

Sivatupaia ramnagarensis and the origin of the subfamily Crocidurinae (Soricidae, Mammalia)

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Taxonomic Note

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Scandentians, commonly known as treeshrews (tree shrews), are the sister group of primates and colugos within the Euarchonta, a clade with an evolutionary history rooted in the Cretaceous (Roberts et al., 2011; Melin et al., 2016). Scandentians are, however, extremely rare in the fossil record (Ni and Qiu, 2012; Li and Ni, 2016) and, other than the Oligocene species *Ptilocercus kylin* Li and Ni, 2016, their earliest undoubted representatives are not older than 18 Ma (Li and Ni, 2016, and references therein).

Recently Sehgal et al. described *Sivatupaia ramnagarensis* Sehgal et al., 2022a, a new genus and species of a purported treeshrew from the Miocene hominoid locality of Dehari (ca. 13.8–12.5 Ma), in the Indian Siwaliks. This occurrence extended the fossil range of the tupaiids in the region by around 2.5–4.0 Myr more than previously reported by Chopra and Vasishat, who described the species *Palaeotupaia sivalicus* Chopra and Vasishat, 1979, from sediments approximately 10.8–8.5 Ma in age. Even though the description of *Sivatupaia* could in principle be considered an advancement on knowledge of the group, there are several features of the holotype of this new species that cast some doubts on its published taxonomic ascription. In fact, we realized that right after the original publication as the same authors published a ‘Corrigendum’ (Sehgal et al., 2022b) to their own work, which we expected to address the same hesitations we have about the taxonomic ascription of *Sivatupaia*. Because we found no mention of that issue, we considered it worthy to formally express our reservations about the taxonomic allocation of this new taxon.

After a thorough inspection of all the data provided, we found several indications to conclude that *Sivatupaia ramnagarensis* does not belong to the family Tupaiidae (Scandentia) and that this holotype can be unequivocally identified as a lower left m1. The identification of the tooth as a first lower molar is because the trigonid and the talonid in the lower molars of scandentians are nearly equal in length and in width in m2 (Butler, 1980). However, such is not the condition displayed by the fossil element described. The talonid of the holotype of *Sivatupaia* is wider than the trigonid. This feature can be found in the m1s of tupaiids (Butler, 1980) as well as in those of many other mammals with tribosphenic molars (see Repenning, 1967, and Reumer, 1984, for Soricidae; Hutchison, 1968, for Talpidae; Butler, 1948, for Erinaceidae; Crochet, 1978, for Tertiary Marsupialia from Europe).

Stronger concerns involve the identification of this taxon. Instead of its original taxonomic placement, there is sound evidence to consider that *Sivatupaia* would be better allocated within the Soricidae (Eulipotyphla). Soricids and scandentians share some peculiar traits in their lower molars, thus easily leading to confusion between both. Mostly, they both retain a clear tribosphenic pattern with the presence of a small cuspid (hypoconulid) in m1 and m2 close to the entoconid but separated from it by a notch.

There are, however, some characters indicating that this tooth belongs to a shrew rather than to a treeshrew. The statement of Sehgal et al. (2022a, p. 1323) that “Shrews and most microchiropteran bats generally have a buccal cingulum as well as a paraconid and metaconid that are more deeply separated than the present specimen” does not seem sufficiently supported, because both criteria demonstrate a wide range of variation when the entire families are considered. The cingula and cingulids of the mammalian teeth have strong effects on their mechanical properties (Anderson et al., 2011), so they are frequently modified by evolutionary constraints. For instance, the genera *Solisorex* and *Soriculus* do not display labial cingulids (Repenning, 1967), and the shrews of the extinct genus *Nesiotites* have shown odd morphologies in their cingulids within a single species (Furió and Pons-Monjo, 2013). In fact, a diverse collection of different conditions in labial and lingual cingulids can be found in the descriptions provided by Repenning (1967) and Reumer (1984) for many extant and extinct soricids.

Following the general descriptions of Butler (1980) for the lower molars, most genera of tupaiids have the three trigonid cuspids arranged in an approximately equilateral triangle,

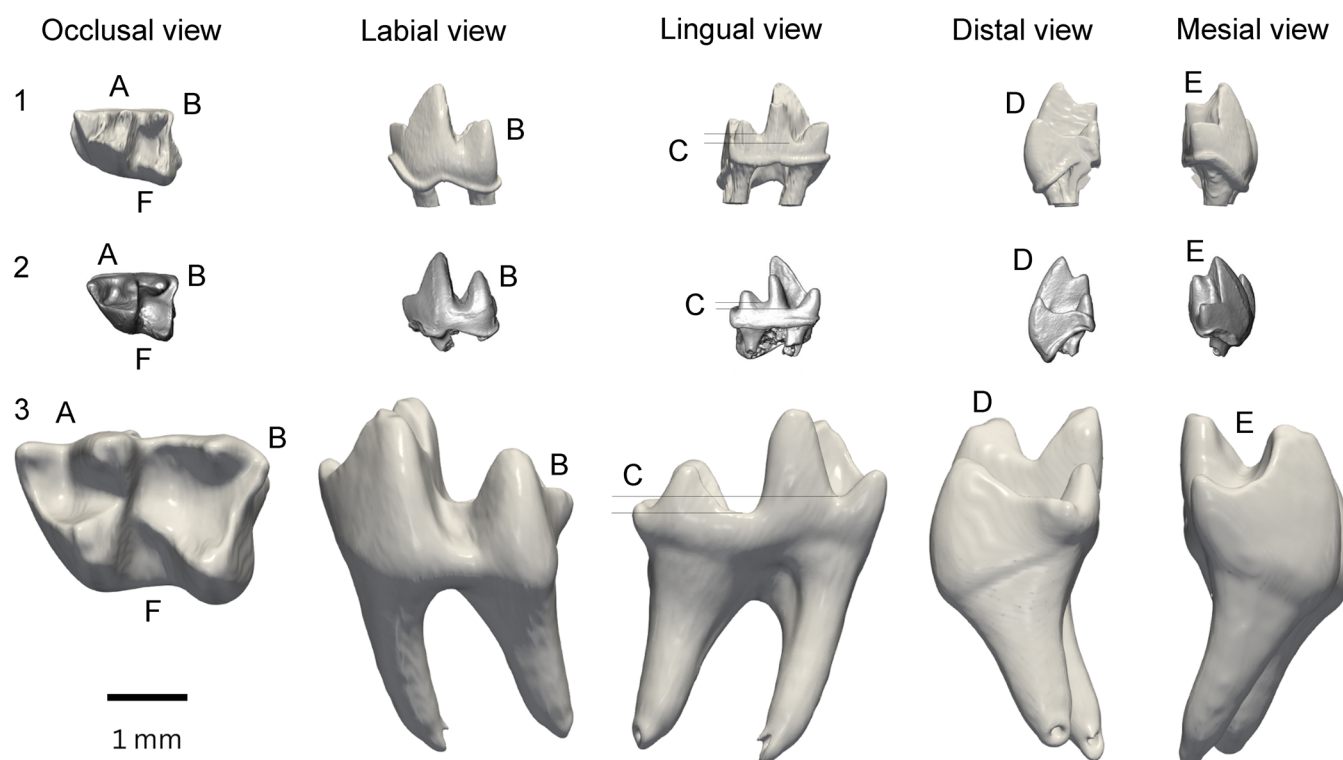


Figure 1. Occlusal, labial, lingual, distal, and mesial views of lower left m1s compared. (1) *Crocidura kornfeldi* from Quibas-Sima (IPHES-QC4/5-1/A1; Catalan Institute of Human Paleoeology and Social Evolution, Spain); (2) *Sivatupaia ramnagarensis* (WIMF/A 4699; Dehari 2, India); (3) *Tupaia tana* Raffles, 1822 (FMNH-14565; Field Museum of Natural History, Morphosource). The characteristic features of the lower molars that make *Sivatupaia* look more similar to a soricid than to a scandentian are: (A) three trigonid cuspids not arranged in equilateral triangle due to the angled morphology of the paracristid in occlusal view (*Crocidura*, *Sivatupaia*); three trigonid cuspids arranged in an approximately equilateral triangle, with a rather smooth curving morphology of the paracristid (*Tupaia*); (B) hypoconulid not protruding the occlusal outline (*Crocidura*, *Sivatupaia*); hypoconulid as a low cusp that overhangs the posterior margin of the tooth (*Tupaia*); (C) lingual opening of the talonid above the lingual opening of the trigonid (*Crocidura*, *Sivatupaia*); lingual opening of the trigonid above the lingual opening of the talonid (*Tupaia*); (D) protoconid clearly higher than metaconid (*Crocidura*, *Sivatupaia*); protoconid slightly lower than (or subequal to) metaconid (*Tupaia*); (E) protolophid showing a soft tilted right angle valley (*Crocidura*, *Sivatupaia*); protolophid showing a deep and rounded intermediate valley (*Tupaia*); and (F) oblique cristid ending almost below the protoconid, leaving little space to develop the reentrant valley (*Crocidura*, *Sivatupaia*); oblique cristid ending less buccally and generating a more pronounced reentrant valley (*Tupaia*).

with the only exceptions of the genera *Anathana* and *Urogale*, in which the trigonids are shortened mesiodistally. The specimen WIMF/A 4699 does not fit the above description (Fig. 1, occlusal view).

However, this is not the only character weakening the argument about the ascription of this fossil to a scandentian species. The most evident one is perhaps the absence of a true hypoconulid, a low cusp that overhangs the posterior margin of the lower molars of the tupaiids (Butler, 1980; Qiu, 1986). This element is connected to the hypoconid by a crest but separated by a groove from the entoconid in all Scandentia. The condition displayed in the fossil from Ramnagar better reproduces the shape of soricids, and more precisely as found in crocidurines (Fig. 1, occlusal and labial views), in which the entoconid cristid of the m1 is usually reduced or absent, the talonid is clearly shorter than the trigonid, the buccal reentrant valley opens high above the cingulum, and there is no trace of pigmentation (Repenning, 1967; Reumer, 1984; Dannelid, 1998).

Other than that, the lingual opening of the trigonid is positioned above the lingual opening of the talonid in *Tupaia*, but the opposite is true in *Crocidura* and *Sivatupaia* (Fig. 1, lingual view), which highlights a distinguishing feature between Soricidae and Tupaiidae (Qiu, 1986).

Another interesting difference observed is the relative sizes of protoconid and metaconid. Whereas in tupaiids the metaconid

is higher than the protoconid or they are both similarly high, in soricids the protoconid is higher than the metaconid (Fig. 1, distal view). Furthermore, the crest linking both cuspids, the protolophid, has a wide valley in tupaiids in distal view. This differs from what is observed in specimen WIMF/A 4699, where the protolophid forms a kind of tilted right angle in frontal view, frequently found in crocidurines. This condition is exemplified by the species *Crocidura kornfeldi* Kormos, 1934 (Fig. 1, mesial view) from the southern Spanish site of Quibas-Sima (Piñero et al., 2020, 2022). Moreover, the position of the contact between the oblique cristid and the protolophid is different, with the contact being closer to the midline of the tooth in *Tupaia*, and nearer the buccal border in *Crocidura* and *Sivatupaia* (Fig. 1, occlusal view).

Finally, size provides an additional clue to this specimen's identification. Better than relative proportions, which are of little value in tribosphenic models, the absolute size of the element found marks a difference between the lower molar of *Sivatupaia* and those of all the species of Scandentia ever known. We have compiled a list of measurements of m1s of shrews and treeshrews (Table 1) based on published data and MorphoSource (Boyer et al., 2016). Figure 2 plots absolute lengths (L) versus talonid widths (TAW) according to the methods in Reumer (1984), placing *Sivatupaia* in the cloud of shrews, far away from the values for treeshrews. Although the larger species of soricids can

Table 1. Measurements of m1 in some fossil and recent species of Soricidae and Scandentia. The sample of soricid fossils is restricted to references in which the measurements have been taken directly by one of the authors to avoid any possible bias in the way of measuring, but Flynn et al. (2020) is also included due to the similar location and aging of the sites sampled. Except for Ni and Qiu (2012), all the measurements in scandentian species have been taken using the data from Morphosource. AMNH = American Museum of Natural History – Mammal Collections, New York City (USA); FMNH = Field Museum of Natural History – Mammal Collection (Zoology), Chicago (USA); IPS = Institut Català de Paleontologia Miquel Crusafont, Barcelona (Spain); IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing (China); MPFI = Max Planck Florida Institute for Neuroscience – Fitzpatrick Lab, Jupiter (USA); QS = Quibas Sima Collection of Museo Arqueológico de Murcia, Murcia (Spain); USNM, National Museum of Natural History – Division of Mammals, Washington D.C. (USA); WIMF/A – Wadia Institute of Himalayan Geology Micro Fossil Collection Series A, Dehradun (India); L = length; TAW = talonid width; ▲ = Soricidae; ● = Scandentia; χ = *Sivatupaia*.

	TAXON	LOCALITY/REGION/MUSEUM	SPECIMEN	L	TAW	REFERENCE/DOI/ARK/ MORPHOSOURCE CODE
▲	<i>Amblyoptus jessiae</i> Doukas in Doukas et al., 1995	Northeastern Spain (Spain)	Mean	3.07	1.40	Furió and Agustí (2017)
▲	<i>Asoriculus gibberodon</i> (Petenyi, 1864)	Capo Mannu D1 (Italy)	Mean	1.59	1.00	Furió and Angelone (2010)
▲	<i>Clapasorex</i> cf. <i>C. alvarezae</i> van den Hoek Ostende, 2003	Turó de les Forques (Spain)	Mean	1.18	0.72	van den Hoek Ostende et al. (2020)
▲	<i>Florinia</i> cf. <i>Florinia</i> sp.	Vallès-Penedès Basin (Spain)	Mean	1.28	0.70	van den Hoek Ostende et al. (2020)
▲	<i>Lartetium</i> cf. <i>Lartetium</i> sp.	Fosso della Fittaia (Italy)	Mean	1.42	1.02	Cirilli et al. (2016)
▲	<i>Oligosorex</i> cf. <i>O. thauensis</i> (Crochet, 1975)	Can Martí Vell 3	IPS - 90097	1.11	0.69	van den Hoek Ostende et al. (2020)
▲	<i>Crocidura kornfeldi</i>	Quibas-Sima (Spain)	Mean	1.42	0.98	Piñero et al. (2022)
▲	<i>Crusafontina endemica</i> Gibert, 1975	Can Feu 2 (Spain)	IPS - 57585	2.04	1.13	Casanovas-Vilar et al. (2012)
▲	<i>Deinsdorfia doukasi</i> Furió and Mein, 2008	Almenara-Casablanca 4 (Spain)	Mean	1.65	0.88	Furió and Mein (2008)
●	<i>Dendrogale melanura</i> (Thomas, 1892)	FMNH (USA)	FMNH 108854	2.24	1.38	ark:/87602/m4/M22226
▲	<i>Dinosorex grycivensis</i> Rzebik-Kowalska & Topachevsky, 1997	Barranc de Can Vila 1 (Spain)	Mean	2.53	1.57	Furió et al. (2011)
▲	<i>Dinosorex grycivensis</i>	Vallès-Penedès Basin (Spain)	Mean	2.58	1.65	Furió et al. (2015)
▲	<i>Miosorex grivensis</i> (Depéret, 1892)	Can Misert (Spain)	Mean	1.45	0.92	Agustí et al. (2005)
▲	<i>Miosorex</i> sp.	Can Martí Vell 2 (Spain)	IPS - 86263	1.38	0.92	van den Hoek Ostende et al. (2020)
▲	<i>Myosorex meini</i> Jammot, 1977	Southeastern Spain (Spain)	Mean	1.32	1.00	Furió et al. (2007)
▲	<i>Neomys</i> sp.	Quibas-Sima (Spain)	QS-1A-03	1.72	1.03	Piñero et al. (2022)
▲	<i>Nesiotites hidalgo</i> Bate, 1944	Canet (Spain)	Mean	2.17	1.43	Pons-Monjo et al. (2012)
▲	<i>Nesiotites meloussae</i> Pons-Moyà and Moyà-Solà, 1980	Binigaus (Spain)	Mean	2.04	1.30	Pons-Monjo et al. (2012)
▲	<i>Nesiotites ponsi-hidalgo</i> Reumer, 1981	Pedrer de s'Onix (Spain)	Mean	2.00	1.27	Pons-Monjo et al. (2012)
▲	<i>Paenelimnoecus repenningi</i> (Bachmayer and Wilson, 1970)	Romerales 2B (Spain)	IPS - 93656	1.02	0.58	Furió and Agustí (2017)
▲	<i>Paenelimnoecus repenningi</i>	Can Vilella (Spain)	Mean	1.10	0.57	Furió and Agustí (2017)
▲	<i>Paenelimnoecus repenningi</i>	Romerales 2C (Spain)	IPS - 93659	1.15	0.61	Piñero et al. (2018)
▲	<i>Paenelimnoecus</i> sp.	Sivas Basin (Turkey)	Mean	1.07	0.65	Furió et al. (2014)
▲	<i>Paenelimnoecus truyolsi</i> (Gibert, 1975)	Calatayud–Montalbán Basin (Spain)	Mean	1.07	0.64	van den Hoek Ostende et al. (2009)
▲	<i>Petenya dubia</i> Bachmayer and Wilson, 1970	Sivas Basin (Turkey)	Mean	1.43	0.87	Furió et al. (2014)
▲	<i>Petenya dubia</i>	Northeastern Spain (Spain)	Mean	1.48	0.84	Furió and Agustí (2017)

(Continued)

Table 1. (Continued.)

	TAXON	LOCALITY/REGION/MUSEUM	SPECIMEN	L	TAW	REFERENCE/DOI/ARK/ MORPHOSOURCE CODE
●	<i>Prodendrogale yunnanica</i> Qiu, 1986	Lufeng, Yunnan (China)	IVPP V 8282.12	2.45	1.60	Ni and Qiu (2012)
	<i>Ptilocercus lowii</i> Gray, 1848	USNM (USA)	USNM 481103	2.60	1.68	doi:10.17602/M2/M6388
	<i>Ptilocercus lowii</i>	USNM (USA)	USNM 481107	2.58	1.73	doi:10.17602/M2/M6391
	<i>Ptilocercus lowii</i>	USNM (USA)	USNM 481108	2.60	1.74	doi:10.17602/M2/M6408
	<i>Ptilocercus lowii</i>	USNM (USA)	USNM 488052	2.73	1.74	doi:10.17602/M2/M6415
	<i>Ptilocercus lowii</i>	USNM (USA)	USNM 488055	2.54	1.67	doi:10.17602/M2/M6418
●	<i>Ptilocercus lowii</i>	USNM (USA)	Mean	2.61	1.71	(Morphosource)
χ	<i>Sivatupaia ramnagarensis</i>	Dehari 2, Ramnagar (India)	WIMF/A 4699	1.17	0.87	Sehgal et al. (2022)
▲	Soricinae indet.	Sivas Basin (Turkey)	Mean	1.34	0.74	Furió et al. (2014)
▲	Soricinae indet.	Bàscara Superior (Spain)	IPS - 33509	1.41	0.84	Furió and Agustí (2017)
▲	Soricinae indet.	El Canyet (Spain)	Mean	1.54	0.98	van den Hoek Ostende et al. (2020)
▲	<i>Suncus honeyi</i> Flynn et al., 2020	Dhok Pathan (Pakistan)	Mean	1.72	1.29	Flynn et al. (2020)
	<i>Tupaia belangeri</i> (Wagner, 1841)	USNM (USA)	USNM 320689	3.70	2.36	doi:10.17602/M2/M6384
	<i>Tupaia belangeri</i>	USNM (USA)	USNM 320655	3.56	2.40	doi:10.17602/M2/M6584
	<i>Tupaia belangeri</i>	USNM (USA)	USNM 320666	3.69	2.46	doi:10.17602/M2/M6605
	<i>Tupaia belangeri</i>	USNM (USA)	USNM 320680	3.61	2.29	doi:10.17602/M2/M6607
	<i>Tupaia belangeri</i>	USNM (USA)	USNM 320690	3.78	2.54	doi:10.17602/M2/M6609
	<i>Tupaia belangeri</i>	AMNH (USA)	AMNH m-272427	3.38	2.08	ark:/87602/m4/M85111
	<i>Tupaia belangeri</i>	AMNH (USA)	AMNH m-272391	3.44	2.14	ark:/87602/m4/M85130
	<i>Tupaia belangeri</i>	MPFI (USA)	l-df:734 BABA	3.51	2.32	doi:10.17602/M2/M6393
●	<i>Tupaia belangeri</i>	AMNH, MPFI, USNM (USA)	Mean	3.58	2.32	(Morphosource)
	<i>Tupaia chrysogaster</i> Miller, 1903	AMNH (USA)	AMNH 103101	3.69	2.66	ark:/87602/m4/M59063
	<i>Tupaia chrysogaster</i>	AMNH (USA)	AMNH 103096	3.70	2.65	doi:10.17602/M2/M59075
	<i>Tupaia chrysogaster</i>	AMNH (USA)	AMNH 103095	3.44	2.54	doi:10.17602/M2/M59072
	<i>Tupaia chrysogaster</i>	AMNH (USA)	AMNH 103110	3.61	2.64	doi:10.17602/M2/M59520
	<i>Tupaia chrysogaster</i>	AMNH (USA)	AMNH 103093	3.55	2.63	doi:10.17602/M2/M59550
●	<i>Tupaia chrysogaster</i>	AMNH (USA)	Mean	3.60	2.62	(Morphosource)
	<i>Tupaia dorsalis</i> Schlegel, 1857	AMNH (USA)	AMNH 32631	3.01	1.89	doi:10.17602/M2/M59090
	<i>Tupaia dorsalis</i>	AMNH (USA)	AMNH 106106	2.96	1.87	doi:10.17602/M2/M59361
	<i>Tupaia dorsalis</i>	AMNH (USA)	AMNH 106104	2.86	1.89	doi:10.17602/M2/M59406
●	<i>Tupaia dorsalis</i>	AMNH (USA)	Mean	2.94	1.88	(Morphosource)
	<i>Tupaia glis</i> (Diard & Duvaucel, 1822)	USNM (USA)	USNM 311305	3.53	2.52	doi:10.17602/M2/M6382
	<i>Tupaia glis</i>	USNM (USA)	USNM 112662	3.47	2.17	doi:10.17602/M2/M6463
	<i>Tupaia glis</i>	USNM (USA)	USNM 311311	3.48	2.22	doi:10.17602/M2/M6698
	<i>Tupaia glis</i>	USNM (USA)	USNM 487950	3.43	2.39	doi:10.17602/M2/M6612
	<i>Tupaia glis</i>	USNM (USA)	USNM 487939	3.48	2.18	doi:10.17602/M2/M15509
●	<i>Tupaia glis</i>	USNM (USA)	Mean	3.48	2.30	(Morphosource)
	<i>Tupaia gracilis</i> Thomas, 1893	AMNH (USA)	AMNH 103850	2.74	1.83	doi:10.17602/M2/M59350
	<i>Tupaia gracilis</i>	AMNH (USA)	AMNH 103620	2.57	1.55	doi:10.17602/M2/M59373

(Continued)

Table 1. (Continued.)

TAXON	LOCALITY/REGION/MUSEUM	SPECIMEN	L	TAW	REFERENCE/DOI/ARK/ MORPHOSOURCE CODE
<i>Tupaia gracilis</i>	AMNH (USA)	AMNH 103619	2.55	1.64	doi:10.17602/M2/M59379
<i>Tupaia gracilis</i>	AMNH (USA)	AMNH 106110	2.46	1.69	doi:10.17602/M2/M59409
● <i>Tupaia gracilis</i>	AMNH (USA)	Mean	2.58	1.68	(Morphosource)
<i>Tupaia javanica</i> Horsfield, 1824	AMNH (USA)	AMNH 101672	2.63	1.89	doi:10.17602/M2/M59376
<i>Tupaia javanica</i>	AMNH (USA)	AMNH 101832	2.60	1.90	doi:10.17602/M2/M59388
<i>Tupaia javanica</i>	AMNH (USA)	AMNH 101663	2.59	1.86	doi:10.17602/M2/M59412
● <i>Tupaia javanica</i>	AMNH (USA)	Mean	2.61	1.88	(Morphosource)
<i>Tupaia minor</i> Günther, 1876	AMNH (USA)	AMNH 103906	2.32	1.55	doi:10.17602/M2/M59353
<i>Tupaia minor</i>	AMNH (USA)	AMNH 102526	2.45	1.55	doi:10.17602/M2/M59382
<i>Tupaia minor</i>	AMNH (USA)	AMNH 102527	2.47	1.64	doi:10.17602/M2/M59385
<i>Tupaia minor</i>	AMNH (USA)	AMNH 102529	2.37	1.57	doi:10.17602/M2/M59394
<i>Tupaia minor</i>	FMNH (USA)	FMNH 141464	2.37	1.72	ark:/87602/m4/M22242
<i>Tupaia minor</i>	FMNH (USA)	FMNH 76865	2.37	1.57	ark:/87602/m4/M30549
● <i>Tupaia minor</i>	AMNH, FMNH (USA)	Mean	2.39	1.60	(Morphosource)
● <i>Tupaia montana</i> Thomas, 1892	FMNH (USA)	FMNH 108831	3.03	2.08	ark:/87602/m4/M22215
<i>Tupaia palawanensis</i> Thomas, 1894	AMNH (USA)	AMNH 207599	3.28	2.25	doi:10.17602/M2/M59356
<i>Tupaia palawanensis</i>	AMNH (USA)	AMNH 29725	3.36	2.56	doi:10.17602/M2/M59391
<i>Tupaia palawanensis</i>	AMNH (USA)	AMNH 207597	3.35	2.45	doi:10.17602/M2/M59397
<i>Tupaia palawanensis</i>	AMNH (USA)	AMNH 175465	3.50	2.62	doi:10.17602/M2/M59523
<i>Tupaia palawanensis</i>	FMNH (USA)	FMNH 62948	3.25	2.37	ark:/87602/m4/M22164
<i>Tupaia palawanensis</i>	FMNH (USA)	FMNH 62976	3.62	2.32	ark:/87602/m4/M28136
● <i>Tupaia palawanensis</i>	AMNH, FMNH (USA)	Mean	3.39	2.43	(Morphosource)
<i>Tupaia salatana</i> Lyon, 1913	AMNH (USA)	AMNH 103612	3.75	2.13	doi:10.17602/M2/M59078
<i>Tupaia salatana</i>	AMNH (USA)	AMNH 103609	3.56	2.56	doi:10.17602/M2/M59087
<i>Tupaia salatana</i>	AMNH (USA)	AMNH 103613	3.46	2.60	doi:10.17602/M2/M59416
<i>Tupaia salatana</i>	AMNH (USA)	AMNH 103614	3.60	2.62	doi:10.17602/M2/M59588
<i>Tupaia salatana</i>	AMNH (USA)	AMNH 103611	3.53	2.53	doi:10.17602/M2/M59591
● <i>Tupaia salatana</i>	AMNH (USA)	Mean	3.58	2.56	(Morphosource)
<i>Tupaia tana</i>	AMNH (USA)	AMNH m-202252	3.61	2.32	ark:/87602/m4/M49395
<i>Tupaia tana</i>	AMNH (USA)	AMNH 102830	3.55	2.22	doi:10.17602/M2/M59081
<i>Tupaia tana</i>	AMNH (USA)	AMNH 102831	3.57	2.28	doi:10.17602/M2/M59084
<i>Tupaia tana</i>	AMNH (USA)	AMNH 102518	3.33	2.34	doi:10.17602/M2/M59422
<i>Tupaia tana</i>	AMNH (USA)	AMNH 102829	3.51	2.47	doi:10.17602/M2/M59578
<i>Tupaia tana</i>	FMNH (USA)	FMNH 145465	3.36	2.18	ark:/87602/m4/M33531
● <i>Tupaia tana</i>	AMNH, FMNH (USA)	Mean	3.49	2.30	(Morphosource)

occasionally fall within the range of tupaiids, *Sivatupaia* is too isolated within the cloud of shrews to be considered a dwarf scandentian according to the available data. Treeshrews (Scandentia) are almost always larger than ‘regular’ shrews (Soricidae), which is likely due to morpho-functional reasons related to their way of living. Many species and subspecies of tupaiids do not differ significantly in size between their mainland and island

counterparts (Juman et al., 2021), even if some patterns of variation combining insularity and latitude are discernible (Juman et al., 2022). Although modern treeshrews occupy a much more restricted geographical distribution than they did in the past (according to their known fossil record), the mean body mass of all present-day species of treeshrews ranges from 45 to 224 grams (Sargis, 2002) and their lengths of head and body range

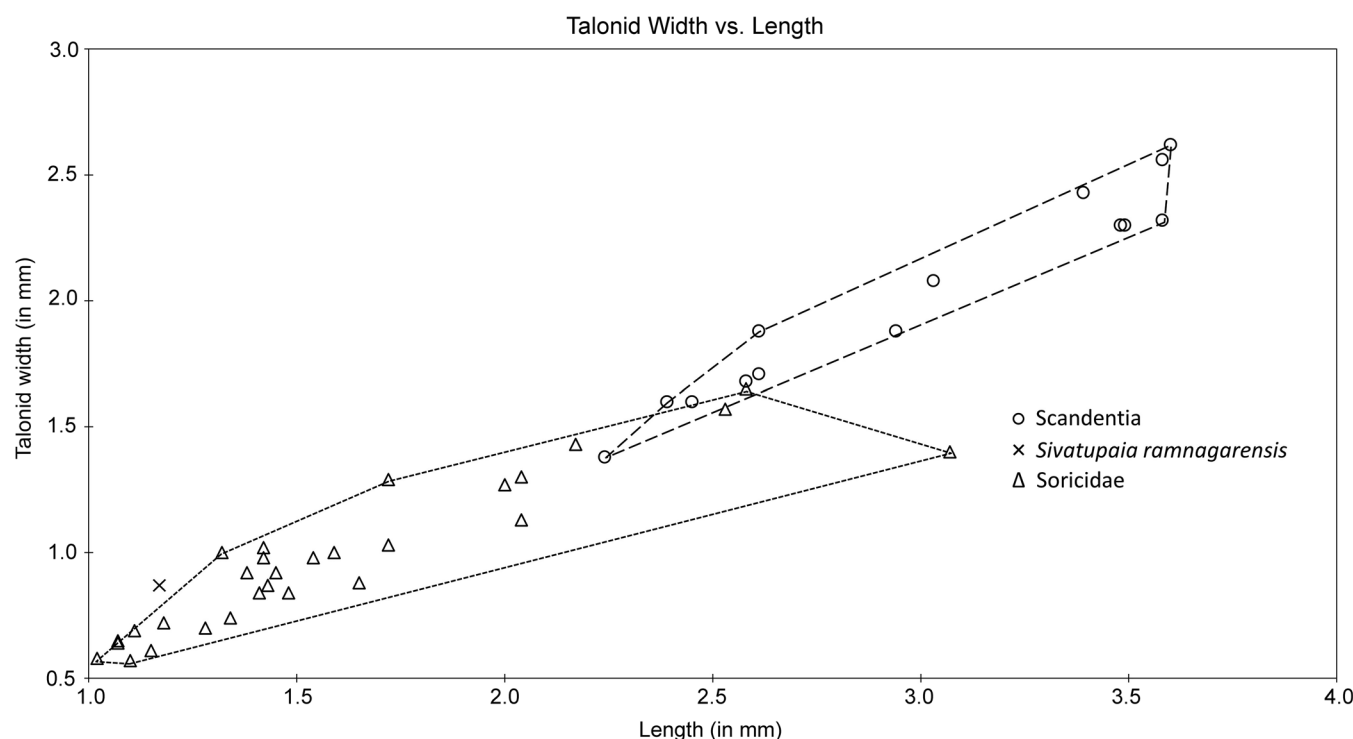


Figure 2. Scatter diagram plotting length (L) versus talonid width (TAW) of m1 in several extinct and extant species of Scandentia and Soricidae. Detailed data and original references for the measurements are provided in [Table 1](#).

from 100 to 225 mm (Stone, 1995), which are out of the expected range for a species with a molar scarcely longer than 1 mm.

For all these reasons, we consider that the specimen WIMF/A 4699 does not belong to a treeshrew. Nevertheless, this likely misidentification of the fossil tooth does not depreciate its real importance. Judging by the ratio between length and width of trigonid and talonid, this lower m1 most likely belongs to a white-toothed shrew. The morphological traits of the m1 of *Sivatupaia ramnagarensis* are typically found in crocidurine species, where the talonid is usually shorter but wider than its corresponding trigonid. Oddly, Crocidurinae and Tupaiidae share their mysterious evolutionary histories, with a gap in the fossil record between their purported origins and their corresponding oldest fossil records.

Some controversy exists on the origin of the white-toothed shrews. Due to its current diversity, Africa has been considered as a likely cradle for the origin of the Crocidurinae (Butler, 1998, 2010). However, the oldest unequivocal records of the subfamily in Africa do not extend in time beyond the Pliocene (Butler, 1998; Stoetzel, 2013). In fact, some molecular studies have suggested more complex evolutionary histories within crocidurines than expected, deducing Eurasian or Afrotropical origins for different genera (Dubey et al., 2007, 2008).

Reumer (1984) considered that there were representatives of the Crocidurinae in Europe from the Early Miocene onwards, but in that work, he included some members with plesiomorphic characters that were finally reallocated into the subfamily Crocidosoricinae (Reumer, 1987). Thus, the fossil record of the subfamily in Europe is strictly limited to the Pliocene and Pleistocene (Rzebik-Kowalska, 1998), apparently restricting its latitudinal distribution for a long time due to climatic oscillations (Rzebik-Kowalska, 1995; Furió et al., 2007; Rofes and Cuenca-Bescós, 2011).

The fossil record of white-toothed shrews is longer in Asia. According to Storch et al. (1998), the oldest unequivocal fossil occurrences of crocidurines in the world come from the Middle Miocene localities of Koçgazi and Sofça (Engesser, 1980), even though they could not be identified at the genus level. However, these occurrences are predated by recent discoveries from the Siwaliks of Pakistan, where crocidurine fossil elements with ages as old as 14 Ma have been reported by Flynn et al. (2020).

All these fossil finds reinforce the idea that the origin of the subfamily must be found in Asia rather than in Africa. In this sense, the holotype of *Sivatupaia ramnagarensis* is important because it aligns with the m1s attributed to the genera *Crociodura* and *Suncus* in Flynn et al. (2020). Indeed, the overall shape of the specimen WIMF/A 4699 exhibits numerous characters in common with the genera *Crociodura* and *Suncus*, such as the rather short talonid compared to the trigonid, the small and low entoconid cristid, the absence of pigmentation, and the small size.

Unfortunately, *Sivatupaia ramnagarensis* is smaller than all the species described by Flynn et al. (2020), so any possible synonymy with the species already identified from the Siwaliks is precluded. In fact, crocidurines display a high rate of phenotypic homoplasy and a low phylogenetic signal of some morphological features (Voyta et al., 2022). Therefore, according to the latter work, the generic identification by Flynn et al. (2020) should be regarded as tentative due to the constraints imposed by the limited available material. Unlike molecular studies, which clearly track the phylogenetic relationships between many extant species, the morphology and the diagnostic characters of the transitional fossil forms between the Crocidosoricinae and the Crocidurinae are still unknown (Voyta et al., 2022). With the only possible exception of *Turiasorex*, which also displays short talonids in its lower molars and no pigmentation in its teeth (van Dam et al., 2011),

there are no clear candidates to fill the evolutionary gap from one group to another group. More surprisingly, no African site has ever provided unequivocal fossils of crocidurines of Miocene age (Butler, 1998, 2010; Stoetzel, 2013).

Therefore, whatever the generic identification of *Sivatupaia ramnagarensis* will eventually be, such a new find of a fossil element of a Crocidurinae (or a closely related Crocidosoricinae ancestor) at ages around 13 Ma reinforces the idea of Western Asia as the source area for the origin of the subfamily. This raises new questions, such as why crocidurines constrained their distribution in this area for so long, whereas in the African continent they radiated rapidly and expanded to all the existing habitats, or what was (or were) the factor (or factors) during the Miocene precluding the expansion of crocidurines into European lands. On the other hand, the question about why it is so hard to find fossil elements of Scandentia remains unsolved. All these questions require new fossil finds and their subsequent studies to be answered.

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References

- Agustí, J., Casanovas-Vilar, I., and Furió, M., 2005, Rodents, insectivores and chiropterans (Mammalia) from the late Aragonian of Can Missert (Middle Miocene, Vallès-Penedès Basin, Spain): *Geobios*, v. 38, p. 575–583.
- Anderson, P.S.L., Gill, P.G., and Rayfield, E.J., 2011, Modeling the effects of cingula structure on strain patterns and potential fracture in tooth enamel: *Journal of Morphology*, v. 272, p. 50–65.
- Bachmayer, F., and Wilson, R.W., 1970, Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria: *Annalen des Naturhistorischen Museums in Wien*, v. 74, p. 533–587.
- Bate, D.M.A., 1944, Pleistocene shrews from the larger western Mediterranean islands: *Annals and Magazine of Natural History*, v. 11, p. 738–769.
- Boyer, D.M., Gunnell, G.F., Kaufman, S., McGeary, T., 2016, MorphoSource—archiving and sharing 3D digital specimen data: *Journal of Paleontology*, v. 22, p. 157–181.
- Butler, P.M., 1948, On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum: *Proceedings of the Zoological Society of London*, v. 118, p. 446–500.
- Butler, P.M., 1980, The tupaiid dentition, in Luckett, W.P., ed., *Comparative Biology and Evolutionary Relationships of Tree Shrews*: New York, Plenum, p. 171–204.
- Butler, P.M., 1998, Fossil history of shrews in Africa, in Wojcik, J.M., and Wolsan, M., eds., *Evolution of Shrews*: Mammal Research Institute, Polish Academy of Science, Białowieża, p. 121–132.
- Butler, P.M., 2010, Neogene Insectivora, in Werdelin, L., and Sanders, W.J., eds., *Cenozoic Mammals of Africa*: Berkeley, California, University of California Press, p. 573–580.
- Casanovas-Vilar, I., Furió, M., Alba, D.M., Moyà-Solà, S., and Méndez, J.M., 2012, Rodents and insectivores from the hominoid-bearing site of Can Feu (Vallès-Penedès Basin, Catalonia, Spain): *Journal of Vertebrate Paleontology*, v. 32, p. 225–230.
- Chopra, S.R.K. and Vasishat, R.N., 1979, Šivalik fossil tree shrew from Haritalyangar, India: *Nature*, v. 281, p. 214.
- Cirilli, O., Benvenuti, M.G., Carnevale, G., Casanovas-Vilar, I., Delfino, M., Furió, M., Papini, M., Villa, A., and Rook, L., 2016, Fosso della Fittiaia: the oldest Tusco-Sardinian Late Miocene endemic vertebrate assemblages (Baccinello-Cinigiano Basin, Tuscany, Italy): *Rivista Italiana di Paleontologia e Stratigrafia*, v. 122, p. 13–34.
- Crochet, J.Y., 1975, Diversité des insectivores soricidés du Miocène inférieur de France: *Colloques Internationaux du Centre National de la Recherche Scientifique*, v. 218, p. 631–652.
- Crochet, J.Y., 1978, *Les Marsupiaux du Tertiaire d'Europe* [PhD thesis]: Montpellier, France, Université des Sciences et Techniques du Languedoc, 360 p.
- Dannellid, E., 1998, Dental adaptations in shrews, in Wojcik, J.M., and Wolsan, M., eds., *Evolution of Shrews*: Mammal Research Institute, Polish Academy of Science, Białowieża, p. 157–174.
- Deperet, C., 1892, La faune de Mammifères Miocènes de la Grive-Sainl-Alban (Isère) et de quelques autres localités du bassin du Rhône: *Archives du Muséum d'Histoire Naturelle de Lyon*, v. 5, p. 1–93.
- Diard, P.M., and Duvaucl, A., 1822, Sur une nouvelle espèce de Sorex – Sorex Glis: *Asiatick Researches, or, Transactions of the Society Instituted in Bengal, for Inquiring into the History and Antiquities, the Arts, Sciences, and Literature of Asia*, v. 14, p. 471–475.
- Doukas, C.S., van den Hoek Ostende, L.W., Theodoropoulos, C., and Reumer, J.W.F., 1995, Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia), in Schmidt-Kittler, N., ed., *The Vertebrate Locality Maramena (Macedonia, Greece) at the Turolian–Ruscinian Boundary*: Münchner Geowissenschaftliche Abhandlungen, v. A28, p. 43–64.
- Dubey, S., Salamin, N., Ohdachi, S.D., Barrière, P., and Vogel, P., 2007, Molecular phylogenetics of shrews (Mammalia: Soricidae) reveal timing of transcontinental colonizations: *Molecular Phylogenetics and Evolution*, v. 44, p. 126–137.
- Dubey, S., Salamin, N., Ruedi, M., Barrière, P., Colyn, M., and Vogel, P., 2008, Biogeographic origin and radiation of the Old World crocidurine shrews (Mammalia: Soricidae) inferred from mitochondrial and nuclear genes: *Molecular Phylogenetics and Evolution*, v. 48, p. 953–963.
- Engesser, B., 1980, Insectivora und Chiroptera (Mammalia) aus dem Neogen der Türkei: *Schweizerische Paläontologische Abhandlungen*, v. 102, p. 47–149.
- Flynn, L.J., Jacobs, L.L., Kimura, Y., Taylor, L.H., and Tomida, Y., 2020, Siwalik fossil Soricidae: a calibration point for the molecular phylogeny of *Suncus. Paludicola*, v. 12, p. 247–258.
- Furió, M., and Agustí, J., 2017, Latest Miocene insectivores from eastern Spain: evidence for enhanced latitudinal differences during the Messinian: *Geobios*, v. 50, p. 123–140.

- Furió, M., and Angelone, C., 2010, Insectivores (Erinaceidae, Soricidae, Talpidae; Mammalia) from the Pliocene of Capo Mannu D1 (Mandriola, central-western Sardinia, Italy): *Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen*, v. 258, p. 229–242.
- Furió, M., and Mein, P., 2008, A new species of *Deinsdorfia* (Soricidae, Insectivora, Mammalia) from the Pliocene of Spain: *Comptes Rendus Palevol*, v. 7, p. 347–359.
- Furió, M., and Pons-Monjo, G., 2013, The use of the species concept in paleontology. Comment on “*Nesiotites rafelinensis* sp. nov., the earliest shrew (Mammalia, Soricidae) from the Balearic Islands, Spain” by Rofes et al., 2012: *Palaeontologia Electronica*, v. 16, 16.2.16A, <https://doi.org/10.26879/336>.
- Furió, M., Santos-Cubedo, A., Minwer-Barakat, J., and Agustí, J., 2007, Evolutionary history of the African soricid *Myosorex* (Insectivora, Mammalia) out of Africa: *Journal of Vertebrate Paleontology*, v. 27, p. 1018–1032.
- Furió, M., Casanovas-Vilar, I., Moyà-Solà, S., Köhler, M., Galindo, J., and Alba, D.M., 2011, Insectivores (Eulipotyphla; Mammalia) from the Middle Miocene of Barranc de Can Vila 1 (Vallès-Penedès Basin, Catalonia, Spain): *Geobios*, v. 44, p. 199–213.
- Furió, M., van Dam, J.A., and Kaya, R., 2014, New insectivores (Lipotyphla, Mammalia) from the Late Miocene of the Sivas Basin, Central Anatolia: *Bulletin of Geosciences*, v. 89, p. 163–181.
- Furió, M., Prieto, J., and van den Hoek Ostende, L.W., 2015, Three million years of ‘Terror-Shrew’ (*Dinosorex*, Eulipotyphla, Mammalia) in the Miocene of the Vallès-Penedès Basin (Barcelona, Spain): *Comptes Rendus Palevol*, v. 14, p. 111–124.
- Gibert, J., 1975, New insectivores from the Miocene of Spain: *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, v. 78, p. 108–133.
- Gray, J.E., 1848, Description of a new genus of Insectivorous Mammalia, or Talpidae, from Borneo: *Proceedings of the Zoological Society of London*, v. 16, p. 23–24.
- Günther, A., 1876, Remarks on some Indian and, more especially, Bornean mammals: *Proceedings of the Zoological Society of London*, v. 1876, p. 424–428.
- Horsfield, T., 1824, *Zoological Researches in Java, and the Neighbouring Islands, Volume 1*: London, Kingsbury, Parbury, & Allen, 328 p.
- Hutchison, J.H., 1968, Fossil Talpidae (Insectivora, Mammalia) from the later Tertiary of Oregon: *Bulletin of the Museum of Natural History of Oregon*, v. 11, p. 1–117.
- Jammot, D., 1977, Les Musaraignes (Soricidae, Insectivora) du Plio-Pleistocene d'Europe. [Ph.D. Thesis]: Dijon, France, Université de Dijon, 341 p.
- Juman, M.M., Woodman, N., Olson L.E., and Sargis E.J., 2021, Ecogeographic variation and taxonomic boundaries in large treeshrews (Scandentia, Tupaiidae: *Tupaia tana* Rafes, 1821) from Southeast Asia: *Journal of Mammalogy*, v. 102, p. 1054–1066.
- Juman, M.M., Millien, V., Olson, L.E., and Sargis E.J., 2022, Recent and rapid ecogeographical rule reversals in northern treeshrews: *Scientific Reports*, v. 12, p. 19689, <https://doi.org/10.1038/s41598-022-23774-w>.
- Kormos, T., 1934, Neue Insektenfresser, Fledermäuse und Nager aus dem Oberpliozän der Villányer Gegend: *Földtani Közlöny*, v. 64, p. 296–321.
- Li, Q., and Ni, X., 2016, An early Oligocene fossil demonstrates treeshrews are slowly evolving “living fossils”: *Scientific Reports*, v. 6, p. 18627, <https://doi.org/10.1038/srep18627>.
- Lyons, M.W., 1913, Treeshrews: an account of the mammalian family Tupaiidae: *Proceedings of the United States National Museum*, v. 45, p. 1–186.
- Melin, A.D., Wells, K., Moritz, G.L., Kistler, L., Orkin, J.D., et al., 2016, Euarchontan opsin variation brings new focus to primate origins: *Molecular Biology and Evolution*, v. 33, p. 1029–1041.
- Miller, G.S., 1903, Seventy new Malayan mammals: *Smithsonian Miscellaneous Collections*, v. 45, p. 1–73.
- Ni, X., and Qiu, Z., 2012, Tupaiine tree shrews (Scandentia, Mammalia) from the Yuanmou *lufengpithecus* locality of Yunnan, China: *Swiss Journal of Palaeontology*, v. 131, p. 51–60.
- Petényi, S.J., 1864, A Beremendi mészkőbánya természetrajz- és őslénytanilag leírva. Hátrahagyott munkái. [Geological and palaeontological description of the Beremend limestone quarry. Posthumous works.]: *Magyar Tudományos Akadémia Kiadása*, v. 1, p. 35–81. [in Hungarian]
- Piñero, P., Agustí, J., Furió, M., and Laplana, C., 2018, Rodents and insectivores from the Late Miocene of Romerales (Fortuna Basin, Murcia): *Historical Biology*, v. 30, p. 336–359.
- Piñero, P., Agustí, J., Oms, O., Blain, H. A., Furió, M., Laplana, C., Sevilla, P., Rosas, A., and Vallverdú, J., 2020, First continuous pre-Jaramillo to Jaramillo terrestrial vertebrate succession from Europe: *Scientific Reports*, v. 10, 1901, <https://doi.org/10.1038/s41598-020-58404-w>.
- Piñero, P., Agustí, J., Laborda, C., Duval, M., Zhao, J.-X., Blain, H.-A., Furió, M., Laplana, C., Rosas, A., and Sevilla, P., 2022, Quibas-Sima: a unique 1 ma-old vertebrate succession in southern Iberian Peninsula: *Quaternary Science Reviews*, v. 283, 107469, <https://doi.org/10.1016/j.quascirev.2022.107469>.
- Pons-Monjo, G., Moyà-Solà, S., and Furió, M., 2012, New data on the origin of *Nesiotites* (Soricidae, Mammalia) in Menorca (Balearic Islands, Spain): *Comptes Rendus Palevol*, v. 11, p. 393–401.
- Pons-Moyà, J., and Moyà-Solà, S., 1980, Nuevo representante del género *Nesiotites* Bate, 1944; *Nesiotites meloussae* nov. sp. (Insectivora, Soricidae) de los rellenos cársticos del Barranc de Binigaus (Es Mercadal, Menorca): *Endins*, v. 7, p. 53–56.
- Qiu, Z., 1986, Fossil tupaiid from the hominoid locality of Lufeng, Yunnan: *Vertebrata Palasiatica*, v. 24, p. 308–319.
- Raffles, T.S., 1822, Descriptive catalogue of a zoological collection made on account of the Honourable East India Company, in the island of Sumatra and its vicinity, under the direction of Sir Thomas Stamford Raffles, Lieutenant-Governor of Fort Malborough; with additional notices illustrative of the natural history of those countries: *The Transactions of the Linnean Society of London*, v. 13, p. 239–274.
- Repenning, C.A., 1967, Subfamilies and genera of the Soricidae: *US Geological Survey Professional Paper*, v. 565, p. 1–74.
- Reumer, J.W.F., 1981, The Pleistocene small mammals from Sa Pedrera de S'Onix, Majorca (Gliridae, Soricidae): *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, v. 84, p. 2–11.
- Reumer, J.W.F., 1984, Ruscinian and Early Pleistocene Soricidae from Tegelen (The Netherlands) and Hungary: *Scripta Geologica*, v. 73, p. 1–173.
- Reumer, J.W.F., 1987, Redefinition of the Soricidae and the Heterosoricidae (Insectivora, Mammalia), with the description of the Crocidisoricinae, a new subfamily of Soricidae: *Revue de Paléobiologie*, v. 6, p. 189–192.
- Roberts, T.E., Lanier, H.C., Sargis, E.J., and Olson, L.E., 2011, Molecular phylogeny of treeshrews (Mammalia: Scandentia) and the timescale of diversification in Southeast Asia: *Molecular Phylogenetics and Evolution*, v. 60, p. 358–372.
- Rofes, J., and Cuenca-Bescós, G., 2011, Evolutionary history and biogeography of the genus *Crociodura* (Mammalia, Soricidae) in Europe, with emphasis on *Crociodura kornfeldi*: *Mammalian Biology*, v. 72, p. 64–78.
- Rzebik-Kowalska, B., 1995, Climate and history of European shrews: *Acta Zoologica Cracoviensis*, v. 38, p. 95–107.
- Rzebik-Kowalska, B., 1998, Fossil history of shrews in Europe, in Wojcik, J.M., and Wolsan, M., eds., *Evolution of Shrews*: Mammal Research Institute, Polish Academy of Science, Białowieża, p. 23–92.
- Rzebik-Kowalska, B., and Topachevsky, V.O., 1997, Insectivora (Mammalia) from the Miocene of Grytsiv in Ukraine. I. Heterosoricidae Viret and Zapfe, 1951: *Acta Zoologica Cracoviensis*, v. 40, p. 237–247.
- Sargis, E.J., 2002, A multivariate analysis of the postcranium of tree shrews (Scandentia, Tupaiidae) and its taxonomic implications: *Mammalia*, v. 66, p. 579–598.
- Schlegel, H., 1857, *Handleiding tot de Beoefening der Dierkunde 1*: Leiden, The Netherlands, Koninklijke Militaire Akademie, Zee- en Landmagt, 532 p.
- Sehgal, R.K., Singh, A.P., Gilbert, C.C., Patel, B.A., Campisano, C.J., Selig, K.R., Patnaik, R., and Singh, N.P., 2022a, A new genus of treeshrew and other micromammals from the Middle Miocene hominoid locality of Ramnagar, Udhampur District, Jammu and Kashmir, India: *Journal of Paleontology*, v. 96, p. 1318–1335.
- Sehgal, R.K., Singh, A.P., Gilbert, C.C., Patel, B.A., Campisano, C.J., Selig, K.R., Patnaik, R., and Singh, N.P., 2022b, A new genus of treeshrew and other micromammals from the Middle Miocene hominoid locality of

- Ramnagar, Udhampur District, Jammu and Kashmir, India – Corrigendum: *Journal of Paleontology*, v. **96**, p. 1482.
- Stoetzel, E.**, 2013, Late Cenozoic micromammal biochronology of northwestern Africa: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. **392**, p. 359–381.
- Stone, R.D.**, 1995, *Eurasian Insectivores and Tree Shrews – Status Survey and Conservation Action Plan*: IUCN (The World Conservation Union), Gland, Switzerland, 108 p., <https://portals.iucn.org/library/sites/library/files/documents/1995-059.pdf>.
- Storch, G., Qiu, Z., and Zazhigin, V.S.**, 1998, Fossil history of shrews in Asia, in Wojcik, J.M., and Wolsan, M., eds., *Evolution of Shrews*: Mammal Research Institute, Polish Academy of Science, Białowieża, p. 93–120.
- Thomas, O.**, 1892, On some new Mammalia from the East-Indian Archipelago: *Annals and Magazine of Natural History*, ser. 6, v. **9**, p. 250–254.
- Thomas, O.**, 1893, Description of a new Bornean Tupaia: *Annals and Magazine of Natural History*, ser. 6, v. **12**, p. 53–54.
- Thomas, O.**, 1894, On the Palawan representative of *Tupaia ferruginea*: *Annals and Magazine of Natural History*, ser. 6, v. **13**, p. 367.
- van Dam J.A., van den Hoek Ostende, L.W., and Reumer J.W.F.**, 2011, A new short-snouted shrew from the Miocene of Spain: *Geobios*, v. **44**, p. 299–307.
- van den Hoek Ostende, L.W.**, 2003. Insectivores (Erinaceomorpha, Soricomorpha, Mammalia) from the Ramblan of the Daroca-Calamocha area: *Coloquios de Paleontología*, v. Extr. 1, p. 281–310.
- van den Hoek Ostende, L.W., Furió, M., and García-Paredes, I.**, 2009, New data on *Paenelimnoecus* from the Middle Miocene of Spain support the shrew subfamily Allosoricinae: *Acta Palaeontologica Polonica*, v. **54**, p. 159–164.
- van den Hoek Ostende, L.W., Casanovas-Vilar, I., and Furió, M.**, 2020, Stuck in the middle. A geographical appraisal of the oldest insectivores – and a marsupial – from the Vallès-Penedès Basin (Early Miocene, Catalonia, Spain): *Comptes Rendus Palevol*, v. **19**, p. 1–25, <https://doi.org/10.5852/cr-palevol2020v19a1>.
- Voyta, L.L., Abramov, A.V., Lavrenchenko, L.A., Nicolas, V., Petrova, E.A., and Kryuchkova, L.Y.**, 2022, Dental polymorphisms in *Crocidura* (Soricomorpha: Soricidae) and evolutionary diversification of crocidurine shrew dentition: *Zoological Journal of the Linnean Society*, v. **196**, p. 1069–1093.
- Wagner, J.A.**, 1841, Das peguanische Spitzhörnchen, in Schreber, J.C.D., *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen*. Vol. Suppl. 2: Erlangen, Expedition des Schreber'schen Säugethier- und des Esper'schen Schmetterlingswerkes, p. 42–43.