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A NEW SPECIES OF *PLESIOSOREX* (MAMMALIA, EULIPOTYPHLA) FROM THE EARLY MIOCENE OF JAPAN: FIRST RECORD OF THE GENUS FROM EAST ASIA

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Abstract: A nearly complete dentary with preserved i2, p3 and m1 of a relatively large soricomorph from the Dota locality, Kani Basin, Early Miocene (ca. 18.5 Ma), Nakamura Formation of the Mizunami Group in central Japan, is described as a new species of *Plesiosorex*. It represents the first record of the genus in East Asia. *Plesiosorex fejfari* sp. nov. has a slender dentary, posteriorly elongated angular and condyloid processes, p3 with two roots, and m1 without hypoconulid or cingulid. Cladistic analysis of *Butselia gracilis* and seven species of *Plesiosorex* shows that *Butselia* is basally positioned with respect to *Plesiosorex*, and it seems likely that *Plesiosorex* originated in Europe at the beginning of the Miocene and expanded its distribution to East Asia and North America during the Early Miocene. Two Middle Miocene North American species are more closely related to each other than to European species of the same age.

Key words: *Plesiosorex fejfari*, Eulipotyphla, Nakamura Formation, Neogene, Kani Basin

Introduction

Fossils of Paleogene and Neogene small mammals – rodents, lagomorphs and eulipotyphlans – are extremely rare in Japan (Tomida et al. 2013). Most of the known fossils come from the Early Miocene Dota locality in the Kani Basin of central Japan (Text-fig. 1). They comprise eight taxa: three castorids, three eomyids, one ochotonid and one plesiosoricid (Tomida 2011, Tomida et al. 2013). Of these eight taxa, three have been described in detail: two castorids *Youngofiber sinensis* and *Minocastor godai*, and one eomyid *Megapeomys repenningi*, the latter two species being known only from Dota (Tomida et al. 1995, Tomida 2011, Mörs et al. 2016), and another castorid is in the process of being described (Mörs and Tomida in press).

The goal of our paper is to describe the plesiosoricid from the Dota locality. It is the first published record of the genus *Plesiosorex* for Japan, if not for all of East Asia, and we assign it to a new species. The specimen described in this paper, a nearly complete dentary with a few teeth in place, is derived from terrestrial Miocene sediments exposed on the southern (left) bank of the Kiso river in Dota village (part of Kani City) in Gifu Prefecture (Text-fig. 1b). The sediments exposed in this area stratigraphically represent an approximately 10 meter thick section near the top of the Nakamura Formation (Text-fig. 1c). They consist of alternations of thin beds of lignite, mudstone, siltstone and fine sandstone, with relatively thick sandstone beds (Shikano 1995). Magnetostratigraphic and radiometric data indicate that Dota has a numerical age of around 18.5 Ma (Text-fig. 1c). For a more detailed discussion of chrono- and biostratigraphy as well as faunal correlations, see Tomida et al. (2013). Other vertebrates comprise cyprinid and amiid fishes (Yasuno 1982, Yabumoto and Grande 2013).

Material and methods

The new specimen was discovered in 1995 by T. Goda in Aichi Prefecture, Japan, on the left bank of the Kiso river (Text-fig. 1), in the Dota area, Kani City. One of the authors (YT) visited the locality with Goda and examined the site and its stratigraphic horizon. Goda prepared the specimen and donated it to the National Museum of Nature
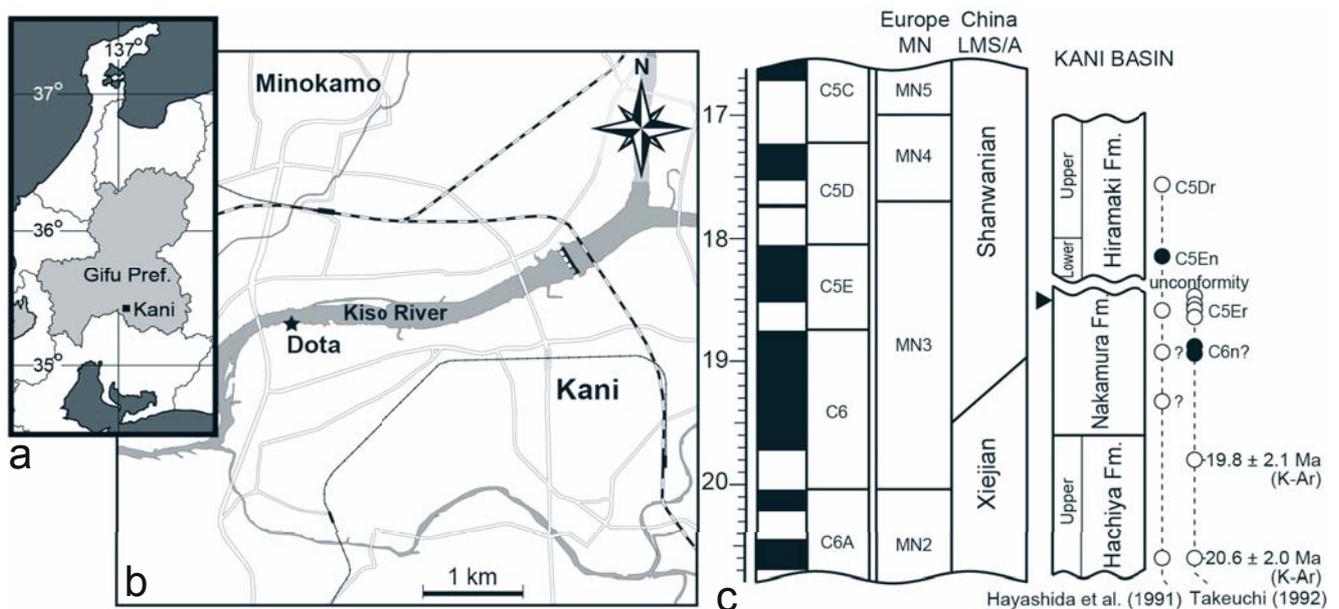
Text-fig. 1. Map showing the locality of *Plesiosorex fejfari* sp. nov. and chronological relationship of the Nakamura Formation (from Mörs et al. 2016). a. general location of Kani City; b. geographical map showing the type locality (solid star) near Dota village in Kani City; c. chronological relationships of the Miocene strata in the Kani Basin. For further information, see Mörs et al. (2016).

and Science. The specimen in the host rock was replicated before the complete preparation, and the cast is catalogued with the original jaw specimen. The host rock is grayish sandstone. The bone and dentine are stained brown, while the enamel of the crown is almost black.

For the morphological terminology and measurements of the mandible and dentition, we follow Jin and Kawamura (1996), which is mainly based on Reumer (1984). Measurements were taken with the caliper tool of a KEYENCE VHX-900 digital microscope and they are presented in Text-fig. 3 and Table 1. Tooth identifications are abbreviated as follows: i1–3 lower incisors, c lower canine, p1–4 lower premolars, m1–3 lower molars. In some species of the genus *Plesiosorex*, the lower dentition is complete (which means 3 incisors, 1 canine, 4 premolars, and 3 molars are readily discernable), but one tooth between i2 and p3 is

missing in other species. We agree with Gunnell et al. (2008: 112) that the missing tooth is a canine. Basic dental formula of the lower dentition in Placentalia is 3·1·4·3, and when a given placental species shows this dental formula, we use the term "complete", or "complete dentition". Dentary height is described as shallow/deep, rather than low/high.

In order to complete the data matrix of character states, data were obtained mainly from the literature and partly from casts of specimens, except for the specimen described in this paper. For details, see the caption for Table 2.

Institutional abbreviations

KU – University of Kansas Museum of Natural History, Lawrence, USA; NMNS – National Museum of Nature and Science, Tokyo, Japan; UNSM – University of Nebraska State Museum, Lincoln, USA.

Systematic palaeontology

Order Eulipotyphla WADDELL, OKADA et HASEGAWA, 1999
Family Plesiosoricidae WINGE, 1917

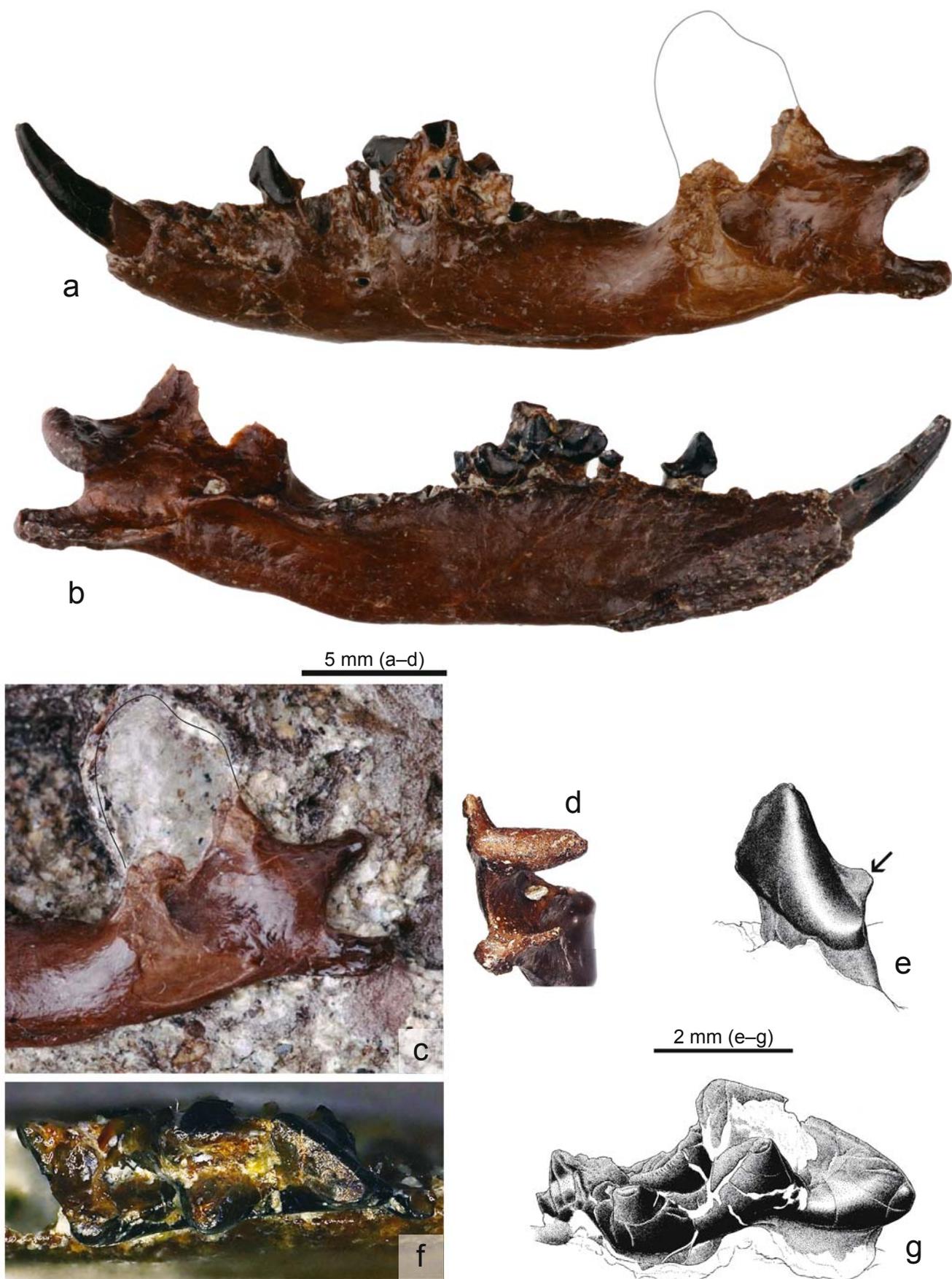**Genus *Plesiosorex* POMEL, 1848**

***Plesiosorex fejfari* sp. nov.**
Text-fig. 2

H o l o t y p e . Nearly complete left mandible with complete i2 and p3, fragment of p4 and incomplete m1 (NMNS PV-20155).

T y p e   l o c a l i t y . Left bank of the Kiso river in Dota village, Kani City, Gifu Prefecture, central Japan (Text-fig. 1).

H o r i z o n   a n d   g e o l o g i c   a g e . Uppermost part of the Nakamura Formation of Mizunami Group; Early Miocene, correlated with European land mammal zone MN 3.

Table 1. Measurements of *Plesiosorex fejfari* lower dentition (NMNS PV-20155, holotype). Measured by digital microscorp KEYENCE VHX-900.

	i2	length of enamel crown	5.29
	p3	length	1.91
		width	1.13
		heigth	2.10
	m1	length	5.45
		width	(broken)
alveolus	m2	length	2.42
		width	1.64
alveolus	m3	length	1.90
		width	1.23

Text-fig. 2. *Plesiosorex fejfari* **(holotype, left mandible, NMNS PV-20155). a. buccal view; b. lingual view; c. buccal view of the impression of the posterior part of the mandible on the host rock; d. posterior view; e. p3 in postero-bucco-dorsal view; f. m1 in occlusal view; g. m1 in postero-linguo-dorsal view; d and f images are depth synthesized by digital microscope (KEYENCE VHX-900).**

Table 2. Data matrix of character states for the cladistic analysis used in this study. Data were obtained mainly from the literature and partly from casts of specimens: *Saturninia gracilis*, Stehlin (1940), Crochet (1974); *Butselia biveri*, Ziegler (2009); *Plesiosorex germanicus*, Seemann (1938), Viret (1940), Ziegler and Mörs (2000); *P. schaffneri*, Engesser (1972, 1979), Franzen et al. (2003); *P. soricinoides*, Engesser (1979), Viret (1940); *P. evolutus*, Ziegler (2006); *P. coloradensis*, Wilson (1960), Engesser (1979), cast of holotype (KU 9989); *P. donroosai*, Green (1977), Martin (2012); *P. latidens*, Hall (1929), Engesser (1979), cast of UNSM 1410-47; *P. aydarlensis*, Kordikova (2000); *P. greeni*, Martin and Lim (2004).

taxa \ character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Saturninia gracilis	0	0	0	0	1	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Butselia biveri	0	0	0	?	1	1	1	?	?	1	1	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1	0	0
P. fejfari	1	0	1	1	1	1	1	0	2	?	1	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. germanicus	0	1	1	1	0	?	2	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1
P. schaffneri	?	?	?	1	?	?	2	?	?	1	1	1	1	1	0	?	?	?	?	1	1	1	1	0	1	1	?	1
P. soricinoides	0	1	1	1	1	1	1	0	1	1	1	0	1	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?
P. evolutus	?	1	?	?	?	?	?	?	?	1	1	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	1
P. coloradensis	0	1	1	1	1	1	2	?	2	1	1	1	1	1	?	1	1	1	1	1	2	1	1	0	1	0	1	1
P. donroosai	1	1	1	1	0	1	2	1	2	?	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. latidens	1	1	1	1	0	1	2	1	2	1	1	0	1	1	?	?	?	?	?	1	1	2	1	0	1	1	1	1
P. aydarlensis	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1	?	?	?	?	1	1	?	1	1	1	0	?	1
P. greeni	1	1	1	1	?	1	2	?	?	?	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?

E t y m o l o g y . Dedicated to Professor Oldřich Fejfar in recognition of his outstanding work on Neogene mammals.

M e a s u r e m e n t s . See Text-fig. 3, Table 1.

D i a g n o s i s . Large-sized species of the genus with elongated mandibular body; ventral margin of the dentary nearly horizontal; both condyloid and angular processes posteriorly elongated; p3 double rooted; neither hypoconulid nor any cingulid present on m1.
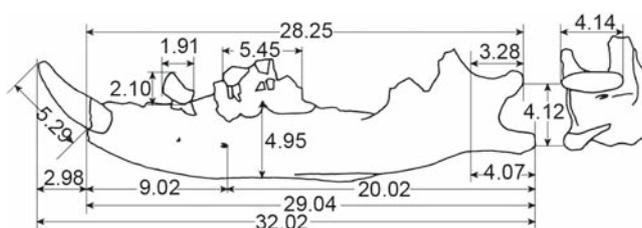
D e s c r i p t i o n . **Left mandible.** It is nearly complete, lacking the coronoid process. Impression of the coronoid process had been preserved on the host rock, but it was lost by the preparation of the specimen (Text-fig. 2c).

The mandibular body in lateral view is relatively horizontal, and it is deepest at the area anterior to p4. The mandibular ramus inclines anteriorly, and the tip of the coronoid process is rounded (Text-fig. 2c), as stated from the impression on the host rock. This lost ascending ramus may have been offset laterally judging from the remaining portion of the ramus. The dentary bends laterally next to m3, with a shelf set between m3 and the ascending ramus. A ridge is present between m3 and the mandibular foramen on the dorso-lingual edge of the dentary, and it becomes sharper posteriorly. The mandibular foramen opens posteriorly but slightly dorsally above that ridge. The upper pterygoid

Text-fig. 3. Measurements of the holotype.

fossa is triangular in outline and shallow. Since the angular process extends postero-lingually, the lower pterygoid fossa is C-shaped in posterior view (Text-fig. 2d), and the bottom of the lower pterygoid fossa is relatively wide and shallow. The condyloid process is extended posteriorly and slightly dorsally, but does not reach posteriorly as far as the angular process, and is transversely almost horizontal and cylindrical in shape. The angular process is significantly elongated posteriorly. The lower sigmoid notch is relatively deep and C-shaped in lateral view. The mandibular symphysis terminates below the posterior margin of p4. The anterior and posterior mental foramina are below the anterior root of p3 and the posterior root of p4, respectively.

Dentition. Dental formula of the lower jaw is 3·0·4·3, lacking c (Gunnel et al. 2008). The i2 and p3 are well preserved, while p4 and m1 are fragmentary and incompletely preserved, respectively. The i1, i3, p1–2, and m2–3 are lost, while their alveoli are preserved. A small cylindrical hole near and ventral to the i2 is considered to be the alveolus of the i1. The i2 is a large piercing, rooted tooth; it gently curves upward, and the tip is sharp. In cross section the i2 crown is D-shaped as the lingual side is worn. The i3, p1 and p2 are single rooted. The alveolus of the i3 is smaller than that of p1, wider than long, and it opens antero-dorsally. The alveolus of the p1 is smaller than that of p2, equal width and length, and it opens antero-dorsally, but slightly more dorsally than in i3. Alveolus of p2 is wider than long and opens antero-dorsally.

The p3 is composed of a large high principal cusp and a distal small cusp, and the occlusal outline of the crown is somewhat rhombus in shape. A sharp edge is developed on the proximal margin, whereas the distal ridge is weak and worn, and a small cusp is weakly developed at the posterior margin (arrow of Text-fig. 2e). The postero-buccal part of the crown widens and slopes gently from the small cusp at the distal end of the crown. The ventral margin of enamel on the

buccal surface descends distinctly posteriorly, while that of the lingual surface does not extend downwards as much. The p3 has two roots, partially visible, the anterior one directed almost vertically, while the posterior one directs postero--ventrally. For the p4, only the lingual half of the posterior root and a small postero-lingual portion of the crown are preserved. The latter preserves a small wear surface with dentine exposed, indicating the presence of an entoconid--like structure. This fact, in addition to the p3 having some structure on the posterior part of the crown, suggests the possibility that p4 had been a submolariform tooth, like that of *P. evolutus* (Ziegler 2006), and not a premolariform, as in *P. styriacus* (Thenius 1949).

The occlusal outline of m1 is trapezoidal. The m1 is extremely large, the largest tooth of the dentition. The trigonid is composed of the protoconid, paraconid and metaconid, while the talonid is composed of the hypoconid and entoconid. Since the buccal side of m1 is damaged, protoconid and hypoconid are somewhat deformed distally. Because of this deformation, m1 length (Tab. 1) is not accurate and is somewhat overestimated. The paraconid, metaconid, and entoconid maintain their original form and positions. The trigonid of m1 is moderately long, with an estimated trigonid/talonid length ratio of ca. 1.6, although it is inaccurate because of the damage mentioned above (Text-fig. 2f). The postero-linguo-dorsal view of m1 (Text-fig. 2g) does not show any distortion due to the viewing angle. The trigonid is higher than the talonid, and the highest cusp of the crown is the protoconid.

Because of the damage to the protoconid, a carnassial--like notch is not observable, but the curvature of the enamel surface in the postero-lingual direction at the postero-buccal end of the paralophid suggests the presence of the carnassial--like notch at the middle of the paralophid. The metaconid is an isolated conical cusp, and the metalophid is not present. The hypoconid is positioned clearly distally to the entoconid, and it projects postero-buccally. The hypoconulid and all cingulid structures are absent in the m1.

The alveolus of the m2 comprises two holes: the proximal one is 0.96 mm long, 1.64 mm wide, while the distal one is 1.19 mm long, 1.61 mm wide, with a total length of 2.42 mm. Estimating from the size of the alveolus, the m2 is much smaller than m1, about one half the length (based on an estimation of m2 length ca. 2.5 mm considering the gap between alveoli of m2 and m3). There are also two holes conforming with the m3 alveolus: the proximal one is nearly ellipsoidal in outline and 0.68 mm long, 1.23 mm wide, whereas the distal one is almost circular and is 0.90 mm long, 1.06 mm wide, and the total length of the two is 1.90 mm.

C o m p a r i s o n . The family Plesiosoricidae is partially characterized by the lower jaw and teeth (Gunnell et al. 2008): i2 hypertrophied into procumbent, piercing teeth; p4 with low, short talonid; dentary with sharply upright or slightly anteriorly inclined coronoid process and transversely cylindrical condyle; symphysis procumbent and extending to anterior root of p4.

The genus *Plesiosorex* is partially characterized by the lower jaw and teeth as well (Gunnell et al. 2008): dental formula complete or reduced by one tooth; molars distinctly graded in size from large m1 to small m3; c1 reduced or
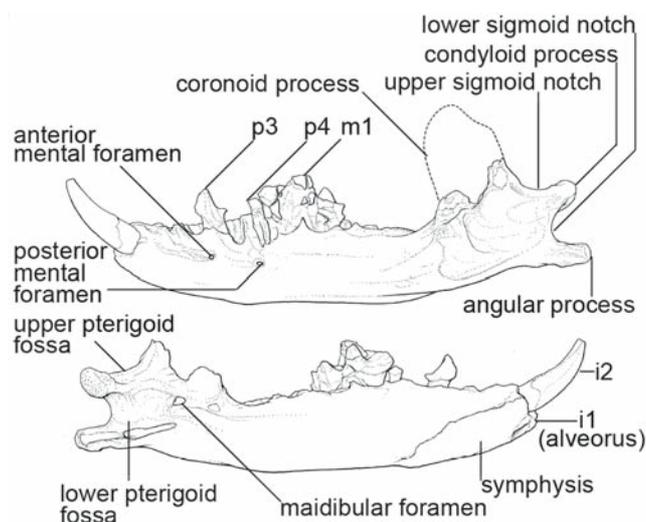
Text-fig. 4. Terminology of the mandible.

absent; i2 enlarged, piercing teeth; p4 semi-molariform; m1 with carnassial-like shear; lower molar hypoconids reduced and centrally located on hypolophids; incisors to p2 and usually p3 single-rooted and unicuspid.

These characters are consistent with those of the specimen described above, and we conclude that it belongs to the genus *Plesiosorex*. Among the family, *Plesiosorex aydarlensis* KORDIKOVA, 2000 (E. – M. Miocene), *Pseudoneurogymnurus shevyrevae* GUREEV, 1979 (E. Oligocene), *Pakilestes lathrius* RUSSEL et GINGERICH, 1981 (M. Eocene), and *Ordolestes ordinatus* LOPATIN, 2006 (E. Eocene) are known in Asia (Ziegler 2009), but *Plesiosorex* is the only genus known from the Early Miocene in Asia, and it is morphologically distinguishable from the Paleogene genera. Twelve species have been identified in the genus *Plesiosorex* globally (Ziegler 2009).

Plesiosorex fejfari differs from all known species with known p3 or p3 alveolus (*P. soricinoides* (DE BLAINVILLE, 1838), *P. germanicus* (SEEMANN, 1938), *P. coloradensis* WILSON, 1960, *P. donroosai* GREEN, 1977, *P. latidens* (HALL, 1929), and *P. greeni* MARTIN et LIM, 2004) in that it has a double rooted p3. Comparisons based on other characters and with the species without p3 follow. Among European species, *P. roosi* FRANZEN, FEJFAR et STORCH, 2003 differs from *P. fejfari* in having nearly upright or only slightly anteriorly inclined coronoid process, posterior mental foramen beneath m1, and high trigonid/talonid length ratio in m1 (Franzen et al. 2003). *Plesiosorex evolutus* ZIEGLER, 2006 is known only from isolated teeth and is somewhat similar to *P. fejfari* in size and trigonid/talonid length ratio in m1, but it differs from *P. fejfari* in having a m1 with cingulids, a deep notch on the entocristid, and small m1/m2 length ratio (Ziegler 2006). *Plesiosorex schaffneri* ENGESSER, 1972 differs from *P. fejfari* in being somewhat smaller in size and in having a lower trigonid/talonid length ratio in m1 and posterior mental foramen beneath m1 (Engesser 1972, 1979, Franzen et al. 2003: 100, Ziegler 2006: 112). *Plesiosorex germanicus* and *P. styriacus* (HOFMANN, 1893) are quite similar to each other (Franzen et al. 2003), but both differ from *P. fejfari* in their smaller size and in having a relatively small trigonid/talonid length ratio in m1 and posterior mental foramen beneath m1

(Franzen et al. 2003). *Plesiosorex soricinoides* (including *P. cf. soricinoides* from Chaveroche, France) differs from *P. fejfari* in having precingulid and ectocingulid on m1, wide occlusal outline and antero-posteriorly shorter trigonid on m1, posterior mental foramen beneath the anterior root of p4, and smaller size (Engesser 1979, Franzen et al. 2003). Because *P. cf. soricinoides* seems to have complete dentition (Viret 1940, Engesser 1979) based on the number of alveoli, we code it as complete lower dentition, although Ziegler (2009) considered it incomplete.

Among North American species, *P. coroladensis* differs from *P. fejfari* in having complete lower dentition, posterior mental foramen beneath the anterior root of m1, antero-posteriorly shorter trigonid in m1, and smaller m1/m2 length ratio (ca. 1.4) (Wilson 1960, Engesser 1979). Although Wilson (1960: 21) indicated "p3 with two roots", if the lower dentition is complete, then the number of alveoli is insufficient, so we follow Ziegler (2009: 370), in which he noted "p3 single-rooted". *Plesiosorex donroosai* differs from *P. fejfari* in having an angular tip on the coronoid process, curved ventral margin of the mandibular body, posterior mental foramen beneath the anterior root of m1, and antero-posteriorly shorter trigonid in m1 (Green 1977, Martin 2012). *Plesiosorex greeni* differs from *P. fejfari* in having a posterior mental foramen beneath the anterior root of m1, m1 with strong external but reduced labial cingulid, antero-posteriorly shorter trigonid in m1, and smaller m1/m2 length ratio (ca. 1.43) (Martin and Lim 2004). *Plesiosorex latidens* (including *Meterix* sp. of Engesser 1979) differs from *P. fejfari* in its angular tip of the coronoid process, curved ventral margin of the mandibular body, posterior mental foramen beneath the anterior root of/ or middle of m1, and antero-posteriorly shorter trigonid in m1 (Hall 1929, Engesser 1979).

Cladistic analysis

Ziegler (2009) cladistically analyzed the relationships among *Butselia biveri* QUINET et MISONNE, 1965 and 9 species of *Plesiosorex*. We originally planned to cite his dataset for our analysis, but we disagreed with some details. Character states of character number 23, for example, should be 0 and 1 only, but he included three 2s in the column of character 23 (Ziegler 2009: 370). Furthermore, he wrote "In the matrix *Meterix latidens* and *Plesiosorex greeni* are synonymised", which means all character states would be the same in the two species, but the latter branched off earlier than the former in his cladogram (Ziegler 2009: 369). Our revised dataset is based mainly on the literature (see the caption of Tab. 2) and on casts of available specimens (Tab. 2).

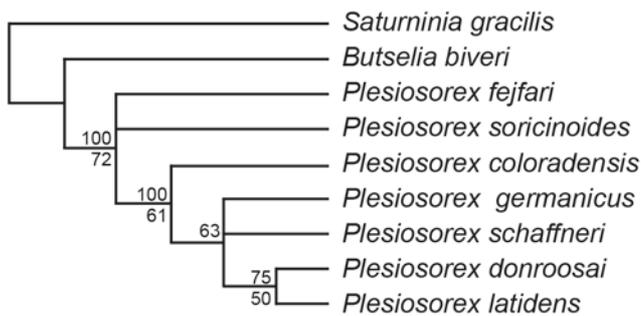Characters of the dentary and lower dentition used for the study
1. dental formula: complete (0), reduced (1)
2. p3: double-rooted (0), single-rooted (1)
3. p2: double-rooted (0), single-rooted (1)
4. i2: cuspulate (0), acuspulate, caniniform (1)
5. ventral margin of dentary: rounded/curved (0), nearly horizontal (1)
6. anterior mental foramen: absent (0), present (1)
7. posterior mental foramen located below: p3 (0), p4 (1), m1 (2)
8. tip of coronoid process: rounded (0), angular (1)
9. coronoid process: inclined posteriorly (0), perpendicular (1), anteriorly (2)
10. p4, base of labial crown: more or less horizontal (0), rising upwards (1)
11. m1/2 hypoconulid: well-developed (0), rudimentary or absent (1)
12. m1 precingulid: present (0), absent (1)
13. m1 paralophid: carnassial notch absent (0), present (1)
14. m1/2 cingulid under hypoconid: present (0), absent (1)
15. m3 talonid: narrower than trigonid (0), as wide as or wider than trigonid (1)

Characters of the upper dentition used for the study
16. P3: occlusal outline triangular (0), trapezoidal (1)
17. P4: metacone present (0), absent (1)
18. P4: hypocone absent (0), present (1)
19. P4 postprotocrista: long (0), absent (1)
20. M1/2 paracone and metacone: situated labially (0), shifted lingually (1)
21. M1/2 ectoflexus concave: slightly (0), distinctly (1)
22. M1 antiparacone (cusp labial to paracone): absent (0), smaller than paracone (1), higher than paracone (2)
23. M1 antimetacone (cusp labial to the metacone): absent (0), present (1)
24. M1 precingulum: present (0), absent (1)
25. M1/2 hypocone: cingular swelling (0), well-developed (1)
26. M1 postprotocrista: continuous (0), short (1)
27. M2 antimetacone: absent (0), present (1)
28. M1/2: relatively wide (0), less wide (1)

Maximum parsimony (MP) analysis was conducted to reconstruct cladograms of *Plesiosorex* and a sister taxon, *Butsera biveri* using PAUP 4.0a. *Saturninia gracilis* STEHLIN, 1940 was selected as outgroup following Ziegler (2009). Although only mandible and lower teeth characters were available for *P. fejfari*, we concatenated 13 characters of upper dentition into the mandible and lower teeth dataset to increase parsimony-informative sites and to recover a more reliable overall topology. We included 26 characters as Ziegler (2009) did, plus two additional characters (i.e., 5th and 8th of the 28 characters above) into our dataset. Of the 12 known *Plesiosorex* species, three species (*P. roosi*, *P. styriacus*, and *P. martinii*) were excluded from the analysis because they share insufficient numbers of comparable characters with the others (i.e., less than 35 %) (Ziegler 2009). We further excluded from the analysis two taxa that lacked more than 60% of the information on the 28 characters above (i.e., *P. aydarlensis* and *P. greeni*). We also excluded *P. evolutus* from the analysis because it lacks more than half of the 15 mandible-lower teeth characters and it shares only four characters with the target taxon, *P. fejfari*. Accordingly, the categorical dataset for the cladistics analysis consisted of 9 taxa and 28 characters (Tab. 2). The MP analysis was conducted with the default settings except "Maxtrees" set to 10,000. Gaps were treated as missing data.

Text-fig. 5. Majority-rule consensus topology of the 16 most parsimonious trees based on 28 mandible and lower and upper dentition characters shown in Table 2 (L = 38). The numbers above branches indicate the percentage of each topology recovered from the 16 most parsimonious trees. Bootstrap values (1,000 replicates) are designated below branches.

Bootstrap analysis was conducted based on the full heuristic search with TBR branch swapping (reconnection limit = 8) and generated 1,000 replicates.

Of the 28 characters in the dataset used for the MP analysis, 12 were parsimony-informative and 16 were parsimony-uninformative. The heuristic analysis found 16 best trees with 38 steps (i.e., tree length L = 38), and the total number of rearrangements was 3,312. The consistency index (CI), retention index (RI) and rescaled retention index (RC) were 0.82, 0.67 and 0.54 respectively. The resulting cladogram is shown in Text-fig. 5.

The cladogram supports the monophyly of the genus *Plesiosorex*, and shows that *P. fejfari* is nested within the *Plesiosorex* clade (Text-fig. 5). The cladogram also suggests that *P. fejfari* and *P. soricinoides* are the earliest diverging lineages in the genus. The two North American Middle – Late Miocene species, *P. donroosai* and *P. latidens*, formed a terminal clade with a moderate bootstrap value (BS = 50%).

Discussion

Morphologically, *P. fejfari* is distinguishable from the 10 known *Plesiosorex* species (other than *P. aydarlensis* and *P. martinii*) as explained in the comparison section above. Differences between *P. fejfari* and each of the ten species are more or less comparable with those among other species, thus *P. fejfari* can be judged as a separate species.

Plesiosorex aydarlensis is represented by four isolated teeth, and none of them can be directly compared with *P. fejfari* (Kordikova 2000). As the m2–3 of *P. aydarlensis* have fairly well-developed cingulids, it may be assumed that m1 also has some cingulid structure. *Plesiosorex martinii* is also known by five isolated teeth (Engesser and Storch 2008), and none of them can be directly compared with *P. fejfari*. Because its m2 has a distinct precingulid, m1 may be assumed to have a similar cingulid. So far, however, we cannot ascertain whether one of them is 100% identical to *P. fejfari*. Given that fossils of *P. fejfari* are assumed to be extremely rare, we consider that proposing *P. feifari* as a new species is a better solution rather than leaving the fossil unnamed until more material from other species under consideration is obtained.

Our cladogram suggests that the branching pattern in the *Plesiosorex* clade has a rather high correlation with their evolutionary pattern, particularly in terms of the geological age and distribution of each species (Text-fig. 5). That is, *Butselia biveri* is derived within MP 21 (ca. 33.6–32.6 Ma) in Europe; *P. soricinoides*, MN 2 (ca. 22.5–20.5 Ma), Europe; *P. fejfari*, MN 3 (ca. 18.5 Ma), East Asia; *P. coloradensis*, Hemmingfordian (He 1, 18.8–17.5 Ma.), North America; *P. germanicus*, MN 4–6 (17.7–13.5 Ma), Europe; *P. schaffneri*, MN 7–9 (13.5–9.7 Ma), Europe; *P. donroosai*, Barstovian (Ba 2, 14.8–12.6 Ma), North America; *P. latidens*, Barstovian-Clarendonian (Ba 1 to Cl 2, 16.0–10.8 Ma), North America (Ziegler 1999, 2009, Gunnell et al. 2008, Janis et al. 2008). Thus, the following scenario emerges based on the results: the genus *Plesiosorex* originated in Europe at the beginning of the Early Miocene (*P. soricinoides*), it expanded its distribution to East Asia during the Early Miocene (*P. fejfari*), and on to North America by the late Early Miocene (*P. coloradensis*), probably through Beringia. It is not clear whether the two lineages evolved independently in Europe (*P. germanicus* and *P. schaffneri*) and in North America (*P. donroosai* and *P. latidens*), or if there was some phylogenetic connection between them. However, the cladistic analysis indicates that the two Middle Miocene North American species are more closely related to each other than the European species of the Middle Miocene.

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