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Tapirus priscus Kaup from the Upper Miocene of Western Europe: palaeontogy, biostratigraphy, and palaeoecology.

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ABSTRACT

Tapirus priscus is anatomically redefined after study of almost all the available material, and compared to modern Tapirs and the fossil Villafranchian (MN 16 and 17) *T. arvernensis arvernensis*. *T. priscus* is to be found in about fifteen West European fossileferous sites and is typical of the Vallesian mammal age; its environment seems analogous to the modern environment of the genus: tropical forest in a warm, wet climate, close to water. Its anatomical resemblance to *T. arvernensis* supports a close phylogenetical relationship between the two species, with some affinities to *T. indicus*.

RÉSUMÉ

L'étude de la presque totalité des restes connus de *Tapirus priscus* Kaup 1833 nous permet de redéfinir cette espèce sur le plan anatomique et de la comparer aux Tapirs actuels et à *T. arvernensis arvernensis* du Villafranchien (MN 16 et 17) d'Europe. *T. priscus* est présent dans une quinzaine de gisements d'Europe occidentale. Bien que toujours rare, il est caractéristique du Vallésien; ses exigences écologiques semblent celles des tapirs actuels: forêt tropicale dense en climat chaud et humide, et proximité de l'eau. Ses ressemblances anatomiques avec *T. arvernensis* sont en faveur d'une proximité phylogénétique entre les deux espèces, avec quelques caractètes évoquant *T. indicus*.

INTRODUCTION

The genus *Tapirus* is represented today by one Asian and three American species. The Asian *T. indicus* is refered to the subgenus *Acrocodia*, the American *T. terrestris*, *T. pinchacus*, and *T. bairdi* to the subgenera *Tapirus*, *Roulini*, and *Elasmognathus*.

The most conspicuous skeletal differences are in size and in cranial shape. *T. bairdi* and *T. indicus* are larger than *T. terrestris* and *T. pinchacus; T. bairdi* has an ossified nasal septum; *T. terrestris* has a huge sagittal crest and a sloping forehead. Other differences whether cranial, dental, or postcranial are less evident.

During the revision of the tapirs initiated some years ago, we had the opportunity of studying in detail numerous recent skeletons, many fossil specimens of the Lower Villafranchian *T. arvernensis arvernensis*, (from Vialette, Perrier, Villafranca d'Asti, and Valdarno) and almost all the known material from *Tapirus priscus*, the most important Upper Miocene species of Western Europe (Guérin and Eisenmann, 1982). *T. priscus* was defined by Kaup in 1833 in the site of Eppelsheim (*Dinotherium* sands from the Rhine Valley, Germany), studied again by Von Meyer (1865-68) and never revised since. Following Von Koenigswald (1930) it is generally accepted that the large *T. priscus* is more similar to the Asian *T. indicus* while the small *T. arvernensis* is closer to the *T. terrestris* type.

The present paper being a revision of *T. priscus*, we concentrated here on the comparison and discussion of those anatomical characters for which information is available in the fossils of *T. priscus* we

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TABLE 1. *Biostratigraphy of* Tapirus priscus *sites in Western Europe.*

	GERMANY	SWITZERLAND	FRANCE	SPAIN
MN 10		Charmoilles (Jura Bernois)	Langemaison (Doubs) Orignac (Pyrénées) Priary (Ain)	
MN9	(Dinother. Formation) Eppelsheim Esselborn Gau Weinhein Kettenheim Westhoffen Wissberg (Bohnerzen) Melchingen Trochtelfingen			El Firal (Seu de Urgell) Can Llobateres (Vallès Penedès)

have seen. As a matter of fact, although about fifteen sites yielded fossils of *T. priscus* (table 1), the material is rather poor. Details about these sites and the material are given in another paper (Guérin and Eisenmann, in press). Using these data, we have tried to find out if indeed the large *T. priscus* is morphologically close to the modern *T. indicus*, and the smaller *T. arvernensis*, to *T. terrestris*.

The skull measurements are nearly the same as those used in *Equus* (Eisenmann, 1986). The limb bones measurements are nearly all the same as the ones recommended by the New York Hipparion Conference (Eisenmann et al., 1988).

COMPARATIVE OSTEOLOGY

a: *Skull*

N.° 40633 from Eppelsheim, London Natural History Museum collections, is a fragmentary skull with most of the palate and a large part of the zygomatic arches (pl. 1, 1). The measurements are in table 2.

Using Simpson's ratio diagrams (fig. 1), we compared the *T. priscus* skull with adult skulls (7 functional cheek teeth) of recent species using *T. terrestris* as a reference, and with the European Villafranchian form *T. arvernensis arvernensis*, represented by 7 incomplete skulls. Comparisons were naturally restricted to the available measurements and their value is limited by the samples size: only one skull for *T. priscus*, only one value for variables 2 and 10 in *T. arvernensis*, only two skulls for *T. pinchacus*. It seems however that:

— *T. terrestris* has narrower choanae than all the other Tapirs;
— Choanal breadth is the only character distinguishing *T. terrestris* and *T. pinchacus*;
— *T. bairdi* differs from *T. indicus* by a longer snout (variable 5), a narrower skull (variables 14 and 6) and much smaller premolars (variable 7);
— *T. priscus* differs from all the recent species by the

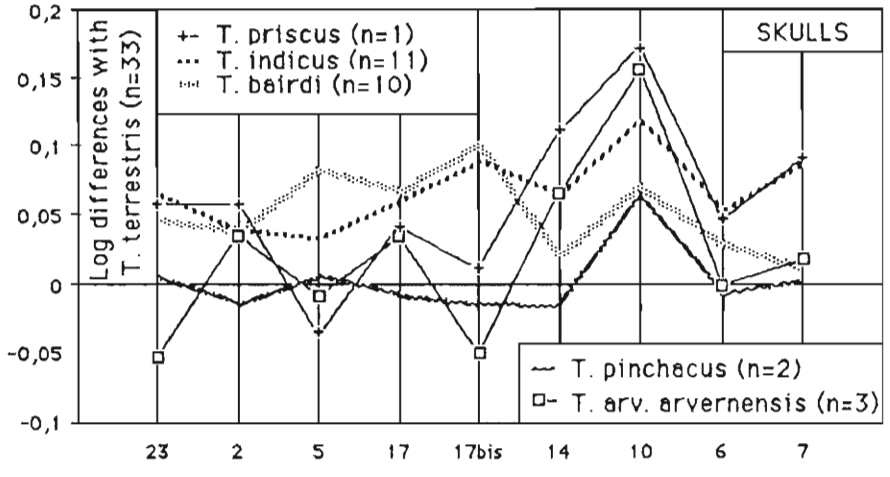

FIGURE 1. Ratio diagram of modern and fossil Tapir skulls. For the definition of the measurements, see captions of Table 2 and Eisenmann, 1986. n = number of specimens (when the number is larger than 1, the ratio diagram is calculated for the mean). Note that both fossil forms have relatively short (5) and narrow snouts at the diastema (17 bis), and wide skulls (14) and choanae (10).

TABLE 2. *Skull measurements of* T. priscus *and* T. arvernensis arvernensis. *(Vialette, n = 5; Etouaires, n = 2; Villafranca d'Asti, n = 1). Measurements defined in Eisenmann (1986) but he palatal length is between the anteriors borders of P1/ and the choanae (Eisenmann et al., 1988).*

		Eppelsheim	Perrier	Vialette	Villafranca
Length of Ant. Ocular Line	23	187.0		145.0	
Palatal length (P1-Choanae)	2	124.5	118.0		
Snout length	5	73.0	77.0	80.0	77.0
Maximal snout breadth	17	47.5	47.0	49.0	44.0
Breadth at the diastema	17 bis	43.0	35.0	35.5	41.0
Bizygomatic breadth	4	233.0		210.0	
Choanal breadth	10	52.0	50.0		
Maximal palatal width	6	73.0	69.0		62.0
Alveolar length P1-P4	7	86.0	76.5	69.2	72.0

shortness of the snout (5), its narrowness at the diastema level (17 bis), the great bizygomatic breadth (14), and the great choanal breadth (10);

— The same characters are exhibited by *T. arvernensis arvernensis*, although the latter is in general smaller.

On the basis of our craniological observations, there is no morphological closeness between *T. priscus* and the modern *T. indicus*, although both are large. Nor is there a special morphological closeness between *T. terrestris* and *T. arvernensis arvernensis*, although both are small. The large *T. priscus* and the smaller *T. arvernensis arvernensis* seem morphologically closer to each other than to any recent species.

b: *Mandible*

Measurements are given in table 3. Still using Simpson's ratio diagrams (fig. 2), we compared adult mandibles (6 functional cheek teeth) of fossil and recent species, again using *T. terrestris* as the reference line.

Some of the variables are lacking in the available material from *T. priscus;* for the rest, the sample varies between 1 specimen (variables 8' and 15) to 8 specimens (variable 4'). For *T. arvernensis arvernensis,* the sample varies between 3 specimens (variables 3, 8', and 15) and 11 specimens (variable 4'). The ratio diagrams show that:

— *T. pinchacus* is in general smaller than *T. terrestris,* and specially by the height in front of P/2 (12) and the thickness under M/3 (14);

— *T. bairdi* differs from *T. indicus* by a longer snout (variable 3), smaller height and thickness of the horizontal ramus (11, 14) and much smaller teeth (4' and 4'');

TABLE 3. *Average mandible measurements of* T. priscus *and* T. arvernensis arvernensis. *(Vialette, n = 8; Etouaires, n = 3; Villafranca d'Asti, n = 2). Measurements closely adapted from those of Eisenmann et al., 1988, but 3 = snout lenqth from I/1 to P/2; 15 = distance from the posterior end of the symphysis to the most posterior point of the mandibular angle.*

T. priscus		n	x	min	max	s	v
Snout length	3						
Alveolar length of P3-P4	4'	8	42.8	39.5	47.5	3.03	7.1
Alveolar length of molars	4''	5	71.5	68.0	77.0	3.50	4.9
Length of symphysis	6						
Minimal symphysis width	7'						
Height at the condyle	8'	1	157.0				
Height under P4-M1	11	7	63.6	61.5	67.0	1.95	3.1
Height in front of P2	12	3	53.8	52.0	56.5	2.36	4.4
Max. thickness under M3	14	5	31.1	28.0	35.5	2.75	8.8
Length symphysis-angle	15	1	280.0				
T. priscus		**n**	**x**	**min**	**max**	**s**	**v**
Snout length	3	3	66,3	65,0	68.0	1.53	2.3
Alveolar length of P3-P4	4'	11	36,6	32.0	39.0	2.21	6.0
Alveolar length of molars	4''	8	61.4	58.5	66.0	2.27	3.7
Length of symphysis	6	4	77.0	70.0	81.0	4.97	6.5
Minimal symphysis width	7'	5	29.0	26.0	33.0	2.89	10.0
Height at the condyle	8'	3	116.0	112.0	122.0	5.29	4.6
Height under P4-M1	11	9	46.1	42.0	49.8	2.60	5.6
Height in front of P2	12	4	39.5	35.0	42.0	3.11	7.9
Max. thickness under M3	14	9	29.0	27.0	31.0	1.50	5.2
Length symphysis-angle	15	3	222.7	211.0	232.0	10,69	4.8

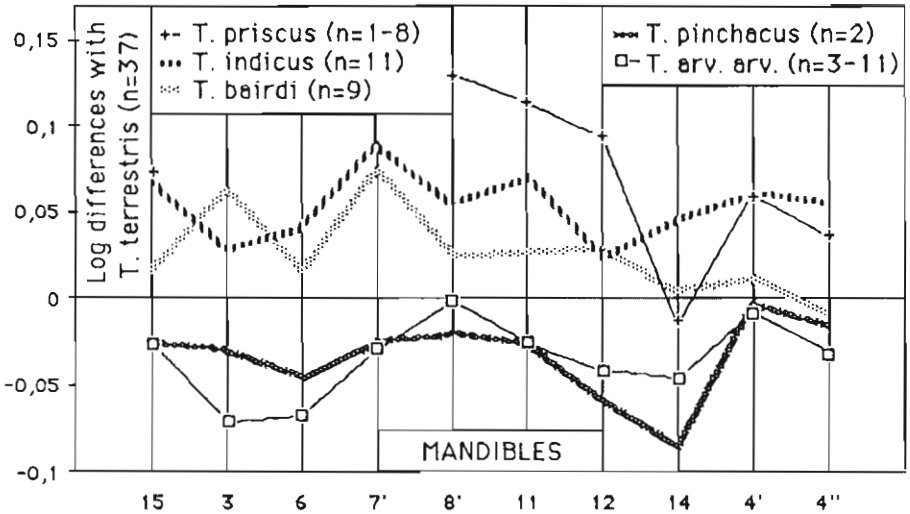

FIGURE 2. Ratio diagram of modern and fossil Tapir mandibles. For the definition of the measurements, see captions of Table 3. n = number of specimens. Note that *T. arv. arvernensis* differs from *T. terrestris*, in particular by the great relative height of the ascending ramus (8'). Several data are lacking for *T. priscus*, but this character is shared by both fossil.

— *T. priscus* seems to have a relatively height ascending ramus (8') and a very thin horizontal branch (14);
— *T. arvernensis arvernensis* has the overall size of *T. pinchacus*, but a shorter snout (3), heigher ascending ramus (8'), and thicker horizontal ramus (14).

No more than skulls do mandibles evidence any morphological closeness between *T. priscus* and *T. indicus*. Moreover, *T. priscus* and *T. arvernensis arvernensis* seen to share et least one character (relative height of the ascending ramus) distinguishing them from the recent species.

c: *Upper cheek teeth*

Among the recent Tapirs, *T. indicus* stays apart because of its very large cheek teeth, with the exception of P1/ which are relatively narrow (fig. 3). *T. bairdi*, *T. terrestris*, and *T. pinchacus* have similar lengths, but *T. pinchacus* has smaller widths.

T. arvernensis arvernensis (table 4) is close to the American Tapirs by the small size of its teeth, but the proportions seem a little different: in our sample, P1/, P2/, and P3/ are relatively large, while M1/, M2/, and M3/ are relatively small. Moreover, and like in *T. indicus*, the posterior widths are subequal on P3/ and P4/ while they are larger on P4/ of the American species (fig. 3).

The interpretation of the material refered to *T. priscus* is difficult. The only two complete series are very different: the teeth of the type skull (DIN 40633) from Eppelsheim (Pl. 1, fig. 1C) are close in size to the average *T. indicus;* the teeth (DIN 1091) from Wissberg (Pl. 1, fig. 2) are close to the average *T. arvernensis arvernensis* (fig. 3). A few isolated teeth do not quite fill the gap in between so that one may wonder if DIN 1091 belongs really to *T. priscus*. The difference

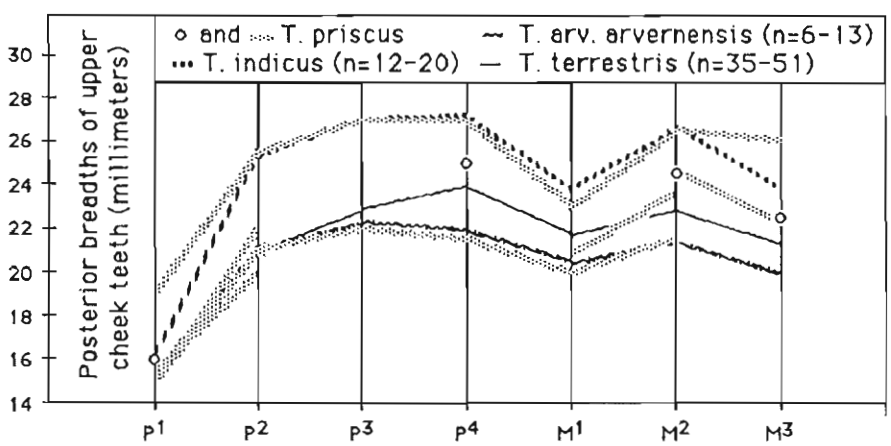

FIGURE 3. Upper cheek teeths of modern and fossil Tapirs: posterior breadths. n = number of specimens. For *T. priscus*, the values for each series are represented separately. Other species are represented by mean values. Note the subequal values of P3/P4/ breadths of both fossils and *T. indicus*, while breadths are larger on P4/ than P3/ in *T. terrestris*.

TABLE 4. *Average measurements of upper cheek teeth of* T. priscus and T. arvernensis arvernensis. m = *number of specimens; x = mean, mind and max = minimal and maximal observed values: s = standard deviation; v = coefficient of variation (100s/x). L = length; b = breadth.*

	Tapirus priscus						Tapirus arvernensis arvernensis					
	n	x	min	max	s	v	n	x	min	max	s	v
P1 L	5	18.2	16.0	20.5	1.68	9.2	10	16.6	15.0	18.0	1.01	6.1
P1 b ant	5	11.4	10.0	13.0	1.52	13.3	8	11.5	10.0	12.5	1.04	9.0
P1 b post	5	16.2	15.0	19.5	1.89	11.7	8	15.2	12.5	16.5	1.33	8.8
P2 L	4	20.1	18.0	22.5	2.02	10.0	10	18.1	16.0	20.5	1.26	7.0
P2 b ant	4	18.3	17.5	19.5	0.87	4.7	9	18.3	17.0	20.0	1.00	5.5
P2 b post	4	21.8	20.0	24.0	1.71	7.9	9	21.0	19.0	23.5	1.32	6.3
P3 L	2	20.8	19.0	22.5	2.47	11.9	6	18.1	17.0	19.5	1.02	5.6
P3 b ant	2	23.3	21.0	25.5	3.18	13.7	5	21.8	20.0	23.0	1.44	6.6
P3 b post	2	24.0	22.0	26.0	2.83	11.8	5	22.3	20.5	24.0	1.35	6.1
P4 L	3	20.8	18.5	22.0	2.02	9.7	9	18.4	17.5	20.5	1.17	6.3
P4 b ant	3	24.5	22.5	26.5	2.00	8.2	8	22.8	21.5	25.0	1.28	5.6
P4 b post	3	24.2	21.5	26.0	2.36	9.8	9	21.9	20.5	25.0	1.36	6.2
M1 L	3	21.0	20.0	22.5	1.32	6.3	11	18.7	17.0	20.0	0.84	4.5
M1 b ant	3	23.8	22.0	27.0	2.75	11.6	10	22.3	20.3	25.0	1.58	7.1
M1 b post	3	21.3	20.0	23.0	1.53	7.2	10	20.4	19.0	23.5	1.45	7.1
M2 L	4	23.9	22.0	25.5	1.49	6.3	13	20.7	19.5	23.5	1.09	5.3
M2 b ant	4	27.3	24.0	29.0	2.22	8.1	12	23.9	22.3	27.6	1.66	6.9
M2 b post	4	23.8	21.5	25.5	1.71	7.2	12	21.4	18.5	25.0	1.75	8.2
Me L	2	24.5	24.0	25.0	0.71	2.9	9	20.2	19.0	22.0	0.97	4.8
M3 b ant	3	26.7	23.0	29.0	3.21	12.1	8	23.9	22.0	26.0	1.43	6.0
M3 b post	2	23.8	22.5	25.0	1.77	7.4	8	19.9	17.0	23.0	2.06	10.3

in size, however, is not so large as to exclude the possibility of a normal intraspecific variation (table 4).

Another interesting point is that both *T. priscus* and *T. arvernensis arvernensis* seem to have the same proportions for the cheek teeth posterior breadths as *T. indicus* (fig. 3).

d: *Lower cheek teeth*

For the cheek lengths, *T. indicus* stays apart because of its very long teeth. *T. bairdi*, although close to *T. terrestris* and *T. pinchacus*, has longer premolars and M/1, and shorter M/2 and M/3. In *T. bairdi*, and more so in *T. indicus*, the P/3 are longer than the P/4; the reverse is true for *T. terrestris* and *T. pinchacus*. For the cheek breadths (fig. 4), *T. indicus* and *T. pinchacus* stay apart because of their (respectively) very large and very small values; *T. bairdi* and *T. terrestris* are very close one to the other.

The sample of *T. priscus* (table 5) is much better than for the upper cheek teeth and looks more homogeneous. The size is in general intermediate between *T. indicus* and the American Tapirs. The P/3 are much longer than the P/4 (more than in *T. indicus*). Breadths of P/2 and P/3 are similar to *T. indicus*, wile breadths of molars are similar to *T. terrestris*; unlike the case of modern Tapirs, breadths of P/3 and P/4 are subequal (fig. 4).

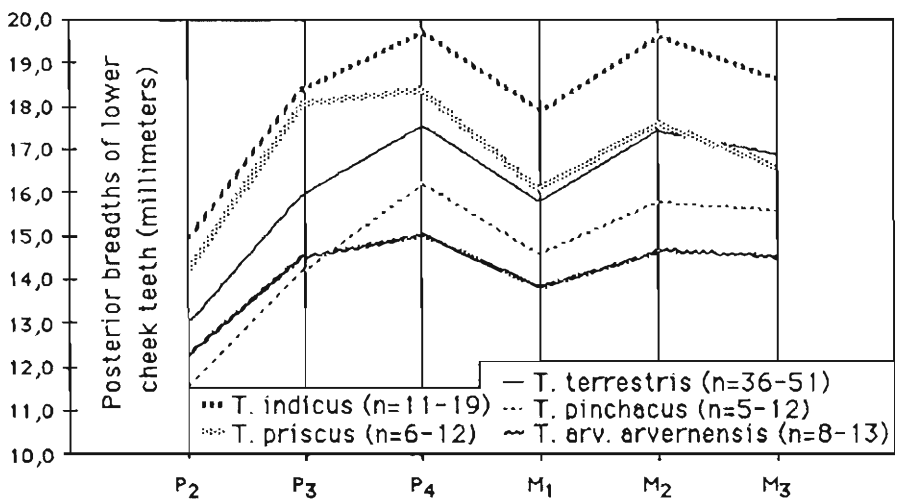

FIGURE 4. Lower cheek teeths of modern and fossil Tapirs: posterior breadths. n = number of specimens. Note the subequal values of P/3P/4 breadths in fossil Tapirs, while P/4 breadths are larger in modern Tapirs.

TABLE 5. *Average measurements of ulower cheek teeth of* T. priscus *and* T. arvernensis arvernensis. m = *number of specimens; x = mean, min and max = minimal and maximal observed values: s = standard deviation; v = coefficient of variation (100s/x). L = length; b = breadth.*

	Tapirus priscus						Tapirus arvernensis arvernensis					
	n	x	min	max	s	v	n	x	min	max	s	v
P2 L	6	23.0	22.0	24.0	0.89	3.89	9	20.8	19.0	22.5	1.06	5.1
P2 b ant	7	12.6	11.0	14.0	0.93	7.40	8	10.6	9.0	12.0	1.03	9.7
P2 b post	6	14.2	13.0	15.0	0.75	5.31	9	12.3	11.0	13.0	0.91	7.4
P3 L	8	22.0	20.0	24.0	1.63	7.39	13	18.5	17.0	21.0	1.36	7.4
P3 b ant	9	15.8	14.5	17.5	1.06	6.70	12	13.3	12.0	14.5	0.72	5.4
P3 b post	9	18.1	17.0	20.3	1.07	5.91	12	14.5	13.0	16.5	1.08	7.4
P4 L	6	20.9	20.0	24.0	1.56	7.47	13	19.0	17.5	21.5	1.06	5.6
P4 b ant	6	17.5	16.0	19.0	1.10	6.26	11	14.8	13.0	16.5	0.96	6.5
P4 b post	6	18.4	17.0	20.2	1.07	5.80	11	15.0	13.5	17.5	1.04	6.9
M1 L	12	21.8	18.0	26.0	1.99	9.17	13	19.4	18.0	21.0	1.02	5.2
M1 b ant	11	16.7	15.0	18.3	1.03	6.14	11	14.6	13.0	16.0	1.00	6.8
M1 b post	12	16.1	14.5	18.0	1.11	6.86	11	13.8	12.5	15.0	0.84	6.1
M2 L	11	24.4	22.5	26.5	1.56	6.40	14	21.6	19.0	24.0	1.45	6.7
M2 b ant	11	18.2	16.0	20.0	1.21	6.65	13	15.7	14.0	17.5	0.83	5.3
M2 b post	11	17.6	16.0	19.0	1.13	6.41	13	14.7	13.5	17.0	1.14	7.8
M3 L	7	24.7	22.5	27.0	1.75	7.09	9	22.1	21.0	25.0	1.19	5.4
M3 b ant	7	18.5	17.0	20.0	1.35	7.26	9	15.7	14.5	17.0	0.83	5.3
M3 b post	7	16.6	15.5	18.0	1.08	6.52	8	14.5	12.5	17.5	1.60	11.1

Lower cheek teeth of *T. arvernensis arvernensis* (table 5) are about the size of *T. pinchacus*, and P/4 are longer than P/3. Breadths are relatively larger on P/2 and P/3 than on other teeth; as in *T. priscus*, posterior breadths are subequal on P/3 and P/4 (fig. 4).

Thus, the two fossil species share one character: the relative breadths of P/3 and P/4. *T. priscus* shares with *T. indicus* (and to a lesser extent with *T. bairdi*) another character: the relative lengths of P/3 and P/4.

e: *Radius*

One radius was found at Eppelsheim; for most of its measurements (table 6); it is larger than the largest from our sample of *T. indicus* (fig. 5). The proximal breadth (measurement 5) is relatively small but otherwise the proportions are similar to *T. indicus*. Compared to *T. terrestris*, the diaphysis is more robust. In *T. arvernensis arvernensis*, the diaphysis is also robust, but the rest of the measurements are like in a small *T. terrestris*.

f: *Talus*

By most of its dimensions (table 7), the Eppelsheim talus is close to the average *T. indicus* (fig. 6) but the medial diameter of the trochlea (measure 2) is much higher and the distal articular antero-posterior diameter is larger (measure 6). Similar proportions are found in the much smaller *T. arvernensis arvernensis* (table 7).

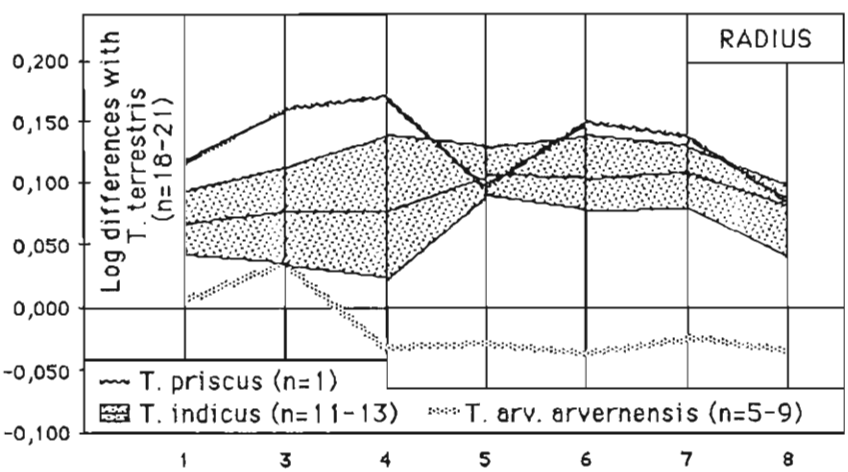

FIGURE 5. Ratio diagram of modern and fossil Tapir radii. For the definition of measurements, see Table 6 and Eisenmann et al., 1988. n = number of specimens. By most of its measurements, the *T. priscus* radius falls outside the range of variation of *T. indicus*. The proximal breadth (5) is surprisingly small.

TABLE 6. *Radius measurements of* T. priscus *and* T. arvernensis arvernensis. *Measurements as in Eisenmann et al., 1988, but 5 = maximal proximal breadth; 7 = articular distal breadth; 8 = articular antero-posterior diameter. Same abreviations as in table 4 and 5.*

	Radius	T. priscus			Tapirus arvernensis arvernensis		
		n	x	min	max	s	v
Maximal length	1	261.0	7	201.8	190.0	213.0	9.25	4.6
Mid-diaphysal width	3	33.5	8	25.1	24.0	29.0	2.62	10.4
Diaph. Ant-Post diameter	4	27.0	8	16.9	16.0	18.0	0.69	4.6
Proximal width	5	60.0	8	45.0	42.0	49.0	3.11	6.9
Prox. And-Post diameter	6	39.0	9	25.4	22.0	29.5	2.40	9.5
Distal articularwidth	7	56.0	5	38.6	35.0	41.0	2.38	6.2
Dist. Ant.-Post diameter	8	31.0	6	23.5	21.0	26.0	2.24	9.5

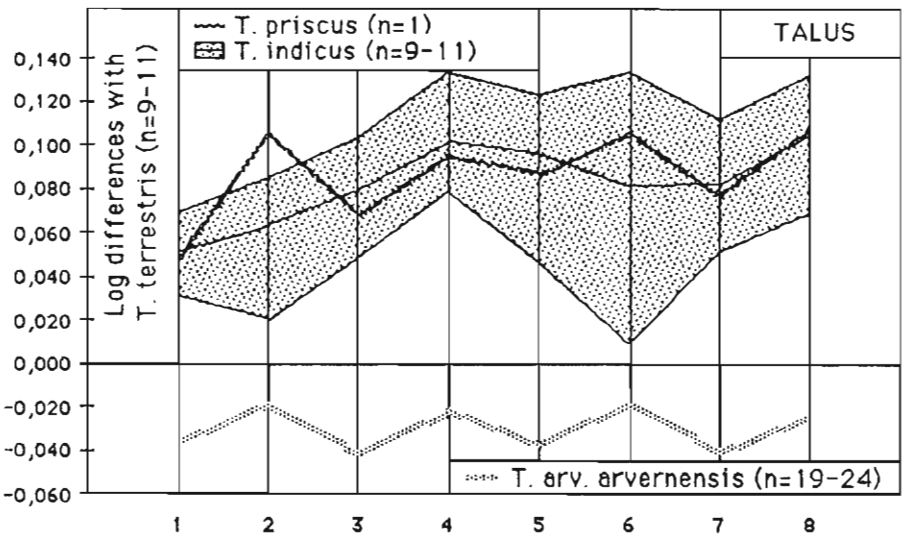

FIGURE 6. Ratio diagram of modern and fossil Tapir tali. For the definition of measurements, see Table 7 and Eisenmann et al., 1988. m = number of specimens. By most of its measurements, the *T. priscus* talus falls inside the range of variation of *T. indicus*. The diameter of the medial condyle is relatively large. Note the similarities in proportions between *T. priscus* and *T. arvernensis arvernensis*.

TABLE 7. *Talus measurements of* T. priscus *and* T. arvernensis arvernensis. *Measurements as in Eisenmann et al., 1988, but 8 = maximal distal breadth. Same abreviations as in table 4 and 5.*

	Talus	T. priscus			Tapirus arvernensis arvernensis		
		n	x	min	max	s	v
Maximal length	1	57.0	23	47.0	43.0	52.0	2.45	5.2
Max. diam. of the med. condyle	2	45.0	22	33.8	32.0	37.0	1.23	3.6
Breadth of the trochlea	3	34.5	22	26.8	24.0	29.0	1.57	5.9
Maximal breadth	4	53.0	23	40.5	38.0	49.0	2.22	5.5
Distal articular breadth	5	46.0	21	34.5	30.0	38.0.	1.66	4.8
Dist. Ant-Post. art. diam.	6	30.0	24	22.5	20.0	26.0	1,50	6.7
Medial Ant-Post diameter	7	36.0	22	27.4	25.0	30.2	1.25	4.6
Distal maximal breadth	8	49.0	19	36.2	33.5	40.0	1.73	4.8

BIOSTRATIGRAPHY

The occurence of *T. priscus* was confirmed in the listed in table 1. Details on these sites and the corresponding bibliography are given in another paper (Guérin and Eisenmann, in press).

Tapirus priscus seems to exist in Western Europe exclusively during the mammalian zones MNQ 9 and 10, and is therefore a typical Vallesian species.

PALAEOECOLOGY

Although found in very different parts of the world, recent tapirs except *T. pinchacus* share the following ecological requirements: hot climate, tropical forest, thick vegetation, wet environment and water proximity; all are good rock climbers when necessary. *T. pinchacus* from the Andes, with thick and bristly hairs, lives in scrub and montane forests between 2000 and 4500 meters, going down to bathe in the valleys and climbing back up every day; its way of life, except for temperature, is very close to other tapir species. The fossil tapirs, with their very similar anatomical structure, probably had the same ecological requirements.

Some data exist on the associated floras. At Orignac the microflora is composed by more than 80% of trees; 50% are Taxodiaceae-Cupressaceae (with numerous exotic genera) and 20% are Conifers of the *Pinus haploxylon* type. These data are good evidence fora a "mostly humid and rather warm climate" (Sauvage, 1969). At Priay there are about 75% of trees including Abietaceae probably growing on the surrounding mountains (according to Méon) and the autochtonous trees (Taxodiaceaea, Cupressaceae, Myricaceae, *Alnus, Carya, Nissa*). At Priay, the environment would be less humid than at Orignac (Combémorel et al., 1970). The Dinotheriensande Formation yielded a macroflora with wet forest characteristics (Wenz, 1921).

TAXONOMY AND PHYLOGENETICAL RELATIONS

Von Koenigswald (1930) considered that individual variability in tapirs is great and that all European Upper Miocene tapirs including the very large *T. antiquus* of the Rhine valley and the little unnamed forms found in the Upper Miocene "Bohnerzen" from Southern Germany are no more than "forms", and as such specifically indistinguishable from *T. priscus*. These forms and the problem of *Tapiruscus pannonicus* of Kretzoi are discussed elsewhere in more detail (Guérin and Eisenmann, in press), but it seems that one tooth at least (from Bermersheim, Dinotheriumsande Formation) refered to *T. antiquus* is too large to belong to *T. priscus*. In the *T. priscus* sample we have seen, most of the material is close in size to *T. indicus*, with the exception of the radius; possibly the latter belongs also to *T. antiquus* and not to *T. priscus*.

Von Koenigswald (1930) considered *T. priscus* and *T. arvernensis* as the last representatives of two different lineages, the first, more similar to the Asian *T. indicus*, with a large *Tapirus* sp. from the MN 6 Göriach Austrian site as direct ancestor, and the second, of the *T. terrestris* anatomical type, descending from the *T. telleri* in the same site of Göriach.

Our study does not support this interpretation since *T. priscus* and *T. arvernensis* are anatomically closer to each other than to any recent tapir. Both fossil tapirs, however, do resemble to *T. indicus* by some teeth characters.

CONCLUSIONS

Despite its rarity, *T. priscus* is now rather welldefined species, characteristic of the Vallesian mammal age and seeming to present the classical ecological requirements of the genus. Its anatomical similarities of proportions, namely for the skull, mandible, cheek teeth and talus, with the Villafranchian *T. arvernensis arvernensis* supports a close phylogenetical relationship between the two species, a few characters being shared with *T. indicus*.

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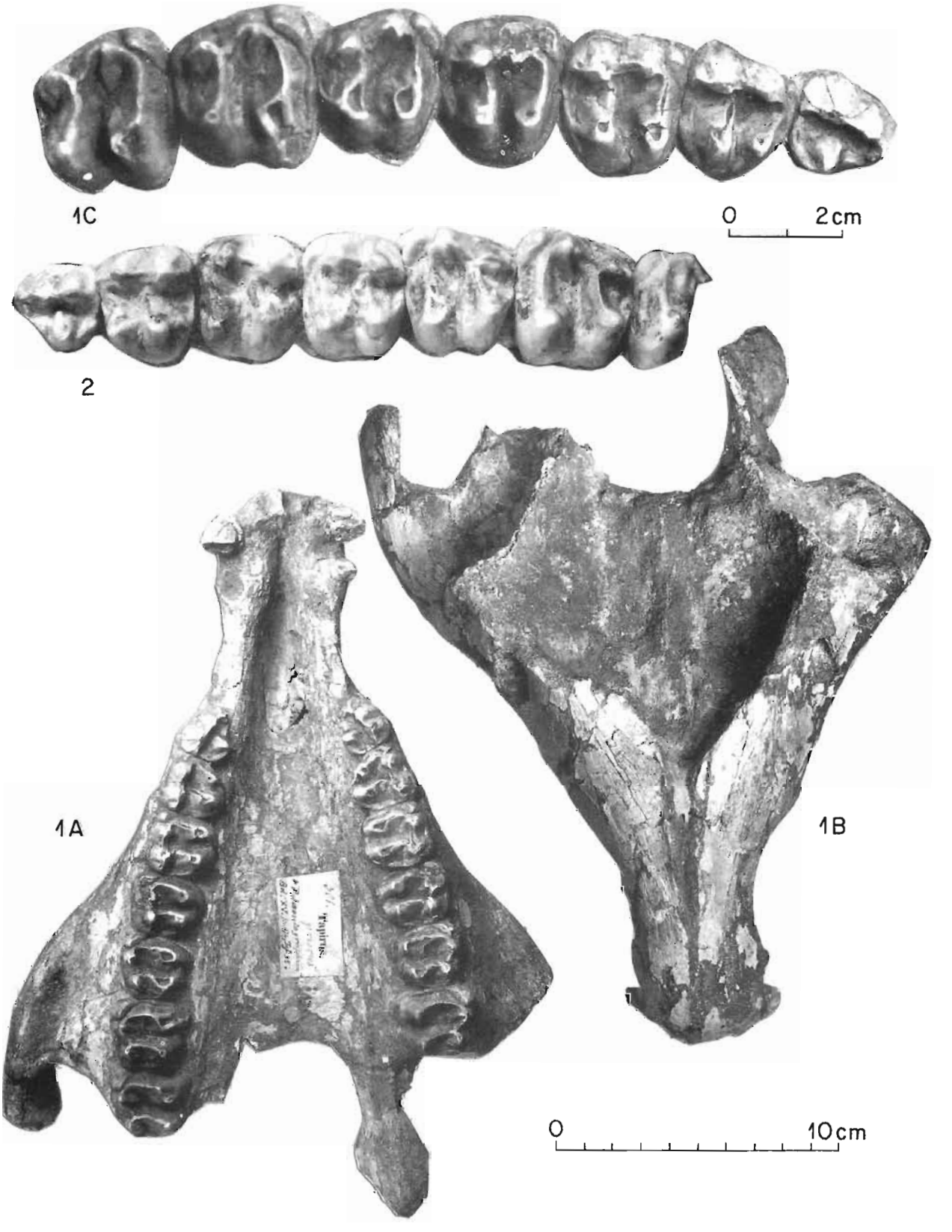

PLATE 1

FIGURE 1. Skull of *Tapirus priscus*, Eppelsheim, n.º 40633 London Natural History collections; 1A: Ventral view; 1B: Dorsal view; 1C: Occlusal view of the Upper right cheek teeth series.

FIGURE 2. Upper left cheek teeth of *Tapirus priscus*, Wissberg, n.º DIN 1091, Hessisches Landesmuseum, Darmstadt; Occlusal view.