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Morphometrical analyses of northern Birch Mice (*Sicista betulina* Pallas, 1779; Mammalia; Rodentia) discovered in a rich locality from the Late Pleistocene of northwestern Switzerland

Analyses morphométriques de sicistes des bouleaux (Sicista betulina Pallas, 1779 ; Mammalia ; Rodentia) découvertes dans un riche gisement du Pléistocène supérieur du Nord-Ouest de la Suisse

Julien Oppliger[a,b,*], Damien Becker[c]

[a] *Département d'archéozoologie, muséum d'histoire naturelle, 1, route de Malagnou, CP 6434, 1211 Genève 6, Switzerland*
[b] *Département d'anthropologie et d'écologie, université de Genève, 12, rue Gustave-Revilliod, 1211 Genève 4, Switzerland*
[c] *Section d'archéologie et paléontologie, république et canton du Jura, office de la culture, hôtel des Halles, CP 64, 2900 Porrentruy 2, Switzerland*

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ABSTRACT

The discovery of 100 isolated teeth of *Sicista betulina* Pallas, 1779 in a doline filling of northwestern Switzerland (Vâ Tche Tchâ locality, Courtedoux, Ajoie) represents, in terms of richness, an exceptional occurrence for the Late Pleistocene of western Europe. This reference collection provides additional data for the identification of *S. betulina*, but also for the distinction of northern Birch Mice (*S. betulina*) and southern Birch Mice (*S. subtilis*) populations by morphometrical analyses (Mahlanobis distance, ratio diagrams) from isolated back teeth. Moreover, the determination of these two species is important for palaeoenvironmental studies, because they are associated to different biotopes.

Mots clés :
Sicista betulina
Pléniglaciaire moyen terminal
Nord-Ouest de la Suisse
Analyse morphométrique

RÉSUMÉ

La découverte de 100 dents isolées de *Sicista betulina* Pallas, 1779 dans le remplissage d'une doline du Nord-Ouest de la Suisse (Vâ Tche Tchâ, Courtedoux, Ajoie) constitue, en termes de richesse, un enregistrement exceptionnel pour le Pléistocène supérieur d'Europe de l'Ouest. Cette importante série de dents apporte des éléments complémentaires pour l'identification de *S. betulina*, mais aussi pour la distinction des populations de sicistes des bouleaux (*S. betulina*) et de sicistes des steppes (*S. subtilis*) par des analyses morphométriques (distance de Mahalanobis, diagrammes de Simpson) sur des dents jugales isolées. De plus, la détermination de ces espèces est importante pour les études paléo-environnementales car elles sont associées à des biotopes différents.

1. Introduction

Due to their very small size, dental and bone remains of *Sicista* (Mammalia; Rodentia) are rarely discovered in Euro-

* Corresponding author.
E-mail address: julien.oppliger@unige.ch (J. Oppliger).

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pean Quaternary sites and generally in small quantities only. The discovery of an important collection of isolated teeth of *Sicista betulina* Pallas, 1779 in a doline filling of the Vâ Tche Tchâ locality in Courtedoux (about 3 km west of Porrentruy, Ajoie, northwestern Switzerland), constitutes a new reference site for the Late Pleistocene of Western Europe (Fig. 1). The referred material, dated to the latest Middle Pleniglacial (Becker et al., 2009), gives additional data for the morphology and morphometry of this taxon. Since the Middle Pleistocene, two species of the genus *Sicista* are known in Europe: the northern Birch Mouse (*Sicista betulina* Pallas, 1779) and the southern Birch Mouse (*Sicista subtilis* Pallas, 1773). However, their distinction is still problematic, particularly for Pleistocene populations.

Today, the populations of *S. betulina* are mainly located in forested areas (taigas) of the eastern Palearctic: from Poland and the Czech Republic to the Lake Baïkal, and from the southern Artic Circle to the Carpathians (Pucek, 1999; Shenbrot et al., 2008). In western Europe, few relic populations persist in restricted refuge areas of Scandinavia, northern Germany, and Austria (Pucek, 1999; Meinig et al., 2008). Regarding *S. subtilis*, its populations inhabit rather open environments (steppes) and its geographical range spreads from Ukraine to the Lake Baïkal and even to northwestern China. Some isolated populations are signalled in Hungary, Romania, Bulgaria and southeastern Poland (Kryštufek et al., 2008). During the Middle and Late Pleistocene, the distribution areas of *Sicista* were strongly enlarged westwards. Occurrences of *S.* cf. *betulina* are also reported in terminal Middle Pleistocene localities from southern France, as in Orgnac 3 (Jeannet, 1981), Abri Vaufrey (Marquet, 1993) and Baume Moula-Guercy (Defleur et al., 2001). During the same time interval, *S. subtilis* is reported in Maastricht-Belvédère (Netherlands) (Kolfschoten, 1993) and probably in France in Baume de Gigny (bed XXIb) (Chaline and Brochet, 1989). During the Late Pleistocene, *S. betulina* showed westward expansions. These incursions are notably recorded in numerous localities from Germany (Brunner, 1949; Brunner, 1953; Brunner, 1956; Heller, 1933; Heller, 1937; Heller, 1957; Koenigswald, 1978; Koenigswald and Taute, 1979; Rabenstein, 1991), France (Chaline, 1972; Marquet, 1993), Italia (Bartolomei, 1966), Belgium (Cordy, 1992) and Switzerland (Stehlin, 1924a; Stehlin, 1924b). In the terminal Late Pleistocene, the localities with *S. betulina* are relatively abundant, but always with few remains. Some populations seem to persist in refuge areas during the Late Glacial of eastern France (Marquet, 1993), during the Preboreal–Boreal interval in southeastern Germany (Brunner, 1949; Heller, 1933; Heller, 1937; Heller, 1957; Rabenstein, 1991) and until the Subboreal–Subatlantic interval in central Germany (Storch, 1994). The records of *S. subtilis* are more incomplete. They include only two localities from the early Late Pleistocene (Early Weichselian), the volcanoes of Wannenköpfe (Kalthoff et al., 2007) in Germany and Baume de Gigny (Chaline and Brochet, 1989) in France. Whereas *S. betulina* still occurs to date in the Austrian Tyrol (Spitzenberger, 2001), its presence in Switzerland was only supposed. Stehlin (Stehlin, 1924a; Stehlin, 1924b) invoked its presence – under the name *S. montana*, synonym of *S. betulina* – in the Magdalenian localities of Ettingen (a right maxilla with P4–M2 and a

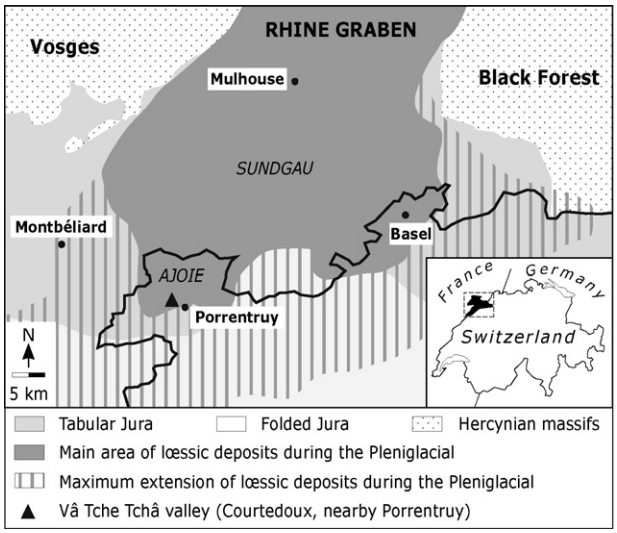

Fig. 1. Geological map of southern Alsace (France) and of the Swiss Jura Mountains (modified after Braillard, 2006). The Pleniglacial loessic deposits are mainly located between the Vosges and Black Forest Hercynian massifs. The southern extension of these deposits is characterized by the first antiforms of the folded Jura. The Vâ Tche Tchâ valley is located in Courtedoux (about 3 km west of Porrentruy, Ajoie, northwestern Switzerland).
Fig. 1. Situation géographique et géologique de la région du Sud de l'Alsace (France) et de la chaîne jurassienne suisse (modifiée d'après Braillard, 2006). La distribution des dépôts lœssiques du Pléniglaciaire est concentrée entre les massifs hercyniens des Vosges et de la Forêt-Noire. Leur extension méridionale est marquée par les premières antiformes du Jura plissé. La Combe de Vâ Tche Tchâ se situe dans la commune de Courtedoux (environ 3 km à l'ouest de Porrentruy, Ajoie, Nord-Ouest de la Suisse).

left mandible with m1) and Thierstein (a left mandible with m1–m3 and a second left one without tooth) in northwestern Switzerland.

Recent palaeontological and archaeological excavations along the construction of the future Transjurane highway A16 in northwestern Switzerland at the Vâ Tche Tchâ locality allowed the excavation of numerous doline fillings (from a diameter of 5 to 50 m), normally covered by Holocene deposits. Nine of them yielded Pleniglacial faunal remains of *Mammuthus primigenius*, *Equus germanicus*, *Bison priscus*, *Coelodonta antiquitatis*, *Cervus elaphus* cf. *simplicidens*, *Megaloceros* sp. and carnivores of diverse sizes (Becker et al., 2009). However, only a single doline (named V1; Fig. 2) yielded a rich small mammal assemblage, which was composed by *Sicista betulina* associated to *Arvicola terrestris*, *Chionomys nivalis*, *Microtus arvalis*, *Microtus agrestis*, *Microtus oeconomus*, *Sorex* group *araneus* and *Talpa europaea*. This paper analyses the rich dental material of *S. betulina* discovered in this doline, and provides additional data for the determination of Late Pleistocene *Sicista* populations in Europe. Moreover, this work tries to distinguish *S. betulina* and *S. subtilis* from isolated teeth, notably by morphometrical approaches.

2. The dolines of the Vâ Tche Tchâ locality

The locality called Vâ Tche Tchâ (Courtedoux, Ajoie, northwestern Switzerland) is the uppermost part of a narrow dry valley, characteristic of the karstic landscape of the Ajoie region (Braillard, 2006). Sedimentary units (D), defined on their lithofacies and chronostratigraphy, allow to describe the sedimentary fillings recorded in the dolines of the Vâ Tche Tchâ valley. They correspond to a stratigraphical range from the Late Pleistocene to present time. It involves a Pleniglacial loessic sequence, which is sometimes very altered and most of time decarbonated (*Lösslehm* of German authors). The sedimentary unit (called D6 base, mainly based on the nomenclature of Aubry et al., 2000; Becker et al., 2009; Braillard, 2006; Guélat, 2006) of the doline V1, which yielded *S. betulina* dental remains, is dated from 42.5–36.5 ka cal BP (radiocarbon calibration from the carbon-14 datings Ua-36664 and Ua-36668 of the Uppsala University in Sweden; Fig. 2c), therefore from the latest Middle Pleniglacial. It probably corresponds to an interstadial stage (Huneborg or maybe Hengelo of the northern Europe chronostratigraphy).

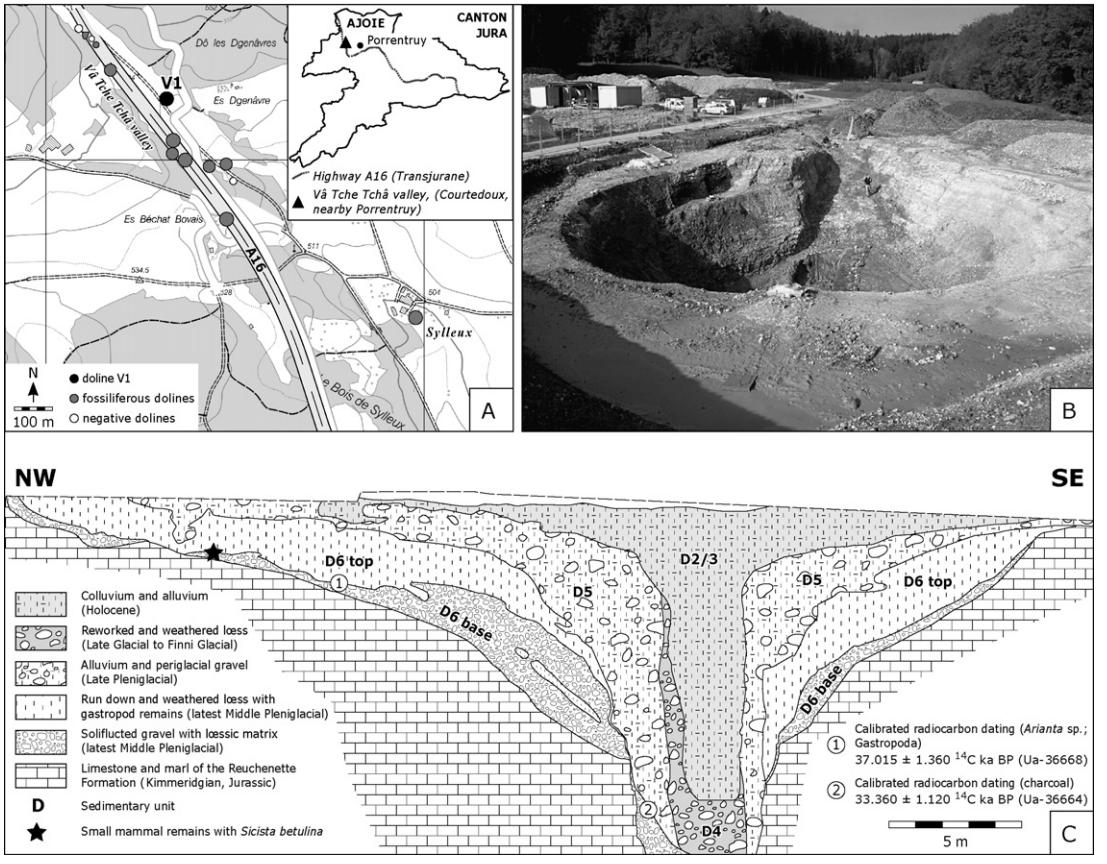

Fig. 2. **A**: location of the Late Pleistocene dolines from the Vâ Tche Tchâ valley (Courtedoux, Ajoie, northwestern Switzerland) along the future Transjurane highway (A16). **B**: photograph of the doline V1 during excavation. **C**: synthetic stratigraphic section of the Late Pleistocene loessic filling within the doline V1. The locations of the small mammal remains and the samples for the radiocarbon datings are represented in projection on the section.

Fig. 2. **A** : localisation des dolines du Pléistocène supérieur de la Combe de Vâ Tche Tchâ (Courtedoux, Ajoie, Nord-Ouest de la Suisse) le long de la future autoroute A16 (Transjurane). **B** : photo de la doline V1 en situation de fouille. **C** : coupe stratigraphique synthétique du remplissage lœssique du Pléistocène supérieur de la doline V1. La position du gisement à micromammifères et des échantillons pour les datations radiocarbones est représentée en projection sur la coupe.

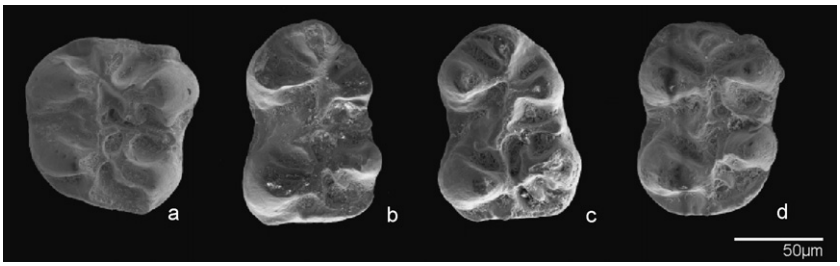

Fig. 3. Scanning Electron Microscope (SEM) pictures (FEI XL30 Sirion FEG; Department of Geosciences, University of Fribourg, Switzerland) of *S. betulina* dental remains from the doline V1 of the Vâ Tche Tchâ valley (latest Middle Pleniglacial; Courtedoux, Ajoie, northwestern Switzerland). The teeth are in occlusal view. **a**: M1 left (MJSN VTA006–692); **b**: m1 left (MJSN VTA006–692); **c**: m1 left (MJSN VTA006–692); **d**: m2 left (MJSN VTA006–692).
Fig. 3. Images obtenues au microscope électronique à balayage (MEB) (FEI XL30 Sirion FEG ; Département de Géosciences, Université de Fribourg, Suisse) des restes dentaires de *S. betulina* de la doline V1 de la Combe de Vâ Tche Tchâ (Pléniglaciaire moyen terminal ; Courtedoux, Ajoie, Nord-Ouest de la Suisse). Les dents sont en vue occlusale. **a** : M1 gauche (MJSN VTA006–692) ; **b** : m1 gauche (MJSN VTA006–692) ; **c** : m1 gauche (MJSN VTA006–692) ; **d** : m2 gauche (MJSN VTA006–692).

3. Material and methods

About 100 kg of sediment from the fossiliferous unit D6 base of the doline V1 were screen-washed, and the micro-remains were collected under the binocular (Fig. 2c). The quantification of the small mammal specimens was defined by the number of remains (NR) and the minimum number of individuals (NMI). The fine sifting (sieve-mesh diameters down to 0.25 mm) allowed collecting 2'549 micro-remains, among which 31 % of dental elements. The bones were very fragmented (87 % of fragmentation), but the teeth were well preserved. The referred specimens, attributed to *S. betulina*, are only back teeth (NR = 100; NMI = 14). They are stored in the *Musée jurassien des sciences naturelles* (MJSN, Porrentruy, Switzerland), collection Palaeontology A16 (VTA006–612, –619, –692, –705, –723).

The morphological analysis of *S. betulina* and *S. subtilis* follows the nomenclature used by Pucek, 1982b. A first distinction between *S. betulina* and *S. subtilis* was based on both the morphology of the molar occlusal face, which is more complex in *S. betulina*, and the dental size, *S. betulina* being smaller. The dental measurements (length and width) were taken twice in order to assess the intra-observator measurement error. The application of paired Student's t-tests underlined no significant difference ($p < 0.05$) between the two measurement sets.

The Mahalanobis distance (Mahalanobis, 1936) and ratio diagram (Simpson, 1941) methods were used from dental measurements to provide confident tools for the distinction of *S. betulina* and *S. subtilis*. Mahalanobis distance allows assessing similarities and differences between these two taxa. It is, for example, successfully applied by Cserkesz et al., 2009 to compare dental measurements of *S. subtilis* subspecies and *S. betulina*, or by Carrasco, 2000 to identify *Dipodomys* subspecies on the base of dental dimensions. All statistical analyses were realized with PAST (PAleontological STatistics) v1.92 statistical software (Hammer et al., 2001).

4. Systematics

Order Rodentia Bowdich, 1821
Family Dipodidae Fischer de Waldheim, 1817
Subfamily Sicistinae Allen, 1901
Genus *Sicista* Gray, 1827
Sicista betulina Pallas, 1779

4.1. Description

In a general way, *Sicista* molars from Vâ Tche Tchâ (Fig. 3) possess additional spurs on the occlusal face, in particular on m1 and m2, conferring a complex structure to these teeth. This character of complexity was not available on upper molars. Moreover, the presence of these additional spurs, both on upper and lower molars, depends strongly on dental wear. Indeed, the state of preservation and wear of *Sicista* teeth from Vâ Tche Tchâ does not permit always to detect full dental structures. However, 13 ($n = 17$) m1 and 14 ($n = 15$) m2 allowed observing a spur in the depression located between the entoconid and the posteroloph, and also 5 m1 on the anterior part of the entoconid. Moreover, all m1 displayed a small concavity between the hypoconid and the protoconid, 13 m1 a few prominent hypoconid on labial side, and 12 m1 a well-developed mesolophid. Dental measurements (length and width) are given in Table 1.

4.2. Taxonomical affinities

According to the *Sicista* dental formula (1/1-0/0-1/0-3/3), the referred specimens correspond to upper premolars and molars, as well as lower molars. The additional spurs observed on the molar occlusal face reveal a dental structure more complex than that of *S. subtilis*. According to Terzea, 1974, this complexity is essentially exhibited on the lower molar talonid and on the half labial side of the upper molar occlusal face. Terzea, 1973 and mainly Kowalski, 1979 specified the position of these additional spurs on m1 and m2. The referred m1 teeth display a combination of typical characters of *S. betulina*, including a strong mesolophid (Kowalski, 1979) and a few prominent hypoconid on the labial side (Storch, 1975; Storch, 1994). The m1 labial concavity, between the hypoconid and the protoconid, seems less important than that underlined in *S. subtilis* by Kalthoff et al., 2007. However, this latter morphological feature does not allow the specific

Table 1
Measurements (in millimetres) of *S. betulina* back teeth from the doline V1 of Vâ Tche Tchâ valley (latest Middle Pleniglacial; Courtedoux, Ajoie, northwestern Switzerland). Abbreviation: **n**: number of specimens; **Min**: minimum value; **Max**: maximum value; **s.d.**: standard deviation; **L**: length; **W**: width.
Tableau 1
Mesures (en millimètres) de la longueur et de la largeur des dents jugales de *S. betulina* provenant de la doline V1 de la Combe de Vâ Tche Tchâ (Pléniglaciaire moyen terminal ; Courtedoux, Ajoie, Nord-Ouest de la Suisse). Abréviations : **n** : nombre de spécimens ; **Min** : valeur minimale ; **Max** : valeur maximale ; **s.d.** : écart-type ; **L** : longueur ; **W** : largeur.

Tooth	Measurement	*n*	Min	Mean	Max	s.d.
P4	L	12	0.48	0.53	0.60	0.04
	W	12	0.53	0.59	0.68	0.05
M1	L	24	0.95	1.01	1.08	0.03
	W	24	0.88	0.97	1.05	0.05
M2	L	15	0.95	1.03	1.05	0.03
	W	15	0.88	0.91	0.93	0.02
M3	L	8	0.58	0.61	0.65	0.02
	W	8	0.68	0.69	0.73	0.02
m1	L	17	1.05	1.11	1.18	0.04
	W	17	0.73	0.78	0.83	0.04
m2	L	15	1.08	1.11	1.15	0.03
	W	15	0.75	0.80	0.85	0.03
m3	L	9	0.73	0.77	0.80	0.02
	W	9	0.63	0.66	0.70	0.03

determination of the *Sicista* population from Vâ Tche Tchâ. According to Kowalski, 1979, comparison with dental morphometrical data, resulting from many research works (Chaline, 1972; Cserkesz et al., 2009; Döppes and Frank, 1997; Kalthoff et al., 2007; Kowalski, 1979; Popov, 2000; Pucek, 1982a; Pucek, 1982b; Spitzenberger, 2001), allowed to point out that M1, M2, m1, and m2 dimensions of the referred population of Vâ Tche Tchâ and Pleistocene *S. betulina* are larger (notably the length) than those of extant *S. betulina* populations. On the other hand, length measurements tend to overlap those of extant *S. subtilis*, but not width measurements, that are smaller in numerous cases. However, according to Chaline, 1972, it is still very difficult to differentiate these two species from P4, M3, and m3 measurements. The reliability and the contingency of specific determination of *S. betulina* and *S. subtilis* from isolated teeth are discussed below.

5. Discussion

After Pucek, 1982b, it is possible to distinguish *S. betulina* from *S. subtilis* by measuring M1, M2, m1, and m2 length and width. However, after Cserkesz et al., 2009, the M1 size is significant only in 92.0 to 94.6 % of cases. In fact, in 5.4 to 8.0 % of cases, *S. subtilis trizona* (the smallest subspecies of *S. subtilis*) could be confused with *S. betulina*. In addition, as already supposed by Storch, 1994, morphometric data of *S. subtilis* reference population from Pucek, 1982b concern *S. subtilis nordmanni* (Cserkesz et al., 2009), which is one of the larger *S. subtilis* European subspecies. Moreover, Late Pleistocene specimens of *S. betulina* and *S. subtilis* have larger dimensions than those of extant populations (Kowalski, 1979; Popov, 2000). The studies on dental size and morphology of Arvicolinae (Montuire and Brunet-Lecomte, 2004; Nadachowski, 1984) and Muridae (Renaud, 1999) species suggest that the size variability is due to several complex phenomena such as environmental or climatic factors, competition and predation. Following Nadachowski, 1984, the problem of correlation between the size of dentition and the size of body is not fully solved and clear at the level of both individuals and populations. Thus, it does not seem possible, as yet, to relate with confidence dental size variations to Bergman's rule.

According to the morphometric data (molars length and width) of published *S. betulina* and *S. subtilis*, five groups can be constituted: extant *S. betulina* (specimens MHNG 913.003 and MHNG 1855.066 from Natural History Museum of Geneva; Kowalski, 1979; Pucek, 1982a; Spitzenberger, 2001), Late Pleistocene *S. betulina* (Chaline, 1972; Döppes and Frank, 1997; Kowalski, 1979), extant *S. subtilis* 1 (Pucek, 1982b), extant *S. subtilis* 2 (Cserkesz et al., 2009) and Late Pleistocene *S. subtilis* (Kalthoff et al., 2007; Kowalski, 1979; Popov, 2000). The extant *S. subtilis* were voluntarily separated in two groups in order to take into account the presence of the small- and large-sized subspecies. The measurements of the Mahalanobis distance between these five groups (Table 2) put together (no significant difference; $p < 0.05$) referred *Sicista* from Vâ Tche Tchâ and Late Pleistocene *S. betulina*, in particular for M1 and m1. The referred material is also close to extant small-sized *S. subtilis* (SS-A2), but differences are regardless significant. Unfortunately, the lack of data for M2 and m2 did not allow confirming these results.

Ratio diagrams allow graphic comparisons of tooth dimensions. Four reference profiles were realized on the basis of dental measurements of Late Pleistocene and extant *S. betulina* and *S. subtilis*. The superposition of these reference profiles and the one of Vâ Tche Tchâ *Sicista* revealed clearly a similarity between fossil and extant *S. betulina* (Fig. 4), whereas the M1, M2, m1, and m2 widths seem to be the discriminating parameters. The use of this method for taxonomical determination of Late Pleistocene specimens appears to be successful, particularly for teeth M1, M2, m1, and m2. Regarding the teeth P4, M3, and m3, caution is required because of the lack of morphometrical data. From isolated teeth, it seems thus possible to distinguish the Late Pleistocene *S. betulina* from *S. subtilis* on the basis of morphometrical methods. Moreover, the presence of additional spurs on unworn or weakly worn molars represents an additional feature to determinate these two species. Therefore, dental morphology and morphometry of the Vâ Tche Tchâ specimens allowed, with confidence, their attribution to *S. betulina*.

Regarding the palaeoenvironnement, the occurrence of this species is consistent with results obtained from other small and large mammals of the doline fillings of Vâ Tche Tchâ. Based essentially on palaeoecological analyses of the mammal assemblage, the palaeoenvironmental reconstruction should correspond to a relatively humid and open landscape, partially covered by bushes, shrubs and trees (Becker et al., 2009). This mosaic environment, comparable to a bushy steppe with wooded and copse (ecological niche of *S. betulina*) areas, probably developed under temperate rather than cold climatic conditions. These results are close

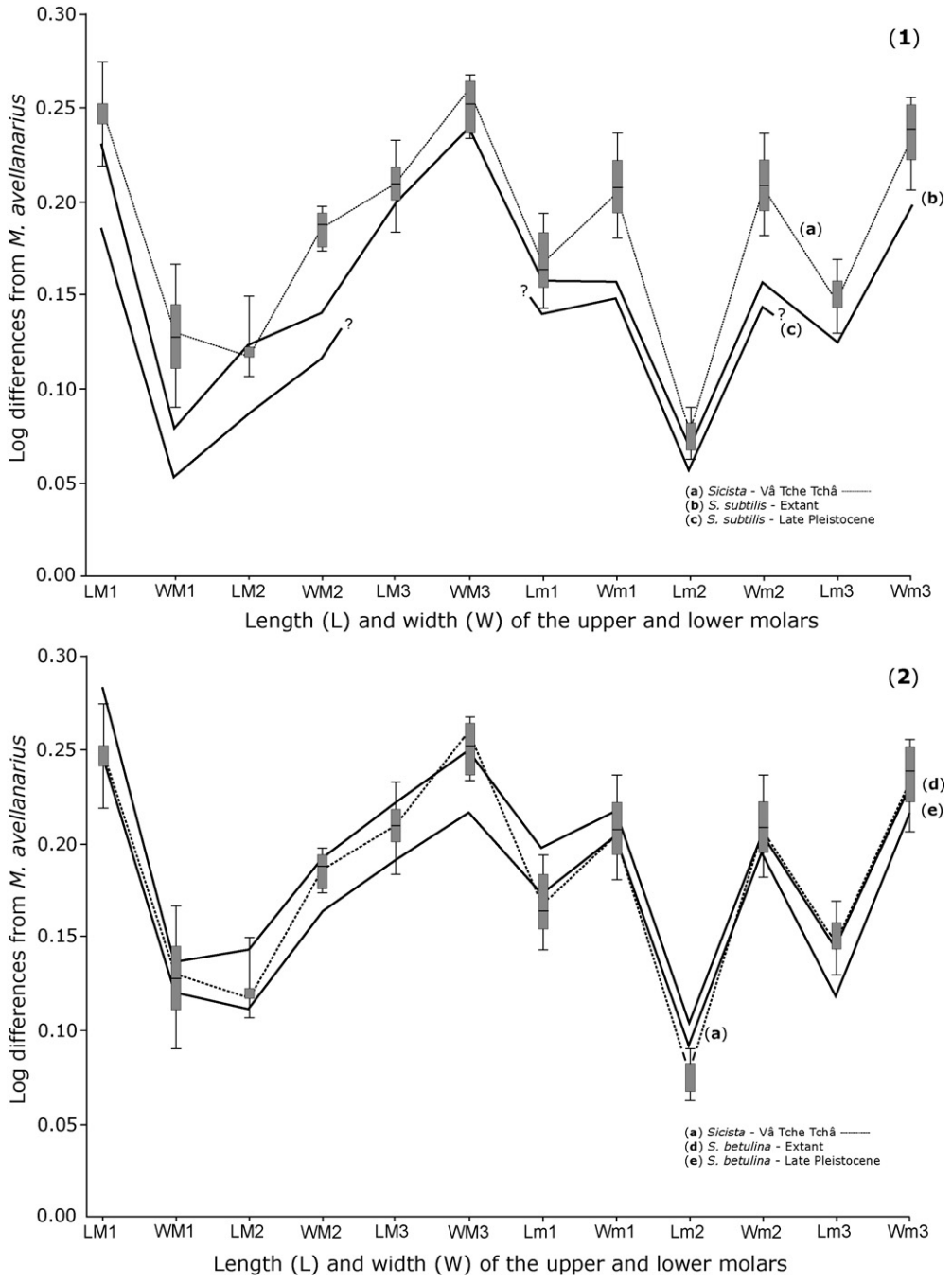

Fig. 4. Ratio diagrams based on (**1**) *S. subtilis* and (**2**) *S. betulina* dental measurements. Mean dental measurements of extant *S. subtilis* are after Pucek, 1982b and Cserkesz et al., 2009, and those of extant *S. betulina* are after Kowalski, 1979, Pucek, 1982a, Spitzenberger, 2001, and two specimens (MHNG 913.003 and MHNG 1855.066) from Natural History Museum of Geneva. Pleistocene data are after Kowalski, 1979, Popov, 2000, and Kalthoff et al., 2007 for *S. subtilis*, and after Chaline, 1972, Kowalski, 1979, and Döppes and Frank, 1997 for *S. betulina*. According to Storch, 1978, dental measurements of *Muscardinus avellanarius* were used as logarithmic scale. Box plots and curve (**a**) represent specimens discovered in the doline V1 from Vâ Tche Tchâ (latest Middle Pleniglacial; Courtedoux, Ajoie, northwestern Switzerland).

Fig. 4. Diagrammes de Simpson basés sur les mesures dentaires de (**1**) *S. subtilis* et (**2**) *S. betulina*. Les mesures dentaires moyennes des populations actuelles sont issues de Pucek, 1982b et Cserkesz et al., 2009 pour *S. subtilis* et de Kowalski, 1979, Pucek, 1982a, Spitzenberger, 2001 et de deux spécimens (MHNG 913.003 et MHNG 1855.066) du Muséum d'histoire naturelle de Genève pour *S. betulina*. Les données du Pléistocène sont extraites de Kowalski, 1979, Popov, 2000 et Kalthoff et al., 2007 pour *S. subtilis* et de Chaline, 1972, Kowalski, 1979 et Döppes and Frank, 1997 pour *S. betulina*. Les mesures dentaires de *Muscardinus avellanarius* de Storch, 1978 ont été utilisées comme base pour l'échelle logarithmique. Les boîtes à moustaches et la courbe (**a**) représentent les spécimens découverts dans la doline V1 de la Combe de Vâ Tche Tchâ (Pléniglaciaire moyen terminal ; Courtedoux, Ajoie, Nord-Ouest de la Suisse).

Table 2
Measurements of Mahalanobis distance, from dental measurements, between data from *Sicista* specimens of the doline V1 of Vâ Tche Tchâ valley (latest Middle Pleniglacial; Courtedoux, Ajoie, northwestern Switzerland) and from specimens of Late Pleistocene and extant *S. betulina* and *S. subtilis*. *P*-value higher than 0.05 allows concluding that there is no significant difference between the two sets of measurements. The presence of a star indicates that the measurement difference is significant. Abbreviations: **VTA**: Vâ Tche Tchâ; **SB-E**: extant *Sicista betulina* (Kowalski, 1979; Pucek, 1982a; Spitzenberger, 2001) and two specimens (MHNG 913.003 and MHNG 1855.066) from Natural History Museum of Geneva; **SB-LP**: Late Pleistocene *Sicista betulina* (Chaline, 1972; Döppes and Frank, 1997; Kowalski, 1979); **SS-E1**: extant *Sicista subtilis* (Pucek, 1982b); **SS-E2**: extant *Sicista subtilis* (Cserkesz et al., 2009); **SS-LP**: Late Pleistocene *Sicista subtilis* (Kalthoff et al., 2007; Kowalski, 1979; Popov, 2000).

Tableau 2
Mesures de la distance de Mahalanobis, à partir des mesures dentaires, entre les données provenant des spécimens de *Sicista* de la doline V1 de la Combe de Vâ Tche Tchâ (Pléniglaciaire moyen terminal ; Courtedoux, Ajoie, Nord-Ouest de la Suisse) et les spécimens du Pléistocène supérieur et actuels de *S. betulina* et *S. subtilis*. Une valeur de *p* supérieure à 0,05 permet de conclure qu'il n'y a pas de différence significative entre les deux séries de mesures. La présence d'une étoile indique que la différence de mesure est significative. Abréviations : **VTA** : Vâ Tche Tchâ ; **SB-E** : *Sicista betulina* actuel (Kowalski, 1979; Pucek, 1982a; Spitzenberger, 2001) et deux spécimens (MHNG 913.003 et MHNG 1855.066) de la collection du Muséum d'histoire naturelle de Genève ; **SB-LP** : *Sicista betulina* Pléistocène supérieur (Chaline, 1972; Döppes and Frank, 1997; Kowalski, 1979) ; **SS-E1** : *Sicista subtilis* actuel (Pucek, 1982b) ; **SS-E2** : *Sicista subtilis* actuel (Cserkesz et al., 2009) ; **SS-LP** : *Sicista subtilis* du Pléistocène supérieur (Kalthoff et al., 2007; Kowalski, 1979; Popov, 2000).

M1	VTA	*p* value		m1	VTA	*p* value	
SB-E	0.3901	< 0.0005	*	SB-E	0.2768	< 0.0005	*
SB-LP	0.1046	0.8040		SB-LP	0.0643	0.4965	
SS-E1	0.4339	< 0.0005	*	SS-E1	0.6402	< 0.0005	*
SS-E2	0.1461	< 0.0005	*	SS-E2	0.1006	0.0445	*
SS-LP	–	–	–	SS-LP	0.6916	< 0.0005	*
M2				m2			
SB-E	0.42340	< 0.0005	*	SB-E	0.4754	< 0.0005	*
SB-LP	–	–	-	SB-LP	–	–	–
SS-E1	1.0120	< 0.0005	*	SS-E1	0.5886	< 0.0005	*
SS-E2	0.2491	< 0.0005	*	SS-E2	–	–	–
SS-LP	1.7070	< 0.0005	*	SS-LP	–	–	–

to those of palynological studies (Drescher-Schneider et al., 2007; Furrer et al., 2007), coleopters (Coope, 2007), and mammoth tooth biogeochemistry (Tütken et al., 2007) of Niederweningen locality (Zürich, Switzerland; ca. 45.5 ka BP (Hajdas et al., 2007)), which is possibly contemporaneous with the Vâ Tche Tchâ locality.

6. Conclusion

For the latest Middle Pleniglacial of Switzerland, the occurrence of a *S. betulina* population with a very high abundance in the doline V1 of Vâ Tche Tchâ is exceptional, and constitutes a new reference population for the Late Pleistocene of western Europe. The morphology as well as the morphometry of isolated molars from Late Pleistocene and extant *S. betulina* and *S. subtilis* allowed us to assign with confidence the studied population to *S. betulina*. It is important to note, that the discovery of this small-sized rodent in Quaternary deposits depends mainly on the screen-washing methodology (notably using sieve-mesh diameters down to 0.25 mm), particularly when the material corresponds to isolated teeth. In fact, the low abundance recorded in the European localities is probably due to a sampling bias, because the smallest sieve-mesh diameter commonly used is 0.5 mm. If populations of *Sicista* are more systematically searched for, then their palaeobiogeographic distribution could be better understood. Finally, new morphometric data should reinforce the results of this study.

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