TAPIRIDAE (PERISSODACTYLA, MAMMALIA) OF THE SWISS MOLASSE BASIN DURING THE OLIGOCENE–MIOCENE TRANSITION

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Abstract—The Tapiridae of the Swiss Molasse Basin from the late Oligocene to the early Miocene are reviewed. Fossil remains that have not previously been described are identified, old descriptions and identifications from previous works are reassessed, and specimens from Switzerland and France are compared, specifically *Protapirus bavaricus* from Ebnat-Kappel (MP28) and Rüfi bei Schänis (MP29), *Protapirus aginensis* from La Milloque (France, MP29), *Protapirus douvillei* from Buchberg 6 (MN4), *Paratapirus helvetius* from Haslen (Switzerland, MP28–30), *Paratapirus intermedius* from Saulcet (France, MN1), Höhronen (MN1), and Brüttelen 1 (MN3a), and *Eotapirus broennimanni* from Wischberg (MN1) and Benken (MN3–4?). These new data enable emended specific diagnoses for *Protapirus bavaricus*, *P. aginensis*, and *P. douvillei*. A late Oligocene (MP28–30) age for the locality of Haslen—the neotype locality of *Paratapirus helvetius*—is also attributed, based upon the literature and personal observations. Furthermore, a new and precise biostratigraphic range of the European Tapiridae at the species level is proposed for the Oligocene and early Miocene of Western Europe. The paleoecology of tapirs and their diversity and evolution through the Oligocene–Miocene transition are discussed and compared with contemporaneous large mammals such as Rhinocerotoidea, Anthracotheriidae, and Suoidea.

INTRODUCTION

Tapirids belong to the tapiroids, a basal perissodactyl group that flourished in the Eocene of Asia and North America (e.g., Prothero and Schoch, 1989; Schoch, 1989). The specific diversity of this lineage decreased drastically after the Oligocene. Today it is represented by only four living species in the monogeneric family Tapiridae Gray, 1821, that are distributed in Central and South America and Southeast Asia (Janis, 1984; Prothero and Schoch, 1989; Schoch, 1989). The Wasatchian genus *Heptodon*, considered by Holbrook (1999) as the earliest known member of the Tapiroidea, suggests that the ancestry of the Tapiridae could be traced back to the early Eocene from North America or Asia. However, *Heptodon* is considered by some authors (e.g., Colbert and Schoch, 1998; Colbert, 1999) as too primitive to be a tapiroid. Eberle (2005) hypothesized an origin from North America based upon the phylogenetically derived biogeographic reconstruction of the oldest and very primitive tapiroids *Helaletes* and *Thuliadanta*. The actual origin of the tapir is thus still in question. The oldest occurrence of Tapiridae is recorded in the early Oligocene of Europe, with the species *Protapirus priscus* in the fillings of Möhren 19 and 20, in Germany (Heissig, 1978, 1999a). Nevertheless, a European origin seems unlikely, given that tapiroids seem to be absent from this continent during the Eocene. The Lophiodontidae—which were predominant in Europe during the Eocene—are no longer considered as Tapiroidea, but as the sister group of Chalicotheriidae (Hooker, 1989).

Despite numerous early analyses (Meyer, 1867; Filhol, 1874, 1877, 1885; Gaudry, 1897; Depéret and Douxami, 1902; Schaub, 1928; Viret, 1929, 1958; von Koenigswald, 1930; Richard, 1938, 1948; Schaub and Hürzeler, 1948; Oettingen-Spielberg, 1952, 1958), the Oligocene and Miocene European fossil record of Tapiridae is very incomplete. The group has a sporadic record in the Oligocene and a limited radiation in the early Miocene. According to Heissig (1999a), the family seems absent after the Proboscidean Datum Event (17 Ma; Tassy, 1989)—excluding the isolated occurrence of *Tapirus telleri* in Göriach (MN6, Austria)—and only showed a short-term occurrence in the earliest late Miocene of Spain (Can Lobaretes, MN9), France (Priay, MN9?), Germany (Eppelsheim, Westhofen, Wissberg, MN9), Austria (Biedermannsdorf, MN9), and Hungary (Rudabanya, MN9; Czákvár, MN10–11). Since the first description by Kaup (1833) of a fossil representative—*Tapirus priscus* from the *Dinotherium* sands of Eppelsheim (late Miocene, MN9, Germany)—the true tapir species have suffered from numerous synonymies and the absence of a precise phylogeny. The most recent study on the systematics of European Tapiridae is by Cerdeño and Ginsburg (1988), who proposed to validate the three well-known genera *Protapirus*, *Paratapirus*, and *Tapirus*. They described a new genus *Eotapirus*, based upon the specimens from Pyrimont-Challonges (early Miocene, MN1, France) and Wischberg (early Miocene, MN1, Switzerland) earlier assigned to *Paratapirus helvetius* by Depéret and Douxami (1902) and *Tapirus broennimanni* by Schaub and Hürzeler (1948), respectively, and ascribed them to *E. broennimanni*. Cerdeño and Ginsburg (1988) also described the new species *E. ruber* from the Phosphorites du Quercy (Oligocene, France) and *Protapirus cetinensis* from Cetina de Aragón and Valquemado (early Miocene, MN2a, Spain). Unfortunately, they did not consider middle and late Miocene records. Only Heissig (1999a) presented the main distribution of the late Miocene *Tapirus priscus* and *T. pannonicus* in his short synthesis of Miocene European tapirs. In the Swiss Molasse Basin, tapirid localities are rare and recorded from only the late Oligocene, probably because the early Oligocene is predominantly marine facies (Berger et al., 2005). In most cases, the recorded material is isolated and fragmentary

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teeth (Aarwangen, MP27; Paudex, MP30; Benken, MN3–4?; Buchberg 6, MN4), fragmentary mandibles (Ebnat-Kappel, MP28; Wischberg, MN1; Höhronen, MN1; Brüttelen 1, MN3a; Würenlos, MN3), and fragmentary maxillae (Ebnat-Kappel, MP28; Rüfi bei Schänis, MP29). Two skulls with complete tooth rows have been discovered in Haslen (MP28–30) by Schaub (1928) and in Wischberg (MN1) by Schaub and Hürzeler (1948).

This study describes the tapir fossils of the Swiss Molasse Basin during the Oligocene–Miocene transition. Emended diagnoses for the species *Protapirus bavaricus*, *P. aginensis*, and *P. douvillei* are proposed. Based on new results and comparisons with the Western European record, a new and precise biostratigraphic range of the tapir species is established and their diversity and evolution are discussed.

GEOLOGICAL SETTING

All of the Swiss localities that contain tapirid fossils (Table 1) occur in the Molasse Basin (North Alpine Foreland Basin): Aarwangen (MP27), Ebnat-Kappel (MP28), Rüfi bei Schänis (MP29), Paudex (MP29), and Haslen (MP28–30) dated to the Chattian (late Oligocene), Wischberg (MN1) and Höhronen (Greit and Sparen) (MN1) dated to the Aquitanian (early Miocene), and Würenlos (MN3), Brüttelen 1 (MN3a), Benken (MN3–4?), and Buchberg 6 (MN4) dated to the Burdigalian (early Miocene) (Fig. 1). The French localities of La Milloque

(MP29; Chattian) and Saulcet (MN1; Aquitanian) are situated in the Aquitaine Basin and the Limagne Graben, respectively (Table 2).

Oligocene Swiss Localities

No tapir fossils have been discovered in the Rupelian of Switzerland (early Oligocene) and all of the Oligocene Swiss localities are dated to the Chattian (late Oligocene). They are precisely biostratigraphically dated (see Table 2 and Fig. 6 for stratigraphic correlations).

Aarwangen (Swiss national grid references 624.025/232.575) is the type locality of the Aarwanger Molasse, an equivalent of the Molasse alsacienne (Picot, 2002; Becker, 2003). It has been dated to the Mammal Biozone MP27 by Engesser and Mayo (1987). Ebnat-Kappel (727.880/235.040) belongs to the Ebnater Schichten and has been dated to the Mammal Biozone MP28 by Engesser and Mödden (1997). Rüfi bei Schänis (722.800/227.550) belongs to the Wintersberg Schichten from the USM (Lower Freshwater Molasse) and has been dated to the Mammal Biozone MP29 by Frei (1979) and Becker (2003). Paudex (541.200/151.720) belongs to the Molasse à Charbon and has been dated to the Mammal Biozone MP29 by Engesser et al. (1984) and Berger (1998).

The locality of Haslen (744–745/249–250) has been the subject of misunderstandings concerning its dating. The tapir remains were found in an isolated sandstone block along the Sitter

TABLE 1. Referred material and housing institutions.

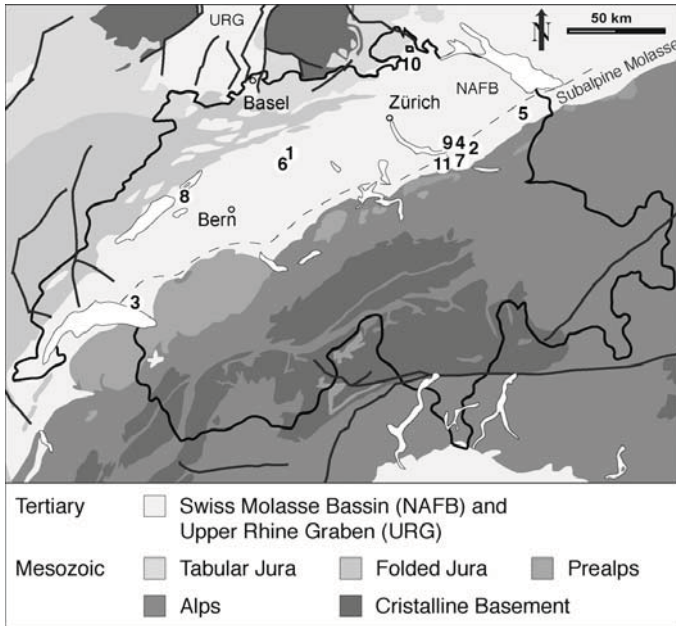| Species	Locality	Country	Anatomy	Inventory number	Direct observation	Housing Institution
Protapirus bavaricus	Ebnat-Kappel	Switzerland	Mandible	EKO-T1	Yes	Private collection U. Oberli
			Fragmentary mandible	EKO-T2	Yes	Private collection U. Oberli
			Fragmentary mandible	EKO-T3	Yes	Private collection U. Oberli
			Fragmentary maxilla	EKO-T4	Yes	Private collection U. Oberli
			Fragmentary maxilla	EKO-T5	Yes	Private collection U. Oberli
			Lower incisor	EKO-T6	Yes	Private collection U. Oberli
	Rüfi bei Schänis	Switzerland	Fragmentary maxilla	A/V79	Yes	PIMUZ
Protapirus aginensis	La Milloque	France	Lower premolar	Lm420	Yes	NMB
			Lower premolar	Lm421	Yes	NMB
			Upper molar	Lm422	Yes	NMB
			Upper molar	Lm1404	Yes	NMB
Protapirus douvillei	Buchberg 6	Switzerland	Upper premolar	A/V690	Yes	PIMUZ
Paratapirus helvetius	Haslen	Switzerland	Skull with maxillae	P1500	Yes	NMSG
			Fragmentary mandible	P1501	Yes	NMSG
Paratapirus intermedius	Höhronen, Greit	Switzerland	Fragmentary mandible	A/V0061	Yes	PIMUZ
			Fragmentary mandible	A/V0063	Yes	PIMUZ
			Fragmentary mandible	A/V64	Yes	PIMUZ
			Fragmentary mandible	A/V0065	Yes	PIMUZ
			Mandible	A/V148	Yes	PIMUZ
			Fragmentary maxilla	A/V64	Yes	PIMUZ
	Höhronen, Sparen	Switzerland	Fragmentary mandible	A/V0062	Yes	PIMUZ
	Brüttelen 1	Switzerland	Fragmentary mandible	501454	Yes	NMBE
			Fragmentary tibia	501453	Yes	NMBE
	Saulcet	France	Fragmentary mandible	Sau2282	Yes	NMB
Eotapirus broennimanni	Wischberg	Switzerland	Upper incisor	D3394	Yes	NMBE
			Fragmentary mandible	D3395	Yes	NMBE
			Juvenile skull with maxillae	As7	Yes	NMB
			Fragmentary mandible	As7	Yes	NMB
			Fragmentary mandible	As7	Yes	NMB
	Benken	Switzerland	Upper premolar	A/V1781	Yes	PIMUZ
			Lower molar	A/V1782	Yes	PIMUZ
			Lower molar	A/V1782	Yes	PIMUZ
			Upper molar	A/V1782	Yes	PIMUZ
Tapiridae indet.	Aarwangen	Switzerland	Upper molar	AW35	Yes	NMB
	Paudex	Switzerland	Fragmentary upper molar	v4108	Yes	MHNG
	Würenlos	Switzerland	Fragmentary mandible	A/V0075	Yes	PIMUZ

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FIGURE 1. Geographic and geological setting of the Swiss Tapiridae localities (modified geological map according to the "Esquisse géologique de la Suisse," Ed. Swisstopo). **1**, Aarwangen; **2**, Ebnat-Kappel; **3**, Paudex; **4**, Rüfi bei Schänis; **5**, Haslen; **6**, Wischberg; **7**, Höhronen; **8**, Brüttelen 1; **9**, Würenlos; **10**, Benken; **11**, Buchberg 6. **Abbreviations**: **NAFB**, North Alpine Foreland Basin; **URG**, Upper Rhine Graben.
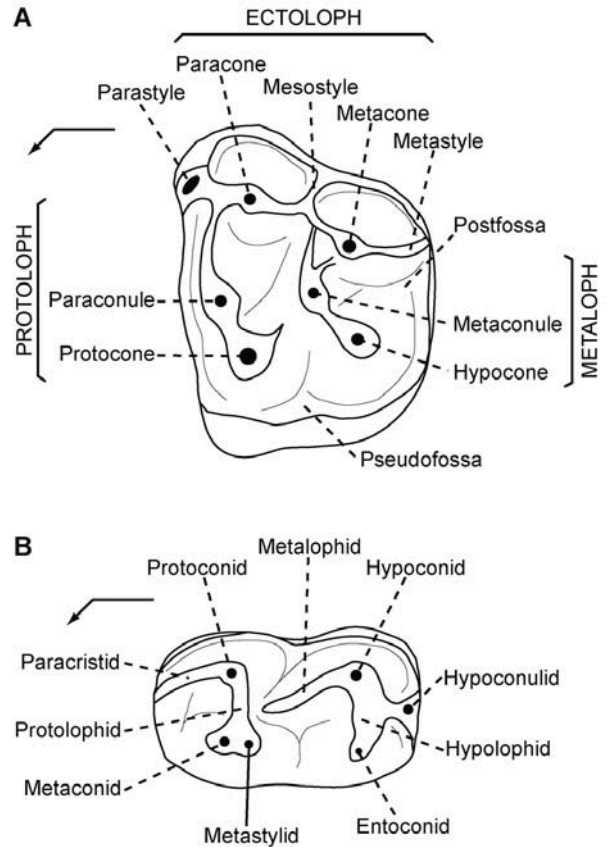

FIGURE 2. Tooth terminology for perissodactyls (modified from Hooker, 1989). **A**, left upper second molar; **B**, right lower second molar. Arrows indicate the mesiolingual side of the teeth.

River, upstream of the Rotbach confluence (Schaub, 1928). The surrounding Kalksandstein Formation is dated to the Chattian (Ludwig et al., 1949). According to Baumberger in Schaub's article on the tapir from Haslen (1928), the block matrix probably also belonged to the Kalksandstein Formation. As there are no such sediments in the OMM (Upper Marine Molasse) of the region, the latter doubtless came from the Chattian outcrop near the village of Haslen. A thin section of the block matrix confirmed this Chattian age, not providing any trace of glauconite nor marine fossils; this sandstone was effectively of fluviatile origin and its belonging to the OMM is, again, excluded. Therefore, a late Chattian (MP28–30) age is the most probable age for this locality. A Burdigalian age, as previously supposed by Cerdeño and Ginsburg (1988), is completely excluded.

Miocene Swiss Localities

Wischberg (624.650/227.630) belongs to the Obere Bunte Mergel from the Aquitanian USM and has been dated to the Mammal Biozone MN1 by Engesser and Mödden (1997). Höhronen (Greit and Sparen) (691.475/223.800 and 692.600/224.175) belongs to the Molasse Grise from the USM and has been dated to the Mammal Biozone MN1 by Engesser and Mödden (1997). Brüttelen 1 (576.800/207.050) belongs to the Sense Schichten from the Burdigalian OMM and has been dated to the Mammal Biozone MN3a by Engesser (1990). Würenlos (669.300/255.720) belongs to the Muschelsandstein Formation from the OMM and is therefore attributed to the Burdigalian (Müller et al., 1984) and probably to the Mammal Biozone MN3. Buchberg 6 (759.210/261.020) belongs to the OSM (Upper Freshwater Molasse) and has been dated by Bolliger (1997) to the Mammal Biozone MN4.

Benken (692.200/278.900) belongs to the St. Galler Schichten from the OMM and the Krokodilen Schichten have been dated to the Mammal Biozones MN3–4 by Bolliger (1992). Neverthe-

less, Engesser (1990) mentioned a reworked fauna from the late Oligocene and the Aquitanian. The species *Eotapirus broennimanni*, as identified at Benken, had so far only been discovered in Wischberg and Pyrimont-Challonges, both dated to the Mammal Biozone MN1. Therefore, the tapir remains from Benken cannot be dated with certainty.

MATERIALS AND METHODS

The referred materials of this study (Table 1) have been partly published in the 19th and 20th centuries (e.g., Meyer, 1867; Schaub, 1928; Schaub and Hürzeler, 1948; Cerdeño and Ginsburg, 1988), but no recent work proposes a complete review. An inventory of the record of European tapirs is presented in Table 2. The private collection of Urs Oberli (St. Gallen) is a non-profit institution and is accessible to all. Visits can be arranged with the Naturhistorisches Museum of St. Gallen.

Taxonomy—The identifications are based upon comparative anatomy, biometric measurements, and the main diagnostic characters reviewed by Cerdeño and Ginsburg (1988). Tooth terminology follows Hooker (1989; Fig. 2). Biometric measurements have an accuracy of 0.5 mm. Length is measured through the ectoloph where the tooth is the longest, width where the tooth is the widest (either through the protoloph or the metaloph), and height (only on unworn or slightly worn teeth) from the base of the crown to the highest cusp (usually the paracone for upper cheek teeth and the protoconid for lower cheek teeth).

TABLE 2. Oligocene and early Miocene European localities recording tapirid fossils, with referred literature.

Species (*type species)	Locality (*type and **neotype locality)	Country	Age	Mammal Zone	References
*Protapirus priscus**	Caylux*	France	Oligocene	—	Filhol, 1874, 1877, 1885; Gaudry, 1897; Zittel, 1894; Depéret and Douxami, 1902; Schaub, 1928; Viret, 1929; von Koenigswald, 1930; Oettingen-Spielberg, 1958; Cerdeño and Ginsburg, 1988
	Möhren 19, 20	Germany	Rupelian	MP21	Heissig, 1978, 1999a
Protapirus bavaricus	Gaimersheim*	Germany	Chattian	MP27	Schaub, 1928; Oettingen-Spielberg, 1952, 1958; Viret, 1958; Cerdeño and Ginsburg, 1988; Schmidt-Kittler et al., 1997
	Ebnat-Kappel	Switzerland	Chattian	MP28	Engesser and Mödden, 1997; Schmidt-Kittler et al., 1997; this study
	Rüfi bei Schänis	Switzerland	Chattian	MP29	Schaub, 1928; Oettingen-Spielberg, 1952, 1958; Frei, 1979; Cerdeño and Ginsburg, 1988; Becker, 2003; this study
Protapirus aginensis	La Milloque*	France	Chattian	MP29	Schaub, 1928; Richard, 1938, 1948; Oettingen-Spielberg, 1958; Cerdeño and Ginsburg, 1988; Schmidt-Kittler et al., 1997; this study
Protapirus douvillei	Saint-Gérand-le-Puy*	France	Aquitanian	MN2a	Filhol, 1885; Gaudry, 1897; Depéret and Douxami, 1902; Schaub, 1928; Viret, 1929; Oettingen-Spielberg, 1958; Cerdeño and Ginsburg, 1988; Heissig, 1999
	Paulhiac	France	Aquitanian	MN1	Schaub, 1928; Oettingen-Spielberg, 1952; Mein, 1989
	Montaigu	France	Aquitanian	MN2a	Schaub, 1928; Oettingen-Spielberg, 1952; Hugueney, 1997
	Fontcaude	France	'mid' Aquitanian	—	Roman, 1919; Cerdeño and Ginsburg, 1988
	Buchberg 6	Switzerland	Burdigalian	MN4	Bolliger, 1997; this study
Protapirus cetinensis	Cetina de Aragon*	Spain	Aquitanian	MN2a	Cerdeño and Morales, 1986; Cerdeño, 1988; Cerdeño and Ginsburg, 1988; Heissig, 1999
	Valquemado	Spain	Aquitanian	MN2a	Cerdeño and Ginsburg, 1988
Protapirus sp.	Espenhain	Germany	Rupelian	MP22	Böhme, 2001
*Paratapirus helvetius**	Othmarsingen*	Switzerland	'late' Chattian	—	Meyer, 1867; Gaudry, 1897; Depéret and Douxami, 1902
	Haslen**	Switzerland	Chattian	MP28-30	Schaub, 1928; Viret, 1929, 1958; Oettingen-Spielberg, 1952; Cerdeño and Ginsburg, 1988; this study
Paratapirus intermedius	Selles-sur-Cher*	France	Aquitanian	MN2b	Filhol, 1885; Zittel, 1894; Depéret and Douxami, 1902; Stehlin, 1909; Schaub, 1928; Oettingen-Spielberg, 1952; Ginsburg and Hugueney, 1980; Cerdeño and Ginsburg, 1988; Heissig, 1999
	Höhronen, Greit	Switzerland	Aquitanian	MN1	Meyer, 1867; Depéret and Douxami, 1902; Engesser and Mödden, 1997; this study
	Höhronen, Sparen	Switzerland	Aquitanian	MN1	Meyer, 1867; Engesser and Mödden, 1997; this study
	Saulcet	France	Aquitanian	MN1	Viret and Hürzeler, 1937; Mein, 1989; this study
	Eggingen-Gemeindesteinbruch	Germany	Aquitanian	MN2	Meyer, 1867; Depéret and Douxami, 1902; von Koenigswald, 1930; Cerdeño and Ginsburg, 1988; Heissig, 1999
	Hessler	Germany	Aquitanian	MN2b	von Koenigswald, 1930; Cerdeño and Ginsburg, 1988; Heissig, 1999
	Budenheim	Germany	Aquitanian	MN2b	von Koenigswald, 1930; Cerdeño and Ginsburg, 1988; Heissig, 1999
	Haslach	Germany	Aquitanian	MN2b	Meyer, 1867; Depéret and Douxami, 1902; von Koenigswald, 1930; Cerdeño and Ginsburg, 1988
	Eselsberg	Germany	Aquitanian	MN2b	Zittel, 1894; von Koenigswald, 1930; Cerdeño and Ginsburg, 1988
	Brux	France	Aquitanian	—	Schlosser, 1910; von Koenigswald, 1930; Cerdeño and Ginsburg, 1988
	Laugnac	France	Aquitanian	MN2b	Viret, 1929; Cerdeño and Ginsburg, 1988; Mein, 1989
	Brüttelen 1	Switzerland	Burdigalian	MN3a	Studer, 1895; Berger, 1985; Engesser, 1990; Kälin, 1997; this study
	Faluns Touraine/Anjou	France	Burdigalian	MN4a	Ginsburg, 1980; Ginsburg et al., 1982; Cerdeño and Ginsburg, 1988
	Eggingen-Mittelhart 3	Germany	Burdigalian	MN4	Sach and Heizmann, 2001
*Eotapirus broennimanni**	Pyrimont-Challonges*	France	Aquitanian	MN1	Depéret and Douxami, 1902; Viret and Hürzeler, 1937; Schaub and Hürzeler, 1948; Cerdeño and Ginsburg, 1988; Mein, 1989; Heissig, 1999
	Wischberg	Switzerland	Aquitanian	MN1	Schaub and Hürzeler, 1948; Cerdeño and Ginsburg, 1988; Engesser and Mödden, 1997; Heissig, 1999; this study
	Benken	Switzerland	Burdigalian?	MN3-4?	Engesser, 1990; Bolliger, 1992; Bolliger, 1997; this study
Eotapirus ruber	Phosphorites du Quercy*	France	Oligocene	—	Cerdeño and Ginsburg, 1988
Tapiridae indet.	Vaumas	France	Oligocene	MP25?	Pomel, 1853; Hugueney, 1997
	Aarwangen	Switzerland	Chattian	MP27	Engesser and Mayo, 1987; this study
	Paudex	Switzerland	Chattian	MP29	Engesser et al., 1984; Berger, 1998; this study
	Würenlos	Switzerland	Burdigalian	MN3	Müller et al., 1984; this study

Biostratigraphy—The biochronological framework is based on the chronological correlations of the Paleogene and Neogene European Land Mammal Zones (MP-Levels and MN-Zones; Mein, 1999; Steininger, 1999; Luterbacher et al., 2004).

Paleoecology—The ecology of the fossil tapir species is extrapolated from the ecology of the associated large-mammal taxa compiled from the literature data (Hellmund, 1991; Fortelius et al., 1996; Becker, 2003; Ginsburg and Chevrier, 2005; B. Mennecart, pers. comm.). The habitats are defined according to the vegetation cover (closed, intermediate, open, not specified) and the relation to water (dry, humid/wet, semi-aquatic, not specified). The ecology of the whole community determines the main paleoecological conditions.

Oligocene–Miocene Transition—The fossil record comprises primarily four large-mammal clades (Tapiridae, Rhinocerotoidea, Anthracotheriidae, Suoidea) of Western Europe in the Oligocene and the early Miocene. The diversity and evolution are based upon FAD (First Appearance Datum) and LAD (Last Appearance Datum) and are compiled from the literature updated with the new tapir data in this paper and personal observations in the Swiss Molasse Basin record.

Institutional Abbreviations—**NMB**, Naturhistorisches Museum Basel (Switzerland); **NMBE**, Naturhistorisches Museum der Burgergemeinde Bern (Switzerland); **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich (Switzerland); **NMSG**, Naturhistorisches Museum Sankt Gallen; **MHNG**, Muséum d'histoire naturelle de Genève.

Anatomical Abbreviations—**I/i**, upper/lower incisor; **C/c**, upper/lower canine; **P/p**, upper/lower premolar; **M/m**, upper/lower molar; **D/d**, upper/lower deciduous tooth.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Suborder TAPIROMORPHA Haeckel, 1866
Infraorder CERATOMORPHA Wood, 1937
Superfamily TAPIROIDEA Gray, 1821
Family TAPIRIDAE Gray, 1821
Genus *PROTAPIRUS* Filhol, 1877

Type Species—*Protapirus priscus* (Filhol, 1874) from the Phosphorites du Quercy, France (Oligocene).

Other Species Referred to the Genus—*P. bavaricus* (Oettingen-Spielberg, 1952), *P. aginensis* (Richard, 1938), *P. cetinensis* Cerdeño and Ginsburg, 1988, *P. douvillei* (Filhol, 1885).

Distribution—Early Oligocene to early Miocene of Europe; late Oligocene of North America (Schoch, 1989).

Diagnosis—Small to medium-sized Tapiridae; un- or weakly molarized upper premolars; lingually convergent protoloph and metaloph on P2, P3, and P4, with protocone and hypocone closing the median valley; skull with incipient proboscis (translation of Cerdeño and Ginsburg, 1988:3).

PROTAPIRUS BAVARICUS (Oettingen-Spielberg, 1952)
(Fig. 3; Table 3)

Type Locality—Gaimersheim bei Ingolstadt, Germany (late Oligocene, MP27).

Synonymy—See Cerdeño and Ginsburg (1988:4) for recent synonymy list.

Distribution—Late Oligocene of Germany and Switzerland (Schaub, 1928; Oettingen-Spielberg, 1952, 1958; Viret, 1958; Cerdeño and Ginsburg, 1988; this study) (Table 2).

Emended Diagnosis—Larger than *Protapirus priscus*; slightly less fused protocone and hypocone on P3 and P4 than in *Protapirus priscus* but more than in *Protapirus aginensis* (translation of Cerdeño and Ginsburg, 1988:5); undeveloped postfossa and absence of lingual pseudofossa on upper premolars.

Referred Specimens—Ebnat-Kappel (Switzerland, MP28; Private collection of Urs Oberli, St. Gallen): incomplete right mandible with p2–m3 (EKO-T1), fragmentary left mandible with m3 (EKO-T2), fragmentary left mandible with m2 (EKO-T3), fragmentary left maxilla with P1–P4 (EKO-T4), fragmentary right maxilla with M1–M3 (EKO-T5), left i1 (EKO-T6); Rüfi bei Schänis (Switzerland, MP29): fragmentary left maxilla with P3–M3 and roots of P1 and P2 (PIMUZ-A/V79).

Description

Upper Dentition—P1 is elongated and triangular, not molarized, with slightly oblique ectoloph. The paracone and metacone are closed, there is a lingual fossa with slightly raised internal wall, a weak parastyle, and no cingula. P2 is subtriangular, not molarized, with slightly oblique ectoloph. The reduced and oblique protoloph and straight metaloph are lingually convergent, and the protocone and hypocone are fused, lingually closing the median valley. The anterior and lingual cingula are not visible (worn tooth), but there is a weak parastyle, a weak continuous posterior cingulum (from the middle of the metacone to the middle of the hypocone), and a subhorizontal and weak posterior labial cingulum around the metacone and joining the posterior cingulum. The postfossa is undeveloped. P3 and P4 are subrectangular, not molarized, with slightly oblique ectoloph. The oblique protoloph and straight metaloph are lingually convergent, and the protocone and hypocone are fused, lingually closing the median valley. There is a weak parastyle, a continuous anterior cingulum (from the parastyle to the middle of the protocone) weak on P3 but slightly developed on P4, a continuous posterior cingulum (from the middle of the metacone to the middle of the hypocone) slightly developed on P3 but developed on P4, an oblique posterior labial cingulum around the metacone and joining the posterior cingulum, weak on P3 but slightly developed on P4, and a short and weak lingual cingulum. The postfossa is undeveloped. M1, M2, and M3 are trapezoidal, with a strongly oblique ectoloph. The reduced and oblique metaloph and lesser oblique protoloph are lingually divergent, and the protocone and hypocone are unfused and well separated, allowing the lingual opening of the median valley. There is a well-developed parastyle on M1 and M2, but strongly developed on M3, a continuous anterior cingulum (from the parastyle to the middle of the protocone) slightly developed on M1 but well developed on M2 and M3, a continuous and developed posterior cingulum (from the middle of the metacone to the middle of the hypocone) on M1 and M2, but short (only at the level of the metacone) and slightly developed on M3, a subhorizontal and slightly developed posterior labial cingulum around the metacone and joining the posterior cingulum, and a short and slightly oblique lingual cingulum, slightly developed on M1 but weak on M2 and M3. The postfossa is undeveloped.

Lower Dentition—p2 is not molarized, with an isolated entoconid (conical entoconid and hypoconid not fused in a hypolophid) and a well-developed paracristid elongated in a paralophid. The cingulids are not visible (worn tooth). p3 and p4 are not molarized, with an isolated entoconid (conical entoconid and hypoconid and not fused in a hypolophid), and a talonid wider than trigonid. The paracristid is developed, and the protolophid is slightly concave. There is a short and weak anterior cingulid on p3 (character not visible on p4), a short and weak posterior cingulid on p3 (character not visible on p4), a short labial cingulid at the level of the median valley weak on p3 but slightly developed on p4, and no lingual cingulid. m1, m2, and m3 have a developed paracristid on m2 and m3 (character not visible on m1), a trigonid wider than talonid, and two subvertical crests on the posterior side of the protolophid. The metastylid is slightly developed, the

TABLE 3. Dental measurements (in mm) of the studied tapir species; range values are in brackets when more than one sample is used for the averaging dimension.

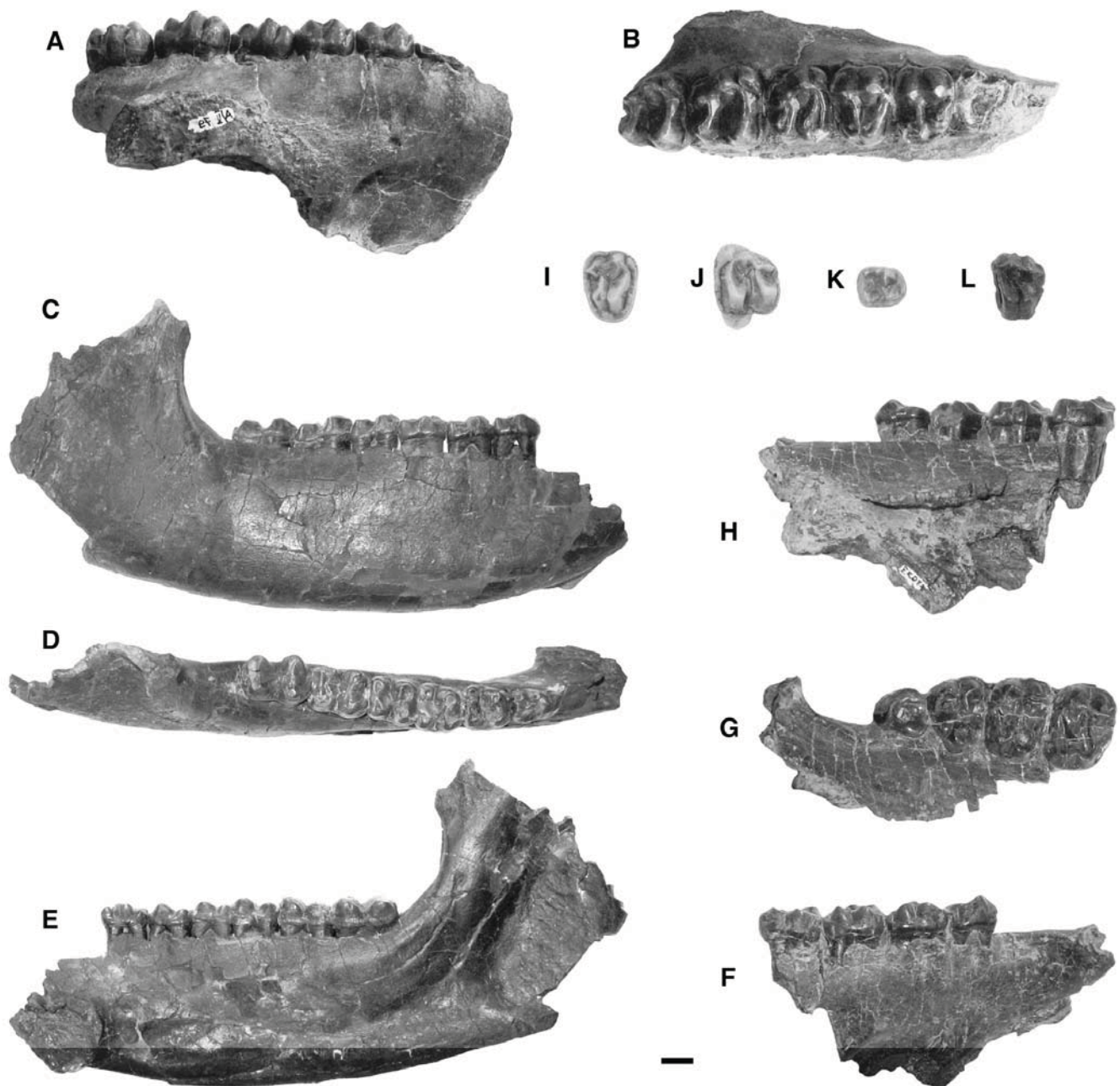| Species	Locality (housing institution-sample number)	Tooth	n	Length	Range value	Width	Range value	Height	Range value
Protapirus bavaricus	Ebnat-Kappel (Oberli-EKO-T1)	p2	1	14.5		9.0		7.5	
	Ebnat-Kappel (Oberli-EKO-T1)	p3	1	13.5		12.5		6.5	
	Ebnat-Kappel (Oberli-EKO-T1)	p4	1	14.0		13.5		6.5	
	Ebnat-Kappel (Oberli-EKO-T1)	m1	1	13.5		13.0		7.5	
	Ebnat-Kappel (Oberli-EKO-T1, EKO-T2)	m2	2	17.8	[16.5–19.0]	13.5	[13.5–13.5]	7.0	[6.5–7.5]
	Ebnat-Kappel (Oberli-EKO-T1, EKO-T2)	m3	2	20.8	[19.5–22.0]	13.8	[13.5–14.0]	7.8	[7.5–8.0]
	Ebnat-Kappel (Oberli-EKO-T4)	P1	1	12.0		11.0		7.0	
	Ebnat-Kappel (Oberli-EKO-T4)	P2	1	14.5		16.0		5.5	
	Ebnat-Kappel (Oberli-EKO-T4)	P3	1	14.5		18.5		6.5	
	Rüfi bei Schänis (PIMUZ-A/V79)	P3	1	14.0		18.5		9.0	
	Ebnat-Kappel (Oberli-EKO-T4)	P4	1	14.0		19.0		7.0	
	Rüfi bei Schänis (PIMUZ-A/V79)	P4	1	14.0		19.0		8.5	
	Ebnat-Kappel (Oberli-EKO-T5)	M1	1	14.5		20.0		6.0.	
	Rüfi bei Schänis (PIMUZ-A/V79)	M1	1	15.0		18.0		7.5	
	Ebnat-Kappel (Oberli-EKO-T5)	M2	1	18.0		21.5		6.0	
	Rüfi bei Schänis (PIMUZ-A/V79)	M2	1	18.5		20.5		8.5	
	Ebnat-Kappel (Oberli-EKO-T5)	M3	1	17.0		19.0		6.0	
	Rüfi bei Schänis (PIMUZ-A/V79)	M3	1	17.5		19.5		11.0	
Protapirus aginensis	La Milloque (NMB-Lm420)	p4	1	16.5		13.5		11.5	
	La Milloque (NMB-Lm421)	P4	1	16.5		21.5		10.0	
	La Milloque (NMB-Lm422, Lm1404)	M2	2	20.3	[20.0–20.5]	21.5	[21.5–21.5]	11.0	[9.0–13.0]
Protapirus douvillei	Buchberg 6 (PIMUZ-A/V690)	P4	1	16.0		20.0		10.0	
Paratapirus helvetius	Haslen (NMSG-P1501)	m1	1	16.5		—		—	
	Haslen (NMSG-P1501)	m2	1	18.5		—		11.0	
	Haslen (NMSG-P1501)	m3	1	19.5		—		11.0	
	Haslen (NMSG-P1500)	P1	2	14.5	[14.5–14.5]	12.5	[12.5–12.5]	9.8	[9.5–10.0]
	Haslen (NMSG-P1500)	P2	2	15.8	[15.5–16.0]	16.5	[16.5–16.5]	10.3	[10.0–10.5]
	Haslen (NMSG-P1500)	P3	2	15.3	[15.0–15.5]	18.5	[18.0–19.0]	9.5	[9.5–9.5]
	Haslen (NMSG-P1500)	P4	1	16.0		19.0		10.0	
	Haslen (NMSG-P1500)	M1	1	17.0		20.0		7.5	
	Haslen (NMSG-P1500)	M2	1	18.0		21.0		9.0	
	Haslen (NMSG-P1500)	M3	1	20.0		22.0		14.5	
Paratapirus intermedius	Höhronen, Greit (PIMUZ-A/V148)	p2	2	17.3	[17.0–17.5]	10.5	[10.5–10.5]	8.0	[8.0–8.0]
	Saulcet (NMB-Sau2282)	p2	1	16.0		12.5		13.0	
	Höhronen, Greit (PIMUZ-A/V0063-0065)	p3	5	15.5	[14.5–17.5]	13.1	[12.5–13.5]	9.6	[8.5–11.5]
	Höhronen, Sparen (PIMUZ-A/V0062)	p3	1	14.0		13.5		8.0	
	Saulcet (NMB-Sau2282)	p3	1	17.0		14.0		11.5	
	Höhronen, Greit (PIMUZ-A/V0064-65, 148)	p4	4	15.6	[15.0–17.0]	13.8	[13.0–15.0]	9.4	[8.5–11.5]
	Höhronen, Sparen (PIMUZ-A/V0062)	p4	1	15.0		15.0		8.5	
	Saulcet (NMB-Sau2282)	p4	1	19.0		13.0		10.0	
	Höhronen, Greit (PIMUZ-A/V0061, 65, 148)	m1	4	17.0	[15.0–19.5]	13.9	[13.5–14.5]	8.5	[7.0–10.5]
	Höhronen, Sparen (PIMUZ-A/V0062)	m1	1	17.5		15.5		8.5	
	Saulcet (NMB-Sau2282)	m1	1	20.0		14.5		9.0	
	Brüttelen (NMBE-5014554)	m1	1	19.5		13.5		8.5	
	Höhronen, Greit (PIMUZ-A/V0061, 148)	m2	3	19.3	[17.0–20.5]	15.5	[15.0–16.0]	9.5	[7.5–11.5]
	Brüttelen (NMBE-5014554)	m2	1	21.0		13.5		9.0	
	Höhronen, Greit (PIMUZ-A/V64)	M1	1	18.0		22.0		10.0	
	Höhronen, Greit (PIMUZ-A/V64)	M2	1	20.5		23.5		12.5	
Eotapirus broennimanni	Wischberg (NMBE-D3395)	p2	1	16.5		11.0		9.5	
	Wischberg (NMBE-D3395, NMB-As7)	p3	2	16.8	[16.5–17.0]	12.3	[11.0–13.5]	7.8	[7.5–8.0]
	Wischberg (NMBE-D3395, NMB-As7)	p4	2	17.3	[17.0–17.5]	12.5	[11.0–14.0]	8.8	[8.5–9.0]
	Benken (PIMUZ-A/V1782)	m1	1	17.5		13.0		9.0	
	Benken (PIMUZ-A/V1782)	m3	1	19.5		14.5		9.0	
	Wischberg (NMB-As7)	P1	2	13.8	[13.5–14.0]	12.3	[12.0–12.5]	7.3	[6.5–8.0]
	Wischberg (NMB-As7)	P2	2	16.5	[16.0–17.0]	15.8	[15.5–16.0]	7.3	[7.0–7.5]
	Benken (PIMUZ-A/V1781)	P2	1	16.5		15.5		7.5	
	Wischberg (NMB-As7)	P3	2	16.0	[15.5–16.5]	15.0	[15.0–15.0]	7.5	[7.5–7.5]
	Wischberg (NMB-As7)	P4	2	17.3	[17.0–17.5]	17.8	[17.5–18.0]	8.0	[8.0–8.0]
	Wischberg (NMB-As7)	M1	1	18.0		19.5		8.5	
	Benken (PIMUZ-A/V1782)	M1	1	17.5		19.5		12.0	

FIGURE 3. Tooth remains of *Protapirus bavaricus*, *P. aginensis*, and *P. douvillei*. **A**, left maxilla of *P. bavaricus* from Rüfi bei Schänis (PIMUZ-A/V79), labial view; **B**, same in occlusal view; **C**, right mandible of *P. bavaricus* from Ebnat-Kappel (EKO-T1), labial view; **D**, same in occlusal view; **E**, same in lingual view; **F**, left maxilla of *P. bavaricus* from Ebnat-Kappel (EKO-T4), labial view; **G**, same in occlusal view; **H**, same in lingual view; **I**, left P4 of *P. aginensis* from La Milloque (NMB-Lm421), occlusal view; **J**, left M2 of *P. aginensis* from La Milloque (NMB-Lm1404), occlusal view; **K**, left p4 of *P. aginensis* from La Milloque (NMB-Lm420), occlusal view; **L**, left P4 of *P. douvillei* from Buchberg 6 (PIMUZ-A/V690), occlusal view. Scale bar equals 1 cm.

protolophid is concave on m1 but straight on m2 and m3, and the hypolophid is straight. There is a short and slightly developed anterior cingulid on m2 (character not visible on m1 and m3), a short posterior cingulid slightly developed on m1 but developed on m2 and m3, a short labial cingulid at the level of the median valley, slightly developed on m1 but weak on m2 and m3 but no lingual cingulid.

Discussion

The comparison of the maxilla of Rüfi bei Schänis with the two fragmentary maxillae of Ebnat-Kappel indicates that the three specimens share the same diagnostic characters: the premolars are not molarized; the protocone and hypocone are strongly fused, closing the median valley; and the protoloph and metaloph

are lingually convergent and not subparallel. These specimens also differ from the type species *Protapirus aginensis* of La Milloque (see further descriptions) with less developed parastyles, cingula, and postfossae, the absence of a lingual pseudofossa, and consequently smaller general size. All of these reasons support the assignment of the specimens from Ebnat-Kappel and Rüfi bei Schänis to *Protapirus bavaricus*.

Cerdeño and Ginsburg (1988) ascribed the left maxilla from Rüfi bei Schänis to the species *Protapirus bavaricus*. According to these authors, the two late Oligocene species of *Protapirus*, *P. bavaricus* and *P. aginensis*, can be distinguished by the relative space between the protocone and the metacone; *Protapirus bavaricus* is a transitional species between *P. priscus* and *P. aginensis*, with P3 and P4 protocones and hypocones more fused in *P. bavaricus* than in *P. aginensis*. Nevertheless, this distinction is not always evident, and the respective diagnoses need to be specified.

PROTAPIRUS AGINENSIS (Richard, 1938)
(Fig. 3; Table 3)

Type Locality—La Milloque, France (late Oligocene, MP29).
Synonymy—See Cerdeño and Ginsburg (1988:5) for recent synonymy list.
Distribution—Late Oligocene of France (Schaub, 1928; Richard, 1938, 1948; Cerdeño and Ginsburg, 1988) (Table 2).
Emended Diagnosis—Similar in size to *Protapirus bavaricus*; less fused protocone and metacone on P3 and P4; less broad P2; stockier anterior part of the lower premolars (translation of Cerdeño and Ginsburg, 1988:5); well-developed postfossa and presence of a lingual pseudofossa on upper premolars.
Referred Specimens—La Milloque (France, MP29): type locality of the species; left p4 (NMB-Lm420), right P4 (NMB-Lm421), two left M2s (NMB-Lm422, NMB-Lm1404).

Description

Upper Dentition—P4 is subrectangular, not molarized, with oblique ectoloph. The oblique protoloph and straight metaloph are lingually convergent, and the protocone and metacone are fused, lingually closing the median valley. There is a developed parastyle, a continuous and developed anterior cingulum (from the parastyle to the middle of the protocone), a continuous and well-developed posterior cingulum (from the middle of the metacone to the middle of the hypocone), an almost continuous and developed labial cingulum only lacking at the level of the paracone, and a short and developed lingual cingulum closing a small pseudofossa. The postfossa is well developed. M2 is trapezoidal, with strongly oblique ectoloph. The reduced and oblique metaloph and straight protoloph are lingually divergent, and the protocone and hypocone are unfused and well separated, allowing the lingual opening of the median valley. There is a strong parastyle, a continuous and developed anterior cingulum (from the parastyle to the middle of the protocone), a continuous and slightly developed posterior cingulum (from the middle of the metacone to the middle of the hypocone), a subhorizontal and slightly developed posterior labial cingulum around the metacone and joining the posterior cingulum, and a short and slightly developed lingual cingulum closing a pseudofossa. The postfossa is slightly developed.

Lower Dentition—p4 is not molarized, with an isolated entoconid (conical entoconid and hypoconid not fused in a hypolophid), and a wider talonid than trigonid. The paracristid is developed, and the protolophid is slightly concave, with two subvertical crests on its posterior side. The metastylid is developed in an accessory cusp. There is a short and slightly developed anterior cingulid, a short, oblique, and developed posterior cingulid, a short and weak labial cingulid at the level of the median valley, but no lingual cingulid.

Discussion

The tapir fossils of La Milloque are described as the type species *Protapirus aginensis* (Oettingen-Spielberg, 1952; Cerdeño and Ginsburg, 1988). The characters of the upper dentition, such as the unmolarized premolars with fused protocone and hypocone and lingually convergent protoloph and metaloph closing the median valley, support assignment to the genus *Protapirus*. The attribution to *Protapirus aginensis* is attested by well-developed parastyles, cingula, and postfossae, the presence of a lingual pseudofossa, and a larger size than *P. bavaricus*.

PROTAPIRUS DOUVILLEI (Filhol, 1885)
(Fig. 3; Table 3)

Type Locality—Saint-Gérand-le-Puy, France (early Miocene, MN2a).
Synonymy—See Cerdeño and Ginsburg (1988:8–9) for recent synonymy list.
Distribution—Early Miocene of France (Filhol, 1885; Gaudry, 1897; Depéret and Douxami, 1902; Roman, 1919; Schaub, 1928; Viret, 1929; Cerdeño and Ginsburg, 1988; Heissig, 1999a) and Switzerland (this study) (Table 2).
Emended Diagnosis—Larger than *Protapirus priscus*; more separated protocone and metacone on P3 and P4 but as fused as in *Protapirus priscus*; no lingual cingulum and highly reduced labial cingula on the upper premolars; narrow P2 and P3; thinned protoloph on P2 (translation of Cerdeño and Ginsburg, 1988:9); developed postfossa and absence of lingual pseudofossa on upper premolars.
Referred Specimens—Buchberg 6 (Switzerland, MN4): left P4 (PIMUZ-A/V690).

Description

Upper Dentition—P4 is subrectangular, not molarized, with oblique ectoloph. The oblique protoloph and straight metaloph are lingually convergent, and the protocone and hypocone are fused, closing the median valley. There is a weak parastyle, a continuous and developed anterior cingulum (from the parastyle to the middle of the protocone), a continuous and slightly developed posterior cingulum (from the middle of the metacone to the front of the hypocone), but no labial nor lingual cingula. The postfossa is developed.

Discussion

This upper premolar shares the characteristics of the genus *Protapirus*: unmolarized premolar with lingually convergent protoloph and metaloph and fused protocone and hypocone closing the median valley. Moreover, the absence of lingual and labial cingula allows its attribution to the species *Protapirus douvillei*. Further observations confirm the differentiation of this specimen from the other species *Protapirus bavaricus* and *Protapirus aginensis* (such as a better-developed postfossa than on *P. bavaricus*, but not as well-developed as on *P. aginensis*, and less developed anterior and posterior cingula than on *P. aginensis*).

Genus *PARATAPIRUS* Depéret and Douxami, 1902

Neotype Species—*Paratapirus helvetius* (Meyer, 1867) from Haslen, Switzerland (late Oligocene, MP28–30).
Other Species Referred to the Genus—*P. intermedius* (Filhol, 1885).
Distribution—Late Oligocene to early Miocene of Europe.
Diagnosis—Medium-sized Tapiridae; square, molarized P2; rectangular P3 and P4 with subparallel and separated protoloph and metaloph and unfused protocone and hypocone, allowing the lingual opening of the median valley (translation of Cerdeño and Ginsburg 1988:10).

PARATAPIRUS HELVETIUS (Meyer, 1867)
(Fig. 4; Table 3)

Neotype Locality—Haslen, Switzerland (late Oligocene, MP28–30).

Synonymy—See Cerdeño and Ginsburg (1988:10) for recent synonymy list.

Distribution—Late Oligocene of Switzerland (Meyer, 1867; Depéret and Douxami, 1902; Schaub, 1928; Viret, 1929, 1958; Cerdeño and Ginsburg, 1988) (Table 2).

Diagnosis—*Paratapirus* with primitive characters; straight and parallel protoloph and metaloph on P3 and P4 (translation of Cerdeño and Ginsburg, 1988:10).

Referred Specimens—Haslen (Switzerland, MP28–30): skull with complete left and right tooth row (NMSG-P1500), right mandible with m1–m3 (NMSG-P1501).

Description

Skull—The partially complete skull lacks the occipital region and the posterior part of the zygomatic arches and bears the complete left and right tooth rows, with broken left P4–M3, left and right I1–I2, right I3, and left and right C. In lateral view, the anterior part of the nasal bones reaches the level of P1, the bottom of the nasal notch is situated between M1 and M2, the anterior part of the orbitotemporal fossa reaches the level of M1, the suborbital process of the orbitotemporal fossa is situated between M2 and M3, and the postorbital process is situated posterior to M3. In vertical view, the nasal bones form an acute anterior point, and the intermaxiliar bones are not drawn aside. In basal view, the intermaxiliar bones are fused anteriorly, as well as fused posteriorly before P1, with a small and lengthened incisor notch (from the middle of I3 to the middle of the C–P1 diastema). There is at least one pair of palatine foramina situated 8 mm anteriorly to the palatine notch, which is situated at the level of M2.

Upper Dentition—I1, I2, and I3 increase in size from I1 to I3, with a well-developed I3 that functionally substitutes for the canine. C is small, with a rounded section. P1 is elongated and triangular, not molarized, with a straight ectoloph. The paracone and metacone are close, and there is a lingual fossa with slightly raised internal wall bearing the protocone and hypocone. The parastyle is weak, and there is a weak but true metastyle. There is a slightly developed posterior cingulum and a slightly developed lingual cingulum. P2 is subquadratic, not molarized, with a slightly oblique ectoloph. The slightly reduced and oblique protoloph and straight metaloph are lingually convergent, and the protocone and hypocone are fused, closing the median valley. The parastyle is weak. There is a continuous and weak anterior cingulum (from the parastyle to the middle of the protocone), a continuous and developed posterior cingulum (from the metacone to the middle of the hypocone), and a continuous and slightly developed lingual cingulum, but no labial cingulum. The postfossa is undeveloped. P3 and P4 are subrectangular, not molarized, with straight ectoloph. The protoloph and metaloph are subparallel and of same length, and the protocone and hypocone are fused, closing the median valley. The parastyle is weak. There is a continuous and weak anterior cingulum (from the parastyle to the middle of the protocone), a continuous and developed posterior cingulum (from the metacone to the middle of the hypocone), a short lingual cingulum slightly developed on P3 but weak on P4, but no labial cingulum. The postfossa is undeveloped. M1, M2, and M3 are trapezoidal, with oblique ectoloph. The highly reduced and oblique metaloph and straight protoloph are lingually divergent, and the protocone and hypocone are well separated, allowing the lingual opening of the median valley. The parastyle is weak on M1 but well developed on M2 and M3. There is a continuous and slightly developed anterior cingulum (from the parastyle to the middle of the metacone), a continu-

ous and slightly developed posterior cingulum (from the metacone to the middle of the hypocone), a short and weak lingual cingulum, but no labial cingulum. The postfossa is slightly developed.

Mandible—The fragmentary right mandible bears the m1–m3 that are broken in two and lack the labial part of each one. The m1 is only a fragment bearing the protoconid. The mandible is not yet fully prepared. No morphological characters can be observed because of the bad preservation of this mandible, but biometrical measurements have been done.

Discussion

The P2 is molarized and square, whereas P3 and P4 are rectangular with parallel protoloph and metaloph, which characterizes the genus *Paratapirus*. The assignment to *Paratapirus helvetius* is supported by the primitive character of fused protocone and hypocone closing the median valley on the premolars. This skull has already been ascribed to the species *Paratapirus helvetius* by Schaub (1928) and Cerdeño and Ginsburg (1988). Meyer (1867) described a skull and a mandible from Othmarsingen (late Oligocene, Switzerland) as the type species *Paratapirus helvetius*. Unfortunately, this skull was missing the cheek teeth—broken at the level of the roots—and later the mandible disappeared from the collections. After the discovery of the tapir skull from Haslen with a complete tooth row and a right mandible, Schaub (1928) designated them as the neotype of *Paratapirus helvetius*.

PARATAPIRUS INTERMEDIUS (Filhol, 1885)
(Fig. 4; Table 3)

Type Locality—Selles-sur-Cher, France (early Miocene, MN2b).

Synonymy—See Cerdeño and Ginsburg (1988:11) for recent synonymy list.

Distribution—Early Miocene of France, Germany, and Switzerland (Filhol, 1885; Zittel, 1894; Depéret and Douxami, 1902; Stehlin, 1909; Schlosser, 1910; Schaub, 1928; Viret, 1929; von Koenigswald, 1930; Ginsburg, 1980; Ginsburg and Hugueney, 1980; Ginsburg et al., 1982; Cerdeño and Ginsburg, 1988; Heissig, 1999a; this study) (Table 2).

Diagnosis—*Paratapirus* with well-molarized P2; subrectangular P2, P3, and P4; P3 and P4 slightly longer than in *Paratapirus helvetius*; slightly lingually convergent protoloph and metaloph on P3; parallel or slightly convergent protoloph and metaloph on P4 (translation of Cerdeño and Ginsburg, 1988:11).

Referred Specimens—Greit, Höhronen (Switzerland, MN1): fragmentary right mandible with m1–m2 (PIMUZ-A/V0061), fragmentary left mandible with p2 broken and p3 (PIMUZ-A/V0063), fragmentary left mandible with p3–p4 (PIMUZ-A/V64), fragmentary right mandible (cast) with p3–p4 (PIMUZ-A/V0065), incomplete mandible with left c–m3 and right p2–m3 (PIMUZ-A/V148), fragmentary left maxilla with M1–M2 (PIMUZ-A/V64); Sparen am Höhronen (Switzerland, MN1): fragmentary right mandible with m1–m3 (PIMUZ-A/V0062); Brüttelen 1 (Switzerland, MN3a): fragmentary left mandible with broken m2–m3 (NMBE-5014554), fragmentary left tibia (NMBE-5014553); Saulcet (France, MN1): fragmentary left subadult mandible with p3–m3 (NMB-Sau2282).

Description

Upper Dentition—M1 and M2 are trapezoidal, with oblique ectoloph on M1 and strongly oblique on M2. The reduced and oblique metaloph and straight protoloph are lingually divergent, and the protocone and hypocone are unfused and well separated, allowing the lingual opening of the median valley. The parastyle is well developed. There is a continuous and developed anterior cingulum (from the parastyle to the middle of the protocone),

FIGURE 4. Tooth remains of *Paratapirus intermedius* and *P. helvetius*. **A**, left mandible of *P. intermedius* from Brüttelen 1 (NMBE-5014554), labial view; **B**, same in occlusal view; **C**, same in lingual view; **D**, right mandible of *P. intermedius* from Höhronen (PIMUZ-A/V0061), labial view; **E**, same in occlusal view; **F**, same in lingual view; **G**, left maxilla of *P. intermedius* from Höhronen (PIMUZ-A/V64), occlusal view; **H**, mandible of *P. intermedius* from Höhronen (PIMUZ-A/V148), lateral view; **I**, same in occlusal view; **J**, subadult left mandible of *P. intermedius* from Saulcet (NMB-Sau2282), labial view; **K**, same in lingual view; **L**, same in occlusal view; **M**, skull of *P. helvetius* from Haslen (NMSG-P1500), basal view; **N**, same in lateral view. Scale bar equals 1 cm.

a short and slightly developed lingual posterior cingulum on M2 (not visible on M1), a slightly developed posterior labial cingulum around the metacone subhorizontal on M1 and oblique on M2, and a short and slightly developed lingual cingulum. The post-fossa is undeveloped on M1 but slightly developed on M2.

Lower Dentition—p2 is not molarized, with an isolated entoconid (conical entoconid and hypoconid not fused in a hypolophid). The paracristid is well developed and elongated in a paralophid. The posterior cingulid is not visible. There is a short and weak labial cingulid at the level of the median valley, but no anterior nor lingual cingulids. p3 and p4 are not molarized, with an isolated entoconid (conical entoconid and hypoconid not fused in a hypolophid), and a wider talonid than trigonid. The paracristid is developed. The protolophid is concave on p3 but slightly concave on p4, and there are three subvertical crests on its posterior side on p3 but only two on p4. The metastylid is developed. There is a short and weak anterior cingulid, a short and slightly developed posterior cingulid, a short and weak labial cingulid at the level of the median valley, but no lingual cingulid. m1, m2, and m3 have a wider trigonid than talonid. The paracristid is slightly developed on m1 and m2 but developed on m3. The protolophid is slightly concave on m1 but straight on m2 and m3, with two subvertical crests on its posterior side. The metastylid is slightly developed. The hypolophid is straight, but without vertical crests on its posterior side. There is a short and weak anterior cingulid on m1 but slightly developed on m2 and m3 around the protoconid, a short and slightly developed posterior cingulid on m1 and m3 but developed on m2, but no labial nor lingual cingulids.

Discussion

The determination of a tapir species with only lower dentitions and upper molars is highly problematic. The tapir species and genera are determined with respect to the upper premolars, because there are no distinguishing characters present on the lower dentition. No remarkable morphological characters could be observed on the specimens from Höhronen (Greit and Sparen), Brüttelen 1, and Saulcet, except for the very large size of the individuals. The genera *Protapirus* and *Eotapirus* are rather small tapirids and only the genera *Paratapirus* and *Tapirus* can reach such dimensions (see Table 3 for the dimensions of *Paratapirus intermedius*). The genus *Tapirus* can be excluded with certainty because of biostratigraphic aspects, because this genus appeared in Europe only in MN9. Studer (1895) described the specimen of Brüttelen 1 as *Tapirus helvetius*—synonym of *Paratapirus helvetius*. We disagree with him because of the larger size of our specimens (around 8% larger than the average size of *Paratapirus helvetius*), which have the same dimensions as the specimens from Höhronen and Saulcet (Table 3). According to Schaub (1928), the specimens from Höhronen, Brüttelen 1, and Saulcet are attributed to *Paratapirus intermedius*, which is the derived form of the small primitive *Paratapirus helvetius*.

EOTAPIRUS Cerdeño and Ginsburg, 1988

Type Species—*Eotapirus broennimanni* (Schaub and Hürzeler, 1948).

Type Locality—Pyrimont-Challonges, France (Aquitanian, MN1).

Other Species Referred to the Genus—*E. ruber* Cerdeño and Ginsburg, 1988.

Distribution—Oligocene to early Miocene of Europe.

Diagnosis—Small-sized Tapiridae; triangular P2 with weakly developed protoloph; subquadratic and highly molarized P3 and P4 with well-separated protocone and hypocone (translation of Cerdeño and Ginsburg, 1988:14).

EOTAPIRUS BROENNIMANNI (Schaub and Hürzeler, 1948)
(Fig. 5; Table 3)

Type Locality—Pyrimont-Challonges, France (early Miocene, MN1).

Synonymy—See Cerdeño and Ginsburg (1988:14) for recent synonymy list.

Distribution—Early Miocene of France and Switzerland (Depéret and Douxami, 1902; Viret and Hürzeler, 1937; Schaub and Hürzeler, 1948; Cerdeño and Ginsburg, 1988; Heissig, 1999a) (Table 2).

Diagnosis—Small-sized Tapiridae; triangular P2 with weakly developed protoloph; subquadratic and highly molarized P3 and P4 with well-separated protocone and hypocone (translation of Cerdeño and Ginsburg, 1988:14).

Referred Specimens—Wischberg (Switzerland, MN1): juvenile skull with left P1–M1 and right P1–DP4 (NMB-As7), fragmentary left juvenile mandible with dp3–dp4 (NMB-As7), fragmentary right juvenile mandible with m1 (NMB-As7), fragmentary right mandible with p2–p4 (NMBE-D3395), left I1 (NMBE-D3394); Benken (MN3–4?): right P2 (PIMUZ-A/V1781), left M1 (PIMUZ-A/V1782), left m1 (PIMUZ-A/V1782), left m3 (PIMUZ-A/V1782).

Description

Upper Deciduous Dentition—DP4 is subquadratic, well molarized, with oblique ectoloph. The slightly reduced but straight metaloph is parallel to the straight protoloph, and the protocone and hypocone are unfused and well separated, allowing the lingual opening of the median valley. The parastyle is well developed. There is a continuous and slightly developed anterior cingulum 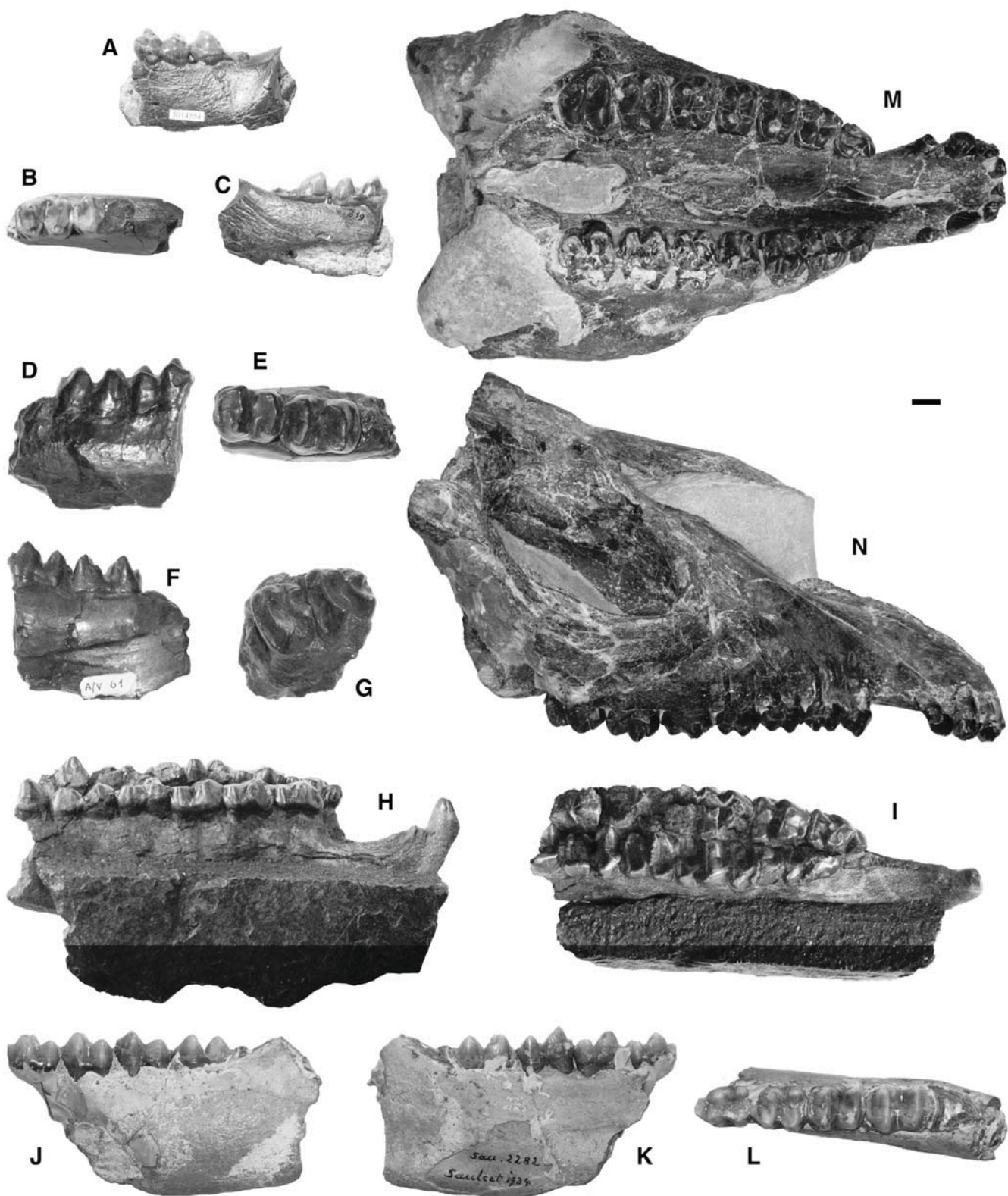(from the parastyle to the middle of the protocone), a continuous and weak posterior cingulum (from the metacone to the middle of the hypocone), a subhorizontal and developed posterior labial cingulum around the metacone and joining the posterior cingulum, and a short and weak lingual cingulum. The postfossa is undeveloped.

Upper Adult Dentition—P1 is elongated and triangular, not molarized, with straight ectoloph. The paracone and metacone are close, and there is a lingual fossa with slightly raised internal wall bearing the protocone and hypocone. The parastyle is slightly developed. There is a weak but true metastyle, but no cingula. P2 is subtriangular, almost molarized, with straight ectoloph. The reduced and slightly oblique protoloph and straight metaloph are lingually convergent, and the protocone and hypocone are unfused and well separated, allowing the lingual opening of the median valley. The parastyle is well developed. There is a continuous and weak anterior cingulum (from the parastyle to the middle of the protocone), a continuous and slightly developed posterior cingulum (from the metacone to the middle of the hypocone), a subhorizontal and slightly developed posterior labial cingulum around the metacone and joining the posterior cingulum, and a short and weak lingual cingulum. The postfossa is undeveloped. P3 is subquadratic, well molarized, with slightly oblique ectoloph. The protoloph and metaloph are subparallel and of same length, and the protocone and metacone are unfused and well separated, allowing the lingual opening of the median valley. The parastyle is well developed. There is a continuous and slightly developed anterior cingulum (from the parastyle to the middle of the protocone), a continuous and slightly developed posterior cingulum (from the metacone to the middle of the hypocone), a subhorizontal and developed posterior labial cingulum around the metacone and joining the posterior cingulum, but no lingual cingulum. The postfossa is undeveloped. M1 is trapezoidal, with oblique ectoloph. The highly reduced but straight metaloph is parallel to the straight protoloph, and the protocone and hypocone are unfused and well separated, allowing the lingual opening of the median valley. The parastyle is strong. There is a continuous and slightly developed anterior cingulum (from the parastyle to the middle of the protocone), a
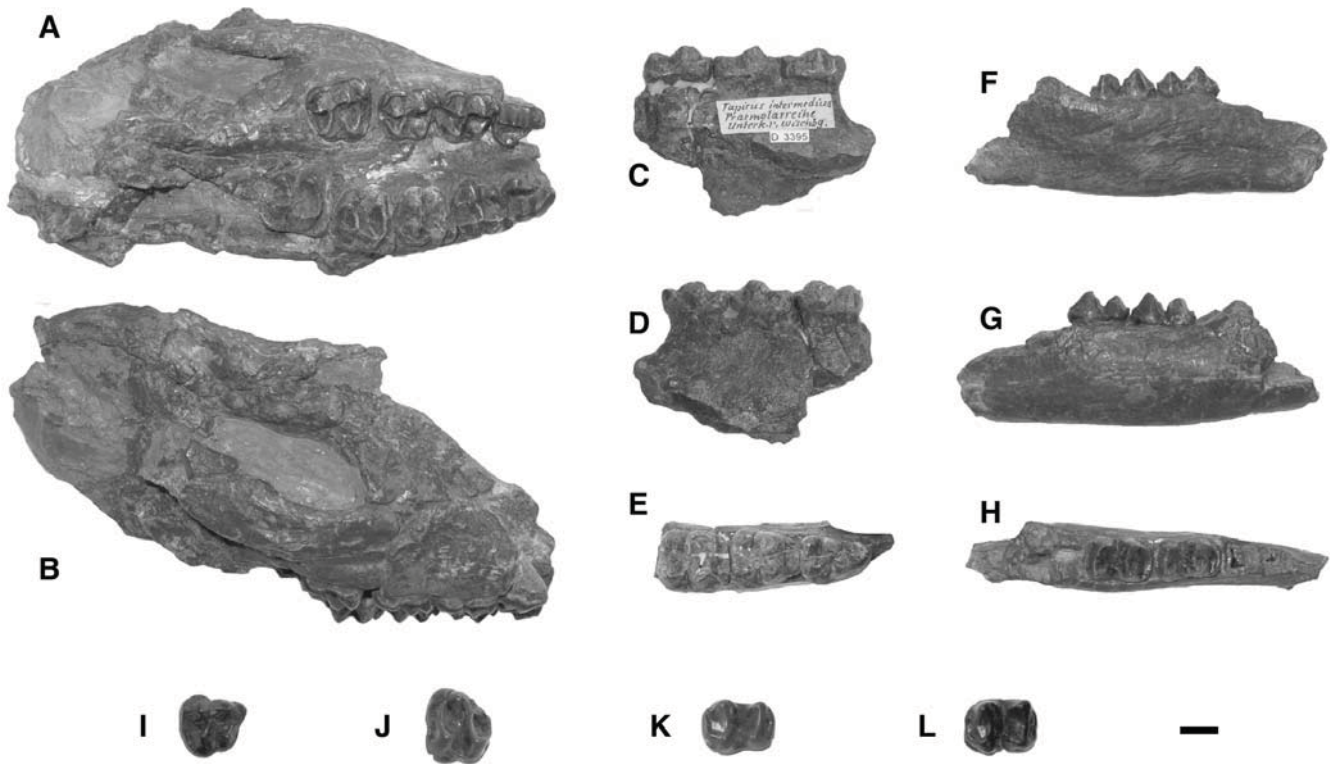
FIGURE 5. Tooth remains of *Eotapirus broennimanni*. **A**, juvenile skull from Wischberg (NMB-As7), occlusal view; **B**, same in lateral view; **C**, right mandible from Wischberg (NMBE-D3395), labial view; **D**, same in lingual view; **E**, same in occlusal view; **F**, juvenile left mandible from Wischberg (NMB-As7), lingual view; **G**, same in labial view; **H**, same in occlusal view; **I**, right P2 from Benken (PIMUZ-A/V1781), occlusal view; **J**, left M1 from Benken (PIMUZ-A/V1782), occlusal view; **K**, left m1 from Benken (PIMUZ-A/V1782), occlusal view; **L**, left m3 from Benken (PIMUZ-A/V1782), occlusal view. Scale bar equals 1 cm.

discontinuous and weak posterior cingulum forming small acute waves, a subhorizontal and developed posterior labial cingulum around the metacone, and a short and weak lingual cingulum closing a pseudofossa. The postfossa is slightly developed.

Lower Deciduous Dentition—dp3 and dp4 are molarized, with a wider talonid than trigonid on dp3 but of same size on dp4. The paracristid is developed. The protolophid is concave on dp3 but slightly concave on dp4, with three subvertical crests on its posterior side. The hypolophid is concave on dp3 but slightly concave on dp4, with four short subvertical crests on its posterior side on dp3, but no one on dp4. The metastylid is slightly developed. There is a slightly developed anterior cingulid around the protoconid, a short and developed posterior cingulid, a short and weak labial cingulid at the level of the median valley, but no lingual cingulid.

Lower Adult Dentition—p2 is not molarized, with an isolated entoconid (conical entoconid and hypoconid not fused in a hypolophid). The paracristid is well developed and elongated in a paralophid. The posterior cingulid is not visible, and there is no anterior, labial, nor lingual cingulids. p3 and p4 are not molarized, with an isolated entoconid (conical entoconid and hypoconid not fused in a hypolophid) and a wider talonid than trigonid. The paracristid is developed. The protolophid is concave on p3 but slightly concave on p4, but subvertical crests and metastylid are not visible (worn teeth). The anterior cingulid is not visible. There is a short and slightly developed posterior cingulid on p4 (not visible on p3), but no labial nor lingual cingulids. m1 and m3 have a wider trigonid than talonid. The paracristid is slightly developed on m1 but developed on m3. The protolophid is slightly

concave on m1 but straight on m3, with two subvertical crests on its posterior side. The metastylid is slightly developed. The hypolophid is straight, with two short subvertical crests on its posterior side. There is a slightly developed anterior cingulid around the protoconid on m1 but weak and short on m3, a short and slightly developed posterior cingulid, but no labial nor lingual cingulids.

Discussion

Cerdeño and Ginsburg (1988) assigned the specimen from Wischberg to the new genus *Eotapirus* and the species *E. broennimanni* based on the characters of the upper dentition. The P2 is triangular with a reduced protoloph lingually convergent to the metaloph, whereas P3 and P4 are well molarized and subquadratic with subparallel protoloph and metaloph. Furthermore, the protocone and metacone of the premolars are unfused and well separated and do not close the lingual part of the median valley. The specimen from Benken shares the same characteristics and no morphological or biometrical differentiations can be observed by comparing both P2s. The specimens from Wischberg and Benken are assigned with confidence to *E. broennimanni*.

Family TAPIRIDAE Gray, 1821

Tapiridae indet—Aarwangen (MP27): left Mx (NMB-AW35); Paudex (MP29): left Mx (MHNG-v4108); Würenlos (MN3): fragmentary right mandible with p3–p4 (PIMUZ-A/V0075).

Description—The isolated upper molar from Aarwangen is worn and incomplete, and bears only the lingual part of the

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protoloph (protocone) with a slightly developed anterior cingulum and a short and slightly developed lingual cingulum. The isolated upper molar from Paudex is worn and incomplete and bears just the labial side of the tooth with a well-developed anterior cingulum and a weak posterior labial cingulum. The fragmentary mandible from Würenlos bears incomplete p3 (broken anterior part) and p4 (broken posterior part); the p3 is not molarized with an isolated entoconid and a short and slightly developed posterior cingulid and the p4 has a slightly concave protolophid and a short and weak anterior cingulid around the protoconid.

Discussion

These fossil remains are too incomplete to be identified beyond Tapiridae indet. Nevertheless, some characters of tapirids can be distinguished clearly on these tooth fragments, such as their bilophodont morphology. This allows their assignment to Tapiridae.

DISCUSSION

Biostratigraphy

The occurrences of early Oligocene to early Miocene European Tapiridae are illustrated in Figure 6 and complete references are given in Table 2. *Protapirus priscus* from the fillings of Möhren 19 and 20 (MP21, Germany) is the first well-dated record of Tapiridae in Europe (Heissig, 1978, 1999a). There is also an M3 described by Böhme (2001) as *Protapirus bavaricus* in Espenhain (MP22, Germany). However, according to the diagnostic characters of the species and the results of this paper, a species cannot be determined based only on lower teeth or upper molars, and this determination is therefore questionable. It would be more reliable to ascribe this tapir from Espenhain to *Protapirus* sp. Regarding *Protapirus priscus* and *Eotapirus ruber* from the Phosphorites du Quercy, these localities are very poorly documented and are not mentioned in the faunal list of Remy et al. (1987), who used only well-dated localities. These two species cannot be better dated than to the interval MP22 to MP28.

Originally described in Gaimersheim (MP27, Germany), the biostratigraphic range of *Protapirus bavaricus* can be extended to the Mammal Biozone MP29 with the determinations of the Swiss specimens from Ebnat-Kappel and Rüfi bei Schänis dated to MP28 and MP29 (base of the biozone), respectively. To date, *Protapirus aginensis* has only been described in La Milloque (MP29, France). According to the anagenetic lineage of *Protapirus* of Cerdeño and Ginsburg (1988), the speciation time from *P. bavaricus* to *P. aginensis* could be dated to around MP29. The last representative species of the genus—*Protapirus douvillei*—occurs mainly in the Aquitanian of France (Saint-Gérand-le-Puy, Fontcaude, Pauhliac, Montaigu). Regarding the record of *Protapirus douvillei* in Buchberg 6 (Switzerland), its geographic distribution is extended eastwards and its biostratigraphy ranges until the end of the Mammal Biozone MN4.

The only Spanish species *Protapirus cetinensis* has been described in Cetina de Aragón and Valquemado (MN2a, Spain). This taxon, very close to *P. aginensis*, seems to have been derived from *P. bavaricus* during the late Oligocene (Cerdeño and Ginsburg, 1988). It supports a sporadic faunal migration between France and the Iberian Peninsula followed by regional endemism, as illustrated by the Spanish evolution of *Anchitherium* during the middle Miocene or *Hipparion* during the Pliocene (e.g., Costeur, 2009).

Paratapirus helvetius is only known to date in the latest Oligocene (MP28–30) of Switzerland (Haslen and Othmarsingen). *Paratapirus intermedius* is commonly described in the early Miocene (MN1 to MN4) of France (Saulcet, Selles-sur-Cher, Laugnac, Brux, Faluns of Touraine and Anjou) and Germany (Eggingen-Gemeindesteinbruch, Eggingen-Mittelhart 3, Hessler,

FIGURE 6. Biostratigraphic range of the European Tapiridae based upon the literature (see Table 2 for complete references) and the new data of this study. New locality data are in italics. Black lines: true occurrences; grey lines: poorly dated occurrences; dashed lines: uncertain occurrences; arrows: supposed speciations as stated in Cerdeño and Ginsburg (1988). The localities sampled in this paper are shown in italics. **Abbreviations**: **Bu**, Budenheim; **CA**, Cetina de Aragon; **EG**, Eggingen-Gemeindesteinbruch; **EM**, Eggingen-Mittelhart 3; **Es**, Eselsberg; **Faluns TA**, Faluns of Touraine and Anjou; **Ha**, Haslach; **He**, Hessler; **La**, Laugnac; **Mo**, Montaigu; **Pa**, Paulhiac; **PC**, Pyrimont-Challonges; **SC**, Selles-sur-Cher; **SGP**, Saint-Gérand-le-Puy; **Va**, Valquemado.

Budenheim, Haslach, Eselsberg) and is also present in Switzerland with the specimens from Höhronen (MN1) and Brüttelen 1 (MN3a).

Eotapirus broennimanni was described in only two European localities dated to the Mammal Biozone MN1: Pyrimont-Challonges in France and Wischberg in Switzerland. A new

occurrence of the species has been identified with the specimens of Benken (MN3–4?, Switzerland). Unfortunately, as this locality records reworked species from the late Oligocene and the early Miocene (see Geological Setting), the biostratigraphy of the tapir species *E. broennimanni* cannot be determined with precision nor extended without any doubt to the end of the Burdigalian.

Paleoecology

Extant tapirs are solitary animals primarily living in forested environments in a warm and wet climate with water proximity (Nowak, 1999). Their brachyodont bilophodont teeth are adapted for a folivorous, browsing diet helped by their short proboscis (Schoch, 1989; Eisenmann and Guérin, 1992). Fossil tapirids share the same anatomical characters as extant species and are inferred to have lived in the same kind of environment (Heissig, 1999a). This statement is reinforced by the ecologic comparison of the fauna associated with the Swiss tapir localities during the Oligocene–Miocene transition, which seems to indicate that they preferred forested and humid habitats (Fig. 7). The Suidae species are considered as forest forms because of their small body size (Fortelius et al., 1996). The anthracotheriid *Microbunodon minimum* was also a species of small size living in humid forested environments and feeding mostly on fruit (Lihoreau and Ducrocq, 2007). According to Becker (2003), most rhinocerotid species indicate rather humid forested environments (*Eggysodon*, *Pleuroceros*, *Protaceratherium*). The genus *Diaceratherium* generally denotes humid forested environments. Only *D. lemanense* seems to have preferred transitional zones between forest and grassland (Becker et al., 2009). The ecology of *Ronzotherium romani* indicates open, rather arid woodland environments (Uhlig, 1999; Becker et al., 2009). The ruminant *Dremotherium quercyi* lived in scattered forests whereas *Palaeomeryx* seems to have preferred open environments (Blondel, 1998). The European Oligocene anthracotheres (*Anthracotherium*, *Elomeryx*, *Brachyodus*) are usually affiliated to water (semi-aquatic); *Anthracotherium* was adapted to aquatic and swampy environments with its long and broad lateral digits (Lihoreau and Ducrocq, 2007).

The Oligocene–Miocene Transition

Climatic and environmental changes occurred in the late Oligocene and the early Miocene, leading to evolutionary responses by mammals. In the Chattian, the climate was quite stable with tropical to temperate influences (Becker, 2003). However, the Late Oligocene Warming (29 to 27 Ma; Vianey-Liaud, 1991; Zachos et al., 1997, 2001) was followed by a decrease in temperature and humidity leading to the Mi-1 Glaciation Event (~22.9 Ma; Zachos et al., 1997, 2001). In the Aquitanian, the temperature increased again to reach the Miocene Climatic Optimum at the end of the early Miocene (17 to 15 Ma; Zachos et al., 2001; Böhme, 2003). The humidity also increased, leading to humid and swampy forested environments in the Burdigalian (Whybrow and Andrews, 2000). Later, in the Langhian (middle Miocene), the temperature began to slowly decrease again (Janis, 1989; Becker, 2003). At the scale of the Western Swiss Molasse Basin, these late Oligocene to early Miocene climatic and environmental changes are also well developed in the sedimentological record (e.g., Berger, 1990; Schlunegger et al., 2001; Becker, 2003), accentuated by the Alpine orogenesis.

Figure 8 illustrates the occurrences of early Oligocene to early Miocene European Tapiridae (according to Heissig, 1978, 1999a; Cerdeño and Ginsburg, 1988; this study), Rhinocerotoidea (Heissig, 1999b; Uhlig, 1999; Antoine et al., 2000; Becker, 2003, 2009; Becker et al., 2009; pers. observ.), Anthracotheriidae (Stehlin, 1910; Hellmund, 1991; Ginsburg and Chevrier, 2005; Lihoreau and Ducrocq, 2007; Lihoreau et al., 2009; pers. observ.), and

FIGURE 7. Associated fauna of the different tapirid localities of the Swiss Molasse Basin, with their environmental and ecological indications (faunal associations according to Hellmund, 1991; Fortelius et al., 1996; Becker, 2003; Ginsburg and Chevrier, 2005; B. Mennecart, pers. comm.; pers. data).

Suoidea (Hellmund, 1992; Fortelius et al., 1996). Three patterns of diversity and evolution can be observed: (1) the Tapiridae and the Suoidea were always represented by a weak abundance; they had a low diversity during the Oligocene and a diachronic diversification in the early Miocene, from MN1 for the Tapiridae and from MN(2)-3 for the Suoidea; (2) the Rhinocerotoidea were rather diverse during both time intervals, but a slight diversity increase occurred during the Oligocene–Miocene transition; and (3) the Anthracotheriidae were common during the Oligocene, but they were represented only by sporadic occurrences in the early Miocene and went extinct at the end of the Burdigalian in Europe.

The changes in the rhinocerotid diversity seem to occur without direct outgroup interactions. We speculate that the less humid climate of the terminal Oligocene (Becker, 2003) could have been stressful for the anthracotheres. The tapirs also affiliated to forested areas were probably more specialized in their
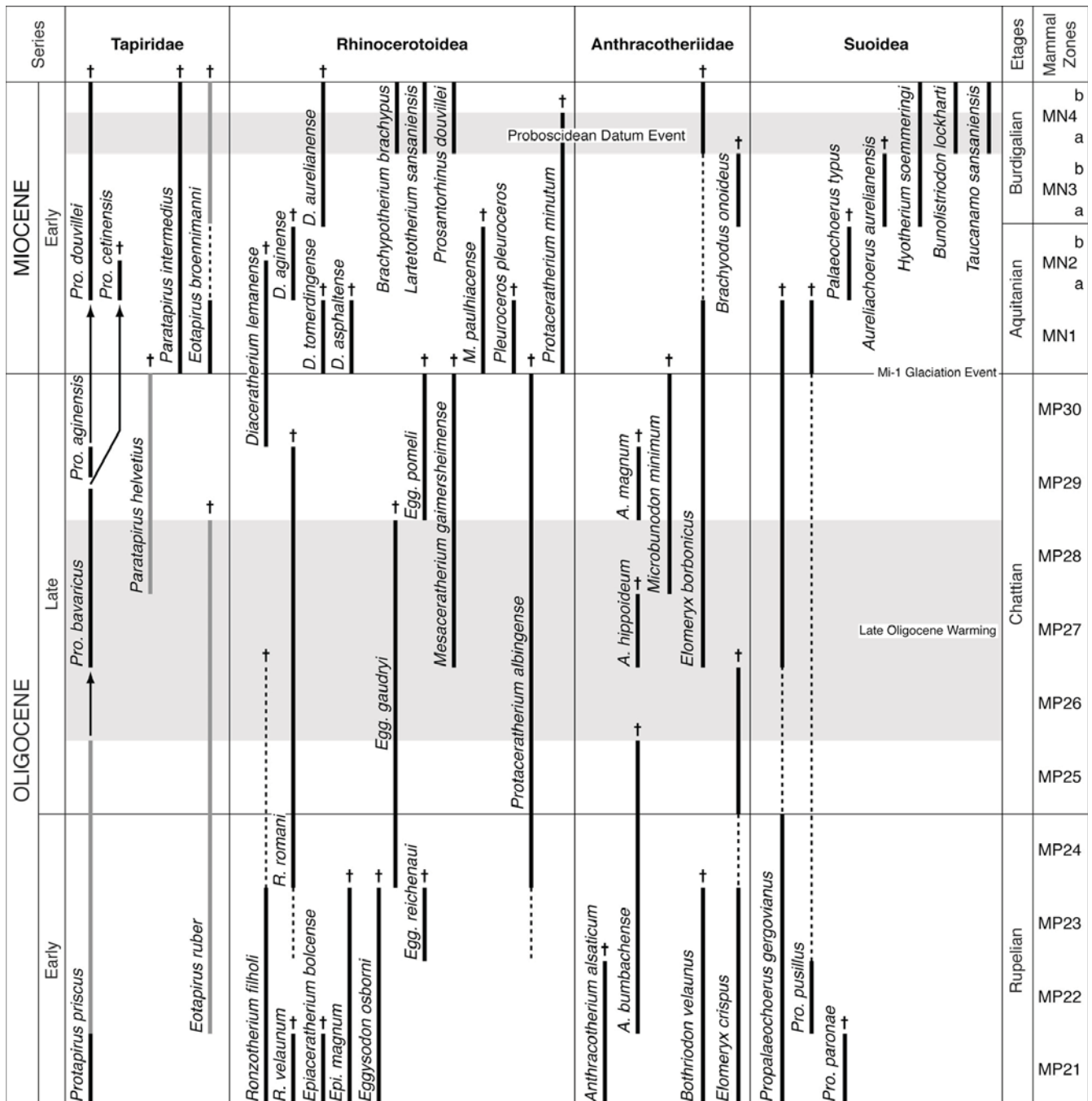
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FIGURE 8. Biostratigraphic range of the genera of terrestrial ungulate mammals (Tapiridae: Heissig, 1978, 1999a; Cerdeño and Ginsburg, 1988; this study; Rhinocerotoidea: Heissig, 1999b; Uhlig, 1999; Antoine et al., 2000; Becker, 2003, 2009; Becker et al., 2009; pers. observ.; Anthracotheriidae: Stehlin, 1910; Hellmund, 1991; Ginsburg and Chevrier, 2005; Lihoreau and Ducrocq, 2007; Lihoreau et al., 2009; pers. observ.; and Suoidea: Hellmund, 1992; Fortelius et al., 1996) during the Oligocene and the early Miocene in Western Europe, related to main climatic and biotic events (Tassy, 1989; Vianey-Liaud, 1991; Zachos et al., 1997, 2001). Black lines: true occurrences; grey lines: poorly dated occurrences; dashed lines: uncertain occurrences; arrows: supposed speciations as stated in Cerdeño and Ginsburg (1988).

diet and social behavior but were probably less dependent on water supply than the semi-aquatic anthracotheriids. We speculate that the combination of competition and environmental changes could have been fatal to the anthracotheres. Thus, the tapirs may have adopted an opportunistic behavior when occupying the scarcer humid forested areas of the terminal Oligocene and in diversifying in the Aquitanian before the arrival of the

suids in the Burdigalian. The latter were less specialized taxa in their diet and were uncommon during the Oligocene. However, successive migrations occurring in MN2 and MN3 with the arrival of *Palaeochoerus*, and *Aureliachoerus* and *Hyotherium*, respectively, have progressively affected the abundance of the tapirs. At the Proboscidean Datum Event, the intensive competition related to massive immigrations (among them the

arrival of the suids *Bunolistriodon* and *Taucanamo*) may have led to the temporary disappearance of tapirs in Europe.

CONCLUSION

The review of the Tapiridae from the Swiss Molasse Basin during the Oligocene and the early Miocene enabled us to emend the diagnoses of three species of the genus *Protapirus*, *P. bavaricus*, *P. aginensis*, and *P. douvillei*, based primarily upon the relative development of the postfossae and cingula as well as to the presence or absence of a lingual pseudofossa on the upper premolars. The new data obtained in this study allowed us to establish a new and precise biostratigraphic range for the European tapir species from the early Oligocene to the early Miocene (from MP21 to MN4). Their paleoecology as forest animals associated with humid environments seems corroborated by the ecologic comparisons of the associated large-herbivorous mammals discovered in seven Swiss localities ranging from the late Oligocene to the late early Miocene (from MP27 to MN4). Furthermore, a general pattern of diversity and evolution has been established for large terrestrial mammals (Tapiridae, Rhinocerotoidea, Anthracotheriidae, and Suoidea) with a focus on the Oligocene–Miocene transition. During this time interval, the climatic and environmental variations were moderate, progressive, and associated with mammalian evolutionary patterns that consisted mainly of local and regional extinctions, successive colonisation events, and speciation. Additionally, the numerous immigrations and the drastic climatic and environmental changes linked to the Proboscidean Datum Event and the Miocene Climatic Optimum implied a more severe and faster faunal response.

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