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

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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 Youngo fiber 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...
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**

*Holotype.* Nearly complete left mandible with complete i2 and p3, fragment of p4 and incomplete m1 (NMNS PV-20155).

**Type locality.** Left bank of the Kiso river in Kota village, Kani City, Gifu Prefecture, central Japan (Text-fig. 1).

**Horizon and geologic age.** Uppermost part of the Nakamura Formation of Mizunami Group; Early Miocene, correlated with European land mammal zone MN 3.
Text-fig. 2. *Plesiosorex fejari* (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   | 1   | 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   | 1   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   | 0   |
| *P. fejfar* | 1   | 0   | 1   | 1   | 1   | 1   | 0   | 2   | ?   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   | 1   | 1   | 1   | 1   |
| *P. germanicus* | 0   | 1   | 1   | 1   | 0   | ?   | 2   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 0   | 1   | 1   | 1   | 1   |
| *P. schaffneri* | ?   | ?   | ?   | 1   | ?   | 2   | ?   | ?   | 1   | 1   | 1   | 1   | 1   | 0   | ?   | ?   | ?   | ?   | 1   | 1   | 1   | 0   | 1   | 1   | 1   | 1   |
| *P. soricinoides* | 0   | 1   | 1   | 1   | 1   | 0   | 1   | 1   | 1   | 0   | 1   | 1   | 0   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   |
| *P. evolutus* | ?   | 1   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   |
| *P. coloradensis* | 0   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 2   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 2   | 1   | 1   | 0   | 1   | 0   |
| *P. donroosai* | 1   | 1   | 1   | 1 | 0   | 1   | 2   | 1   | 2   | ?   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 2   | 1   | 1   | 0   | 1   | 0   | 1   |
| *P. latidens* | 1   | 1   | 1   | 1   | 0   | 1   | 2   | 1   | 2   | ?   | 1   | 1   | 1   | 1   | 0   | 1   | 1   | 1   | 1   | 1   | 1   | 1   | 0   | 1   | 1   |
| *P. aydarlensis* | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   |
| *P. greeni* | 1   | 1   | 1   | 1   | 0   | ?   | 1   | 2   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   | ?   |

Text-fig. 3. Measurements of the holotype.
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-lingual-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.

Comparison. 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 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 unicuspic.

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 aydarnensis KORDIKOVA, 2000 (E. – M. Miocene), Pseudoneurogymnurus shevyrevae GUREEV, 1979 (E. Oligocene), Pakilestes laithrus 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. soricoides (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. roosis 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: cuspatulate (0), acuspatulate, 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),
8. p4 (1), m1 (2)
9. tip of coronoid process: rounded (0), angular (1)
10. coronoid process: inclined posteriorly (0), perpendicular (1), anteriorly (2)
11. p4, base of labial crown: more or less horizontal (0), rising upwards (1)
12. m1/2 hypoconulid: well-developed (0), rudimentary or 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 paracne and metacone: situated labially (0), shifted lingually (1)
21. M1/2 ectoflexus concave: slightly (0), distinctly (1)
22. M1 antiparacne (cusp labial to paracne): absent (0), smaller than paracne (1), higher than paracne (2)
23. M1 antitracone (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 antitracone: 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. martini) 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.
Consideration is obtained. More material from other species under a new species is a better solution rather than leaving the fossil unnamed until more material from other species under consideration is obtained. We consider that proposing a new species is a better solution rather than leaving the fossil unnamed until more material from other species under consideration is obtained.

The two North American Middle-Miocene species, *Plesiosorex fejfari* and *P. aydarlensis*, are represented by four isolated teeth (Engesser and Storch 2000). 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. fejfari* as a new species is a better solution rather than leaving the fossil unnamed until more material from other species under consideration is obtained.

**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* (Kordíkova 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. fejfari* 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, *Butselsia biveri* is derived within MP 21 (ca. 33.6–32.6 Ma) in Europe; *P. soricoides*, 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. soricoides*), 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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