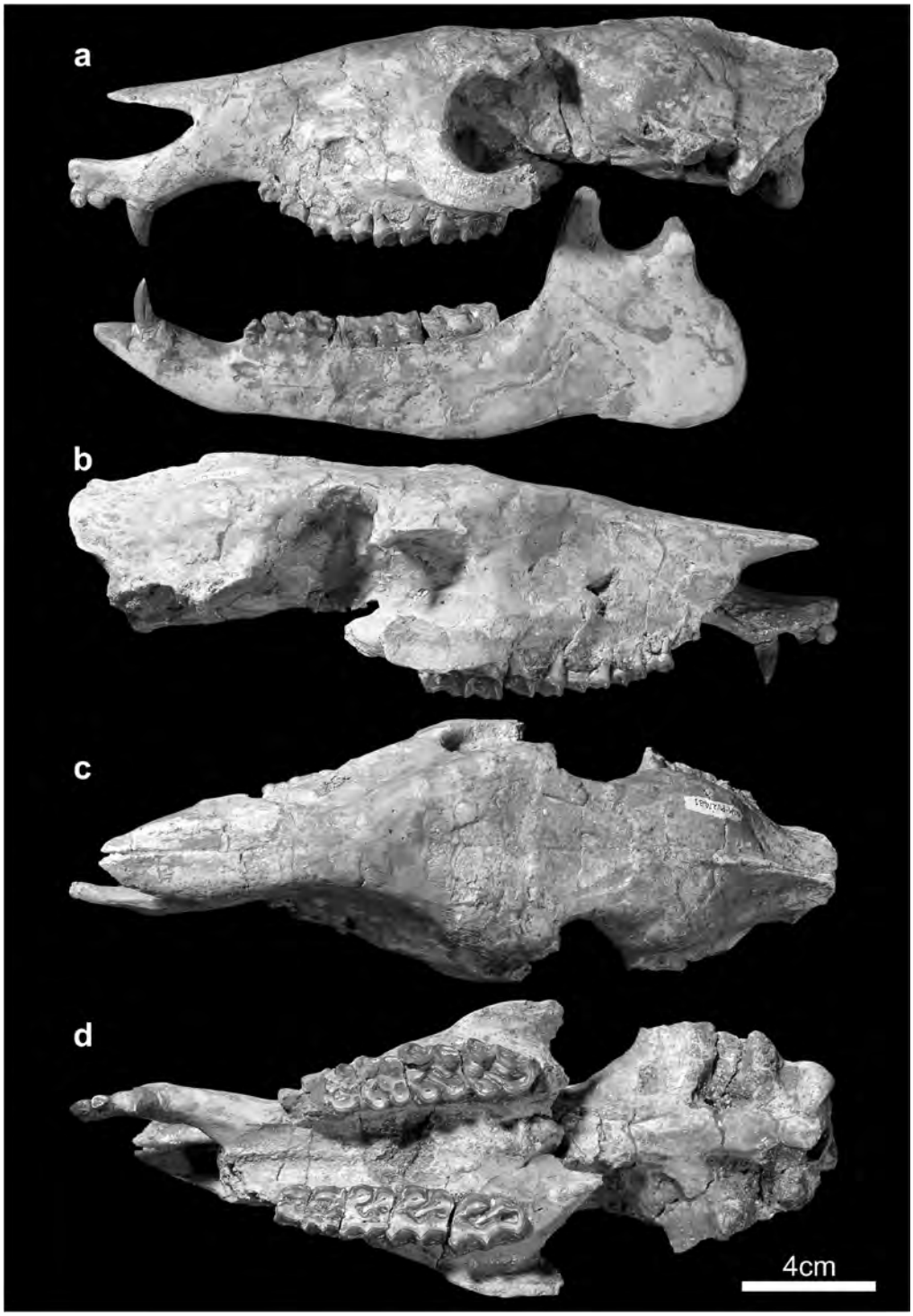

Fig. 47. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Baby. NMNS-PV 21431, incomplete skull with right P3–M3, broken left P4, and M1–3 and left mandibular fragment with m1–3 in left lateral (a) view (note the artificial parts: nasals, left premaxilla, anterior part of left maxilla, left P2–3, left mandible anterior to m1, and vertical ramus of left mandible); the skull in right lateral (b), dorsal (c), and ventral (d) views.

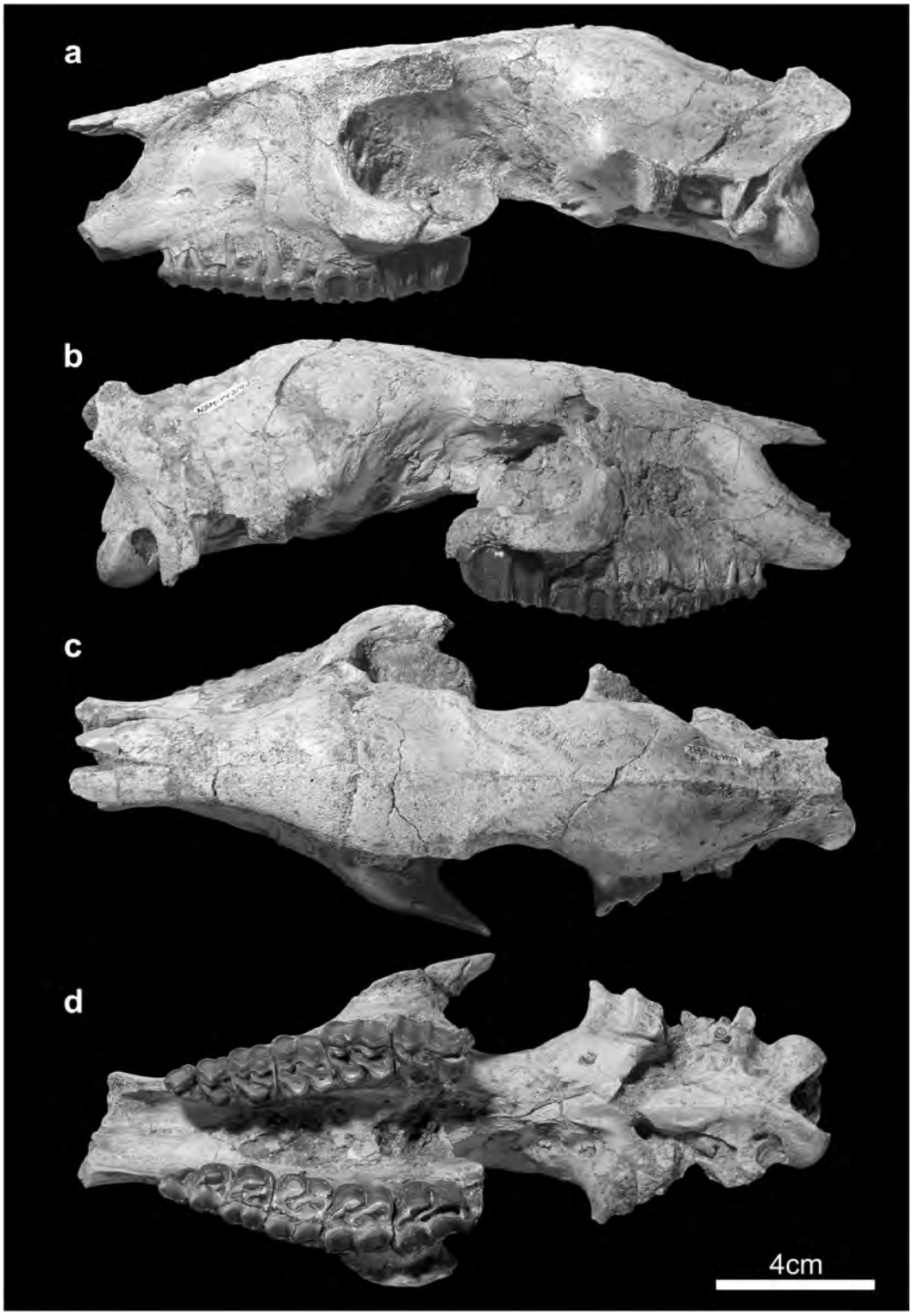

Fig. 48. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Baby. NMNS-PV 21432, incomplete skull with right and left P2–M3s in left lateral (a), right lateral (b), dorsal (c), and ventral (d) views.

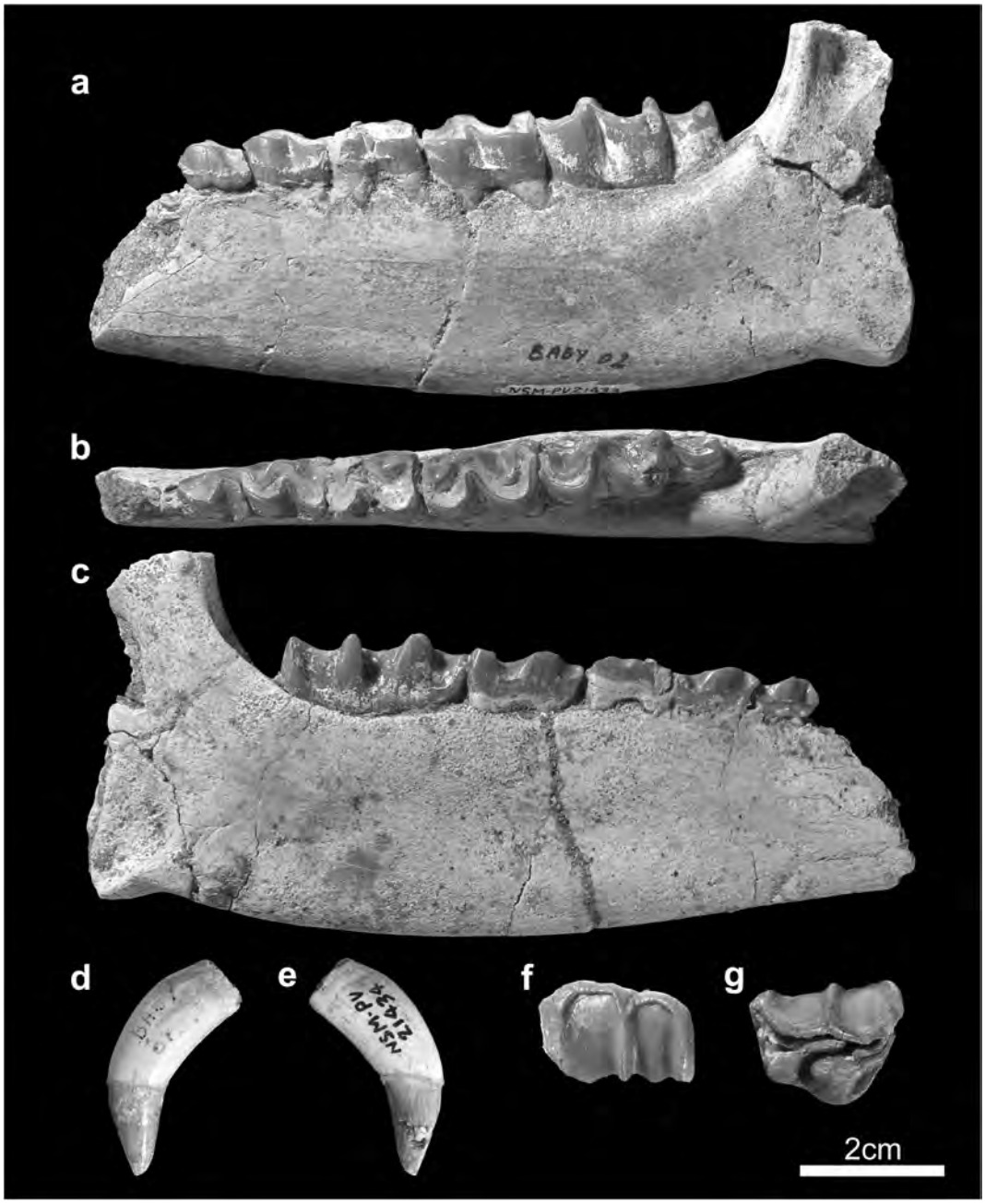

Fig. 49. *Plagiolophus* (*Paloplotherium*) *annectens* (Owen, 1848b) from Baby. NMNS-PV 21433, left mandibular fragment with p2 roots and p3–m3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21434, left C1 in labial (d) and lingual (e) views. NMNS-PV 21437, broken right M3 in labial (f) and occlusal (g) views.

Capraise d'Eymet preserves a large M1 (22.2 × 20.9 mm, Appendix 1), supporting the assignment to *P. major* (Fig. 50). The specimen is derived from a young individual and is partially restored at the roots of the anterior premolars. The incisors (I2 and I3) and canine are not fully erupted in NMNS-PV 21544. The post-canine teeth except for M1 can be referred to a DP2 and molariform DP3 and DP4

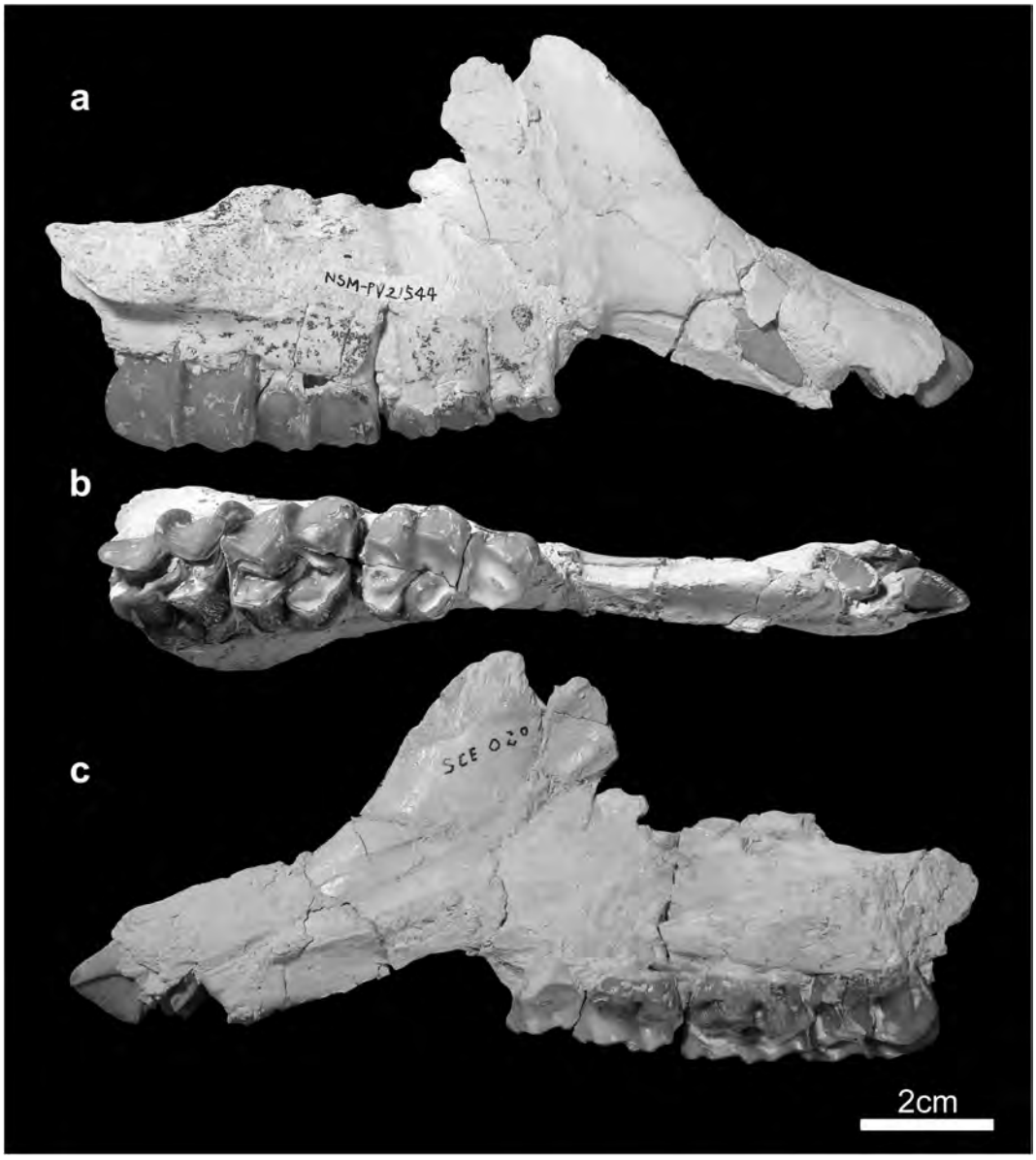

Fig. 50. *Plagiolophus* (*Paloplotherium*) *major* (Brunet and Jehenne, 1989) from St. Capraise d'Eymet. NMNS-PV 21544, right maxillary and premaxillary fragments with I2–3, C1, DP2–4, and M1 in labial (a), occlusal (b), and lingual (c) views.

based on the morphology and tooth wear, although the radiograph of NMNS-PV 21544 does not show any hint of the germs of premolars in the maxilla (Fig. 51).

***Plagiolophus* (*Paloplotherium*) *oweni* Depéret, 1917**

(Figs. 52–54)

Localities and Materials: Civrac de Blaye: NMNS-PV 21378, right mandibular fragment with p3–

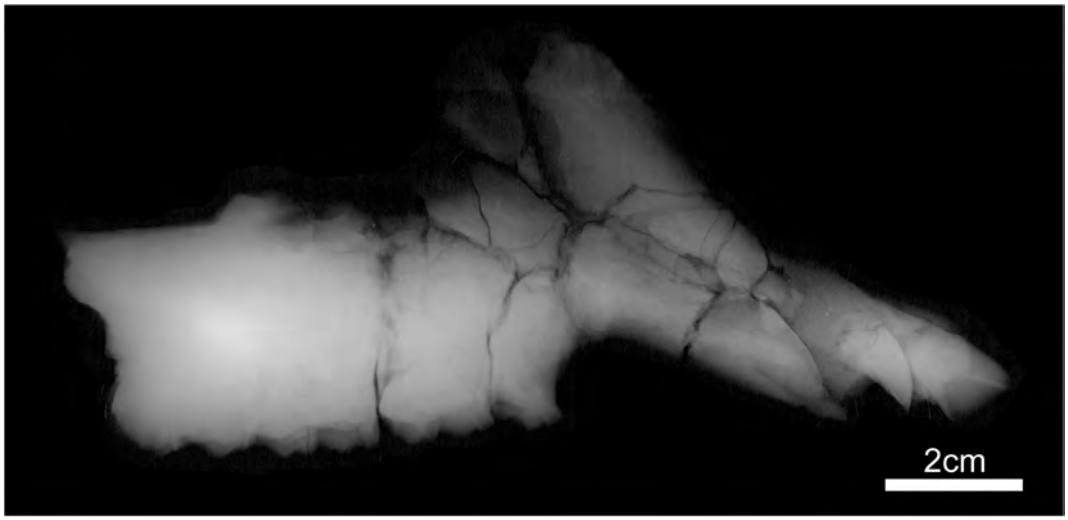

Fig. 51. The radiograph of NMNS-PV 21544, right maxillary and premaxillary fragments with I2–3, C1, DP2–4, and M1 of *Plagiolophus* (*Paloplotherium*) *major* (Brunet and Jehenne, 1989) from St. Capraise d'Eymet.

m3; 21379, right M3.

La Débruge: NMNS-PV 21496, anterior part of compressed skull with right I2, C1, P2–M3, left I1–3, C1, and P2–M3; 21497, left mandibular fragment with p3–m3; 21498, right M3.

Comments: *Plagiolophus oweni* is larger than *P. minor* and has a dental morphology intermediate between *P. minor* and earlier *P. annectens* (Remy, 2004). However, *P. oweni* cannot be readily distinguished from *P. annectens* in dental size, although the former has generally larger cheek teeth than in the latter (Remy, 2004). *P. oweni* has a long nasal and a short post-canine diastema as seen in *P. annectens*, but the skull of *P. oweni* is characterized by a shallower nasal incision and a slightly more anterior orbit than in *P. annectens*.

No cranial material is preserved in the specimens from Civrac de Blaye. NMNS-PV 21378 (Fig. 52a–c) has a deeper mandible and larger molars (47.9 mm in m1–3 length) than those of *P. minor.* The molars and mandible are similar to those of a larger species, *P. annectens* or *P. oweni.* However, *P. annectens* is supposed to be known only from MP 16 and 17, and has not been recorded from the younger Civrac de Blaye, MP 18 (Remy, 2004). The M3 from Civrac de Blaye (Fig. 52d–f, NMNS-PV 21379) is also larger than that of *P. minor* and is closely similar to the M3 of the *P. oweni* skull from La Débruge (Fig. 53, NMNS-PV 21496).

Compared to the specimens of *P. annectens* and *P. oweni* housed in the collections of the Université des Sciences et Techniques du Languedoc, Montpellier (FMO), the upper dental characters of NMNS-PV 21496 are actually close to either those of *P. oweni* from Faveirol (Grès de Célas, FMO FAV-1) or of *P. annectens* from Euzèt (FMO EUZ 5616–5618). However, NMNS-PV 21496 has the definitive shallow nasal incision of *P. oweni* (Fig. 53), distinguishable from *P. annectens*. In NMNS-PV 21496, robust canines, I2 larger than I3, and cementum layers on labial surfaces of M1–3 are also preserved. NMNS-PV 21498 from La Débruge (Fig. 54d, e), a right M3 with a cementum layer on labial surface, is also similar to that of NMNS-PV 21496.

The mandibular material from La Débruge (Fig. 54a–c, NMNS-PV 21497) has a smaller p3 and slightly more hypsodont cheek teeth with weak lingual cingulid, compared to those of Euzèt *P. annectens*. The teeth of NMNS-PV 21497 are identical with those of MNHN LDB-397 and 617 from La Débruge (collections of Muséum National d'Histoire Naturelle, Paris), which belong to the type series

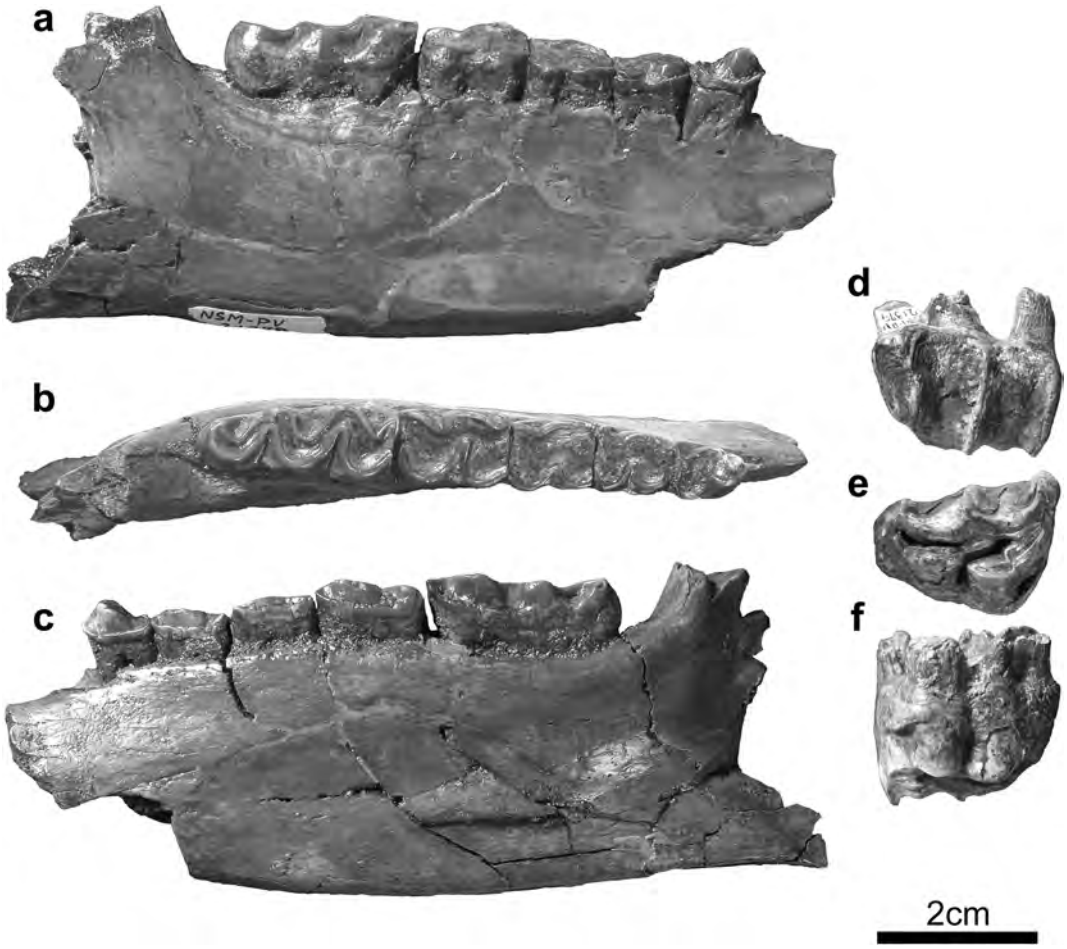

Fig. 52. *Plagiolophus* (*Paloplotherium*) *oweni* Depéret, 1917 from Civrac de Blaye. NMNS-PV 21378, right mandibular fragment with p3–m3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21379, right M3 in labial (d), occlusal (e), and lingual (f) views.

of *P. oweni* (Remy, 2004).

Subgenus *Plagiolophus* Pomel, 1847a
***Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804)**
(Figs. 55–63)

Localities and Materials: La Débruge: NMNS-PV 21500, anterior part of mandible with right i1–3, c1, left i1 root, and i2; 21501, right mandible with c1, p2–m3, and left symphysial part on matrix; 21502, right mandible with p2–m3 on matrix; 21503, left mandible with c1, p2–m3, and right symphysial part on matrix; 21504, left mandible with p2–m3 on matrix; 21505, left mandible with p2–m3; 21506, right and left mandibles with right c1 root, p4–m3, left c1 root, and p3–m3; 21507, incomplete skull with right P2–M3, left P2–3, and M1–3; 21508, left maxillary fragment with broken P4 and M1–3; 21509, right maxillary fragment with P2–M3 on matrix; 21510, possible right i1; 21511, right astragalus; 21512, left mandibular fragment with m2–3; 21513, right mandibular fragment with broken

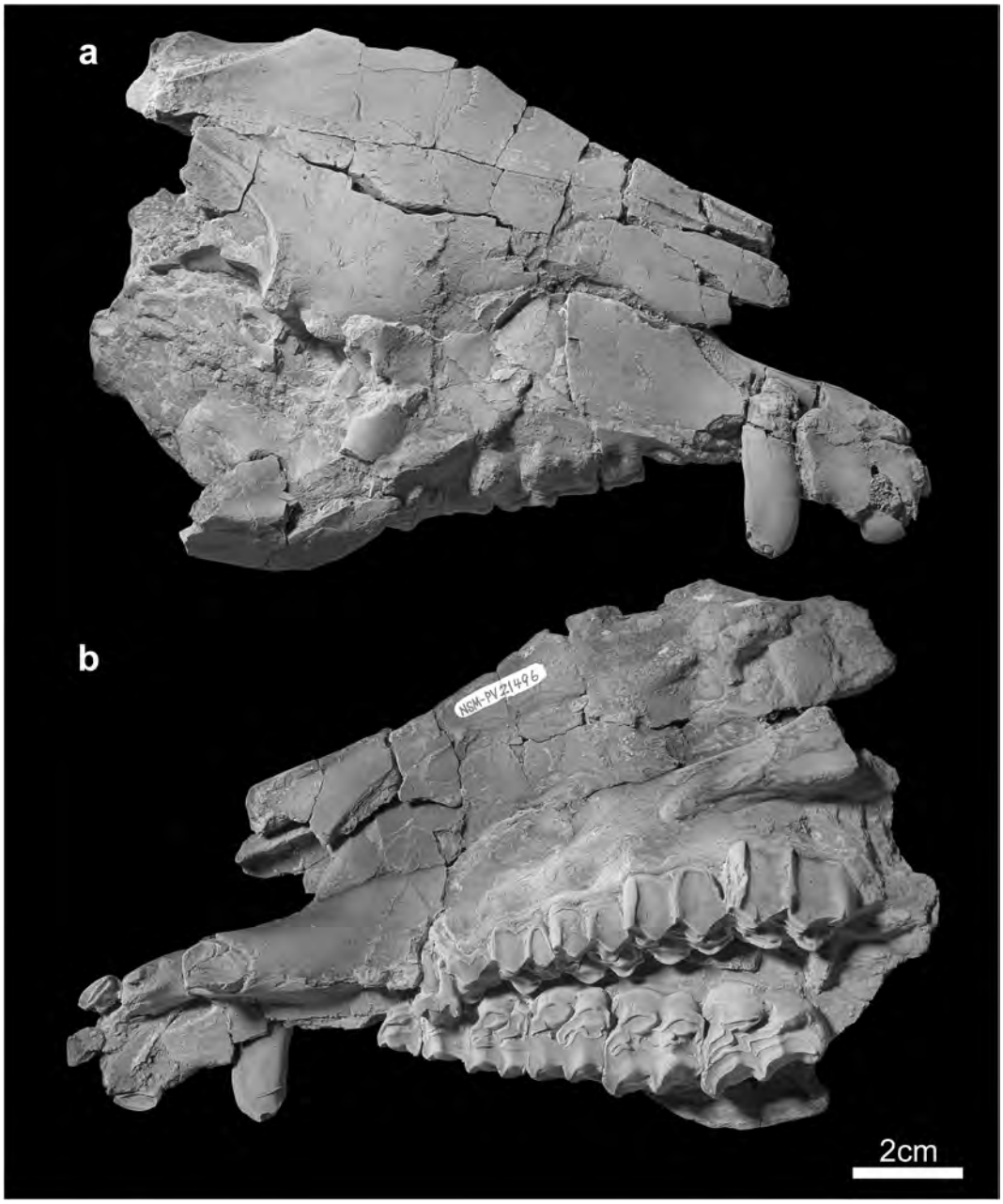

Fig. 53. *Plagiolophus* (*Paloplotherium*) *oweni* Depéret, 1917 from La Débruge. NMNS-PV 21496, anterior part of compressed skull with right I2, C1, P2–M3, left I1–3, C1, and P2–M3 in dorsal (a) and ventral (b) views.

m1 and m2–3; 21514, broken right M2; 21515, possible left maxillary fragment with broken C1 and isolated right P3; 21517, possible left C1; 21520, left maxillary fragment with possible DP1 and DP2–4.

St. Capraise d'Eymet: NMNS-PV 21532, left maxillary fragment with DP3–4 on matrix; 21547, right mandibular fragment with m3; 21549, left maxillary fragment with P2–M3; 21550, broken left M2; 21551, left mandible with p2 root, p3–m3, and right symphysial part with c1; 21552, left mandibular fragment with p3–m2 and unerupted m3; 21553, possible right I1; 21554, right c1; 21555, possi-

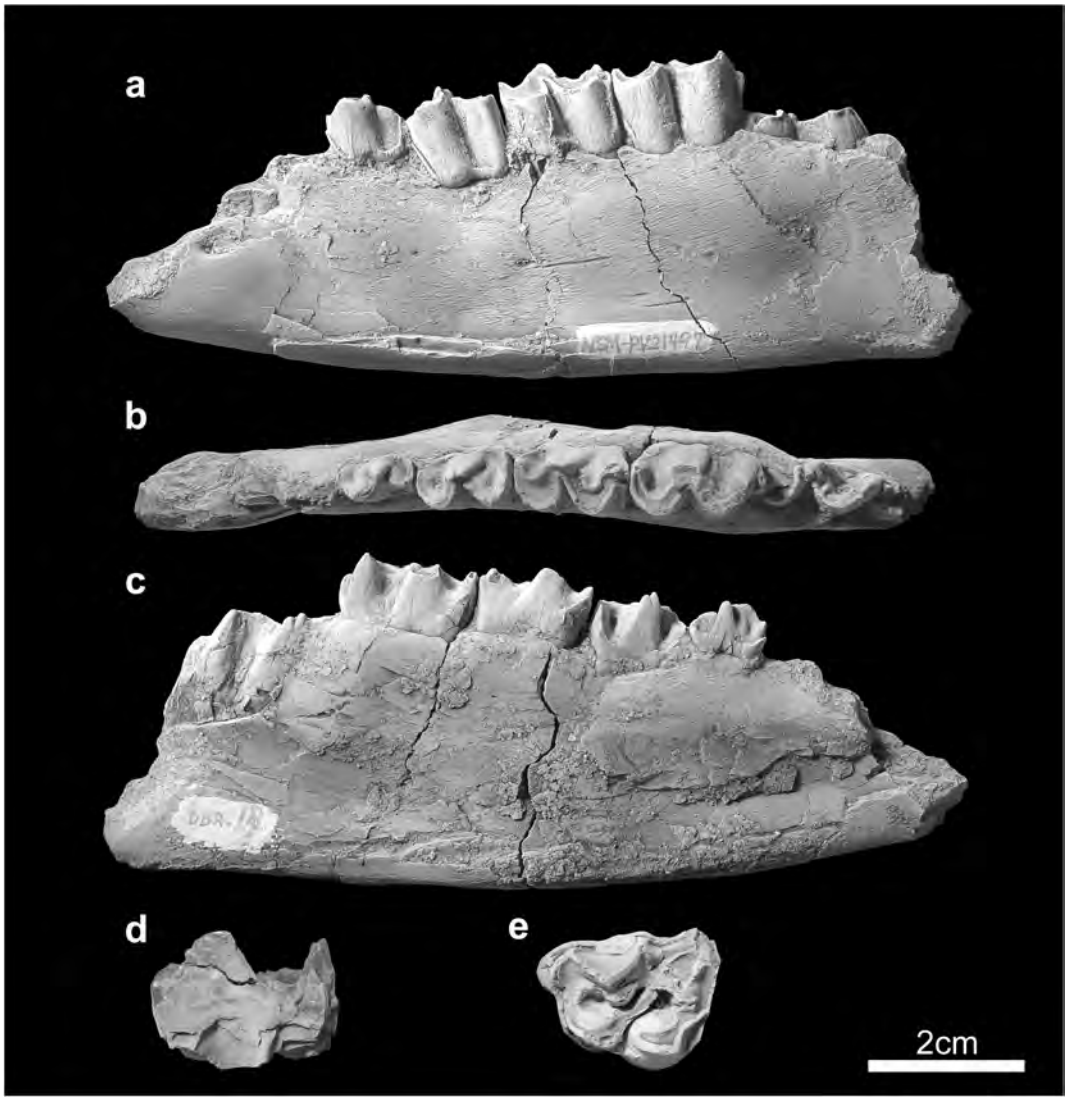

Fig. 54. *Plagiolophus* (*Paloplotherium*) *oweni* Depéret, 1917 from La Débruge. NMNS-PV 21497, left mandibular fragment with p3–m3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21498, right M3 in labial (d) and occlusal (e) views.

ble right c1.

Comments: *Plagiolophus minor* is well-documented and is the most widely distributed species of the genus; *P. minor* has been recorded from MP 18 to MP 22 (Priabonian–Rupelian) and has been described from various Eocene localities in France, Switzerland, England, and Spain (Remy, 2004). The specimens of *P. minor* cataloged here, except for a few not fully prepared (NMNS-PV 21501, 21503, and 21504), clearly show the typical dental morphologies of the species.

According to Remy (2004), *Plagiolophus minor* is the smallest species of the genus (57–73 mm in P2–M3 length, 60–70 mm in p2–m3 length). The post-canine diastemata between C1 and P2 and between c1 and p2 vary within 25–45 % for P2–M3 length and 36–48% for p2–m3 length, respectively; the ratios of diastemata are greater than in *P. annectens* (Remy, 2004).

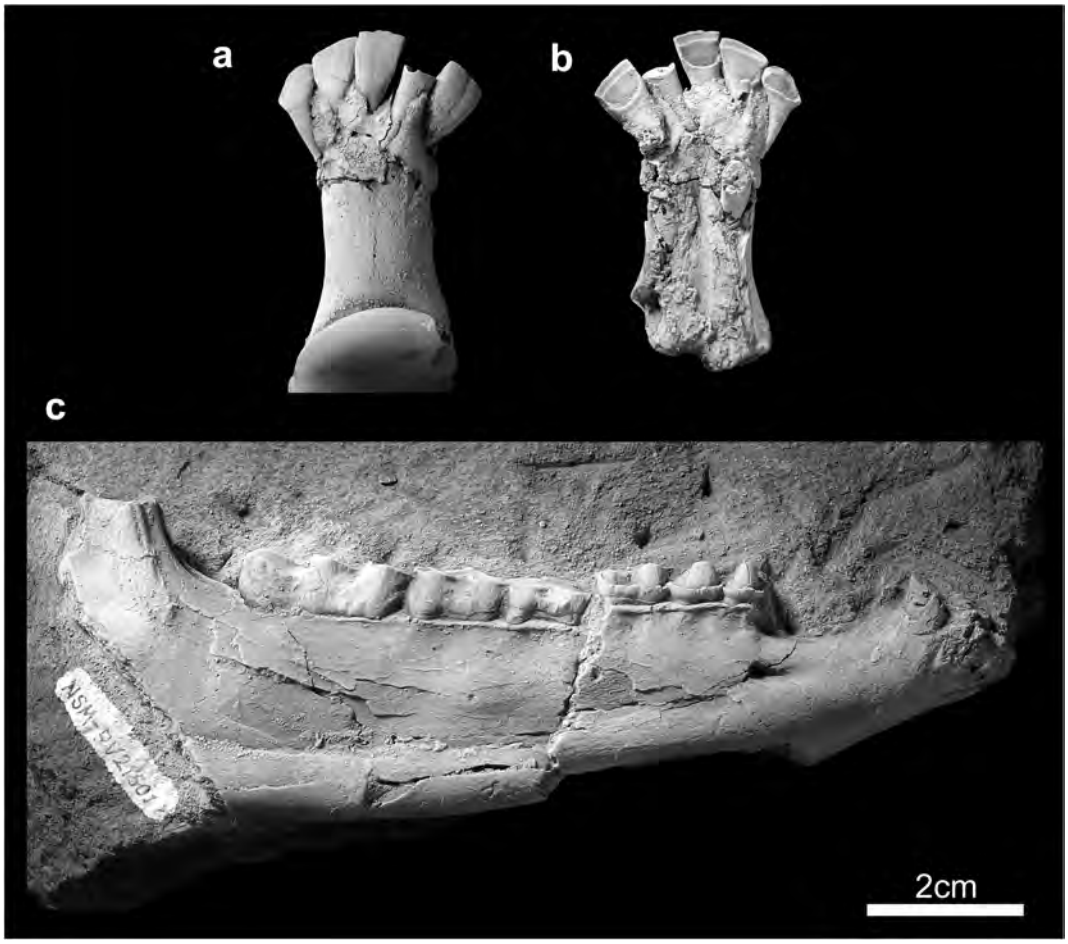

Fig. 55. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21500, anterior extremity of mandible with right i1–3, c1, left i1 root, and i2 in ventral (a) and occlusal (b) views. NMNS-PV 21501, right mandible with c1, p2–m3, and left symphysial part on matrix (c) in labial view.

The mandibles (Figs. 55–58, NMNS-PV 21500–21506) from La Débruge demonstrate the small size of this species (61.7–67.0 mm in p2–m3 length, Appendix 1) and show minor variations in mandibular depth (22.7–26.2 mm, Appendix 1). NMNS-PV 21500 is an anterior part of mandible showing detailed features of the canine and incisors of *P. minor* (Fig. 55a, b). The canine is relatively small in NMNS-PV 21500 and 21501 but is larger in NMNS-PV 21503 and 21506, suggesting that *P. minor* was sexually dimorphic (Appendix 1).

The isolated incisors and canines from La Débruge and St. Capraise d'Eymet are also referable to *P. minor* based on their small size (Figs. 60 g, h, 61j, k, and 63 g–k; NMNS-PV 21510, 21517, and 21553–21555). NMNS-PV 21555 (Fig. 63k) is a small caniniform tooth with a posteriorly curved root which differs from the more robust canine, NMNS-PV 21554 (Fig. 63i, j). These isolated upper and lower canines can be identified by the presence of wear facet on the anterior and posterior edges of crown, respectively.

The lower cheek teeth of NMNS-PV 21551 from St. Capraise d'Eymet (Fig. 63a–c) are almost identical with those of NMNS-PV 21547 and 21552 from the same locality (Figs. 62d–f and 63d–f). However, NMNS-PV 21551 has a slightly longer length of p2–m3 (ca. 73.8 mm, Appendix 1) exceed-

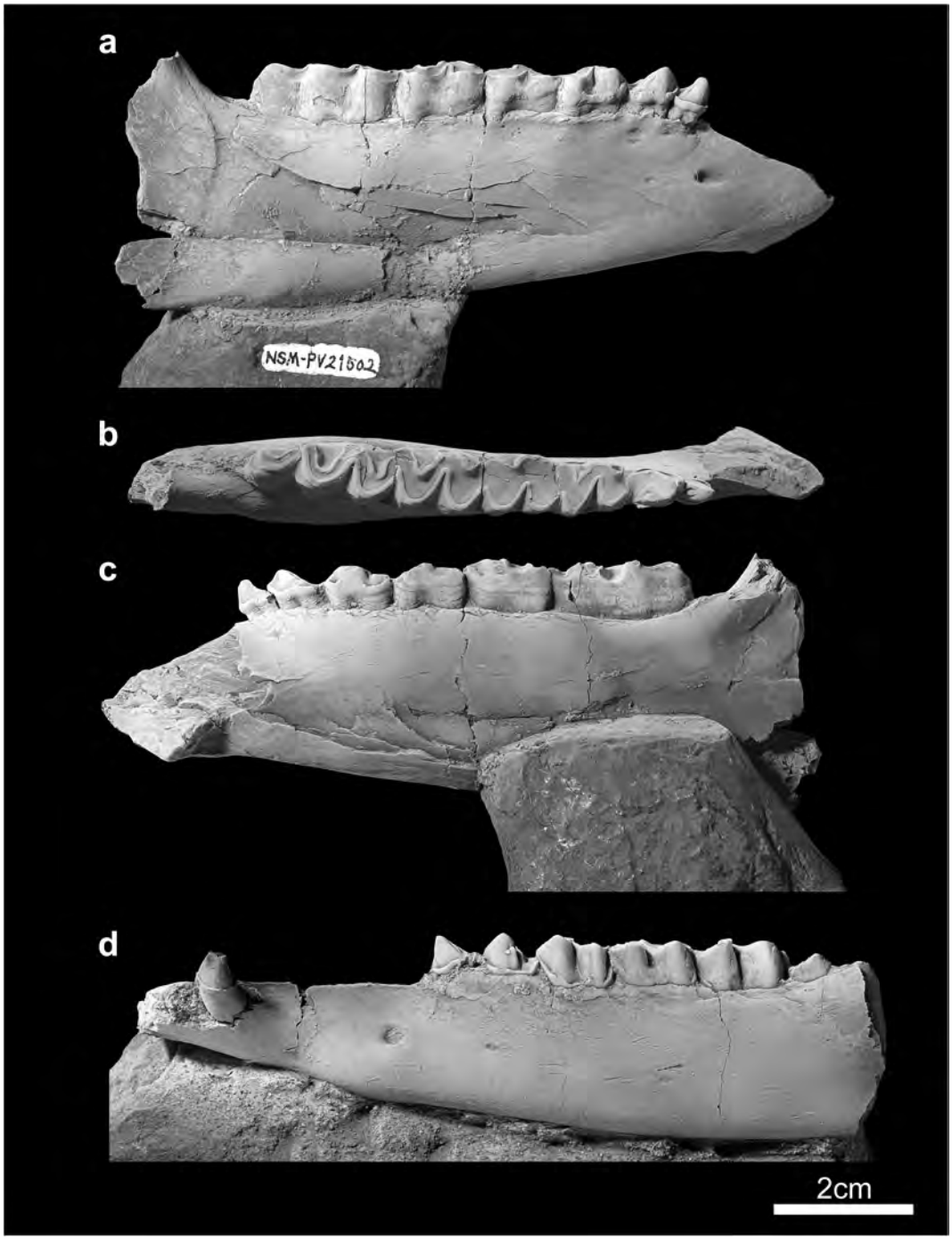

Fig. 56. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21502, right mandible with p2–m3 on matrix in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21503, left mandible with c1, p2–m3, and a right symphysial part on matrix (d) in labial view.

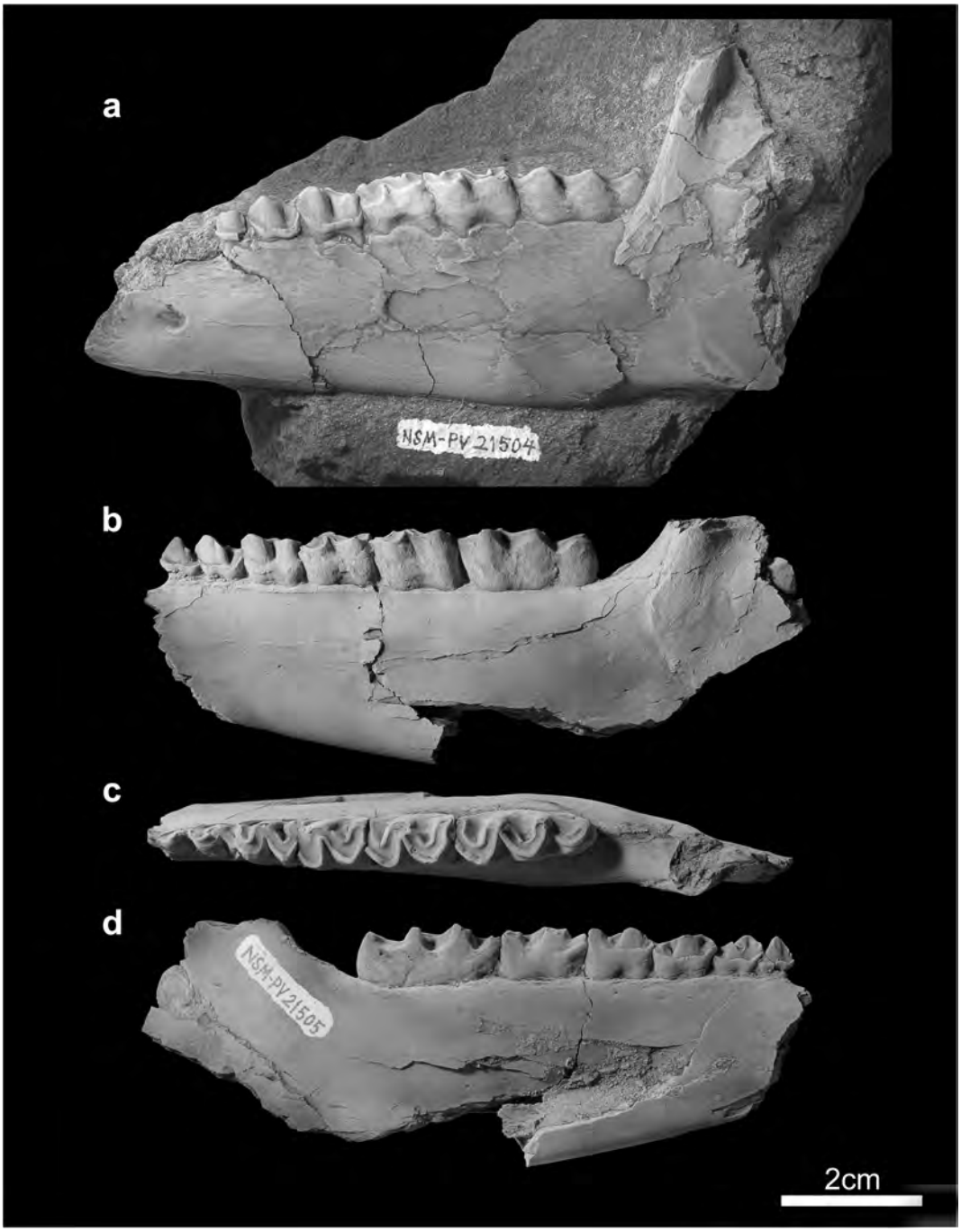

Fig. 57. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21504, left mandible with p2–m3 (a) on matrix in labial view. NMNS-PV 21505, left mandible with p2–m3 in labial (b), occlusal (c), and lingual (d) views.

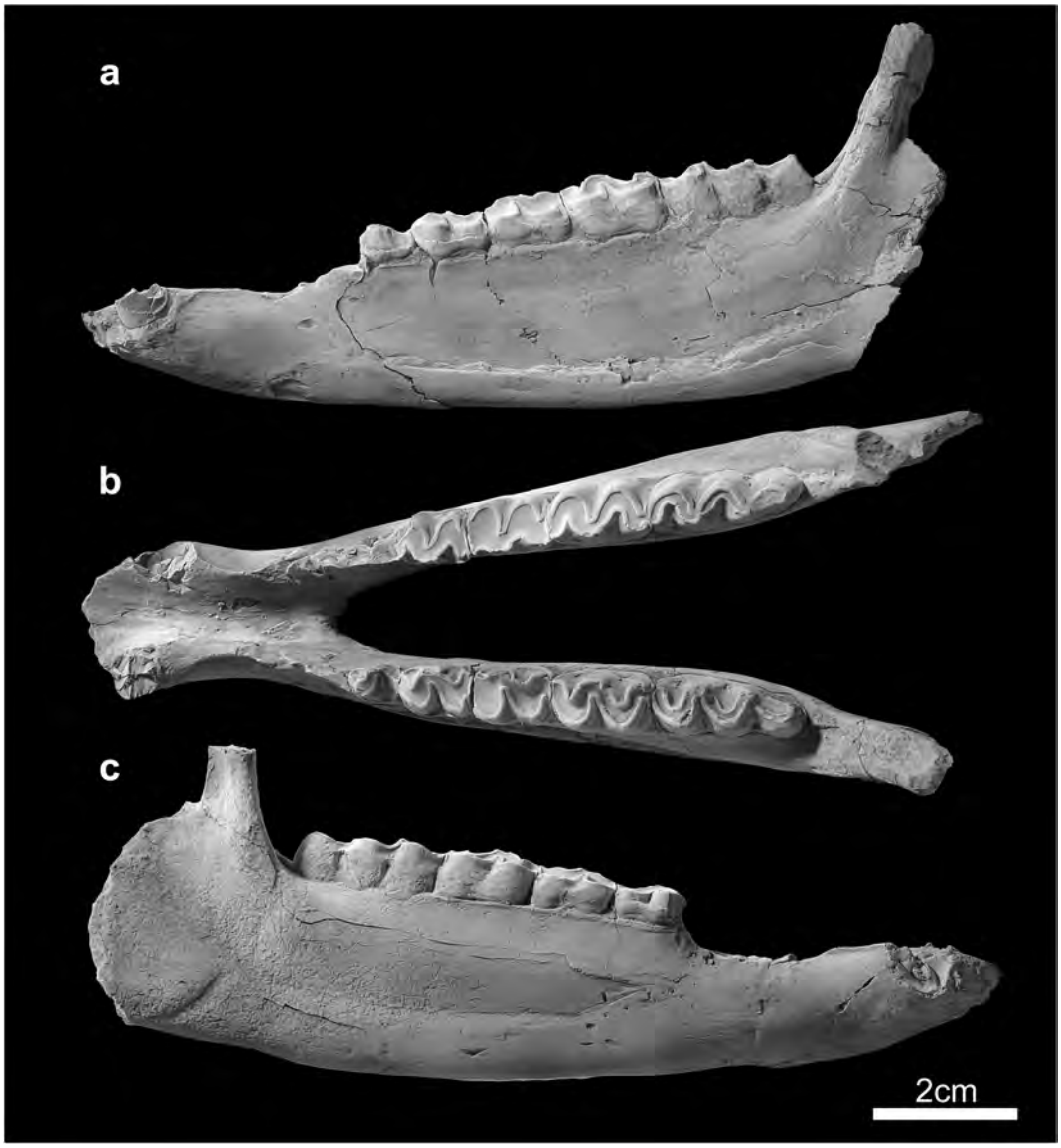

Fig. 58. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21506, right and left mandibles with right c1 root, p4–m3, left c1 root, and p3–m3 in left lateral (a), occlusal (b), and right lateral (c) views.

ing the observed range of *P. minor* (approximately 60–70 mm) provided by Remy (2004). Besides, NMNS-PV 21551 preserves a slender p3 and the alveoli for a p1; p1 is normally absent but is likely present in young individuals of *P. minor* (p1 disappeared early during life; Remy, 2004). Despite these differences from the La Débruge form mentioned above, the St. Capraise d'Eymet specimens are most likely referable to *P. minor*.

The anterior skull morphology is shown in NMNS-PV 21507 from La Débruge (Fig. 59), despite the deformation of specimen (dorsoventral compression). The nasals in NMNS-PV 21507 are expanded anteriorly, possibly beyond the position of canine. The P2–M2 length of NMNS-PV 21507 is compatible with p2–m3 lengths of NMNS-PV 21504 and 21505 from the same locality. The M2–3

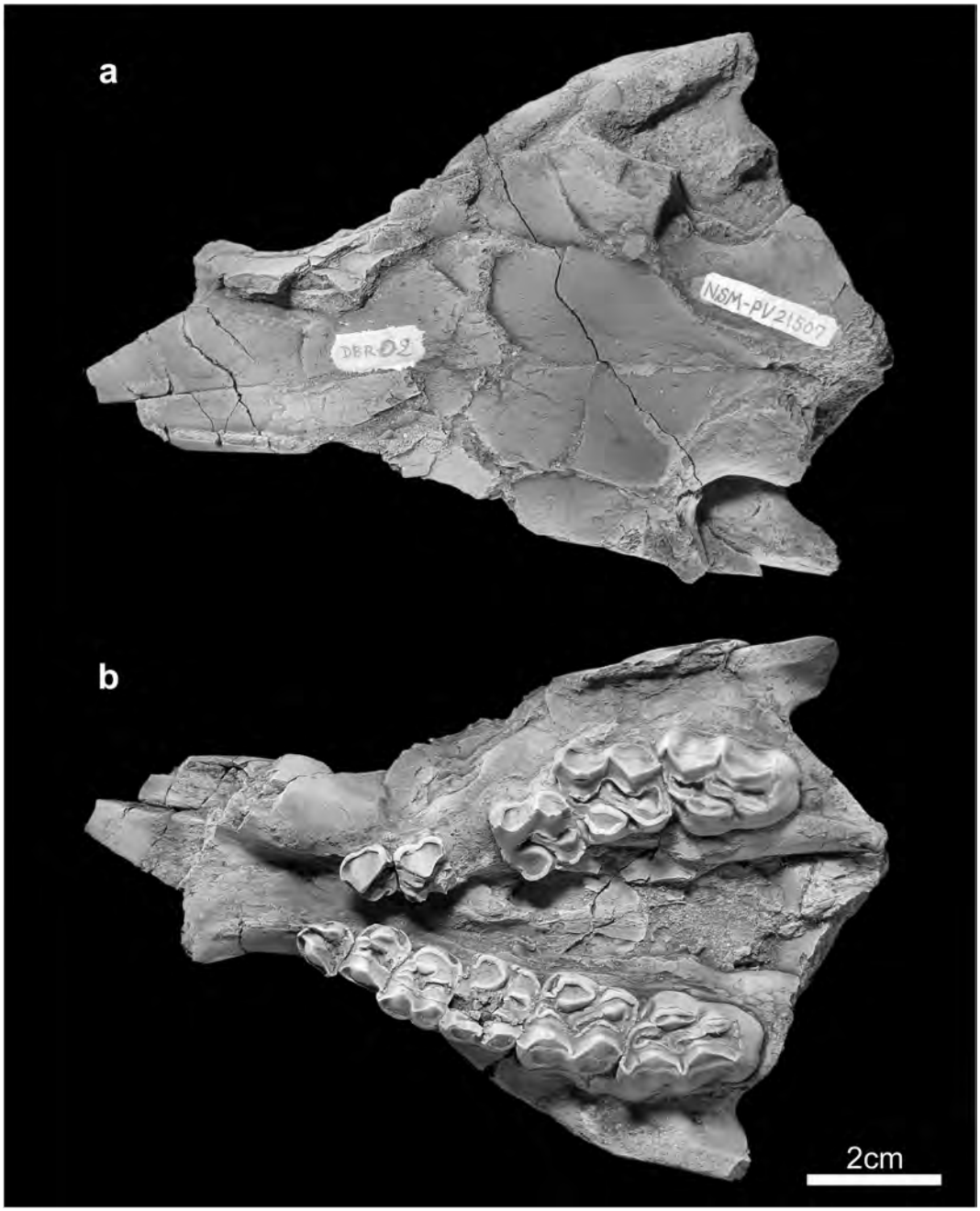

Fig. 59. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21507, incomplete skull with right P2–M3, left P2–3, and M1–3 in dorsal (a) and occlusal (b) views.

in NMNS-PV 21507 preserve cementum layers on the labial surfaces as do the upper molars of NMNS-PV 21508 and 21509 (Fig. 60a–f). The M2s of *P. minor* cataloged here have weaker parastyles than those of *P. annectens*, which are markedly expanded labially.

NMNS-PV 21509 displays a unique occlusal pattern of the molariform premolars (P2–4) unlike in

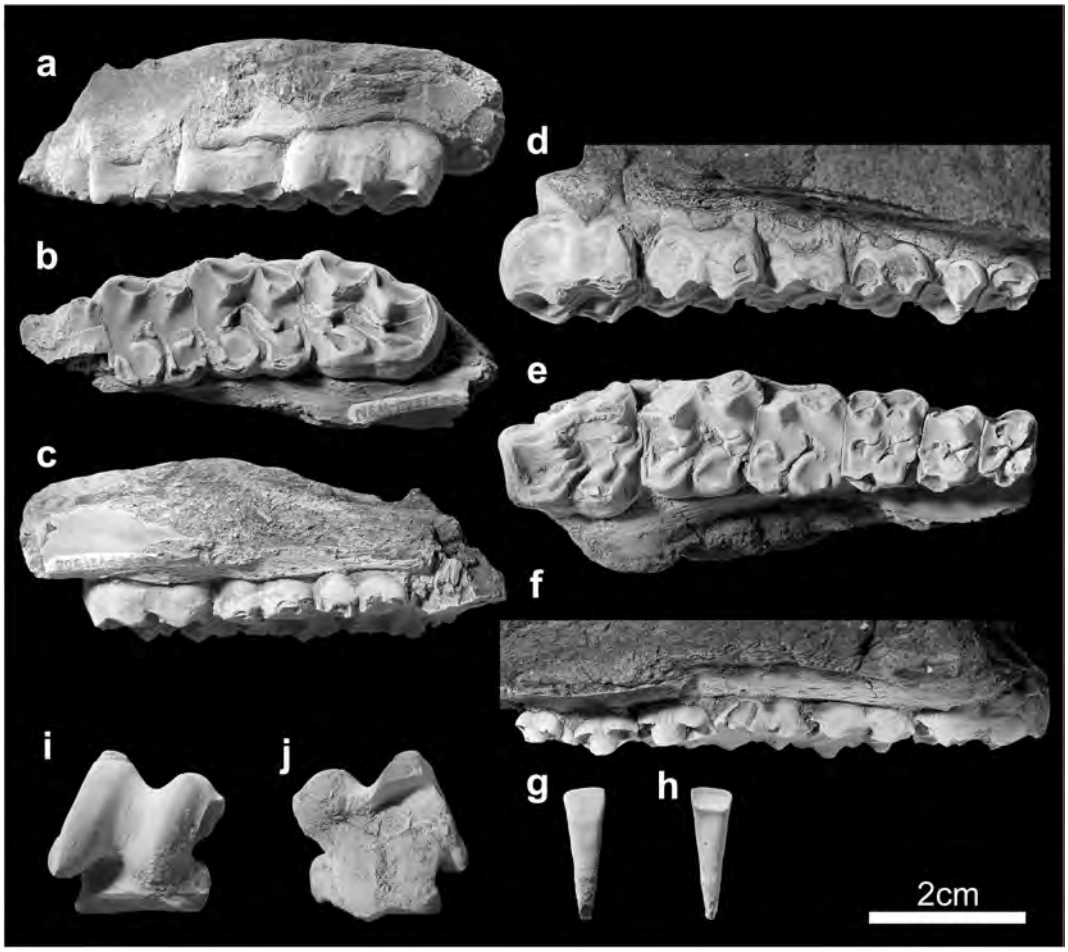

Fig. 60. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21508, left maxillary fragment with broken P4 and M1–3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21509, right maxillary fragment with P2–M3 on matrix in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21510, possible right i1 in labial (g) and lingual (h) views. NMNS-PV 21511, right astragalus in dorsal (i) and plantar (j) views.

NMNS-PV 21507 (Figs. 59b and 60d–f); the protocones are constricted anteroposteriorly, shelf-like lingual cingula are present posterior to the protocones, and P2 possesses a stout metaloph-like crest extending to the posterolingual side of the paracone. The premolar protocones in the St. Capraise d'Eymet specimens are never constricted unlike in NMNS-PV 21509 (Fig. 62h, NMNS-PV 21549). However, the differences in premolars seem to be a general variation of *P. minor* (see also Remy, 2004).

The deciduous upper premolars are preserved in NMNS-PV 21520 and 21532 (Figs. 61l, m and 62a–c) and can be easily distinguished from the permanent premolars. DP2 is narrow anteroposteriorly and bears large para- and metastyles, and DP4 is narrow labiolingually. The jugal position also supports the tooth identification in NMNS-PV 21520.

Among the material referred to *P. minor* is a right astragalus, NMNS-PV 21511 (Fig. 60i, j), which is smaller than those of other *Plagiolophus* species (cf. the dimensions of astragali in Remy, 2000).

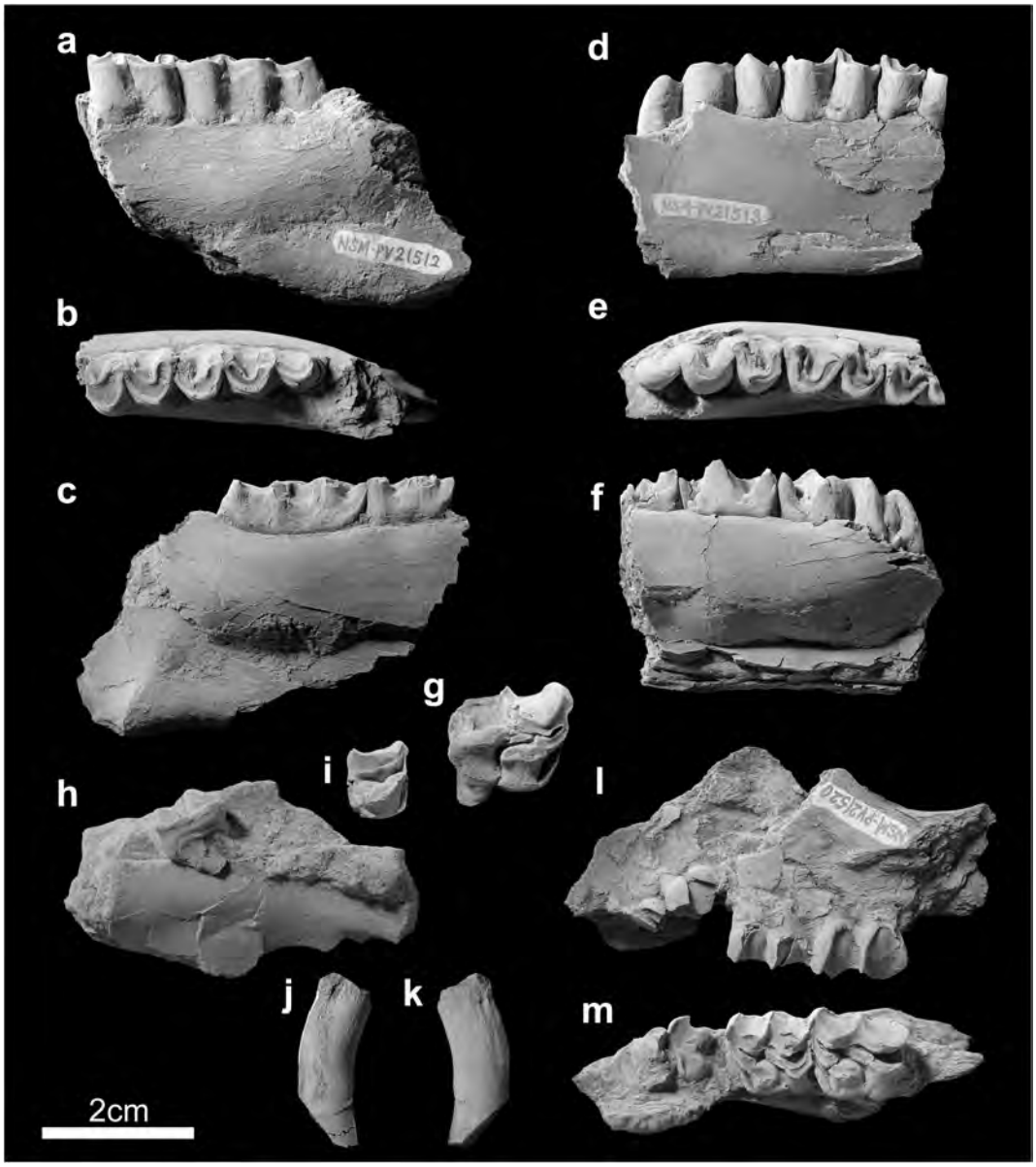

Fig. 61. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from La Débruge. NMNS-PV 21512, left mandibular fragment with m2–3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21513, right mandibular fragment with broken m1 and m2–3 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21514, a broken right M2 (g) in occlusal view. NMNS-PV 21515, possible left maxillary fragment with broken C1 (h) and isolated right P3 (i). NMNS-PV 21517, possible left C1 in labial (j) and lingual (k) views. NMNS-PV 21520, left maxillary fragment with possible DP1 and DP2–4 in labial (l) and occlusal (m) views.

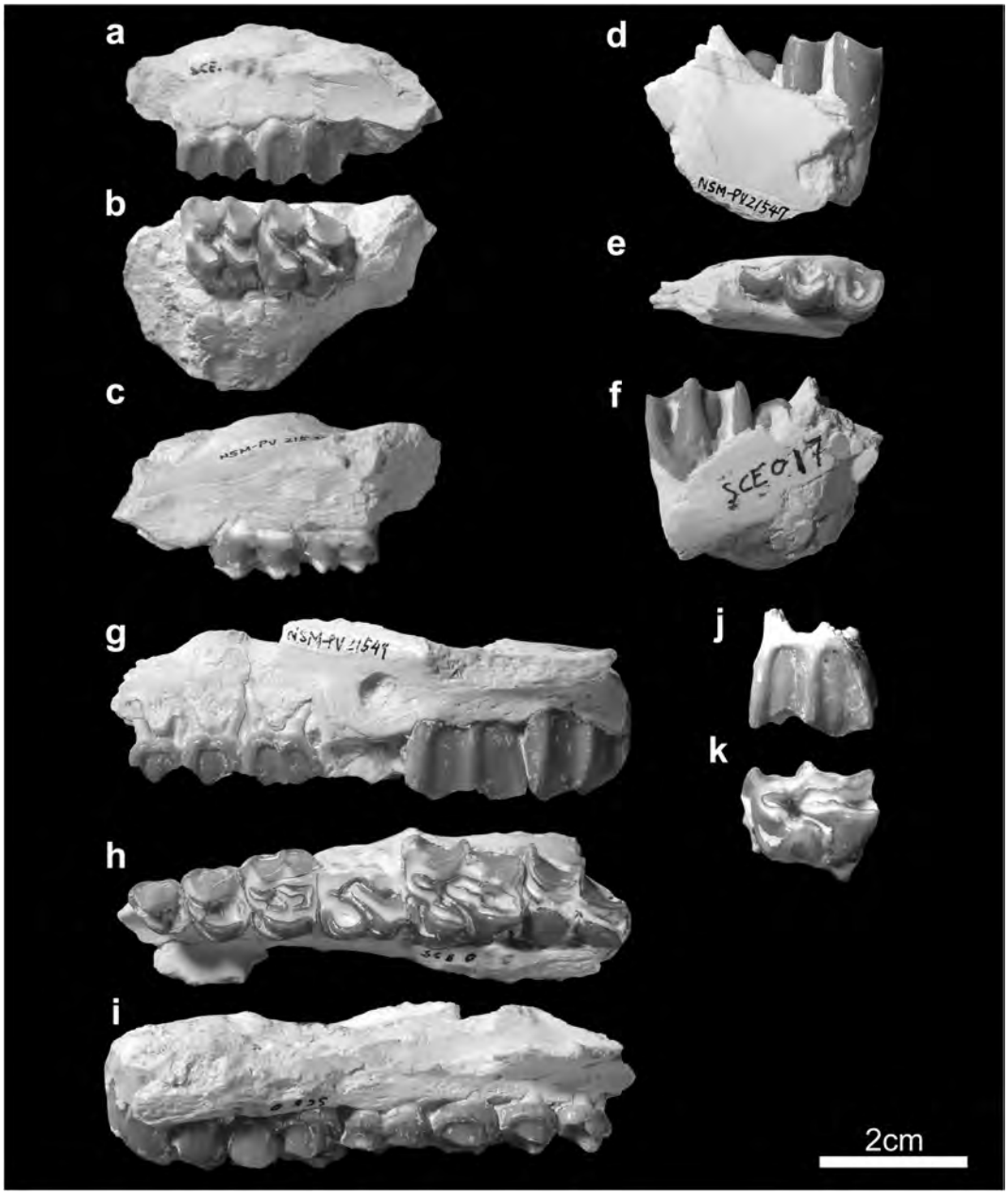

Fig. 62. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from St. Capraise d'Eymet. NMNS-PV 21532, left maxillary fragment with DP3–4 on matrix in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21547, right mandibular fragment with m3 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21549, left maxillary fragment with P2–M3 in labial (g), occlusal (h), and lingual (i) views. NMNS-PV 21550, broken left M2 in labial (j) and occlusal (k) views.

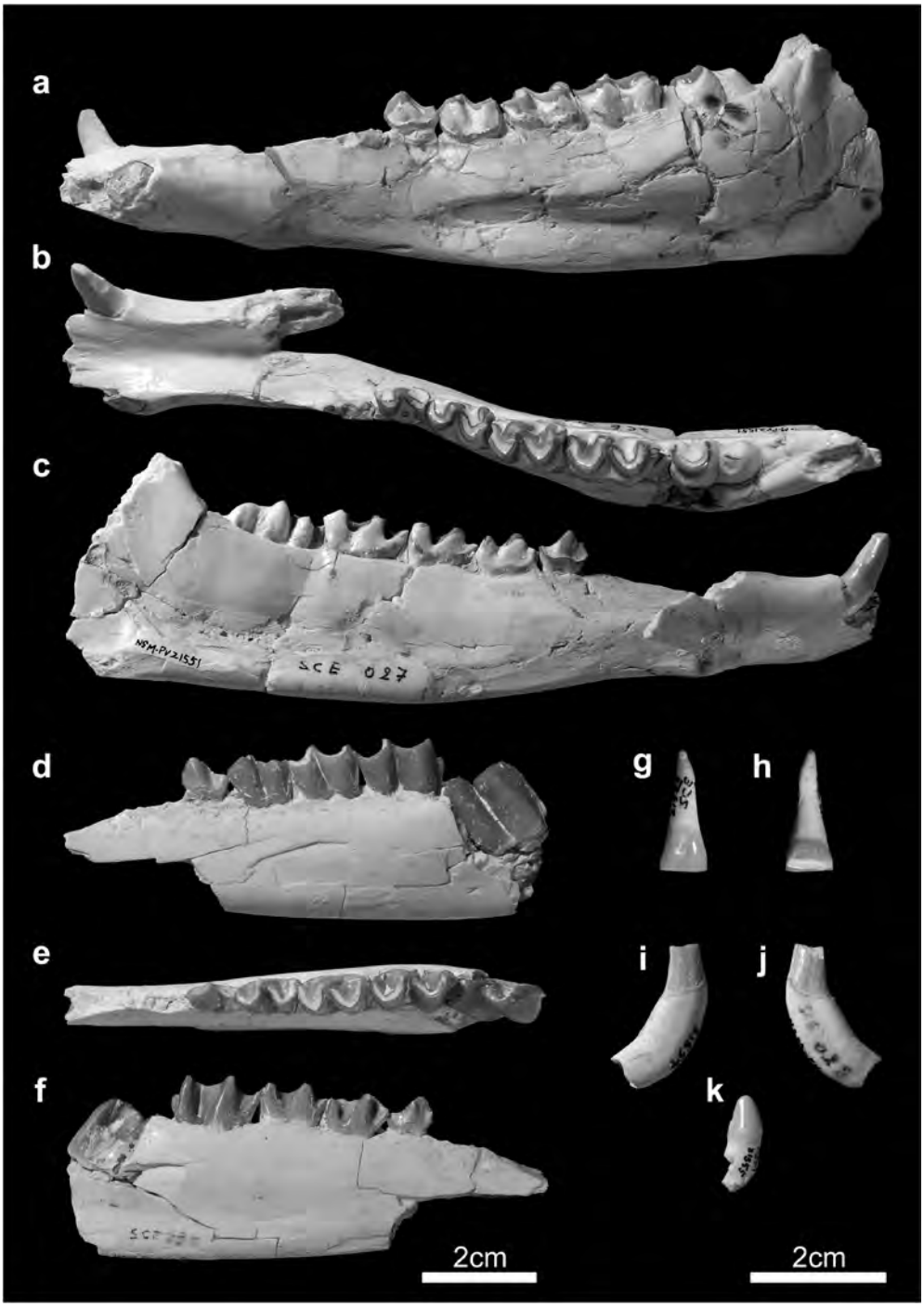

Fig. 63. *Plagiolophus* (*Plagiolophus*) *minor* (Cuvier, 1804) from St. Capraise d'Eymet. NMNS-PV 21551, left mandible with p2 root, p3–m3, and a right symphysial part with c1 in left lateral (a), occlusal (b), and left lingual (c) views. NMNS-PV 21552, left mandibular fragment with p3–m2 and unerupted m3 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21553, possible right I1 in labial (g) and lingual (h) views. NMNS-PV 21554, right c1 in labial (i) and lingual (j) views. NMNS-PV 21555, possible right c1 (k) in labial view. Scale bar for g–k is shown at bottom right.

***Plagiolophus* sp.**
(Fig. 64)

Localities and Materials: Le Bretou: NMNS-PV 21199, possible left p4 or m1; 21200, possible right C1.

Robiac: NMNS-PV 21346, left p4 or m1.

Euzèt les Bains: NMNS-PV 21411, possible left c1; 21418, right I2 or left i2.

La Débruge: NMNS-PV 21518, possible right I3; 21519, possible right I2 or left i2.

St. Capraise d'Eymet: NMNS-PV 21548, right M1; 21557, left astragalus; 21558, left astragalus.

Comments: All of the specimens cataloged here are isolated. The isolated teeth from Le Bretou are comparable to those of *P. annectens* or *P. mamertensis* from Robiac in size and morphology (Fig. 64a–e, NMNS-PV 21199 and 21200). The upper canine (Fig. 64d, e) has a faint wear facet on the anterior

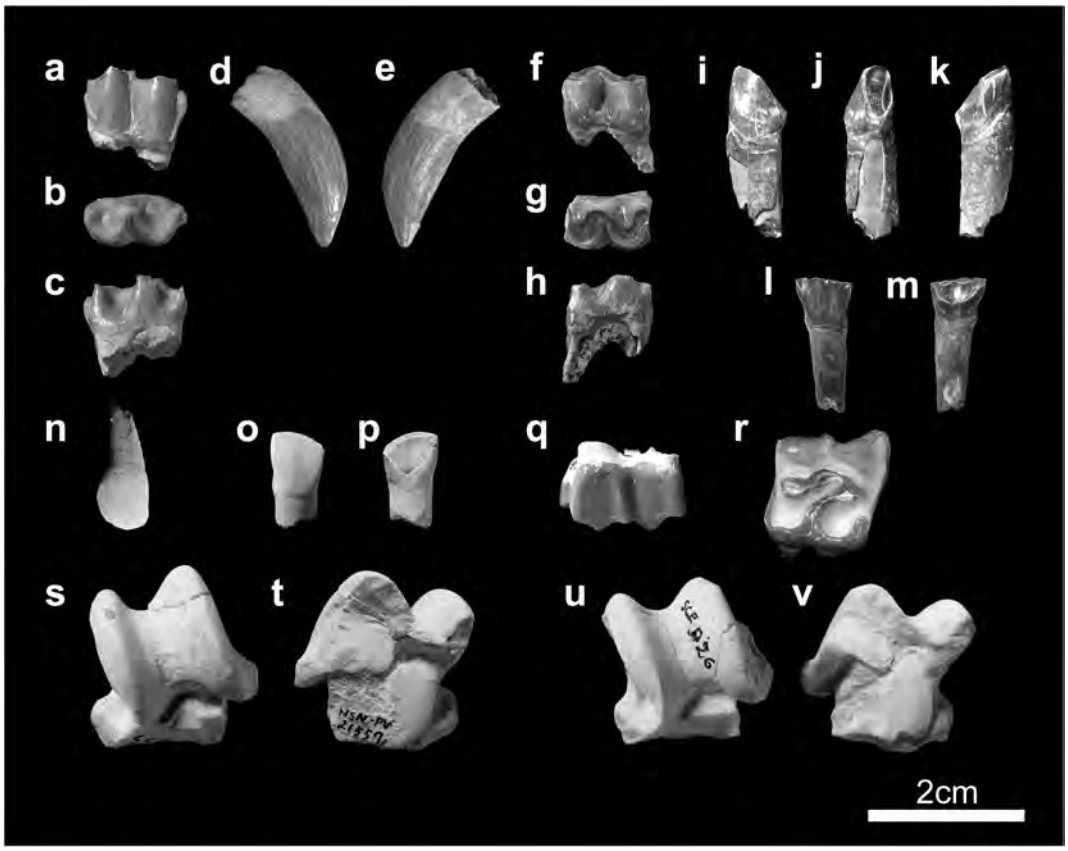

Fig. 64. *Plagiolophus* sp. from Le Bretou (NMNS-PV 21199 and 21200), Robiac (NMNS-PV 21346), Euzèt les Bains (NMNS-PV 21411 and 21418), La Débruge (NMNS-PV 21518 and 21519), and St. Capraise d'Eymet (NMNS-PV 21548, 21557, and 21558). NMNS-PV 21199, possible left p4 or m1 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21200, possible right C1 in labial (d) and lingual (e) views. NMNS-PV 21346, left p4 or m1 in labial (f), occlusal (g), and lingual (h) views. NMNS-PV 21411, possible left c1 in labial (i), distal (j), and lingual (k) views. NMNS-PV 21418, right I2 or left i2 in labial (l) and lingual (m) views. NMNS-PV 21518, possible right I3 (n) in labial view. NMNS-PV 21519, possible right I2 or left i2 in labial (o) and lingual (p) views. NMNS-PV 21548, right M1 in labial (q) and occlusal (r) views. NMNS-PV 21557, left astragalus in dorsal (s) and plantar (t) views. NMNS-PV 21558, left astragalus in dorsal (u) and plantar (v) views.

edge of crown. NMNS-PV 21346 from Robiac (Fig. 64f–h) has a broad talonid and is too small to identify with that of *P. annectens*, but it is similar to that of *P. minor* in size. NMNS-PV 21411 (Fig. 64i–k) has a stout root and a distinct wear facet as seen in lower canines of *Plagiolophus*. The incisors from Euzèt les Bains and La Débruge (Fig. 64l–p; NMNS-PV 21418, 21518, and 21519) are typical incisors of *Plagiolophus*. NMNS-PV 21418 and 21519 are distinguished from I3 and i3, which are distinct asymmetrical; the former (NMNS-PV 21418) might be a left i2 because it has a thin labiolingual crown, while the latter (NMNS-PV 21519) has a stout root which is more robust than that of *P. minor* (see also Fig. 55, NMNS-PV 21500). NMNS-PV 21518 (Fig. 64n) is similar to the right I3 in having an asymmetrical outline of crown and a thin distal edge. The m1 from St. Capraise d'Eymet (Fig. 64q, r; NMNS-PV 21548) is smaller than that of *P. major* and is slightly larger than that of *P. minor*. The astragali from St. Capraise d'Eymet (Fig. 64s–v, NMNS-PV 21557 and 21558) are larger compared to those of *P. minor* (Appendix 1).

Cf. *Plagiolophus* sp.

(Fig. 65)

Localities and Materials: Le Bretou: NMNS-PV 21198, right mandibular fragment with p4.

Baby: NMNS-PV 21435, proximal half of left femur, thoracic and lumbar vertebrae, patella, distal fragment of possible right humerus, tooth fragment, and unidentified bone fragment; NMNS-PV 21436, right m1 or m2; 21438, right mandibular fragment with possible dp3 and broken dp4.

La Débruge: NMNS-PV 21516, upper molar fragment.

St. Capraise d'Eymet: NMNS-PV 21545, right P2.

Comments: All of these specimens are remains of palaeotheriids, probably referable to *Plagiolophus*. The mandibular fragment from Le Bretou (Fig. 65a–c, NMNS-PV 21198) preserves a molariform tooth similar to p4 of *P. annectens*, but the mandible is too shallow (approximately half the depth of *P. annectens*). Although the postcranial material from Baby (Fig. 65d–g, NMNS-PV 21435) might not be from a single individual, the femur possesses a well developed third trochanter and a greater trochanter projecting high above the proximal articular head. The lower molar with no root from Baby (Fig. 65h–j, NMNS-PV 21436) appears to be at an immature stage. The mandibular fragment from Baby (Fig. 65k–m, NMNS-PV 21438) preserves a possible dp3 bearing a small paraconid and metastylid. NMNS-PV 21545 (Fig. 65o, p) is a unique P2 without labial cingulum, whereas NMNS-PV 21516 is a fragment of a heavily worn upper molar (Fig. 65n).

Genus *Leptolophus* Remy, 1965

Type species: *Leptolophus stehlini* Remy, 1965

Comments: Remy (1998) recognized three species in the genus: *Leptolophus magnus* Remy, 1998; *L. nouleti* (Stehlin, 1904a); and *L. stehlini*. The first and last species are, respectively, the largest and smallest species of the genus, and Robiac is the type locality for both species (Remy, 1998). *Leptolophus* is known from MP 16 in southern France and Switzerland (Remy, 1998), and apparently extends from MP 16 to 18 in Spain (Cuesta, 1994b; Badiola et al., 2002).

Leptolophus sp.

(Fig. 66)

Localities and Materials: Robiac: NMNS-PV 21345, double-roots of possible right m1 and m2 in

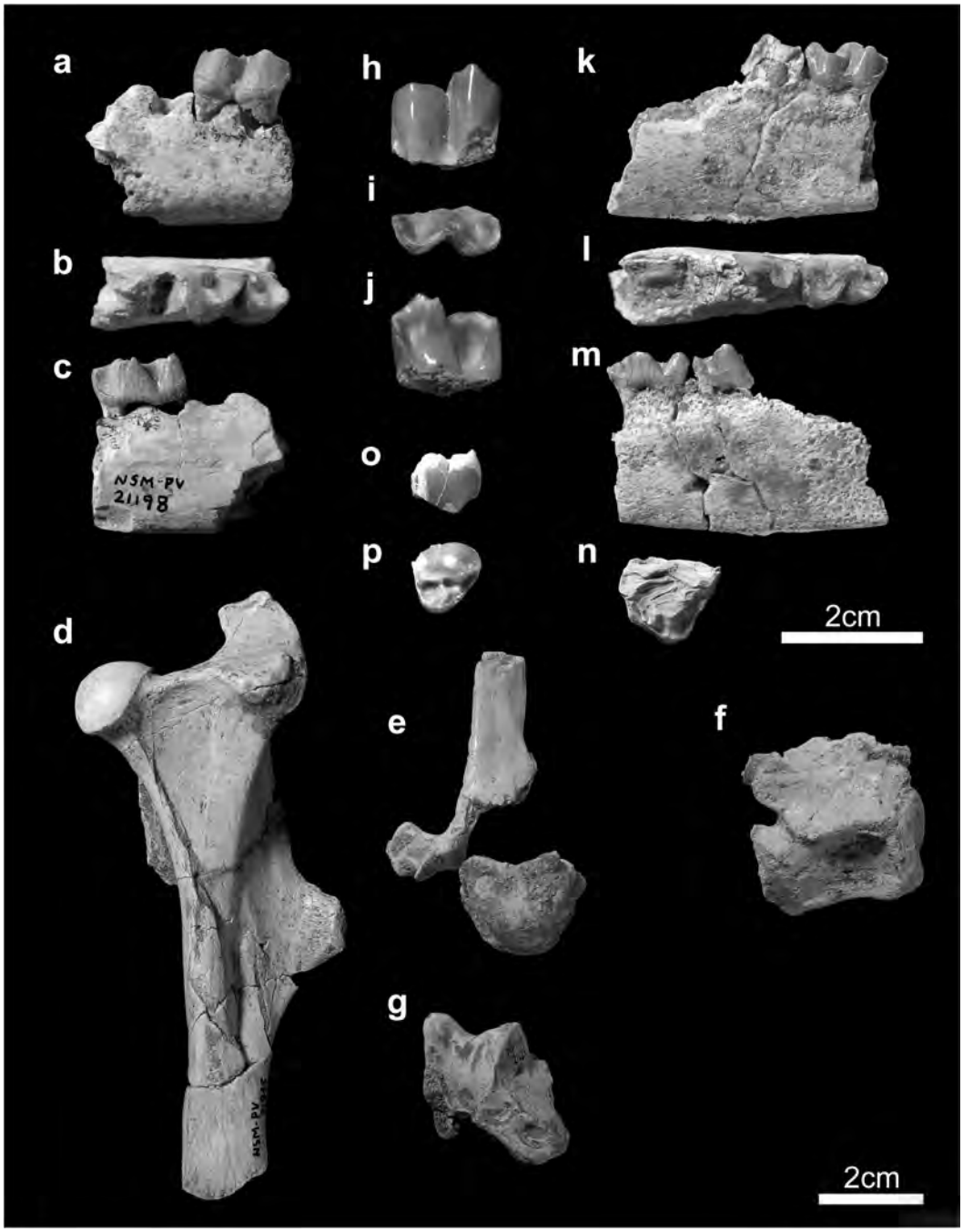

Fig. 65. Cf. *Plagiolophus* sp. from Le Bretou (NMNS-PV 21198), Baby (NMNS-PV 21435, 21436, and 21438), La Débruge (NMNS-PV 21516), and St. Capraise d'Eymet (NMNS-PV 21545). NMNS-PV 21198, right mandibular fragment with p4 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21435 (selected), proximal half of left femur (d) in anterior view, a thoracic vertebra (e) in anterior view, lumber vertebra (f) in lateral view, and a distal fragment of possible right humerus (g). NMNS-PV 21436, right m1 or m2 in labial (h), occlusal (i), and lingual (j) views. NMNS-PV 21438, right mandibular fragment with possible dp3 and broken dp4 in labial (k), occlusal (l), and lingual (m) views. NMNS-PV 21516, upper molar fragment (n) in occlusal view. NMNS-PV 21545, right P2 in labial (o) and occlusal (p) views. Scale bar for d–g is shown at bottom right.

Fig. 66. *Leptolophus* sp. from Robiac: NMNS-PV 21345, double-roots of possible right m1 and m2 in matrix in labial (a), occlusal (b), and lingual (c) views.

matrix.

Comments: The molariform tooth in NMNS-PV 21345 is hypsodont and labiolingually narrow, showing a typical feature of *Leptolophus*. Based on the dental dimensions provided by Remy (1998), the molariform tooth is most likely referable to M2 of *L. stehlini* or *L. nouleti*. Considering the size of the double-roots anterior to the molariform tooth, NMNS-PV 21345 is potentially assigned to *L. stehlini*.

Suborder Tapiromorpha Haeckel, 1866
Family Pachynolophidae Pavlow, 1888, sensu (Hooker, 1989, 1994)

Genus *Pachynolophus* Pomel, 1847b

Type species: *Pachynolophus duvali* Pomel, 1847b.

Comments: The genus *Pachynolophus* Pomel, 1847b is known from MP 10 to MP 18 or 20(?) with roughly a dozen species (Savage et al., 1965; Cuesta, 1994a; Badiola et al., 2005). Based on a phylogenetic analysis, Badiola et al. (2005) recognized seven species forming a monophyletic group as valid. They concluded that *P. bretovensis* Remy, 1988 does not have any synapomorphic characters shared with *Pachynolophus*. Therefore, its systematic status remains questionable. However, despite its debatable systematic position, *P. bretovensis* is allocated to the genus in this chapter. The *Pachynolophus* specimens cataloged here come from Aumelas (MP 13) and Robiac (MP 16).

***Pachynolophus bretovensis* Remy, 1988**
(Fig. 67)

Localities and Materials: Robiac: NMNS-PV 21325, left maxillary fragment with P4–M2 and broken M3; 21326, mandibular fragments with right m1–3, broken left p2, p3–m3, isolated right p4, and possible right M3 in matrix.

Comments: Among the known species of *Pachynolophus*, *P. bretovensis* has been recorded only from MP 16 (Badiola et al., 2005). The specimens cataloged here were assigned to this species by comparison with the type specimen from Le Bretou (BRT-130, collection of the Université des Sciences et Techniques du Languedoc, Montpellier; see also Remy, 1988). The maxillary fragment (Fig. 67a–c; NMNS-PV 21325) preserves upper molars bearing strong paraconules, faint metaconules, and almost no mesostyle; the molars are rather lophodont unlike in *Lophiotherium* and resemble those of BRT-130. The P4 of NMNS-PV 21325 has a triangular outline with no hypocone as seen in the type specimen (Fig. 67b). Although the lower cheek teeth (Fig. 67d, NMNS-PV 21326) are worn out, they have weak cingulids on the labial and lingual surfaces suggesting pachynolophine affinity. The upper

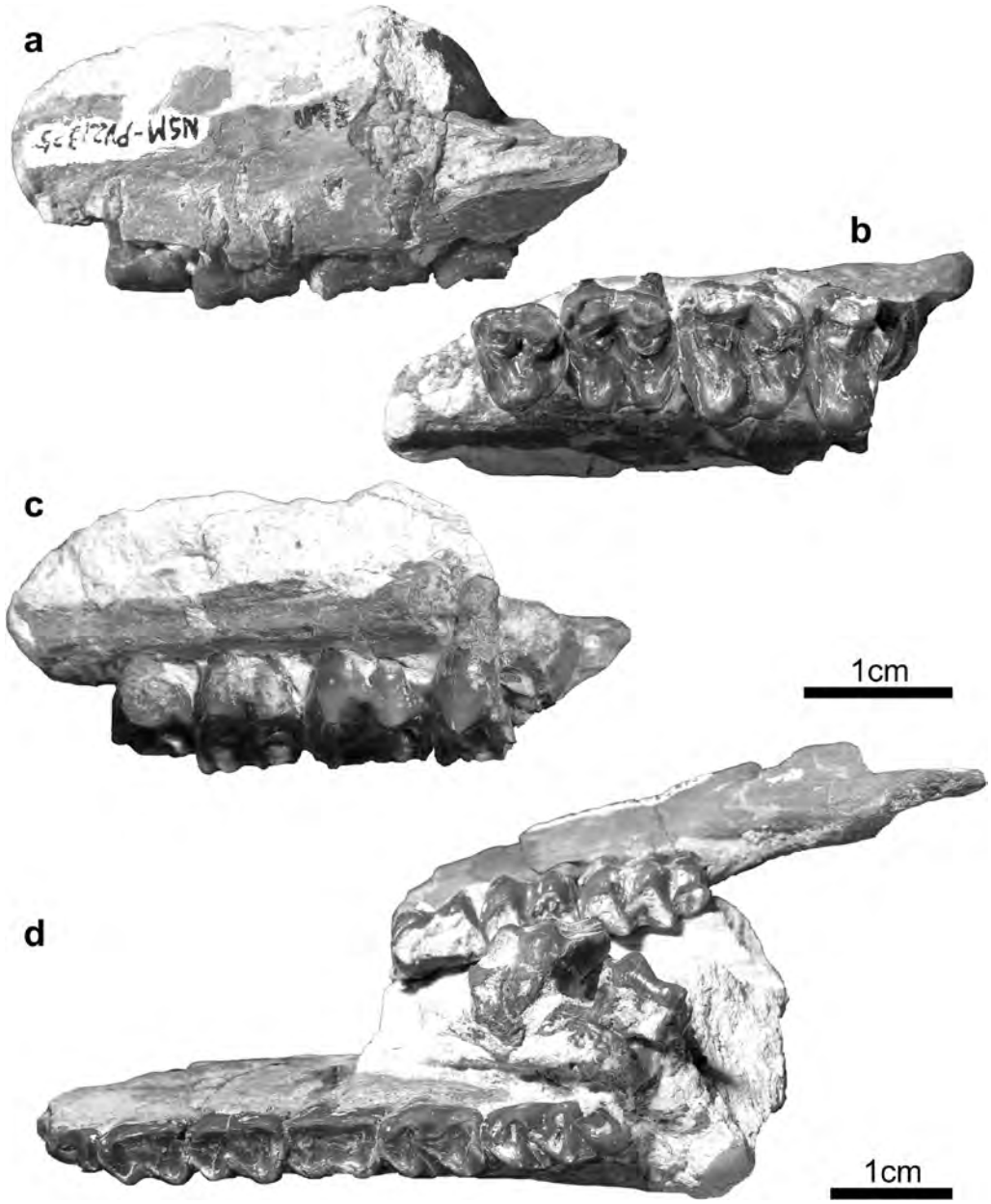

Fig. 67. *Pachynolophus bretovensis* Remy, 1988 from Robiac: NMNS-PV 21325, left maxillary fragment with P4–M2 and broken M3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21326, mandibular fragments with right m1–3, broken left p2, p3–m3, isolated right p4, and possible right M3 in matrix (d). Scale bar for d is shown at bottom right.

molar associated with the mandible (a possible right M3) is heavily worn but is also similar to that of *P. bretovensis*.

***Pachynolophus* sp. cf. *P. bretovensis* Remy, 1988**

(Fig. 68)

Localities and Materials: Robiac: NMNS-PV 21303, broken left posterior lower premolar or anterior lower molar; 21328, possible right m1 or m2; 21329, left mandibular fragment with possible m2.

Comments: All of these teeth are similar to those of the specimens referred to *Pachynolophus bretovensis* mentioned above. The lower molariform teeth display stout labial crests and weak entoconids unlike in *Lophiotherium* and *Anchilophus* from Robiac. However, the specimens are too fragmentary to make a more definitive assignment.

***Pachynolophus duvali* Pomel, 1847b**

(Figs. 69 and 70)

Localities and Materials: Aumelas: NMNS-PV 21125, incomplete skull with right P2–3, DP4, M1–3, and left M1–3 (partially restored); 21126, left maxillary fragment with broken P4 and M1–3 in

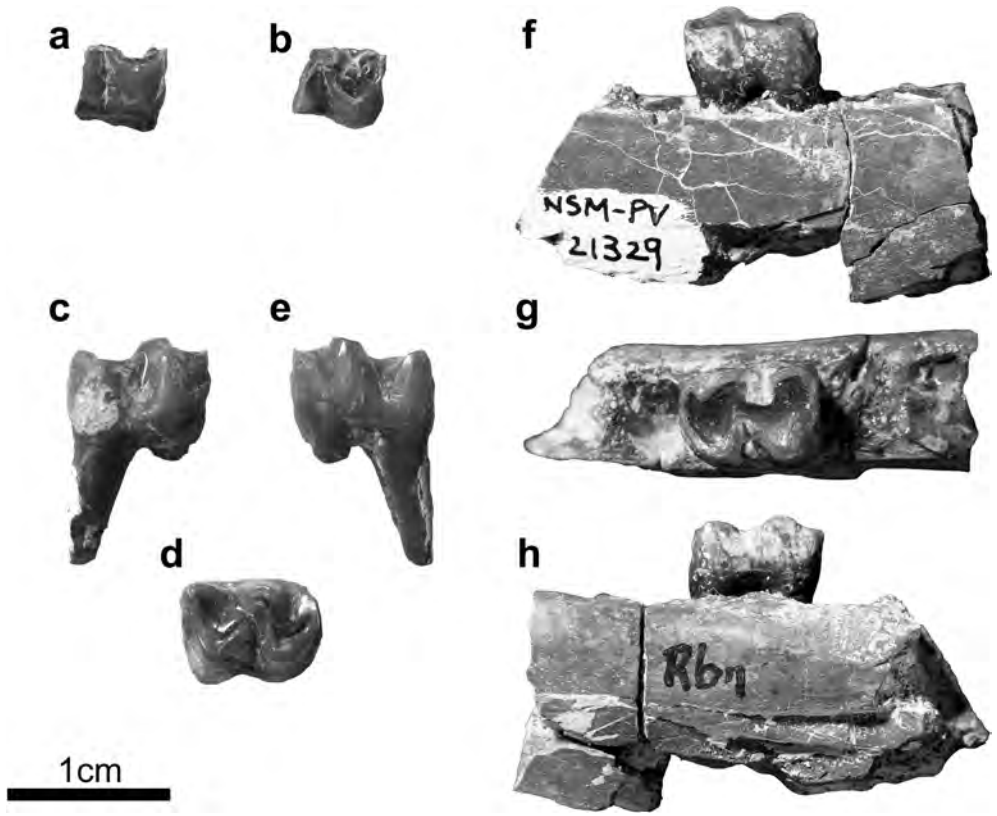

Fig. 68. *Pachynolophus* sp. cf. *P. bretovensis* Remy, 1988 from Robiac: NMNS-PV 21303, broken left posterior lower premolar or anterior lower molar in labial (a) and occlusal (b) views. NMNS-PV 21328, possible right m1 or m2 in labial (c), occlusal (d), and lingual (e) views. NMNS-PV 21329, left mandibular fragment with possible m2 in labial (f), occlusal (g), and lingual (h) views.

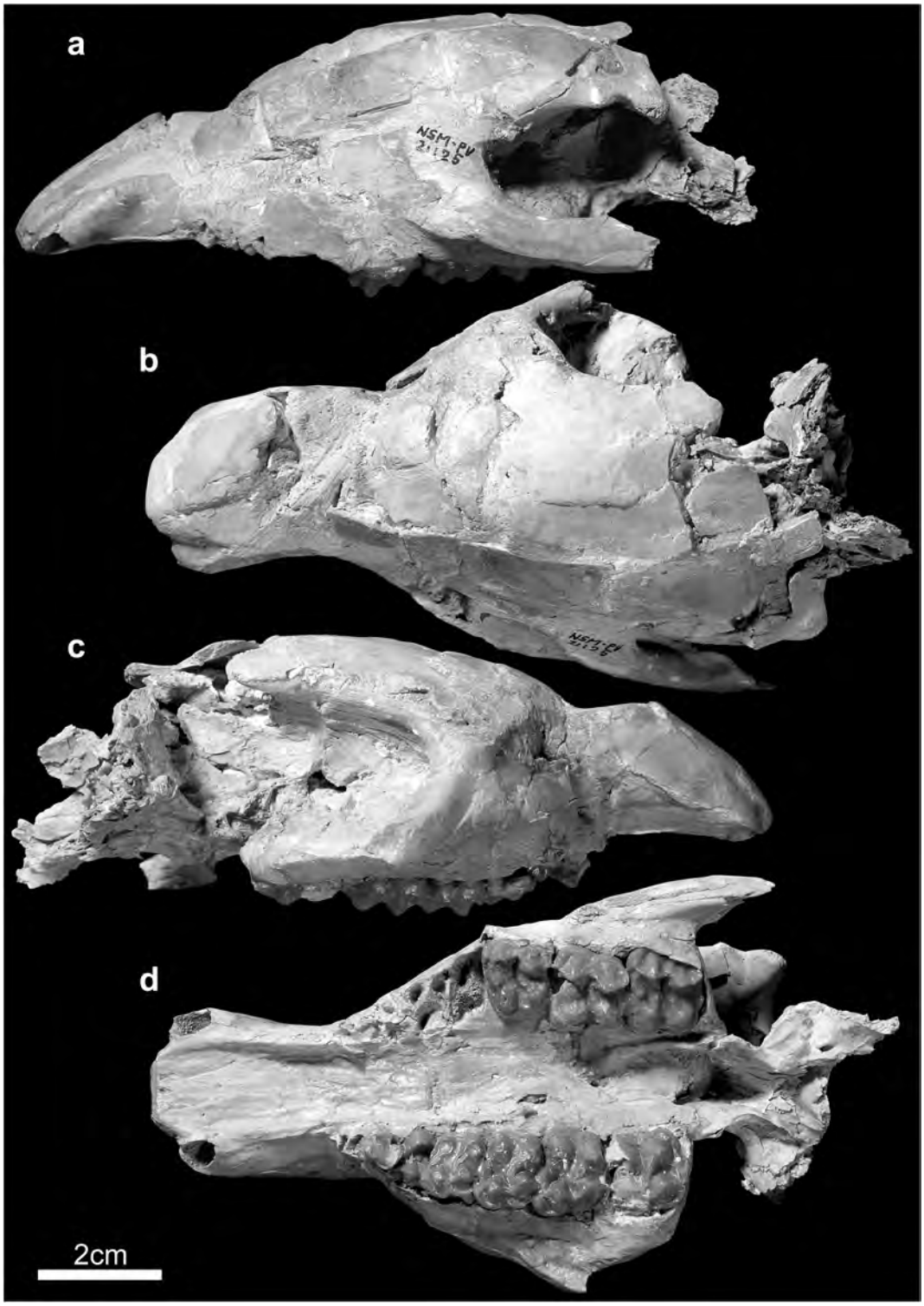

Fig. 69. *Pachynolophus duvali* Pomel, 1847b from Aumelas: NMNS-PV 21125, incomplete skull with right P2–3, DP4, M1–3, and left M1–3 (partially restored) in left lateral (a), dorsal (b), right lateral (c), and ventral (d) views.

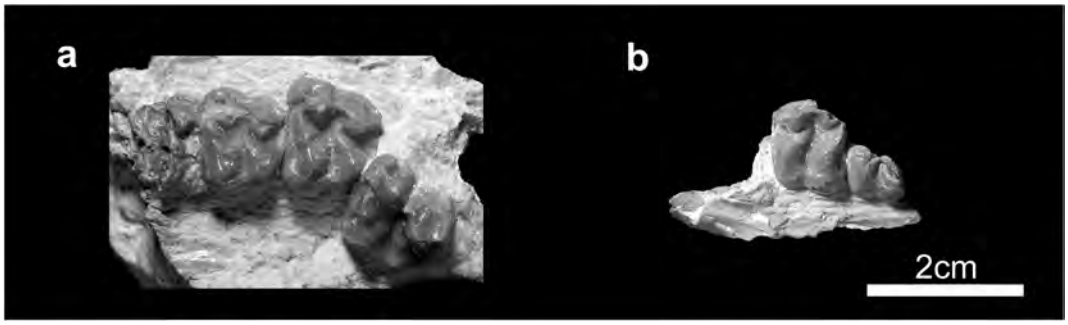

Fig. 70. *Pachynolophus duvali* Pomel, 1847b from Aumelas: NMNS-PV 21126, left maxillary fragment with broken P4 and M1–3 (a) in occlusal view. NMNS-PV 21127, right maxillary fragment with lingual part of M1 and broken M2 (b) in occlusal view.

matrix; 21127, right maxillary fragment with lingual part of M1 and broken M2.

Comments: *Pachynolophus duvali* is known from MP 12 to 13 (Franzen, 1987; Badiola et al., 2005). Although NMNS-PV 21125 is partially restored (Fig. 69, largely on the right half), the left lateral side from maxilla to jugal and palatine appears to retain its original shape. The skull preserves long post-canine diastemata and a nearly complete upper cheek tooth series with deciduous premolars, all of which show the typical dental features of *Pachynolophus*. The right P3 is not fully erupted, and the P4 is present under the DP4. The permanent molars are almost unworn and bear small protoconules and reduced metaconules. There is no apparent mesostyle on the molars (Fig. 69d), but a faint enamel swelling on the labial surface of ectoloph is present between the paracone and metacone in each upper molar, as noted in Savage et al. (1965). The other specimens from Aumelas (Fig. 70, NMNS-PV 21126 and 21127) preserve upper molars identical to those of NMNS-PV 21125, supporting the assignment to the same species.

Genus *Anchilophus* Gervais, 1852

Type species: *Anchilophus desmaresti* Gervais, 1852.

Comments: The genus *Anchilophus* is more closely related to *Paranchilophus* Casanovas and Santafé, 1989 than to *Pachynolophus*, although these three genera form a monophyletic clade (Badiola et al., 2005). Savage et al. (1965) recognized five species in the genus *Anchilophus*, but they did not attempt to review *Anchilophus* in detail. *Anchilophus* is known from MP 13 to 19 (Franzen, 1987; Hooker, 1987; Legendre, 1987). The specimens of *Anchilophus* cataloged here were collected from Le Bretou, Robiac, and Euzèt les Bains; the first two localities correlate with MP 16 and preserve three species including the type species. The other two species are *A. gaudini* Pictet and Humbert, 1869 and *A. dumasi* (Gervais, 1852), both of which extend into MP 17 (Legendre, 1987).

***Anchilophus* sp. cf. *A. desmaresti* Gervais, 1852**

(Fig. 71)

Localities and Materials: Robiac: NMNS-PV 21322, right maxillary fragment with M1–3; 21323, left mandibular fragment with p4–m3; 21324, possible right M1 or M2.

Comments: All of these specimens are larger compared to the type specimen of *A. desmaresti* (MP-20, collections of Muséum National d'Histoire Naturelle, Paris; see also Savage et al.,1965) but

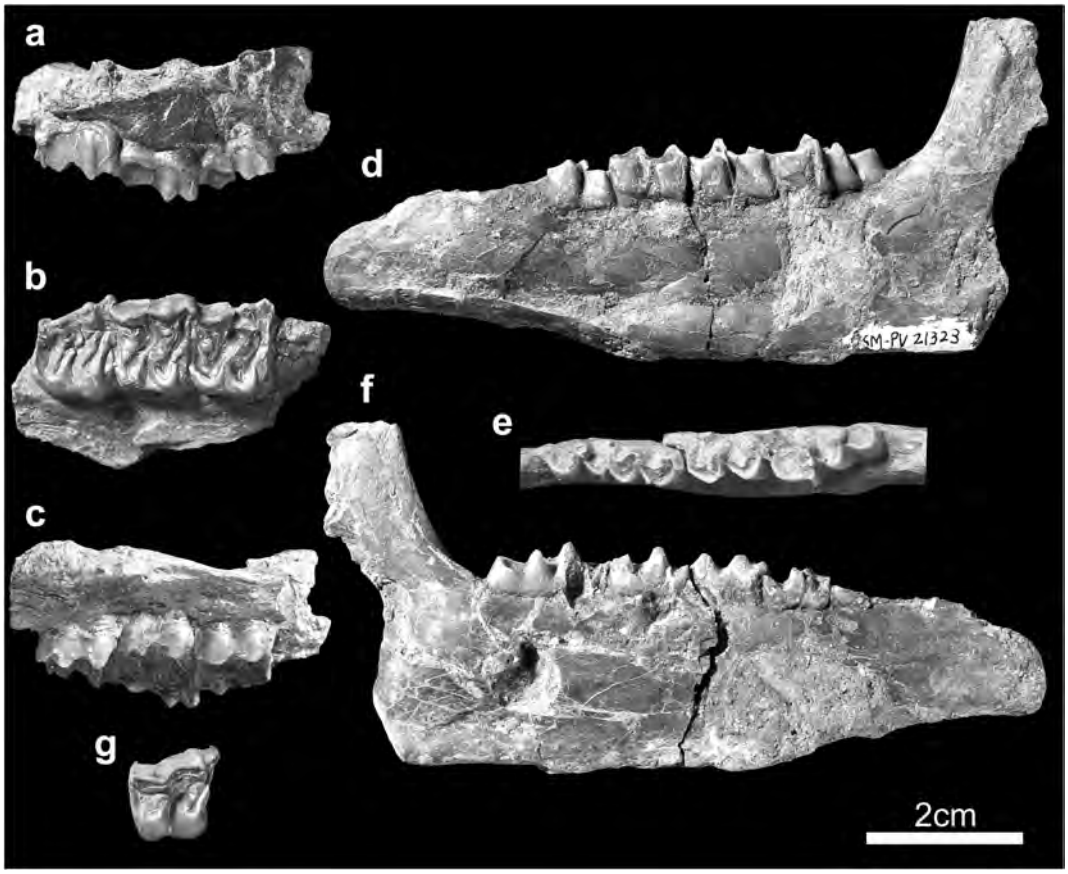

Fig. 71. *Anchilophus* sp. cf. *A. desmaresti* Gervais, 1852 from Robiac: NMNS-PV 21322, right maxillary fragment with M1–3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21323, left mandibular fragment with p4–m3 in labial (d), occlusal (e, p4–m3 only), and lingual (f) views. NMNS-PV 21324, possible right M1 or M2 (g) in occlusal view.

are apparently smaller compared to *A. dumasi* from Euzèt (Fig. 72, Appendix 1). The upper molars (Fig. 71a–c, g; NMNS-PV 21322 and 21324) have a more flattened ectoloph with strong paracone ribs and more distinct para- and metalophs than in *A. gaudini*. There is a faint indentation on the posterior wall in NMNS-PV 21324, suggesting that it represents M1 or M2. NMNS-PV 21323 (Fig. 71d–f) exhibits high lingual molar cusps (meta- and entoconids) and a stout m3 hypoconulid positioned close to the entoconid. The mandible is shallower than in *A. dumasi*.

***Anchilophus dumasi* (Gervais, 1852)**

(Fig. 72)

Localities and Materials: Euzèt les Bains: NMNS-PV 21386, right mandibular fragment with c1, p1–4, and broken m1–2 in matrix; 21387, right mandibular fragment with m1–3 in matrix.

Comments: Euzèt is the type locality of *A. dumasi* (Savage et al., 1965; Remy, 1988). Although the *Anchilophus* specimens from Euzèt are not completely prepared, the two mandibles (Fig. 72, NMNS-PV 21386 and 21387) represent the largest species of the genus, *A. dumasi*. NMNS-PV 21386 preserves

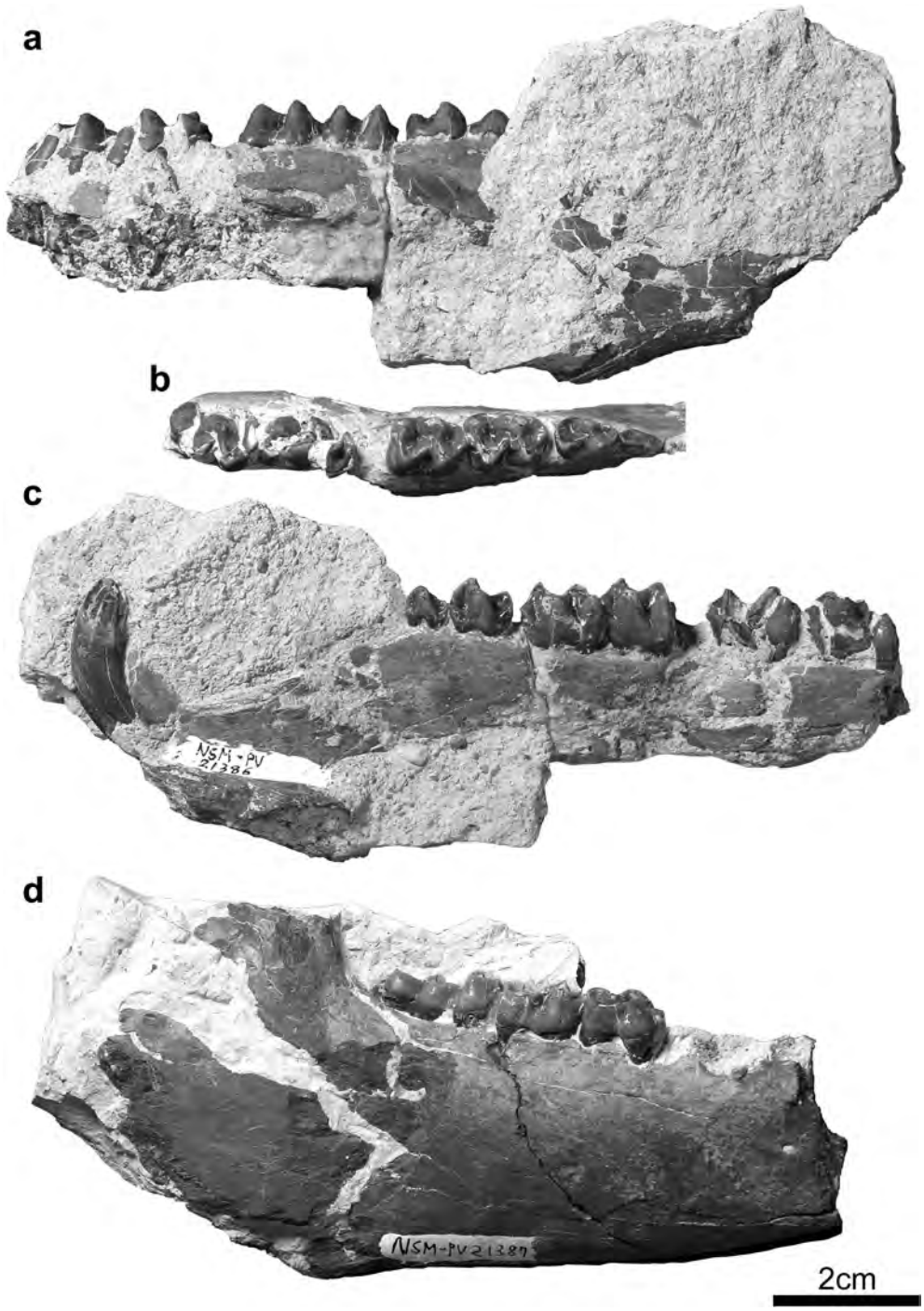

Fig. 72. *Anchilophus dumasi* (Gervais, 1852) from Euzèt les Bains: NMNS-PV 21386, right mandibular fragment with c1, p1–4, and broken m1–2 in matrix in labial (a), occlusal (b, p1–m3 only), and lingual (c) views. NMNS-PV 21387, right mandibular fragment with m1–3 in matrix (d) in labial view.

almost unworn cheek teeth showing the complete premolar morphology and a long post-canine diastema which is a characteristic of the genus. The p4 of NMNS-PV 21386 is more molariform than in *A. desmaresti* with deep trigonid and talonid basins.

Anchilophus sp. cf. *A. gaudini* Pictet and Humbert, 1869
(Fig. 73)

Localities and Materials: Le Bretou: NMNS-PV 21193, possible right M3; 21194, right maxillary fragment with M3; 21195, possible left P4 or M1; 21197, left M2.

Robiac: NMNS-PV 21327, possible left P4 or M1; 21330, right maxillary fragment with possible P3–4; 21331, possible left M2 or M3.

Comments: Remy (1988) described *Anchilophus* materials from Le Bretou, which are now housed in the Université des Sciences et Techniques du Languedoc, Montpellier. The cataloged specimens were identified by comparison with *Anchilophus* specimens described by Remy (1988).

The La Bretou and Robiac specimens are too fragmentary for exact determinations on species level. However, these molars are smaller than those of *A. dumasi*, they bear ectolophs with faint but visible ribs on paracones and metacones, have a less developed metastyle, and display slightly lower lophs than in *A. desmaresti* (Fig. 73). The possible P3 of NMNS-PV 21330 is molariform with a discrete hypocone (Fig. 73i). NMNS-PV 21193 and 21194 are assignable to M3, which has a shelf-like posterior cingulum and no indentation on the posterior wall (Fig. 73b, c). NMNS-PV 21331 is incomplete but also has no distinct indentation on the posterior wall (Fig. 73j).

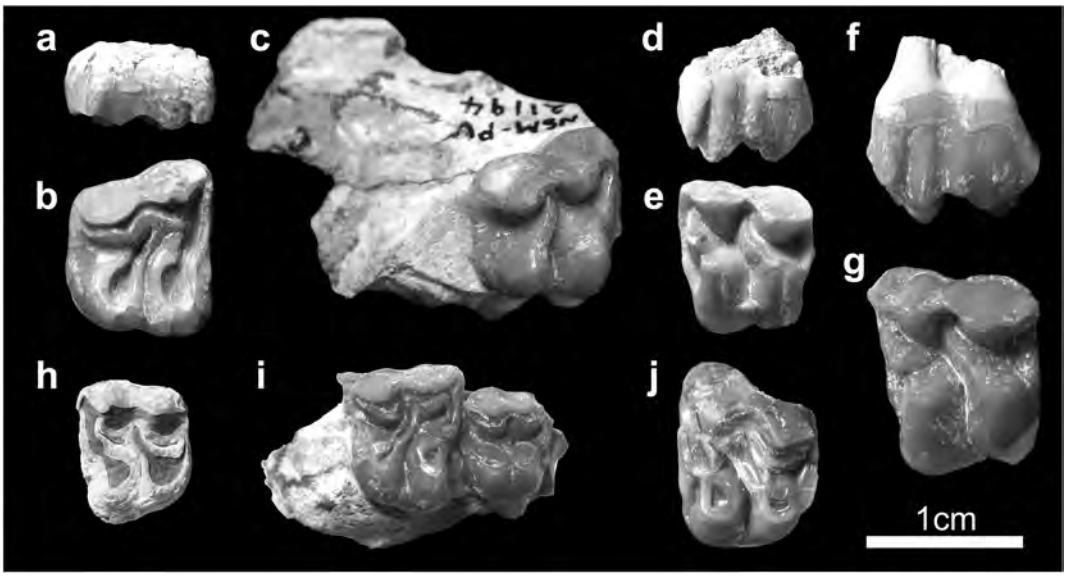

Fig. 73. *Anchilophus* sp. cf. *A. gaudini* Pictet and Humbert, 1869 from Le Bretou (NMNS-PV 21193–21195 and 21197) and Robiac (NMNS-PV 21327, 21330, and 21331): NMNS-PV 21193, possible right M3 in labial (a) and occlusal (b) views. NMNS-PV 21194, right maxillary fragment with M3 (c) in occlusal view. NMNS-PV 21195, possible left P4 or M1 in labial (d) and occlusal (e) views. NMNS-PV 21197, left M2 in labial (f) and occlusal (g) views. NMNS-PV 21327, possible left P4 or M1 (h) in occlusal view. NMNS-PV 21330, right maxillary fragment with possible P3–4 in occlusal (i) view. NMNS-PV 21331, possible left M2 or M3 (j) in occlusal view.

Cf. *Anchilophus* sp.
(Fig. 74)

Localities and Materials: Le Bretou: NMNS-PV 21192, possible right P2; 21196, possible right c1.

Comments: The specimens from Le Bretou are potentially referable to those of *Anchilophus*, but they are too fragmentary for specific assignments. NMNS-PV 21192 (Fig. 74a–c) is similar to P2 of *Anchilophus* in morphology but is smaller than those of any species of the genus, being closer to the P2 of *Pachynolophus* in size. NMNS-PV 21196 (Fig. 74d, e) is referable to a lower canine (c1) based on its shape and the presence of a faint wear facet on the posterior edge of the crown.

Infraorder Ancylopoda Cope, 1889
Family Lophiodontidae Gill, 1872

Genus *Lophiodon* Cuvier, 1822

Type species: *Lophiodon tapiroides* (Cuvier, 1812)

Comments: Although about a dozen species of *Lophiodon* have been regarded as valid since Cuvier (1822), the classification of the genus remains debatable (e.g., Hooker, 1986; Cuesta, 1994c). Moreover, the closely related genera *Rhinocerolophiodon* Fischer, 1977 and *Paralophiodon* Dedieu, 1977 are considered to be synonymous with *Lophiodon* (Holbrook, 2009). Although a systematic review of *Lophiodon* is beyond the scope of this monograph, most of the *Lophiodon* specimens cataloged here are derived from Robiac. They can be assigned to a very large species, *Lophiodon lautricense*. At least one specimen (NMNS-PV 21129) from Aumelas represents a smaller species than *L. lautricense*.

Lophiodon lautricense Noulet, 1851
(Figs. 75–81)

Localities and Materials: Robiac: NMNS-PV 21348, right and left mandibles with right i2, left i1–2, right and left c1s, p2–m3s; 21349, right maxillary fragment with P3–M2; 21350, right and left

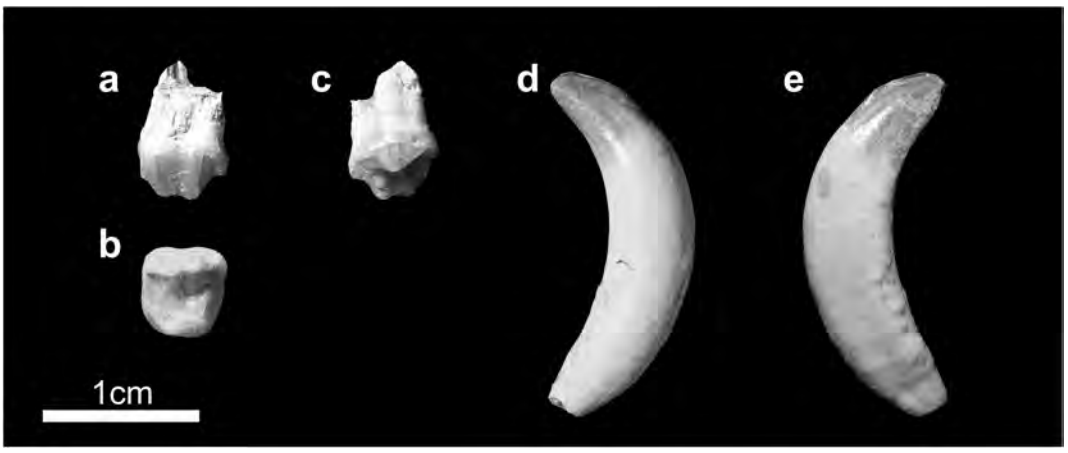

Fig. 74. Cf. *Anchilophus* sp. from Le Bretou: NMNS-PV 21192, possible right P2 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21196, possible right c1 in labial (d) and lingual (e) views.

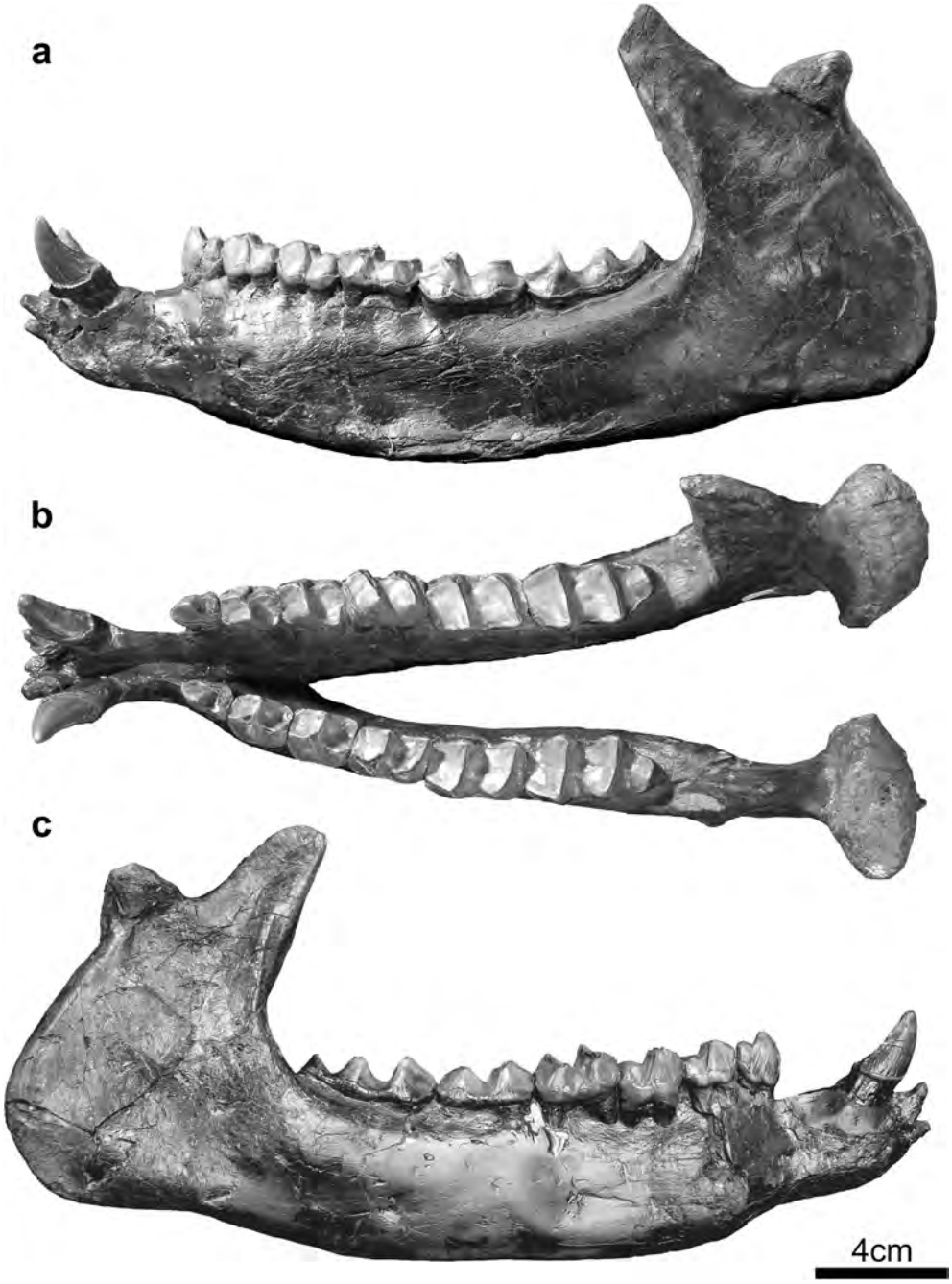

Fig. 75. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21348, right and left mandibles with right i2, left i1–2, right and left C1s, p2–m3s in left lateral (a), occlusal (b), and right lateral (c) views.

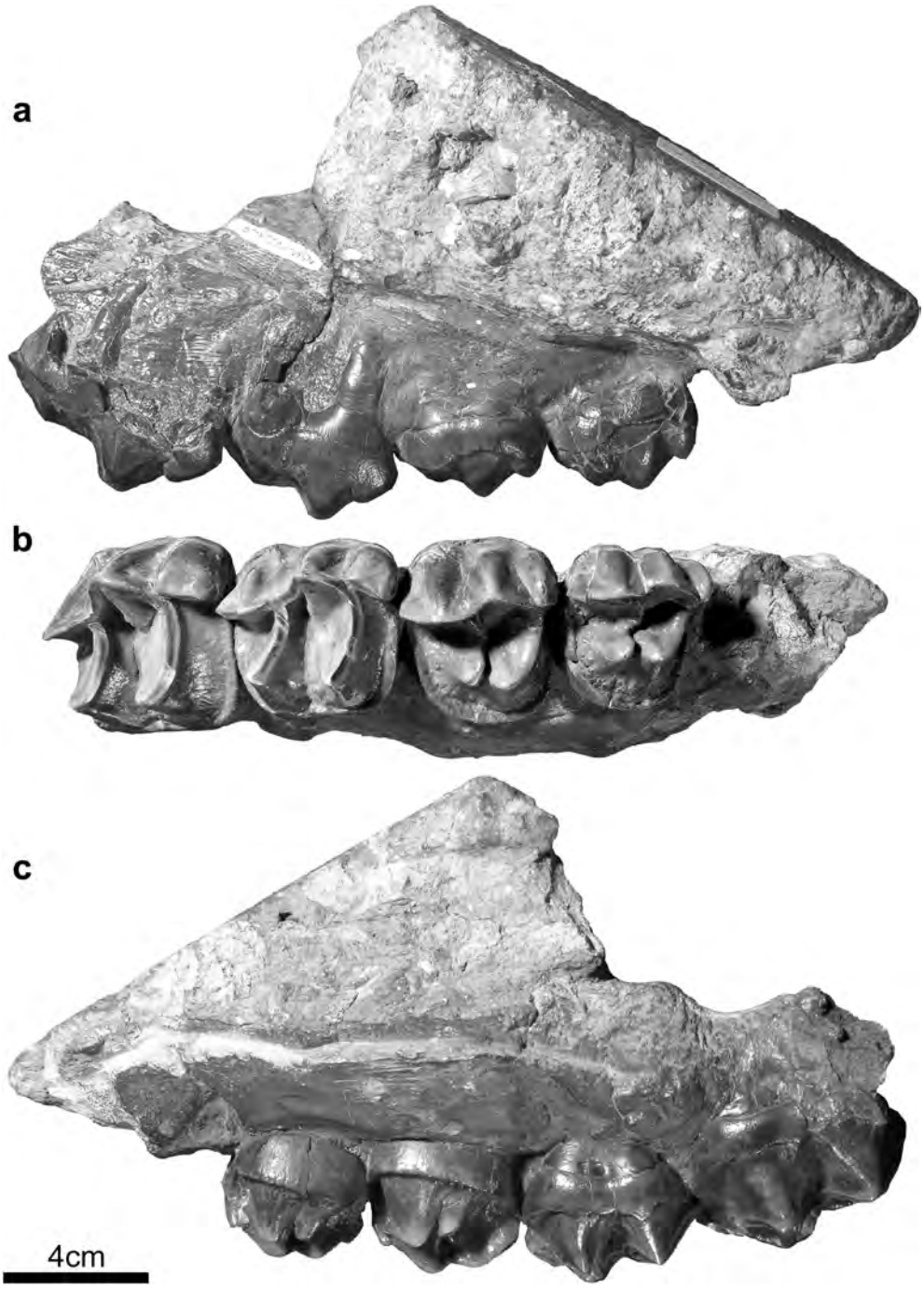

Fig. 76. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21349, right maxillary fragment with P3–M2 in labial (a), occlusal (b), and lingual (c) views.

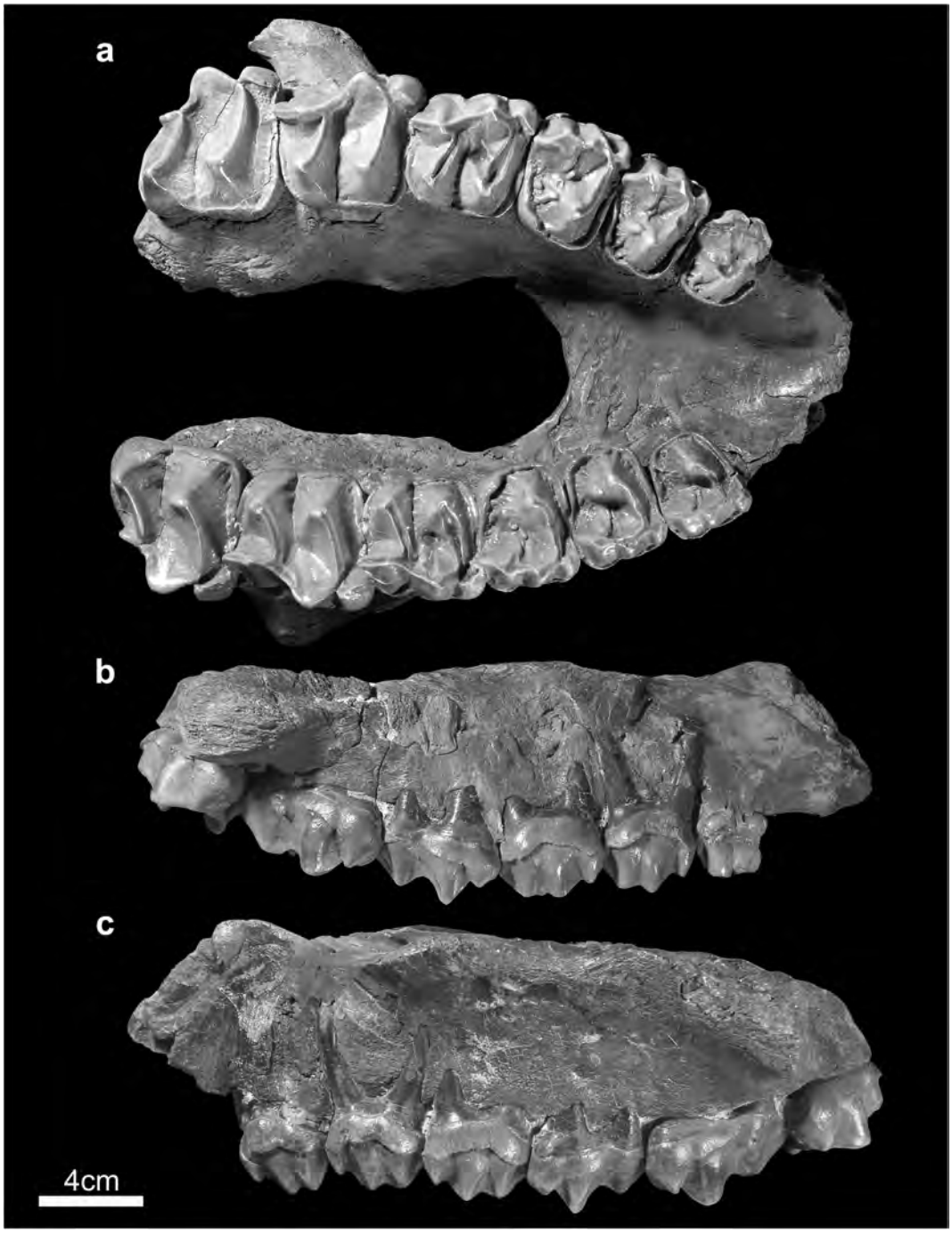

Fig. 77. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21350, right and left maxillae with P2–M3s in occlusal (a), right lateral (b), and left lateral (c) views.

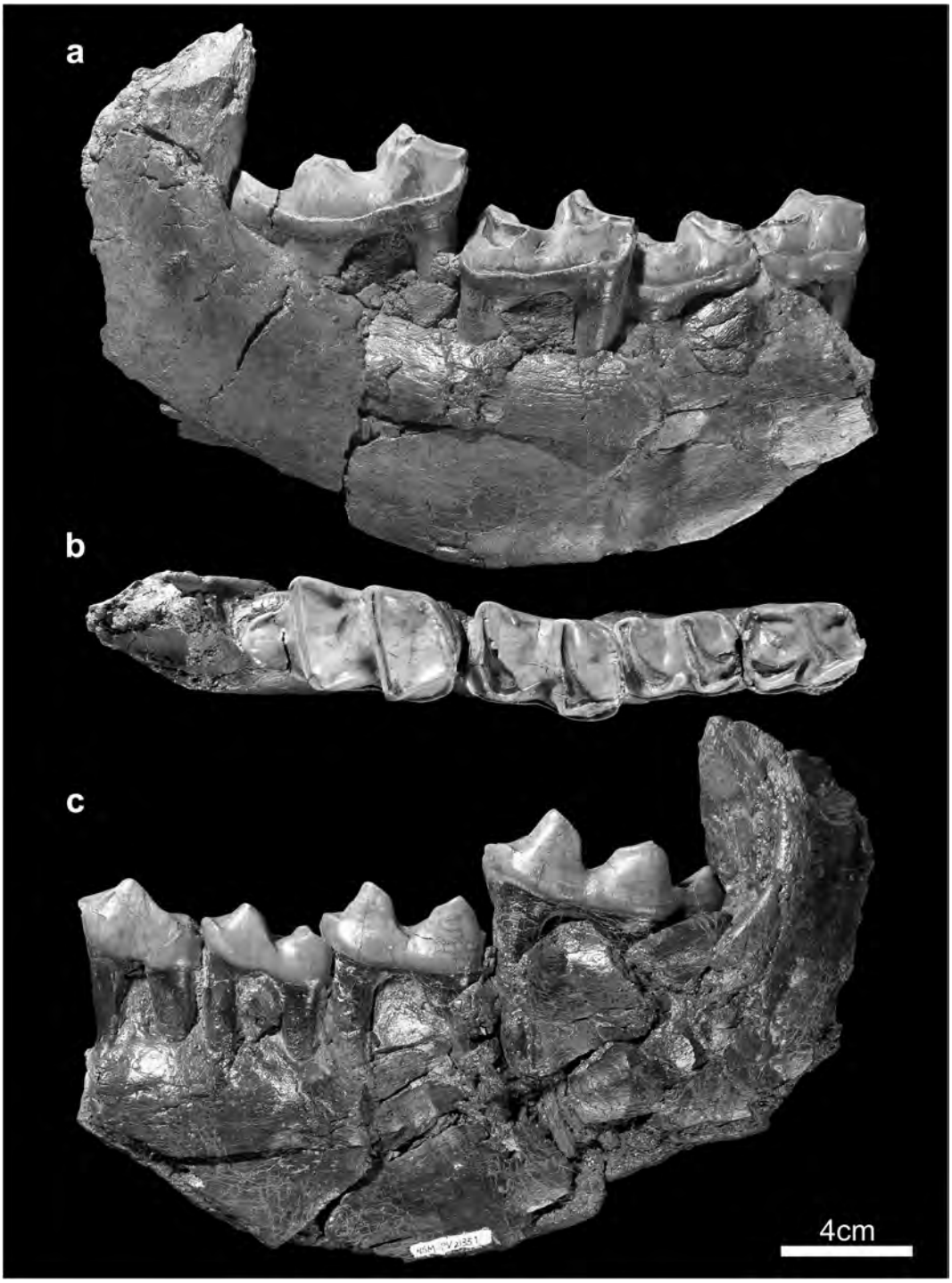

Fig. 78. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21351, right mandibular fragment with p4–m3 in labial (a), occlusal (b), and lingual (c) views.

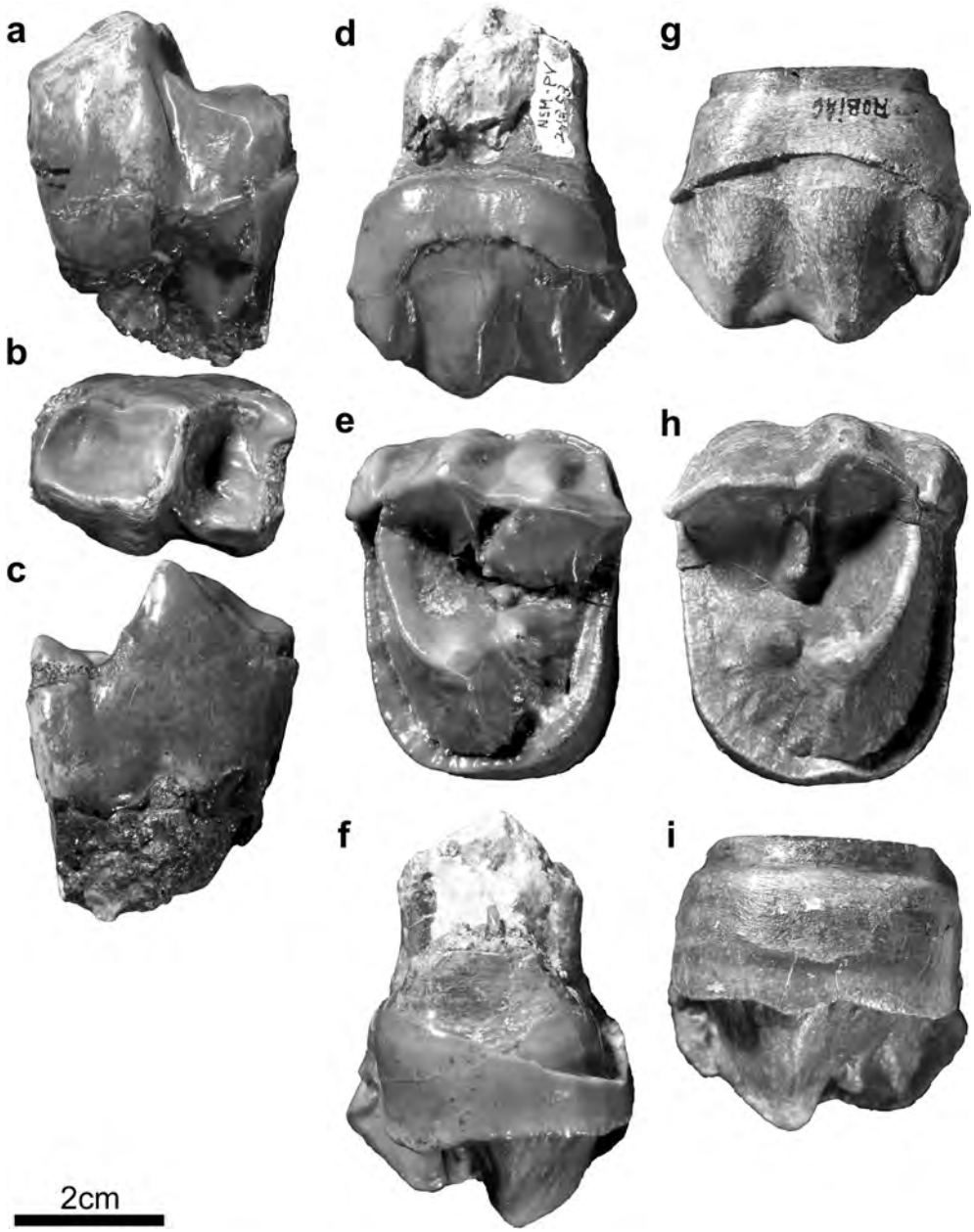

Fig. 79. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21352, left p3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21353, left P4 in labial (d), occlusal (e), and lingual (f) views. NMNS-PV 21354, right P4 (basal crown is restored) in labial (g), occlusal (h), and lingual (i) views.

maxillae with P2–M3s; 21351, right mandibular fragments with p4–m3; 21352, left p3; 21353, left P4; 21354, right P4 (basal crown is restored); 21355, left M3; 21356, right M2; 21357, left P4; 21359, right maxillary fragment with broken DP2 and DP3–4.

Comments: *Lophiodon lautricense* is a very large species and an index taxon for reference level MP 16 (Hooker, 1987; Cuesta, 1994c). The dental morphological variation was previously documented (e.g.,

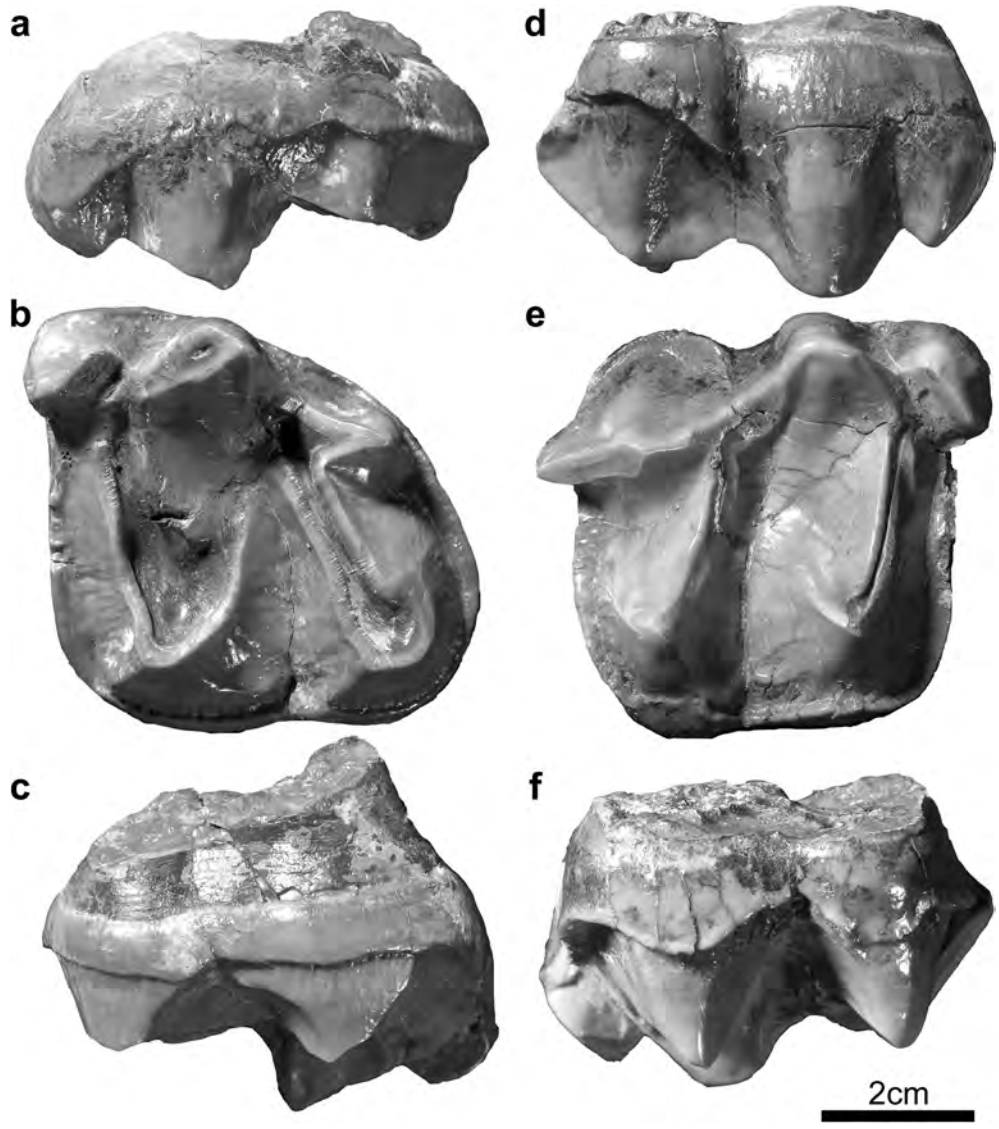

Fig. 80. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21355, left M3 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21356, right M2 in labial (d), occlusal (e), and lingual (f) views.

Sudre, 1971), although a formal diagnosis seems not available (Hooker, 1986).

The specimens of *L. lautricense* include mandibles and maxillae with beautifully preserved cheek teeth. The best-preserved mandible (Fig. 75, NMNS-PV 21348) and maxilla (Fig. 77, NMNS-PV 21350) exhibit the complete lower and upper cheek tooth series, respectively. NMNS-PV 21348 is partially restored at the symphysial portion of mandible and preserve two incisors referable to left i1–2, a possible right i2, and an alveolus for right i1. The restored symphysial portion of NMNS-PV 21348 does not have alveoli for an i3. The Robiac specimens also include isolated cheek teeth, showing almost identical morphology with NMNS-PV 21348 and 21350.

As Sudre (1971) clarified, there is considerable morphological variation within the premolars of *L. lautricense*. Some morphological differences, particularly in the development of premolar hypocones

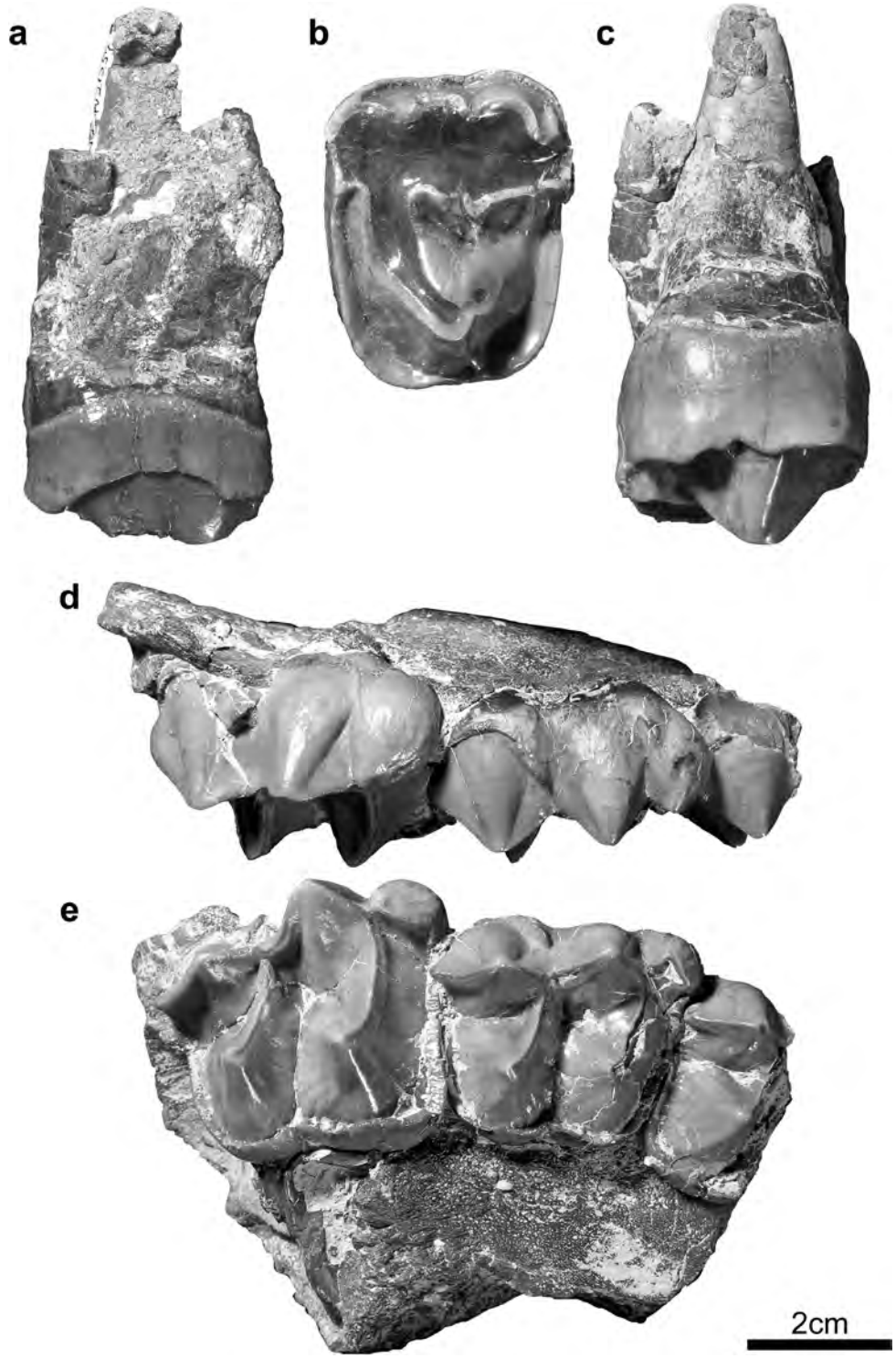

Fig. 81. *Lophiodon lautricense* Noulet, 1851 from Robiac. NMNS-PV 21357, left P4 in labial (a), occlusal (b), and lingual (c) views. NMNS-PV 21359, right maxillary fragment with broken DP2 and DP3–4 in labial (d) and occlusal (e) views.

(molarization of premolars), are observable among the present specimens; the hypocone in the premolars (P3–4) of NMNS-PV 21349 (Fig. 76) is well separated from protocone and bears a weak loph extending to the ectoloph, whereas other upper premolars (Figs. 77, 79d–i, and 81a–c; NMNS-PV 21350, 21353, 21354, and 21357) show small and conical hypocones less separated from the protocones. Given the dental variation documented by Sudre (1971), all of these specimens can be unambiguously assigned to a single species, *L. lautricense.*

***Lophiodon* sp.**
(Fig. 82)

Localities and Materials: Aumelas: NMNS-PV 21129, left mandibular fragment with possible p4 root and broken M1–3; 21130, right upper or left lower incisor

Robiac: NMNS-PV 21358, right upper or left lower incisor

Comments: The mandibular fragment from Aumelas (Fig. 82a, b; NMNS-PV 21129) is poorly preserved, thus making its specific assignment difficult. Despite the incompleteness, the dimensions of NMNS-PV 21129 suggest that it belongs to a small species like *L. remensis* Lemoine, 1878 or *L. tapirotherium* Desmarest, 1822. In any case, it is a smaller species than *Paralophiodon isselense* (Fischer, 1829) (see also Savage et al., 1966; Cuesta, 1994c). The incisor from Aumelas (Fig. 82c–e, NMNS-PV 21130) can not be directly compared to NMNS-PV 21129. It appears too large to be allocated to the same species as NMNS-PV 21129, while the Robiac incisor (Fig. 82f–h, NMNS-PV 21358) probably belongs to *L. lautricense*.

Systematic Paleontology
(Miocene Perissodactyls)

Order Perissodactyla Owen, 1848a
Suborder Hippomorpha Wood, 1937
Superfamily Equoidea Gray, 1821
Family Equidae Gray, 1821

Genus *Anchitherium* Meyer, 1844

Type species: *Anchitherium aurelianense* (Cuvier, 1825)

Comments: *Anchitherium* is a common genus in Miocene mammalian faunas in Europe. It flourished from MN 3 to MN 9 or 10 (Abusch-Siewert, 1983; Forstén, 1991). About ten species have been described from Europe as valid (Miyata and Tomida, 2010).

***Anchitherium aurelianense* (Cuvier, 1825)**
(Fig. 83a)

Localities and Materials: Faluns de Touraine: NMNS-PV 21672, left M3

Comments: The occurrence of *A. aurelianense* from Faluns de Touraine was reported previously (Ginsburg, 2001). Faluns de Touraine is believed to be correlated to MN5 (Burdigalian–Langhian, late Early to early Middle Miocene; Luterbacher et al., 2004), and the locality has also provided various

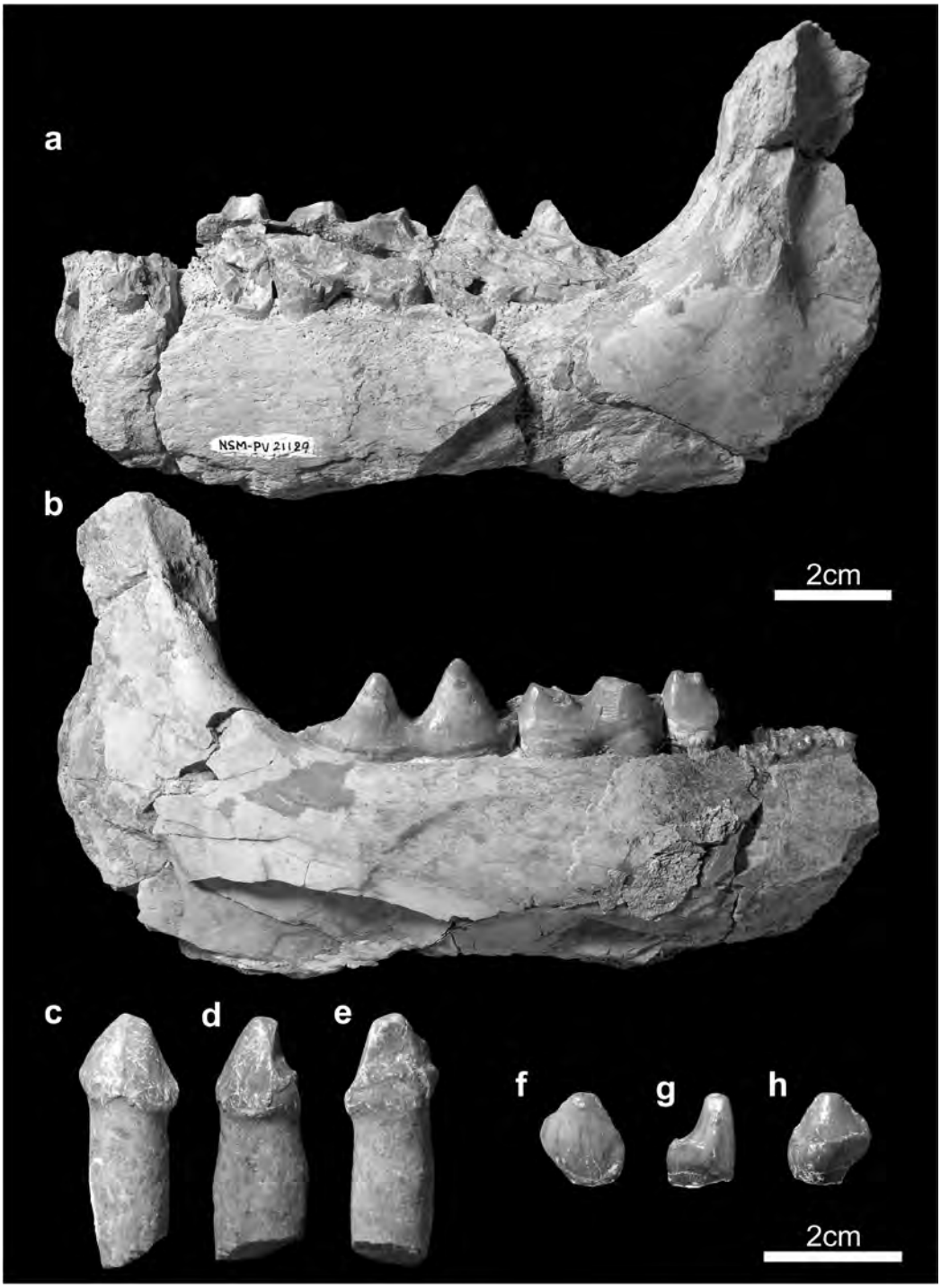

Fig. 82. *Lophiodon* sp. from Aumelas (NMNS-PV 21129 and 21130) and Robiac (NMNS-PV 21358). NMNS-PV 21129, left mandibular fragment with possible p4 root and broken M1–3 in labial (a) and lingual (b) views. NMNS-PV 21130, right upper or left lower incisor in labial (c), distal (d), and lingual (e) views. NMNS-PV 21358, right upper or left lower incisor in labial (f), mesial (g), and lingual (h) views. Scale bar for c–h is shown at bottom right.

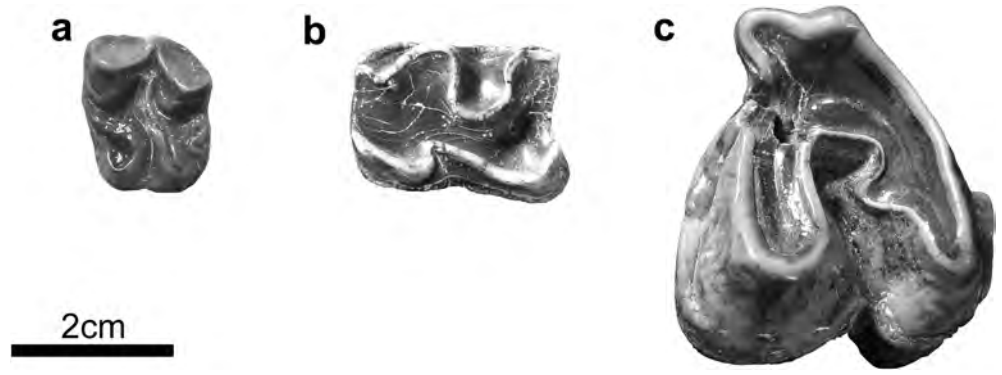

Fig. 83. *Anchitherium aurelianense* (Cuvier, 1825) (NMNS-PV 21672), Rhinocerotidae gen. et sp. indet. 1 (NMNS-PV 21673), and 2 (NMNS-PV 21674) from Faluns de Touraine. NMNS-PV 21672, left M3 (a) in occlusal view. NMNS-PV 21673, possible left p3 or p4 (b) in occlusal view. NMNS-PV 21674, left M3 (c) in occlusal view.

reworked fossils from older MN 2 and MN 3 deposits (Ginsburg, 2001). NMNS-PV 21672 has a brachydont crown that is narrower posteriorly, as in the M3 of *Anchitherium*. NMNS-PV 21672 is referable to M3 of *A. aurelianense* based on size and morphology, but it is overall damaged by abrasion, suggesting that it is a reworked fossil.

Suborder Tapiromorpha Haeckel, 1866
Infraorder Ceratomorpha Wood, 1937
Superfamily Rhinocerotoidea Gray, 1821
Family Rhinocerotidae Gray, 1821

Gen. et sp. indet. 1
(Fig. 83b)

Localities and Materials: Faluns de Touraine: NMNS-PV 21673, possible left p3 or p4

Comments: About six Miocene rhinocerotid genera have been reported from the Miocene Faluns de Touraine and vicinity (Ginsburg, 2001). This lower premolar has a shallow trigonid basin, lacks a developed anterior crest from metaconid, and has a distinct labial cingulid unlike in *Protaceratherium* Abel, 1910, *Diaceratherium* Dietrich, 1931, and *Hispanotherium* Crusafont and Villalta, 1947.

Gen. et sp. indet. 2
(Fig. 83c)

Localities and Materials: Faluns de Touraine: NMNS-PV 21674, left M3

Comments: This M3 is too large to be allocated to the same species as NMNS-PV 21673, which is mentioned above. NMNS-PV 21674 has a short crochet on the metaloph and a faint antecrochet as seen in *Prosantorhinus* Heissig, 1974 and in *Plesiaceratherium* Young, 1937, but it apparently differs from that of *Hispanotherium.* NMNS-PV 21674 is damaged by abrasion as well as NMNS-PV 21672 (left M3 of *Anchitherium aurelianense*), implying that both are reworked.

Acknowledgments

I wish to express my gratitude to Drs. Jens L. Franzen (Forschungsinstitut Senckenberg Frankfurt, Germany, and Naturhistorisches Museum Basel, Switzerland), Gregg F. Gunnell (University of Michigan, Museum of Paleontology, Ann Arbor, U.S.A.), and Jean A. Remy (Université Montpellier II, Montpellier, France) for critically reading and making many of helpful suggestions, which improved the early manuscript. The classification of perissodactyls cataloged here owes largely to generous helps of Drs. Jens L. Franzen and Jean A. Remy. I thank Drs. Bernard Marandat (Université Montpellier II, Montpellier, France) and Pascal Tassy (Muséum National d'Histoire Naturelle, Paris, France) for their helpful assistance and access to comparable specimens.

Literatures Cited

Abel O., 1910. Kritische Untersuchungen über die paläogenen Rhinocerotiden Europas. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt, Wien*, **20**: 1–52.

Abusch-Siewert, S., 1983. Gebißmorphologische Untersuchungen an eurasiatischen Anchitherien (Equidae, Mammalia) unter besonderer Berücksichtigung der Fundstelle Sandelzhausen. *Courier Forschungsinstitut Senckenberg*, **62**: 1–361.

Badiola, A., H. Astibia, X. Pereda Suberbiola, and X. Murelaga, 2002. First record of the genus *Leptolophus* Remy, 1965 (Mammalia, Perissodactyla) in the late Eocene (Priabonian) of Europe. *Geodiversitas*, **24**: 841–848.

Badiola, A., X. Pereda-Suberbiola, and M. A. Cuesta, 2005. Una nueva especie de *Pachynolophus* (Mammalia, Perissodactyla) de Zambrana (Álava, Región Vasco-Cantábrica). Análisis filogenético de *Pachynolophus* y primera cita en el Eoceno superior de la Península Ibérica. *Géobios*, **38**: 1–16.

Blainville, H. M. D. de, 1846 (1839–1864). *Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie*. 4 vols., Paris.

Bonaparte, C.-L., 1850. Conspectus Systematis Mastozoologiae. Editio altera reformata. *In*: *Conspectus Systemanum Vertebratorum*, Leiden.

Brunet, M. and Y. Jehenne, 1989. Révision des genres *Plagiolophus* Pomel, 1847 et *Paloplotherium* Owen, 1848, Mammalia, Palaeotheriidae du Paléogène d'Europe; intéret biochronologique. *Annales de Paléontologie*, **75**: 23–52.

Casanovas-Cladellas, M. L., 1975. Datos sobre los Perisodáctilos del yacimiento de Roc de Santa; la nueva especie *Palaeotherium crusafonti*. *Acta Geológica Hispánica*, **10**: 121–126.

Casanovas-Cladellas, M. L. and J. V. Santafé-Llopis, 1980. El *Palaeotherium* de talla grande (Palaeotheriidae, Perissodactyla) del yacimiento ludiense de Sossis (Tremp, Lerida). *Boletín Informativo Instituto Provincial de Paleontología de Sabadell*, **12**: 21–29.

Casanovas-Cladellas, M. L. and J. V. Santafé-Llopis, 1989. Dos nuevos Paleotéridos (Mammalia, Perissodactyla) del yacimiento eocénico de Llamaquique (Oviedo). *Trabajos de Geología, Universidad de Oviedo*, **18**: 37–52.

Casanovas-Cladellas, M. L. and J. V. Santafé-Llopis, 1991. Los Paleotéridos (Mammalia, Perissodactyla) del yacimiento de Llamaquique (Oviedo, España). *Boletín de Ciencias de la Naturaleza, Instituto de Estudios Asturianos*, **41**: 101–188.

Casanovas-Cladellas, M. L., L. Checa Soler, and J. V. Santafé-Llopis, 1992. Éléments du squelette postcrânien du genre *Palaeotherium* (Perissodactyla) du Ludien de Roc de Santa (Province de Lerida, Espagne). *Géobios*, **25**: 535–552.

Cope, E. D., 1889. The vertebrata of the Swift Current River, II. *American Naturalist*, **23**: 151–155.

Crusafont-Pairó, M. and J. F. de Villalta Comella, 1947. Sobre un interesante rinoceronte (*Hispanotherium* nov. gen.) del Mioceno del valle del Manzanares. *Las Ciencias*, **12**: 869–883.

Cuesta Ruiz-Colmenares, M. Á., 1993. Los Palaeotheriidae (Perissodactyla, Mammalia) del Eoceno de la Cuenca del Duero (Castilla y Leon, España). *Estudios Geológicos*, **49**: 87–109.

Cuesta Ruiz-Colmenares, M. Á., 1994a. Los Pachynolophinae (Equoidea, Perissodactyla, Mammalia) del Eoceno de la Cuenca del Duero (Castilla y León, España). *Stvdia Geologica Salmanticensia*, **30**: 21–63.

Cuesta Ruiz-Colmenares, M. Á., 1994b. Los Plagiolophinae (Remy, 1976) nuevo rango (Perissodactyla, Mammalia) del Eoceno de la Cuenca del Duero (Castilla y Leon, España). *Estudios Geológicos*, **50**: 253–279.

Cuesta Ruiz-Colmenares, M. Á., 1994c. Los Lophiodontidae (Perissodactyla, Mammalia) del Eoceno de la Cuenca del Duero (Castilla y León, España). *Stvdia Geologica Salmanticensia*, **29**: 23–65.

Cuesta Ruiz-Colmenares, M. Á., 1996. Primeros hallazgos de Lophiodontidae **(**Perissodactyla**,** Mammalia) en el yacimiento eocénico de Mazaterón (Cuenca del Duero, España): Implicaciones bioestratigráficas. *Stvdia Geologica Salmanticensia*,

32: 39–48.

Cuvier, G., 1804. Sur les espèces d'animaux dont proviennent les os fossiles répandus dans la pierre à plâtre des environs de Paris. (1.–3. mém, 1. sect.). *Annales du Muséum National d'Histoire Naturelle, Paris*, **3**: 275–303, 364–387, 442–472.

Cuvier, G., 1805. Sur les espèces d'animaux dont proviennent les os fossiles répandus dans la pierre à plâtre des environs de Paris. (3. mém, 2. sect.): restitution des pieds de devant. *Annales du Muséum National d'Histoire Naturelle, Paris*, **6**: 253–283.

Cuvier, G., 1812. *Recherches sur les ossemens fossiles de quadrupèdes, où l'on rétablit les caractères de plusieurs espèces d'animaux que les révolutions du globe paroissent avoir détruites*. 4 vols., Déterville, Paris.

Cuvier, G., 1822–25. *Recherches sur les ossemens fossiles (Nouvelle Edition)*. G. Dufour et E. d'Ocagne, Paris.

Dedieu, P., 1977. Sur la systématique des Tapiroidea (Mammalia) de l'Eocène européen. *Comptes Rendus de l'Académie des Sciences, Paris*, **284**: 2219–2222.

Depéret, C., 1901. Révision des formes européennes de la famille des Hyracothéridés. *Bulletin de la Société Géologique de France, Paris*, **4**: 199–225.

Depéret, C., 1917. Monographie de la faune de mammifères fossiles du Ludien inférieur d'Euzèt-les-Bains (Gard). *Annales de l'Université de Lyon, Nouvelle Série (I. Sciences, Médecine)*, **40**: 1–290.

Desmarest, A. G., 1822. *Mammalogie ou description des espèces de mammifères. Seconde partie, contenant les ordres des Rongeurs, des Édentés, des Pachydermes, des Ruminans et des Cétacés*. Mme Veuve Agasse, Imprimeur-Libraire, Paris.

Dietrich, W. O., 1931. Neue Nashornreste aus Schwaben (*Diaceratherium tomerdingensis* n. g. n. sp.). *Zeitschrift für Säugetierkunde*, **6**: 203–220.

Fischer, J. B., 1829. *Synopsis Mammalium*. J. G. Cottae, Stuttgart. 752 pp.

Fischer, K. H., 1977. Neue Funde von *Rhinocerolophiodon* (n. gen.), *Lophiodon*, und *Hyrachyus* (Ceratomorpha, Perissodactyla, Mammalia) aus dem Eozän des Geiseltals bei Halle (DDR). 1. Teil. *Rhinocerolophiodon*. *Zeitschrift für geologische Wissenschaft, Berlin*, **5**: 909–919.

Forstén, A., 1991. Size trends in holarctic Anchitherines (Mammalia, Equidae). *Journal of Paleontology*, **65**: 147–159.

Fraas, O., 1869. *Die geognostische Sammlung Württembergs im Erdgeschoss des Königlichen Naturalien-Cabinets zu Stuttgart. Ein Führer für die Besucher desselben*. Kosten des Verfassers gedruckt, Stuttgart. 57 pp.

Franzen, J. L., 1968. *Revision der Gattung Palaeotherium Cuvier 1804 (Palaeotheriidae, Perissodactyla, Mammalia)*. Inaugural-Dissertation zur Erlangung der Doktorwürde der Naturwissenschaftlich-mathematischen Fakultät der Albert-Ludwigs Universität zu Freiburg i. Br., Band 1 (Text), 181 pp. and 2 (Tafel und Tabellen).

Franzen, J. L., 1987. Mammalian reference levels MP 11–13. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 24–25.

Franzen, J. L., 1989. Origin and systematic position of the Palaeotheriidae. *In*: D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford Monographs on Geology and Geophysics, **15**, Oxford University Press, Oxford. p. 102–108.

Franzen, J. L., 1999. *Lophiotherium sondaari* n. sp. (Mammalia, Perissodactyla, Equidae) aus der oberen Unterkohle des Geiseltales bei Halle (Saale). *Deinsea*, **7**: 187–194.

Franzen, J. L., 2006. *Eurohippus* n.g., a new genus of horses from the Middle to Late Eocene of Europe. *Senckenbergiana lethaea*, **86**: 97–102.

Franzen, J. L. and H. Haubold, 1986. Revision der Equoidea aus den eozänen Braunkohlen des Geiseltales bei Halle (DDR). *Palaeovertebrata*, **16**: 1–34.

Froehlich, D. J., 1999. Phylogenetic systematics of basal perissodactyls. *Journal of Vertebrate Paleontology*, **19**: 140–159.

Froehlich, D. J., 2002. Quo vadis *Eohippus*? The systematics and taxonomy of the early Eocene equids (Perissodactyla). *Zoological Journal of the Linnean Society*, **134**: 141–256.

Gervais, P., 1849. Recherches sur les mammifères fossiles des genres *Palaeotherium* et *Lophiodon*, et sur les autres animaux de la même classe que l'on a trouvés avec eux dans le midi de la France. *Comptes Rendus de l'Académie des Sciences, Paris*, **29**: 381–384, 568–579.

Gervais, P., 1852 (1848–52). *Zoologie et paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivants et fossiles de la France*. 3 vols., 1st édition. Bertrand, Paris. 271 pp.

Gervais, P., 1859. *Zoologie et paléontologie françaises ou nouvelles recherches sur les animaux vertébrés dont on trouve les ossements enfouis dans le sol de la France et sur leur comparaison avec les espèces propres aux autres régions du globe*. Bertrand, Paris, 544 pp.

Gervais, P., 1875. *Palaeothérium* du calcaire grossier. *Journal de Zoologie*, **4**: 421–422.

Gill, T., 1872. Arrangement of the families of mammals with analytical tables. *Smithsonian Miscellaneous Collections*, **11**:

1–98.

Ginsburg, L., 2001. Les faunes de mammifères terrestres du Miocène moyen des Faluns du bassin de Savigné-sur-Lathan (France). *Geodiversitas*, **23**: 381–394.

Gray, J. E., 1821. On the natural arrangement of vertebrose animals. *London Medical Repository, Monthly Journal and Review*, **15**: 296–310.

Haeckel, E., 1866. *Generelle Morphologie der Organismen. Band 1: Allgemeine Anatomie der Organismen*. Georg Reimer, Berlin.

Haupt, O., 1925. Die Palaeohippiden der eocänen Süßwasserablagerungen von Messel bei Darmstadt. *Abhandlungen der Hessischen Geologischen Landesanstalt zu Darmstadt*, **6**: 1–159.

Heissig, K., 1974. Neue Elasmotherini (Rhinocerotidae, Mammalia) aus dem Obermiozän Anatoliens. *Mitteilungen der Bayerische Staatssammlung für Paläontologie und Historische Geologie*, **14**: 21–35.

Holbrook, L. T., 2009. Osteology of *Lophiodon* Cuvier, 1822 (Mammalia, Perissodactyla) and its phylogenetic implications. *Journal of Vertebrate Paleontology*, **29**: 212–230.

Hooker, J. J., 1986. Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. *Bulletin of the British Museum (Natural History), London (Geology)*, **39**: 1–478.

Hooker, J. J., 1987. Mammalian reference levels MP 14–16. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 26–27.

Hooker, J. J., 1989. Character polarities in early perissodactyls and their significance for *Hyracotherium* and infraordinal relationships. *In*: D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford Monographs on Geology and Geophysics, **15**, Oxford University Press, Oxford. p. 79–101.

Hooker, J. J., 1994. The beginning of the equoid radiation. *Zoological Journal of the Linnaean Society*, **112**: 29–63.

Hooker, J. J., 2005. Perissodactyla. *In*: K. D. Rose and J. D. Archibald (eds.), *The rise of placental mammals: origins and relationships of the major extant clades*. The Johns Hopkins University Press, Baltimore. p. 199–214.

Laurillard, C. L., 1849. *Lophiodon*. *In*: A. d'Orbigny, *Dictionnaire Universel d'Histoire Naturelle*, Paris, 7. p. 438–439.

Legendre, S., 1987. Mammalian reference levels MP 17–20. *In*: N. Schmidt-Kittler (ed.), International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 28–29.

Lemoine, V., 1878. Communication sur les ossements fossiles des terrains tertiaires inférieures des environs de Reims faite à la Société d'Histoire Naturelle de Reims. *Bulletin de la Société d'Histoire Naturelle, Reims*, **2**: 90–113.

Luterbacher, H. P., J. R. Ali, H. Brinkhuis, F. M. Gradstein, J. J. Hooker, S. Monechi, J. G. Ogg, J. Powell, U. Röhl, A. Sanfilippo, and B. Schmitz, 2004. The Paleogene Period. *In*: F. M. Gradstein, J. G. Ogg, and A. G. Smith (eds.), *A Geological Time Scale 2004*. Cambridge University Press, Cambridge, United Kingdom. p. 384–408.

Matthes, H. W., 1977. Die Equiden aus dem Eozän des Geiseltales. 1. Die Zähne. *In*: H. W. Matthes and B. Thaler (eds.), *Eozäne Wirbeltiere des Geiseltales*. Wissenschaftliche Beiträge der Martin-Luther-Universität, Halle-Wittenberg, 1977/2 (P5). p. 5–39.

McKenna, M. C. and S. K. Bell, 1997. *Classification of mammals above the species level*. Columbia University Press, New York. 631 pp.

Meyer, H. von, 1844. Über die fossilen Knochen aus dem Tertiär-Gebilde des Cerro de San Isidro bei Madrid. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, **1844**: 289–310.

Meyer, H. von, 1852. Mittheilungen an Professor Bronn gerichtet. *Neues Jahrbuch für Mineralogische, Geognosie, Geologische und Petrefaktenkunde*, **1852**: 831–833.

Miyata, K. and T. Tomida, 2010. *Anchitherium* (Mammalia, Perissodactyla, Equidae) from the Early Miocene Hiramaki Formation, Gifu Prefecture, Japan, and its implication for the early diversification of Asian *Anchitherium*. *Journal of Paleontology*, **84**: 763–773.

Noulet, J.-B., 1851. Note sur une nouvelle espèce de Pachyderme fossile du genre *Lophiodon* (*Lophiodon lautricense*). *Mémoires de l'Académie des Sciences, Inscription et Belles Lettres de Toulouse*, 4 sér., **1**: 245–250.

Noulet, J.-B., 1863. Etude sur les fossiles du terrain éocène supérieur du bassin de l'Agout (Tarn). *Mémoires de l'Académie des Sciences, Inscription et Belles Lettres de Toulouse*, 6e sér., **1**: 181–206.

Owen, R., 1848a. Description of teeth and portions of jaws in two extinct anthracotheroid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, **4**: 103–141.

Owen, R., 1848b. On the fossil remains of Mammalia referable to the genus *Palaeotherium*, and to two genera *Paloplotherium*

and *Dichodon*, hitherto undefined, from the Eocene Sand at Hordle, Hampshire. *Quarterly Journal of the Geological Society of London*, **4**: 17–42.

Pavlow, M., 1888 (1887–1888). Études sur l'Histoire Paléontologique des ongulés en Amérique et en Europe. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 1–80.

Pictet, F.-J., 1857. Seconde partie: description des ossements fossiles trouvés au Mauremont. *In*: F. J. Pictet, C.-T. Gaudin, and P. Delaharpe, 1855–1857, *Mémoire sur les animaux vertébrés trouvés dans le terrain sidérolithique du canton de Vaud et appartenant à la faune éocène*. Matériaux pour la Paléontologie, Suisse, (1)2: 27–120.

Pictet, F.-J. and A. Humbert, 1869. *Mémoire sur les animaux vertébrés trouvés dans le terrain sidérolithique du canton de Vaud et appartenant à la faune éocène. Supplément*. Matériaux pour la Paléontologie, Suisse, (5)2: 125–197.

Pomel, A., 1847a. Note critique sur le genre *Palaeotherium*. *Bulletin de la Société Géologique de France*, **2**: 584–587.

Pomel, A., 1847b. Notes sur les mammifères et reptiles fossiles des terrains éocènes de Paris, inférieurs au dépôt gypseux. *Archives des Sciences Physiques et Naturelles de Genève*, **4**: 326–330.

Pomel, A., 1853. *Catalogue méthodique et descriptif des vertébrés fossiles découverts dans le bassin hydrographique supérieur de la Loire, et surtout dans la vallée de son affluent principal l'Allier*, Baillière, Paris. 193 pp.

Prothero, D. R. and R. M. Schoch, 1989. Origin and evolution of the Perissodactyla: summary and synthesis. *In*: D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford Monographs on Geology and Geophysics, **15**, Oxford University Press, Oxford. p. 504–529.

Pulgar, J. A., M. Gutiérrez-Claverol, and M. Torres Alonso, 1999. Constitución geológica y características geotécnicas del subsuelo urbano de La Tenderina-Ventanielles (Oviedo). *Trabajos de Geología, Universidad de Oviedo*, **21**: 295–307.

Remy, J. A., 1965. Un nouveau genre de Paléothéridé (Perissodactyla) de l'Eocène supérieur du Midi de la France. *Comptes Rendus de l'Académie des Sciences, Paris*, **260**: 4362–4364.

Remy, J. A., 1976. *Étude comparative des structures dentaires chez les Palaeotheriidae et divers autres périssodactyles fossiles*. Thèse 3e cycle, Université de Strasbourg I, Strasbourg, France, 207 pp.

Remy, J. A., 1985. Nouveaux gisements de mammifères et reptiles dans les Grès de Célas (Eocène sup. du Gard), étude des Palaeothériidés (Perissodactyla, Mammalia). *Palaeontographica*, **A189**: 171–225.

Remy, J. A., 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. VIII. Périssodactyles. *Palaeontographica*, **A205**: 155–172.

Remy, J. A., 1992. Observations sur l'anatomie crânienne du genre *Palaeotherium* (Perissodactyla, Mammalia): mise en évidence d'un nouveau sous-genre *Franzenitherium*. *Palaeovertebrata*, **21**: 103–224.

Remy, J. A., 1998. Le genre *Leptolophus* (Perissodactyla, Mammalia): morphologie et histologie dentaires, anatomie crânienne, implications fonctionnelles. *Palaeovertebrata*, **27**: 45–108.

Remy, J. A., 2000. *Plagiolophus huerzeleri*, une nouvelle espèce de Palaeotheriidae (Perissodactyla, Mammalia) de l'Oligocène inférieur (Rupélien, MP 23), à Murs (Vaucluse, France). *Géobios*, **33**: 489–503.

Remy, J. A., 2001. Sur le crâne de *Propalaeotherium isselanum* (Mammalia, Perissodactyla, Palaeotheriidae) de Pépieux (Minervois, Sud de la France). *Geodiversitas*, **23**: 105–127.

Remy, J. A., 2004. Le genre *Plagiolophus* (Palaeotheriidae, Perissodactyla, Mammalia): révision systématique, morphologie et histologie dentaires, anatomie crânienne, essai d'interprétation fonctionnelle. *Palaeovertebrata*, **33**: 17–281.

Savage, D. E., D. E. Russell, and P. Louis, 1965. European Eocene Equidae (Perissodactyla). *University of California Publications, Geological Sciences*, **56**: 1–94.

Savage, D. E., D. E. Russell, and P. Louis, 1966. Ceratomorpha and Ancylopoda (Perissodactyla) from the Lower Eocene Paris Basin, France. *University of California Publications, Geological Sciences*, **66**: 1–38.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene—Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A*, **10**: 1–312.

Schoch, R. M., 1989. A review of the tapiroids. *In*: D. R. Prothero and R. M. Schoch (eds.), *The Evolution of Perissodactyls*. Oxford Monographs on Geology and Geophysics, **15**, Oxford University Press, Oxford. p. 298–320.

Stehlin, H. G., 1904a. Sur les mammifères des sables bartoniens du Castrais. *Bulletin de la Société géologique de France, Paris*, 4e sér., **4**: 445–475.

Stehlin, H. G., 1904b. Die Säugetiere des schweizerischen Eocaens. Critischer Catalog der Materialien. Zweiter Teil: *Palaeotherium*. *Plagiolophus*. *Propalaeotherium*. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **31**: 155–258.

Sudre, J., 1971. Etude de la variabilité chez *Lophiodon lautricense* Noulet. *Palaeovertebrata*, **4**: 67–95.

Wood, H. E., 1937. Perissodactyl suborder. *Journal of Mammalogy*, **18**: 106.

Young, C.-C., 1937. On a Miocene mammalian fauna from Shantung. *Bulletin of the Geological Society of China*, **17**: 209–238.

Appendix 1. Measurements (in mm) of the perissodactyl specimens. Abbreviations: alv=at alveolus, D=depth, H=height, L=length, W=width. An asterisk (*) and a dash (—) means estimate (damaged) and not available to measure, respectively.

Eocene Perissodactyls

Propalaeotherium sp. cf. *P. isselanum* from Aumelas
NMNS-PV 21128: right M2 L = 13.7, W = 16.8
right M3 L = 13.5, W = 17.1*
Lophiotherium cervulum from Euzèt les Bains
NMNS-PV 21388: left M1–3 L = 22.0
left P3 L = 6.7, W = 8.0
left P4 L = 6.7, W = 8.9
left M1 L = 6.6, W = 8.8
left M2 L = 7.9, W = 10.3
left M3 L = 7.7, W = 10.5
NMNS-PV 21389: left M1–3 L = —
left DP3 L = 6.6, W = 7.4
left DP4 L = 7.0, W = 8.1
left M1 L = 7.0, W = 9.2
left M2 L = 7.3, W = 9.8
left M3 L = —, W = —
NMNS-PV 21390: left c1 L = 4.4, W = 3.4
diastema between left c1 and p2 = 30.0 alv
left mandibular D below m3 trigonid = 23.8
left p2–m3 L = 43.6*
left m1–3 L = 25.1*
left p2 L = 5.2, W = 5.6
left p3 L = 5.9, trigonid W = 4.5, talonid W = 4.7
left p4 L = 6.7, trigonid W = 5.4, talonid W = 5.5
left m1 L = 7.0, trigonid W = 5.5, talonid W = 5.3*
left m2 L = 7.7, trigonid W = 6.0, talonid W = 5.8
left m3 L = 10.7*, trigonid W = 5.3*, talonid W = 4.6*
right c1 L = 4.1*, W = 3.5*
NMNS-PV 21391: left mandibular D below m3 trigonid = —
possible left p3 L = 6.1, trigonid W = 3.1*, talonid W = 3.8
possible left p4 L = 6.4, trigonid W = 3.9, talonid W = 4.4
left m1 L = 6.9, trigonid W = 4.3, talonid W = 4.6
left m2 L = 7.2, trigonid W = 5.3, talonid W = 5.5
NMNS-PV 21392: right left mandibular D below m3 trigonid = 20.0*
right p2–m3 L = 42.0*
right m1–3 L = 23.9
right p2 L = 5.3, W = 3.1
right p3 L = 6.4, trigonid W = 4.3, talonid W = 5.0
right p4 L = 6.6, trigonid W = 5.2, talonid W = 5.5
right m1 L = 6.8, trigonid W = 5.5, talonid W = 5.4
right m2 L = 7.5, trigonid W = 5.9, talonid W = 5.7
right m3 L = 10.2, trigonid W = 5.6, talonid W = 4.7*
NMNS-PV 21393: possible left M1 L = —, W = —
possible left M2 L = 8.5, W = 11.9
possible left M3 L = 8.5, W = 11.4
Palaeotherium castrense robiacense from Robiac
NMNS-PV 21332: right M3 L = 35.6, W = 23.8
NMNS-PV 21333: left P3 L = 22.1, W = 29.2
NMNS-PV 21334: possible left p3 L = 27.2, trigonid W = 16.6, talonid W = 17.6
possible left p4 L = 30.8, trigonid W = 18.2, talonid W = 18.5
NMNS-PV 21335: right P2 L = 18.4, W = 22.8
right P3 L = 23.7, W = 29.2
right P4 L = 22.8*, W = 31.6
Palaeotherium curtum frohnstettense from St. Capraise d'Eymet
NMNS-PV 21543: right M2 L = 23.8*, W = 27.1*
right M3 L = 29.5, W = 31.2
left M1 L = —, W = 25.3*
left M2 L = 25.5, W = 31.3
left M3 L = 29.3, W = 31.2

Appendix 1. Continued

Palaeotherium curtum villerealense from Civrac de Blaye
NMNS-PV 21366: mandibular D below m3 trigonid = 37.0
left p2–m3 L = 110.2*
left p2–4 L = 44.9*
left m1–3 L = 67.2*
left p2 L = 11.9*, trigonid W = —, talonid W = —
left p3 L = 15.8, trigonid W = 9.9, talonid W = 9.9
left p4 L = 15.6, trigonid W = 11.0, talonid W = 10.8
left m1 L = 18.3, trigonid W = 11.8, talonid W = 11.5
left m2 L = 20.2, trigonid W = 12.8, talonid W = 11.8
left m3 L = 28.9*, trigonid W = 13.1, talonid W = 10.6
NMNS-PV 21367: right P2–M3 L = 106.4*
right P2–4 L = 43.8*
right M1–3 L = 64.7
right P2 L = 12.3*, W = —
right P3 L = 15.4, W = 20.2
right P4 L = 16.9, W = 22.6
right M1 L = 19.0, W = 22.8
right M2 L = 22.5, W = 26.2
right M3 L = 26.3, W = 26.7
NMNS-PV 21368: right P2–4 L = 45.3
right P2 L = 13.9, W = 15.4
right P3 L = 15.8, W = 20.0
right P4 L = 16.6, W = 21.7
right M1 L = 18.1, W = 24.0
right M2 L = 22.1, W = 26.1
NMNS-PV 21369: mandibular D below m3 trigonid = 41.9
right m3 L = 28.3, trigonid W = 13.7, talonid W = 12.0
NMNS-PV 21370: mandibular D below m3 trigonid = 37.5
mandibular height from ventral margin to condylar process = 97.1*
left m1–3 L = 64.9
left p3 L = 14.9, trigonid W = 9.4, talonid W = 10.4
left p4 L = 15.3, trigonid W = 10.4, talonid W = 11.2
left m1 L = 16.5, trigonid W = 10.7, talonid W = 11.6
left m2 L = 19.1, trigonid W = 11.4, talonid W = 11.6
left m3 L = 28.2, trigonid W = 12.1, talonid W = 10.0
NMNS-PV 21376: right P3 L = 17.4, W = 19.9
right P4 L = 18.2, W = 21.4
right M1 L = 20.2, W = 23.3
Palaeotherium curtum villerealense from La Débruge:
NMNS-PV 21468: mandibular D below p4 = 21.7
right p3 L = 17.6*, trigonid W = 9.4, talonid W = 9.6
right p4 L = 20.1, trigonid W = 9.7, talonid W = 9.8
NMNS-PV 21469: mandibular D below p4 = 24.3
right p2–4 L = 55.0
right p1 L = 8.0, W = 5.1
right p2 L = 17.0, trigonid W = 7.9, talonid W = 9.6
right p3 L = 18.0, trigonid W = 10.3, talonid W = 11.6
right p4 L = 18.9, trigonid W = 11.7, talonid W = 12.4
NMNS-PV 21490: right p2 L = 17.8, trigonid W = —, talonid W = —
right p3 L = 18.8, trigonid W = —, talonid W = 11.5
Palaeotherium sp. cf. *P. curtum* from La Débruge
NMNS-PV 21470: possible right p3 or p4 L = 17.7, trigonid W = 10.9, talonid W = 12.1
Palaeotherium sp. cf. *P. curtum* from St. Capraise d'Eymet
NMNS-PV 21540: possible right P2 L = 14.6, W = 18.6
NMNS-PV 21541: possible left P2 L = 13.0, W = 17.9
NMNS-PV 21542: labial fragment of possible upper premolar, L = 17.6
Palaeotherium lautricense from Robiac
NMNS-PV 21336: left m1–3 L = —
left p3 L = 10.7, trigonid W = 6.5, talonid W = 6.6
left p4 L = 11.0, trigonid W = 7.3, talonid W = 7.3
left m1 L = 12.2, trigonid W = 7.5, talonid W = 8.3
left m2 L = 13.7, trigonid W = 8.8, talonid W = 8.5

Appendix 1. Continued

left m3 L = —, trigonid W = 8.2, talonid W = 6.5
NMNS-PV 21337: possible left p4 or m1 L = 13.8, trigonid W = 8.4, talonid W = 8.6*
NMNS-PV 21338: mandibular D below m2 talonid = 26.0
left m1–3 L = 46.0*
left p3 L = 10.8, trigonid W = 7.3, talonid W = 7.8
left p4 L = 11.4, trigonid W = 8.2, talonid W = 8.6
left m1 L = 11.7, trigonid W = 8.4, talonid W = 8.6
left m2 L = 13.8, trigonid W = 9.0, talonid W = 9.0
left m3 L = 20.2*, trigonid W = 8.0*, talonid W = 7.6
NMNS-PV 21339: mandibular D below m3 trigonid = 31.6*
mandibular height from ventral margin to coronoid process = 74.8*
right m1–3 L = 46.0*
right m1 L = 12.0*, trigonid W = —, talonid W = 8.7
right m2 L = 13.0, trigonid W = 8.6, talonid W = 8.7
right m3 L = 20.7, trigonid W = 8.3, talonid W = 7.5
NMNS-PV 21340: right p3 L = 12.4, trigonid W = 7.6, talonid W = 8.8
NMNS-PV 21341: right p3 L = 11.1, trigonid W = 6.4, talonid W = 7.5
NMNS-PV 21344: left M3 L = 16.6, W = 16.8
Palaeotherium magnum girondicum from Civrac de Blaye
NMNS-PV 21365: left M2 L = 32.2, W = 33.4
NMNS-PV 21371: mandibular D below m3 trigonid = 58.0
right p2–m3 L = 188.9
right p2–4 L = 81.8
right m1–3 L = 107.0
right p2 L = 25.6, trigonid W = 15.3, talonid W = 16.5
right p3 L = 29.2 trigonid W = 18.7, talonid W = 18.5
right p4 L = 30.3, trigonid W = 20.4, talonid W = 19.8
right m1 L = 30.5, trigonid W = 19.8, talonid W = 19.3
right m2 L = 33.3, trigonid W = 21.0, talonid W = 19.2
right m3 L = 47.4, trigonid W = 22.1, talonid W = 17.8
NMNS-PV 21372: right P2–M3 L = 187.2
right P2–4 L = 81.3
right M1–3 L = 107.7
right P2 L = 26.8, W = 26.7
right P3 L = 27.3, W = 30.0
right P4 L = 30.0, W = 30.7
right M1 L = 32.0, W = 33.4
right M2 L = 37.6, W = 39.6
right M3 L = 42.2, W = 39.2
NMNS-PV 21373: right M2 L = 30.0, W = 36.5
right M3 L = 37.8, W = —
NMNS-PV 21374: possible right I2 or left i2 L = 13.9, W = 10.0
NMNS-PV 21375: possible right C1 or left c1 L = 20.5, W = 15.9
Palaeotherium magnum girondicum from La Débruge
NMNS-PV 21471: left M1–3 L = 114.5
left P3 L = —, W = —
left P4 L = 29.5, W = 34.0*
left M1 L = 32.2, W = 35.6
left M2 L = 40.1, W = 39.8
left M3 L = 43.0*, W = —
NMNS-PV 21472: right P4 L = 29.0, W = 32.8
right M1 L = 31.3, W = 36.7
NMNS-PV 21473: right p2 L = 33.6, trigonid W = 12.2*, talonid W = 16.5
NMNS-PV 21474: left p2 L = 31.8, trigonid W = 13.9, talonid W = 16.5
NMNS-PV 21475: right anterior premolar, talonid W = 13.8*
NMNS-PV 21476: left P4 or M1 L = 31.5, W = 36.5
NMNS-PV 21477: anterior incisor L = 13.1, W = 13.0
NMNS-PV 21478: anterior incisor L = 13.0, W = 13.4
NMNS-PV 21479: right C1 L = 23.4, W = 18.2
Palaeotherium medium euzetense from Euzèt les Bains
NMNS-PV 21394: right c1 L = 12.3, W = 9.1
right p2 L = 14.7, trigonid W = 7.3*, talonid W = 8.1*
right p3 L = 15.9, trigonid W = 8.4*, talonid W = 9.1

Appendix 1. Continued

left mandibular D below m3 trigonid = 45.6
diastema between left c1 and p1 = 13.8 alv
left c1 L = 11.2, W = 8.1
left p1–m3 L = 113.9
left p2–m3 L = 106.7
left p2–4 L = 46.7
left m1–3 L = 60.5
left p1 L = 6.8, W = 4.7
left p2 L = 14.8, trigonid W = 7.2, talonid W = 6.9
left p3 L = 16.0, trigonid W = 9.1, talonid W = 9.2
left p4 L = 16.9, trigonid W = 10.6, talonid W = 10.7*
left m1 L = 15.8*, trigonid W = 10.4, talonid W = 11.4
left m2 L = 18.5, trigonid W = 11.8, talonid W = 12.2
left m3 L = 26.9, trigonid W = 11.9, talonid W = —

NMNS-PV 21395: mandibular D below m3 trigonid = 39.2
left m1–3 L = 70.1
left p3 L = —, trigonid W = —, talonid W = 10.8
left p4 L = 18.4, trigonid W = 12.0, talonid W = 12.5
left m1 L = 19.1, trigonid W = 11.7, talonid W = 12.7
left m2 L = 21.2, trigonid W = 13.5, talonid W = 13.8
left m3 L = 30.6, trigonid W = 13.1, talonid W = 12.1

NMNS-PV 21396: right M2 L = 22.3, W = 24.1

NMNS-PV 21398: mandibular D below m3 trigonid = 44.6*
left m2 L = 20.2, trigonid W = 13.2, talonid W = 12.4
left m3 L = 29.9, trigonid W = 12.8, talonid W = 11.3

Palaeotherium medium perrealense from La Débruge

NMNS-PV 21480: left P2–M3 L = 110.0*
left P2–4 L = 50.1*
left M1–3 L = 63.6
left P3 L = 16.5*, W = —
left P4 L = 17.8, W = 21.4
left M1 L = 19.2, W = 21.7
left M2 L = 23.3, W = 24.1
left M3 L = 25.0, W = 24.1

NMNS-PV 21481: right M3 L = 25.3, W = 24.4

NMNS-PV 21482: right DP3 L = 19.7, W = 18.2
right DP4 L = 21.2, W = 20.3

NMNS-PV 21483: left P3 L = 17.5, W = 21.0
left P4 L = 18.2, W = 21.6

NMNS-PV 21485: possible right P3 L = 17.1, W = 18.5

NMNS-PV 21486: mandibular D below m3 trigonid = 41.9
left m1–3 L = 73.1
left p4 L = 19.4, trigonid W = 12.5, talonid W = 12.9
left m1 L = 19.9, trigonid W = 12.3, talonid W = 12.5
left m2 L = 22.8, trigonid W = 12.9, talonid W = 12.6
left m3 L = 32.8, trigonid W = 13.3, talonid W = 10.9

NMNS-PV 21487: mandibular D below m3 trigonid = 47.9
right m1–3 L = 71.3
right p3 L = 18.7, trigonid W = 10.2, talonid W = 11.8
right p4 L = 19.2, trigonid W = 12.7, talonid W = 13.5
right m1 L = 19.5, trigonid W = 12.6, talonid W = 12.8
right m2 L = 21.5, trigonid W = 13.6, talonid W = 13.1
right m3 L = 30.2*, trigonid W = 13.6, talonid W = 10.9

NMNS-PV 21489: right P2–4 L = 47.0*
right P2 L = 16.0*, W = 17.5
right P3 L = 17.2*, W = 20.5

Palaeotherium sp. cf. *P. medium* from La Débruge

NMNS-PV 21484: possible right p4 or m1, L = 20.0, trigonid W = 11.7, talonid W = 12.7

NMNS-PV 21491: left m1 L = 18.7, trigonid W = 10.9, talonid W = 11.9
left m2 L = 20.6, trigonid W = 10.9, talonid W = 11.9

NMNS-PV 21493: labial part of right M3, L = 26.0

Palaeotherium muehlbergi thaleri from La Débruge

NMNS-PV 21494: right P2–M3 L = 113.7*

Appendix 1. Continued

right P2–4 L = 49.6
right M1–3 L = 68.2*
right P2 L = 15.3, W = 19.2
right P3 L = 17.8, W = 23.8
right P4 L = 19.1, W = 26.5
right M1 L = 20.6, W = 28.2
right M2 L = 25.5, W = 31.0*
right M3 L = 30.9, W = 31.5
NMNS-PV 21495: right m1 or m2 L = 22.4, trigonid W = 13.2, talonid W = 14.0
Palaeotherium sp. from Euzèt les Bains
NMNS-PV 21397: left C1 L = 14.0, W = 10.5
NMNS-PV 21399: right lower or left upper incisor L = 7.5, W = 8.7
Palaeotherium sp. from Baby
NMNS-PV 21422: right c1 L = 15.8, W = 11.7
NMNS-PV 21423: right tibia L = 239.8, proximal W = 75.5
NMNS-PV 21424: left lower molar trigonid W = 8.6
NMNS-PV 21425: possible left m2 talonid W = 15.0
NMNS-PV 21429: right upper molar L = 21.4*
NMNS-PV 21430: left P2 L = 12.8*
Palaeotherium sp. from Civrac de Blaye
NMNS-PV 21364: right C1 L = 16.1, W = 12.5
Palaeotherium sp. from La Débruge
NMNS-PV 21492: mandibular D below p3 = 27.3
right p3 L = 18.0, trigonid W = 9.7, talonid W = 10.4
Cf. *Palaeotherium* sp. from Baby
NMNS-PV 21426: vertebra anteroposterior L (preserved part only) = 44.5
maximum W = 66.5*
column L = 18.8
NMNS-PV 21427: possible fibular shaft L (preserved part only) L = 117.6
shaft maximum diameter (preserved part only) = 10.2
NMNS-PV 21428: right proximal femur L (preserved part only) = 38.0
shaft mediolateral diameter = 19.5
proximal W = 39.0*
femoral head anteriorposterior diameter = 18.6
Cf. *Palaeotherium* sp. from Civrac de Blaye
NMNS-PV 21377: transverse W of condyles = 51.6
transverse diameter of magnum foramen = 23.1
Cf. *Palaeotherium* sp. from La Débruge
NMNS-PV 21488: vertebra anteroposterior L (preserved part only) = 40.8
column L = 38.3, W = 19.9
Plagiolophus (*Paloplotherium*) *annectens* from Robiac
NMNS-PV 21342: left M2 L = 14.2, W = 16.4
left M3 L = 23.5, W = 18.5
NMNS-PV 21343: right M1–3 L = 42.2
right M1 L = 11.4, W = 15.0
right M2 L = 12.8, W = 14.9
right M3 L = 20.2, W = 16.1
NMNS-PV 21347: right M3 L = 19.6, W = 15.5
Plagiolophus (*Paloplotherium*) *annectens* from Euzèt les Bains
NMNS-PV 21400: right mandibular D below m3 trigonid = 35.6
diastema between right c1 and p2 = 20.5 alv
right c1 L = 8.5, W = 7.9
right p2–m3 L = 86.7
right m1–3 L = 56.4
right p2 L = 8.3, W = 5.4
right p3 L = 10.2, W = 7.6
right p4 L = 12.3, trigonid W = 9.1, talonid W = 8.8
right m1 L = 14.3, trigonid W = 9.6, talonid W = 10.0
right m2 L = 16.9, trigonid W = 11.3, talonid W = 10.4
right m3 L = 26.6, trigonid W = 10.7, talonid W = 8.9
diastema between left c1 and p2 = 22.9* alv
left c1 L = 9.9, W = 6.8
left p2–m3 L = 87.5

Appendix 1. Continued

left m1–3 L = 56.4
left p2 L = 7.7, W = 5.7
left p3 L = 10.8, W = 7.5
left p4 L = 12.4, trigonid W = 9.1, talonid W = 9.0
left m1 L = 13.7, trigonid W = 9.7, talonid W = 10.0
left m2 L = 16.7, trigonid W = 11.1, talonid W = 10.6
left m3 L = 27.4, trigonid W = 10.6, talonid W = 8.9

NMNS-PV 21401: right mandibular D below m3 trigonid = 28.8
diastema between right c1 and p2 = 17.3* alv
right p2–m3 L = —
right m1–3 L = —
right p2 L = 8.8, W = 6.2
right p3 L = —, W = —
right p4 L = 13.3, trigonid W = 9.2, talonid W = 9.9
right m1 L = 14.2, trigonid W = 9.9, talonid W = 10.1
right m2 L = 17.9, trigonid W = 11.5*, talonid W = 10.5
right m3 L = —, trigonid W = 9.9, talonid W = 8.8*
left mandibular D below m2 = 26.0*
diastema between left c1 and p2 = 19.5 alv
left c1 L = 9.6, W = 6.6
left p2 L = —, W = —
left p3 L = 11.8, W = 8.5
left p4 L = 12.5, trigonid W = 8.9, talonid W = 9.9
left m1 L = 14.5, trigonid W = 9.3*, talonid W = 9.3*

NMNS-PV 21402: diastema between right C1 and P2 = 17.0 alv
right P2–M3 L = 74.3*
right M1–3 L = 49.3
right P2 L = —, W = —
right P3 L = 9.5, W = 13.3
right P4 L = 10.8, W = 15.2
right M1 L = 13.2, W = 16.3
right M2 L = 17.5, W = 18.7
right M3 L = 20.3, W = 17.1*
left I3 L = —, W = —
left P2–M3 L = 76.9*
left M1–3 L = 49.1*
left P2 L = —, W = —
left P3 L = 10.0, W = —
left P4 L = 10.5, W = 14.3*
left M1 L = 14.4, W = 15.9*
left M2 L = 16.8, W = 17.8*
left M3 L = 20.1*, W = 18.2

NMNS-PV 21403: right c1 L = 9.7*, W = 7.8*
left mandibular D below m3 trigonid = 29.5
diastema between left c1 and p2 = —
left p2–m3 L = —
left m1–3 L = 55.3*
left p3 L = —, W = —
left p4 L = 12.1, trigonid W = 7.5*, talonid W = 8.3*
left m1 L = 12.8, trigonid W = 7.8*, talonid W = 8.7*
left m2 L = 16.8, trigonid W = 10.3, talonid W = 10.2
left m3 L = 25.7, trigonid W = 10.2, talonid W = 9.3

NMNS-PV 21404: right m1 L = 14.5, trigonid W = 8.5, talonid W = 9.1

NMNS-PV 21405: right mandibular D below m3 trigonid = 28.2
right p2–m3 L = 83.6
right m1–3 L = 55.4
right p2 L = 7.9, W = —
right p3 L = 9.6, W = —
right p4 L = 12.6, trigonid W = —, talonid W = —
right m1 L = 14.0, trigonid W = —, talonid W = —
right m2 L = 17.2, trigonid W = —, talonid W = —
right m3 L = 24.8, trigonid W = —, talonid W = —

NMNS-PV 21406: left radius, mediolateral W at proximal end= 24.5

Appendix 1. Continued

anteroposterior W at proximal end = 11.4
proximal shaft diameter = 17.1
NMNS-PV 21407: left calcaneum, length (preserved part only) = 31.0
tuberosity maximum W = 14.0
NMNS-PV 21408: right astragalus maximum H = 24.9
maximum W = 24.4
NMNS-PV 21409: left M2 L = 18.3, W = 16.9
NMNS-PV 21410: broken right M3 L = 21.0*, W = 16.2
NMNS-PV 21412: broken right M2 L = 17.1, W = 16.5
NMNS-PV 21413: broken left P4 L = 11.5, W = 15.5
NMNS-PV 21414: left p4 L = 12.7, trigonid W = 8.4, talonid W = 8.8
NMNS-PV 21415: right m3 L = 23.6*, trigonid W = 9.0, talonid W = 7.9
NMNS-PV 21416: left DP3 L = 13.3, W = 13.0
left DP4 L = 15.8, W = 14.5
left M1 L = 16.5, W = 15.4
NMNS-PV 21417: right DP3 L = 14.3, W = 13.2
Plagiolophus (*Paloplotherium*) *annectens* from Baby
NMNS-PV 21431: right P2–M3 L = —
right M1–3 L = 52.9
right P3 L = 9.1, W = 12.2
right P4 L = 10.8, W = 14.3
right M1 L = 13.2, W = 15.7
right M2 L = 16.6, W = 17.9
right M3 L = 23.2, W = 17.5
left M1–3 L = 50.8
left P4 L = 8.2*, W = 14.7
left M1 L = 13.2, W = 15.8
left M2 L = 16.5, W = 18.2
left M3 L = 22.8, W = 17.8
left mandibular D below m3 trigonid = 32.3
left m1–3 L = 50.5
left m1 L = 11.5, trigonid W = 8.9, talonid W = 9.1
left m2 L = 14.5, trigonid W = 8.9, talonid W = 8.9
left m3 L = 24.6, trigonid W = 9.2, talonid W = 8.2
NMNS-PV 21432: right P2–M3 L = 77.4
right M1–3 L = 51.5
right P2 L = 8.7, W = 9.5
right P3 L = 9.3, W = 12.7
right P4 L = 11.9, W = 16.0
right M1 L = 13.4, W = 17.8
right M2 L = 17.5, W = 17.3
right M3 L = 22.2, W = 17.6
left P2–M3 L = 76.4
left M1–3 L = 49.9
left P2 L = 8.9, W = 9.7
left P3 L = 8.4, W = 12.3
left P4 L = 11.9, W = 15.2
left M1 L = 13.2, W = 15.8
left M2 L = 17.4, W = 17.5
left M3 L = 21.3, W = 17.8*
NMNS-PV 21433: left mandibular D below m3 trigonid = 29.9
left p2–m3 L = 79.0*
left m1–3 L = 53.0*
left p2 L = —, W = —
left p3 L = 10.7, W = 7.5
left p4 L = 12.8, trigonid W = 7.8, talonid W = 8.8
left m1 L = 11.8*, trigonid W = 8.8, talonid W = 9.8
left m2 L = 16.7, trigonid W = 9.7, talonid W = 10.3
left m3 L = 25.1, trigonid W = 9.3, talonid W = 8.6
NMNS-PV 21434: left C1 L = 8.0, W = 7.2
NMNS-PV 21437: right M3 L = 22.2*, W = 17.2
Plagiolophus (*Paloplotherium*) *major* from St. Capraise d'Eymet
NMNS-PV 21544: right I2 L = 12.9, W = 6.6

Appendix 1. Continued

right I3 L = —, W = —
right C1 L = —, W = —
right DP2 L = 11.3, W = 12.4
right DP3 L = 14.6, W = 17.2
right DP4 L = 20.0, W = 19.6
right M1 L = 22.2, W = 20.9

Plagiolophus (*Paloplotherium*) *oweni* from Civrac de Blaye

NMNS-PV 21378: right mandibular D below m3 trigonid = 30.7
right m1–3 L = 47.9
right p3 L = 10.0, W = 7.0
right p4 L = 9.8, trigonid W = 7.7, talonid W = 8.2
right m1 L = 11.0, trigonid W = 8.7, talonid W = 8.9
right m2 L = 13.7, trigonid W = 9.5, talonid W = 9.3
right m3 L = 24.2, trigonid W = 9.2, talonid W = 8.3

NMNS-PV 21379: right M3 L = 23.6, W = 16.0

Plagiolophus (*Paloplotherium*) *oweni* from La Débruge

NMNS-PV 21496: right I2 L = 8.8, W = 3.3
right C1 L = 10.1, W = 8.9
diastema between right C1 and P2 = 18.7* alv
right P2–M3 L = 82.4
right M1–3 L = 54.9
right P2 L = 8.2, W = 9.5
right P3 L = 8.0, W = 10.8*
right P4 L = 11.6, W = 16.3
right M1 L = 14.2, W = 17.5
right M2 L = 18.4, W = 19.1
right M3 L = 24.4, W = 20.8
left I1 L = 5.9, W = 2.3
left I2 L = 7.9, W = 3.8
left I3 L = 5.5*, W = 2.3
left C1 L = 11.2, W = 9.6
diastema between left C1 and P2 = 28.5 alv
left P2–M3 L = 81.5
left M1–3 L = 54.8
left P2 L = 8.5, W = —
left P3 L = 8.3, W = 11.6*
left P4 L = 11.6, W = 15.8*
left M1 L = 13.8, W = 17.0*
left M2 L = 18.4, W = 19.2*
left M3 L = 24.1*, W = 20.1*

NMNS-PV 21497: left mandibular D below m3 trigonid = 30.9
left m1–3 L = 53.0*
left p3 L = 9.8, W = 5.8
left p4 L = 12.0, trigonid W = 7.5, talonid W = 8.0
left m1 L = 14.2, trigonid W = 9.0, talonid W = 9.4
left m2 L = 17.0, trigonid W = 9.7, talonid W = 9.8
left m3 L = 22.5*, trigonid W = —, talonid W = 9.6*

NMNS-PV 21498: right M3 L = 23.4*, W = 17.7

Plagiolophus (*Plagiolophus*) *minor* from La Débruge

NMNS-PV 21500: right i1 L = 3.8, W = 5.8
right i2 L = 3.7, W = 6.5
right i3 L = 2.9, W = 6.2
right c1 L = 4.4, W = 3.6
left i1 L = —, W = —
left i2 L = 4.1, W = 6.1

NMNS-PV 21501: right mandibular D below m3 trigonid = 25.4
diastema between right c1 and p2 = 17.7 alv
right c1 L = 4.8, W = 3.9*
right p2–m3 L = 67.0
right m1–3 L = 44.6
right p2 L = 6.4, W = 4.2*
right p3 L = 7.5, W = 6.4*
right p4 L = 9.5, trigonid W = 7.2*, talonid W = 7.7*

Appendix 1. Continued

right m1 L = 10.6, trigonid W = 7.8*, talonid W = 8.2*
right m2 L = 12.4, trigonid W = 8.2*, talonid W = 8.5*
right m3 L = 21.4, trigonid W = 7.6*, talonid W = 7.8*
NMNS-PV 21502: right mandibular D below m3 trigonid = 26.2
right p2–m3 L = 65.0
right m1–3 L = 43.7
right p2 L = 5.3, W = 3.7
right p3 L = 8.0, W =5.8
right p4 L = 9.9, trigonid W = 7.0, talonid W = 7.6
right m1 L = 10.9, trigonid W = 8.2, talonid W = 8.5
right m2 L = 12.2, trigonid W = 9.0, talonid W = 8.9
right m3 L = 20.1, trigonid W = 8.5, talonid W = 7.4
NMNS-PV 21503: left mandibular D below m3 trigonid = 22.7
diastema between left c1 and p2 = 26.7 alv
left c1 L = 5.6, W = 4.2
left p2–m3 L = —
left m1–3 L = —
left p2 L = 6.7, W = 4.2*
left p3 L = 8.4, W = 4.7*
left p4 L = 10.3, trigonid W = 5.8*, talonid W = 6.0*
left m1 L = 12.3, trigonid W = 6.7*, talonid W = 6.7*
left m2 L = 14.7, trigonid W = 6.8, talonid W = 6.2
left m3 L = —, trigonid W = —, talonid W = —
NMNS-PV 21504: left mandibular D below m3 trigonid = 26.2
left p2–m3 L = 61.7*
left m1–3 L = 42.2
left p2 L = 3.8, W = 4.0*
left p3 L = 6.5, W = 4.8*
left p4 L = 9.4, trigonid W = 6.6*, talonid W = 7.4*
left m1 L = 10.0, trigonid W = 7.9*, talonid W = 8.2*
left m2 L = 12.5, trigonid W = 8.8, talonid W = 8.1
left m3 L = 20.8*, trigonid W = 8.9*, talonid W = 6.5*
NMNS-PV 21505: left mandibular D below m2 talonid = 25.0
left p2–m3 L = 62.1
left m1–3 L = 42.1
left p2 L = 5.7, W = 3.6
left p3 L = 6.9, W = 5.3
left p4 L = 8.8, trigonid W = 6.4, talonid W = 7.2
left m1 L = 10.2, trigonid W = 7.2, talonid W = 7.2
left m2 L = 12.2, trigonid W = 7.6, talonid W = 7.5
left m3 L = 19.9, trigonid W = 7.9, talonid W = 7.0
NMNS-PV 21506: right mandibular D below m3 trigonid = 26.0
right m1–3 L = 45.5
right p4 L = 10.7, trigonid W = 7.2, talonid W = 7.6
right m1 L = 11.3, trigonid W = 7.9, talonid W = 8.2
right m2 L = 13.8, trigonid W = 8.3, talonid W = 8.4
right m3 L = 21.0, trigonid W = 8.1, talonid W = 7.7
left mandibular D below m3 trigonid = 25.2
left c1 L = 6.8, W = 6.0
left m1–3 L = 45.3
left p3 L = 7.7, W = 5.4
left p4 L = 10.2, trigonid W = 6.9, talonid W = 7.6
left m1 L = 11.1, trigonid W = 7.9, talonid W = 8.1
left m2 L = 13.5, trigonid W = 8.3, talonid W = 8.3
left m3 L = 21.0, trigonid W = 8.0, talonid W = 7.7
NMNS-PV 21507: right P2–M3 L = 70.0
right M1–3 L = 46.4
right P2 L = 8.2, W = 8.2
right P3 L = 7.4, W = 10.0
right P4 L = 10.8, W = 12.4
right M1 L = 12.1, W = 14.1
right M2 L = 15.3, W = 15.3
right M3 L = 20.6, W = 15.6

Appendix 1. Continued

left P2 L = 8.4, W = 8.1
left P3 L = 8.0, W = 9.7*
left M1 L = 11.9, W = 13.7
left M2 L = 15.8, W = 15.2
left M3 L = 21.0, W = 15.9
NMNS-PV 21508: left M1–3 L = 44.6
left P4 L = —, W = —
left M1 L = 11.8, W = 14.0
left M2 L = 14.2, W = 15.0
left M3 L = 20.7, W = 15.6
NMNS-PV 21509: right P2–M3 L = 68.5
right M1–3 L = 44.2
right P2 L = 8.1, W = 10.0
right P3 L = 7.9, W = 10.6
right P4 L = 10.7, W = 12.8
right M1 L = 11.2, W = 13.7
right M2 L = 15.9, W = 15.7
right M3 L = 18.4, W = 16.0
NMNS-PV 21510: possible right i1 L = 3.9, W = 5.4
NMNS-PV 21511: right astragalus maximum H = 20.9
maximum W = 20.7
NMNS-PV 21512: left m2 L = 12.5, trigonid W = 8.5, talonid W = 8.7
left m3 L = 19.4, trigonid W = 8.3, talonid W = 7.1
NMNS-PV 21513: right mandibular D below m3 trigonid = —
right m1 L = —, trigonid W = —, talonid W = 7.2
right m2 L = 13.1, trigonid W = 7.9, talonid W = 8.1
right m3 L = 20.3, trigonid W = 7.7, talonid W = 7.1
NMNS-PV 21514: broken right M2 L = 16.9*, W = 14.4*
NMNS-PV 21515: broken left C1 L = 6.0*, W = 6.7*
right P3 L = 8.0, W = 10.0
NMNS-PV 21517: possible left C1 L = 7.2, W = 6.4
NMNS-PV 21520: possible left DP1 L = —, W = —
left DP2 L = 7.7, W = 8.6
left DP3 L = 11.0, W = 11.0
left DP4 L = 13.1, W = 11.5
Plagiolophus (*Plagiolophus*) *minor* from St. Capraise d'Eymet
NMNS-PV 21532: left DP3 L = 10.7, W = 11.6
left DP4 L = 12.6, W = 12.3
NMNS-PV 21547: right m3 L = 20.4*, trigonid W = 8.3, talonid W = 6.5
NMNS-PV 21549: left P2–M3 L = 67.8
left M1–3 L = 43.5
left P2 L = 7.1, W = 7.5
left P3 L = 7.9, W = 10.2
left P4 L = 10.6, W = 11.9
left M1 L = 11.6, W = 13.3*
left M2 L = 16.4, W = 14.8
left M3 L = 18.8, W = 13.4*
NMNS-PV 21550: left M2 L = 16.6, W = 14.0*
NMNS-PV 21551: right c1 L = 6.9, W = 5.2
left mandibular D below m3 trigonid = 28.2*
diastema between left c1 and p2 = 33.8 alv
left p2–m3 L = 73.8*
left m1–3 L = 48.8*
left p3 L = 9.3, W = 6.2
left p4 L = 10.5, trigonid W = 6.7, talonid W = 7.2
left m1 L = 12.6, trigonid W = 8.2, talonid W = 8.6
left m2 L = 15.6, trigonid W = 8.7, talonid W = 8.1
left m3 L = 20.0*, trigonid W = 7.6, talonid W = 6.7
NMNS-PV 21552: left mandibular D below m2 talonid = 23.4
left p3 L = 8.1, W = 4.7
left p4 L = 11.3, trigonid W = 5.6, talonid W = 6.1
left m1 L = 11.8, trigonid W = 6.8, talonid W = 7.0
left m2 L = 15.2, trigonid W = 7.5, talonid W = 7.3

Appendix 1. Continued

left m3 L = —, trigonid W = 7.6, talonid W = 7.1
NMNS-PV 21553: possible right I1 L = 4.6, W = 7.0
NMNS-PV 21554: right c1 L = 7.8, W = 5.8
NMNS-PV 21555: possible right c1 L = 5.3, W = 3.9
Plagiolophus sp. from Le Bretou
NMNS-PV 21199: possible left p4 or m1 L = 13.4, trigonid W = 6.4, talonid W = 6.9
NMNS-PV 21200: possible right C1 L = 7.5, W = 5.3
Plagiolophus sp. from Robiac
NMNS-PV 21346: left p4 or m1 L = 11.2, trigonid W = 7.0, talonid W = 7.6
Plagiolophus sp. from Euzèt les Bains
NMNS-PV 21411: possible left c1 L = 7.5, W = 6.2
NMNS-PV 21418: incisor, assignable to right I2 or left i2 L = 7.1, W = 3.6
Plagiolophus sp. from La Débruge
NMNS-PV 21518: possible right I3 L = —, W = 6.8
NMNS-PV 21519: possible left i2 or right I2 L = 4.1, W = 7.0
Plagiolophus sp. from St. Capraise d'Eymet
NMNS-PV 21548: right M1 L = 14.5, W = 15.6
NMNS-PV 21557: left astragalus maximum H = 23.2
maximum W = 22.4
NMNS-PV 21558: left astragalus maximum H = 21.1
maximum W = 21.4
Cf. *Plagiolophus* sp. from Le Bretou
NMNS-PV 21198: right p4 L = 13.7, trigonid W = 7.8, talonid W = 8.2
Cf. *Plagiolophus* sp. from Baby
NMNS-PV 21435: femoral L (preserved part only) = 115.3*
NMNS-PV 21436: right m1 or m2 L = 15.1, trigonid W = 7.2, talonid W = 6.2
NMNS-PV 21438: right mandibular D below possible dp3 = 18.2
possible right dp3 L = 12.0, trigonid W = 5.6, talonid W = 6.8
possible right dp4 L = —, trigonid W = —, talonid W = —
Cf. *Plagiolophus* sp. from La Débruge
NMNS-PV 21516: upper molar fragment L (preserved part only) = 14.3*
Cf. *Plagiolophus* sp. from St. Capraise d'Eymet
NMNS-PV 21545: right P2 L = 9.9, W = 10.2
Leptolophus sp. from Robiac
NMNS-PV 21345: possible right m1 L = 10.0*, trigonid W = —, talonid W = —
possible right m2 L = 15.8, trigonid W = 7.5, talonid W = 7.8
Pachynolophus bretovensis from Robiac
NMNS-PV 21325: left P4 L = 6.1, W = 7.4
left M1 L = 7.3, W = 9.2
left M2 L = 8.8, W = 10.0
left M3 L = —, W = 10.2
NMNS-PV 21326: right M3 L = 7.5, W = 9.3*
right mandibular D below m3 trigonid = —
right m1–3 L = 26.4
right p4 L = 7.4, trigonid W = 4.7, talonid W = 5.4
right m1 L = 7.7, trigonid W = 5.5, talonid W = 5.2
right m2 L = 8.1, trigonid W = 5.2, talonid W = 4.7
right m3 L = 11.2, trigonid W = 5.5, talonid W = 5.4
left mandibular D below m3 trigonid = 20.1
left p2–m3 L = 46.6*
left m1–3 L = 26.7
left p2 L = 6.0*, W = 3.6
left p3 L = 7.4, trigonid W = 4.9, talonid W = 5.3
left p4 L = 7.6, trigonid W = 5.2, talonid W = 5.4
left m1 L = 7.5, trigonid W = 5.5, talonid W = 5.4
left m2 L = 8.3, trigonid W = 6.0, talonid W = 5.5
left m3 L = 11.3, trigonid W = 5.4, talonid W = 5.1
Pachynolophus sp. cf. *P. bretovensis* from Robiac
NMNS-PV 21303: left lower molariform tooth L = —, W = 4.9
NMNS-PV 21328: possible right m1 or m2 L = 8.6, trigonid W = 6.2, talonid W = 6.0
NMNS-PV 21329: possible right m2 L = 8.1, trigonid W = 6.1, talonid W = 6.3
Pachynolophus duvali from Aumelas
NMNS-PV 21125: diastema between right C and P1 = 19.7 alv

Appendix 1. Continued

right P1–M3 L = 53.2
right P2–M3 L = 53.2
right M1–3 L = 34.1
right P2 L = 7.8, W = 5.8*
right P3 L = 7.4*, W = 9.2
right DP4 L = 9.5, W = 10.6
right M1 L = 11.0, W = 12.9
right M2 L = 12.5, W = 14.5
right M3 L = 13.1*, W = 12.8*
diastema between left C and P1 = 19.7 alv
left M1–3 L = 34.4
left M1 L = 11.1, W = 13.3
left M2 L = 12.1, W = 13.7
left M3 L = 12.3, W = 14.6
NMNS-PV 21126: left M1–3 L = 34.2*
left P4 L = —, W = 12.1
left M1 L = 10.6, W = 12.2
left M2 L = 11.8, W = 13.8
left M3 L = 12.9, W = 15.0*
NMNS-PV 21127: right M1 L = —, W = —
right M2 L = 11.5, W = 13.3
Anchilophus sp. cf. *A. desmaresti* from Robiac
NMNS-PV 21322: right M1–3 L = 30.2
right M1 L = 10.9, W = 12.6
right M2 L = 11.7, W = 13.0
right M3 L = 11.3, W = 12.9
NMNS-PV 21323: left mandibular D below m3 trigonid = 21.5
left m1–3 L = 35.8
left p4 L = 9.1, trigonid W = 4.6, talonid W = 5.2
left m1 L = 10.0, trigonid W = 5.0, talonid W = 5.0
left m2 L = 10.7, trigonid W = 4.9, talonid W = 6.1
left m3 L = 15.0, trigonid W = 6.9*, talonid W = 5.4
NMNS-PV 21324: possible right M1 or M2 L = 12.2, W = 12.6
Anchilophus dumasi from Euzèt les Bains
NMNS-PV 21386: right mandibular D below m3 trigonid = —
diastema between right c1 and p1 = 38.7* alv
right c1 L = 7.0, W = —
right p2–4 L = 36.7
right p1 L = 6.0, W = 3.7
right p2 L = 8.6, trigonid W = 5.3, talonid W = 5.8
right p3 L = 11.2, trigonid W = 7.0, talonid W = 7.9
right p4 L = 10.5, trigonid W = 7.7, talonid W = 7.8
right m1 L = 13.1*, trigonid W = 7.1*, talonid W = 7.9*
right m2 L = 13.2*, trigonid W = 8.4*, talonid W = 8.0*
NMNS-PV 21387: right mandibular D below m3 trigonid = 31.5
right m1–3 L = 38.4
right m1 L = 10.9, trigonid W = 8.2, talonid W = 7.3
right m2 L = 11.9, trigonid W = —, talonid W = —
right m3 L = 16.2, trigonid W = —, talonid W = —
Anchilophus sp. cf. *A. gaudini* from Le Bretou
NMNS-PV 21193: possible right M3 L = 9.9, W = 11.5
NMNS-PV 21194: right M3 L = 9.5, W = 11.0
NMNS-PV 21195: possible left P4 or M1 L = 9.0, W = 10.1
NMNS-PV 21197: left M2 L = 11.1, W = 13.4
Anchilophus sp. cf. *A. gaudini* from Robiac
NMNS-PV 21327: possible left P4 or M1 L = 7.1, W = 9.3
NMNS-PV 21330: right P4 L = 5.7, W = 7.1
right M1 L = 7.3, W = 9.3
NMNS-PV 21331: possible left M2 or M3 L = 9.0, W = 10.8*
Cf. *Anchilophus* sp. from Le Bretou
NMNS-PV 21192: possible right P2 L = 5.4, W = 5.9
NMNS-PV 21196: possible right c1 L = 5.7, W = 3.5
Lophiodon lautricense from Robiac

Appendix 1. Continued

NMNS-PV 21348: right mandibular D below m3 trigonid = 79.1
right mandibular height from ventral margin to coronoid process = 227.0, and to condylar process = 190.0
right i1 L = —, W = —
right i2 L = 19.1, W = 16.1
diastema between right c1 and p2 = 40.6 alv
right c1 L = 28.0, W = 23.8
right p2–m3 L = 269.0
right p2–4 L = 94.6
right m1–3 L = 176.4
right p2 L = 26.6, W = 17.7
right p3 L = 33.4, trigonid W = 23.5, talonid W = 24.6
right p4 L = 37.5, trigonid W = 28.8, talonid W = 32.2
right m1 L = 46.6, trigonid W = 29.7, talonid W = 30.3
right m2 L = 56.2, trigonid W = 35.7, talonid W = 33.6
right m3 L = 75.1, trigonid W = 40.5, talonid W = 36.1
left mandibular D below m3 trigonid = 75.5
left mandibular height from ventral margin to coronoid process = 231.0, and to condylar process = 188.0
left i2 L = 12.4, W = 13.7
left i3 L = 18.9, W = 16.5
diastema between left c1 and p2 = 37.8 alv
left c1 L = 29.7, W = 23.4
left p2–m3 L = 266.8
left p2–4 L = 98.0
left m1–3 L = 173.5
left p2 L = 28.1, W = 19.4
left p3 L = 33.2, trigonid W = 25.9, talonid W = 24.6
left p4 L = 34.9, trigonid W = 29.7, talonid W = 29.0
left m1 L = 45.0, trigonid W = 28.9, talonid W = 27.6
left m2 L = 56.8, trigonid W = 36.3, talonid W = 33.5
left m3 L = 76.7, trigonid W = 38.0, talonid W = 35.8
NMNS-PV 21349: right P3 L = 40.9, W = 44.9
right P4 L = 42.9, W = 50.9
right M1 L = 51.7, W = 47.3
right M2 L = 64.8, W = 56.5
NMNS-PV 21350: right P2–M3 L = 234.0*
right P2–4 L = 101.3*
right M1–3 L = 152.9
right P2 L = 29.8*, W = 35.3
right P3 L = 34.7, W = 44.1
right P4 L = 36.6, W = 46.4
right M1 L = 47.8, W = 46.6
right M2 L = 57.8, W = 51.1
right M3 L = 55.3, W = 57.7
left P2–M3 L = 241.2
left P2–4 L = 102.9
left M1–3 L = 149.4
left P2 L = 32.8, W = 37.3
left P3 L = 33.9, W = 43.3
left P4 L = 37.2, W = 45.4
left M1 L = 46.7, W = 45.6
left M2 L = 58.8, W = 51.1
left M3 L = 54.4, W = 58.3
NMNS-PV 21351: right mandibular D below m3 trigonid = —
right m1–3 L = 158.0*
right p4 L = 40.3, trigonid W = 26.7, talonid W = 28.2
right m1 L = 40.7, trigonid W = 26.9, talonid W = 26.7
right m2 L = 53.4, trigonid W = 32.4, talonid W = 31.7
right m3 L = 72.6, trigonid W = 35.5, talonid W = 34.8
NMNS-PV 21352: left p3 L = 35.6, trigonid W = 25.2, talonid W = 26.4
NMNS-PV 21353: left P4 L = 38.3, W = 46.6
NMNS-PV 21354: right P4 L = 40.5, W = 49.4
NMNS-PV 21355: left M3 L = 55.8, W = 57.1

Appendix 1. Continued

NMNS-PV 21356: right M2 L = 60.3, W = 54.6
NMNS-PV 21357: left P4 L = 34.7, W = 45.2
NMNS-PV 21359: right DP2 L = —, W = 30.4
right DP3 L = 37.3, W = 31.5
right DP4 L = 42.9, W = 36.7
Lophiodon sp. from Aumelas
NMNS-PV 21129: left m1–3 L = 85.3*
left p4 L = —, trigonid W = —, talonid W = —
left m1 L = 21.2*, trigonid W = —, talonid W = —
left m2 L = 25.0, trigonid W = 18.1*, talonid W = 17.1*
left m3 L = 39.9*, trigonid W = 20.2*, talonid W = 16.7*
NMNS-PV 21130: incisor L = 12.3, W = 10.5
NMNS-PV 21358: incisor L = 12.7, W = 10.3

Miocene Perissodactyls

Anchitherium aurelianense from Faluns de Touraine
NMNS-PV 21672: left M3 L = 15.8, W = 19.2
Rhinocerotidae gen. et sp. indet. 1 from Faluns de Touraine
NMNS-PV 21673: left p4, m1, or m2 L = 26.4, trigonid W = 18.3, talonid W = 19.4
Rhinocerotidae gen. et sp. indet. 2 from Faluns de Touraine
NMNS-PV 21674: left M3 L = 37.7, W = 41.8

National Museum of Nature and Science Monographs, No. 55, pp. 179–213, 2025

Chapter 8

ARTIODACTYLA

Takehisa Tsubamoto

Earth Sciences, Graduate School of Science and Engineering, Ehime University, Matsuyma, Ehime 790–8577, Japan
(e-mail: tsubamoto.takehisa.yt@ehime-u.ac.jp)

Introduction

Artiodactyl collection catalogued in this paper consists of total 113 specimens from total nine localities. The localities consist of six Eocene French, one Oligocene English, one Oligocene German, and one Miocene French localities. The Eocene French collection includes 102 specimens, the Oligocene English collection includes five specimens, the Oligocene German collection includes one specimen, and the Miocene French collection includes five specimens.

Classification of taxa mostly follows Erfurt and Métais (2007) and Lihoreau and Ducrocq (2007). Several other important references concerning the artiodactyl taxa catalogued here and not indicated in the Systematic Paleontology section are listed below: von Meyer (1832), Pomel (1847), Fraas (1870), de Bonis (1964), Sudre (1972, 1973, 1974, 1978a), Hartenberger (1974), Russell *et al*. (1982), Savage and Russell (1983), Hooker (1986), Sudre *et al*. (1990), Sudre and Ginsburg (1993), Martinez and Sudre (1995), McKenna and Bell (1997), Hooker and Weidmann (2000), Blondel (2005), and Erfurt *et al*. (2007).

The list of the artiodactyl taxa reported in this paper is shown in Table 1. Measurements are shown in Appendix 1. Measurement positions of astragalus are shown in Fig. 1.

Abbreviations: I/i, upper/lower incisor; C/c, upper/lower canine; P/p, upper/lower premolar; M/m, upper/lower molar; DI/di, upper/lower deciduous incisor; DC/dc, upper/lower deciduous canine; DP/dp, upper/lower deciduous premolar.

Systematic Paleontology

Order Artiodactyla Owen, 1848
Suborder indet.
Family Anthracotheriidae Leidy, 1869
Subfamily Bothriodontinae Scott, 1940
Genus *Bothriodon* Aymard, 1846

Bothriodon sp.

(Fig. 2)

Material: NMNS-PV 21656, left M1 or M2; NMNS-PV 21657, left M3; NMNS-PV 21658, left m3; NMNS-PV 21659, right m2.

Locality: Isle of Wight (England). Upper Hamstead Bed.

Age: earliest Oligocene (Rupelian). Calcareous nannoplankton zone NP21; polarity chron C13n–

Table 1. List of artiodactyl taxa reported in this paper.

- Artiodactyla Owen, 1848
  - Suborder indet.
    - Anthracotheriidae Leidy, 1869
      - Bothriodontinae Scott, 1940
        - *Bothriodon* Aymard, 1846
          - *Bothriodon* sp.
        - *Elomeryx* Marsh, 1894
          - *Elomeryx crispus* (Gervais, 1849)
    - Cebochoeridae Lydekker, 1883
      - *Cebochoerus* Gervais, 1852
        - *Cebochoerus* sp. cf. *C. helveticus* (Pictet and Humbert, 1869)
        - *Cebochoerus robiacensis* Depéret, 1917
        - *Cebochoerus* sp.
    - Choeropotamidae Owen, 1845
      - *Choeropotamus* Cuvier, 1822
        - *Choeropotamus parisiensis* Cuvier, 1822
        - *Choeropotamus* sp.
      - *Tapirulus* Gervais, 1850
        - *Tapirulus* sp. cf. *T. schlosseri* Stehlin, 1910
    - Cainotheriidae Camp and Van der Hoof, 1940
      - Robiaciinae Sudre, 1977
        - *Robiacina* Sudre, 1969
          - *Robiacina minuta* Sudre, 1969
          - Cf. *Robiacina minuta* Sudre, 1969
    - Anoplotheriidae Bonaparte, 1850
      - Anoplotheriinae Bonaparte, 1850
        - *Anoplotherium* Cuvier, 1804
          - *Anoplotherium commune* Cuvier, 1822
          - *Anoplotherium laurillardi* Pomel, 1851
        - *Diplobune* Rütimeyer, 1862
          - *Diplobune* sp.
      - Dacrytheriinae Depéret, 1917
        - *Dacrytherium* Filhol, 1876
          - *Dacrytherium ovinum* (Owen, 1857)
        - *Catodontherium* Depéret, 1908
          - *Catodontherium robiacense* (Depéret, 1906)
    - Xiphodontidae Flower, 1884
      - *Xiphodon* Cuvier, 1822
        - *Xiphodon castrensis* Kowalevsky, 1873
        - Cf. *Xiphodon castrensis* Kowalevsky, 1873
        - *Xiphodon gracile* Cuvier, 1822
        - *Xiphodon* sp. cf. *X. gracile* Cuvier, 1822
        - Cf. *Xiphodon gracile* Cuvier, 1822
      - *Dichodon* Owen, 1848
        - *Dichodon cervinus* (Owen, 1841)
        - *Dichodon* sp.
      - *Haplomeryx* Schlosser, 1886
        - *Haplomeryx* sp. cf. *H. picteti* Stehlin, 1910
    - Amphimerycidae Stehlin, 1910
      - *Amphimeryx* Pomel, 1848
        - Cf. *Amphimeryx murinus* (Cuvier, 1822)
      - *Pseudamphimeryx* Stehlin, 1910
        - *Pseudamphimeryx* sp.
        - Cf. *Pseudamphimeryx* sp.
  - Suiformes Jaeckel, 1911
    - Suoidea Gray, 1821
      - Family indet.
        - Gen. et sp. indet.
  - Ruminantia Scopoli, 1777
    - Family indet.
      - Gen. et sp. indet.
- ?Artiodactyla Owen, 1848
  - Family indet.
    - Gen et sp. indet.

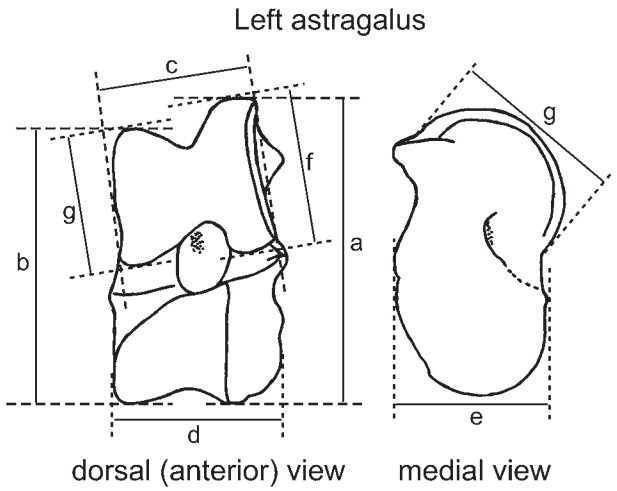

Fig. 1. Measurement positions of artiodactyl astragalus (after Tsubamoto and Tsogtbaatar, 2008).

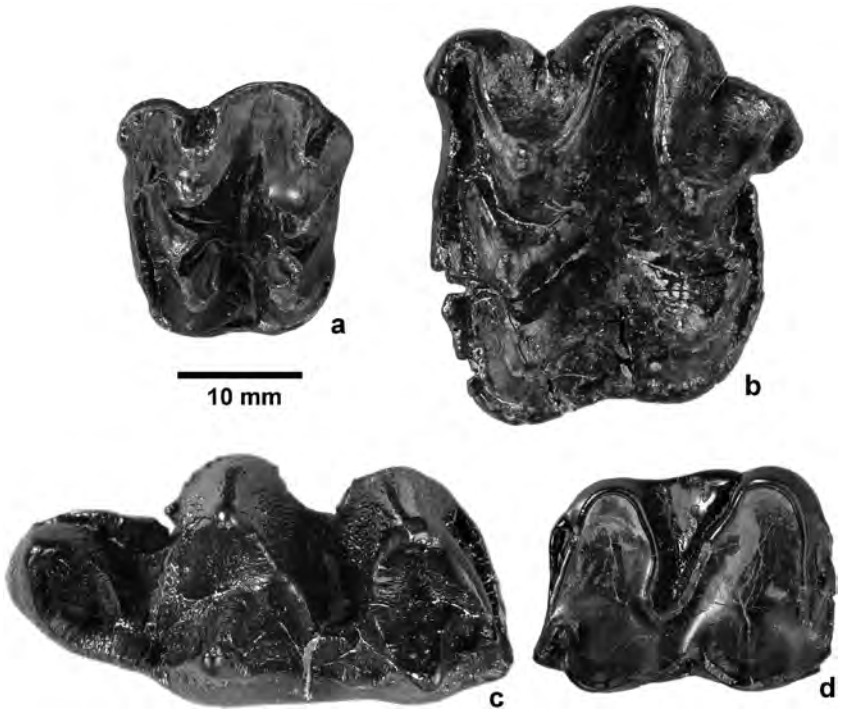

Fig. 2. *Bothriodon* sp. in occlusal view. (a) NMNS-PV 21656, left M1 or M2. (b) NMNS-PV 21657, left M3. (c) NMNS-PV 21658, left m3. (d) NMNS-PV 21659, right m2.

C12r; European mammal zone MP 21 (Hooker *et al*., 2004, fig. 3).

Comments: NMNS-PV 21656 (upper molar) has an interstitial wear facet on the distal face, implying that the tooth is M1 or M2. The present upper molars are strongly selenodont with a well-developed paraconule and a buccally well-protruded and loop-like mesostyle. Three species of *Bothriodon* have been recognized in the early Oligocene of western Europe (Lihoreau and Ducrocq, 2007): *Both-*

riodon velaunus, *Bothriodon leptorhynchus*, and *Bothriodon aymardi*. Judging from the figures by Filhol (1883, figs. 91–95), *B. aymardi* is the smallest in size, *B. velaunus* is medium-sized, and *B. leptorhynchus* is the largest. However, the size variations of these species are unknown.

Genus *Elomeryx* Marsh, 1894

***Elomeryx crispus* (Gervais, 1849)**
(Fig. 3)

Material: NMNS-PV 21655, left maxillary fragment with M3.

Locality: Isle of Wight (England). Upper Hamstead Bed.

Age: earliest Oligocene (Rupelian). Calcareous nannoplankton zone NP21; polarity chron C13n–C12r; European mammal zone MP 21 (Hooker *et al*., 2004, fig. 3).

Comments: The present upper molar is less selenodont than that of *Bothriodon*; and its parastyle and mesostyle are much smaller than those of *Bothriodon*. This molar is referable in size and morphology to that of *Elomeryx crispus*, which is the only recorded species among the genus in the early Oligocene of England (Lihoreau and Ducrocq, 2007).

Family Cebochoeridae Lydekker, 1883
Genus *Cebochoerus* Gervais, 1852
(in Gervais, 1848–1852)

Cebochoerus* sp. cf. *C. helveticus
(Pictet and Humbert, 1869)
(Fig. 4)

Material: NMNS-PV 21163, right maxillary fragment with P2–M1; NMNS-PV 21164, right P3; NMNS-PV 21165, right DP4; NMNS-PV 21166, right ?P2 or left ?p3.

Locality: Le Bretou (Quercy, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: In the Le Bretou locality, *Cebochoerus helveticus* is recorded among the genus (Erfurt

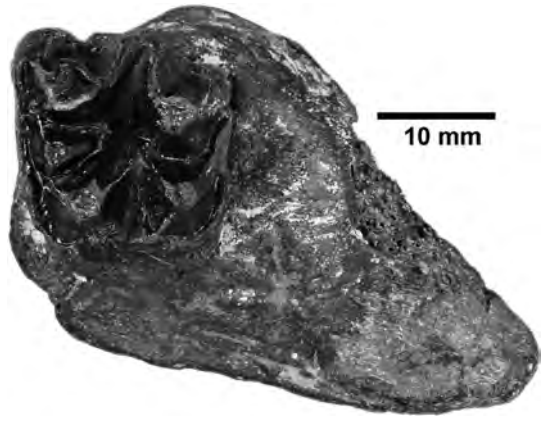

Fig. 3. *Elomeryx crispus* (Gervais), NMNS-PV 21655, left maxillary fragment with M3, occlusal view.

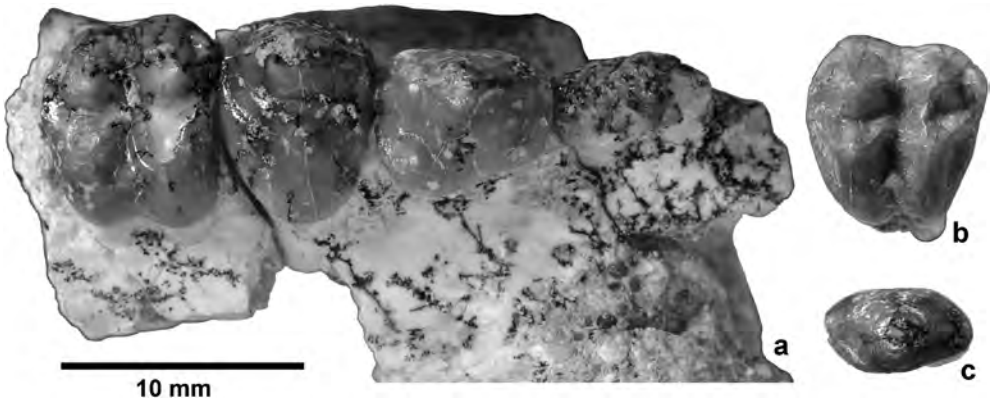

Fig. 4. *Cebochoerus* sp. cf. *C. helveticus* (Pictet and Humbert) in occlusal view. (a) NMNS-PV 21163, right maxillary fragment with P2–M1. (b) NMNS-PV 21165, right DP4. (c) NMNS-PV 21166, right ?P2 or left ?p3.

Fig. 5. *Cebochoerus robiacensis* Depéret in occlusal view. (a) NMNS-PV 21301, left m3. (b) NMNS-PV 21302, right p3.

and Métais, 2007). The resent specimens are distinguished from the specimens of *C. helveticus* stored in Université Montpellier II (Montpellier, France) in that the P3 protocone is more distally shifted compared to the latter.

***Cebochoerus robiacensis* Depéret, 1917**

(Fig. 5)

Material: NMNS-PV 21301, left m3; NMNS-PV 21302, right p3.

Locality: Robiac (150 km northwest of Marseille, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: In the Robiac locality, *Cebochoerus helveticus* and *Cebochoerus robiacensis* are recorded among the genus (Erfurt and Métais, 2007). *C. robiacensis* is smaller than *C. helveticus*. The present specimens are referable to *C. robiacensis* in size.

***Cebochoerus* sp.**

(Fig. 6)

Material: NMNS-PV 21164, right P3.

Locality: Le Bretou (Quercy, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The present P3 is smaller than that of *Cebochoerus helveticus*. It is also distinguished from P3 of *C. helveticus* stored in Université Montpellier II (Montpellier, France) in that the protocone is more distally shifted.

Family Choeropotamidae Owen, 1845
Genus *Choeropotamus* Cuvier, 1822

***Choeropotamus parisiensis* Cuvier, 1822**
(Fig. 7)

Material: NMNS-PV 21533, cast of a left maxillary fragment with M1–3.

Locality: St. Capraise d'Eymet (Dordogne, France).

Age: late Eocene (Priabonian). European mammal zone MP20 (Schmidt-Kittler, 1987).

Comments: The information of the original fossil specimen is unknown. *Choeropotamus parisiensis* is the only species among the genus recorded in the St. Capraise d'Eymet (Erfurt and Métais, 2007). This species is the largest among the genus (Erfurt and Métais, 2007).

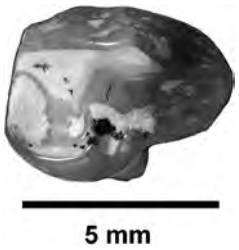

Fig. 6. *Cebochoerus* sp. NMNS-PV 21164, right P3, occlusal view.

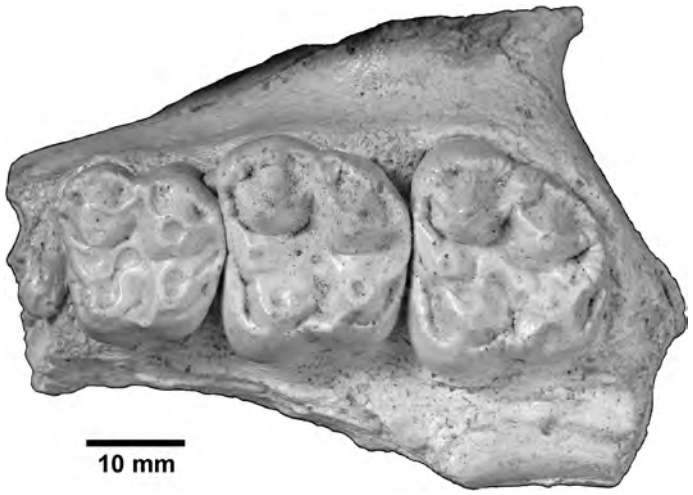

Fig. 7. *Choeropotamus parisiensis* Cuvier. NMNS-PV 21533, cast of a left maxillary fragment with M1–3, occlusal view.

***Choeropotamus* sp.**
(Fig. 8)

Material: NMNS-PV 21459, right mandibular fragment with dp4.
Locality: La Débruge (Apt, Cereste, Vaucluse, 70 km north of Marseille, France).
Age: late Eocene (Priabonian). European mammal zone MP18 (Schmidt-Kittler, 1987).
Comments: Judging from the locality and its large size, this specimen is referable either to *Choeropotamus affinis* or *Choeropotamus parisiensis*.

Genus *Tapirulus* Gervais, 1850

***Tapirulus* sp. cf. *T. schlosseri* Stehlin, 1910**
(Fig. 9)

Material: NMNS-PV 21167, left DP4; NMNS-PV 21168, right M1 or M2.
Locality: Le Bretou (Quercy, France).
Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).
Comments: *Tapirulus* is characterized by the bilophodont dentition. In the Le Bretou locality, *Tapirulus schlosseri* and *Tapirulus* sp. cf. *T. schlosseri* have been recorded among the genus (Erfurt and Métais, 2007).

Fig. 8. *Choeropotamus* sp. NMNS-PV 21459, a right mandibular fragment with dp4, occlusal view.

Fig. 9. *Tapirulus* sp. cf. *T. schlosseri* Stehlin in occlusal view. (a) NMNS-PV 21167, left DP4. (b) NMNS-PV 21168, right M1 or M2.

Family Cainotheriidae Camp and Van der Hoof, 1940
Subfamily Robiaciinae Sudre, 1977
Genus *Robiacina* Sudre, 1969

***Robiacina minuta* Sudre, 1969**
(Figs. 10–11)

Material: NMNS-PV 21185, left mandibular fragment with p4–m1 and a trigonid fragment of m2; NMNS-PV 21284, left mandibular fragment with m3; NMNS-PV 21285, left mandibular fragment with p3 talonid and p4, and with associated incisor; NMNS-PV 21286, right mandibular fragment with m1–3; NMNS-PV 21287, right maxillary fragment with M3; NMNS-PV 21289, right upper molar; NMNS-PV 21290, right upper molar; NMNS-PV 21291, left P4; NMNS-PV 21292a right upper molar; NMNS-PV 21293, right upper molar; NMNS-PV 21295, left upper molar; NMNS-PV 21296, right m1 or m2; NMNS-PV 21297, left m1 or m2; NMNS-PV 21298, right m1 or m2; NMNS-PV 21299, right m1 or m2.

Locality: NMNS-PV 21185 is from Le Bretou (Quercy, France). The other specimens (NMNS-PV 21284–21287, 21289–21293, 21295–21299) are from Robiac (150 km northwest of Marseille, France).

Age: late middle Eocene (Bartonian); European mammal zone MP16 (Schmidt-Kittler, 1987).

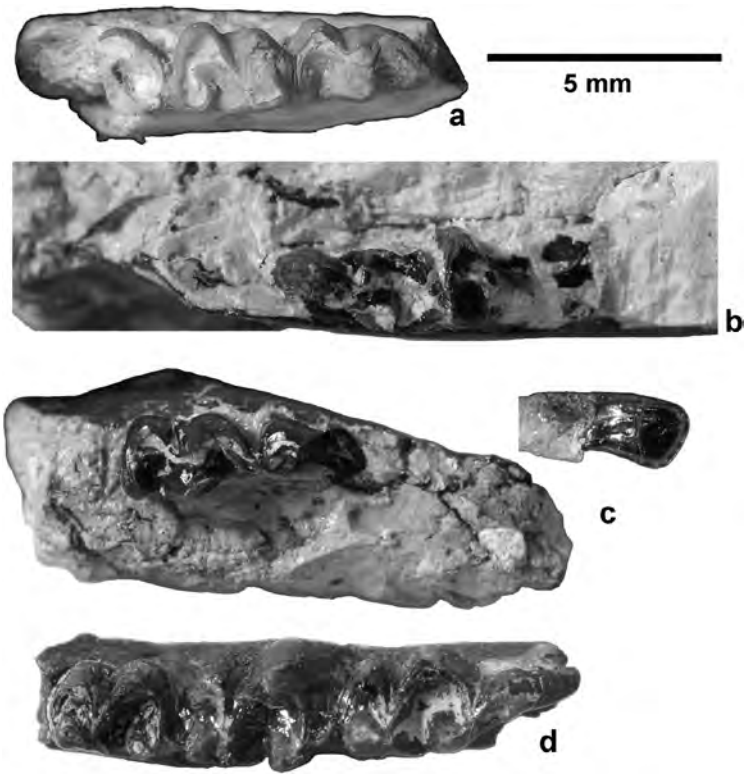

Fig. 10. *Robiacina minuta* Sudre in occlusal view. (a) NMNS-PV 21185, left mandibular fragment with p4–m1 and a trigonid fragment of m2. (b) NMNS-PV 21284, left mandibular fragment with m3. (c) NMNS-PV 21285, left mandibular fragment with p3 talonid and p4, and with an associated incisor. (d) NMNS-PV 21286, right mandibular fragment with m1–3.

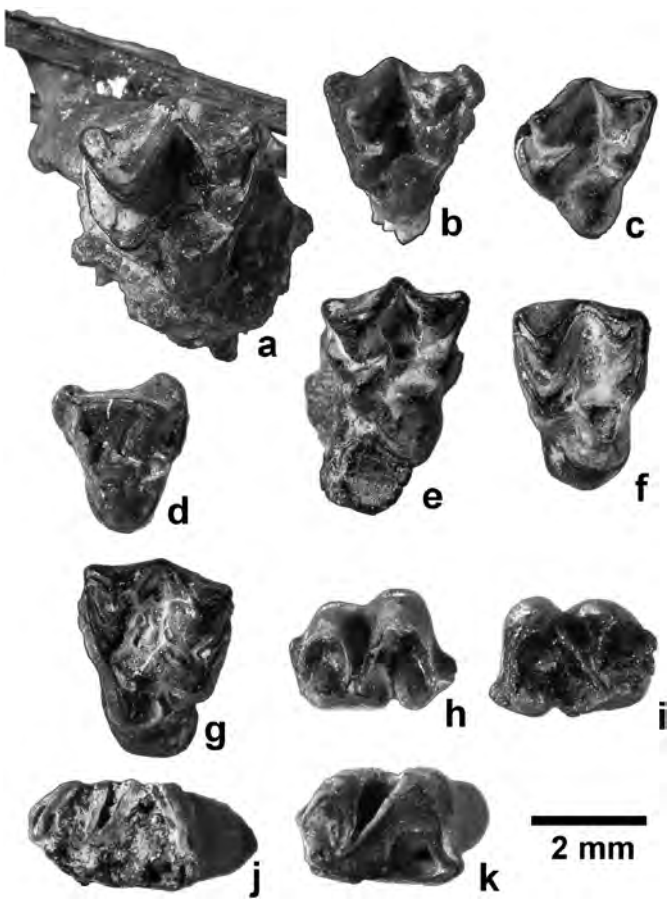

Fig. 11. *Robiacina minuta* Sudre in occlusal view. (a) NMNS-PV 21287, right maxillary fragment with M3. (b) NMNS-PV 21289, right upper molar. (c) NMNS-PV 21290, right upper molar. (d) NMNS-PV 21291, left P4. (e) NMNS-PV 21292, right upper molar. (f) NMNS-PV 21293, right upper molar. (g) NMNS-PV 21295, left upper molar. (h) NMNS-PV 21296, right m1 or m2. (i) NMNS-PV 21297, left m1 or m2. (j) NMNS-PV 21298, right m1 or m2. (k) NMNS-PV 21299, right m1 or m2.

Comments: *Robiacina minuta* is the only species recorded in the Le Bretou and Robiac localities among the genus (Erfurt and Métais, 2007).

Cf. *Robiacina minuta* Sudre, 1969
(Fig. 12)

Material: NMNS-PV 21288, right P3.

Locality: Robiac (150 km northwest of Marseille, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: This specimen is roughly comparable to P3 or P4 of *Robiacina minuta* in size and morphology. However, it is distinguished from P4 of *Robiacina* in having a less developed protocone and in that the buccal part of the crown is mesiodistally more elongated. It differs from P3 of *Robiacina* in having more developed and more mesially shifted protocone. It has similarity with P3 of *Mix-*

Fig. 12. cf. *Robiacina minuta* Sudre. NMNS-PV 21288, right P3, occlusal view.

totherium lavergensis (= *Robiacina lavergensis* Sudre, 1977) in the development of protocone. However, it differs from P3 of *M. lavergensis* in having a mesiobuccally oriented preparacrista (the preparacrista of P3 of *M. lavergensis* is mesiodistally oriented). And, *Mixtotherium* has not been recorded in Robiac (Erfurt and Métais, 2007).

Family Anoplotheriidae Bonaparte, 1850
Subfamily Anoplotheriinae Bonaparte, 1850
Genus *Anoplotherium* Cuvier, 1804
(in Cuvier, 1804–1805)

***Anoplotherium commune* Cuvier, 1822**
(Figs. 13–15)

Material: NMNS-PV 21449, right maxillary fragment with DP2–3; NMNS-PV 21450, right ?C1 or ?DP1; NMNS-PV 21451, right mandibular fragment with dp3; NMNS-PV 21452, left I3; NMNS-PV 21458, left mandibular fragment with m2; NMNS-PV 21525, skull and mandibles with right P2–M3, right p2–M3, left C1–M3, and left p2–m3; NMNS-PV 21526, 14 caudal vertebrae on matrix; NMNS-PV 21527, right and left mandibles with right teeth (p1, dp2–4, m1–2) and left teeth (?di1, di3, dc1, p1, dp2–4, m1–2); NMNS-PV 21528, left maxillary fragment with DP2–4 and M1; NMNS-PV 21529, left mandibular fragment including condyle with p2–m3; NMNS-PV 21530, left maxillary fragment with M2–3; NMNS-PV 21531, left maxillary fragment with P1 and DP2–4; NMNS-PV 21546, left ?I3.

Locality: NMNS-PV 21449–21452 and 21458 are from La Débruge (Apt, Cereste, Vaucluse, 70 km north of Marseille, France). NMNS-PV 21525–21531 are from St. Capraise d'Eymet (Dordogne, France).

Age: La Débruge: late Eocene (Priabonian); European mammal zone MP 18. St. Capraise d'Eymet: late Eocene (Priabonian); European mammal zone MP20 (Schmidt-Kittler, 1987).

Comments: *Anoplotherium commune* is larger than *Anoplotherium laurillardi*, although several intermediate-sized specimens are present in the collection of the Muséum National d'Histoire Naturelle (Paris, France).

***Anoplotherium laurillardi* Pomel, 1851**
(Fig. 16)

Material: NMNS-PV 21453, left mandibular fragment with p1–2; NMNS-PV 21454, right p2;

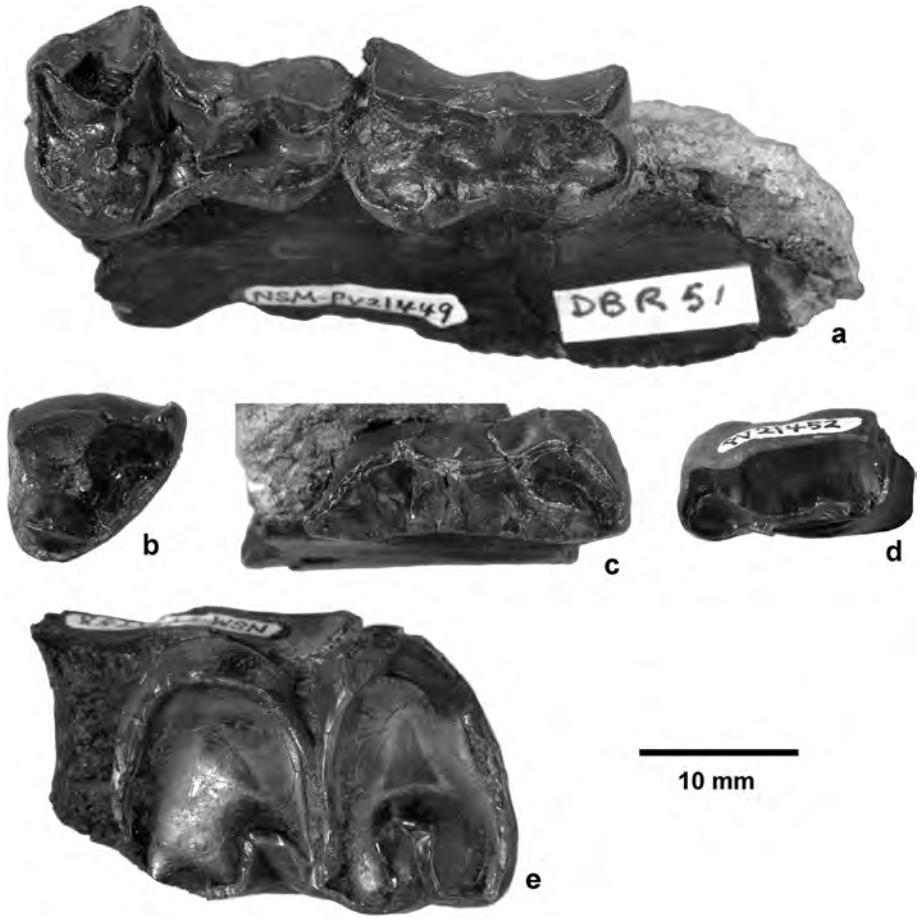

Fig. 13. *Anoplotherium commune* Cuvier in occlusal view. (a) NMNS-PV 21449, right maxillary fragment with DP2–3. (b) NMNS-PV 21450, right ?C1 or ?DP1 (c) NMNS-PV 21451, right mandibular fragment with dp3. (d) NMNS-PV 21452, left I3. (e) NMNS-PV 21458, left mandibular fragment with m2.

NMNS-PV 21455, left I2; NMNS-PV 21456, left mandibular fragment with dp3; NMNS-PV 21457, left mandibular fragment including condyle with dp1–4 and m1, and associated proximal radius attached to the mandible; NMNS-PV 21499, right maxillary fragment with distal part of M1, and M2.

Locality: La Débruge (Apt, Cereste, Vaucluse, 70 km north of Marseille, France).

Age: late Eocene (Priabonian); European mammal zone MP18 (Schmidt-Kittler, 1987).

Comments: *Anoplotherium laurillardi* is smaller than *Anoplotherium commune*.

Genus *Diplobune* Rütimeyer, 1862

***Diplobune* sp.**
(Fig. 17)

Material: NMNS-PV 21661, right maxillary fragment with M1–3.

Locality: Mittelfranken (middle part of northern Bayern Province, Germany).

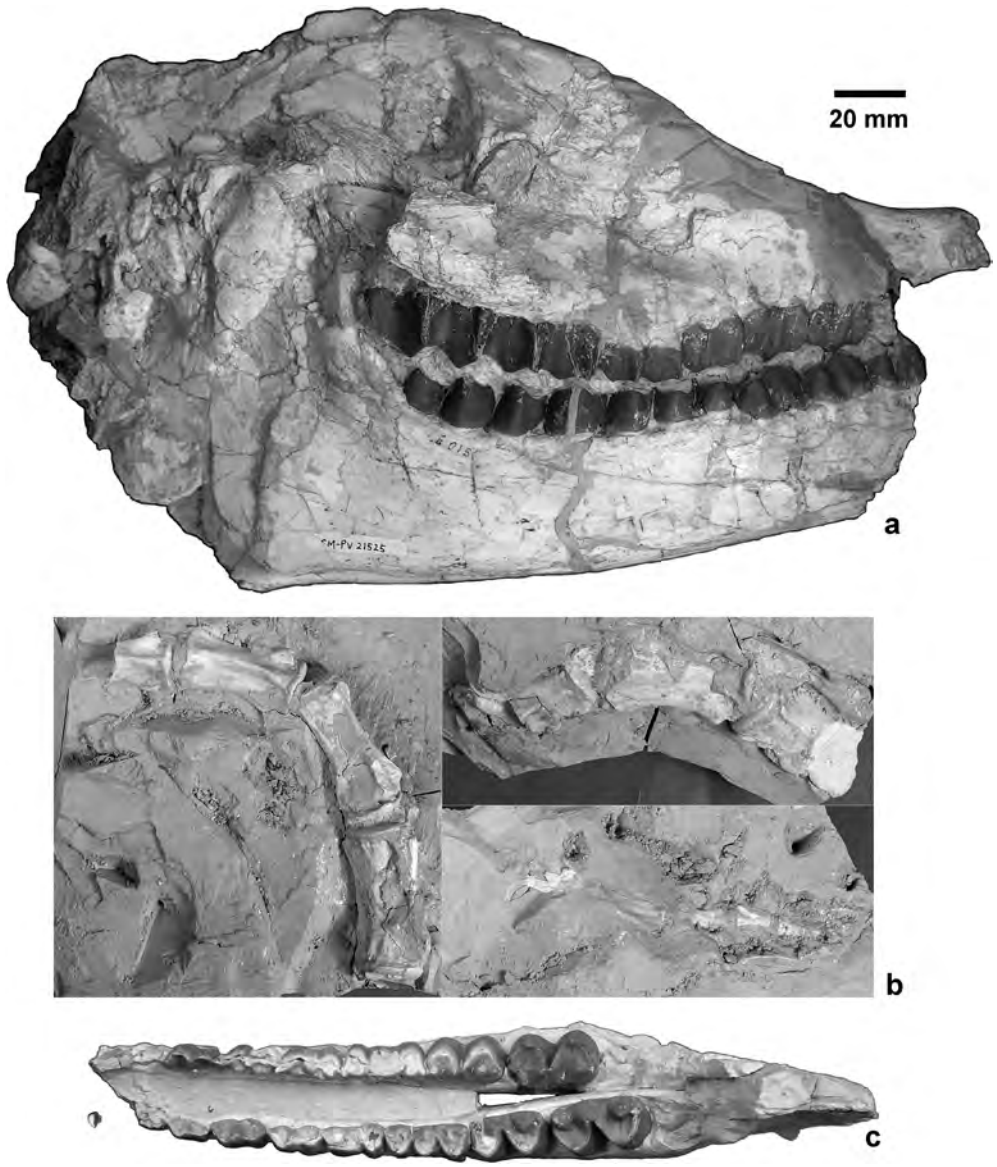

Fig. 14. *Anoplotherium commune* Cuvier. (a) NMNS-PV 21525, skull with right P2–M3, right p2–M3, left C1–M3, and left p2–m3, right lateral view. (b) NMNS-PV 21526, 14 caudal vertebrae on matrix. (c) NMNS-PV 21527, right and left mandibles with right teeth (p1, dp2–4, m1–2) and left teeth (?di1, di3, dc1, p1, dp2–4, m1–2), occlusal view.

Age: early Oligocene (Rupelian).

Comments: Although the precise locality is unknown, if this specimen is from Pappenheim City of Mittelfranken Division, the specimen is probably assigned to *Diplobune bavarica*, which is the only recorded species of the genus *Diplobune* in Pappenheim (Erfurt and Métais, 2007).

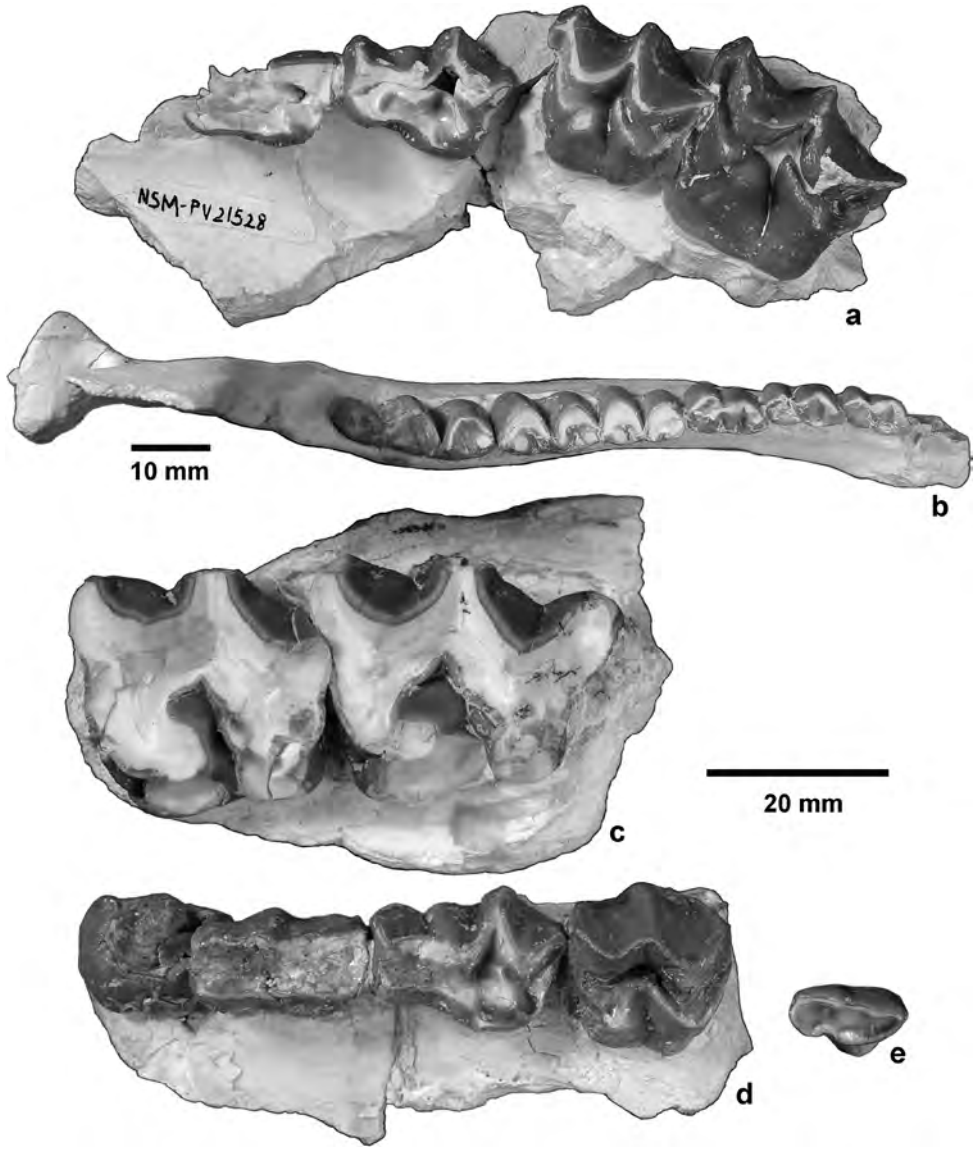

Fig. 15. *Anoplotherium commune* Cuvier in occlusal view. (a) NMNS-PV 21528, left maxillary fragment with DP2–4 and M1. (b) NMNS-PV 21529, left mandibular fragment including condyle with p2–m3. (c) NMNS-PV 21530, left maxillary fragment with M2–3. (d) NMNS-PV 21531, left maxillary fragment with P1 and DP2–4. (e) NMNS-PV 21546, left ?I3. Upper scale corresponds to b; lower scale corresponds to a, c, d, e.

Subfamily Dacrytheriinae Depéret, 1917
Genus *Dacrytherium* Filhol, 1876

***Dacrytherium ovinum* (Owen, 1857)**
(Fig. 18)

Material: NMNS-PV 21385, right mandibular fragment with dp3–4, posterior part of dp2, and erupting m1.

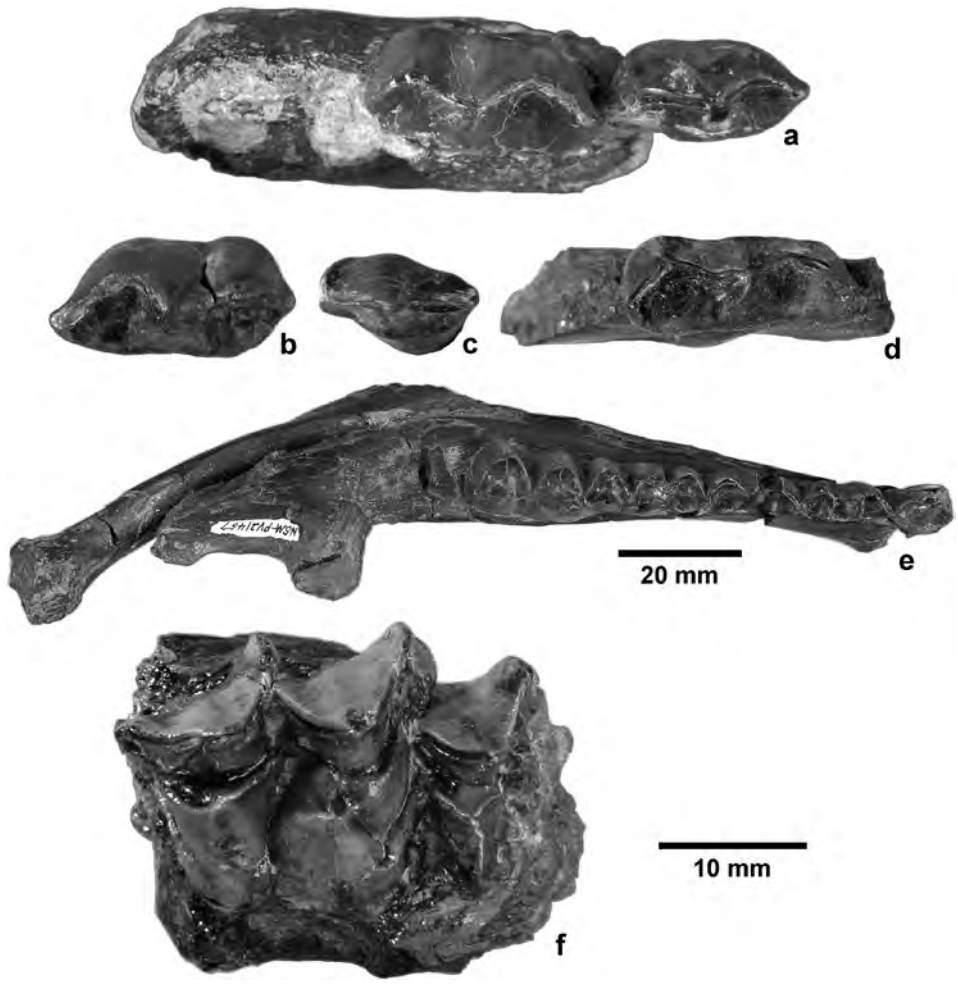

Fig. 16. *Anoplotherium laurillardi* Pomel in occlusal view. (a) NMNS-PV 21453, left mandibular fragment with p1–2. (b) NMNS-PV 21454, right p2. (c) NMNS-PV 21455, left I2. (d) NMNS-PV 21456, left mandibular fragment with dp3. (e) NMNS-PV 21457, left mandibular fragment including condyle with dp1–4 and m1, and an associated proximal radius attached to the mandible. (f) NMNS-PV 21499, right maxillary fragment with distal part of M1, and M2.

Locality: Euzet les Bains, (Gard, 200 km northwest of Marseille, France)

Age: late Eocene (Priabonian). European mammal zone MP17 (Schmidt-Kittler, 1987).

Comments: *Dacrytherium ovinum* is the only species among the genus that recorded in Euzet les Bains (Sudre, 1978b).

Genus *Catodontherium* Depéret, 1908

***Catodontherium robiacense* (Depéret, 1906)**
(Fig. 19)

Material: NMNS-PV 21304, right maxillary fragment with M1–3; NMNS-PV 21305, right m2.

Locality: Robiac (150 km northwest of Marseille, France).

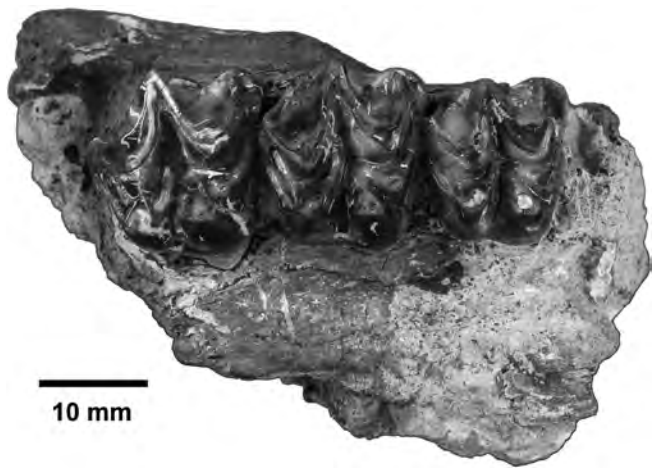

Fig. 17. *Diplobune* sp. NMNS-PV 21661, right maxillary fragment with M1–3, occlusal view.

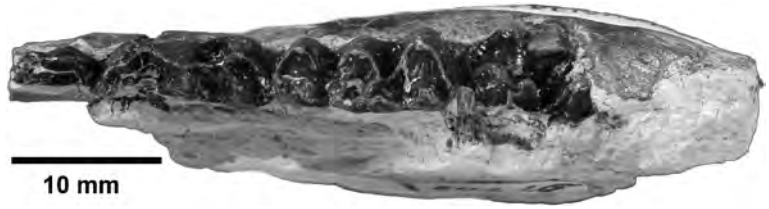

Fig. 18. *Dacrytherium ovinum* (Owen). NMNS-PV 21385, right mandibular fragment with dp3–4, posterior part of dp2, and erupting m1, occlusal view.

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: *Catodontherium robiacense* is the only species among the genus that recorded in Euzet les Bains (Erfurt and Métais, 2007).

Family Xiphodontidae Flower, 1884
Genus *Xiphodon* Cuvier, 1822

***Xiphodon castrensis* Kowalevsky, 1873**
(Figs. 20–22)

Material: NMNS-PV 21169, left dp4; NMNS-PV 21170, left ?p2; NMNS-PV 21176, left mandibular fragment with m1–3; NMNS-PV 21177, left ?P2 or ?P1 in matrix; NMNS-PV 21178, right maxillary fragment with ?P2; NMNS-PV 21179, left m1 (with roots); NMNS-PV 21180, left m1 or 2 (without roots); NMNS-PV 21306, right mandibular fragment with m3; NMNS-PV 21307, right maxillary fragment with M3; NMNS-PV 21308, left mandibular fragment with p4–m2; NMNS-PV 21309, left mandibular fragment with m1–2 and m3 trigonid; NMNS-PV 21311, left p4; NMNS-PV 21313, left upper molar; NMNS-PV 21314, right upper molar; NMNS-PV 21315, right upper molar; NMNS-PV 21316, left upper molar; NMNS-PV 21317, right m3 talonid; NMNS-PV 21319, left ?P2; NMNS-PV 21320, left P4; NMNS-PV 21321, eleven teeth fragments.

Locality: NMNS-PV 21169–21170 and 21176–21180 are from Le Bretou (Quercy, France).

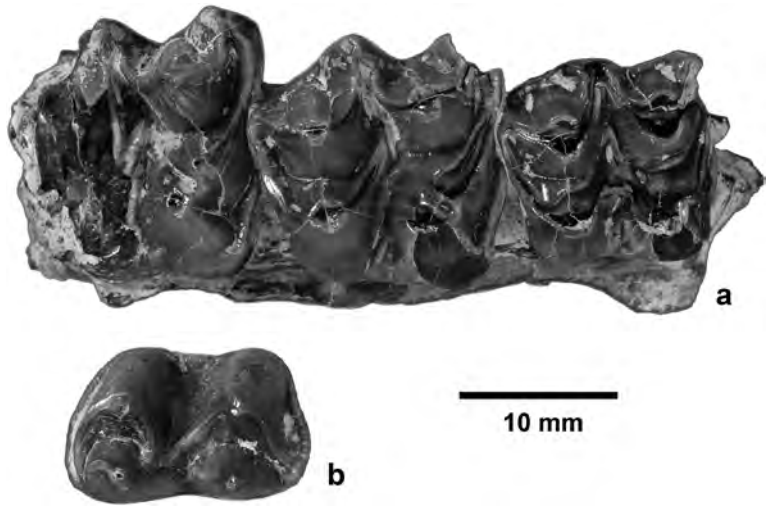

Fig. 19. *Catodontherium robiacense* (Depéret) in occlusal view. (a) NMNS-PV 21304, right maxillary fragment with M1–3. (b) NMNS-PV 21305, right m2.

NMNS-PV 21306–21317 and 21319–21321 are from Robiac (150 km northwest of Marseille, France).

Age: late middle Eocene (Bartonian); European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: *Xiphodon castrensis* is the only species among the genus recorded in the Le Bretou and Robiac localities (Erfurt and Métais, 2007). It is smaller than *Xiphodon gracile*.

Cf. *Xiphodon castrensis* Kowalevsky, 1873

(Fig. 23)

Material: NMNS-PV 21181, lower left or upper right ?incisor; NMNS-PV 21189, phalange; NMNS-PV 21190, tarsal bone (?cuboid); NMNS-PV 21191, carpal or tarsal bone (?navicular); NMNS-PV 21310, right ?dp3; NMNS-PV 21312, left ?dp2.

Locality: NMNS-PV 21181 and 21189–21191 are from Le Bretou (Quercy, France). NMNS-PV 21310 and 21312 are from Robiac (150 km northwest of Marseille, France).

Age: late middle Eocene (Bartonian); European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Judging from the size, the postcranial specimens (NMNS-PV 21189–21191) is probably referable to *Xiphodon castrensis*. The dental specimens (NMNS-PV 21181, 21310, and 21312) were originally labeled as *Xiphodon castrensis*, but their identifications are still tentative.

Xiphodon gracile Cuvier, 1822

(Fig. 24–25)

Material: NMNS-PV 21460, right maxillary fragment with M1–3; NMNS-PV 21461, right maxillary fragment with M1–3; NMNS-PV 21462, right mandibular fragment with p3–m3; NMNS-PV 21463, left mandibular fragment with dp4 and m1; NMNS-PV 21464, left mandibular fragment with m2 and trigonid of m3; NMNS-PV 21466, right P4; NMNS-PV 21534, right mandibular fragment with m1–3 and three anterior teeth (?i1–3); NMNS-PV 21535, left P4; NMNS-PV 21536, left maxillary fragment with

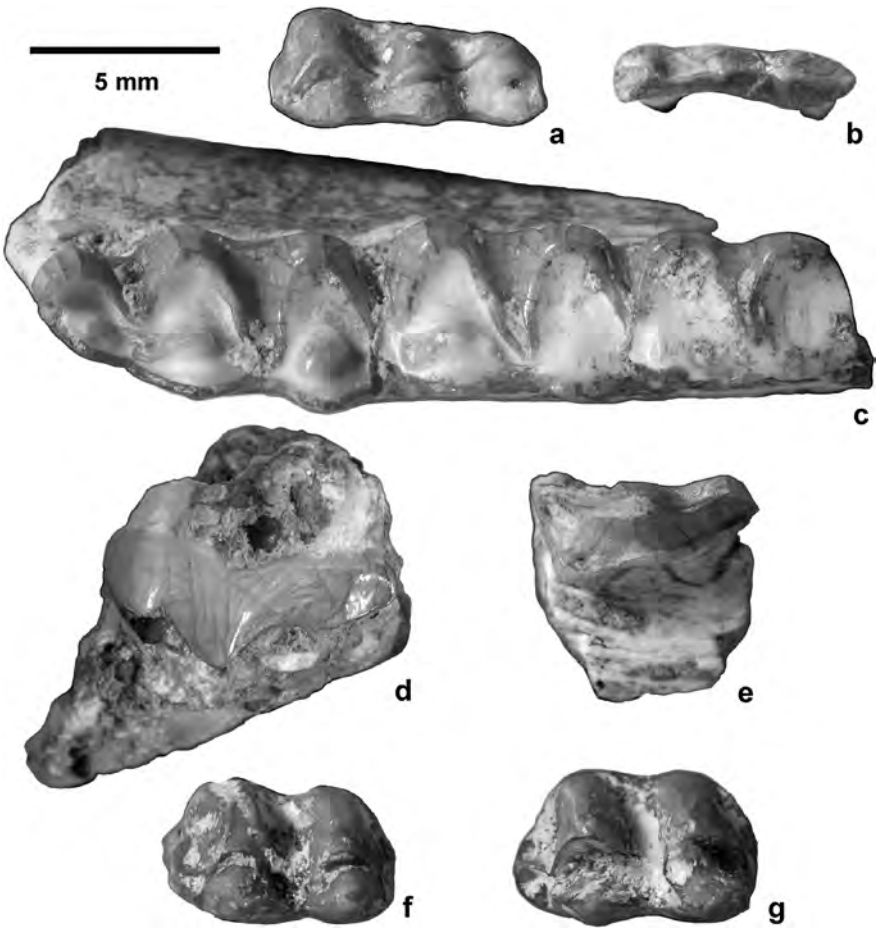

Fig. 20. *Xiphodon castrensis* Kowalevsky. (a) NMNS-PV 21169, left dp4, occlusal view. (b) NMNS-PV 21170, left ?p2, occlusal view. (c) NMNS-PV 21176, left mandibular fragment with m1–3, occlusal view. (d) NMNS-PV 21177, left ?P2 or ?P1 in matrix, buccal view. (e) NMNS-PV 21178, right maxillary fragment with ?P2, occlusal view. (f) NMNS-PV 21179, left m1, occlusal view. (g) NMNS-PV 21180, left m1 or 2, occlusal view.

P4; NMNS-PV 21537, left maxillary fragment with an upper molar; NMNS-PV 21538, right mandibular fragment with p3; NMNS-PV 21539, right mandibular fragment with m2 talonid and m3.

Locality: NMNS-PV 21460–21464 and 21466 are from La Débruge (Apt, Cereste, Vaucluse, 70 km north of Marseille, France). NMNS-PV 21534–21539 are from St. Capraise d'Eymet (Dordogne, France).

Age: La Débruge: late Eocene (Priabonian); European mammal zone MP18. St. Capraise d'Eymet: late Eocene (Priabonian); European mammal zone MP20 (Schmidt-Kittler, 1987).

Comments: *Xiphodon gracile* is the only species among the genus recorded in the La Débruge and St. Capraise d'Eymet localities (Erfurt and Métais, 2007). It is larger than *Xiphodon castrensis*.

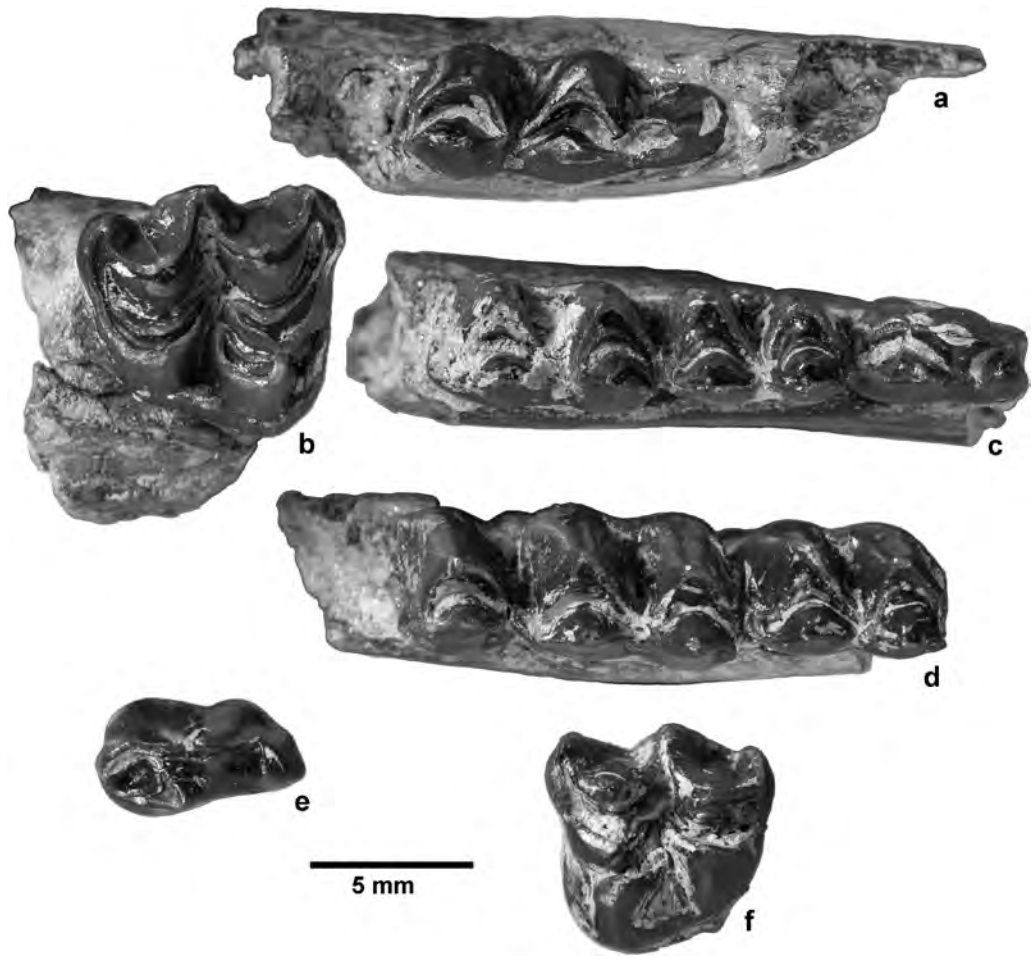

Fig. 21. *Xiphodon castrensis* Kowalevsky in occlusal view. (a) NMNS-PV 21306, right mandibular fragment with m3. (b) NMNS-PV 21307, right maxillary fragment with M3. (c) NMNS-PV 21308, left mandibular fragment with p4–m2. (d) NMNS-PV 21309, left mandibular fragment with m1–2 and m3 trigonid. (e) NMNS-PV 21311, left p4. (f) NMNS-PV 21313, left upper molar.

***Xiphodon* sp. cf. *X. gracile* Cuvier, 1822**

(Fig. 26)

Material: NMNS-PV 21363, left mandibular fragment with p4–m3.

Locality: Civrac de Blaye (Gironde, south of Bordeaux, France).

Age: late Eocene (Priabonian); European mammal zone MP18 (Schmidt-Kittler, 1987).

Comments: The dental morphology and size are comparable to those of *Xiphodon gracile*; but this locality (Civrac de Blaye) is not listed in the localities of the species by Erfurt and Métais (2007).

Cf. *Xiphodon gracile* Cuvier, 1822

(Fig. 27)

Material: NMNS-PV 21465, right astragalus.

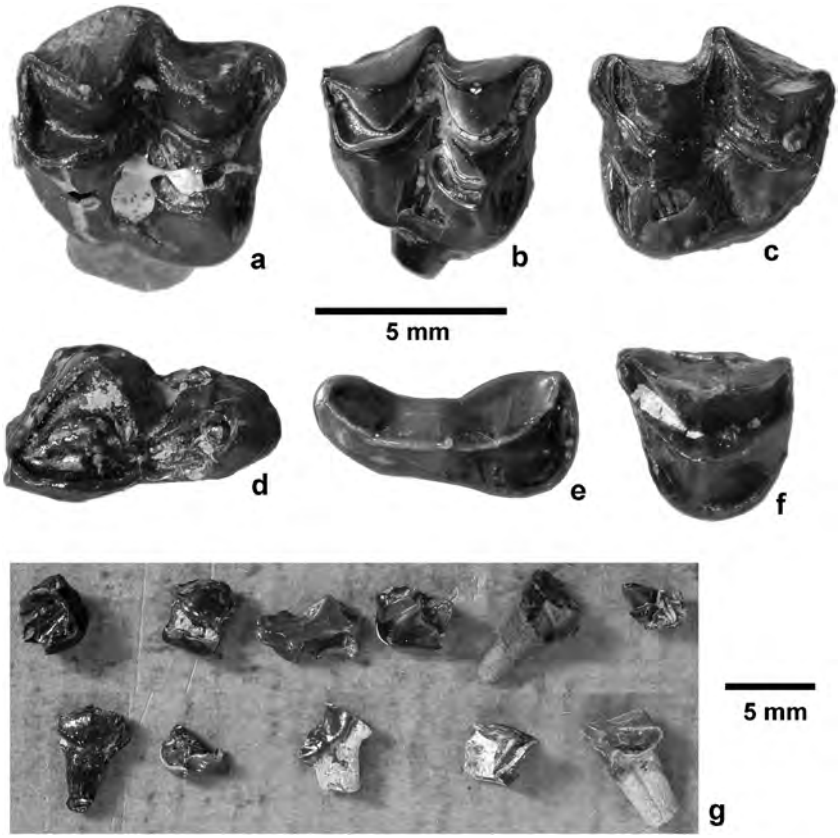

Fig. 22. *Xiphodon castrensis* Kowalevsky. (a) NMNS-PV 21314, right upper molar, occlusal view. (b) NMNS-PV 21315, right upper molar, occlusal view. (c) NMNS-PV 21316, left upper molar, occlusal view. (d) NMNS-PV 21317, right m3 talonid, occlusal view. (e) NMNS-PV 21319, left ?P2, occlusal view. (f) NMNS-PV 21320, left P4, occlusal view. (g) NMNS-PV 21321, eleven teeth fragments. Upper scale corresponds to a–f; lower scale corresponds to g.

Locality: La Débruge (Apt, Cereste, Vaucluse, 70 km north of Marseille, France).

Age: late Eocene (Priabonian); European mammal zone MP 18 (Schmidt-Kittler, 1987).

Comments: Judging from the size, this artiodactyl astragalus is probably referable to *Xiphodon gracile*.

Genus *Dichodon* Owen, 1848

***Dichodon cervinus* (Owen, 1841)**
(Fig. 28)

Material: NMNS-PV 21384, right mandibular fragment with p2–m3.

Locality: Euzet les Bains (Gard, 200 km northwest of Marseille, France).

Age: late Eocene (Priabonian). European mammal zone MP17 (Schmidt-Kittler, 1987).

Comments: *Dichodon cervinus* is the only species among the genus that recorded in Euzet les Bains (Erfurt and Métais, 2007).

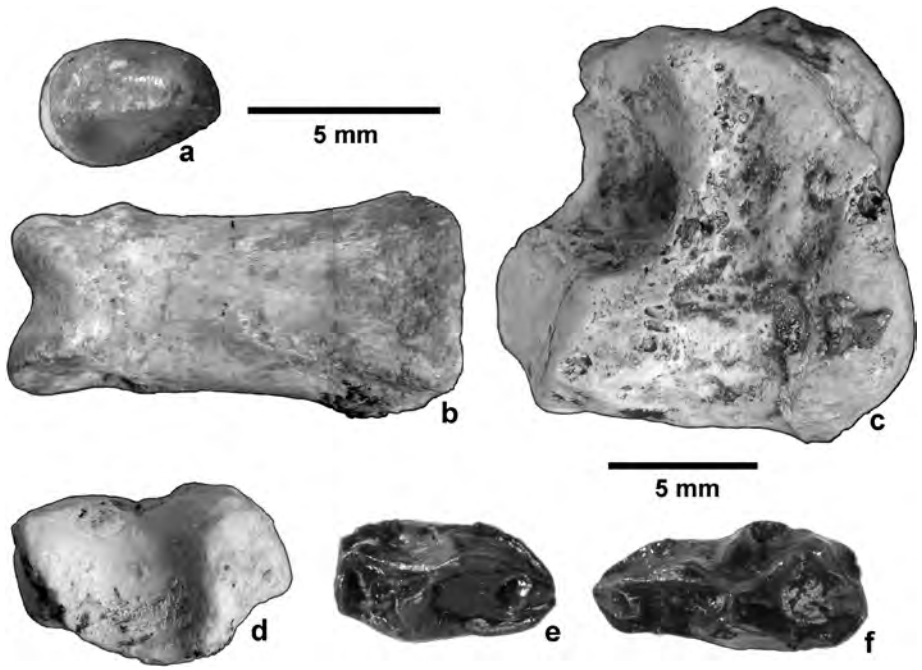

Fig. 23. Cf. *Xiphodon castrensis* Kowalevsky. (a) NMNS-PV 21181, lower left or upper right ?incisor, occlusal view. (b) NMNS-PV 21189, phalange, dorsal (anterior) view. (c) NMNS-PV 21190, tarsal bone (?cuboid). (d) NMNS-PV 21191, carpal or tarsal bone (?navicular). (e) NMNS-PV 21310, right ?dp3, occlusal view. (f) NMNS-PV 21312, left ?dp2, occlusal view. Left upper scale corresponds to a, e, f; right lower scale corresponds to b–d.

***Dichodon* sp.**

(Fig. 29)

Material: NMNS-PV 21175, right mandibular fragment with p3–4 and m2.

Locality: Le Bretou (Quercy, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: This specimen has trilobed p4 with two cusps on the anterior lobe, indicating that the specimen is referable to *Dichodon*. It is comparable in size to *Dichodon vidalenci*, which is recorded in the Le Bretou locality (Erfurt and Métais, 2007); and it is smaller than *Dichodon cervinus*. However, the present specimen lacks a strong "oreilles" (ears) on the lower molars, which is one of the diagnostic characters of *D. vidalenci* (Sudre, 1988).

Genus *Haplomeryx* Schlosser, 1886

***Haplomeryx* sp. cf. *H. picteti* Stehlin, 1910**

(Fig. 30)

Material: NMNS-PV 21172, right maxillary fragment with M2–3; NMNS-PV 21174, left P4; NMNS-PV 21294, left ?M1.

Locality: NMNS-PV 21172 and 21174 are from Le Bretou (Quercy, France). NMNS-PV 21294 is from Robiac (150 km northwest of Marseille, France).

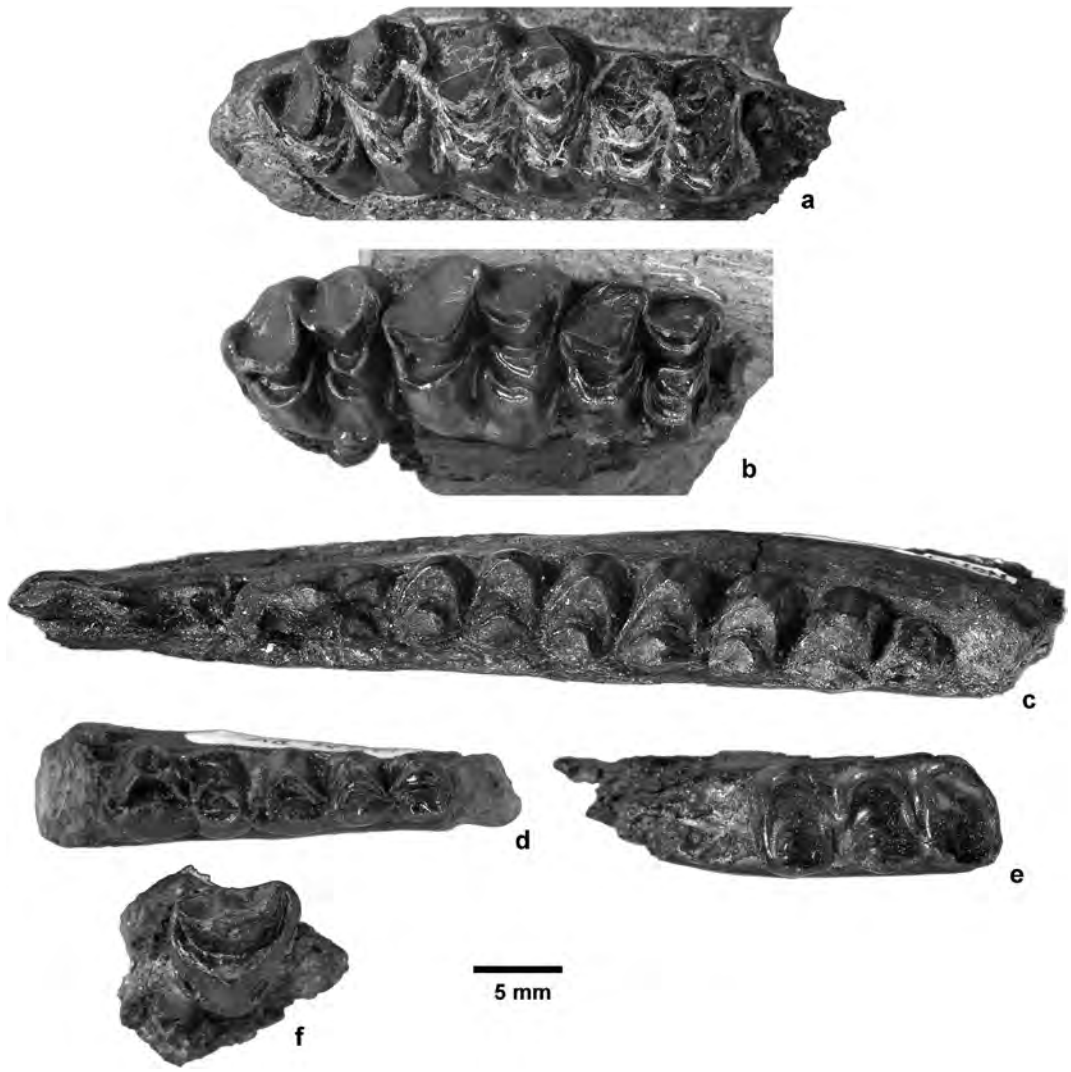

Fig. 24. *Xiphodon gracile* Cuvier in occlusal view. (a) NMNS-PV 21460, right maxillary fragment with M1–3. (b) NMNS-PV 21461, right maxillary fragment with M1–3. (c) NMNS-PV 21462, right mandibular fragment with p3–m3. (d) NMNS-PV 21463, left mandibular fragment with dp4 and m1. (e) NMNS-PV 21464, left mandibular fragment with m2 and trigonid of m3. (f) NMNS-PV 21466, right P4.

Age: late middle Eocene (Bartonian). European mammal zone MP 16 (Schmidt-Kittler, 1987).

Comments: The upper molars of *Haplomeryx* are distinguished from those of *Robiacina* in lacking a distinct paraconule and a crista connecting the paracone and parastyle. In the Le Bretou and Robiac localities, *Haplomeryx picteti* and *Haplomeryx* sp. cf. *H. picteti* have been recorded among the genus (Erfurt and Métais, 2007).

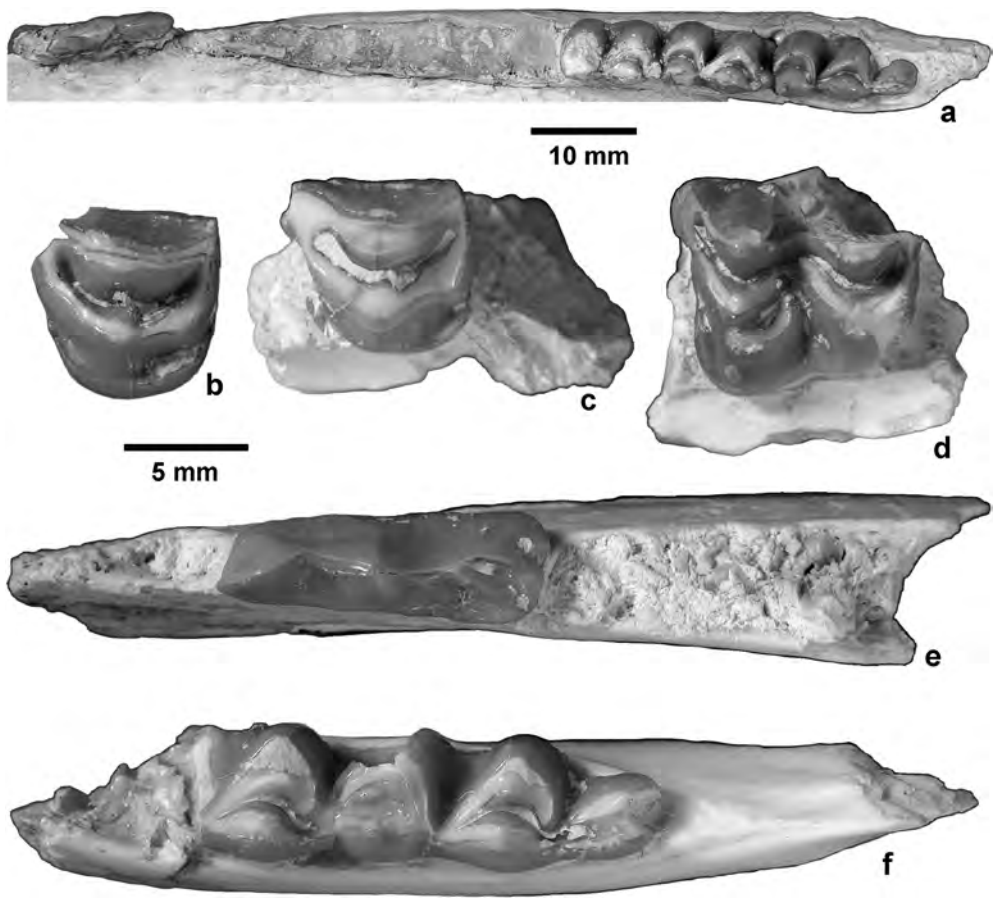

Fig. 25. *Xiphodon gracile* Cuvier in occlusal view. (a) NMNS-PV 21534, right mandibular fragment with m1–3 and three anterior teeth (?i1–3). (b) NMNS-PV 21535, left P4. (c) NMNS-PV 21536, left maxillary fragment with P4. (d) NMNS-PV 21537, left maxillary fragment with an upper molar. (e) NMNS-PV 21538, right mandibular fragment with p3. (f) NMNS-PV 21539, right mandibular fragment with m2 talonid and m3. Upper scale corresponds to a; lower scale corresponds to b–f.

Fig. 26. *Xiphodon* sp. cf. *X. gracile* Cuvier. NMNS-PV 21363, left mandibular fragment with p4–m3, occlusal view.

Fig. 27. Cf. *Xiphodon gracile* Cuvier. NMNS-PV 21465, right astragalus, dorsal (anterior) view.

Fig. 28. *Dichodon cervinus* (Owen). NMNS-PV 21384, right mandibular fragment with p2–m3, occlusal view.

Fig. 29. *Dichodon* sp. NMNS-PV 21175, right mandibular fragment with p3–4 and m2, occlusal view.

Family Amphimerycidae Stehlin, 1910
Genus *Amphimeryx* Pomel, 1848

Cf. *Amphimeryx murinus* (Cuvier, 1822)
(Fig. 31)

Material: NMNS-PV 21467, left m1 or m2.

Locality: La Débruge (Apt, Cereste, Vaucluse, 70 km north of Marseille, France).

Age: late Eocene (Priabonian); European mammal zone MP18 (Schmidt-Kittler, 1987).

Comments: The present lower molar is heavily worn, so that its precise morphology cannot be examined. The overall size and morphology match that of *Amphimeryx murinus*.

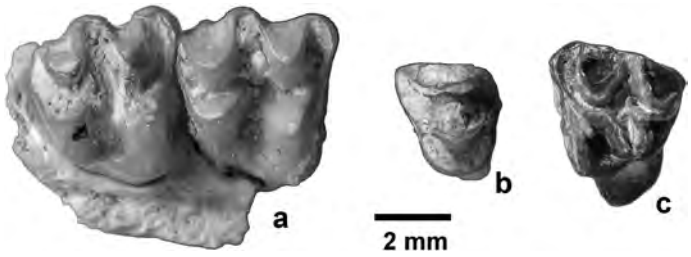

Fig. 30. *Haplomeryx* sp. cf. *H. picteti* Stehlin in occlusal view. (a) NMNS-PV 21172, right maxillary fragment with M2–3. (b) NMNS-PV 21174, left P4. (c) NMNS-PV 21294, left ?M1.

Fig. 31. Cf. *Amphimeryx murinus* (Cuvier). NMNS-PV 21467, left m1 or m2, occlusal view.

Genus *Pseudamphimeryx* Stehlin, 1910

***Pseudamphimeryx* sp.**
(Fig. 32)

Material: NMNS-PV 21171, left mandibular fragment with p3–m3; NMNS-PV 21173, left m1 or m2; NMNS-PV 21182, right mandibular fragment with p4–m3; NMNS-PV 21183, left M1 or M2; NMNS-PV 21184, left upper molar.

Locality: Le Bretou (Quercy, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Judging from the locality, these specimens are referable either to *Pseudamphimeryx pavloviae* or *Pseudamphimeryx renevieri*.

Cf. *Pseudamphimeryx* sp.
(Fig. 33)

Material: NMNS-PV 21186, left astragalus; NMNS-PV 21187, right astragalus.

Locality: Le Bretou (Quercy, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: Judging from the size, these artiodactyl astragali are probably referable to *Pseusamphimeryx*.

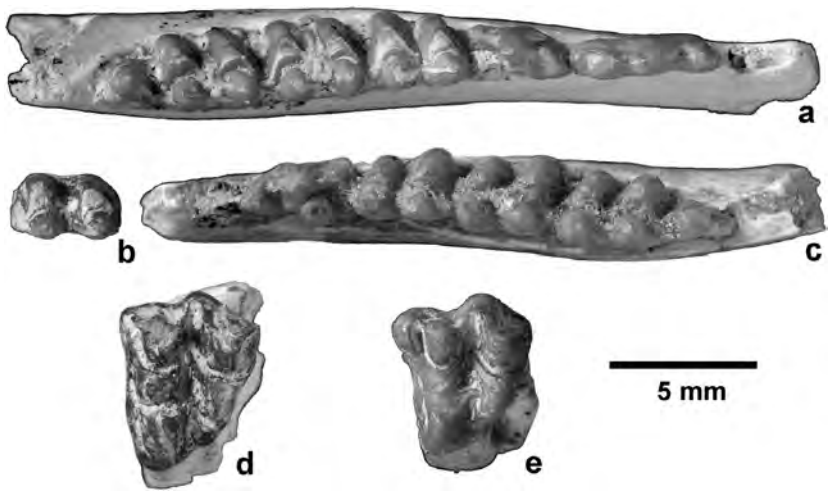

Fig. 32. *Pseudamphimeryx* sp. in occlusal view. (a) NMNS-PV 21171, left mandibular fragment with p3–m3. (b) NMNS-PV 21173, left m1 or m2. (c) NMNS-PV 21182, right mandibular fragment with p4–m3. (d) NMNS-PV 21183, left M1 or M2. (e) NMNS-PV 21184, left upper molar.

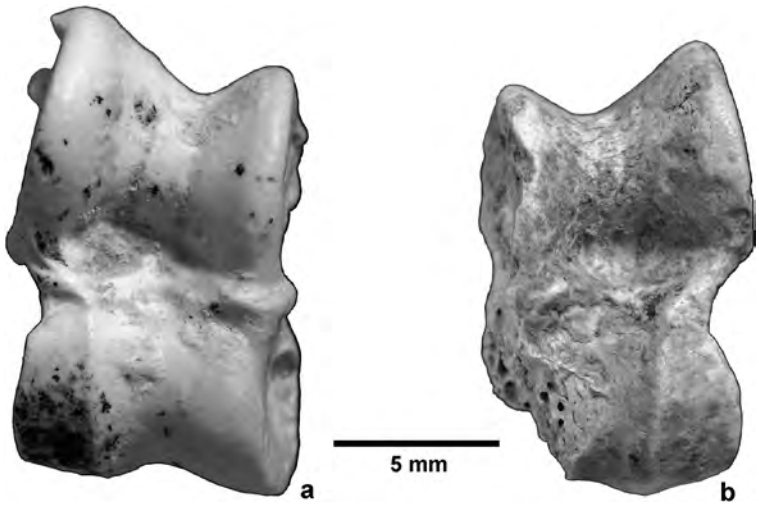

Fig. 33. Cf. *Pseudamphimeryx* sp., astragalus, dorsal (anterior) view. (a) NMNS-PV 21186, left astragalus. (b) NMNS-PV 21187, right astragalus.

Suborder Suiformes Jaeckel, 1911
Superfamily Suoidea Gray, 1821

Suoidea fam., gen et sp. indet.
(Fig. 34)

Material: NMNS-PV 21666, upper right incisor; NMNS-PV 21667, right P4.
Locality: Faluns de Touraine, (Loire, 300 km southwest of Paris, France).
Age: Basal part of middle Miocene (Langhian). European mammal zone MN5 (Steininger *et al.*,

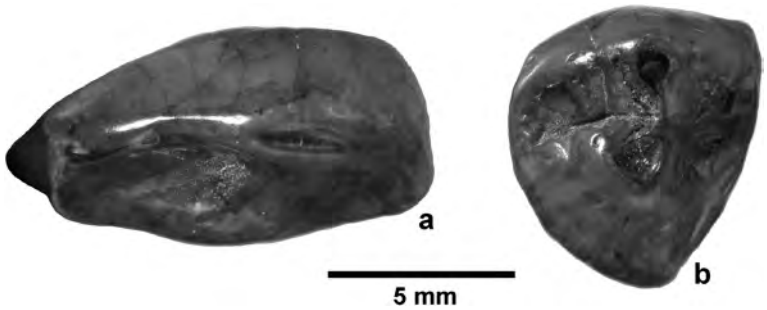

Fig. 34. Suoidea fam., gen. et sp. indet. in occlusal view. (a) NMNS-PV 21666, upper right incisor. (b) NMNS-PV 21667, right P4.

1996).

Comments: The dental morphologies of these specimens show a typical dental morphology of suoids. In the faunal list of the locality (Faluns de Touraine) by Ginsburg (1990), the following four suoid species were listed: *Aureliachoerus aurelianensis*, *Hyotherium soemmeringi*, *Bunolistriodon lockharti*, and *Taucanamo sansaniensis*.

Suborder Ruminantia Scopoli, 1777

Ruminantia fam., gen et sp. indet.
(Fig. 35)

Material: NMNS-PV 21669, right astragalus; NMNS-PV 21670, proximal phalange; NMNS-PV 21671, left p3 or p4.

Locality: Faluns de Touraine (Loire, 300 km southwest of Paris, France).

Age: Basal part of middle Miocene (Langhian). European mammal zone MN5 (Steininger *et al.*, 1996).

Comments: These specimens are roughly referable in size to those of sheep-sized ruminants. The lower premolar (NMNS-PV 21671) has a typical posterior premolar (p3 or p4) morphology of ruminants. The astragalus (NMNS-PV 21669) has a tibial trochlea that is parallel to the distal trochlea, indicating that it is probably referable to that of ruminants. The phalange (NMNS-PV 21670) is relatively slender and is tentatively assigned to the Ruminantia. In the faunal list of the locality (Faluns de Touraine) by Ginsburg (1990), the following eight genera (*Dorcatherium*, *Procervulus*, *Amphimoschus*, *Stephanocemas*, *Lagomeryx*, *Dicrocerus*, *Palaeomeryx*, and *Eotragus*) and 12 species of ruminants were listed.

Order ?Artiodactyla Owen, 1848

?Artiodactyla fam., gen et sp. indet.
(Fig. 36)

Material: NMNS-PV 21318, left lower premolar.

Locality: Robiac (150 km northwest of Marseille, France).

Age: late middle Eocene (Bartonian). European mammal zone MP16 (Schmidt-Kittler, 1987).

Comments: The classification of the tooth is unknown. It is possibly not referable to the Artiodactyla.

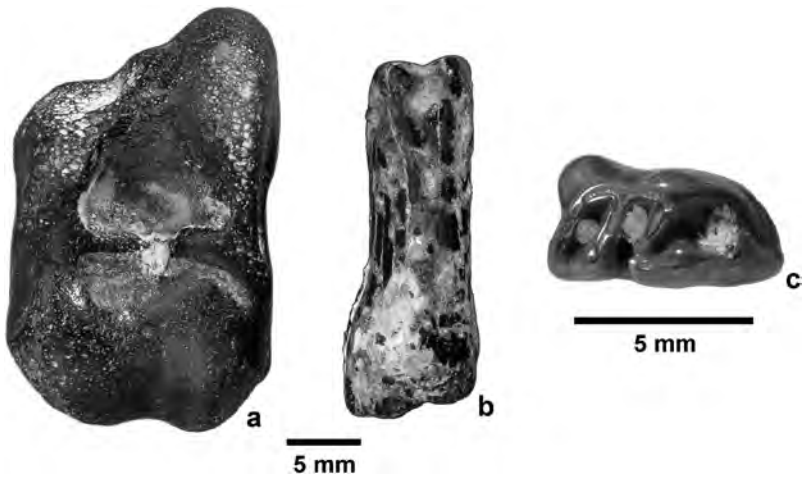

Fig. 35. Ruminantia fam., gen. et sp. indet. (a) NMNS-PV 21669, right astragalus, dorsal (anterior) view. (b) NMNS-PV 21670, proximal phalange, dorsal (anterior) view. (c) NMNS-PV 21671, left p3 or p4, occlusal view. Left scale corresponds to a–b; right scale corresponds to c.

Fig. 36. ?Artiodactyla fam., gen. et sp. indet., NMNS-PV 21318, a left lower premolar, occlusal view.

Acknowledgments

I am grateful to Drs. Bernard Marandat, Laurent Marivaux, and Jean Sudre (Université Montpellier II, Montpellier, France) and to Drs. Christine Argot, Pascal Tassy, Claire Sagne, Martin Pickford, and Brigitte Senut (Muséum National d'Histoire Naturelle, Paris, France) for graciously providing access to the collections and literatures in their institutions.

Literature Cited

Aymard, A., 1846. Essai monographique sur un nouveau genre de mammifère fossile trouvé dans la Haute-Loire, et nommé *Entelodon*. *Annales de la Société d'agriculture, sciences, arts et commerce du Puy,* **12** (1842–46): 227–67.

Blondel, C., 2005. New data on the Cainotheriidae (Mammalia, Artiodactyla) from the early Oligocene of south-western France. *Zoological Journal of the Linnean Society,* **144**: 145–166.

Bonaparte, C. L., 1850. *Conspectus systematis mastozoologiae (ornithologiae, etc.). Editio altera reformata; J. E. Brill, Leiden.*

Camp, C. L. and V. L. Van der Hoof, 1902. Bibliography of fossil vertebrates 1928–1933. *Geological Society Special Publication,* **27**: 1–503.

Cuvier, G., 1804–1805. Sur les espèces d'animaux dont provinnent les os fossiles répandus dans la pierre à plâtre des environs de Paris. *Annales du Muséum d'Histoire Naturelle Paris,* **3**: 275–472.

Cuvier, G., 1822. *Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux, dont les révolutions du globe ont détruit les espèces. G. Dufour et E. d'Ocagne, Paris*: 1–412.

de Bonis, L., 1964. Étude de Quelques mammifères du Ludien de la Débruge (Vaucluse). *Annales de Paléontologie (Vertébrés)*, **50** (2): 120–154.

Depéret, C., 1906. Los vertebrados del Oligocenio inferior de Tárrega (prov. de Lerida). *Memorias de la Academia de Ciencias y Artes de Barcelona*, **3**: 401–451.

Depéret, C., 1908. L'histoire géologique et la phylogénie des anthracothériidés. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **146**: 158–162.

Depéret, C., 1917. Monographie de la fauna de mammifères fossiles du Ludien inférieur d'Euzet-les-Bains (Gard). *Annales de l'Université de Lyon. I. Sciences, Médecine*, **40**: 1–290.

Erfurt, J. and G. Métais, 2007. Endemic European Paleogene artiodactyls: Cebochoeridae, Choeropotamidae, Mixtotheriidae, Cainotheriidae, Anoplotheriidae, Xiphodontidae, and Amphimerycidae. *In*: D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls. Johns Hopkins University Press, Baltimore*: 59–84.

Erfurt, J., G. Métais, and J. Sudre, 2007. Diversity of European Paleogene Artiodactyla (Mammalia), and their biostratigraphic significance for European Land Mammal Ages. *Abstracts Volume of the 5th Meeting of the European Association of Vertebrate Palaeontologists and 12th European Workshop of Vertebrate Palaeontology (Carcassonne-Espéraza, May 15–19, 2007)*: 21–27.

Filhol, H., 1876. Mammiferes fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **82**: 288–289.

Filhol, H., 1883. Etude des mammiferes fossiles de Ronzon (Haut-Loire). *Annales des sciences géologiques, Paris*, **12** (3): 1–271.

Flower, W. H., 1884. *Catalogue of the specimens illustrating the osteology and dentition of vertebrate animals, recent and extinct, contained in the Museum of the Royal College of Surgeons of England. Taylor and Francis, London*: 779 p.

Fraas, O., 1870. *Diplobune Bavaricum*. *Palaeontographica* **17**: 177–184.

Gervais, P., 1848–1852. *Zoologie et Paléontologie françaises (animaux vertébrés) ou Nouvelles Recherches sur les Animaux Vivants et Fossiles de la France. Arthus Bertrand, Paris*: 271 p.

Gervais, P., 1849. Recherches sur les mammifères fossiles des genres *Palaeotherium* et *Lophiodon* et sur les autres animaux de la même classe que l'on a trouvés avec eux dans le midi de la France. *Comptes Rendus de l'Académie des Sciences, Paris*, **29**: 381–384 and 568–579.

Gervais, P., 1850. Nouvelles recherches sur relatives aux mammifères d'espèces éteintes qui sont enfouies auprès d'Apt, avec des *Palaeotherium* identiques à ceux de Paris. *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences*, **30**: 602–604.

Ginsburg, L., 1990. The faunas and stratigraphical subdivisions of the Orleanian in the Loire Basin (France). *In*: E. H. Lindsay, V. Fahlbusch, and P. Mein (eds.), *European Neogene Mammal Chronology. Plenum Press, New York*: 157–176.

Gray, J. E., 1821. On the natural arrangement of vertebrose animals. *London Medical Repository*, **15**: 296–310.

Hartenberger, J.-L., B. Gige, and J. Sudre, 1974. La plus ancienne gaune de mammifere du Quercy: La Bretou. *Palaeovertebrata*, **6** (3–4): 177–196.

Hooker, J. J., 1986. Mammals from the Bartonian (middle/late Eocene) of the Hampshire Basin, southern England. *Bulletin of British Museum of Natural History (Geology)*, **39** (4): 191–478.

Hooker, J. J., M. E. Collinson, and N. P. Sille, 2004. Eocene–Oligocene mammalian faunal turnover in the Hampshire Basin, UK: calibration to the global time scale and the major cooling event. *Journal of the Geological Society, London*, **161**: 161–172.

Hooker, J. J. and M. Weidmann, 2000. The Eocene mammal faunas of Mormont, Switzerland. *Schweizerische Paläontologische Abhandlungen, Mémoires suisses de Paléontologie*, **120**: 1–141.

Jaeckel, O. M. J., 1911. *Die Wirbeltiere. Eine Überzicht über die fossilen und lebenden Formen. Gebrüder Borntraeger, Berlin*: viii + 252 p.

Kowalevsky, W., 1873. On the osteology of the Hyopotamidae. *Philosophical Transactions of the Royal Society of London*, **163**: 19–94.

Leidy, J., 1869. The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences of Philadelphia (Ser. 2)* **7**: 1–472.

Lihoreau, F. and S. Ducrocq, 2007. Family Anthracotheriidae. *In*: D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls. Johns Hopkins University Press, Baltimore*: 89–105.

Lydekker, R., 1883. Indian Tertiary and Post-Tertiary Vertebrata. Part 5. Siwalik Selenodont Suina. *Palaeontologia Indica (Series 10)*, **2** (5): 143–177.

Marsh, O. C., 1894. Description of Tertiary artiodactyls. *American Journal of Science (Series 3)*, **48**: 259–274.

Martinez, J.-N. and J. Sudre, 1995. The astragalus of Paleogene artiodactyls: comparative morphology, variability and prediction of body mass. *Lethaia*, **28**: 197–209.

McKenna, M. C. and S. K. Bell, 1997. *Classification of mammals above the species level. Columbia University Press, New York*: 631 p.

Owen, R., 1841. Description of some fossil remains of *Choeropotamus*, *Palaeotherium, Anoplotherium* and *Dichobune*, from the Eocene formation, Isle of Wight. *Transactions of the Geological Society of London*, **6**: 41–45.

Owen, R., 1845. *Odontography; or a treatise on the comparative anatomy of the teeth; their physiological relations, mode of development, and microscopic structure, in the vertebrate animals (2 volumes issued in parts). Hippolyte Bailliere, London.* **3**: 289–655.

Owen, R., 1848. Description of teeth and portions of jaw of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N.W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of pachyderms by the number of their toes. *Quarterly Journal of the Geological Society of London*, **4** (1): 103–141.

Owen R., 1857. Description of the lower jaw and teeth of an anoplotherioid quadruped (*Dichobune ovina*, Ow.) of the size of the *Xiphodon* gracilis, Cuv., from the upper Eocene Marl, Isle of Wight. *Quarterly Journal of the Geological Society of London*, **13**: 254–260.

Pictet, J. F. and A. Humbert, 1869. Mémoire sur les animaux vertébrés trouvés dans le terrain sidérolithique du Canton de Vaud et appartenant à la faune éocène. Supplément. *Matériaux Paléontologie Suisse*, **5**: 121–197.

Pomel, A., 1847. Note critique sur les caractères et les limites du genre *Paleotherium*. *Archives des sciences physiques et naturelles*, **5**: 200–207.

Pomel, A., 1848. Sur la classification des mammifères ongulés. *Bulletin de la Société Géologique de France*, **5**: 256–259.

Pomel, A., 1851. Nouvelles observations sur la structure des pieds dans les animaux de la famille des *Anoplotherium*, et dans le genre *Hyemoschus*. *Comptes Rendus de l'Académie des Sciences, série IIa*, **33**: 16–18.

Russell, D. E., J.-L. Hartenberger, C. Pomerol, S. Sen., N. Schmidt-Kittler, and M. Vianey-Liaud, 1982. The Paleontology of Europe: Mammals and stratigraphy. *Palaeovertebrata, Mémoire extraordinaire*: 1–77.

Rütimeyer, L., 1962. Eocäene Säugetiere aus dem Gebiet des Schweizerischen Jura. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften*, **19**: 1–98.

Savage, D. E. and D. E. Russell 1983. *Mammalian Paleofaunas of the World. Addison-Wesley Publishing Company, London*: 432 p.

Schlosser, M., 1886. Beiträge zur Kenntnis der Stammesgeschichte der Hufthiere und versuch einer Systematik der Paar- und Unpaarhufer. *Morphologische Jahrbuch*, **12**: 1–136.

Schmidt-Kittler, N. (ed.), 1987. International symposium on mammalian biostratigraphy and Paleoecology of the European Paleogene–Mainz, February 18th–21st 1987. *Münchner Geowissenschaftliche Abhandlungen, Reihe A* , **10**: 1–312.

Scopoli, G.A., 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague, Gerle*: 506 p.

Scott, W. B., 1940. The mammalian fauna of the White River Oligocene (Scott, W. B. and Jepsen, G. L. eds.), Part IV: Artiodactyla. *Transactions of the American Philosophical Society, New Series*, **28** (4): 363–746.

Stehlin, H. G., 1910. Die Säugetiere des schweizerischen Eocaens. Teil 6. *Abhandlungen der Schweizerischen Paläontologischen Gesellschaft*, **36**: 839–1164.

Steininger, F. F., W. A. Berggren, D. V. Kent, R. L. Bernor, S. Sen, and J. Agusti, 1996. Circum-Mediterranean Neogene (Miocene and Pliocene) marine–continental chronologic correlations of European Mammal Units. *In*: R. L. Bernor, V. Fahlbusch, and H.-W. Mittmann (eds.), *The Evolution of Western Eurasian Neogene Mammal Faunas. Columbia University Press, New York*: 7–46.

Sudre, J., 1969. Les gisements de Robiac (Eocène supérieur) et leurs faunes de Mammifères. *Palaeovertebrata*, **2**: 95–156.

Sudre, J., 1972. Révision des artiodactyles de l'Éocène moyen de Lissieu (Ehône). *Palaeovertebrata*, **5**: 111–156.

Sudre, J., 1973. Un *Dichodon* géant de La Débruge et une nouvelle interprétation phylétique du genre. *Bulletin du Muséum National d'Histoire naturelle, Paris, 3e* série, **133** (Sciences de la Terre 25): 73–78.

Sudre, J., 1974. D'Importants restes de *Diplobune minor* Filhol a Itardies (Quercy). *Palaeovertebrata*, **6** (1–2): 47–54.

Sudre, J., 1977. L'évolution du genre *Robiacina* Sudre 1969, et l'origine des Cainotheriide; implications systématiques. *Géobios, Mémoire special*, **1**: 213–231.

Sudre, J., 1978a. La poche à phosphate de Ste.-Néboule (Lot) et sa faune de vertébrés du Ludien supérieur. 9. Primates et Artiodactyles. *Palaeovertebrata*, **8**: 269–290.

Sudre, J., 1978b. Les artiodactyles de l'Eocène moyen et supérieur d'Europe occidentale. Systematique et évolution. *Mémoires et Travaux de l'Institut de Montpellier de l'Ecole Pratique des Hautes Etudes*, **7**: 1–229.

Sudre, J., 1988. Le gisement du Bretou (Phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de vertébrés de l'Eocène supérieur. VII. Artiodactyles. *Palaeontographica Abt. A*, **205** (1–6): 129–154.

Sudre, J. and L. Ginsburg, 1993. La faune de mammifères de la Défense (Calcaire grossier; Lutétien supérieur) à Puteaux près Paris; artiodactyles et *Lophiodon parisiense* Gervais, 1848–1852. *Bulletin du Muséum National d'Histoire naturelle, Paris, 4e* série, **15** (section C) (1–4): 155–181.

Sudre, J., B. Sigé, J. A. Remy, B. Marandat, J.-L. Hartenberger, M. Godinot, and J.-Y. Crochet, 1990. Une faune du niveau d'Egerkingen (MP 14; Bartonien inferieur) dans les Phosphorites du Quercy (sud de la France). *Palaeovertebrata*, **20** (1): 1–32.

Tsubamoto, T. and Kh. Tsogtbaatar, 2008. New specimens of anthracotheriid artiodactyls from the upper Eocene Ergilin Dzo Formation of Mongolia. *Paleontological Research*, **12** (4): 371–386.

von Meyer, H., 1832: *Palaeologica, zur Geschichte der Erde und ihrer Geschöpfe*. *Frankfurt am Main*: 560 p.

Appendix 1. Measurements (in mm) of artiodactyl specimens. Abbreviations: *, estimate; L, length; W, width. For the measurement position of astragalus (a–g), see Fig. 1.

Bothriodon sp.
NMNS-PV 21656: left M1 or M2 L = 19.2; W = 20.84
NMNS-PV 21657: left M3 L = 31.4; W = 35.2
NMNS-PV 21658: left m3 L = 44.1; trigonid W = 20.8; talonid W = 23.3
NMNS-PV 21659: right m2 L = 24.1; trigonid W = 17.3; talonid W = 18.1
Elomeryx crispus
NMNS-PV 21655: left M3 L = 19.3; W = 21.5
Cebochoerus sp. cf. *C. helveticus*
NMNS-PV 21163: right P2 L = 6.5; W = —
right P3 L = 7.3; W = 6.1
right P4 L = 6.4; W = 8.5
right M1 L = 7.2; W = 8.8
NMNS-PV 21165: right DP4 L = 7.3; W = 7.8
NMNS-PV 21166: ?right P2 or ?left p3 L = 6.5; W = 3.6
Cebochoerus robiacensis
NMNS-PV 21301: left m3 L = 8.1; trigonid W = 5.0; talonid W = 4.0
NMNS-PV 21302: right p3 L = 5.6; W = 3.1
Cebochoerus sp.
NMNS-PV 21164: right P3 L = 5.6; W = 4.5
Choeropotamus parisiensis
NMNS-PV 21533: left M1 L = 17.5; W = 18.8
left M2 L = 20.2; W = 23.8
left M3 L = 21.0; W = 24.6
Choeropotamus sp.
NMNS-PV 21459: right dp4 L = —; trigonid W = —; talonid W = 9.1
Tapirulus sp. cf. *T. schlosseri*
NMNS-PV 21167: left DP4 L = 4.7; W = 4.0
NMNS-PV 21168: right M1 or M2 L = 5.2; W = 5.9
Robiacina minuta
NMNS-PV 21185: left p4 L = 3.1; trigonid W = 1.7; talonid W = 1.9
left m1 L = 2.7; trigonid W = 2.1; talonid W = 2.1
NMNS-PV 21284: left m3 L = 4.7; trigonid W = 2.3; talonid W = —
NMNS-PV 21285: left p3 L = —; trigonid W = —; talonid W = 1.3
left p4 L = 3.1; trigonid W = 1.5; talonid W = 1.8
incisor L = 1.5; W = 0.6
NMNS-PV 21286: right m1 L = 3.0; trigonid W = 2.0; talonid W = 2.1
right m2 L = 3.4; trigonid W = 2.5; talonid W = 2.6
right m3 L = 4.2; trigonid W = 2.1; talonid W = 2.4
NMNS-PV 21287: right M3 L = 3.3; W = 3.6
NMNS-PV 21289: right upper molar L = 2.8; W = 2.7
NMNS-PV 21290: right upper molar L = 2.8; W = 2.6*
NMNS-PV 21291: left P4 L = 2.4; W = 2.6
NMNS-PV 21292: right upper molar L = 2.6; W = 3.0
NMNS-PV 21293: right upper molar L = 2.4; W = 3.0
NMNS-PV 21295: left upper molar L = 2.7; W = 3.0
NMNS-PV 21296: right m1 or m2 L = 2.9; trigonid W = 1.8; talonid W = 2.1
NMNS-PV 21297: left m1 or m2 L = 2.9; trigonid W = 2.0; talonid W = 2.2
NMNS-PV 21298: right m1 or m2 L = 3.0; trigonid W = 1.8; talonid W = 1.9
NMNS-PV 21299: right m1 or m2 L = 2.9; trigonid W = 1.9; talonid W = 2.0
Cf. *Robiacina minuta*
NMNS-PV 21288: right P3 L = 3.1; W = 2.9
Anoplotherium commune
NMNS-PV 21449: right DP2 L = 19.0; W = 12.2
right DP3 L = 21.1; W = 15.1
NMNS-PV 21450: right ?C1 or ?DP1 L = 11.5; W = 11.0
NMNS-PV 21451: right dp3 L = 21.0; trigonid W = 7.7; talonid W = 9.1
NMNS-PV 21452: left I3 L = 13.7; W = 8.1
NMNS-PV 21458: left m2 L = 26.3; trigonid W = 18.2; talonid W = 16.9
NMNS-PV 21525: right P2 L = 18.9; W = —
right P3 L = 19.7; W = —
right P4 L = 17.7; W = —
right M1 L = 24.3; W = —

Appendix 1. Continued

right M2 L = 31.0; W = —
right M3 L = 36.9; W = —
left C1 L = 15.2; W = —
left P1 L = 15.4; W = —
left P2 L = 18.7; W = —
left P3 L = 19.9; W = —
left P4 L = 17.7*; W = —
left M1 L = 22.6; W = —
left M2 L = 30.1; W = —
left M3 L = 35.6; W = —
right p2 L = 19.0; trigonid W = —; talonid W = —
right p3 L = 22.0; trigonid W = —; talonid W = —
right p4 L = 23.3; trigonid W = —; talonid W = —
right m1 L = 23.0; trigonid W = —; talonid W = —
right m2 L = 27.7; trigonid W = —; talonid W = —
right m3 L = 38.3; trigonid W = —; talonid W = —
left p2 L = 19.0; trigonid W = —; talonid W = —
left p3 L = 20.0; trigonid W = —; talonid W = —
left p4 L = 20.0; trigonid W = —; talonid W = —
left m1 L = 22.1; trigonid W = —; talonid W = —
left m2 L = 27.5; trigonid W = —; talonid W = —
left m3 L = 38.0; trigonid W = —; talonid W = —

NMNS-PV 21526: no measurements

NMNS-PV 21527: left ?i1 L = 4.6; W = 3.6
left i3 L = 10.7; W = —
left c1 L = 12.8; W = 5.2
left p1 L = 16.8; trigonid W = 8.1; talonid W = 8.7
left dp2 L = 16.5; trigonid W = 7.4; talonid W = 8.6
left dp3 L = 19.0; trigonid W = 8.4; talonid W = 10.3
left dp4 L = 23.9; anterior lobe W = 9.7; central lobe W = 9.4; posterior lobe (talonid) W = 11.6
left m1 L = 22.7*; trigonid W = 13.8; talonid W = 15.5
left m2 L = 26.5; trigonid W = 17.2; talonid W = —
right p1 L = 16.7; trigonid W = 8.2; talonid W = 8.8
right dp2 L = 16.9; trigonid W = —; talonid W = —
right dp3 L =19.4; trigonid W = 8.5; talonid W = 9.7
right dp4 L = 23.9; anterior lobe W = 10.2; central lobe W = 9.7; posterior lobe (talonid) W = 11.6
right m1 L = 22.6; trigonid W = 14.3; talonid W = 16.0
right m2 L = 26.6*; trigonid W = 17.1; talonid W = 18.1

NMNS-PV 21528: left DP2 L = 18.5*; W = 11.5
left DP3 L = 19.2; W = 15.1
left DP4 L = 19.8; W = 18.3
left M1 L = 25.0; W = 22.9

NMNS-PV 21529: left p2 L = 19.6; trigonid W = 10.5; talonid W = 10.6
left p3 L = 21.5; trigonid W = 11.7; talonid W = 11.6
left p4 L = 21.7; trigonid W = 12.5; talonid W = 13.7
left m1 L = 22.1; trigonid W = 13.3; talonid W = 15.3
left m2 L = 26.2; trigonid W = 15.9; talonid W = 16.9
left m3 L = 41.3; trigonid W = 16.7; talonid W = 15.3

NMNS-PV 21530: left M2 L = 29.0; W = 28.3
left M3 L = 35.2; W = 28.5

NMNS-PV 21531: left P1 L = 18.7; W = 13.3
left DP2 L = 20.1; W = 12.4
left DP3 L = 22.1; W = 16.6
left DP4 L = 19.5*; W = —

NMNS-PV 21546: left ?I3 L = 13.2; W = 6.8

Anoplotherium laurillardi

NMNS-PV 21453: left p1 L = 14.7; W = 6.9
left p2 L = 16.7; W = 8.8

NMNS-PV 21454: right p2 L = 17.2; W = 8.8

NMNS-PV 21455: left I2 L = 11.1; W = 6.0

NMNS-PV 21456: left dp3 L = 16.9; trigonid W = 6.5; talonid W = 7.1

NMNS-PV 21457: left dp1 L = 11.7; W = 6.5
left dp2 L = 15.0; trigonid W = 6.5; talonid W = 6.4

Appendix 1. Continued

left dp3 L = 16.5; trigonid W = —; talonid W = 7.0
left dp4 L = 20.4; anterior lobe W = 7.2; central lobe W = 8.4; posterior lobe (talonid) W = 8.7
left m1 L = 18.2; trigonid W = 11.5; talonid W = 12.0
NMNS-PV 21499: right ?M1 L = —; W = —
right ?M2 L = 22.3; W = 19.2

Diplobune sp.
NMNS-PV 21661: right M1 L = 13.5; W = 15.5
right M2 L = 15.3; W = 17.6
right M3 L = 16.7; W = 17.3

Dacrytherium ovinum
NMNS-PV 21385: right dp2 L = —; W = 2.7
right dp3 L = 12.3; anterior lobe W = 4.0; central lobe W = 4.1; posterior lobe (talonid) W = 4.8
right dp4 L = 12.5; anterior lobe W = 4.7; central lobe W = 5.3; posterior lobe (talonid) W = 5.8

Catodontherium robiacense
NMNS-PV 21304: right M1 L = 14.3; W = 13.7
right M2 L = 16.6; W = 16.4
right M3 L = —; W = 17.4
NMNS-PV 21305: right m2 L = 16.2; trigonid W = 10.4; talonid W = 10.3

Xiphodon castrensis
NMNS-PV 21169: left dp4 L = 7.4; anterior lobe W = 2.4; central lobe W = 2.6; posterior lobe (talonid) W = 3.1
NMNS-PV 21170: left ?dp2 L = 6.4; W = 1.6
NMNS-PV 21176: left m1 L = 6.1; trigonid W = 3.9; talonid W = 4.2
left m2 L = 6.8; trigonid W = 4.6; talonid W = 4.7
left m3 L = 9.4; trigonid W = 4.7; talonid W = 4.6
NMNS-PV 21177: left ?P2 or ?P1 L = 7.9; W = —
NMNS-PV 21178: right ?P2 L = 6.1; W = 3.0
NMNS-PV 21179: left m1 L = 6.0; trigonid W = 3.9; talonid W = 4.0
NMNS-PV 21180: left m1 or m2 L = 6.6; trigonid W = 4.1; talonid W = 4.1
NMNS-PV 21306: right m3 L = 10.1; trigonid W = 4.4; talonid W = 4.4
NMNS-PV 21307: right M3 L = 8.3; W = 7.6
NMNS-PV 21308: left p4 L = 5.7; W = 3.4
left m1 L = 6.1; trigonid W = 3.7; talonid W = 4.0
left m2 L = 7.2; trigonid W = 4.4; talonid W = 4.5
NMNS-PV 21309: left m1 L = 6.3; trigonid W = 4.2; talonid W = 4.2
left m2 L = 7.3; trigonid W = 4.8; talonid W = 4.9
left m3 L = —; trigonid W = 4.6; talonid W = —
NMNS-PV 21311: right p4 L = 6.5; W = 3.7
NMNS-PV 21313: left upper molar L = 7.1; W = 6.9
NMNS-PV 21314: right upper molar L = 7.1; W = 7.0
NMNS-PV 21315: right upper molar L = 6.2; W = 6.1
NMNS-PV 21316: left upper molar L = 6.5; W = 6.1
NMNS-PV 21317: right m3 L = —; trigonid W = 4.2; talonid W = —
NMNS-PV 21319: left ?P2 L = 7.1; W = 3.5
NMNS-PV 21320: left P4 L = 4.7; W = 4.5
NMNS-PV 21321: no measurements

Cf. *Xiphodon castrensis*
NMNS-PV 21181: ?Incisor L = 4.2; W = 3.2
NMNS-PV 21189: Phalange: maximum length = 15.8; maximum width = 7.7; maximum height = 7.2
NMNS-PV 21190: no measurements
NMNS-PV 21191: no measurements
NMNS-PV 21310: right ?dp3 L = 7.3; W = 3.5
NMNS-PV 21312: right ?dp2 L = 5.8; W = 3.4

Xiphodon gracile
NMNS-PV 21460: right M1 L = 8.5*; W = —
right M2 L = 9.2*; W = 10.4
right M3 L = 10.7; W = 10.5
NMNS-PV 21461: right M1 L = 9.5; W = 9.5
right M2 L = 10.7; W = 11.0
right M3 L = 10.4; W = 10.4
NMNS-PV 21462: right p3 L = 12.7; W = 3.8
right p4 L = 9.1; W = 5.0
right m1 L = 8.2; trigonid W = 5.8; talonid W = 6.1
right m2 L = 9.1; trigonid W = 6.4; talonid W = 6.6

Appendix 1. Continued

right m3 L = 13.3; trigonid W = 5.8; talonid W = 6.1
NMNS-PV 21463: left dp4 L = 11.4; anterior lobe W = 4.0; central lobe W = 4.3; posterior lobe (talonid) W = 4.9
left m1 L = 8.8; trigonid W = —; talonid W = 5.8
NMNS-PV 21464: left m2 L = 9.2; trigonid W = 6.6; talonid W = 6.2
left m3 L = —; trigonid W = 6.4; talonid W = —
NMNS-PV 21466: right P4 L = 7.3; W = 7.6
NMNS-PV 21534: right ?i1 L = —; W = —
right ?i2 L = 7.1; W = 2.8
right ?i3 L = 7.1; W = 2.7
right m1 L = 9.7; trigonid W = 5.8; talonid W = 6.2
right m2 L = 10.5; trigonid W = 6.4; talonid W = 6.3
right m3 L = 13.9; trigonid W = 6.4; talonid W = 5.9
NMNS-PV 21535: left P4 L = 8.0*; W = 7.7
NMNS-PV 21536: left P4 L = 7.9*; W = 7.2
NMNS-PV 21537: left upper molar L = 10.3; W = 9.1
NMNS-PV 21538: right p3 L = 13.5; W = 4.8
NMNS-PV 21539: right m2 L = —; trigonid W = —; talonid W = 6.0
right m3 L = 13.7*; trigonid W = 5.9*; talonid W = 5.8

Xiphodon sp. cf. *X. gracile*
NMNS-PV 21363: left p4 L = 8.9; W = 4.9
left m1 L = 9.1; trigonid W = 5.3; talonid W = 5.6
left m2 L = 10.2; trigonid W = 6.1; talonid W = 6.3
left m3 L = 13.6; trigonid W = 6.3; talonid W = 6.1

Cf. *Xiphodon gracile*
NMNS-PV 21465: right astragalus: a = 25.5; b = 22.9; c = 13.1; d = 13.9; e = 13.4; f = 13.2; g = 13.3

Dichodon cervinus
NMNS-PV 21384: right p2 L = 10.9; W = 3.5
right p3 L = 11.1; W = 3.5
right p4 L = 10.6; trigonid W = 4.6; talonid W = 5.2
right m1 L = 8.2; trigonid W = 5.5; talonid W = 6.0
right m2 L = 9.1; trigonid W = 6.2; talonid W = 6.6
right m3 L = 13.2; trigonid W = 6.4; talonid W = 6.5

Dichodon sp.
NMNS-PV 21175: right p3 L = 10.2; W = 2.4
right p4 L = 9.5; trigonid W = 3.1; talonid W = 3.6
right m2 L = 7.3; trigonid W = 4.4; talonid W = 4.7

Haplomeryx sp. cf. *H. picteti*
NMNS-PV 21172: right M2 L = 4.2; W = 4.6
right M3 L = 4.3; W = 4.5
NMNS-PV 21174: left P4 L = 2.8; W = 3.0
NMNS-PV 21294: left ?M1 L = 3.5; W = 3.5

Cf. *Amphimeryx murinus*
NMNS-PV 21467: left m1 or m2 L = 4.1; trigonid W = 2.5; talonid W = 2.7

Pseudamphimeryx sp.
NMNS-PV 21171: left p3 L = 5.1; W = 1.4
left p4 L = 3.5; W = 1.9
left m1 L = 3.6; trigonid W = 2.5; talonid W = 2.8
left m2 L = 3.7; trigonid W = 2.8; talonid W = 2.9
left m3 L = 5.3; trigonid W = 2.9; talonid W = 2.8
NMNS-PV 21173: left m1 or m2 L = 3.8; trigonid W = 2.1; talonid W = 2.2
NMNS-PV 21182: right p4 L = 4.0; W = 2.1
right m1 L = 3.4; trigonid W = 2.3; talonid W = 2.6
right m2 L = 3.6; trigonid W = 2.7; talonid W = 2.9
right m3 L = 5.3; trigonid W = 2.7; talonid W = 2.5
NMNS-PV 21183: left M1 or M2 L = 4.8; W = 6.3
NMNS-PV 21184: left upper molar L = 4.7; W = 5.3

Cf. *Pseudamphimeryx* sp.
NMNS-PV 21186: right astragalus: a = 14.2; b = 13.0; c = 7.8; d = 7.8; e = 7.4; f = 8.1; g = 8.4
NMNS-PV 21187: left astragalus: a = 14.1; b = —; c = 7.2; d = —; e = 6.2; f = 7.4; g = —

Suoidea fam., gen, et sp. indet.
NMNS-PV 21666: right upper incisor L = 10.6; W = 6.0
NMNS-PV 21667: right P4 L = 6.6; W = 7.8

Appendix 1. Continued

Ruminantia fam., gen. et sp. indet.
NMNS-PV 21669: right astragalus: a = —; b = 29.4; c = —; d = —; e = —; f = —; g = —
NMNS-PV 21670: phalange: maximum L = 24.0; maximum W = 8.8; maximum height = 9.5
NMNS-PV 21671: left p3 or p4 L = 6.5; W = 3.4
?Artiodactyla fam., gen. et sp. indet.
NMNS-PV 21318: left lower anterior premolar L = 5.2; W = 3.0

National Museum of Nature and Science Monographs

(Nos. 1–35 were published as "National Science Museum Monographs)

No. 1*. Early Cretaceous marine and brackish-water Gastropoda from Japan. By Tomoki Kase, 199 pp., 31 pls., 1984.

No. 2*. A taxonomic study on the subfamily Herminiinae of Japan (Lepidoptera, Noctuidae). By Mamoru Owada, 208 pp., 1987.

No. 3*. Small mammal fossils and correlation of continental deposits, Safford and Duncan Basins, Arizona, USA. By Yukimitsu Tomida, 141 pp., 1987.

No. 4. Late Miocene floras in northeast Honshu, Japan. By Kazuhiko Uemura, 174 pp., 11 pls., 1988.

No. 5. A revisional study of the spider family Thomisidae (Arachnida, Araneae) of Japan. By Hirotsugu Ono, 252 pp., 1988.

No. 6. The taxonomic study of Japanese dictyostelid cellular slime molds. By Hiromitsu Hagiwara, 131 pp., 1989.

No. 7. A systematic study of the Japanese Chiroptera. By Mizuko Yoshiyuki, 242 pp., 1989.

No. 8. Rodent and lagomorph families of Asian origins and diversification: Proceedings of Workshop WC-2 29th International Geological Congress, Kyoto, Japan. Edited by Yukimitsu Tomida, Chuankuei Li, and Takeshi Setoguchi, 195 pp., 1994.

No. 9. A microevolutional history of the Japanese people as viewed from dental morphology. By Hirofumi Matsumura, 130 pp., 1995.

No. 10. Studies on the human skeletal remains from Jiangnan, China. Edited by Bin Yamaguchi and Huan Xianghon, 108 pp., 3 pls., 1995.

No. 11. Annoted checklist of the inshore fishes of the Ogasawara Islands. By John E. Randall, Hitoshi Ida, Kenji Kato, Richard L. Pyle, and John L. Earle, 74 pp., 19 pls., 1997.

No. 12. Deep-sea fauna and pollutants in Suruga Bay. By Tsunemi Kubodera and Masaaki Machida, *et al*., 336 pp., 12 pls., 1997.

No. 13. Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo. Families Polynoidae and Acoetidae. By Minoru Imajima, 131 pp., 1997.

No. 14. Advance in vertebrate paleontology and geochronology. Edited by Yukimitsu Tomida, Lawrence J. Flynn, and Louis L. Jacobs, 292 pp., 1998.

No. 15. Proceedings of the Second Gondwanan Dinosaur Symposium. Edited by Yukimitsu Tomida, Thomas H. Rich, and Patricia Vickers-Rich, 296 pp., 1999.

No. 16. Onuphidae (Annelida, Polychaeta) from Japan, excluding the genus *Onuphis*. By Minoru Imajima, 115 pp., 1999.

No. 17. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), northeastern Brazil. By Alexander W. A. Kellner and Yukimitsu Tomida, 135 pp., 2000.

No. 18. Proceedings of the First and Second Symposia on Collection Building and Natural History Studies in Asia. Edited by Keiichi Matsuura, 188 pp., 2000

No. 19. A taxonomic revision of the marine species of *Cladophora* (Chlorophyta) along the coasts of Japan and the Russian Far-east. By Christiaan van den Hoek and Mitsuo Chihara, 242 pp., 2000.

No. 20. Deep-sea fauna and pollutants in Tosa Bay. Edited by Toshihiko Fujita, Hiroshi Saito and Masatsune Takeda, 380 pp., 2001.

No. 21. Marine Fauna of the Shallow Waters around Hainan Island, South China Sea. Edited by Keiichi Matsuura, 126 pp., 2001.

No. 22. Proceedings of the Third and Fourth Symposia on Collection Buildings and Natural History Studies in Asia and the Pacific Rim. Edited by Tsunemi Kubodera, Masanobu Higuchi, and Ritsuro Miyawaki, 193 pp., 2002.

No. 23. Polychaetous Annelids from Sagami Bay and Sagami Sea Collected by the Emperor Showa of Japan and Deposited at the Showa Memorial Institute, National Science Museum, Tokyo (II). Orders included within the Phyllodocida, Amphinomida, Spintherida and Eunicida. By Minoru Imajima, 221 pp., 2003.

No. 24. Proceedings of the Fifth and Sixth Symposia on Collection Building and Natural History Studies in Asia and the Pacific Rim. Edited by Shinobu Akiyama, Ritsuro Miyawaki, Tsunemi Kubodera, and Masanobu Higuchi 292 pp., 2004.

No. 25. Revision of scydmaenid beetles of the genus *Syndicus* Motschulsky (Coleoptera, Scydmaenidae). By Pawel Jaloszynski, 108 pp., 2004.

No. 26. A new specimen of *Apatosaurus ajax* (Sauropoda: Diplodocidae) from the Morrison Formation (Upper Jurassic) of Wyoming, USA. By Paul Upchurch, Yukimitsu Tomida, and Paul M. Barrett, 108 pp., 10 pls., 2004.

No. 27. Leaf-rolling Sawflies of the *Pamphilius vafer* complex (Hymenoptera, Pamphiliidae). By Akihiko Shinohara, 116 pp., 2005.

No. 28. Types of Japanese Bird. By Hiroyuki Morioka, Edward C. Dickinson, Takashi Hiraoka, Desmond Allen and Takeshi Yamasaki, 154 pp., 2005.
No. 29. Deep-sea fauna and pollutants in Nansei Islands. Edited by Kazunori Hasegawa, Gento Shinohara and Masatsune Takeda, 476 pp., 2005.
No. 30. Phenology and Growth Habits of Tropical Trees: Long-term Observations in the Bogor and Cibodas Botanic Garden, Indonesia. Edited by Hiroaki Hatta and Dedy Darnaedi, 436 pp., 2005.
No. 31. The Cretaceous System in the Makarov area, southern Sakhalin, Russian Far East. Edited by Yasunari Shigeta and Haruyoshi Maeda, 136 pp., 2005.
No. 32. Revision of the Palearctic species of the myrmecophilous genus *Pella* (Coleoptera, Staphylinidae, Aleocharinae). By Munetoshi Maruyama, 207 pp., 2006.
No. 33. Checklist of Japanese lichens and allied fungi. By Syo Kurokawa and Hiroyuki Kashiwadani, 157 pp., 2006.
No. 34. Proceedings of the Seventh and Eighth Symposia on Collection Building and Natural History Studies in Asia and the Pacific Rim. Edited by Yukimitsu Tomida, Tsunemi Kubodera, Shinobu Akiyama and Taiju Kitayama, 294 pp., 2006.
No. 35. Anatomy of a Japanese Tomistomine Crocodylian, *Toyotamaphimeia Machikanensis* (Kamei et Matsumoto, 1965), from the Middle Pleistocene of Osaka Prefecture: The Reassessment of its Phylogenetic Status within Crocodylia. By Yoshitsugu Kobayashi, Yukimitsu Tomida, Tadao Kamei and Taro Eguchi, 121 pp., 2006.
No. 36. A systematic study of the genus *Siriella* (Crustacea: Mysida) from the Pacific and Indian oceans, with descriptions of fifteen new species. Edited by Masaaki Murano and Kouki Fukuoka, 173 pp., 2008.
No. 37. Chromosome atlas of flowering plants in Japan. Edited by Tsunehiko Nishikawa, 706 pp., 2008.
No. 38. The Lower Triassic System in the Abrek Bay area, South Primorye, Russia. Edited by Yasunari Shigeta, Yuri D. Zakharov, Haruyoshi Maeda and Alexander M. Popov, 218 pp., 2009.
No. 39. Deep-sea Fauna and Pollutants off Pacific Coast of Northern Japan. Edited by Toshihiko Fujita, 755 pp., 2009.
No. 40. Joint Haeckel and Ehrenberg Project: Reexamination of the Haeckel and Ehrenberg Mircofossil Collections as a Historical and Scientific Legacy. Edited by Yoshihiro Tanimura and Yoshiaki Aita, 106 pp., 2009.
No. 41. Middle and Late Miocene Marie Bivalvua from the Northeern Kanto Region, Central Japan. Edited by Yukito Kurihara, 87 pp., 2010.
No. 42. Chemical Compositions of Electrum Grains in Ore and Placer Deposits in the Japanese Islands. By Kazumi Yokoyama, Shogo Takeuchi, Izumi Nakai, Yukiyasu Tsutsumi, Takashi Sano, Masako Shigeoka, Ritsuro Miyawaki and Satoshi Matsubara, 80 pp., 2011.
No. 43 Digeneans (Trematoda) Parasitic in Freshwater Fishes (Osteichthyes) of the Lake Biwa Basin in Shiga Prefecture, Centeral Honshu, Japan. By Takeshi Shimazu, Misako Urabe and Mark J. Grygier, 105 pp., 2011.
No. 44 Deep-sea Fauna of the sea of Japan. Edited by Toshihiko Fujita, 291 pp., 2014.
No. 45 Olenekian (Early Triassic) Stratigraphy and Fossil Assemblages in Northeastern Vietnam. Edited by Yasunari Shigeta, Toshifumi Komatsu, Takumi Maekawa and Huyen Dang Tran, 309 pp., 2014.
No. 46 The Subfamily Steninae Macleay, 1825 (Coleoptera: Staphylinidae) of Japan Part 1. *Dianous and Stenus* (*S. comma* Group to *S. guttalis* Group). By Shun-Ichiro Naomi, Shûhei Nomura and Volker Puthz, 339 pp., 2017.
No. 47 Bio-Anthropological Studies of Early Holocene Hunter-Gatherer Sites at Huiyaotian and Liyupo in Guangxi, China. By Hirofumi Matsumura, Hsiao-chun Hung, Li Zhen and Kenichi Shinoda, 228 pp., 2017.
No. 48 Flavonoids of the Plants Composing Flora of Japan. By Tsukasa Iwashina, 649 pp., 2018.
No. 49 Checklist of Lichens and Allied Fungi of Japan. By Yoshihito Ohmura and Hiroyuki Kashiwadani, 143 pp., 2018.
No. 50 Campanian (Late Cretaceous) ammonoids and inoceramids from the Ribira River area, Hokkaido, northern Japan. By Yasunari Shigeta, Masataka Izukura and Tomohiro Nishimura, 139 pp., 2019.
No. 51 The Subfamily Steninae Macleay, 1825 (Coleoptera: Staphylinidae) of Japan Part 2. *Stenus Asyura*-Group to *S. Cirrus*-Group. By Shun-Ichiro Naomi, Shûhei Nomura and Volker Puthz, 255 pp., 2019.
No. 52 Checklist of planktonic diatoms in the coastal waters of western Japan. By Keisuke Tezaki, Megumi Saito-Kato and Kazumi Matsuoka, 151 pp., 2021.

No. 53 The subfamily Steninae Macleay, 1825 (Coleoptera: Staphylinidae) of Japan Part 3. *Stenus satsuki*-group and *S. cephalotes*-group. By Shun-Ichiro Naomi, Shûhei Nomura and Volker Puthz, 310 pp., 2022.

No. 54 Olenekian (Early Triassic) ammonoids and conodonts from southern Thailand. By Kittichai Tongtherm, Yasunari Shigeta, Apsorn Sardsud, Kaito Asato, Takumi Maekawa, Takuma Haga, Sachiko Agematsu and Katsuo Sashida, 171 pp., 43 pls., 2023.

(* out of print)

All inquiries concerning the Monographs should be addressed to:
Library
National Museum of Nature and Science
4–1–1 Amakubo, Tsukuba, Ibaraki 305–0005, Japan