

<b>Zeitschrift:</b>	Eclogae Geologicae Helvetiae
<b>Herausgeber:</b>	Schweizerische Geologische Gesellschaft
<b>Band:</b>	89 (1996)
<b>Heft:</b>	3
<b>Artikel:</b>	The biostratigraphical position of the Oligocene French fossil localities Saint-Martin-de-Castillon (Apt basin) and Vialenc (Aurillac basin) based on the Issiodoromyini (Mammalia, Rodentia, Theridomyidae)
<b>Autor:</b>	Hugueny, Marguerite / Mödden, Clemens
<b>DOI:</b>	<a href="https://doi.org/10.5169/seals-167943">https://doi.org/10.5169/seals-167943</a>

#### **Nutzungsbedingungen**

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

#### **Conditions d'utilisation**

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

#### **Terms of use**

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

**Download PDF:** 07.01.2026

**ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>**

# The biostratigraphical position of the Oligocene French fossil localities Saint-Martin-de-Castillon (Apt basin) and Vialenc (Aurillac basin) based on the Issiodoromyini (Mammalia, Rodentia, Theridomyidae).

MARGUERITE HUGUENEY<sup>1</sup> & CLEMENS MÖDDEN<sup>2</sup>

*Key words:* Biostratigraphy, Oligocene, Europe, Mammalia, Rodentia, Theridomyidae

## ZUSAMMENFASSUNG

Die Vertreter der Issiodoromyini sind für die biostratigraphische Einstufung oligozäner, kontinental beeinflusster Sedimente in Mittel-, Südwest- und Westeuropa aufgrund rascher Veränderungen in der Morphologie ihrer Zähne von grosser Bedeutung. Aus dem oligozänen, biostratigraphischen Mammalia-Standard-Niveau MP 24 (Referenzlokalität: Heimersheim) waren bisher keine Issiodoromyini bekannt. Diese Lücke wird mit dieser Arbeit geschlossen, da die hier aus den französischen Fundstellen St.-Martin-de-Castillon und Vialenc beschriebenen Issiodoromyini aufgrund ihrer Zahnmorphologie intermediär zwischen den aus den Standard-Niveaus MP 23 und MP 25 beschriebenen Issiodoromyini stehen.

## ABSTRACT

The taxa of the Issiodoromyini are very important for the determination of the biostratigraphic position of Oligocene continental (influenced) sediments of Central, Southwest, and Western Europe, because the morphology of their teeth changes very rapidly. Until now, no Issiodoromyini have been described from the Oligocene biostratigraphic mammal standard level MP 24 (reference locality: Heimersheim). This gap is closed here. According to their morphology, the teeth of the Issiodoromyini from St.-Martin-de-Castillon and Vialenc described here show an evolutionary level intermediate between the known Issiodoromyini from MP 23 and MP 25; consequently, they are ascribed to the biostratigraphic mammal standard level MP 24.

## RESUME

Du fait des changements très rapides de leur morphologie dentaire, les différents taxa de la tribu des Issiodoromyini (Mammalia, Rodentia, Theridomyidae) sont d'une importance primordiale pour la biozonation des dépôts continentaux oligocènes de l'Europe centrale, de l'Ouest et du Sud-Ouest. Or jusqu'à présent, aucun Issiodoromyini n'était connu dans le niveau mammalien standard MP 24 (localité-repère: Heimersheim). Les dents d'Issiodoromyini, décrites ici et provenant des gisements de St.-Martin-de-Castillon et Vialenc, montrent un niveau d'évolution intermédiaire entre les Issiodoromyini connus en MP 23 et ceux de MP 25. Ces gisements représentent donc bien le niveau MP 24.

<sup>1</sup> Centre de Paléontologie stratigraphique et de Paléoécologie de l'Université Claude-Bernard, Lyon I, associé au C.N.R.S.(UMR 5565), 27–43 bvd du 11 novembre, F-69622 Villeurbanne Cedex

<sup>2</sup> Naturhistorisches Museum, Augustinergasse 2, CH-4001 Basel

## Introduction

The Oligocene mammal site St.-Martin-de-Castillon, first described by Hugueney et al. (1971), was placed in the biostratigraphic mammal age zone of Heimersheim (Ducréux et al. 1985). However, Brunet et al. (1977) described the fauna from the locality of Vialenc and placed it near the level of Antoingt. In the International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene in Mainz (Schmidt-Kittler ed. 1987: Tab. 2), Heimersheim became the international reference locality for the fossil mammal-based biostratigraphic standard level MP 24; but the locality of St.-Martin-de-Castillon was placed in standard level MP 23 and the mammal site of Vialenc in MP 25 (Schmidt-Kittler ed. 1987: Tab. 2). In Hugueney (1994), however, it is shown that the localities of St.-Martin-de-Castillon could have the mammal-based biostratigraphic level of MP 24.

At the end of the Early Oligocene and during the Late Oligocene the phylogenetic development of the teeth of the Issiodoromyini tribe – which includes only the two genera *Issiodoromys* and *Elfomys* (Mödden 1994) – allow a very exact age determination of the sediments which contain them. In St.-Martin-de-Castillon and Vialenc, teeth of Issiodoromyini have been found, but no Issiodoromyini are known from the reference locality Heimersheim. Until now there are no localities placed in MP 24 from which Issiodoromyini have been described, so an age determination of St.-Martin-de-Castillon and Vialenc by direct comparison of the teeth of the Issiodoromyini is not possible. But the Issiodoromyini from standard levels MP 23 and MP 25 are known and Vianey-Liaud (1976) stated for the first time that the species *Elfomys medius* (MP 23) is the direct ancestor of *Issiodoromys minor* (MP 25). Later authors came to the same conclusion. So the teeth of the Issiodoromyini from standard level MP 24 must show characteristics intermediate between *Elfomys medius* and *Issiodoromys minor*. In this paper we demonstrate that the teeth of the Issiodoromyini from the sites of St.-Martin-de-Castillon and Vialenc show exactly these characteristics and so the mammals from both localities are to be placed in the biostratigraphic mammal level MP 24.

## Material

The locality of Saint-Martin-de-Castillon is situated in the Apt basin (for a map and further details see Ducréux et al. 1985); there are several layers which belong to different profiles (Hugueney et al. 1971). The mammal fossils of Saint-Martin-de-Castillon were excavated in 1970–1971 and more intensively in 1974 when three tons of sediment were recovered from the main level Saint-Martin-de-Castillon C (StMc in the following text) and where other mammal-bearing levels were discovered: namely Saint-Martin-de-Castillon 6 (the stratigraphically uppermost layer in the same profile as StMc) and the Saint-Martin-de-Castillon éboulis (StMeb in the following text), in another profile not directly correlatable. StMeb yielded, however, the same groups of mammals as StMc but the size of the cricetids, particularly *Paracricetodon*, is smaller than in StMc; so StMeb is considered as older than StMc. Teeth of Issiodoromyini have been found, especially in StMc and StMeb, and these two localities make it possible to follow the morphological transformation of the Issiodoromyini within the stratified layers of a single basin.

The mammal fossils of Vialenc were excavated in 1976 and 1977 (Brunet et al. 1977);

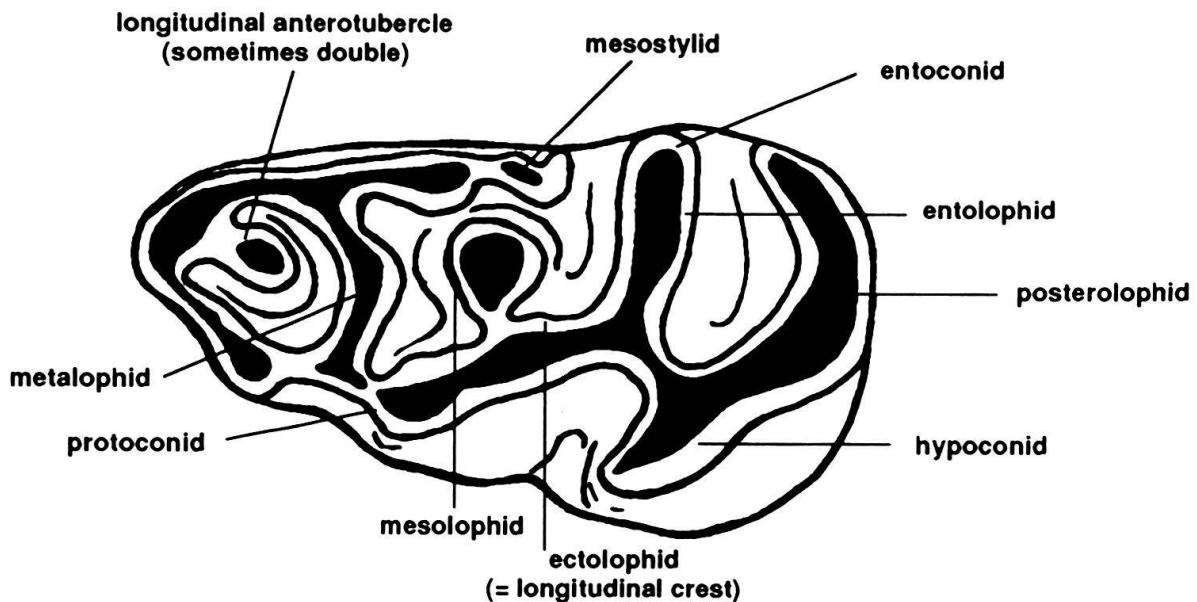


Fig. 1. Terminology of the lower deciduous teeth (D<sub>4</sub>) in Issiodoromyini.

additional and hitherto unpublished material was recovered later by M. Hugueney. All the fossils from Vialenc come from a thin layer of grey-green coloured marls.

The materials from Saint-Martin-de-Castillon and Vialenc are stored in the collections of the University Claude-Bernard, Lyon I, except part of the Vialenc material which is stored at the University of Poitiers.

The Issiodoromyini from St.-Martin-de-Castillon and Vialenc are compared with the material of *Elfomys mediis* described by Vianey-Liaud (1976) from the fissure fillings La Plante 2 and Roqueprune 2 (Quercy, France) which have been placed in MP 22 and MP 23 respectively (Schmidt-Kittler ed. 1987: Tab. 2) and also with the material of *Issiodoromyis minor* from the fissure filling Belgarite IVa (Quercy) described by Mödden (1994). The fauna of Belgarite IVa belongs to MP 25 because of the occurrence of *Protechimys gracilis* (this species is restricted to the MP 25 level, Schmidt-Kittler ed. 1987: Tab. 7).

### Terminology and method

In the description of the permanent cheek teeth we follow the terminology given in Bosma (1974). The deciduous teeth are important to determine the biostratigraphic age of the Issiodoromyini but their morphology is different from that of the permanent cheek teeth; therefore, the terminology employed for the lower D<sub>4</sub> is shown in figure 1.

The measurements of length and height are given according to Schmidt-Kittler & Vianey-Liaud (1987: Fig. 1). The measurement of width is analogous with and perpendicular to length. Because the length and width increase during wear in cheek teeth of Issiodoromyini, especially in late wear stages, the measurements of length, width and of height / length – ratio (= H/L, = “taux d’hypsodontie”) were made only in wear stages 0 and 1–2 according to Vianey-Liaud (1976: Fig. 42).

### Abbreviations:

Belg 1	Belgarric 1, Collection of the University of Montpellier
Belg IVa	Belgarite IVa, Collection of the Rijksuniversiteit Utrecht
CP	Collection of the University of Poitiers
CU	Collection of the Rijksuniversiteit Utrecht, Faculteit Aardwetenschappen, Postbus 80.021, Budapestlaan 4, NL-3508 TA Utrecht
FSL	Collection of the Centre de Paléontologie stratigraphique et de Paléoécologie de l'Université Claude-Bernard, Lyon I, associé au C.N.R.S.
StMc	Saint-Martin-de-Castillon C
StMeb	Saint-Martin-de-Castillon éboulis

### Description of Issiodoromyini from Saint-Martin-de-Castillon and Vialenc

Family	Theridomyidae ALSTON, 1876
Sub-Family	Issiodoromyinae TULLBERG, 1899 (1884)
Tribe	Issiodoromyini

Comparison of measurements between these localities and other localities will be given in the next chapter.

### Lower teeth

#### D<sub>4</sub>: StMc (8 teeth): Fig. 2 e–f.

They are conspicuously longer than P<sub>4</sub>. Their anterior part is sharp; the anterior synclinid is entirely closed by the mesolophid joining the mesostylid fused in an oval border crest; in 1 tooth out of 8 the mesolophid is more oblique and joins the border crest before the mesostylid; the border crest is often granulated. In the anterior synclinid, there is always a more or less longitudinal crest and sometimes a smaller crest or a granulation in the antero-internal part. 2/8 teeth show an interrupted mesolophid compounded of independent granulations. Mesolophid and entolophid join in their labial ends and none of the teeth shows an ectolophid; this crest begins to develop conspicuously in *I. minor* from Belgarite IVa (Mödden 1994) and becomes longer in the further evolution of the genus *Issiodoromys* (Fig. 2 a–b). The entolophid is curved, the concave part being directed forward. The posterosynclinid is largely open lingually so that, in lingual view, its notch is as deep as that of the middle synclinid. There is a little ectostylid at the labial opening of the sinusid.

#### D<sub>4</sub>: StMeb (5 teeth): Fig. 2 g–h.

They are just a little longer than P<sub>4</sub>. The pattern of the crests is the same as in StMc but the mesolophid joins the labial part of the border crest in only 4/6 teeth; the mesolophid is always directed more obliquely to the anterior part and fuses (when it is the case) clearly before the mesostylid; the entolophid is only slightly directed obliquely to the anterior part of the teeth and is rectilinear and not curved. A short ectolophid exists in some teeth (Fig. 2 h). The posterolophid is directed to the tip of the entoconid, so that, in lingual view, the notch separating them is clearly less deep than that of the middle synclinid.

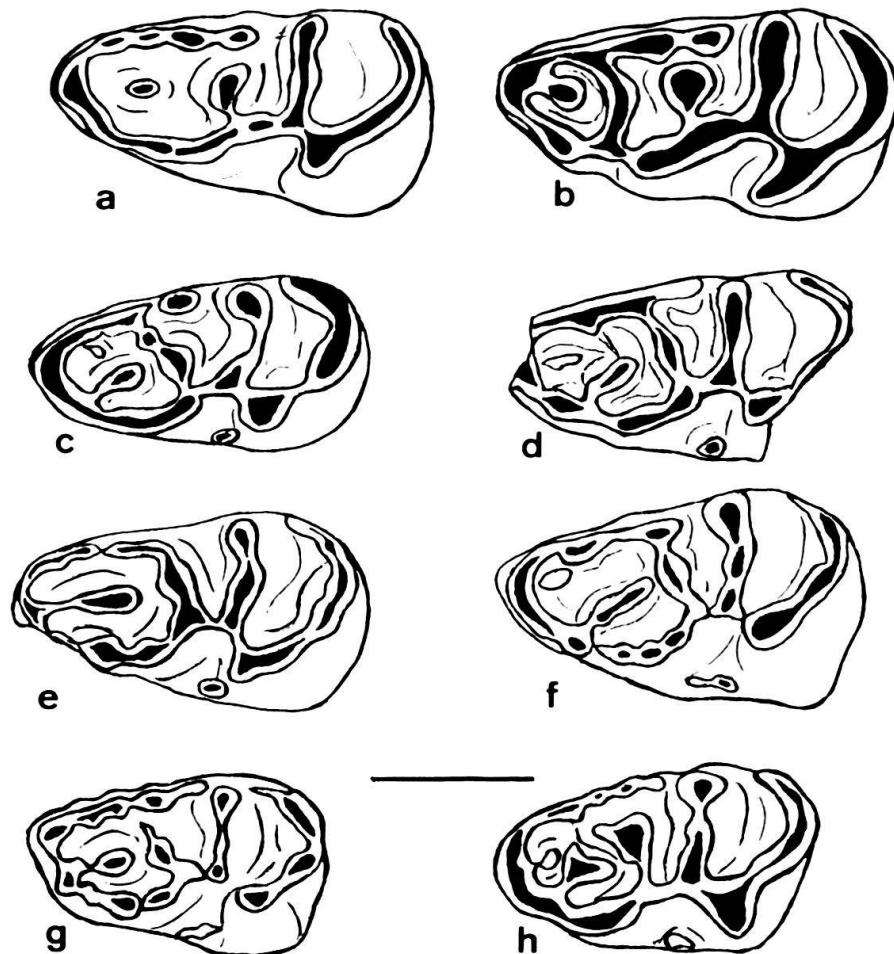


Fig. 2. D<sub>4</sub> of Issiodoromyini from the studied localities to show their increasing length.  
 a-b) Belgarite IVa; c-d) Vialenc; e-f) Saint-Martin-de-Castillon c (nov. spec.); g-h) Saint-Martin-de-Castillon  
 eb: a) left D<sub>4</sub> (CU, Bel IVa 1708), b) right D<sub>4</sub> (CU, Bel IVa 1709, reversed), c) left D<sub>4</sub> (CP), d) left D<sub>4</sub> (FSL 97922), e) left D<sub>4</sub> (FSL 97900), f) left D<sub>4</sub> (FSL 97901), g) left D<sub>4</sub> (FSL 97911), h) left D<sub>4</sub> (FSL 97912). Scale bar  
 represents 1 mm.

**D<sub>4</sub>: Vialenc** (1 complete but slightly damaged tooth, 13 damaged teeth): Fig. 2 c-d.  
 Their size is difficult to assess but seems to be close to that of StMc. The mesolophid seems to be more oblique than in StMc and is directed toward the mesostyliid in all cases, but one. A short ectolophid is indicated in 2 teeth. The entolophid is rectilinear in 2 teeth, curved in 7 teeth. The longitudinal anterotubercle is single in 4 teeth, double in 7 teeth.

In 2 teeth, a short crest springs from the lingual border to the main anterotubercle and shows a tendency to form a metalophid as seen in Belgarite IVa (Fig. 2 b). On three observable teeth, the postero- and anterolophid does not reach the entolophid.

**P<sub>4</sub>: StMc** (8 teeth): Fig. 3a-a'.

The anterior border of the tooth is rectilinear; only 1 tooth (wear stage = 0) shows a slight median division. All the teeth show a short longitudinal crest inside the anterior synclinid; on one of them, this crest curves to the labial border and isolates a small pit

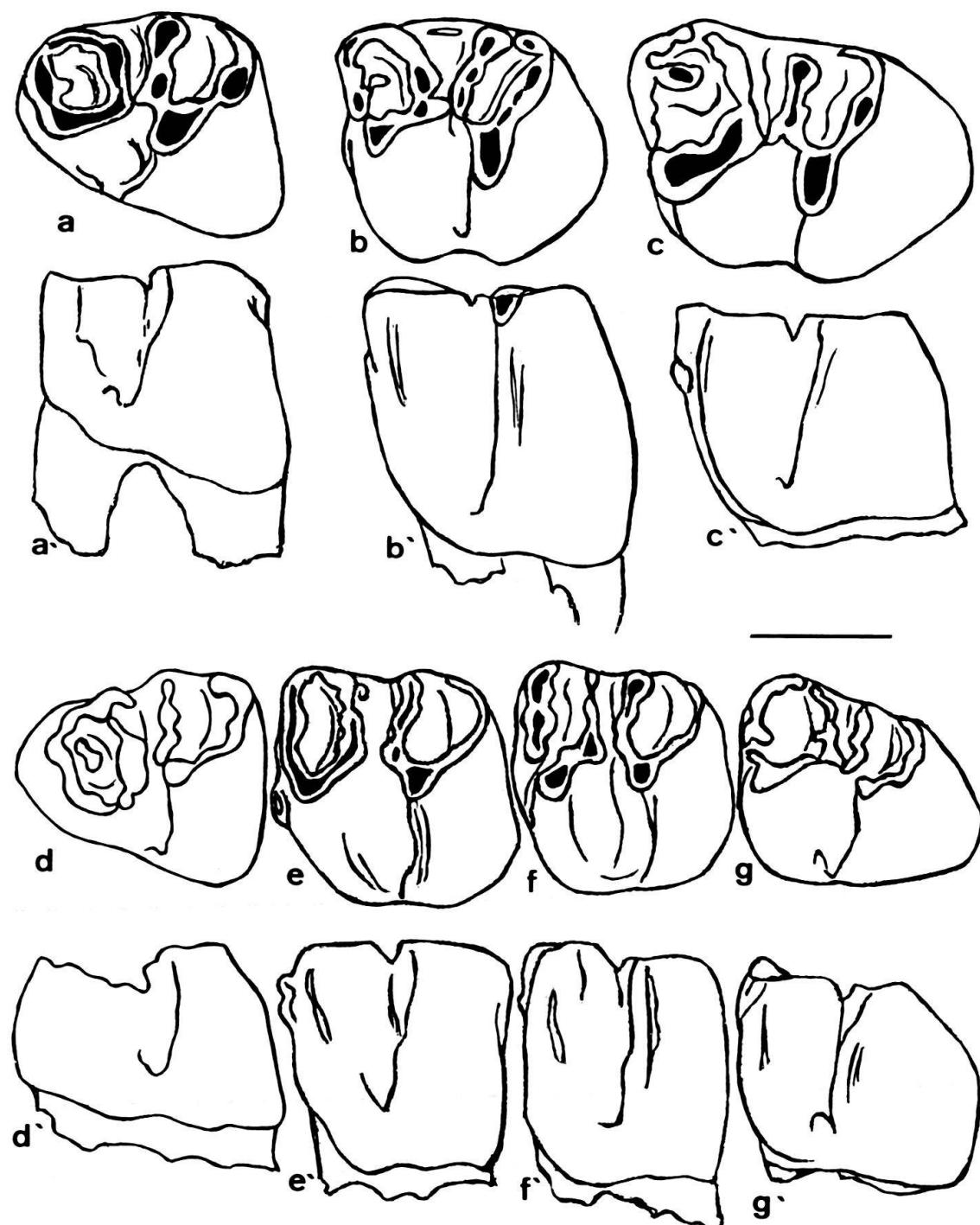


Fig. 3. Lower teeth of *Issiodoromyini* from Saint-Martin-de-Castillon c (a–c, nov. spec.) and Saint-Martin-de-Castillon eb (d–g): a) left P<sub>4</sub> (FSL 97902), occlusal view; a') labial view; b) left M<sub>1–2</sub> (FSL 97903), occlusal view; b') labial view; c) left M<sub>3</sub> (FSL 97904), occlusal view; c') labial view; d) right P<sub>4</sub> (FSL 97913, reversed), occlusal view; d') labial view; e) left M<sub>1–2</sub> (FSL 97914), occlusal view; e') labial view; f) left M<sub>1–2</sub> (FSL 97915), occlusal view; f') labial view; g) left M<sub>3</sub> (FSL 97916), occlusal view; g') labial view. Scale bar represents 1 mm.

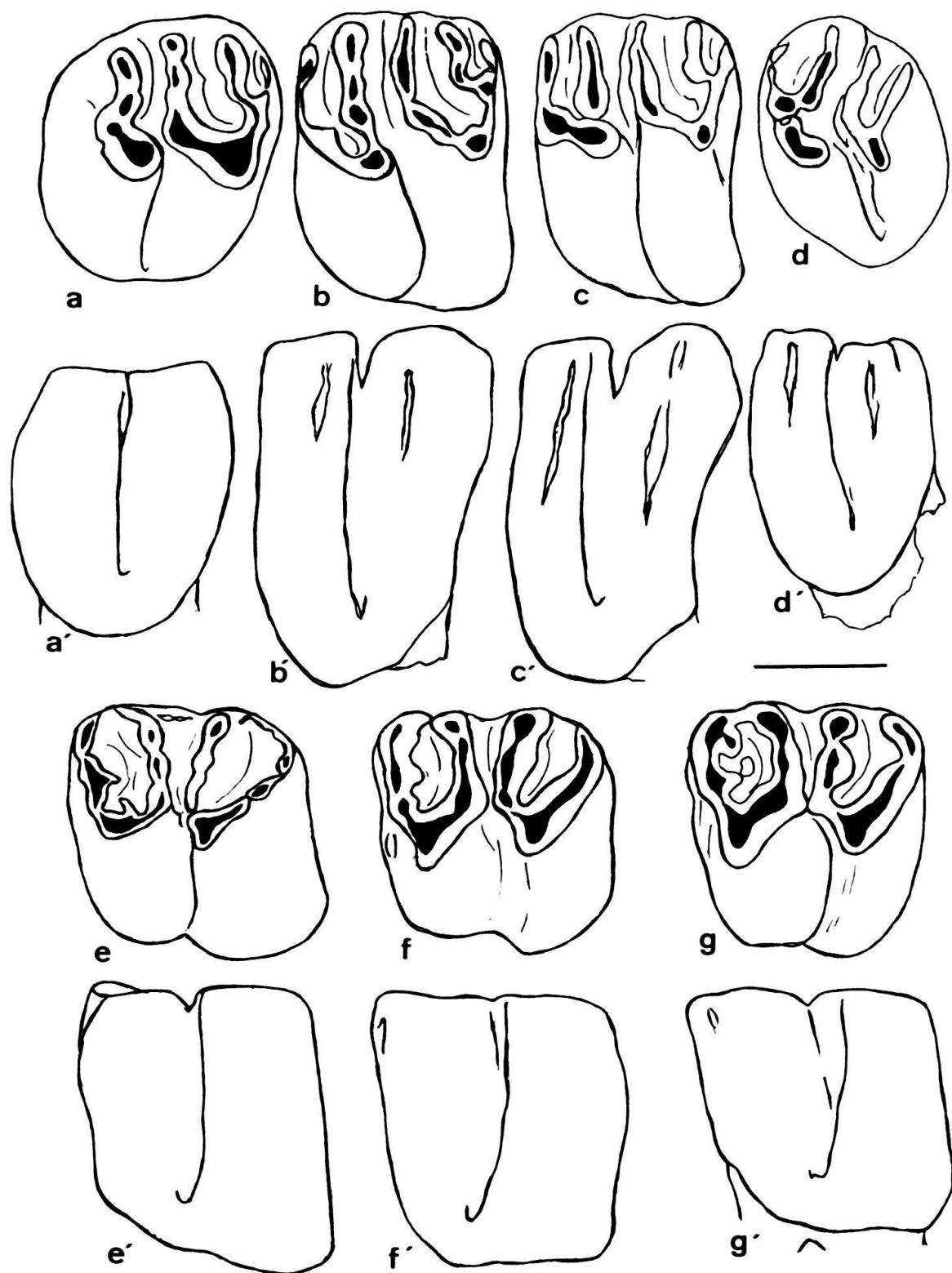


Fig. 4. Upper and lower teeth of Issiodoromyini from Vialenc: a) right  $P^4$  (FSL 97456, reversed), occlusal view; a') labial view; b) left  $M^{1-2}$  (FSL 97923), occlusal view; b') labial view; c) left  $M^{1-2}$  (FSL 97924), occlusal view; c') labial view; d) left  $M^3$  (FSL 97925), occlusal view; d') labial view; e) left  $M_{1-2}$  (FSL 97926), occlusal view; e') labial view; f) left  $M_{1-2}$  (FSL 97927), occlusal view; f') labial view; g) right  $M_{1-2}$  (FSL 97454, reversed), occlusal view; g') labial view. Scale bar represents 1 mm.

(? synclinid I). The talonid is open on the lingual side at approximately the same level as the middle synclinid. The length of  $P_4$  is, on average, a little smaller than that of the  $M_{1-2}$ .

**P<sub>4</sub>: StMeb** (1 tooth): Fig. 3d–d'.

The length of the unique  $P_4$  is about the same as that of  $M_{1-2}$ ; the tooth has the same morphology as in StMc but, as in D<sub>4</sub>, the mesolophid joins the lingual border before a well expressed mesostyliid.

**P<sub>4</sub>: Vialenc** (not represented)

**M<sub>1-2</sub>: StMc** (36 teeth): Fig. 3b–b'.

wear stage / n: (0/4); (1–2/ 26); (3/1); (4/5)

The  $M_{1-2}$  generally show two roots but out of the four entirely worn teeth, three have developed a double anterior root. The pattern with four transverse and parallel crests – the mesolophid being a little more oblique and fused with the metaconid and the posterosynclinid open – is that of all the Oligocene Issiodoromyinae.

On the anterior wall of the teeth of StMc, an anteroconid is more or less indicated on 16 teeth/30, 6 teeth/30 have nothing and 8 teeth/30 show an anteroconid with a faint antesisinusid (on the other teeth, this characteristic cannot be observed); in only 1 tooth, this antesisinusid appears on the wear surface of the tooth (wear stage 3), as is the case in *E. medius* from Les Chapelins in wear stage 2 (Vianey-Liaud 1976: Fig. 24).

9 teeth show short longitudinal crests in the anterior synclinid, generally one, but in 2 cases there are 2 crests fused to enclose a minute synclinid. 2 entirely worn teeth exhibit an isolated circle-like synclinid III.

**M<sub>1-2</sub>: StMeb** (10 teeth): Fig. 3e–e', f–f'.

$M_1$  and  $M_2$  seem to be more easily distinguishable than in StMc, the posterior half of  $M_1$  being slightly wider than the anterior part, the two halves of  $M_2$  being equivalent; 1 tooth shows a small synclinid I, the others have no longitudinal crests in the anterior synclinid.

Anteroconid and antesisinusid exist in 9/10 teeth and are more marked than in StMc; but they are also situated well under the tip of the tooth. Generally, the anterior transverse crest joins the protoconid a little more anteriorly than in StMc and makes a notch before the protoconid; it resembles more the pattern of *E. medius*.

**M<sub>1-2</sub>: Vialenc** (10 complete and 5 damaged teeth): Fig. 4e–e', f–f', g–g'.

wear stage / n: (0/3); (1–2/ 6); (4/1).

The pattern of the teeth is the same as in StMc. Anteroconid and antesisinusid exist in 3 teeth, marked anteroconid in 2 teeth, weak anteroconid in 6 teeth and a smooth anterior wall in 4 teeth.

**M<sub>3</sub>: StMc** (11 teeth): Fig. 3c–c'.

All the teeth with roots are biradiculate. The general pattern is the same as for  $M_{1-2}$  but the posterolophid is lower than the other crests and also rounded. The mean length is the same as for  $M_{1-2}$ . Six teeth present two short longitudinal crests in the anterior synclinid and in two cases these crests are fused to form a synclinid I. Six teeth show an anteroconid, two show anteroconid and antesisinusid and in two teeth the anterior wall is smooth; anteroconid and antesisinusid are always conspicuously below the tip of the unworn tooth.

Tab. 1a: Length, width and height of the teeth of the Issiodoromyini from Vialenc (mm).

		length					width					height			
	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.			
D4/	1		1.93		1		1.18		1		1.07				
P4/	1		1.35		1		1.14		1		1.83				
M1-2/	11	1.35	1.49	1.57	11	0.93	1.15	1.54	9	1.99	2.33	2.72			
M3/	2	1.08	1.18	1.28	2	1.10	1.17	1.25	1		2.02				
M/1-2	9	1.42	1.54	1.72	9	0.87	1.03	1.23	5	1.68	1.87	2.03			

Tab. 1b: Length, width and height of the teeth of the Issiodoromyini from Saint-Martin-de-Castillon c (mm).

		length					width					height			
	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.			
D4/	6	1.75	1.82	1.87	6	1.00	1.12	1.26	5	0.75	0.82	0.91			
P4/	8	1.42	1.52	1.64	8	1.02	1.31	1.55	8	1.33	1.78	2.12			
M1-2/	40	1.40	1.53	1.64	40	1.00	1.25	1.82	37	1.51	2.48	2.13			
M3/	8	1.17	1.36	1.59	8	0.89	1.17	1.64	8	1.26	1.75	2.04			
D/4	3	2.18	2.22	2.25	3	1.09	1.11	1.14	4	0.74	0.81	0.86			
P/4	10	1.32	1.57	1.92	10	0.73	1.09	1.63	8	1.13	1.61	1.82			
M/1-2	36	1.50	1.65	1.85	36	0.89	1.21	1.97	30	1.30	1.84	2.24			
M/3	11	1.46	1.61	1.72	11	1.03	1.17	1.30	8	1.53	1.75	2.15			

Tab. 1c: Length, width and height of the teeth of the Issiodoromyini from Saint-Martin-de-Castillon eb (mm).

		length					width					height			
	n	min.	mean	max.	n	min.	mean	max.	n	min.	mean	max.			
D4/	3	1.60	1.61	1.62	3	0.95	1.14	1.48	2	0.94	0.94	0.95			
P4/	1		1.46		1		1.17		1		1.58				
M1-2/	9	1.43	1.50	1.56	9	1.02	1.14	1.26	7	1.76	2.08	2.31			
M3/	2	1.09	1.19	1.30	2	0.98	1.07	1.16	2	1.59	1.80	2.01			
D/4	5	1.79	1.91	2.05	5	0.95	1.00	1.06	5	0.70	0.80	0.93			
P/4	1		1.54		1		1.13		1		1.38				
M/1-2	10	1.31	1.53	1.73	10	0.96	1.12	1.22	9	1.50	1.79	1.96			
M/3	2	1.29	1.30	1.32	2	0.90	0.96	1.02	2	1.45	1.59	1.72			

**M<sub>3</sub>: StMeb** (2 teeth, wear stage 0): Fig. 3 g–g'.

Same pattern as in StMc; one with anteroconid and one without.

**M<sub>3</sub>: Vialenc** (1 tooth, wear stage 4)

It is very worn with a nearly closed synclinid III (figured in Brunet et al. 1977: Fig. 8).

*Upper teeth***D<sup>4</sup>: StMc** (8 teeth): Fig. 5 d–e.

The general pattern is comparable with closely related Issiodoromyini. The length of D<sup>4</sup> is smaller than that of D<sub>4</sub>. Their outline is regularly trapezoidal without conspicuous expansion of the anterior part; the protocone is isolated in unworn teeth. The mesoloph is a well marked and oblique crest joined to the anterior part of the hypocone. The metaloph is always short and joins the posterior part of the posterior cingulum. Additional crests often develop: a border crest between mesoloph and posterior cingulum, and a crest joining metaloph and mesoloph or ending free. The longitudinal crest is always deeply interrupted.

**D<sup>4</sup>: StMeb** (3 teeth): Fig. 5 f.

Smaller and more quadrate than in StMc; the pattern is the same, but the protocone, isolated from the protoloph, is smaller and more firmly joined to the anterior cingulum.

**D<sup>4</sup>: Vialenc** (1 tooth): Fig. 5 c.

The protocone is large and isolated; it shows no additional crest.

**P<sup>4</sup>: StMc** (10 teeth): Fig. 6 a–a', Fig. 10.

Distinguishable from the upper molars only by the anteroloph which is always short and dips into the anterior wall. The basis of the protocone is often inflated anteriorly. The size seems to vary from teeth distinctly larger than the upper molars to those with more reduced teeth. Sometimes a labial border crest develops between mesoloph and metaloph.

**P<sup>4</sup>: StMeb** (1 tooth): Fig. 6 e–e'.

Same pattern as in StMc.

**P<sup>4</sup>: Vialenc** (1 tooth): Fig. 4 a–a'.

The protoloph joins the anterior arm of the protocone and the anteroloph is extremely small.

**M<sup>1-2</sup>: StMc** (40 teeth): Fig. 6 b–b', c–c'.

The pentalophodont structure with interruption of the longitudinal crest is the same as in other Issiodoromyinae. It is almost impossible to separate M<sup>1</sup> and M<sup>2</sup>, even if some teeth (?M<sup>2</sup>) seem to be more compressed antero-posteriorly. The protoloph generally joins the posterior arm of the protocone but in 5 teeth it is double and in 6 teeth, the protoloph joins the anterior arm of the protocone. The labial part of the anticlines normally ends free, but on 14 teeth the metacone forms a crest directed to the mesostyl and joins it in 4 teeth.

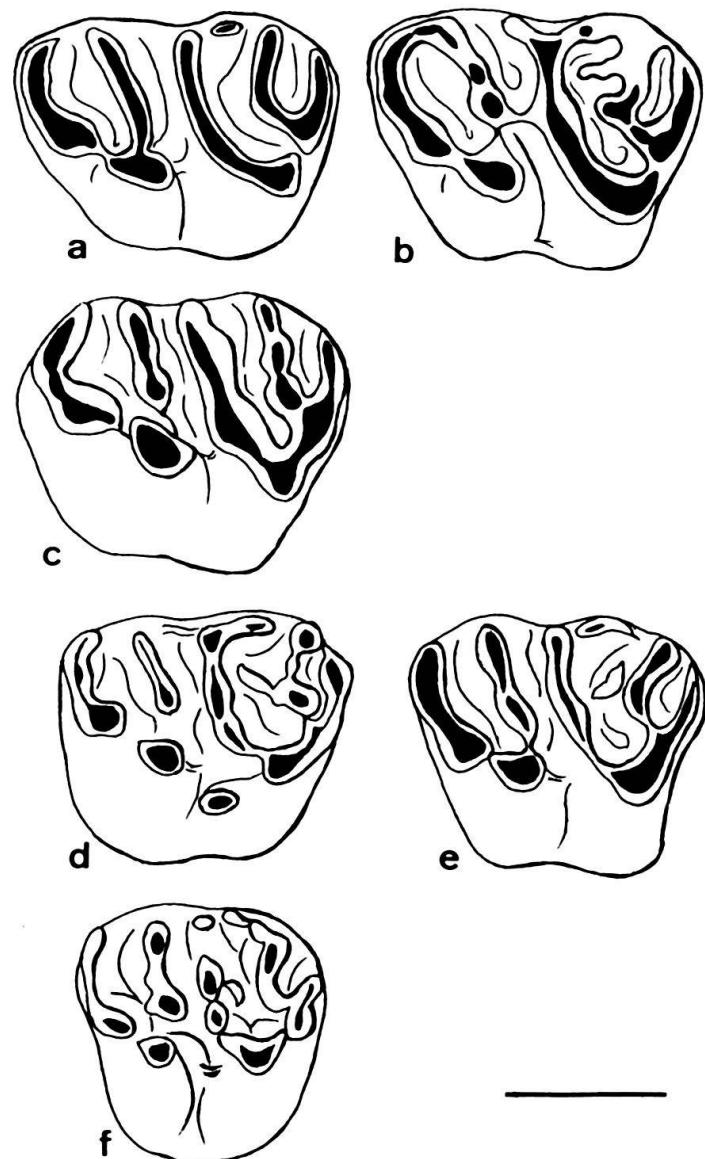


Fig. 5. D<sup>4</sup> of Issiodoromyini from the studied localities. a-b) Belgarite IVa; c) Vialenc; d-e) Saint-Martin-de-Castillon c (nov. spec.); f) Saint-Martin-de-Castillon eb: a) left D<sup>4</sup> (CU, Bel IVa 1702), b) left D<sup>4</sup> (CU, Bel IVa 1703), c) right D<sup>4</sup> (FSL 97928, reversed), d) left D<sup>4</sup> (FSL 97905), e) left D<sup>4</sup> (FSL 97906), f) left D<sup>4</sup> (FSL 97917). Scale bar represents 1 mm.

**M<sup>1-2</sup>: StMeb** (10 teeth): Fig. 6 f-f', g-g'.

Same pattern as in StMc but the protoloph always joins the posterior part of the protocone; 4 teeth show a labial border crest from metaloph to mesoloph.

**M<sup>1-2</sup>: Vialenc** (11 teeth & 2 entirely worn maxillary tooth rows): Fig. 4 b-b', c-c'.

The pattern is the same as in StMc. The protoloph joins the posterior arm of the protocone in 2 teeth and the anterior arm in 1 tooth, it is double in 2 teeth. In the other cases,

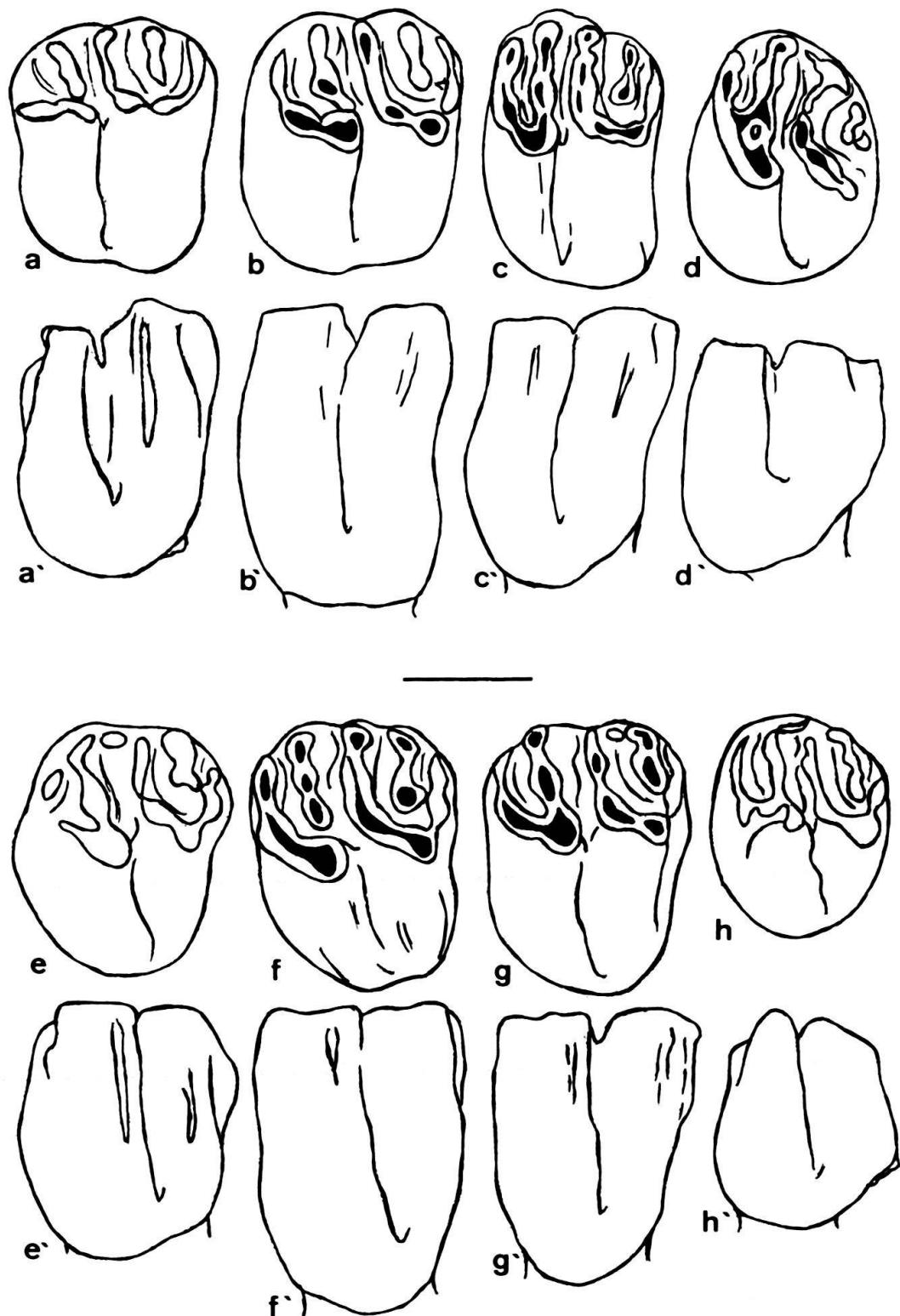


Fig. 6. Upper teeth of *Issiodoromyini* from Saint-Martin-de-Castillon c (a-d, nov. spec.) and Saint-Martin-de-Castillon eb (e-h): a) left  $P^4$  (FSL 97907), occlusal view; a') labial view; b) left  $M^{1-2}$  (FSL 97908), occlusal view; b') labial view; c) left  $M^{1-2}$  (FSL 97909), occlusal view; c') labial view; d) left  $M^3$  (FSL 97910), occlusal view; d') labial view; e) right  $P^4$  (FSL 97918, reversed), occlusal view; e') labial view; f) right  $M^{1-2}$  (FSL 97919, reversed), occlusal view; f') labial view; g) right  $M^{1-2}$  (FSL 97920, reversed), occlusal view; g') labial view; h) right  $M^3$  (FSL 97921, reversed), occlusal view; h') labial view. Scale bar represents 1 mm.

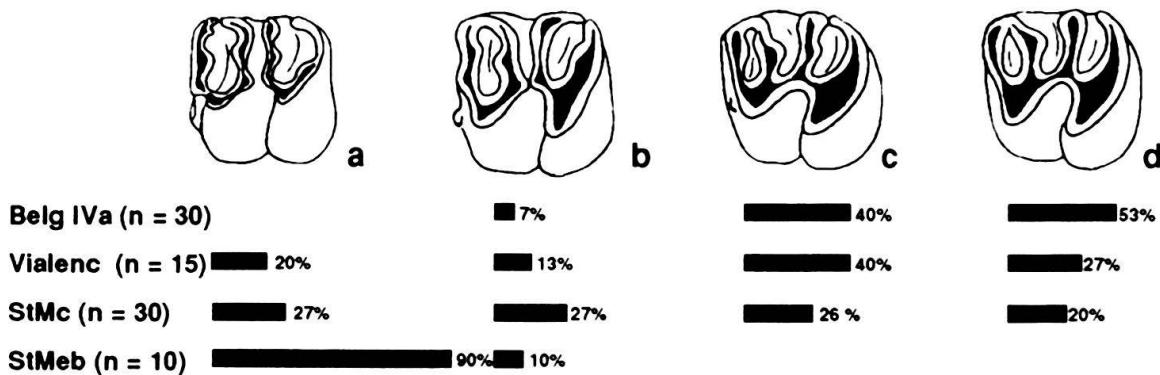


Fig. 7. Schematic representation of four different morphological stages in the evolution of the  $M_{1-2}$  of the *Elfomys-Issiodoromys* lineage and their repartition (in %) in the studied localities [from a) primitive pattern to d) most evolved pattern]. a) with anteroconid and antesusinid, b) well expressed anteroconid, c) weak anteroconid, d) no anteroconid. For abbreviations see under "Terminology and method".

it is difficult to decide because the protocone is compressed and directed obliquely. In 2 teeth the metacone forms a crest directed to the mesostyl.

#### **M<sup>3</sup>: StMc** (9 teeth): Fig. 6 d-d'.

Same pattern as  $M^{1-2}$  but more compressed anteroposteriorly and with the posterior part generally reduced (metaloph and posterior cingulum reduced or absent). The protoloph has a double connection with the protocone in 4 teeth.

#### **M<sup>3</sup>: StMeb** (2 teeth): Fig. 6 h-h'.

Same pattern as in StMc, one of the teeth is proportionally large but very reduced posteriorly so that it shows only 3 transverse crests.

#### **M<sup>3</sup>: Vialenc** (2 teeth): Fig. 4 d-d'.

Similar to those of StMc. The protoloph is always directed toward the anterior arm of the protocone.

## Results and discussion

In order to determine the biostratigraphic position of St.-Martin-de-Castillon and Vialenc important dental characteristics of the Issiodoromyini (e.g. antesusinid, length, H/L-ratio) from these sites are compared with those of La Plante 2 (MP 22) and Roqueprune 2 (MP 23), Belgarrie and Rigal-Jouet (MP 25), all described by Vianey-Liaud (1976), as well as with those of Belgarite IVa (MP 25) described by Mödden (1994). Until now no Issiodoromyini have been described from MP 24.

According to Vianey-Liaud (1976: 101), three characters in the teeth of the *Elfomys-Issiodoromys* lineage make it possible to differentiate between these two genera: on the one hand *Elfomys medius* from the biostratigraphic mammal levels of MP 22 and MP 23 and on the other hand, its successor *Issiodoromys minor* from MP 25. These three characters are: 1. Lower molars with well individualized antesusinid in *Elfomys*. 2. Upper mo-

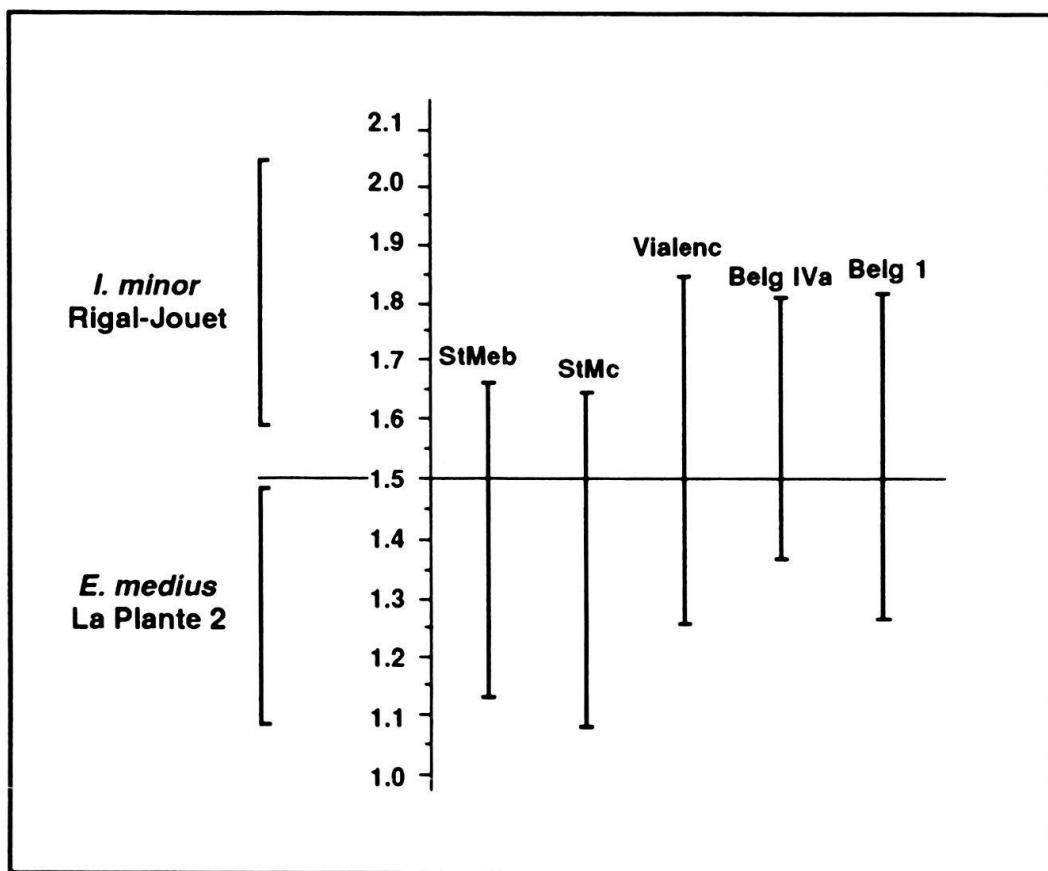


Fig. 8. Height/Length values (= H/L = "taux de hypsodontie") of the  $M^{1-2}$  (wear stages 0 and 1–2) of Issiodoromyini in the studied localities, compared with the data of Vianey-Liaud (1976) for La Plante 2, Belgarrie 1 and Rigal-Jouet. The horizontal line – situated at 1.50 – indicates the discriminating value between the two genera *Elfomys* and *Issiodoromys* as supposed by Vianey-Liaud (1976). For abbreviations see under "Terminology and method".

lars with a height/length-ratio less than 1.5 in *Elfomys*. 3. External synclines of the upper molars incised in the labial wall of the crown in *Elfomys*. These characters are discussed here and it is shown that their expression in the Issiodoromyini of the sites StMc and StMeb is intermediate between *Elfomys medius* and *Issiodoromys minor*.

First character (Antesinusid): The degree of expression of the anteroconid in the lower molars has been measured by ascribing the teeth to four groups: a) anteroconid with incised antesinusid, b) distinct anteroconid, c) weak expressed anteroconid, d) no anteroconid. According to their pattern, the  $M_{1-2}$  of the studied localities have been distributed into these groups and the result (in %) is shown in Fig. 7.

The most primitive stage investigated in relation to this character is to be found in StMeb where 90% of the teeth show a well marked antesinusid; so the Issiodoromyini from StMeb are morphologically more closely related to *E. medius* than to *I. minor* and are designated as *E. aff. medius*.

On the contrary, the lower molars from StMc and Vialenc pertain certainly to *Issiodoromys*, because they always show a reduced antesinusid, conspicuously below the oc-

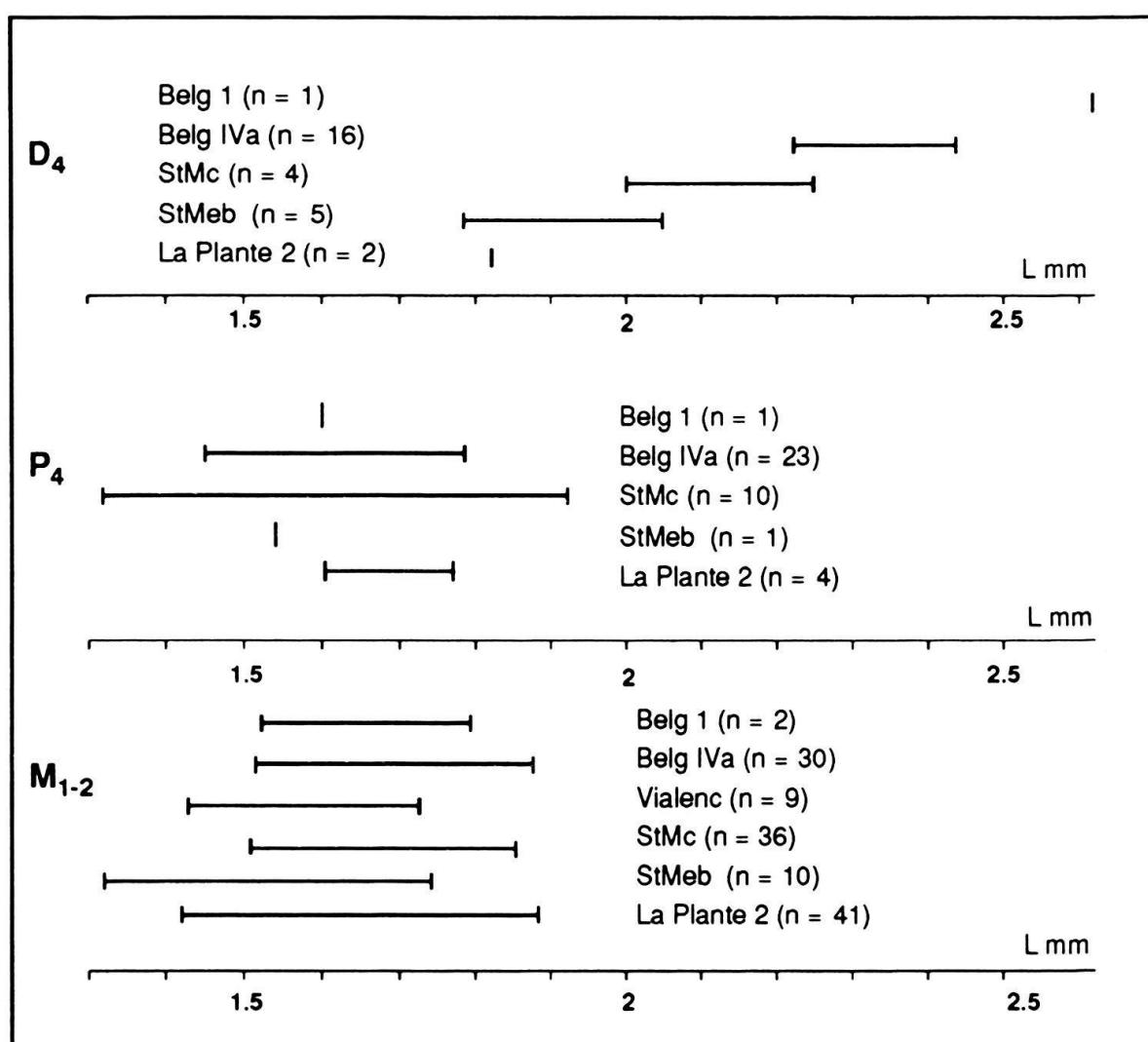


Fig. 9. Length of the lower teeth (wear stages 1-2) of Issiodoromyini in the studied localities, compared with data given by Vianey-Liaud (1976) for La Plante 2 and Belg. 1. For abbreviations see under "Terminology and method".

clusal surface in the unworn lower molars and which is only exceptionally visible on the wear surface; they resemble much more the teeth of *I. minor* from Belgarite IVa.

So, this character seems to change very rapidly and as it is very easy to detect both on unworn and worn teeth, it seems to be very useful for the distinction between *Elfomys* and *Issiodoromys*.

Second character (H/L-ratio less than 1.5): in wear stages 0 and 1-2 the upper molars ( $M^{1-2}$ ) of *Issiodoromys minor* show a height/length-ratio ("taux d'hypsodontie") higher than 1.5 and differ in this point from *Elfomys medius* from La Plante 2 (MP 22) and Roqueprune 2 (MP 23). From StMeb, 1 out of 7  $M^{1-2}$  has a H/L-ratio  $\geq 1.5$  (14.3%); from StMc, 12 out of 37  $M^{1-2}$  have a H/L-ratio  $\geq 1.5$  (32.4%); from Vialenc, 6 out of 9  $M^{1-2}$  have a H/L-ratio  $\geq 1.5$  (66.7%), from Belgarite IVa, 15 out of 20  $M^{1-2}$  have a H/L-ratio  $\geq$

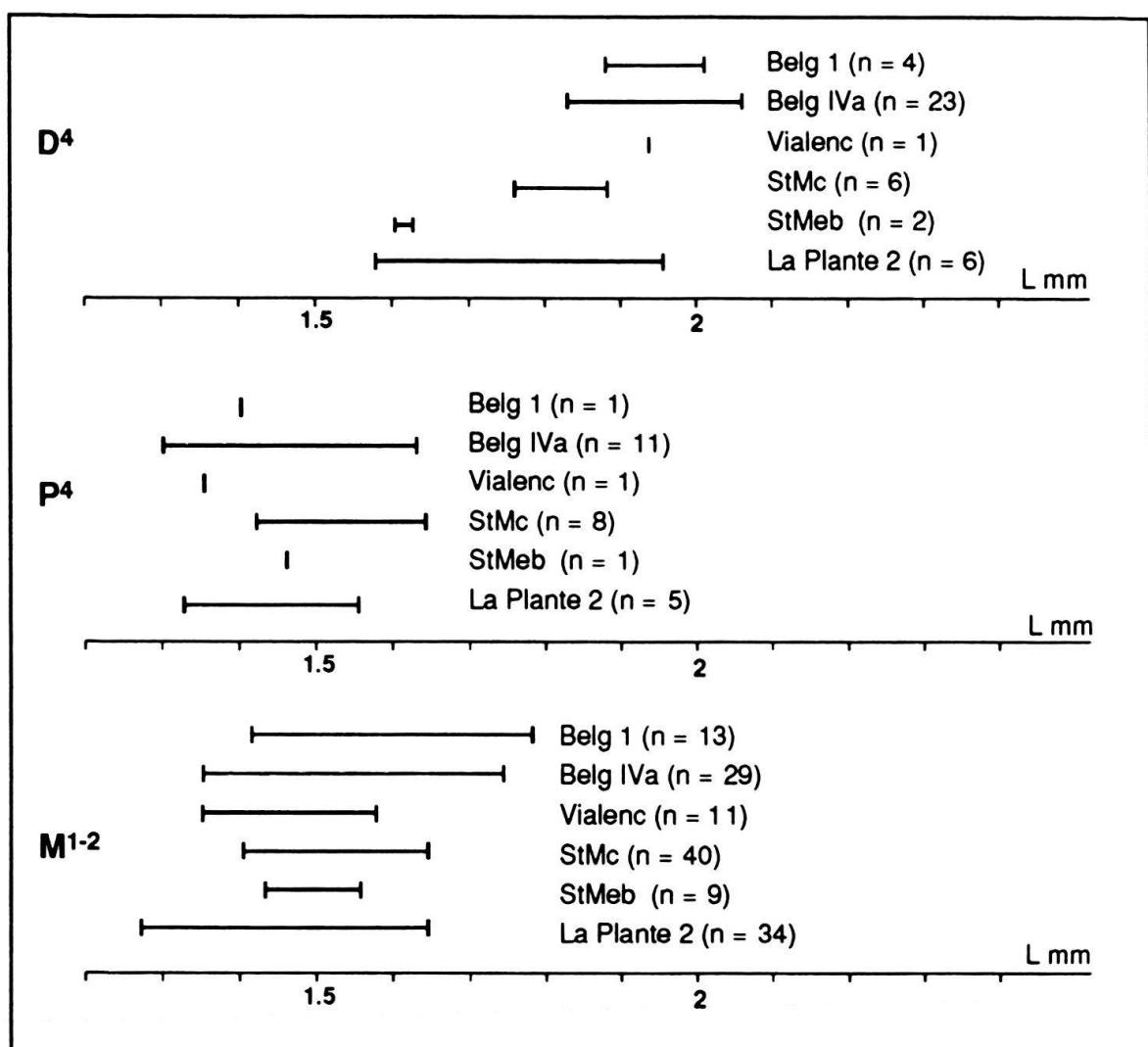


Fig. 10. Length of the upper teeth (wear stages 1–2) of Issiodoromyini in the studied localities, compared with data given by Vianey-Liaud (1976) for La Plante 2 and Belg. 1. For abbreviations see under "Terminology and method".

1.5 (75.0%). The distribution of the H/L-ratio in the studied localities is shown in figure 8. As can be seen in this figure it is not possible to differentiate between *Elfomys* and *Issiodoromys* in MP 24 on the base of the H/L-ratio. However, taking into account the fact that there are very few teeth in StMeb, the H/L-ratio character gives a slight hint that the Issiodoromyini from StMeb are more primitive than those of StMc and Vialenc.

Third character (synclines incised in buccal wall): it seems to be difficult to differentiate *E. medius* and *I. minor* with this character, first because a restriction was made by Vianey-Liaud (1976) herself ("au moins sur une partie de la population") and secondly because the question "incised or not incised" is often difficult to decide.

Thus, from these three characters used to differentiate between *Elfomys medius* and *Issiodoromys minor* the most important seems to be the expression of the anteroconid.

But other possibilities to assess the evolutionary stage of the Issiodromyini in levels MP 22–25 are length (Fig. 9 and 10/table 1) and occlusal pattern of the lower D<sub>4</sub>.

The total length of the lower D<sub>4</sub> increases gradually from StMeb to Belgarite IVa (the unique complete D<sub>4</sub> of Vialenc is in a very late wear stage and should not be measured). We have to note, however, that the length of the lower D<sub>4</sub> decreases very rapidly in late wear stages and so only early and middle wear stages should be measured.

Moreover, there are also changes in the occlusal pattern of the lower D<sub>4</sub> because the crest connecting the anterior and posterior part of the tooth (= ectolophid or “crête longitudinale”) becomes longer from StMeb to Belgarite IVa (Fig. 2).

Upper D<sup>4</sup> can also give a slight hint about the biostratigraphic position of the Issiodromyini of the levels MP 22–25. The synclines of the upper D<sup>4</sup> from StMc and StMeb (especially the anterosyncline and posterosyncline) seem to be more incised in the occlusal surface than in the upper D<sup>4</sup> of Belgarite IVa and other more evolved Issiodromyini.

According to Vianey-Liaud (1976: Fig. 45), no important change in the length of the upper molars (M<sup>1–2</sup>) took place during the biostratigraphic interval MP 22–MP 25 (La Plante 2–Belgarric). However, according to Schmidt-Kittler & Vianey-Liaud (1987) there is little change in the length of the lower molars (M<sub>1–2</sub>). Figure 9 shows the length of the lower M<sub>1–2</sub> in StMc, StMeb, Vialenc and Belgarite IVa. The mean of the length is not given, because it depends on the distribution of the teeth inside the wear stages in the different localities and perhaps, it may also depend on the respective number of M<sub>1</sub> and M<sub>2</sub>.

The length distribution displays considerable overlap in M<sub>1–2</sub> and P4 (Fig. 9 and 10/table 1a–c) and, as the width varies much more during wear, it is not possible to distinguish *E. medius* and *I. minor* by the occlusal size of molars and premolars.

## Conclusion

Since Stehlin & Schaub (1951: 363) and Vianey-Liaud (1976) it is known that the evolutionary development of the Issiodromyini (*Elfomys-Issiodromys* lineage) presents good possibilities for indicating the biostratigraphical, fossil mammal based standard levels (MP zones) of the Oligocene. It has been shown that the characters of the Issiodromyini from the stratified sites of St.-Martin-de-Castillon (StMc and StMeb) and Vialenc are intermediate between the known *Elfomys medius* from MP 22 and MP 23 (Vianey-Liaud 1976) and the known *Issiodromys minor* from MP 25 (Vianey-Liaud 1976 and Mödden 1994). This intermediate morphology between *E. medius* and *I. minor* is mainly shown by the following characters (relative to *E. medius*): decrease of the expression of antesisusid and anteroconid in the lower molars; increase of total length of the lower D<sub>4</sub>; and increase of length of its ectolophid. However, these characters do not reach the evolutionary degree of *I. minor* from MP 25. The morphologically intermediate stage of these Issiodromyini leads to the assumption that St.-Martin-de-Castillon c and eb and Vialenc belong to the biostratigraphical mammal standard level MP 24 and so here the first description of Issiodromyini of MP 24 is given.

Direct comparison between the Issiodromyini of the two levels of St.-Martin-de-Castillon show that the Issiodromyini from StMeb have a more primitive morphology than those of StMc and resemble *Elfomys medius* more; so they are ascribed to *Elfomys* aff. *medius*. On the contrary, the more evolved teeth of StMc and Vialenc are ascribed to *Issiodromys* aff. *minor*. We are convinced that *Issiodromys* from StMc is morphologi-

cally different from *Issiodoromys minor* from Belgarrie and Garouillas and that it represents a new species, but, as announced in Mödden (1994), before establishing this new species one problem has to be solved: what taxonomically is *Issiodoromys minor*? The answer is in preparation by Mödden and Vianey-Liaud.

In the reference-locality of MP 24, Heimersheim, discriminating taxa (Issiodoromyini) are missing and peculiar theridomorphs (*Theridomys heimersheimensis*, *Toeniodus hexalophodus*) occur; consequently precise correlations are difficult and this perhaps indicates a certain amount of endemicity. The fossil mammals of St.-Martin-de-Castillon and Vialenc give valuable additional support to the recognition of the MP 24 level; moreover, being stratified localities and, in the case of St.-Martin-de-Castillon, yielding two successive populations, they give us very precise information about the evolutionary development and variability of the Issiodoromyini and other mammal groups in this level.

### Acknowledgements

We thank Monique Vianey-Liaud (Montpellier) and Hans de Bruijn (Utrecht) for access to the collections under their care. The research of one of us (C. M.) was supported by the Swiss National Science Foundation (project No 21-37357.93) and the Deutsche Forschungsgemeinschaft (DFG) (Az.: Schm 452/17-2). We are also grateful to Thomas Bolliger (Zürich) and an anonymous reviewer for instructive comments and suggestions.

### REFERENCES

BOSMA, A. A. 1974: Rodent Biostratigraphy of the Eocene-Oligocene transitional strata of the Isle of Wight. Utrecht Micropal. Bull., Spec. Publ. 1, 1-128.

BRUNET, M., HUGUENEY, M. & JEHENNE, Y. 1977: Première découverte d'une faune de petits mammifères dans le Paléogène du bassin d'Aurillac (Cantal); implications stratigraphiques. Geobios 10/5, 749-752.

DUCREUX, J.-L., HUGUENEY, M. & TRUC, G. 1985: La formation des calcaires et lignites de Sigonce (Oligocène moyen, bassin de Forcalquier, Alpes-de-Haute-Provence): datation à l'aide des mammifères; reconstitution des milieux de dépôts. Geobios 18/1, 109-114.

HUGUENEY, M. 1994: *Theridomys truci* de l'Oligocène de Saint-Martin-de-Castillon (Vaucluse, France) nouvelle espèce du genre *Theridomys* (Rodentia, Mammalia) et sa relation avec la lignée de *Theridomys lembronicus*. Scripta Geol. 104, 115-127.

HUGUENEY, M., TRUC, G. & PHILIPPE, M. 1971: Nouveaux gisements à Micromammifères et Mollusques continentaux dans l'Oligocène Moyen du synclinal d'Apt (Vaucluse, Sud-Est de la France). C. R. Acad. Sc. Paris, 272, D, 2430-2433.

MÖDDEN, C. 1994: Systematik und Nomenklatur der Issiodoromyinae Tullberg, 1899 (1884) (Rodentia, Theridomyidae) des europäischen Paläogen. Eclogae geol. Helv. 87/3, 1037-1066.

SCHMIDT-KITTLER, N. (ed.) 1987: International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene vom 18.-21. Februar 1987 in Mainz. Münchener Geowiss. Abh. 10

SCHMIDT-KITTLER, N. & VIANEY-LIAUD, M. 1987: Morphometric analysis and evolution of the dental pattern of the genus *Issiodoromys* (Theridomyidae, Rodentia) of the European Oligocene as a key to its evolution. Proc. Koninkl. Nederl. Akad. van Wetenschappen B 90/3, 281-306.

STEHLIN, H. G. & SCHAUB, S. 1951: Die Trigonodontie der simplicidentaten Nager. Schweiz. paläont. Abh. 67, 1-385.

VIANEY-LIAUD, M. 1976: Les Issiodoromyinae (Rodentia, Theridomyidae) de l'Éocène supérieur à l'Oligocène supérieur en Europe Occidentale. Palaeovertebrata 7/1, 1-115.

Manuscript received July 20, 1995

Revision accepted April 16, 1996