

# Morphology-based taxonomic re-assessment of the Arctic lamprey, *Lethenteron camtschaticum* (Tilesius, 1811) and taxonomic position of other members of the genus

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## Abstract

The lamprey genus *Lethenteron* Creaser & Hubbs, 1922 is widespread across Eurasia and North America, but the number and distribution of its constituent species is not firmly established. After a morphological examination of extant type material of the currently recognized species and their synonyms, *Lethenteron mitsukurii* (Hatta, 1901) is resurrected with *Le. matsubarai* Vladykov & Kott, 1978 as its junior synonym. Amongst nonparasitic species *Le. reissneri* (Dybowski, 1869) and *Le. mitsukurii* are confirmed as present in Japan and the former is also present on Sakhalin. An in-depth study of large samples of nonparasitic lamprey adults from Japan and Sakhalin Island is needed to determine whether the lower trunk myomere (< 66) individuals from these areas represent one or more undescribed species, or *Le. mitsukurii*, or *Le. reissneri*, or a mixture of these three alternatives. The material from the Anadyr Estuary identified by Berg (1931, 1948) as *Lampetra japonica kessleri* has been re-identified as *Le. camtschaticum* and there is no evidence that *Le. kessleri* occurs there. *Lethenteron reissneri* is reported from the Angara River system, Yenisei River drainage, Russia. *Lethenteron alaskense* Vladykov & Kott, 1978 is provisionally considered to be a junior synonym of *Le. kessleri* (Anikin, 1905). *Petromyzon ernstii* Dybowski, 1872, *Ammocoetes aureus* Bean, 1881, *Petromyzon dentex* Anikin, 1905, *Lampetra mitsukurii major* Hatta, 1911, and *Lampetra japonica septentrionalis* Berg, 1931 are junior synonyms of *Petromyzon marinus camtschaticus* Tilesius, 1811. A key is provided to adults of the six species recognized as belonging in the genus *Lethenteron*.

**Keywords**

Arctic lamprey, *Lethenteron* species, synonyms, taxonomic key

**Introduction**

The lamprey genus *Lethenteron* Creaser & Hubbs, 1922 is widely distributed across the Northern Hemisphere, but the number and distribution of its constituent species is not firmly established. Originally erected by Creaser and Hubbs (1922) as a subgenus of *Entosphenus* Gill, 1862, the cladistic study of Gill et al. (2003) based on morphological characters of parasitic species only, showed that *Entosphenus* is a monophyletic group supported by two synapomorphies, and *Lethenteron* belongs to a sister clade, also supported by two synapomorphies, that includes *Eudontomyzon* Regan, 1911 and *Lampetra* Bonnaterre, 1788. Furthermore, the cladogram by Gill et al. (2003) suggests that *Lethenteron* is sister to *Eudontomyzon-Lampetra*. However, no derived character defined *Lethenteron*, while the latter clade was supported by a single synapomorphy. Until a phylogenetic study more definitely resolves the relationships among the three genera, we choose to recognize *Lethenteron* as a distinct genus. According to Vladykov and Follett (1967), the genus *Lethenteron* is characterized by the presence of a single row of posterial teeth, a 2–2–2 endolateral formula, and the absence of exolateral teeth. However, the latter character shows variation (Kott 1974; Vladykov and Kott 1978a; Renaud and Naseka 2015).

Kottelat (1997) resurrected *Lethenteron camtschaticum* (Tilesius, 1811) for the Arctic lamprey, and thus, the long-standing name *Lethenteron japonicum* (von Martens, 1868) became the junior synonym. The type for *Le. camtschaticum* being lost, Kottelat (1997) designated the lectotype of *Le. japonicum* (ZMB 6475) as the neotype for the former making the type locality for *Le. camtschaticum* Tokyo (appeared as Jeddo) and Yokohama, Honshu Island, Japan as defined by the neotype. However, while the scientific name for the taxon has been fixed, its taxonomic limits are still not clear. Berg (1931) separated what he called *Lampetra japonica* into three subspecies: the nominotypical subspecies, to which he gave the common name Pacific river lamprey, distributed in the North Pacific Ocean basin in an arc from the Sea of Japan basin (Korean Peninsula, areas of Gensan, now known as Wŏnsan in North Korea and Fusan, now known as Busan in South Korea; Japan; Russian Far East, Tumen River and Suchan River, now known as Partizanskaya River), the Amur River, the Kamchatka Peninsula and across to the Yukon River in North America; a second subspecies *La. j. septentrionalis* Berg, 1931, to which he gave the common name Arctic lamprey, restricted to the Arctic Ocean basin from the White Sea basin to the Ob' River drainage; and a third subspecies *La. j. kessleri* (Anikin, 1905), the Siberian lamprey, distributed in the intervening zone between the two (Ob' River to Kolyma and Anadyr rivers, and Sakhalin Island).

Berg (1931) considered *La. j. japonica* and *La. j. septentrionalis* to be large migratory (anadromous) forms in which the larvae at metamorphosis were much smaller

than the adults and *La. j. kessleri* to be a small non-migratory (i.e., resident) form in which the larvae at metamorphosis were larger than the adults. Altukhov et al. (1958) reported that anadromous *La. japonica* migrate 400 or more kilometers up the Severnaya (or Northern) Dvina and Mezen' rivers, White Sea basin, while in the Amur River Morozova (1956) reported upstream migrations varying between 766 and 905 km, and according to Chereshnev (2008), even up to a remarkable 1,700 km. Although Berg (1931) made no statement in regard to adult feeding, the implication of his dichotomy was that the first two were parasitic lampreys while the third was a nonparasitic lamprey. Furthermore, Berg (1931) likened the relationship between *La. j. septentrionalis* and *La. j. kessleri* to that of *La. fluviatilis* (Linnaeus, 1758) and *La. planeri* (Bloch, 1784), thus corroborating the parasitic-nonparasitic argument. Another level of complexity introduced by Berg (1931) is the concept that migratory lampreys may be represented by two sympatric forms; one large and one small (i.e., f. *praecox*), and that the small, earlier-maturing form may be migratory or paradoxically resident (i.e., non-migratory) in lakes. A single female of *La. j. septentrionalis* 247 mm total length from the Onega River (type locality), Russia was identified by Berg (1931) as belonging to the forma *praecox*. However, *praecox* is not an available name according to article 1.3 of the International Code of Zoological Nomenclature (ICZN 1999) because it was proposed as an infrasubspecific rank. Berg (1948), without justifying his action, synonymized *La. j. septentrionalis* with the nominotypical subspecies under the common name Arctic lamprey, and increased the re-defined taxon's western range to include the Barents Sea basin at least to Motovsky Bay, Russia and perhaps to Varanger Fjord, Norway, and in the eastern range included mainland rivers of the Okhotsk Sea basin (Okhota, Kukhtui, Taui, and Ola) and Sakhalin Island, Russia. Despite this, the common name Pacific lamprey has persisted in the Russian literature in reference to this taxon (Birman 1950; Morozova 1956; Nikol'sky 1956; Martynov 2002; Gritsenko et al. 2006; Bugayev et al. 2007; Savvaitova et al. 2007; Chereshnev 2008).

Berg (1931, 1948) noted the wide discontinuity in the distribution of the anadromous populations of *La. j. japonica*; none being present between the Gulf of Ob' and Kamchatka. However, Berg (1948) still recognized the subspecies *La. j. kessleri* and increased its western range to include the Pechora River, Barents Sea basin and suggested that this taxon was probably also present in Alaska. Ioganzen (1935a, 1935b) compared the morphometrics and dentition of *La. j. kessleri* and *La. j. septentrionalis* collected sympatrically in the Ob' River drainage including at the type locality of the former (Tom' River near Tomsk), and, other than total length (i.e., 132–207 mm versus 215–408 mm, respectively), could not find any significant differences between the two. Furthermore, Ioganzen (1935a) dismissed the wide discontinuity between the distributions of *La. j. septentrionalis* and *La. j. japonica* by suggesting that their similar dentition was not indicative of their common origin and that *La. j. septentrionalis* was in fact derived from *La. fluviatilis*, and should therefore be called *La. fluviatilis septentrionalis*. However, Ioganzen (1935b) accepted the close phylogenetic relationship between *La. j. kessleri* and its presumed ancestor *La. j. japonica*.

Holčík (1986a, 1986b) recognized the genus *Lethenteron* and elevated *Le. kessleri* to the rank of species, as originally proposed by Anikin (1905) followed by Poltorykhina (1974). Holčík (1986b) stated that *Le. kessleri* was most probably nonparasitic and usually indistinguishable morphologically from other satellite (i.e., nonparasitic) species of *Le. camtschaticum* (appeared as *Le. japonicum*), namely, *Le. reissneri* (Dybowski, 1869), *Le. wilderi* (Gage in Jordan & Evermann, 1896), *Le. meridionale* Vladykov, Kott & Pharand-Coad, 1975, *Le. alaskense* Vladykov & Kott, 1978, and *Le. matsubaraei* Vladykov & Kott, 1978, and that these are possibly conspecific. He thus called for an urgent critical revision, earlier advocated by Hubbs and Potter (1971), and this has been most recently reiterated by Dyldin et al. (2019a). Two of the species recognized by Holčík (1986b), *Le. wilderi* and *Le. meridionale*, are junior synonyms of different species. The former is a questionable synonym of *Lethenteron appendix* (DeKay, 1842) (see Renaud 2011) and the latter a synonym of *Lampetra aepyptera* (Abbott, 1860) (see Walsh and Burr 1981). The generic allocation of *La. aepyptera* is not clear. It is either *Lampetra* or *Okkelbergia* Creaser & Hubbs, 1922, but not *Lethenteron* (see Potter et al. 2015), and therefore, it will not be dealt with further.

Ren et al. (2016) examined the mitogenome of *Le. camtschaticum*, *Le. reissneri*, *Le. appendix*, *Le. morii*, *La. aepyptera*, and *La. fluviatilis*. Their phylogenetic tree using a maximum likelihood method with the Tamura-Nei substitution model suggested that there were two *Lethenteron* lineages; one consisting of the clade *Le. camtschaticum*-*Le. appendix*-*Le. morii*-*Le. reissneri* sister to a *La. aepyptera*-*La. fluviatilis* clade and another consisting of *Le. camtschaticum*-*Le. reissneri* that was sister to those two clades. Ren et al. (2016) stated that morphological comparisons of closely related lampreys can be difficult, and may have resulted in mistaken species identification leading to this confusing result. Misidentifications notwithstanding, it is difficult to explain how species of *Lampetra* distributed in eastern North America (*La. aepyptera*) and Europe (*La. fluviatilis*) are more closely related to Asian species of *Lethenteron* (*Le. camtschaticum* and *Le. reissneri*), but not to another species pair of *Le. camtschaticum*-*Le. reissneri*, unless the latter represent entirely new species. Moreover, the resolution of the relationships between *Lampetra*, *Lethenteron*, and *Eudontomyzon* is beyond the scope of this study and will be the object of future inquiry.

The goals of this study are to:

- re-assess the taxonomic status of the three subspecies of *Lampetra japonica* proposed by Berg (1931), as well as that of the following nominal taxa that have been considered as synonyms, either tentatively or not, of one or the other of these putative subspecies by Berg (1931, 1948): *Petromyzon ernstii* Dybowski, 1872 described from the mouth of the Amur River, Russia, *Ammocoetes aureus* Bean, 1881 described from Anvik, Yukon River, Alaska, U.S.A., and *Petromyzon dentex* Anikin, 1905 described from the mouth of the Yenisei River, near Gol'chikha, Russia;
- establish the relationship with *Le. camtschaticum* of two lamprey species, *Lampetra mitsukurii* Hatta, 1901 described from small watercourses on Hondo (= Honshu), Shikoku, Kyushu, and Hokkaido islands, Japan and *Le. matsubaraei*

described from Shokotsu River, Hokkaido Island, Japan. The first was synonymized with *La. reissneri* by Berg (1931) and later tentatively resurrected by Hubbs and Potter (1971), while the second was synonymized with *Le. kessleri* by Iwata et al. (1985).

- re-evaluate synonymization of *Le. kessleri* with *Le. reissneri* by Yamazaki et al. (2006) and the two names with *Le. camtschaticum* by Kucheryavyy (2014) as not based on a re-examination of all of the relevant type material.

- establish relationships of *Lampetra mitsukurii minor* Hatta, 1911 and *La. m. major* Hatta, 1911 with *Le. camtschaticum*. Berg (1931) considered *La. m. minor* a synonym of *La. reissneri* and *La. m. major* a synonym of *La. japonica japonica*.

Molecular data of Lang et al. (2009), Pu et al. (2016), and Ren et al. (2016) have suggested that *Lampetra (Eudontomyzon) morii* Berg, 1931 should be assigned to *Lethenteron* and we will provide a justification for its placement in *Eudontomyzon*.

The remaining three species recognized by Potter et al. (2015) as belonging to the genus *Lethenteron*, *Le. alaskense*, *Le. appendix*, and *Le. ninae* Naseka et al. 2009, will be included in a taxonomic key to the adults of the species of the genus that will also include the other species as established in this study. Artamonova et al. (2011) synonymized *Le. ninae* with *Le. camtschaticum*, but Tuniyev et al. (2016) confirmed the specific distinctiveness of the former. Although Tuniyev et al. (2016) showed that *Le. ninae* usually possesses a row of posterial teeth (complete or incomplete) characteristic of the genus *Lethenteron*, other morphological evidence (tricuspid middle endolateral, low number of trunk myomeres, straight longitudinal laminae, no velar wings) suggested that it should be assigned to *Lampetra*. However, they recommended the status quo until a total evidence cladistic analysis had been completed that incorporated parasitic and nonparasitic species and morphological and molecular characters to prevent re-assignment of a species to a different genus based on incomplete information.

## Materials and methods

Material examined follows the method of Renaud (2011) and for the gular pigmentation of Vladykov and Kott (1978a). TL refers to total length. All collection dates are according to the Gregorian calendar. We restricted our study to adults (i.e., metamorphosed individuals) because the diagnostic characters in the original descriptions and the type material of the three nominal subspecies and their synonyms were based on this life stage only.

## Abbreviations:

CMNFI	Canadian Museum of Nature Fish Collection, Ottawa, Canada
TGU	Tomsk State University, Tomsk, Russia;
ZIN (ZISP also used)	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia;
ZMB	Museum für Naturkunde, Berlin, Germany.

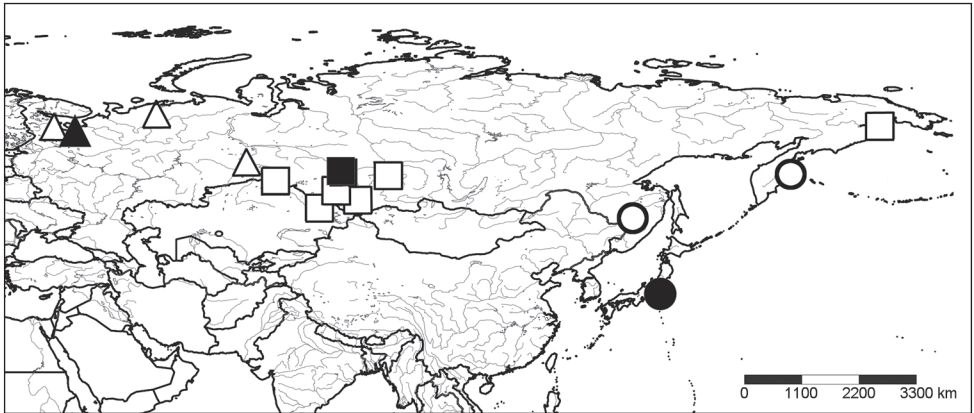
### Type material (Fig. 1):

- ZMB 6475, 1 adult, 418.3 mm TL, neotype of *Petromyzon marinus camtschaticus* Tilesius, 1811 and lectotype of *Petromyzon japonicus* von Martens, 1868, Japan: Tokyo (originally Jeddo) and Yokohama, Honshu Island, Pacific Ocean basin, 1860–1863.
- ZMB 6476, 1 adult, 397.3 mm TL, paralectotype of *Petromyzon japonicus*, Japan: Tokyo (originally Jeddo) and Yokohama, Honshu Island, Pacific Ocean basin, 1860–1863.
- TGU 3 [no. 3699 in Ioganzen (1935b, table 3)], 1 adult, 182 mm TL, syntype of *Petromyzon kessleri* Anikin, 1905, Russia: Kirgizka River near Tomsk, Tom' River system, Ob' River drainage, Kara Sea basin, Arctic Ocean basin, 24 Dec. 1899, A. Neiland.
- TGU 9 [no. 3696 in Ioganzen (1935b, table 3)], 6 of 10 adults, 128–165 mm TL, syntypes of *Petromyzon kessleri*, Russia: near mouth of Tom' River at Kozyulino, taken from a Common gull's (*Larus canus*) digestive tract, Ob' River drainage, Kara Sea basin, Arctic Ocean basin, 28 June 1903, G.E. Ioganzen.
- ZIN 12159, 8 of 10 adults, 281–374 mm TL, syntypes of *Lampetra japonica septentrionalis* Berg, 1931, Russia: Onega River at Podporozh'e, White Sea basin, Arctic Ocean basin, December 1901, N.A. Varpakhovskiy.
- ZMB 20638, 2 adults, 138.3–140.1 mm TL, syntypes of *Lampetra mitsukurii* Hatta, 1901, Japan: small watercourses on Hondo (= Honshu), Shikoku, Kyushu, and Hokkaido islands, Pacific Ocean basin.
- CMNFI 1984–274, 2 adults, 147.5–163.5 mm TL, paratypes of *Lethenteron matsubarae* Vladikov & Kott, 1978, Japan: Shokotsu River, Hokkaido Island, 44°22'N, 143°20'E, Sea of Okhotsk basin, Pacific Ocean basin, 1950–1952, T. Hikita.
- CMNFI 2008–59, 1 adult, 149.5 mm TL, paratype of *Lethenteron ninae* Naseka, Tuniyev & Renaud, 2009, Russia: Chakhtsutsyr Stream at Gumariya, Sochi District, Psou River drainage, Black Sea basin, 17–24 Dec. 2006, S.B. Tuniyev.

### Non-type material (Fig. 1):

#### Identified by Berg (1931) as *Lampetra japonica japonica*:

- ZIN 15188, 5 of 16 adults, 391.5–436.5 mm TL, Russia: Amur River, 6 km below Khabarovsk, Pacific Ocean basin, V.K. Soldatov.
- ZIN 23440, 1 adult, 170 mm TL, Russia: backwater of Kamchatka River near Ust-Kamchatsk, Pacific Ocean basin, 7 July 1908, P.J. Schmidt, beach seine.
- ZIN 23441, 1 adult, 187 mm TL, Russia: Kamchatka River near Ust-Kamchatsk, Pacific Ocean basin, June 1908, P.J. Schmidt, beach seine, lamprey descending towards the ocean.
- ZIN 23590, 2 adults, 154.5–198 mm TL, Russia: Kamchatka River near Ust-Kamchatsk, Pacific Ocean basin, 7 July 1909, P.J. Schmidt, lamprey descending towards the ocean.



**Figure 1.** Geographic distribution of the lamprey genus *Lethenteron* in Eurasia based strictly on the examination of type material of *Petromyzon marinus camtschaticus* (●), *Petromyzon kessleri* (■), *Lampetra japonica septentrionalis* (▲) and ZIN material identified by Berg (1931) as *Lampetra japonica japonica* (○), *La. j. kessleri* (□), and *La. j. septentrionalis* (Δ). Note that the easternmost record of *La. j. kessleri* from the Anadyr Estuary has been re-identified as *Le. camtschaticum*.

#### Identified by Berg (1931) as *La. j. kessleri*:

- ZIN 6174, 3 adults, 202–212 mm TL, Russia: Ob' River at Barnaul, Kara Sea basin, Arctic Ocean basin, Goebler.
- ZIN 6310, 1 adult, 187.5 mm TL, Russia: Ob' River between Lake Teletskoye and Barnaul, Kara Sea basin, Arctic Ocean basin, 1876, Slovtsov.
- ZIN 6311, 1 adult, 144 mm TL, Russia: Irtysh River at Omsk, Ob' River drainage, Kara Sea basin, Arctic Ocean basin, 1877, Poliakov.
- ZIN 7815, 1 adult, 186 mm TL, Kazakhstan: tributary to Irtysh River near Semipalatinsk (now Semey), Ob' River drainage, Kara Sea basin, Arctic Ocean basin, 1887, Suvorcev.
- ZIN 14371, 1 adult re-identified as *Le. camtschaticum* because it possesses the silvery body coloration of an anadromous downstream migrant, 144 mm TL, Russia: Anadyr Estuary (Liman) at Novo-Mariinsk (now Anadyr), Bering Sea basin, Pacific Ocean basin, N. Gondatti.
- ZIN 14441, 1 adult, 122.5 mm TL, Russia: Yenisei River at Bazaikha, Kara Sea basin, Arctic Ocean basin, 29 June 1906.

#### Identified by Berg (1931) as *La. j. septentrionalis*:

- ZIN 7814, 1 adult, 351 mm TL, Russia: Tobol River at Tobolsk, Irtysh River system, Ob' River drainage, Kara Sea basin, Arctic Ocean basin, 1887, I. Slovtsov.
- ZIN 8545, 1 adult, 301.5 mm TL, Russia: Vyg River at Soroka (now Belomorsk), White Sea basin, Arctic Ocean basin, 1886, Mizrakhanov.
- ZIN 20802, 1 adult, 334 mm TL, Russia: Shapkina River, Pechora River drainage, Barents Sea basin, Arctic Ocean basin, 5 Sept. 1921, G.D. Richter.

### Supplementary topotype material of *La. j. septentrionalis* (Fig. 1):

- ZIN uncat., 11 adults, 290–347 mm TL, Russia: Onega River, 25 km upstream from its mouth, White Sea basin, Arctic Ocean basin, 1 Nov. 2011, A.P. Novoselov.

## Results

The morphometric, countable, shape, and pigmentary character states for the extant adult type material of *Petromyzon marinus camtschaticus*, *P. japonicus*, *P. kessleri*, and *La. j. septentrionalis* are given in Tables 1–3. The original descriptions of these nominal taxa are also an integral part of this section because they supplement our observations on the type material and because they were published in various languages (Latin, German, Russian, and English, respectively), they are presented below in English for ease of comparison. Additionally, as they span a period (1811–1931) when lamprey dentition nomenclature in particular was not yet standardized (see Vladykov and Follett 1967, Hubbs and Potter 1971), we used the current tooth nomenclature or added the equivalent name in parentheses.

The morphometric, countable, shape, and pigmentary character states in all non-type adults identified by Berg (1931) as *La. j. japonica*, *La. j. kessleri*, and *La. j. septentrionalis* available to us are given in Tables 4–6. Furthermore, the original descriptions of two species, *Petromyzon ernstii* and *P. dentex*, for which extant type material of neither could be found, are presented below in their English translation of the original German and Russian, respectively. Berg (1931) considered the former to be junior synonym of *La. j. japonica* and the latter, tentatively, as a junior synonym of *La. j. kessleri*. Berg (1931) considered *Ammocoetes aureus* to be a junior synonym of *La. j. japonica* and although its extant holotype was not examined, its original English description is presented below.

The morphometric, countable, shape, and pigmentary character states for extant adult type material of *La. mitsukurii* and *Le. matsubarai* are given in Tables 7–9 and their original English descriptions are also presented. Finally, the English translation of the original German descriptions of *La. m. minor* and *La. m. major* are presented.

### Original description of *Petromyzon marinus camtschaticus* Tilesius, 1811: 240–247, pl. IX, figs I, II.

The common name in Itelmen, formerly Kamchadal, a language spoken in Kamchatka, is Canaháisch. The written description and the drawings of the body (life size) and of the oral disc (enlarged) are based on a metamorphosed specimen collected 30 July 1804 (Julian calendar; 11 August 1804 Gregorian calendar) from marine waters in the harbor of Petropavlovsk-Kamchatsky, Russia. The drawing of the body in side view is thrown into three curves and by using a string along the curves we estimated the total length to be 308 mm. Disc length is ca. 16 mm ( $\approx 5.2\%$  TL) and urogenital papilla length ca. 9.5 mm ( $\approx 3.1\%$  TL). The two dorsal fins are separate; the interspace

**Table 1.** Morphometrics in adult types of *Petromyzon marinus camtschaticus* Tilesius, 1811, *Petromyzon japonicus* von Martens, 1868, *Petromyzon kessleri* Anikin, 1905, *Lampetra japonica septentrionalis* Berg, 1931 and adult topotypes of the latter. Numbers in parentheses are sample sizes.

	<i>Petromyzon marinus camtschaticus</i> ZMB 6475 (neotype)	<i>Petromyzon japonicus</i> ZMB 6476 (paralectotype)	<i>Petromyzon kessleri</i> TGU 3, TGU 9 (7 syntypes) <sup>1</sup>	<i>Lampetra japonica septentrionalis</i> ZIN 12159 (8 syntypes)	<i>La. j. septentrionalis</i> ZIN uncat. (11 topotypes)
Type locality	Tokyo and Yokohama, Japan	Tokyo and Yokohama, Japan	Tom' and Kirgizka rivers, Russia	Onega River, Russia	Onega River, Russia
Total length (TL, mm)	418.3	397.3	128–182 (7)	281–374 (8)	290–347 (11)
Dorsal fin interspace ( $D_1$ – $D_2$ , mm)	12.4	10.2	undetermined (7)	undetermined (8)	4.0–21.2 (11)
Intestinal diameter, mm	undetermined	undetermined	0.5 (3)	1.0–4.5 (8)	1.6–4.9 (11)
<b>% TL</b>					
Prebranchial length ( $d$ – $B_1$ )	9.8	9.3	9.1–13.7 (5)	9.0–10.9 (8)	9.6–10.6 (11)
Branchial length ( $B_1$ – $B_7$ )	10.5	11.4	9.7–11.2 (4)	9.1–10.9 (8)	8.7–10.6 (11)
Trunk length ( $B_7$ – $a$ )	53.0	52.2	46.8–47.4 (2)	50.6–55.6 (8)	51.4–56.2 (11)
Cloacal slit length ( $a$ )	1.6	1.6	1.5 (1)	0.8–1.2 (8)	0.8–1.3 (11)
Tail length ( $a$ – $C$ )	25.2	27.6	29.5 (1)	23.4–27.9 (8)	24.9–27.5 (11)
Disc length ( $d$ )	4.8	4.1	4.2–6.0 (5)	4.6–5.5 (8)	4.0–5.7 (11)
Prenostril length ( $d$ – $n$ )	5.6	5.1	1.9–6.9 (5)	5.0–6.8 (8)	5.4–6.3 (11)
Snout length ( $d$ – $O$ )	6.2	5.8	4.8–7.8 (5)	5.7–7.1 (8)	6.1–7.0 (11)
Eye length ( $O$ )	1.5	1.5	2.0–2.4 (5)	1.3–2.0 (8)	1.1–1.5 (11)
Postocular length ( $O$ – $B_1$ )	2.7	2.8	1.9–3.2 (5)	2.2–2.9 (8)	2.4–2.8 (11)
Interbranchial opening length ( $B_1$ – $B_2$ )	1.4	1.2	1.3–1.6 (4)	1.1–1.5 (8)	1.2–1.5 (11)
Interocular width ( $I$ )	3.3	3.0	2.5–3.2 (5)	2.6–3.4 (8)	2.9–3.8 (11)
Urogenital papilla length	undetermined	0.7	0.5–0.8 (3)	0.0–0.8 (8)	0.4–0.7 (11)

<sup>1</sup> Six of the seven syntypes (TGU 9) were collected from the digestive tract of a Common gull (*Larus canus*) and their condition was such that not all morphometrics could be measured.

being ca. 22 mm. Caudal fin is lanceolate (= spade-like). Dentition: teeth are yellow; supraoral lamina with two bicuspid teeth separated by a wide bridge; two bicuspid endolaterals on each side; infraoral lamina with seven unicuspid teeth; transverse lingual lamina u-shaped, with seven blunt unicuspid teeth, the median one not enlarged in the figure, but noted as distinct in the text. The figure of the oral disc also shows a total of eleven anterials arranged in two rows; the first one consisting of five unicuspid teeth. Posterior and marginal teeth are not mentioned in the text, nor are they shown in the figure of the oral disc. Body pigmentation is not mottled, dorsal surface of head olive-brown, ventral body surface bluish-silvery, and tips of fins blackish; further on in the text he specifies that the posterior (= second) dorsal fin is blackish. The type specimen is lost, but Kottelat (1997) designated the lectotype of *Petromyzon japonicus* von Martens, 1868 as the neotype of *Petromyzon marinus camtschaticus* Tilesius, 1811, and it was studied (Tables 1–3).

### Original description of *Petromyzon japonicus* von Martens, 1868: 3–5, pl. I, fig. 2.

The Japanese common name is Yats'-me-anango meaning eight-eyes-eel, in reference to the eye and seven branchial openings on the side of the body and eel-like body shape. The written description and the drawing of the oral disc (scale not provided) are based



**Figure 2.** Oral disc of neotype of *Petromyzon marinus camtschaticus* and lectotype of *P. japonicus*, ZMB 6475, 418.3 mm TL.

on an unspecified number of metamorphosed specimens collected between 1860 and 1863 from Tokyo (appeared as Jeddo) and Yokohama, Honshu Island, Japan. It is not clearly stated whether von Martens collected these himself or if they were obtained from the fish market. The habitat from which they came (i.e., freshwater, brackish or marine) is, therefore, not certain. Total length, 454 mm; snout length, 29 mm (= 6.4% TL). The two dorsal fins are separate, the interspace is 2.5 times the eye diameter (eye diameter not provided). Dentition (Fig. 2): row of similarly-sized, slender and pointed marginals; between the marginals and the infraoral lamina is a row of 16 small posteriors (we counted 19 on the drawing); between the marginals and supraoral lamina are several larger teeth in a quincunx arrangement (the quincunx arrangement is not

**Table 2.** Trunk myomeres, dentition, oral papillae and oral fimbriae in adult types of *Petromyzon marinus camtschaticus* Tilesius, 1811, *Petromyzon japonicus* von Martens, 1868, *Petromyzon kessleri* Anikin, 1905, *Lampetra japonica septentrionalis* Berg, 1931, and adult topotypes of the latter. Numbers in parentheses are frequencies of character states. Abbreviations: b, bicuspid; u, unicuspid.

	<i>Petromyzon marinus camtschaticus</i> ZMB 6475 (neotype)	<i>Petromyzon japonicus</i> ZMB 6476 (paralectotype)	<i>Petromyzon kessleri</i> TGU 3, TGU 9 (7 syntypes) <sup>1</sup>	<i>Lampetra japonica septentrionalis</i> ZIN 12159 (8 syntypes)	<i>La. j. septentrionalis</i> ZIN uncat. (11 topotypes)
Type locality	Tokyo and Yokohama, Japan	Tokyo and Yokohama, Japan	Tom' and Kirgizka rivers, Russia	Onega River, Russia	Onega River, Russia
Trunk myomeres	75	70	70 (2), 73, 74, undetermined (3)	undetermined (8)	68, 71, 72 (4), 73, 74 (3), 76
Supraoral lamina	1u–1u	1u–1u	1u–1u (5), undetermined (2)	1u–1u (8)	1u–1u (11)
Endolateral formula	2–2–2 (2)	2–2–2 (2)	2–2–2 (9), 2–2–3, undetermined (4)	2–2–2 (14), 2–2–1 (2)	2–2–2 (22)
Infraoral lamina	1b4u1b	1b5u	1b4u1b (3), 1b5u1b (2), undetermined (2)	1b4u1b (8)	1b4u1b (10), 1b7u
Rows of anteriorials	2	2	2 (2), 3 (3), undetermined (2)	2 (6), 3 (2)	2 (4), 3 (7)
Rows of exolaterals	0 (2)	0 (2)	0 (10), undetermined (4)	0 (16)	0 (22)
Rows of posteriorials	1	1	1 (3), undetermined (4)	1 (8)	1 (11)
First anterior row	5u	3u	5u (5), undetermined (2)	3u (4), 4u (3), 5u	3u (9), 4u, 5u
First posterior row	20u	19u	24u (2), 29u, undetermined (4)	19u (3), 20u, 21u (2), 22u, 24u	18u, 19u, 20u (2), 21u, 22u (4), 23u (2)
Transverse lingual lamina	2u–I–6u	2u–I–3u	5u–I–7u, 7u–I–7u, undetermined (5)	4u–I–4u (2), 4u–I–5u, 6u–I–7u, 7u–I–6u, 7u–I–7u (2), 7u–I–8u	6u–I–5u, 6u–I–6u (2), 7u–I–6u (3), 7u–I–7u (2), 7u–I–8u (2), 8u–I–8u
Longitudinal lingual laminae	undetermined (2)	7u, 8u	undetermined (14)	undetermined (16)	9u (3), 10u (5), 11u, 12u (2), 13u, undetermined (10)
Oral papillae	undetermined	undetermined	undetermined (7)	13, 16 (3), 18 (4)	12, 14, 15 (2), 16, 18 (2), 21, undetermined (3)
Oral fimbriae	undetermined	undetermined	undetermined (7)	85, 91, 94, 97 (2), 98, 102, 103	88, 89 (2), 90, 92, 94 (2), 96, undetermined (3)

<sup>1</sup> Six of the seven syntypes (TGU 9) were collected from the digestive tract of a Common gull (*Larus canus*) and their condition was such that not all counts could be made.

apparent on the drawing); supraoral lamina is crescent shaped, each side with a strong unicuspid tooth; three bicuspid endolaterals on each side (the drawing shows 1–2–2 on the left and 2–2–1–2 on the right side); infraoral lamina with six unicuspid teeth (we counted seven on the drawing), the two outermost larger (smaller on the drawing); transverse lingual lamina without a furrow, with a strong middle unicuspid tooth and four unicuspid teeth on each side (only three unicuspid teeth on each side were discernible on the drawing); longitudinal lingual laminae paired, narrow, with numerous cusps facing each other. Body pigmentation is slate gray on the dorsal surface and silvery on the lateral and ventral surfaces. One lectotype and one paralectotype was studied (Tables 1–3).

**Table 3.** Shape and pigmentary characters in adult types of *Petromyzon marinus camtschaticus* Tilesius, 1811, *Petromyzon japonicus* von Martens, 1868, *Petromyzon kessleri* Anikin, 1905 and *Lampetra japonica septentrionalis* Berg, 1931 and adult topotypes of the latter. Numbers in parentheses are frequencies of character states. Pigmentation coverage as follows: -, absent to < 1%; +, 1 to < 25%; +++, ≥ 75%.

	<i>Petromyzon marinus camtschaticus</i> ZMB 6475 (neotype)	<i>Petromyzon japonicus</i> ZMB 6476 (paralectotype)	<i>Petromyzon kessleri</i> TGU 3, TGU 9 (7 syntypes) <sup>1</sup>	<i>Lampetra japonica septentrionalis</i> ZIN 12159 (8 syntypes)	<i>La. j. septentrionalis</i> ZIN uncat. (11 topotypes)
Type locality	Tokyo and Yokohama, Japan	Tokyo and Yokohama, Japan	Tom' and Kirgizka rivers, Russia	Onega River, Russia	Onega River, Russia
Caudal fin shape	spade-like	spade-like	undetermined (7)	spade-like (8)	spade-like (11)
<b>Pigmentation</b>					
Caudal fin	+++	+++	undetermined (7)	+++ (7), undetermined	+++ (10), undetermined
Second dorsal fin	with blotch	with blotch	undetermined (7)	no blotch, with blotch (6), undetermined	with blotch (10), undetermined
Lateral line neuromasts	undetermined	undetermined	undetermined (7)	pigmented, undetermined (7)	unpigmented (2), pigmented, undetermined (8)
Gular	undetermined	undetermined	undetermined (7)	- (7), undetermined	- (7), + (2), +++, undetermined

<sup>1</sup> Six of the seven syntypes (TGU 9) were collected from the digestive tract of a Common gull (*Larus canus*) and their condition was such that no characters could be evaluated.

Original description of *Petromyzon kessleri* Anikin, 1905: 10–15.

The written description is based on 16 metamorphosed specimens (Fig. 3) collected in the Tom' River and at the mouth of its tributary the Kirgizka River, Ob' River drainage; both localities near Tomsk, Russia. Total length, 160–210 mm. Two dorsal fins; the interspace varying from 0 (touching at their bases with swelling at the site of contact) to 10 mm. The second dorsal fin is usually angular and 1.5–2 times higher than the rounded first dorsal fin. The second dorsal fin is continuous with the caudal fin. The caudal fin shape is rhomboid (= spade-like). Dentition: row of minute marginals; 20–25 anterials becoming progressively smaller towards the anterior end of the oral disc and arranged in staggered order in five rows; supraoral lamina with two large, either sharp, blunt or intermediate shape, usually dark yellow teeth separated by a bridge; three bicuspid endolaterals on each side; infraoral lamina with six or seven, usually six, exceptionally nine (Mean = 6.6), large, either sharp or blunt, usually dark yellow teeth, the lateralmost being bicuspid and the internal ones unicuspid; a single row of 20–25 small posterials; semi-circular transverse lingual lamina with a large, sharp median tooth and eight or nine smaller teeth on each side; pair of longitudinal lingual laminae with an unspecified number of fine teeth facing each other. Body pigmentation is pale brown, ash gray or black on the dorsal surface, white or yellowish on the ventral surface and the end of the tail is dark brown. The line of demarcation between the dorsal and ventral pigmentation is not always distinct. The dorsal and caudal fins are white or yellowish except that the apex of the second dorsal fin is ash gray and the tip of the caudal fin is dark brown. Seven syntypes were studied (Tables 1–3).



**Figure 3.** Syntype of *Petromyzon kessleri*, TGU 3 [no. 3699 in Loganzen (1935b: table 3)], 182 mm TL.

**Original description of *Lampetra japonica septentrionalis* Berg, 1931: 93, 100–102, pl.V, fig. 4.**

The written description is based on ten metamorphosed specimens from the Onega River at Podporozh'e, White Sea basin, Russia, collected December 1901 by N.A. Varpakhovskiy (ZIN 12159). The common name given is Arctic lamprey. Total length, 284–377 mm (Mean = 327 mm). Dentition: infraoral lamina with six sharp teeth (Berg's notation is 1+4+1, but he does not explain the reason for the distinction between the types of teeth). Berg (1931) provides a drawing of the oral disc of a non-type specimen collected from the type locality in December 1929 (Berg 1931: pl. V, fig. 4) and it becomes clear that 1+4+1 means four unicuspid teeth flanked on each side by one enlarged bicuspid tooth. This is the condition (1b4u1b) of all eight syntypes examined in this study (Table 2). The drawing also shows a row of marginals, two rows of anterials, the first row with three unicuspid teeth, one row of posterials with 19 unicuspid teeth, no exolaterals on either side, supraoral lamina with two unicuspid teeth separated by a wide bridge, three bicuspid endolaterals on each side, transverse lingual lamina with an enlarged median cusp flanked on the left side by six unicuspid teeth and on the right by at least five. Additional characteristics reported by Berg (1931) in non-type specimens from the Onega River are an infraoral lamina count of 1+6+1 and four adult individuals with their ventral body surface mottled brown and one with the body entirely black. In a specimen from the Tura River the infraoral lamina count is 1+5+1 and in a specimen from the Vyg River a third cusp is placed asymmetrically between the two larger cusps on the supraoral lamina. Based on material examined and literature, Berg (1931) determined that the distribution of *La. j. septentrionalis* occurs from the White Sea basin to the Ob' River drainage. The specific rivers listed from west to east are: Umba (only apparently because based on an ammocoete), Vyg, Onega, Severnaya Dvina, Pesh, Shapkina (Pechora River drainage), Tura, Tobol, Irtysh, Tom', and also the Gulf of Ob'. The shortest adult is 227 mm TL from the Vyg River at Soroka (= Belomorsk) and the longest is 430 mm TL from the Tura River at Tyumen. In the

**Table 4.** Morphometrics in adults identified by Berg (1931) as *Lampetra japonica japonica* (von Martens, 1868), *La. j. kessleri* (Anikin, 1905), and *La. j. septentrionalis* Berg, 1931. Numbers in parentheses are sample sizes.

	<i>Lampetra japonica japonica</i>		<i>Lampetra japonica kessleri</i>				<i>Lampetra japonica septentrionalis</i>		
Locality	Amur River	Kamchatka River	Ob' River	Irtys River system	Yenisei River	Anadyr Estuary	Tobol River	Vyg River	Shapkina River
ZIN catalogue no.	15188	23440, 23441, 23590	6174, 6310	6311, 7815	14441	14371 <sup>1</sup>	7814	8545	20802
Total length (TL, mm)	391.5–436.5 (5)	154.5–198 (4)	187.5–212 (4)	144–186 (2)	122.5 (1)	144 (1)	351 (1)	301.5 (1)	334 (1)
Intestinal diameter, mm	1.0–2.5 (5)	2.5–4.5 (4)	0.7–1.3 (3), undetermined	0.7, undetermined	0.5	0.5	5.0	2.5	3.0
% TL									
Prebranchial length (d–B <sub>1</sub> )	9.4–10.8 (5)	12.6–14.2 (4)	9.6–12.0 (4)	10.8–11.8 (2)	11.4	12.8	11.0	10.6	9.9
Branchial length (B <sub>1</sub> –B <sub>2</sub> )	10.0–10.9 (5)	9.4–10.4 (4)	8.2–9.6 (4)	9.0–9.1 (2)	10.6	9.4	9.3	10.9	9.6
Trunk length (B <sub>2</sub> –a)	54.1–55.3 (5)	46.9–51.8 (4)	49.1–51.2 (4)	47.3–47.9 (2)	51.4	50.7	49.7	50.9	50.6
Cloacal slit length (a)	0.7–0.9 (5)	0.8–1.2 (4)	0.5–1.2 (4)	0.7–1.1 (2)	0.8	0.7	0.6	1.0	0.7
Tail length (a–C)	24.1–25.9 (5)	24.2–27.8 (4)	29.2–30.3 (4)	30.2–31.7 (2)	26.5	27.4	28.1	25.5	29.0
Disc length (d)	4.6–5.4 (5)	6.4–7.1 (4)	4.0–6.7 (4)	5.6–5.9 (2)	4.1	4.5	5.8	5.6	4.6
Prenostiril length (d–n)	5.6–6.8 (5)	7.2–8.1 (4)	5.2–7.2 (4)	6.2–6.4 (2)	6.1	6.6	6.0	5.6	5.5
Snout length (d–O)	5.6–7.0 (5)	8.0–9.1 (4)	5.4–7.7 (4)	6.7–6.9 (2)	6.1	7.6	7.1	6.6	6.4
Eye length (O)	1.2–1.4 (5)	2.1–2.5 (4)	1.7–2.4 (4)	2.7–2.8 (2)	2.4	2.4	1.6	1.8	1.2
Postocular length (O–B <sub>1</sub> )	2.6–2.9 (5)	2.7–3.0 (4)	2.0–2.7 (4)	2.4 (2)	3.3	3.1	2.3	2.3	2.7
Interbranchial opening length (B <sub>1</sub> –B <sub>2</sub> )	1.1–1.4 (5)	1.2–1.3 (4)	1.1–1.6 (4)	1.0–1.1 (2)	1.6	1.4	1.1	1.3	1.2
Interocular width (I)	3.2–3.8 (5)	3.2–3.7 (4)	2.2–3.7 (4)	2.7–2.8 (2)	3.7	2.1	2.7	3.6	3.1
Urogenital papilla length	0.0–0.4 (5)	0.5–0.8 (4)	0.0–1.0 (4)	0.7–1.1 (2)	1.2	0.0 <sup>2</sup>	0.6	0.7	0.6

<sup>1</sup> Re-identified as *Lethenteron camtschaticum* because it possesses the silvery body coloration of an anadromous downstream migrant.  
<sup>2</sup> The urogenital papilla did not protrude beyond the cloacal slit.

Onega River it is fished commercially. Berg (1931) diagnosed this subspecies from *La. j. japonica* based on the smaller length of its upstream migrants (227–430 mm TL versus 352–625 mm TL, respectively) and its lower fecundity: 24,086–25,144 eggs in two females, 335–339 mm TL, collected from the Onega River at the end of November 1929 compared to 80,825–107,015 eggs in six females, 403–492 mm TL, respectively (the TL of the female with the lowest fecundity was unknown), collected from Tneyvakh, below Nikolayevsk-on-Amur, lower Amur River, Russia between September and 20 November 1929. Berg (1931) diagnosed this subspecies from *La. j. kessleri* based on the latter having few eggs (no specific numbers given) and adults only reaching a maximum of 260 mm TL. Eight syntypes were studied (Tables 1–3).

**Table 5.** Trunk myomeres, dentition, oral papillae and oral fimbriae in adults identified by Berg (1931) as *Lampetra japonica japonica* (von Martens, 1868), *La. j. kessleri* (Anikin, 1905), and *La. j. septentrionalis* Berg, 1931. Numbers in parentheses are frequencies of character states. Abbreviations: b, bicuspid; u, unicuspid.

Locality	<i>Lampetra japonica japonica</i>			<i>Lampetra japonica kessleri</i>			<i>Lampetra japonica septentrionalis</i>		
	Amur River	Kamchatka River	Ob' River	Irrish River system	Yenisei River	Anadyr Estuary	Tobol River	Vyg River	Shapkina River
ZIN catalogue no.	15188	23440, 23441, 23590	6174, 6310	6311, 7815	14441	14371 <sup>1</sup>	7814	8545	20802
Trunk myomeres	undetermined (5)	73, undetermined (3)	76–77 (2), undetermined (2)	75, undetermined	76	undetermined	undetermined	undetermined	undetermined
Supraoral lamina	1u–1u (5)	1u–1u (4)	1u–1u (3), 1u–1u–1u	1u–1u (2)	1u–1u	1u–1u	1u–1u	1u–1u	1u–1u
Endolateral formula	2–2–2 (10)	2–2–2 (8)	2–2–2 (8)	2–2–2 (3), 2–2–2 <sup>2</sup>	2–2–2 (2)	2–2–2 (2)	2–2–2 (2)	2–2–2 (2)	2–2–2 (2)
Infraoral lamina	1b4u1b (3), 1b5u1b, 1b6u1b	1b4u1b, 1b5u1b (2), 1b1u1b2u1b	1b4u1b, 1b5u1b (3)	1b4u1b, 1b5u1b	1b3u1b	1b5u1b	1b4u1b	1b4u1b	1b4u1b
Rows of anteriors	2, 3 (4)	2 (3), 3	3 (4)	2 (2)	2	2	3	2	2
Rows of exolaterals	0 (10)	0 (8) <sup>2</sup>	0 (8) <sup>3</sup>	0 (3), undetermined	0 (2)	0 (2)	0 (2) <sup>4</sup>	0 (2)	0 (2)
Rows of posteriors	1 (5)	1 (3), 2 <sup>5</sup>	1 (4)	1 (2)	1	1	1	1	1
First anterior row	3u (3), 4u (2)	3u (3), 5u	3u (2), 4u, 6u	4u, undetermined	2u	5u	3u	4u	1u
First posterior row	18u, 19u (2), 20u, 22u	20u, 21u, 22u, 7u2b13u	25u, 28u, 31u, undetermined	21u, ≈30u	18u	undetermined	23u	20u	21u
Transverse lingual lamina	6u–1–7u, 7u–1–6u, 7u–1–7u (2), ?–1–?	8u–1–7u, ?–1–8u, undetermined (2)	7u–1–7u (2), 7u–1–8u, 9u–1–7u	6u–1–5u, 6u–1–6u	undetermined	8u–1–8u	8u–1–9u	?–1–?	4u–1–4u
Longitudinal lingual laminae	undetermined (10)	undetermined (8)	12u (2), undetermined (6)	7u (2), ≈13u (2)	undetermined	undetermined	undetermined	undetermined	undetermined
Oral papillae	16, 17 (2), 22, undetermined	18, 20, undetermined (2)	17, 26, undetermined (2)	undetermined (2)	undetermined	undetermined	undetermined	undetermined	19
Oral fimbriae	96, 100, 111, 126, undetermined	92, undetermined (3)	≈110, 121, 122, undetermined	>120, undetermined	≈82	undetermined	undetermined	undetermined	98

<sup>1</sup> Re-identified as *Lethenteron camtschaticum* because it possesses the silvery body coloration of an anadromous downstream migrant. <sup>2</sup> One exolateral tooth on the right side and one on the left side in the middle of the lateral field between the first and second endolaterals in one specimen. <sup>3</sup> One exolateral tooth on the right side next to the marginals between the first and second endolaterals in one specimen. <sup>4</sup> One exolateral tooth on the left side between the third endolateral and the marginals. <sup>5</sup> Two unicuspid teeth in the second row of posteriors.

**Table 6.** Shape and pigmentary characters in adults identified by Berg (1931) as *Lampetra japonica japonica* (von Martens, 1868), *La. j. kessleri* (Anikin, 1905), and *La. j. septentrionalis* Berg, 1931. Numbers in parentheses are frequencies of character states. Pigmentation coverage as follows: -, absent to < 1%; +, 1% to < 25%; ++, 25% to < 75%; +++, ≥ 75%.

Locality	<i>Lampetra japonica japonica</i>			<i>Lampetra japonica kessleri</i>			<i>Lampetra japonica septentrionalis</i>		
	Amur River	Kamchatka River	Ob' River	Irtys' River system	Yenisei River	Anadyr Estuary	Tobol River	Vyg River	Shapkina River
ZIN catalogue no.	15188	23440, 23441, 23590	6174, 6310	6311, 7815	14441	14371 <sup>1</sup>	7814	8545	20802
Caudal fin shape	spade-like (2), undetermined (3)	spade-like (4)	spade-like (3), undetermined	spade-like (2)	spade-like	undetermined	spade-like	spade-like	spade-like
<b>Pigmentation:</b>									
Caudal fin	+++ (4), undetermined	+++ (4)	+++ undetermined (3)	+++ (2)	+++	undetermined	undetermined	+++	+++
Second dorsal fin	with blotch (5)	with blotch (4)	with blotch, undetermined (3)	with blotch, undetermined	with blotch	with blotch	undetermined	with blotch	with blotch
Lateral line neuromasts	undetermined (5)	unpigmented (2), undetermined (2)	unpigmented, undetermined (3)	unpigmented, undetermined	undetermined	undetermined	undetermined	undetermined	unpigmented
Gular	-(4), +	-, + (2), ++	-(2), +, undetermined	+, +++	+++	undetermined	-	+	-

<sup>1</sup> Re-identified as *Lathenteron camtschaticum* because it possesses the silvery body coloration of an anadromous downstream migrant.

### Original description of *Petromyzon ernstii* Dybowski, 1872: 220.

The written description is based on a 310 mm TL metamorphosed specimen from the mouth of the Amur River, Russia. At the periphery of the suctorial disc is a series of small pointed teeth (= marginals); a second more centrally-located circular series of teeth consists in its lower zone of a row of small pointed teeth (= posterials), in its central zone, on each side, of three transversely-positioned tooth plates (= endolaterals), of which only the top two are bicuspid (the condition of the bottom endolateral is not given), and in its upper zone of two rows of more pointed conical teeth (= anterials) numbering eleven. Maxillary arch (= supraoral lamina) with two strong, sharp canine teeth. Mandibular arch (= infraoral lamina) with an average (therefore, the description involved more than one individual, but only one measuring 310 mm TL is mentioned) of four smaller-pointed teeth, and on either side a strong bicuspid tooth. Tongue crescent bar (= transverse lingual lamina) with 19 teeth; a narrow, weakly convex-concave (= parenthesis-shaped) bar (longitudinal lingual lamina) with 12 pointed teeth at both extremities of the crescent bar. First dorsal fin separated from the higher second dorsal fin by a wide gap. Body ash gray colored above and silvery below. The whereabouts of the type specimen is unknown and is presumed lost.

### Original description of *Petromyzon dentex* Anikin, 1905: 15–17.

The written description is based on two metamorphosed specimens ca. 160 mm long collected in the summer of 1903 at the mouth of the Yenisei River near Gol'chikha, Russia. These specimens were presumed to have come from the digestive system of a bird or a fish because their mucous layer was absent and all the fins were destroyed, leaving only occasional shreds. The dorsal body surface was black and the ventral surface yellowish white, with a sharp boundary between the two areas. The posterior end of the body and the tip of the caudal fin were black. Dentition is identical to that of *P. kessleri* in terms of number and arrangement of teeth in the upper jaw (= supraoral lamina), lower jaw (= infraoral lamina), paired lateral teeth (= endolaterals) and all the fine teeth (= anterials and posterials), but resembles that of *Petromyzon* (= *Lampetra*) *fluviatilis* in the teeth being larger and sharp. It may be assumed that the Siberian lampreys are represented by two forms, parallel to the European *Petromyzon* (= *Lampetra*) *planeri* and *P. fluviatilis*; *P. planeri* corresponds to *P. kessleri* and *P. fluviatilis* corresponds to *P. dentex*. The teeth are brown. The number of teeth on the infraoral lamina is not the same in the two specimens; one has six teeth, and the other has eight teeth, with two of the inside teeth being incompletely separated. This indicates that each of these incompletely divided teeth originate from a single tooth, resulting in the total number of eight instead of six teeth. The outermost teeth of the infraoral lamina have two inconspicuous cusps (i.e., bicuspid) in both specimens. There are 17–20 anterials arranged in four oblique rows and these teeth decrease in size from the center to the periphery of the oral disc. The row of small posterial teeth extends from one side to the other, its ends reaching the lower lateral pairs of teeth (= endolaterals). The two syntypes are presumed lost because Ioganzen (1935b) could not find them at TGU where they had been deposited and nor could AMN during his visit in 2011.

### Original description of *Ammocoetes aureus* Bean, 1881: 159.

The written description is based on one metamorphosed specimen (holotype, USNM 21524) 15 inches (= 381 mm) TL collected in 1877 (Bean 1882) from the Yukon River at Anvik (63°N, 160°W), Alaska, U.S.A. Dentition: maxillary (= supraoral lamina) with two cusps and mandibular (= infraoral lamina) with seven, the lateralmost one on each side enlarged. Eye length (O), nearly twice the width of the largest branchial opening, but the latter not given. Head or prebranchial length (d-B<sub>1</sub>), 9.7% of TL; tail length (a-C), 25% of TL (uncertain proportion because not clear if the measurement was taken from the anterior or posterior edge of the cloaca). Two dorsal fins with an interspace of ca. 24 mm. Coloration (in alcohol) of the back plumbeous, sides and belly golden yellow (hence, the specific name), and underside of the head and branchial region silvery. The collector, L.M. Turner, noted that the species was extremely abundant and used for food. The holotype was not studied.

### Original description of *Lampetra mitsukurii* Hatta, 1901: 22–24.

The written description is based on an unspecified number of metamorphosed specimens measuring 80–156 mm TL and collected from small watercourses (streamlets between fields, springs, and small canals) on Hondo [= Honshu], Shikoku, Kyushu, and Hokkaido islands, Japan. Hatta (1901) states that the new species is distinct from *La. japonica* measuring 390–507 mm TL that occurs in waterbodies (rivers, lakes, and ponds) of Honshu and Hokkaido islands, Sea of Japan basin, Japan. Additionally, it is diagnosable from *La. japonica* by having a more protruded suctorial disc; less prominent and more obtuse teeth; an unspecified lesser number of teeth in the series outside the mandibular tooth-plate (row of posterial teeth); the cusps at the lateral extremities of the mandibular tooth-plate (infraoral lamina) not bifurcated; the first and second dorsal fins are not separated by an interspace, only a notch; the anal fin (= fin-like fold) is of considerable height in females during the spawning season; the labial tentacles (= oral fimbriae) are mostly palmate; the skin is dark brown with faint irregular spots. Hatta (1901) notes that the two most important diagnostic characters are the smaller body size (80–156 versus 390–507 mm TL) and the unicuspid (versus bicuspid in *La. japonica*) lateralmost teeth on either side of the infraoral lamina. He suggests that the American brook lamprey, *La. wilderi* is probably the closest relative to *La. mitsukurii*. Two syntypes were studied (Fig. 4, Tables 7–9).

### Original descriptions of *Lampetra mitsukurii minor* Hatta, 1911: 263–266, 268, pl. IX, figs 3, 4, 7, 8 and *La. m. major* Hatta, 1911: 266–268, pl. IX, figs 1, 2, 5, 6.

The written description of *Lampetra mitsukurii minor* is based on an unspecified number of metamorphosed specimens measuring 80–165 mm TL from 14 localities across Japan as follows: Sapporo (Hokkaido Island), Tsuyama, Takayama, Akita, Aganogawa, Tamagawa, Kawagoye, Yamagata, Yamaguchi, Sakura, Hamamatsu,



**Figure 4.** Syntypes of *Lampetra mitsukurii*, ZMB 20638, 138.3 (a) and 140.1 (b) mm TL.

Gifu (eleven localities on Honshu Island), Matsuyama (Shikoku Island), Kumamoto (Kyushu Island). It is supplemented by drawings of the body of a spawning male and a spawning female from Sapporo in side-view, as well as close-ups of their cloacal regions (Hatta 1911: figs 3, 4 and 7, 8, respectively). The written description of *La. m. major* is based on an unspecified number of metamorphosed specimens measuring 350–410 mm TL from Sapporo (Hokkaido Island); the maximum TL in the range having been determined from Hatta (1911: fig. 1). It is supplemented by drawings of the body of a spawning male and a spawning female in side-view, as well as close-ups of their cloacal regions (Hatta 1911: figs 1, 2 and 5, 6, respectively). The males of both subspecies possess well-developed urogenital papillae and the females of both subspecies possess well-developed anal fin-like folds. Both subspecies are diagnosable from Japanese *La. japonica* because the latter is larger (450–507 mm TL), not externally sexually dimorphic, its supraoral and infraoral laminae cusps are sharp instead of blunt and its intestine relatively thick instead of thread-like. Additionally, while *La. m. major* arrives on its spawning grounds at the end of April, *La. japonica* arrives on its spawning grounds in late May or early June. *La. m. major* is sympatric with *La. m. minor* at Sapporo and is often found attached to the latter, but is allopatric with *La. japonica*. No type material was studied.

#### Original description of *Lethenteron matsubarai* Vladykov & Kott, 1978: 1792–1800.

The written description is based on seven metamorphosed specimens (holotype + six paratypes) measuring 150–174 mm TL collected in 1950–1952 from Shokotsu River, Hokkaido Island, Japan (44°22'N, 143°20'E). It is supplemented by photographs of the holotype (whole body in side-view and oral disc) and paratypes (intestine and velar apparatus). *Lethenteron matsubarai* is diagnosable from five metamorphosed *Le. japonicum* (= *Le. camtschaticum*) collected sympatrically and measuring 172–372 mm TL by being nonparasitic (intestinal diameter < 1 mm versus 3.5 mm), having

**Table 7.** Morphometrics in adult types of *Lampetra mitsukurii* Hatta, 1901 and *Lethenteron matsubarai* Vladyskov & Kott, 1978. Numbers in parentheses are sample sizes.

	<i>Lampetra mitsukurii</i> ZMB 20638 (2 syntypes)	<i>Lethenteron matsubarai</i> CMNFI 1984-274 (2 paratypes)
Type locality	Japan	Shokotsu River, Hokkaido Island, Japan
Total length (TL, mm)	138.3–140.1	147.5–163.5
Dorsal fin interspace (D <sub>1</sub> –D <sub>2</sub> , mm)	0.0 (2)	0.0 (2)
Intestinal diameter, mm	undetermined (2)	0.5, undetermined
% TL		
Prebranchial length (d–B <sub>1</sub> )	9.9–10.6	11.9(2)
Branchial length (B <sub>1</sub> –B <sub>7</sub> )	10.7–10.9	8.9–9.2
Trunk length (B <sub>7</sub> –a)	49.1–51.0	48.1–48.6
Cloacal slit length (a)	0.8–1.1	0.7–1.2
Tail length (a–C)	27.6–28.8	30.2–31.2
Disc length (d)	4.9–5.2	5.4–5.5
Prenostil length (d–n)	4.8–5.3	5.8–6.1
Snout length (d–O)	5.9–6.7	7.0–7.1
Eye length (O)	1.6–1.7	1.5–2.4
Postocular length (O–B <sub>1</sub> )	2.6–2.7	3.1 (2)
Interbranchial opening length (B <sub>1</sub> –B <sub>2</sub> )	1.2–1.3	1.2–1.4
Interocular width (I)	3.3–3.6	2.7–3.1
Urogenital papilla length	undetermined (2)	0.0–0.6

weaker dentition (poorly cornified, pale yellow blunt cusps versus strongly cornified, orange sharp cusps) and by the absence of pigmentation versus dark pigmentation on the second dorsal and caudal fins. Additionally, disc length and eye diameter, as a percentage of TL, was respectively, 4.4–5.3 and 1.7–2.3 in *Le. matsubarai* measuring 150–174 mm TL versus 5.3–6.0 and 2.6–3.2 in sympatric *Le. camtschaticum* measuring 172–193 mm TL. Dentition: supraoral lamina with one cusp at each end; three bicuspid endolaterals on each side; infraoral lamina with six cusps; single row of 18–23 unicuspid posteriors; transverse lingual lamina with an enlarged median cusp and up of eleven cusps in total. Body pigmentation in 4–5% formalin is light brown on back and sides and very light brown on ventral aspect. Trunk myomeres are 66–70 and velar tentacles seven or eight. Vladyskov and Kott (1979b) provided an amended caption to a figure in the original description (Vladyskov & Kott, 1978b: fig. 4). Two paratypes were studied (Tables 7–9).

Discussion

One or multiple species

Hubbs (1925) proposed that what he called *Entosphenus mitsukurii* was a degenerate, dwarf, brook lamprey derived from anadromous, parasitic *Entosphenus japonicus* (= *Le. camtschaticum*). Whether morphologically-similar (other than maximum adult size attained), but trophically distinct paired subspecies or species sensu Zanandrea (1959) or stem-satellite species sensu Vladyskov and Kott (1979a) [reviewed and

**Table 8.** Trunk myomeres, dentition, oral papillae, and oral fimbriae in adult types of *Lampetra mitsukurii* Hatta, 1901 and *Lethenteron matsubarai* Vladikov & Kott, 1978. Numbers in parentheses are frequencies of character states. Abbreviation: u, unicuspid.

	<i>Lampetra mitsukurii</i> ZMB 20638 (2 syntypes)	<i>Lethenteron matsubarai</i> CMNFI 1984-274 (2 paratypes)
Type locality	Japan	Shokotsu River, Hokkaido Island, Japan
Trunk myomeres	66–67	69–70
Supraoral lamina	1u–1u (2)	1u–1u (2)
Endolateral formula	2–2–2 (4)	2–2–2 (3), 2–2–1
Infraoral lamina	6u (2)	6u (2)
Rows of anterials	1, 2	2 (2)
Rows of exolaterals	0 (4) <sup>1</sup>	0 (4)
Rows of posterials	1, 2 <sup>2</sup>	1 (2)
First anterior row	4u, 5u	3u, 4u
First posterior row	20u, 21u	18u, 19u
Transverse lingual lamina	undetermined (2)	2u–1–4u, 3u–1–3u
Longitudinal lingual laminae	undetermined (2)	4u, undetermined
Oral papillae	11, 23	19, 20
Oral fimbriae	87, 106	undetermined (2)

<sup>1</sup> One exolateral tooth on the left side and two on the right side in one specimen.

<sup>2</sup> 22 unicuspid teeth are present in the second row of posterials.

updated by Salewski (2003)] represent distinct taxa, or a single trophically-plastic taxon sensu McPhail and Lindsey (1970), Yamazaki et al. (1998), Sawatzky et al. (2007), Kucheryavyy et al. (2007a, 2007b), Kucheryavyy et al. (2010a, 2010b, 2016), April et al. (2011), Nazarov et al. (2011), Yamazaki et al. (2011), Makhrov et al. (2013), Yamazaki and Nagai (2013), Kucheryavyy (2014), Artamonova et al. (2015), Makhrov and Popov (2015), and Yamazaki and Goto (2016) needs to be treated on a case by case basis as there appears to be a continuum of differentiation within lampreys [see reviews by Docker (2009) and Docker and Potter (2019)]. Between 17–21 June 1972 Savvaitova and Maksimov (1978) observed communal spawning of two forms (large and small) of *La. japonica* (= *Le. camtschaticum*) in Levyy Kolkalvayam River, tributary to Utkholok River, Sea of Okhotsk basin, western Kamchatka, Russia. The communal redds of large spawners (230–320 mm total length) and small spawners (100–140 mm total length) were located 60–80 km from the sea while redds consisting of small spawners only were located both closer to the coast and further upriver. Savvaitova and Maksimov (1978) proposed that the large spawners are the anadromous form and the small spawners the precociously mature resident freshwater form of *Le. camtschaticum*. Gritsenko (2002) also reported communal spawning of *Le. japonicum* (= *Le. camtschaticum*) (340–570 mm TL) and what he identified as *Le. kessleri* (< 230 mm TL), but could belong to another species (see below ‘Sympatric parasitic and nonparasitic taxa’, page 40) in the Tym’ River, Sakhalin Island, Sea of Okhotsk basin, Russia. However, he concluded that the two species were distinct because, in addition to their difference in total lengths, their trunk myomeres were non-overlapping by over 90%. In their review of lampreys in the Eurasian Arctic, encompassing over 70 rivers from the basins of the Barents, White, Kara, Laptev, East Siberian, Chukchi, and Bering seas, Makhrov et al. (2013) determined that *Le. camtschaticum* comprised both anadromous parasitic and resident

**Table 9.** Shape and pigmentary characters in adult types of *Lampetra mitsukurii* Hatta, 1901 and *Lethenteron matsubarai* Vladykov & Kott, 1978. Numbers in parentheses are frequencies of character states. Pigmentation coverage as follows: -, absent to < 1%.

	<i>Lampetra mitsukurii</i> ZMB 20638 (2 syntypes)	<i>Lethenteron matsubarai</i> CMNFI 1984-274 (2 paratypes)
Type locality	Japan	Shokotsu River, Hokkaido Island, Japan
Caudal fin shape	spade-like (2)	spade-like, undetermined
<b>Pigmentation</b>		
Caudal fin	- (2)	- (2)
Second dorsal fin	no blotch, undetermined	no blotch (2)
Lateral line neuromasts	unpigmented (2)	unpigmented (2)
Gular	undetermined (2)	- (2)

nonparasitic forms and considered the latter form, represented by *Le. kessleri*, to be a junior synonym. Kucheryavyy et al. (2007a) had previously treated sympatric lampreys in the Utkholok River drainage possessing three distinct modes of life [i.e., normally-maturing anadromous lampreys feeding as adults, early-maturing (i.e., praecox form) anadromous lampreys that spend up to a year at sea, presumably for feeding, although this is not explicitly stated, but in Savvaitova et al. (2007) and Kucheryavyy et al. (2010b) it is, and freshwater-resident lampreys non-feeding as adults] as belonging to a single species, *Le. camtschaticum*. Kucheryavyy et al. (2007a, 2010b) proposed a mechanism to explain the co-existence of these morphologically-similar, other than mature adult total length attained (i.e., respectively, 174–350 mm, 145–220 mm, and 100–165 mm), and synchronously spawning lampreys. They suggested that what determined the adult mode of life was the larval diet, with the larvae that switch from their usual diet of organic detritus and algae to an energy-rich diet of decomposing carcasses of Pacific salmon (*Oncorhynchus* spp.) forego feeding as an adult and become residents, while those that fed only on organic detritus and algae begin feeding post-metamorphosis in fresh water and later at sea before returning to fresh water for spawning. Unfortunately, this does not explain why there are normally maturing and praecox anadromous forms (Renaud 2011). Additionally, while decaying salmonids may be available in this particular river drainage, this is not the case in other parts of Russia and in Kazakhstan where nonparasitic lamprey occur thousands of kilometers from the sea, namely the upper Ob’ and Irtysh rivers, respectively (Romanov et al. 2017). Kucheryavyy et al. (2010a) also suggested that size differences in spawning individuals of *Le. camtschaticum* was not a barrier to successful spawning in that species. In the Kolkavayam River, Utkholok River drainage, communal and paired matings of different size individuals of all three forms (i.e., means of 270–280 mm, 170 mm, ≈130 mm TL for anadromous, praecox-anadromous, and resident, respectively) in various combinations during spawning ensure what Kucheryavyy et al. (2010a) refer to as evolutionary stasis. Kucheryavyy et al. (2007b) had previously reported on six so-called spawning balls of *Le. camtschaticum* in the Utkholok River drainage that varied in size from six to 44 individuals, three of which (six, seven, 43 individuals) consisted of the resident form only and the other three (eight, 27, 44 individuals) consisted of a mixture of anadro-

mous and resident forms in which the resident form was always predominant, constituting respectively, 62, 85, and 98% of individuals. On the other hand, Mateus et al. (2013) found 166 fixed allelic differences, 12 of which were assigned to genes, some of them controlling migratory behavior (i.e., anadromy vs. freshwater residency), between the species pair *La. fluviatilis* (anadromous parasitic) and *La. planeri* (resident nonparasitic) collected sympatrically at a spawning site in Portugal; thus indicating reproductive isolation. While such a study has not been conducted on *Le. camtschaticum* and its nonparasitic derivatives, we treat lampreys with different trophic modes of life as distinct species until this hypothesis has been falsified. Renaud et al. (2009) proposed common garden experiments as a way to elucidate this conundrum. Interestingly, preliminary studies by Yamazaki et al. (2011) and Yamazaki and Nagai (2013) indicate significant differences in allelic frequencies of polymorphic nuclear microsatellite loci between anadromous and what they characterize as fluvial nonparasitic landlocked (10 dams separating them from the sea) populations of *Le. camtschaticum* in Japan, and this may represent the first step in lamprey speciation. However, the results of these studies must be taken with caution because the two nonparasitic populations of *Le. camtschaticum* identified were represented only by ammocoetes (Ina and Tateiwa rivers, Agano River system, Honshu Island). Yamazaki and Goto (2000a) had previously proposed that in Japan speciation of lampreys of the genus *Lethenteron* had occurred from ancestral populations of anadromous parasitic *Le. japonicum* (= *Le. camtschaticum*) via precocious dwarf individuals leading independently to distinct nonparasitic *Le. kessleri* and what they called a northern form of *Le. reissneri* (see below ‘Taxonomic identity of nonparasitic lampreys in Japan and Sakhalin Island, Russia with low trunk myomere counts’, page 42). Salewski (2003) argued that the worldwide trend of satellite species in lampreys perhaps represented cases of sympatric speciation. Although lamprey species are usually either parasitic or nonparasitic, *Le. appendix* is the only nonparasitic species within the genus that exhibits very rarely what has been termed facultative parasitism (Docker 2009; Renaud 2011; Renaud and Cochran 2019). Eight “giant” *Le. appendix* adults (260–354 mm in total length) have been reported from Lake Huron and Lake Michigan basins (Manion and Purvis 1971; Vladykov and Kott 1980; Cochran 2008). Because these adults exceed the maximum total length of 240 mm reported for the larvae of the species (Mundahl et al. 2005) they must have fed post-metamorphosis. The retained capacity of some individuals to feed post-metamorphosis argues for a recent divergence of *Le. appendix* from *Le. camtschaticum* (Renaud 2011; Renaud and Cochran 2019).

### *Lethenteron* species with exolaterals

A number of individuals of various *Lethenteron* species possess exolaterals [see Kott (1974) in reference to *Le. appendix* (appeared as *Lethenteron lamottei*), in which 21.1% of individuals possessed one or two exolaterals in one or both exolateral fields; Vladykov and Kott (1978a) in reference to *Le. alaskense*, in which the holotype possesses one exolateral in each one of the exolateral fields and one paratype possesses on

both exolateral fields a complete exolateral row, which they refer to as a supplementary marginal row; Renaud and Naseka (2015) in reference to one individual each of *Le. reissneri* and *Le. camtschaticum*, in which they respectively possessed two and one exolateral teeth on one of the fields]. In this study, we recorded one or two exolaterals per exolateral field in two individuals of *Le. camtschaticum* (one from the Kamchatka River and one from the Tobol River), one individual of *Le. kessleri* from the Ob' River and in one syntype of *Le. mitsukurii* (Tables 5, 8).

### *Petromyzon japonicus*, a synonym of *P. marinus camtschaticus*

The original description of *P. marinus camtschaticus* based on a single adult (now lost) is very different from that of *P. japonicus* represented by two extant adult syntypes, one of which was selected as the neotype of the former taxon by Kottelat (1997) thereby making it a lectotype of the latter taxon. The original description of *P. marinus camtschaticus* refers to a supraoral lamina bearing two bicuspid teeth separated by a wide bridge, two pairs of bicuspid endolaterals and no row of posterial teeth is mentioned or depicted, while in that of *P. japonicus* (Fig. 2) the supraoral lamina has two unicuspid teeth separated by a wide bridge, three pairs of bicuspid endolaterals (although the accompanying drawing shows 1–2–2 on the left and 2–2–1–2 on the right side) and a single row of posterials. However, both taxa exceed 300 mm TL indicating that they represent parasitic species and possess a u-shaped transverse lingual lamina with an enlarged median cusp. The number of teeth on the transverse lingual lamina in the original description of *P. m. camtschaticus* is seven and nine in that of *P. japonicus* although in the type material from Japan we counted 2u–I–6u and 2u–I–3u (Table 2). The disc length of 5.2% TL estimated from the original description of *P. m. camtschaticus* is similar to the disc length of 4.1–4.8% TL for the type material from Japan (Table 1). The original description of *P. m. camtschaticus* reports seven unicuspid teeth on the infraoral lamina and that of *P. japonicus* reports six unicuspid teeth (although we counted seven in the accompanying drawing). However, the type material from Japan exhibits counts of 1b4u1b and 1b5u (Table 2). The second dorsal fin is stated to be blackish in the original description of *P. m. camtschaticus* and although no mention is made of its condition in the original description of *P. japonicus* both types from Japan exhibited a blotch on the second dorsal fin (Table 3). We agree with the action by Kottelat (1997) of making *P. japonicus* a synonym of *P. marinus camtschaticus* and suggest that the specimen described by Tilesius (1811) is atypical in the condition of its supraoral lamina and number of bicuspid endolaterals, while the absence of a row of posterials is an oversight on his part as these teeth are relatively small in comparison to the others that he did describe.

### Identity of the lamprey in Steller's unpublished manuscript

Because Tilesius (1811) had one lamprey specimen only, he added the unpublished description (Indice Piscium Camtschaticorum, manuscript F) by Georg Wilhelm Steller (1709–1746) of a metamorphosed lamprey collected near the mouth of Bolschaja River

brought to the latter on 18 June 1738 (Julian calendar; 29 June 1738 Gregorian calendar). However, Steller left St. Petersburg in January 1738 to join the Second Kamchatka Expedition (1733–1743) of Vitus Jonassen Bering (1681–1741), and by January 1739, had only reached Yeniseysk (on the Yenisei River), where he met Johann Georg Gmelin (1709–1755); still over 3,900 km from the Kamchatka Peninsula. Although there is a Bolshaya River on the western coast of Kamchatka, it is, therefore, improbable that this lamprey was obtained from there. It is more probable that the lamprey came from the Yenisei River, the name being derived from Ionessi (= Yonessi) meaning Bolschaja (= Bolshaya) voda or Big water in Evenki, the language spoken by the local Evenks people. This 333 mm TL lamprey adult is described as having variegated (mottled) body coloration with a brown dorsal surface and brown lines extending down in a wavy pattern into the shiny green-bronze sides of the body while the type of *P. m. camtschaticus* is not mottled. Otherwise, the characters described are similar to those of *P. m. camtschaticus*: body anguilliform; two dorsal fins, interspace between them ca. seven mm; posterior (second) dorsal fin blackish at the top; teeth yellowish; supraoral lamina with two teeth; infraoral lamina with six teeth. Additional characters described are: snout length is ca. 25 mm ( $\approx 7.5\%$  TL); eye length is ca. 2.5 mm ( $\approx 0.8\%$  TL); iris bronze colored. The common name Kanaháisch of this variegated lamprey is almost identical (Canaháisch) to the one reported for *P. m. camtschaticus* by Tilesius (1811). Although both *Le. camtschaticum* and *Le. kessleri* occur in the Yenisei River (see below ‘Sympatric parasitic and nonparasitic taxa’, page 40), the lamprey in Steller’s manuscript is *Le. camtschaticum* based on its size (333 mm TL). The only other study that reports a mottled body coloration in metamorphosed lampreys from Russia is that of Berg (1931) based on four non-type adults of *La. j. septentrionalis* [= *Le. camtschaticum*; see below ‘*Lampetra japonica septentrionalis* a synonym of *Petromyzon japonicus*’, page 26] measuring 279–345 mm TL from the Onega River.

### *Lampetra japonica septentrionalis* not derived from *La. fluviatilis*

We reject the hypothesis proposed by Ioganzen (1935a) that the similar dentition of *La. j. septentrionalis* and *La. j. japonica* is not indicative of their common origin and that *La. j. septentrionalis* is instead derived from *La. fluviatilis* and should therefore be called *La. fluviatilis septentrionalis*. Ioganzen (1935a) argued that the differences in dentition in *La. j. septentrionalis* versus *La. fluviatilis* in the second endolateral tooth (bicuspid versus tricuspid, exceptionally quadricuspid, respectively) and posterior row (present versus absent, respectively) were not stable taxonomic characters to distinguish the two. However, Ioganzen (1935a) provided no evidence for the presence of a tricuspid or quadricuspid second endolateral tooth in *La. j. septentrionalis* and merely suggested that this was due to insufficient samples. Berg (1948) hypothesized that the absence of lower labials (i.e., posteriors) in three of 19 adults of *La. japonica* from the Vyg River, White Sea basin, could be explained through hybridization of this species with *La. fluviatilis* in the post-Tertiary period during which the White and Baltic sea basins were in communication. Unfortunately, we did not examine this particular material, although the single adult we did examine from the Vyg River (Table 5,

ZIN 8545) possessed a row of posterials. Given that all lamprey individuals that we examined and were stated by Berg (1931) to be without posterials in fact possessed them (this study; Renaud and Naseka 2015), we believe that the hybridization explanation does not need to be invoked. Additionally, the cladistic analysis of Gill et al. (2003) based on morphological characters that included dentition showed that *La. fluviatilis* was not sister to *Le. camtschaticum*.

### *Lampetra japonica septentrionalis*, a synonym of *Petromyzon japonicus*

Berg (1931) distinguished *La. j. septentrionalis* from *La. j. japonica* by the smaller length of its upstream migrants (227–430 mm TL versus 352–625 mm TL, respectively) and its lower fecundity (24,086–25,144 eggs versus 80,825–107,015 eggs, respectively). Although Berg (1948) did not explain why he synonymized *La. j. septentrionalis* with *La. j. japonica*, he stated that the upstream migrating lampreys from the Mezen' River, White Sea basin, were not smaller than those of the Pacific Ocean basin [540 mm TL (Manteyfel' 1945) versus 625 mm TL (Berg 1931), respectively], and hence, one of his two diagnostic characters no longer held. Furthermore, Berg (1948) stated that the average number of eggs within lamprey from the Taui River, Okhotsk Sea basin, was ca. 40,000. This is intermediate between the 24,086–25,144 eggs for *La. j. septentrionalis* and 80,825–107,015 eggs for *La. j. japonica* reported in Berg (1931), thereby weakening the strength of his second diagnostic character. Additionally, Morozova (1956) recorded fecundities ranging from 50,000 to 124,000 eggs in *La. japonica* measuring 335–481 mm TL from the Amur River near Elabuga and Malmyzh, Russia, Yamazaki et al. (2001a) recorded fecundities ranging from 62,936–119,180 eggs in *Le. japonicum* measuring 363–442 mm TL from Hokkaido and Honshu islands, Japan, and Nursall and Buchwald (1972) recorded fecundities ranging from 9,790 to 29,780 eggs in 18 mature *Le. japonicum* females (TL not stated) from Great Slave Lake, Slave River, and Hay River, Northwest Territories, Canada. Our comparison of morphometrics, trunk myomeres, dentition, oral papillae and fimbriae, caudal fin shape and pigmentary characters of the type material of *Petromyzon marinus camtschaticus*, *P. japonicus* and *La. j. septentrionalis* (Tables 1–3) did not reveal any diagnostic differences between these three nominal taxa and we therefore consider them to be synonyms. Makhrov and Lajus (2018) suggest that *Le. camtschaticum* originated in the Pacific Ocean basin and colonized the Eurasian Arctic Ocean basin postglacially because in the median joining network analysis of mtDNA haplotypes, the Northern European haplotypes occur at the end of branches indicating their recent origin. Furthermore, on the eastern portion of its distribution, Walters (1955) proposes that *Le. camtschaticum* (appeared as *La. japonica*) colonized Arctic Canada through two possible routes: Arctic Alaska and the Yukon Valley; and that this could have occurred during the presence of the Bering Strait land bridge linking Eurasia and North America. Walters (1955) further states that *Le. camtschaticum* can also disperse across marine waters, and therefore, this is another possible route for its colonization of Arctic Canada. Yamazaki et al. (2014) provide evidence based on their study of seven polymorphic nuclear microsatellite loci

in 12 anadromous *Le. camtschaticum* populations distributed between Velikaya River, Chukotka, Russia in the north and Jinzu River, Honshu Island, Japan in the south, that the species has considerable marine dispersal ability and low homing ability. There is a caveat, however, associated with that study. Only three localities on Honshu and Hokkaido islands, Japan out of the 12 contained adults; the remaining samples were ammocoetes which are notoriously difficult to identify to species and were not dealt with in the present study.

### *Petromyzon ernstii*, a synonym of *Lethenteron camtschaticum*

*Petromyzon ernstii* is considered a junior synonym of *Le. camtschaticum* on the basis of its adult total length of 310 mm (Dybowski 1872a). The adult size attained by *P. ernstii* indicates that it feeds post metamorphosis and *Le. camtschaticum* is the only species to do so in the genus. The dentition of *P. ernstii* is not fully described by Dybowski (1872a), but what is described generally agrees with that of the neotype of *P. m. camtschaticus* (Table 2): supraoral lamina with two strong cusps; three endolaterals on each side with the top two endolaterals bicuspid (the type of the bottom endolateral is not given); infraoral lamina with two bicuspid teeth laterally and an average of four unicuspid teeth internally; two rows of anterials; one row of posterials. While the counts of 19 teeth on the transverse lingual lamina and 12 on each of the longitudinal lingual laminae reported by Dybowski (1872a) are respectively lower (9) and undetermined in the neotype of *P. m. camtschaticus* (Table 2), in the types of the latter's junior synonyms, *P. japonicus* and *La. j. septentrionalis*, the ranges observed are much closer to reaching those values (respectively, 6–16 and seven or eight; Table 2). If we include topotypes of *La. j. septentrionalis* the counts are even closer or encompassing (respectively, 12–17 and 9–13; Table 2). Notwithstanding the fact that we did not observe a count of 19 teeth on the transverse lingual lamina, we found a count of 18 in a specimen from the Tobol River identified as *La. j. septentrionalis* by Berg (1931) (Table 5), and therefore, we believe that *P. ernstii* is a junior synonym of *Le. camtschaticum*.

### Variability in the infraoral lamina dentition of *Le. camtschaticum*

Berg (1948) reported that *La. j. japonica* + *La. j. septentrionalis* (= *Le. camtschaticum*) usually had six mandibular (infraoral) teeth, occasionally seven (exceptionally nine in the Kamchatka River). We found six in the types (Table 2) and six to eight in the non-types (Table 5). According to Kucheryavii et al. (2007a), the infraoral lamina in typically anadromous *Le. camtschaticum* from the Utkholok River drainage, Kamchatka possessed one bicuspid tooth on either side, and three to seven unicuspid teeth internally, giving a total of five to nine teeth. Kucheryavii et al. (2007a) and Nazarov et al. (2011) for the Kol' River drainage, Kamchatka, also reported that rarely one of the lateralmost teeth was unicuspid. We also found a lateralmost unicuspid tooth in the paralectotype of *Petromyzon japonicus* (ZMB 6476; Table 2) and one topotype of *La. j. septentrionalis* (ZIN uncat.; Table 2).

## Real or perceived distributional discontinuity between the populations of parasitic *Le. camtschaticum* in Russia?

In regard to the wide discontinuity in the distributions of the populations of parasitic *Le. camtschaticum* reported by Berg (1931) as *La. j. septentrionalis* and *La. j. japonica* and later (Berg 1948) combined as *La. j. japonica*, this study has re-identified as *Le. camtschaticum* some of the samples in the intervening Siberian waters and considered by the aforementioned author as well as Ioganzen (1935b) as nonparasitic *La. j. kessleri*, thereby narrowing the gap between the distributions. Firstly, Berg (1931, 1948) tentatively considered and Ioganzen (1935b) undoubtedly considered *P. dentex* Anikin, 1905 to be a junior synonym of *La. j. kessleri*. However, we suggest instead that it is a junior synonym of *Le. camtschaticum* because Anikin (1905) stated that the teeth of the two approximately 160 mm TL specimens collected at the mouth of the Yenisei River are brown (indicating strong keratinization) instead of dark yellow as they usually are in *P. kessleri* and that although they have the same number and arrangement of teeth as in *P. kessleri*, these are larger and sharp, resembling those of *Petromyzon* (= *Lampetra*) *fluviatilis* rather than *P.* (= *La.*) *planeri*. Furthermore, Egorov (1985) reports the presence of *La. j. kessleri* adults up to 322 mm TL from the Yenisei Gulf, which on the basis of size we identify as *Le. camtschaticum*. Therefore, in our opinion, the range of *Le. camtschaticum* extends further east than the Ob' River drainage to the Yenisei River. Secondly, six specimens from the Anadyr Liman (= Estuary) are also re-identified as *Le. camtschaticum* rather than *Le. kessleri*. Anikin (1905) stated that *La. j. kessleri* (appeared as *P. kessleri*) reached an adult TL of 210 mm, but Berg (1931) stated that it reached, albeit rarely, 220–260 mm. Although we acknowledge that a TL of 221 mm can be attained (Table 4, ZIN 6174; only 212 mm when re-measured by us likely caused by shrinkage over time), we suggest that the 258 mm TL spent female [ZIN 23154 in Berg (1931)] is a *Le. camtschaticum* rather than *La. j. kessleri* because it was collected in brackish water of the Anadyr Estuary and was attached to a dog salmon, also called chum salmon (*Onchorhynchus keta*). Furthermore, it exceeds by 38 mm the longest ammocoete reported by Berg (1931) for *La. j. kessleri* (ZIN 6306, 220 mm TL from the Irtysh River at Omsk) even without taking into account the shrinkage in body length that occurs in a nonparasitic species between the beginning of metamorphosis and spawning. The two adults 135–138 mm TL (ZIN 23158) with very sharp teeth identified as *La. j. kessleri* by Berg (1931) are also re-identified as *Le. camtschaticum* because they were also collected in brackish water and attached to a chum salmon. The adult 144 mm TL (ZIN 14371) identified as *La. j. kessleri* by Berg (1931) is also re-identified as *Le. camtschaticum* (Tables 4–6) because it possesses the silvery body coloration of an anadromous downstream migrant. Later, Berg (1948) suggested that what he called *La. j. japonica* is possibly present in the Anadyr River based on a 260 mm specimen with sharp teeth collected in its estuary on 7 August 1938. Two other specimens with sharp teeth and thick intestines from the Anadyr Estuary identified by Berg (1948) as *La. j. kessleri* are re-identified as *Le. camtschaticum*; one (155 mm TL) was attached

to a sculpin (Cottidae) and the other (144 mm TL) to a chum salmon. Chereshnev (2008) also reports the presence of anadromous *Le. camtschaticum* in the Anadyr River from the estuary to ca. 600 km upstream. Therefore, we believe that *Le. camtschaticum* occurs in the Anadyr River and this extends its range northward from Kamchatka. Between the Yenisei and Anadyr River drainages are only two major rivers: the Lena and Kolyma; both within the region of Yakutia, also known as Republic of Sakha. According to Kirillov and Chereshnev (2006) and Kirillov et al. (2014), only nonparasitic *Lethenteron* lampreys occur in this entire region from the Anabar (west of the Lena) to the Kolyma rivers. However, these authors provide very little information about the lampreys and two things suggest that, at least in the case of the Kolyma River, anadromous, parasitic lamprey may be present. According to Kirillov et al. (2014) the mature adults at the beginning of the spawning season attain 240 mm TL, which slightly exceeds the maximum total length of 230 mm attained by *Le. kessleri* (see below), and lamprey are known down to the estuary, which would not be expected in a brook lamprey. Further investigations are required to confirm this.

### Adult total length attained by *Le. kessleri*

Although Berg (1931) considered *La. j. kessleri* to be a small non-migratory (i.e., resident) form in which the larvae at metamorphosis were larger than the adults, the material at his disposal did not support this contention. Berg (1931) stated that the longest ammocoete was 220 mm and adults reached 220–260 mm. We have explained above that *Le. kessleri* adults reach 221 mm TL, but have no direct evidence that they exceed this value. However, Poltorykhina (1971, 1974) conducted the most extensive studies of *Le. kessleri* examining 50 ammocoetes, 104 metamorphosing ammocoetes and 100 adults in the first study and 300 adults in the second study collected from the upper Irtys River system (Ob' River drainage) and reports that 218 mm is the mean TL attained by 50 ammocoetes, 233 mm is the mean TL attained by 12 metamorphosing ammocoetes at the penultimate stage of metamorphosis, and 230 mm is the maximum TL attained by adults. According to Poltorykhina (1971) the apparent increase in length between ammocoetes and adults is not the result of parasitic feeding post metamorphosis, but due to continued feeding of metamorphosing ammocoetes, at first on detritus and unicellular algae and later exclusively on unicellular algae, even though the oral cirri are lost and replaced by the rudiments of teeth over the course of metamorphosis. The latter is perhaps achieved through grazing of unicellular algae on rocks via the action of the lingual laminae and piston cartilage as suggested by Renaud (2011). Although Poltorykhina (1971) did not comment on whether or not the digestive tract remained open throughout metamorphosis, one must assume that it is patent at least for most of the period because growth occurred and algae were found in the intestine up until and including the last stage of metamorphosis. According to Poltorykhina (1971, 1974) the adults possess 67–72 trunk myomeres, which overlaps the range based on our examination of *Le. kessleri* type material (70–74; Table 2).

## Variability in the dentition of *Le. kessleri*

Ioganzen (1935b) reported that *La. j. kessleri* from the Ob' River drainage usually has two teeth on the supraoral lamina ( $n = 15$ ) and exceptionally four ( $n = 1$ ). However, his drawing (1935b: fig. 7) of the supraoral lamina in the latter specimen from the Ob' River near Bogorodskoye is interpreted as two bicuspid teeth instead of four unicuspid teeth and Egorov (1985) is also in agreement with this interpretation. However, Zhuravlev and Lomakin (2017) reported the case and provided a photograph of four unicuspid teeth on the supraoral lamina, one at each end and two on the bridge, in one of 54 individuals of *Le. kessleri* from the Belokurikha River, upper Ob' drainage (53 individuals had only one tooth at each end). In her extensive study of *Le. kessleri* from the upper Irtysh River system (Ob' River drainage), Poltorykhina (1974) reported usually two teeth on the supraoral lamina ( $n = 297$ ) and three cases in which an additional tooth was found on the bridge. We also found a case of three teeth on the supraoral lamina (ZIN 6310, Table 5). Poltorykhina (1974) stated that the infraoral lamina possesses five to ten teeth, usually six or seven, with the lateralmost being bicuspid and in 16 of 300 individuals some of the internal ones are also bicuspid. In five syntypes of *P. kessleri* (Table 2) we found six or seven teeth, with the lateralmost bicuspid and in one individual from the Yenisei River (ZIN 14441, Table 5) we recorded five teeth with the lateralmost bicuspid. Ioganzen (1935b) reported four bicuspid endolaterals on either side of the oral disc in a syntype of *P. kessleri* from the Tom' River (Ioganzen 1935b: table 3, TGU 3700). We did not find this specimen during AMN's visit to TGU in 2011. All of the syntypes that we examined (Table 2) had three endolaterals only on either side, most of which were bicuspid ( $n = 9$ ) and one with the formula 2–2–3. Additionally, Anikin (1905) only reported three bicuspid endolaterals in the original description of *P. kessleri*. Poltorykhina (1974) also only recorded three endolaterals on either side of the oral disc ( $n = 300$ ), and while the majority were bicuspid, in 36 individuals the formula was 2–2–1 and in 16 it was 2–1–2. Nazarov (2012) stated that usually there were three, but sometimes only two endolaterals on one side in material from the middle Yenisei River drainage. Nazarov (2012) reported three to five teeth in the first anterior row in individuals from the middle Yenisei River drainage, while we recorded invariably five in five syntypes of *P. kessleri* (Table 2) and two to six in non-types of *Le. kessleri* (Table 5). Poltorykhina (1974) reported that the lower circumoral teeth (= first posterial row) consist of a single row with 16–25 teeth and an unspecified number of individuals do not possess any. We recorded 24–29 teeth in three syntypes of *P. kessleri* (Table 2) and 18–31 in non-types of *Le. kessleri* (Table 5).

## *Lethenteron kessleri* without posterials?

The presence of well-developed lower labial teeth (= posterial row) in *Le. kessleri* versus weakly developed or completely absent lower labial teeth in *Le. reissneri* was the diagnostic character used by Berg (1931, 1948) to distinguish the two taxa. However, Renaud and Naseka (2015) showed that a complete and well-developed posterial row

was usually present in *Le. reissneri*. Berg (1931) reported “a very aberrant specimen” of *Le. kessleri* from the upper Yenisei River (ZIN 14441) without teeth on the lower lip (i.e., no posterials) and Berg (1948) suggested that it was possibly an aberrant *Le. kessleri* resembling *Le. reissneri*. However, we re-examined this specimen and found one row of posterials with 18 unicuspid teeth (Table 5). This situation is reminiscent of the case of three specimens identified by Berg (1931) as *Le. reissneri* without posterials, but found by Renaud and Naseka (2015) to possess them. While one of the three specimens was determined by Renaud and Naseka (2015) to be *Le. reissneri* (Shangshi River, People’s Republic of China), they re-identified the other two as *Le. camtschaticum* (Samarga and Sedanka rivers, Russia).

We suggest that the ten syntypes of *P. kessleri* retrieved in relatively good condition from the digestive tract of a Common gull [TGU 9 = TGU 3696 in Ioganzen 1935b: table 3] on 28 June 1903 were spawning because lampreys congregate in shallow waters during that time making them susceptible to bird predation. This was also the contention of Holčík (1986b). Additionally, Ioganzen (1935b) stated that the two dorsal fins touched in all ten individuals indicating that they were mature adults.

### Identity of lampreys in the Utkholok River drainage, Kamchatka

Kucheryavyy et al. (2007a) reported the presence of three forms of *Lethenteron camtschaticum* in the Utkholok River drainage, Kamchatka, Russia; typically anadromous, anadromous forma praecox, and resident. All three forms spawned together in June 2005 and possessed a dark blotch at the apex of their second dorsal fin and well pigmented spade-like caudal fins. The total lengths of the three forms were: 174–350 mm (typically anadromous, mature individuals of both sexes combined), 145–220 mm (anadromous forma praecox, mature individuals of both sexes combined), and 100–165 mm (resident, mature individuals of both sexes combined). Kucheryavyy (2014) reported anadromous adults of *Le. camtschaticum* on the Kamchatka Peninsula up to 452 mm TL. The supraoral lamina in the three forms possessed one unicuspid tooth on either end and in the case of the typically anadromous form rarely one bicuspid tooth on either end, as was also the case in the specimen of *P. m. camtschaticus* in Tilesius (1811: pl. IX, fig. II). The endolaterals in the three forms generally consisted of three bicuspid teeth on either side. Rarely, in the case of the typically anadromous form, the lower left or right endolateral was unicuspid or there were four bicuspid endolaterals or there were three bicuspid with one unicuspid tooth at the lower position, and rarely in the case of the resident form, the lower endolateral was unicuspid or there were four bicuspid endolaterals. The infraoral lamina in the three forms generally possessed one bicuspid tooth on either side, and respectively, three to seven, four or five, and four to six unicuspid teeth internally. Rarely, in the case of the typically anadromous form, one of the lateralmost teeth was unicuspid, and in the case of the resident form, one or both lateralmost teeth were unicuspid. The number of posterials for the three forms was respectively, 13–28, 12–22, and 12–25. These values are lower than the combined values of 18–29 posterials, based on our examination of type or topotype material of

*P. m. camtschaticus*, *P. japonicus*, *P. kessleri*, and *La. j. septentrionalis* (Table 2), but may reflect the larger sample sizes examined by Kucheryavyi et al. (2007a). Remarkably, the range in trunk myomeres for the three forms was extremely broad for a small river drainage being respectively 55–79, 57–71, and 57–78. The lower end counts may at least partly be explained by the method of counting which was based on a vertical line drawn in front of the cloaca rather than using the lower angle of the posterior myoseptum lying at or anterior to the anterior edge of the cloaca as in Renaud (2011). We interpret the typically anadromous form as being *Le. camtschaticum* and both the anadromous forma praecox and the resident form as being *Le. kessleri*. The resident form is stated by Kucheryavyi et al. (2007a) as not feeding after metamorphosis. The reasons we identify the anadromous forma praecox as *Le. kessleri* is because there is no clear evidence that it is anadromous or feeding as an adult as the intestinal contents of 16 individuals were examined by Kucheryavyi et al. (2007a), and while five did not contain any food, six contained small algae and five contained brown material similar in color to the food of ammocoetes, and furthermore, their adult size range (145–220 mm TL) falls under the maximum 230 mm TL reported for adults of the species by Poltorykhina (1974). If the anadromous forma praecox had spent several months to a year in the sea, as Kucheryavyi et al. (2007a) contend, one would not expect any remnants of larval food in their intestine. While we identify as *Le. camtschaticum* four small adults collected in the Kamchatka River and measuring 154.5–198 mm TL (Table 4: ZIN 23440, 23441, 23590), these individuals possessed intestinal diameters 2.5–4.5 mm (Table 4) and were therefore at the beginning of their adult life unlike the spawning individuals in the Utkholok River drainage presumed by Kucheryavyi et al. (2007a) to be anadromous forma praecox *Le. camtschaticum*. In fact, Berg (1931) stated that three of the four individuals collected June 1908 (ZIN 23441) and 7 July 1909 (ZIN 23590) measuring a combined 154.5–198 mm TL were descending towards the ocean. The fecundity of the typically anadromous form was 12,272–34,586 eggs (Kucheryavyi et al. 2007a), which overlaps the lower end of the fecundity (24,086–107,015 eggs) recorded by Berg (1931, 1948) for *Le. camtschaticum*. Kucheryavyi et al. (2007a) did not record the fecundity for the anadromous forma praecox, but stated that the fecundity of the resident form was 468–3,441 eggs. This we take to be the fecundity for *Le. kessleri*. It broadly overlaps with the fecundity reported by Poltorykhina (1973) [cited in Holčík (1986b) and Makhrov et al. (2013)] for *Le. kessleri* (i.e., 1,820–5,800 eggs) from the upper Irtysh River system, Ob' River drainage, as well as the fecundity reported by Zhuravlev and Lomakin (2017) for *Le. kessleri* (i.e., 465–1,350 eggs) from the Belokurikha River, Ob' River drainage, and slightly overlaps with the fecundity reported by Karasev (2008) for *Le. kessleri* in the lower Tobol River (i.e., 3,161–7,208 eggs), also in the Ob' River drainage, and is very close to the fecundity reported by Kuderskiy and Mel'nikova (1970) for *Le. kessleri* (i.e., 651–3,096 eggs) in the Yemtsa River (Severnaya Dvina River drainage), and to that of *Le. alaskense* provisionally suggested here as a synonym of *Le. kessleri* (see below 'Taxonomic key to adults of *Lethenteron*', page 53). The fecundity of *Le. alaskense* from Brooks River, Alaska, U.S.A. and Martin River, Northwest Territories, Canada was reported by Vladykov

and Kott (1978a) as 2,188–3,477 eggs. It is also very similar to the fecundity recorded by Karasev (1987) for *Le. reissneri* from the Ingoda River, Russia (1,720–3,360 eggs). The extremely low fecundity of 117 eggs recorded by Novikov (1966), in a 134 mm TL *Le. kessleri* retrieved from the stomach of a Northern pike, *Esox lucius*, collected in July 1963 in the Kolyma River, Russia, may have been a partially spent female.

### Identity of lampreys in the Kol' River drainage, Kamchatka

Similar to the case reported above in the Utkholok River drainage, Nazarov et al. (2011) stated the presence of three forms of *Le. camtschaticum* in the Kol' River drainage, Kamchatka, Russia; typically anadromous (243–297 mm TL, mature individuals sexes combined), anadromous forma praecox (190.5–237 mm TL, two spent females only), and resident (110–141 mm TL, mature individuals sexes combined). However, whereas all three forms are reported to possess a blotch on the second dorsal fin (their table 2), only the typically anadromous and anadromous forma praecox possess one (their fig. 5a, b, respectively), whereas the resident form appears to possess none (their fig. 5c depicting a male and a female). Additionally, the typically anadromous and anadromous forma praecox possess a strongly pigmented caudal fin (their fig. 5a and 5b, respectively), whereas the resident form appears to possess no caudal fin pigmentation (their fig. 5c). The two anadromous forms are said to be parasitic and the resident form nonparasitic. The supraoral lamina in the three forms possessed one unicuspid tooth on either end. The endolaterals in the three forms generally consisted of three bicuspid teeth on either side. Rarely, in the case of the typically anadromous form, and sometimes, in the case of the resident form, the lower left or right endolateral was unicuspid. The infraoral lamina in the three forms generally possessed one bicuspid tooth on either side, and respectively, four to seven, five or six, and five or six unicuspid teeth internally. Rarely, in the case of the typically anadromous form, one of the lateralmost teeth was unicuspid. The number of posteriors for the three forms was respectively, 13–20, 17–22, and 15–21. The range in trunk myomeres for the three forms was respectively, 71–76, 73–75, and 67–74. The fecundity of the typically anadromous form was 24,038–31,050 eggs, which virtually completely overlaps with the lower end of the fecundity (24,086–107,015 eggs) recorded by Berg (1931, 1948) for *Le. camtschaticum*. Nazarov et al. (2011) did not record the fecundity for the anadromous forma praecox, as the only two females were spent, but stated that the fecundity of the resident form was ca. 3,200 eggs. Nazarov et al. (2011) reported that resident lamprey either spawned communally with typically anadromous and anadromous forma praecox or independently. This is reminiscent of the situation reported by Savvaitova and Maksimov (1978) of communal spawning between large (230–320 mm TL) and small (100–140 mm TL) lampreys and independent spawning of small lamprey in the Levyy Kolkalvayam River, Utkholok River drainage. We interpret the typically anadromous and anadromous forma praecox as being *Le. camtschaticum* and the resident form as very similar to *Le. mitsukurii* in terms of the absence of a blotch on the second dorsal fin and the unpigmented caudal fin, but different in its possession of bicuspid

rather than unicuspid lateralmost teeth on the infraoral lamina (see below ‘*Lethenteron mitsukurii*’ distinct from *Le. kessleri* and *Le. reissneri*’, page 37). We, therefore, defer judgment on the identity of the resident form until more information becomes available. However, it is significant that Vladykov and Kott (1979c) reported the presence of *Le. matsubarai* on the Kamchatka Peninsula (see below ‘*Lethenteron matsubarai*’, a synonym of *Le. mitsukurii*’, page 38). Khusainova and Karpenko (2017) confirmed the presence of *Le. camtschaticum* in the Kol’ River based on prespawning individuals measuring 312–351 mm TL.

### Identity of lampreys in the Lake Azabach’e basin, Kamchatka

Karpenko et al. (2013) described 37 spawning individuals of *Lethenteron* measuring 147.1–172.0 mm TL and collected on 12 July 2012 from Dyakonovskiy Creek, Lake Azabach’e basin, but they could not identify them to species. It would appear that the individuals were partially spent because the four females examined possessed only 16–126 eggs and in the two in which the eggs were measured they were ca. 1.0 mm in length. According to Karpenko et al. (2013) these adults possess two or three teeth on the supraoral lamina (usually one unicuspid tooth at each end, but in one case the tooth at one end is bicuspid, and in another case an additional unicuspid tooth is present on the bridge between the unicuspid lateral teeth), three bicuspid endolaterals on each side, the infraoral lamina usually with two lateralmost teeth bicuspid and four or five internal teeth unicuspid (sometimes the two lateralmost as well as the four, five or six internal teeth are unicuspid), one row of small posteriors, and 66–74 trunk myomeres. While the characters of dentition and trunk myomeres all agree with *Lethenteron*, the small total length of the spawning individuals would indicate a nonparasitic species; either *Le. reissneri* or *Le. kessleri*. However, the diagnostic characters distinguishing these two species (i.e., second dorsal fin pigmentation and transverse lingual lamina dentition; see below ‘*Lethenteron kessleri*’ distinct from *Le. reissneri*’, page 35) were not recorded, and therefore, we cannot determine the species’ identity. Bugayev et al. (2007) had reported the presence of *Le. reissneri* in Lake Azabach’e, but we have re-identified the 185 mm TL adult as *Le. camtschaticum* because its intestine contained half-digested fish flesh. Lake Azabach’e belongs to the Kamchatka River drainage, and the presence of *Le. camtschaticum* is well documented in this river drainage (Berg 1931, 1948; Bugayev et al. 2007). Khusainova and Karpenko (2017) collected additional spawning individuals from Dyakonovskiy Creek in 2014 (n = 145) and compared them with prespawning material from the Kol’ River (western Kamchatka) collected in 2013 (n = 19). These authors concluded based on total length that the lamprey from the Dyakonovskiy Creek measuring 132–190 mm TL is *Le. reissneri* and the one from the Kol’ River measuring 312–351 mm TL is *Le. camtschaticum*. While we agree with the identification of *Le. camtschaticum* for the Kol’ River material, we believe that the identification of the material from Dyakonovskiy Creek cannot be established because, as in Karpenko et al. (2013), neither the second dorsal fin pigmentation nor the transverse lingual lamina dentition was examined by Khusainova and Karpenko (2017).

### *Ammocoetes aureus*, a synonym of *Le. camtschaticum*

Despite having been placed in the genus *Ammocoetes*, *A. aureus* is clearly based on an adult individual. The holotype measures 381 mm TL, and it possesses supraoral and infraoral laminae and eyes. Even though the original description is fragmentary, the size of the adult individual, the condition of its supraoral (two cusps) and infraoral (seven cusps, the lateralmost one on either end enlarged) laminae indicate that *A. aureus* is a junior synonym of *Le. camtschaticum*. Nelson (1887) reports that *A. aureus* (= *Le. camtschaticum*) ascends the Yukon River, Alaska, at least up to Nulato and that the native Alaskan name for the Arctic lamprey is Nû-mug-û-shûk. He further reports that the upstream-migrating lamprey passed through Anvik in the evening of 26 Nov. 1879 and that the native Alaskans catch them through holes in the ice with sticks having two short cross bars at the lower end or dipnets and extract their oil for eating and as a substitute for seal oil in lamps. On the other hand, Turner (1886) reports that *A. aureus* (= *Le. camtschaticum*) ascends the Yukon River in the latter part of December, reaches the Russian Mission – Anvik river section by the middle of February and by the latter part of April, Fort Yukon, Alaska, over 1,600 km upriver of the mouth. Turner (1886) also states that the spawning run passing through a given locality lasts approximately three weeks.

### *Lethenteron alaskense*, a synonym of *Le. kessleri*?

Because no character was found to distinguish the adults of *Le. kessleri* from those of *Le. alaskense*, we provisionally consider the latter to be a junior synonym of the former despite the fact that they occur on separate, but adjoining continents; *Le. kessleri* in Eurasia and *Le. alaskense* in North America. Further study is required to test this hypothesis. Interestingly, Berg (1948) had suggested that what he called *La. j. kessleri* was probably also present in Alaska and Poltorykhina (1974) treated the Alaskan *La. japonica* of Heard (1966) as *La. kessleri*. Additionally, in the original description of *Le. alaskense*, Vladykov and Kott (1978a) stated that they did not compare it to *Le. kessleri* because they lacked sufficient material for comparison. Holčík (1986c) treated *Le. alaskense* as a landlocked form of *Le. japonicum* (= *Le. camtschaticum*), but we reject this on the basis that the former is nonparasitic and the latter parasitic.

### *Lethenteron kessleri* distinct from *Le. reissneri*

A comparison of the original descriptions and extant type material of these two nominal taxa (this study; Renaud and Naseka 2015) did not reveal any significant differences other than total length (160–210 mm in *P. kessleri* versus 120–140 mm in *P. reissneri*), and this we believe is due to the incomplete descriptions and the poor condition of the specimens, in particular *Le. reissneri*, preventing a full comparison. However, Renaud and Naseka (2015) reported that the adult specimen identified by Berg (1931) and accepted by them as *Le. reissneri* (ZIN 14457) from the Shangshi River, Amur River

drainage, does not have a blotch at the apex of its second dorsal fin and has a transverse lingual lamina with 2u–I–2u while the original description of *Petromyzon kessleri* Anikin, 1905 stated that the apex of the second dorsal fin is ash gray (i.e., blotched) and the transverse lingual lamina has a large median tooth flanked by eight or nine smaller teeth (i.e., 8u–I–8u or 9u–I–9u and combinations thereof). In two of the seven syntypes of *P. kessleri* for which we could determine the character state of the transverse lingual lamina (Table 2) these were 5u–I–7u and 7u–I–7u. Therefore, the pigmentation of the second dorsal fin and the transverse lingual lamina dentition are diagnostic characters for these two taxa. The suggestion by Yamazaki et al. (2006) that *Le. kessleri* is a synonym of *Le. reissneri* on the basis of similarities in their larval trunk myomere counts and identical electrophoretic profiles is thus rejected. Sato (1951) was the first to suggest that *Le. kessleri* (appeared as *La. j. kessleri*) was present on Hokkaido Island on the basis of 26 spawning adults 144–193 mm TL collected in the Shibechari River (now known as Shizunai River). However, we have re-identified this material as *Le. reissneri* because according to the description by Sato (1951) the specimens do not have a dark blotch on their second dorsal fin, but do have a pigmented caudal fin (++, +++; according to his fig. 1), an infraoral lamina bearing five to seven teeth, the lateralmost being bicuspid, usually three bicuspid endolaterals on each side, the third one rarely unicuspid on one or both sides, 17–23 teeth in the first posterial row, and 66–74 trunk myomeres. Additionally, material from the Shizunai River have an identical electrophoretic profile to *Le. reissneri* from the type locality of Onon River, Siberia (Yamazaki et al. 2006).

### *Lethenteron reissneri* present in the Angara River drainage, Russia

In their redescription of the species, Renaud and Naseka (2015) restricted the distribution of *Le. reissneri* to the Shilka and Songhua river systems within the Amur River drainage, until a more geographically comprehensive study is undertaken. Loshakova and Knizhin (2015) reported the presence of a nonparasitic lamprey in the geographically proximate Angara River drainage, Yenisei River system, Russia; specifically, in the Chuksha River. Their reported adult TL of 135–182 mm, caudal fin strongly pigmented [i.e., +++, based on figs 3, 4 in Loshakova and Knizhin (2015)], trunk myomeres 66–77, supraoral lamina with two unicuspid teeth, three bicuspid endolaterals on either side, infraoral lamina with usually four, less frequently five unicuspid teeth and one bicuspid lateralmost tooth on either side, 18–26 posteriors, spawning at the end of May middle of June, absolute fecundity of 1,042–3,166 eggs with diameter 0.79–0.87 mm, all point to the identity being *Le. reissneri* and the reported absence of a dark blotch on the second dorsal fin distinguishes it from *Le. kessleri* (see above '*Lethenteron kessleri* distinct from *Le. reissneri*', page 35). Indeed, Karasev (1987) reported an almost identical adult TL (i.e., 137–182 mm) for lamprey, identified as *Le. reissneri* by Renaud and Naseka (2015), from the upper Amur basin (Ingoda [type locality of *Le. reissneri*] and Shilka rivers), as well as a fecundity in females from the Ingoda River of 1,720–3,360 eggs with diameter 0.68–0.84 mm. Both syntypes of *Le. reissneri* examined by Renaud and Naseka (2015) also had a supraoral lamina with two unicuspid teeth and the only

one in which endolaterals and trunk myomeres could be determined had three bicuspid endolaterals and 70 trunk myomeres. Although the only syntype in which the infraoral lamina could be studied had only one lateralmost bicuspid and five unicuspid teeth, another individual from the Shangshi River (Songhua River drainage, Amur River system), and identified by Berg (1931) as *Le. reissneri*, had two lateralmost bicuspid and four internal unicuspid teeth, as well as 24 posteriors, a strongly pigmented (i.e., +++) caudal fin and no blotch on its second dorsal fin (see Renaud and Naseka 2015). Finally, Dybowski (1869) stated that *Le. reissneri* spawns in June. Unfortunately, the number of cusps on the transverse lingual lamina, another diagnostic character distinguishing *Le. reissneri* from *Le. kessleri*, was not recorded by Loshakova and Knizhin (2015). According to Enikeev (2018) a Transbaikalian paleolake existed in the Late Pleistocene connecting the Angara River to the upper Amur including the Onon and Ingoda rivers, the type locality of *Le. reissneri*, and we believe this could explain the present-day occurrence of this lamprey species in the Angara and Amur River drainages.

### *Lethenteron mitsukurii* distinct from *Le. kessleri* and *Le. reissneri*

*Lampetra mitsukurii* is placed by us in the genus *Lethenteron* because it possesses a row of posteriors according to the original description (Hatta 1901) and the examination of two syntypes (Table 8). *Lethenteron mitsukurii* is distinct from *Le. kessleri* based on the absence of bicuspid lateralmost teeth on the infraoral lamina (Hatta 1901; Table 8) and the absence of pigmentation on its second dorsal and caudal fins (Table 9). The original description of *Le. kessleri* states that the lateralmost teeth on the infraoral lamina are bicuspid (Anikin 1905) and this was confirmed in five syntypes for which the character could be determined (Table 2). While examination of the pigmentary characters was uninformative in the syntypes of *Le. kessleri* (Table 3), the original description states that the apex of the second dorsal fin is ash gray (Anikin 1905) and an adult identified by Berg (1931) as *La. j. kessleri* from the Ob' River (ZIN 6310, Table 6) has a heavily pigmented caudal fin (+++). *Lethenteron mitsukurii* is distinct from *Le. reissneri* based on syntypes of the latter possessing a bicuspid tooth on one or both sides of the infraoral lamina (Dybowski 1869; Renaud and Naseka 2015) and a heavily pigmented caudal fin (+++) in the adult from the Shangshi River, Amur River system (ZIN 14457) identified by Berg (1931) and accepted by Renaud and Naseka (2015) as *Le. reissneri*.

### Identity of the lamprey from Siberia described in Hatta (1901)

Hatta (1901) identified as *La. mitsukurii* a recently metamorphosed 150 mm TL female from Pervaya Rechka Brook near Vladivostok, Russia. Contrary to what is stated in Hatta (1901) this brook is not a tributary to the Amur River, but empties directly into the Sea of Japan. He notes that the first and second dorsal fins are separated by a deep notch; the supraoral lamina has two well separated blunt cusps; the infraoral lamina has six blunt cusps; three bicuspid endolaterals occur on each side; other labial teeth are simple and form a circle immediately inside the fringe of labial tentacles

(= oral fimbriae). The latter character refers to the row of marginals. There is no mention of a row of posterials. Renaud and Naseka (2015) identified as *Le. camtschaticum* a 161.5 mm TL adult, previously identified by Berg (1931) as *La. reissneri*, from the Sedanka River emptying directly into the Sea of Japan near Vladivostok. Although the six unicuspid teeth on the infraoral lamina point to *Le. mitsukurii*, the absence of information on other key diagnostic characters (i.e., posterial row, second dorsal fin and caudal fin pigmentation) prevent us from confidently identifying as such the specimen from Siberia in Hatta (1901).

### *Lethenteron matsubarae*, a synonym of *Le. mitsukurii*

In our opinion *Le. matsubarae* is a junior synonym of *Le. mitsukurii* because both possess only unicuspid teeth on the infraoral lamina (Table 8) and unpigmented second dorsal and caudal fins (Table 9), three diagnostic characters that distinguish them from *Le. camtschaticum*, in which the infraoral lamina possesses at least one bicuspid tooth, the second dorsal fin has a blotch at its apex, and the caudal fin is strongly pigmented (Tables 2, 3). Likewise, the infraoral lamina of both *Le. reissneri* and *Le. kessleri* possess at least one bicuspid tooth (Renaud and Naseka 2015; Table 2). Unfortunately, the poor condition of the type material of *Le. reissneri* (see Renaud and Naseka 2015) and *Le. kessleri* (Table 3) did not permit an evaluation of the pigmentation of their second dorsal and caudal fins. However, Renaud and Naseka (2015) determined the second dorsal fin to be unpigmented (i.e., no blotch) and the caudal fin to be strongly pigmented in an adult of *Le. reissneri* from the Shangshi River (Amur River system), People's Republic of China and Anikin (1905) described *Le. kessleri* as having the apex of the second dorsal and caudal fins pigmented, thus further distinguishing both species from *Le. mitsukurii*. Therefore, we reject the synonymy of *Le. matsubarae* with *Le. kessleri* proposed by Iwata et al. (1985), which was based on material presumed as belonging to the latter species that came from Hokkaido Island following Sato (1951) instead of examining type material or using the original description. The material identified as *Le. kessleri* by Sato (1951) has been re-identified by us as *Le. reissneri* (see above '*Lethenteron kessleri* distinct from *Le. reissneri*', page 35). The material identified as *Le. kessleri* by Iwata et al. (1985) we believe to be a mixture of *Le. reissneri* and *Le. mitsukurii* because the authors report it to possess 65–73 trunk myomeres, an unpigmented second dorsal fin and a strongly pigmented caudal fin; a few individuals however having an unpigmented caudal fin. Those individuals with a strongly pigmented caudal fin correspond to *Le. reissneri*, while those with an unpigmented caudal correspond to *Le. mitsukurii*.

### Taxonomic identity of *Lampetra mitsukurii minor* and *La. m. major*

Hatta (1911) described two forms of *Lampetra mitsukurii*; one small (80–165 mm TL) with a widespread Japanese distribution he called *minor* and one large (350–410 mm

TL) restricted to Sapporo, Hokkaido Island, he called *major*. The two forms occurred sympatrically on spawning grounds at Sapporo. Both were distinct from *La. japonica* (= *Le. camtschaticum*) based on characteristics related to sexual maturity (i.e., well-developed urogenital papilla in males and anal fin-like fold in females in the former versus undeveloped structures in both sexes in the latter, blunt cusps on the supraoral and infraoral laminae and thread-like intestines in the former versus sharp cusps on these laminae and relatively thick intestines in the latter). The subspecies *minor* is a junior synonym of *Le. mitsukurii* (Hatta, 1901) based on their very similar total lengths (80–165 versus 80–156 mm, respectively) and their identical geographic distributions (i.e., Hokkaido, Honshu, Shikoku, and Kyushu islands). The subspecies *major* is distinct from *La. mitsukurii* because figs 5 and 6 in Hatta (1911) showing close-ups of the cloacal regions of male and female *La. m. major*, respectively, possess a dark blotch at the apex of the second dorsal fin similarly to fig. 9 showing a close-up of the cloacal region of *La. japonica* (= *Le. camtschaticum*), whereas our study of a *La. mitsukurii* syntype revealed that its second dorsal fin is unpigmented (Table 9). Thus, even though Hatta (1911) states that the forms *minor* and *major* were often found attached to each other while spawning, they belong to distinct species. We therefore agree with Creaser and Hubbs (1922) and Berg (1931) that *La. m. major* is a synonym of what they respectively called *Entosphenus* (*Le.*) *japonicus* and *La. j. japonica* (= *Le. camtschaticum*). We disagree with Berg (1931) that *La. m. minor* is a synonym of *Le. reissneri* (see above '*Lethenteron mitsukurii* distinct from *Le. kessleri* and *Le. reissneri*', page 37). Ioganzen (1935c) reported on adults of nine *La. m. minor* (130.7–162.3 mm TL) and two *La. m. major* (334.0–366.0 mm TL) identified by Prof. S. Hatta and collected sympatrically in Sapporo in April 1911. These were sent to Tomsk State University where they were studied in 1914 by the author's father, Prof. G. E. Ioganzen. Unfortunately, in 1933 Ioganzen (1935c) could only find the *La. m. minor* and AMN could find neither when he visited TGU in 2011. According to Ioganzen (1935c) the supraoral lamina in both forms consisted invariably of two teeth while the infraoral lamina in *La. m. minor* possessed either 6(2), 7(4) or 9(1) unicuspid teeth or the formulae 5u1b(1) or 2b3u1b(1). Additionally, one count of six unicuspid teeth and three counts of seven unicuspid teeth are followed by unexplained exclamation marks and one count of seven unicuspid teeth is followed by an unexplained question mark. Both *La. m. major* possessed six teeth. However, since these two individuals were not personally examined by Ioganzen (1935c), we do not know whether the counts given represent only unicuspid or a mixture of unicuspid and lateralmost bicuspid teeth. While Hatta (1911) did not give tooth counts in his descriptions of *La. m. minor* and *La. m. major*, the presence of one or two bicuspid teeth on the infraoral lamina in two of the nine *La. m. minor* specimens is perplexing because it is different from the original description of *La. mitsukurii* by Hatta (1901) and our study of two syntypes (Table 8). Because this material of *La. m. minor* and *La. m. major* is now lost and relied in part on second-hand information, we treat it with suspicion and stand by our interpretations of the taxonomic identities of *La. m. minor* and *La. m. major*.

### *Lethenteron mitsukurii* not the spawning phase of *Le. camtschaticum*

Sato (1951) hypothesized that *Le. mitsukurii* was *Le. camtschaticum* (appeared as *La. j. japonica*) in its spawning phase. However, type material of *Le. mitsukurii* has unpigmented second dorsal and caudal fins (Table 9) and that of *Le. camtschaticum* is pigmented for both those characters (Table 3), and thus, we reject this hypothesis.

### Sympatric parasitic and nonparasitic taxa

According to Berg (1931) and Ioganzen (1935a, 1935b) the parasitic *La. j. septentrionalis* (= *Le. camtschaticum*) is distributed throughout the Ob' River drainage, where it occurs sympatrically with the nonparasitic *La. j. kessleri* (= *Le. kessleri*). Specifically, Berg (1931) stated that *La. j. septentrionalis* (ZIN 6308: 355 mm TL) was sympatric with *La. j. kessleri* (ZIN 6307, ZIN 6311: 180–224 mm TL [ZIN 6311 as measured by us is very shriveled and only 144 mm instead of 180 mm as measured by Berg]) in the Irtysh River at Omsk and based on literature in the Tom' River near Tomsk (the type locality of *P. kessleri*). In regard to the Tom' River, Berg (1931) placed the 389 mm TL adult reported by Ruzskiy (1920) under the synonymy of *La. j. septentrionalis* contrasting with the 160–210 mm TL type series of *P. kessleri* reported by Anikin (1905). Ioganzen (1935a, 1935b) also stated that these two taxa were sympatric in the Tom' River near Tomsk based on two adults of *La. j. septentrionalis* 215–408 mm TL and 12 adult syntypes of *P. kessleri* 132–207 mm TL. Six of the latter syntypes (TGU 9 = TGU 3696 in Ioganzen 1935b, table 3) were 128–165 mm TL as measured by us. In their study of the fishes of the Ob'-Irtysh system, Pavlov and Mochek (2006) reported *Le. camtschaticum* (appeared as *Le. japonicum*) to be sympatric with *Le. kessleri* in the Upper Ob' and Middle Irtysh regions, as well as in the Southern and Northern Ob'-Taz Guba estuaries. The reported presence, albeit rare, of the nonparasitic *Le. kessleri* in estuarine waters is unexpected and may perhaps be explained by extensive freshwater plumes. It appears that the lower Tobol River, Ob' River drainage, also contains both *Le. camtschaticum* and *Le. kessleri*. In the lower Tobol River Karasev (2008) reported (as *Le. kessleri*) five lamprey adults measuring 200–407 mm TL and seven mature females, the latter collected in late April and May, with absolute fecundity 3,161–7,208 eggs. We believe that the adults measuring over 230 mm TL (see above 'Adult total length attained by *Le. kessleri*', page 29) refer to *Le. camtschaticum* while the adults with the reported fecundity < 10,000 eggs refer to *Le. kessleri*. Unfortunately, Karasev (2008) did not report the total lengths of the females with the recorded fecundities. Contrary to the contention by Zhuravlev and Lomakin (2017) that anadromous *Le. camtschaticum* is presumed to have become extirpated from the upper Ob' River drainage since the mid-20<sup>th</sup> century, it would appear that it is still present (Pavlov and Mochek 2006; Karasev 2008). Further west, *Le. camtschaticum* and *Le. kessleri* are sympatric in the Severnaya Dvina River drainage (Berg 1931; Altukhov et al. 1958; Kuderskiy and Mel'nikova 1970; Sotnikov and Solov'ev 2002). According to Berg (1948) *Le. camtschaticum* and *Le. kessleri* are sympatric in the Pechora River drainage based on

a 349 mm TL adult of the former from Shapochnaya (= Shapkina) River (ZIN 20802: 334 mm TL as measured by us, Table 4) and a 118 mm TL spent female of the latter from the Pechora River (ZIN 23909: 110 mm TL as measured by us). *Lethenteron camtschaticum* and *Le. kessleri* are also sympatric in the Yenisei River based on our re-interpretation of *P. dentex* as a junior synonym of *Le. camtschaticum* (see above ‘Real or perceived distributional discontinuity between the populations of parasitic *Le. camtschaticum* in Russia?’, page 28) and one individual (ZIN 14441) of *Le. kessleri* (Tables 4–6). Nazarov (2012) also reports Siberian lamprey (= *Le. kessleri*) in the middle Yenisei (i.e., Chernaya and Beryozovka rivers) based on 152 adults 122–211 mm TL. *Lethenteron camtschaticum* and *Le. kessleri* are sympatric in the Utkholok River drainage, Kamchatka (see above ‘Identity of lampreys in the Utkholok River drainage, Kamchatka’, page 31) based on our re-interpretation of the data presented in Kucheryavyy et al. (2007a). *Lethenteron camtschaticum* and an unidentified nonparasitic species very similar to *Le. mitsukurii* are sympatric in the Kol’ River drainage, Kamchatka (see above ‘Identity of lampreys in the Kol’ River drainage, Kamchatka’, page 33). *Lethenteron camtschaticum* and an unidentified nonparasitic species are also sympatric in Lake Azabach’e basin, Kamchatka (see above ‘Identity of lampreys in the Lake Azabach’e basin, Kamchatka’, page 34). On Sakhalin Island, *Le. camtschaticum* is sympatric with nonparasitic *Le. reissneri* in the Tym’ River (Gritsenko 1968, 2002; Dyldin and Orlov 2016; this study – see below ‘Taxonomic identity of nonparasitic lampreys in Japan and Sakhalin Island, Russia with low trunk myomere counts’, page 42). While Gritsenko (2002) recorded the presence of another nonparasitic species in the Tym’ River, *Le. kessleri*, the identity of the species was not clearly established because he used the number of trunk myomeres to distinguish it from *Le. reissneri* and the number recorded (i.e., 64–74) could apply to either species as the type material of *Le. kessleri* possessed 70–74 (this study) and that of *Le. reissneri* possessed 70 (Renaud and Naseka 2015). Interestingly, out of several hundred specimens of brook lamprey from the Tym’ River examined by Gritsenko (2002), three possessed two rows of posteriors, like the specimen of *Le. reissneri* mentioned above that we identified from that river. Unfortunately, the key diagnostic characters separating the two species (i.e., the pigmentation of the second dorsal fin and the transverse lingual lamina dentition; see above ‘*Lethenteron kessleri* distinct from *Le. reissneri*’, page 35) were not recorded. In the People’s Republic of China, *Le. camtschaticum* (as *La. japonica*) is sympatric with nonparasitic *Le. reissneri* in the Mudan River (not Mutantiang River), tributary to Sungari (Songhua) River (Hensel 1963). Li and Liu (2011) confirm the presence of *Le. camtschaticum* (as *La. japonica* or *Le. japonicum* used interchangeably) in the Songhua River system based on prespawning adults 385–470 mm TL. In Japan, *Le. camtschaticum* is sympatric with nonparasitic *Le. mitsukurii* in Sapporo, Hokkaido Island (see above ‘Taxonomic identity of *Lampetra mitsukurii minor* and *La. m. major*’, page 38) and Shokotsu River, Hokkaido Island (Vladykov and Kott 1978b in which *Le. matsubarai* is a synonym of *Le. mitsukurii*). Additionally, Yamazaki et al. (1998) reported the presence of mature dwarf male and female *Le. camtschaticum* (as *Le. japonicum*), which they suggested were nonparasitic, together with anadromous *Le. camtschaticum* (also as *Le. japonicum*) in the Ohno River,

Hokkaido Island, Japan. However, neither photograph of a male and a female dwarf individual in their figure 1 exhibit a dark blotch on the second dorsal fin, and therefore, these would not be *Le. camtschaticum*, but rather belong to an unidentified nonparasitic species. Later, Yamazaki and Goto (2016) provided another photograph of a mature nonparasitic lamprey, measuring 140–160 mm TL, from the Ohno River (their photo 2–1B) showing a dark blotch on the second dorsal fin and a heavily pigmented caudal fin, which in our opinion could be *Le. kessleri*, but this needs confirmation. Yamazaki et al. (2011) and Yamazaki and Goto (2016) referred to the nonparasitic lamprey from the Ohno River as a population of fluvial *Le. camtschaticum*. In Lake Sopochnoe basin, Iturup Island, Kuril Archipelago, Russia, *Le. camtschaticum* is sympatric with *Le. kessleri* (Sidorov and Pichugin 2005). However, these authors used the identification criteria of Iwata et al. (1985) and we have argued above (see '*Lethenteron matsubaraei*, a synonym of *Le. mitsukurii*', page 38) that the specimens identified as *Le. kessleri* by the latter represented a mixture of *Le. reissneri* and *Le. mitsukurii*. Unfortunately, Sidorov and Pichugin (2005) did not comment on the pigmentation of the caudal fin, and therefore, we cannot make a definitive identification between these two species. In Alaska, *Le. camtschaticum* (as *Le. japonicum* in Vladykov and Kott 1978a) is sympatric with nonparasitic *Le. alaskense* (= *Le. kessleri*?; see key below, page 53) in the Naknek River system (Vladykov and Kott 1978a), as well as the Chatanika and Chena rivers, Yukon River drainage (Vladykov and Kott 1978a; Sutton 2017).

### Taxonomic identity of nonparasitic lampreys in Japan and Sakhalin Island, Russia with low trunk myomere counts

The nonparasitic *Le. reissneri* has long been reported from Japan (Berg 1931, 1948; Mori 1936; Okada 1960; Hubbs and Potter 1971; Vladykov and Kott 1978a, 1978b; Sato 1984). However, in the redescription of this species Renaud and Naseka (2015) restricted its distribution to mainland Asia (Russia, Mongolia, People's Republic of China) pending a more comprehensive study across a wider geographic range, because of a marked difference in the number of trunk myomeres between *Le. reissneri* from mainland Asia versus nonparasitic lamprey in Japan. Indeed, the number of trunk myomeres in adult *Le. reissneri* (including a syntype) from mainland Asia is 70–72 (Renaud and Naseka 2015) versus 57–63 in adults referred to this species from Japan and Sakhalin Island (Vladykov and Kott 1978a). There are two available names for nonparasitic species described from Japan, *Le. mitsukurii* and its junior synonym *Le. matsubaraei*. Their adults possess 66–70 trunk myomeres (Table 8; Vladykov and Kott 1978b), higher counts than the 57–63 recorded for Japanese "*Le. reissneri*" by Vladykov and Kott (1978a). Interestingly, the basis for the first report of *Le. reissneri* in Japan was the synonymy by Berg (1931) of *Le. mitsukurii* with *Le. reissneri* due to his re-identification of Japanese adult lamprey 86–147 mm TL (erroneously reported as 92–145 mm TL) with 56–67 trunk myomeres identified as *Le. mitsukurii* (appeared as *Entosphenus mitsukurii*) by Jordan and Hubbs (1925). Hubbs and Potter (1971) had remarked that

unidentified nonparasitic lampreys from Hokkaido (Japan) and Siberia (Russia) possessed ca. 70 or more trunk myomeres, contrasting with the lower counts of Jordan and Hubbs (1925). It is important to note that Berg (1931) did not examine type material of *Le. mitsukurii* or *Le. reissneri* in reaching his conclusion. Yamazaki and Goto (1996) discovered fixed alternate allelic differences at eleven loci (AAT-1, G6PDH, GPI-2, IDHP-1, IDHP-2, IDHP-3, IDHP-4, MDH-3, MDH-4, MEP-1, PGM) among what they assumed were Japanese populations of *Le. reissneri* collected from 27 rivers across Hokkaido and Honshu islands, which they identified as northern (N) and southern (S) groups. Furthermore, they detected no evidence of hybridization between three sympatric river populations on Honshu Island (i.e., Uono, Shou-gawa, and Shoushu rivers) implying that the northern and southern groups were reproductively isolated. Yamazaki et al. (1999) extended the range of the S-group to include Shikoku and Kyushu islands, Japan, and the Korean Peninsula. They also added five other rivers on Honshu where the two forms (N and S) were sympatric (Ushiwatari, Takifuchi, Shouzenji, Makino, and Shourai) and Yamazaki et al. (2001a) added a further one (Gakko). Despite an overlap in the spawning season and size at spawning of the two forms in the Ushiwatari River, tributary to the Gakko River, Yamazaki and Goto (2000b) found only males and females of a given form on their own nests and no evidence of gene exchange between the two forms, which they suggested may be due to an unidentified premating isolating mechanism ensuring that they remain distinct. Additionally, Yamazaki et al. (2003) found differences in the mtDNA COI sequences (1095 bp) between the N and S forms. Interestingly, the mean percentage sequence differences between them (9.1%) was greater than between either of them and *La. fluviatilis* (7.0–8.8%). However, Yamazaki and Goto (1997) could find no diagnostic morphometric, countable (trunk myomere and dentition) or pigmentation (caudal fin) characters to distinguish adults of the two. Yamazaki and Goto (1997) state that the caudal fin of the northern and southern groups is translucent or slightly pigmented. This is highly significant because the caudal fin pigmentation of *Le. reissneri* is heavily pigmented (+++) according to Renaud and Naseka (2015), while it is unpigmented (-) in *Le. mitsukurii* (Table 9). Additionally, the range in adult total length reported by Yamazaki and Goto (1997) for the northern and southern groups combined (87.9–169.1 mm) is very similar to that (80–156 mm) reported in the original description of *Le. mitsukurii*. According to Yamazaki et al. (2006) the two undescribed *Lethenteron* spp. from Japan are distinguished from *Le. reissneri* of the upper Amur River system (from the type locality) on the basis of the number of larval trunk myomeres: 65–73 (upper Amur *Le. reissneri*), 51–66 (*Lethenteron* sp. N), and 49–62 (*Lethenteron* sp. S). Yamazaki et al. (2006) further added that *Le. reissneri* from the type locality (Onon and Ingoda rivers) and *Le. sp. S* from the Naktong (= Nakdong) River, South Korea are fixed for alternate alleles at eight loci (AAT-1, IDHP-1, IDHP-2, IDHP-3, IDHP-4, MDH-3, MDH-4, PGM). Remarkably, based on a strict consensus tree generated from maximum parsimony of a partial sequence of the mtDNA COI gene (1009 bp), *Le. sp. N* is sister to a *Lethenteron* clade (100% bootstrap support) that includes

*Le. japonicum* (= *Le. camtschaticum*), *Le. reissneri*, and *Le. kessleri*, while *Le. sp. S* is sister to an *Entosphenus–Lampetra–Lethenteron* clade (99% bootstrap support) that also includes *Le. sp. N* (Yamazaki et al. 2006). Yamazaki and Goto (1998) conducted an electrophoretic analysis of *Le. japonicum* (= *Le. camtschaticum*) and *Le. kessleri* collected from Hokkaido and Honshu islands, Japan, and the Far Eastern region of Russia. These were identified based on morphological features reported by Iwata et al. (1985). Although Yamazaki and Goto (1998) found that the two species were fixed for alternate alleles at one locus (MDH–3) at the three Hokkaido Island localities (Sarufutsu, Hororo, and Mena rivers) where they were sympatric, the identity of *Le. kessleri* is in question because it did not possess a pigmented second dorsal fin as reported in the original description and none of its samples came from the type locality. Yamazaki et al. (2006) found that lamprey material from the type locality of *Le. reissneri* (Onon and Ingoda rivers, Russia) and from the Ob' River drainage, the same river drainage as for the type locality of *Le. kessleri* (Tom' and Kirgizka rivers, Russia), although very distantly removed from the latter (Irtysh and Uba rivers, Kazakhstan), shared the same MDH–3 allele. However, we have shown above that two morphological characters (transverse lingual lamina counts and pigmentation of the second dorsal fin) distinguish those two species. At this point, only two nonparasitic species are confirmed to occur in Japan: *Le. reissneri* (Shizunai River, Hokkaido Island, this study) and *Le. mitsukurii*. As adults of both *Le. mitsukurii* and *Le. reissneri* have high trunk myomere counts (66–72: this study; Renaud and Naseka 2015), an in-depth study of large samples of nonparasitic lamprey adults from Japan and Sakhalin Island is needed to determine whether the lower trunk myomere (< 66) individuals from these areas represent one or more undescribed species, or *Le. mitsukurii*, or *Le. reissneri*, or a mixture of these three alternatives. Yamazaki and Goto (2000a) made the suggestion that perhaps *Lethenteron* form N or *Le. form S* could in fact be *Le. mitsukurii*. Recently, using data extracted from two theses, Dyldin et al. (2019b) could not determine the specific identity of adult *Lethenteron* lampreys from four Sakhalin rivers (Bol'shoi Garomai, Nitui, Novikovka, Pugachovka) measuring 116–220 mm TL and with 65–75 trunk myomeres. In this regard we have identified as *Le. reissneri* a 146 mm TL (158 mm originally) adult with 68 trunk myomeres from Tym' River, Sakhalin Island, Russia (ZIN 25204) that was treated as *Lethenteron* sp. in Tuniyev et al. (2016). Although placed under the *La. reissneri* species account in Berg (1948), he added (p. 43, fig. 30) that it was possibly a new species because it possessed multiple posterial rows. Two posterial rows have been reported by Renaud and Naseka (2015) in a specimen of *La. reissneri* from the Shangshi River, People's Republic of China (ZIN 14457). We diagnosed the specimen from Sakhalin (Fig. 5) as *Le. reissneri* because it possesses two rows of posterials, the first one with 20 unicuspid teeth, the endolateral formula is 2–2–2, the infraoral lamina is 1b5u1b, the second dorsal fin is unpigmented and the caudal fin heavily pigmented (+++). According to Nikoforov et al. (1994), the paleo-Amur was hypothesized to be connected to the eastern littoral of Sakhalin Island in the geological past, and we believe this may explain the presence of *Le. reissneri* in the Tym' River in present times. One of the syntypes of *La. mitsukurii* (Table 8) also possessed two rows of posterials indicating that this condition is not restricted to *Le. reissneri*.



**Figure 5.** Oral disc of *Lethenteron reissneri*, ZIN 25204, 146 mm TL with two rows of posteriors from Tym' River, Sakhalin Island, Russia.

### Synonymy of *Lethenteron camtschaticum* (Tilesius, 1811), the Arctic lamprey

Synonyms, new combinations, and misidentifications are included.

*Petromyzon marinus Camtschaticus* Tilesius, 1811: 240–247, pl. IX, figs I, II [original description, marine waters of St. Peter and Paul Camtschatici (= Petropavlovsk-Kamchatsky) harbor, Russia].

- Petromyzon Fluvialis* (non Linnaeus, 1758) – Richardson 1823: 705 [misspelling of *P. fluviatilis* Linnaeus, 1758; common name: Lesser lamprey, Great Slave Lake, Northwest Territories, Canada, attached to an Inconnu, *salmo Mackenzii* (= *Stenodus leucichthys*)]; Richardson 1836: 294 [common name: River lamprey, refers to the individual in the previous reference].
- Petromyzon borealis* Girard, 1858: 377 [available by indication to *Petromyzon fluviatilis* Richardson, 1836].
- Petromyzon Japonicus* von Martens, 1868: 3–5, pl. I, fig. 2 [original description, Tokyo (appeared as Jeddo) and Yokohama, Honshu Island, Japan].
- Petromyzon Kameraticus* – Dybowski, 1869: 948 [misspelling of *P. camtschaticus* Tilesius, 1811; treated as a distinct species, not a subspecies of *P. marinus* as Tilesius (1811) intended, ascends to Stretensk on the Shilka River, a tributary of the Amur River, Russia].
- Petromyzon fluviatilis* (non Linnaeus, 1758) – Günther 1870: 504 [presence of a transverse series of small teeth behind the mandibular tooth (= row of posterials) in *Petromyzon japonicus* von Martens, 1868 from Japan judged insufficient by Günther (1870) to distinguish it from *P. fluviatilis*.]
- Petromyzon Ernstii* Dybowski, 1872: 220 [original description, mouth of the Amur River, Russia].
- Petromyzon Kameralicus* – Dybowski 1872b: 221 [misspelling of *P. camtschaticus* Tilesius, 1811].
- Petromyzon kamtschaticus* – Dybowski 1872b: 221 [misspelling of *P. camtschaticus* Tilesius, 1811].
- Ammocoetes aureus* Bean, 1881: 159 [original description, Yukon River at Anvik (63°N, 160°W), Alaska, U.S.A.].
- Petromyzon (Ammocoetes) fluviatilis* var. (non Linnaeus, 1758) – Smitt 1895: 1190–1191, fig. 353 [Archangel, Russia, 315 mm TL male with middle pair of the lateral (= endolateral) teeth bicuspid and a curved but irregular row of teeth in the posterior part of the disc (= row of posterials)].
- Lampetra aurea* – Jordan and Evermann 1896: 13 [comb. nov., Yukon River]; Jordan and Gilbert 1899: 434 [Yukon River]; Schmidt 1904: 336 [northern Bering Sea]; Evermann and Goldsborough 1907: 222, 227 [common name: Lamprey eel, Bering Sea basin].
- Entosphenus camtschaticus* – Jordan and Gilbert 1899: 434 [comb. nov., allocation to *Entosphenus* is proposed as probable, but not certain, Kamchatka].
- Lampetra japonica* – Hatta 1901: 22–24 [comb. nov., Honshu and Hokkaido islands, Sea of Japan basin, Japan]; Jordan and Snyder 1901b: 733 [Japanese common name: Yatsumeunagi, which translates to eight-eyed eel, 470 mm TL, Shinano River, Honshu Island, Japan]; Soldatov and Lindberg 1930: 2–3 [common name: Japanese lamprey, adults up to 350 mm TL, but fig. 1 indicates 452 mm, Tumen River, Maikhe River mouth, Ussuri Bay, Amur estuary, Vorovskaya River (Kamchatka), Russia]; Mori 1936: 3, 6, 10, 15 [Maritime, Karafuto (= Sakhalin), Hokkaido, Amur zoogeographical districts, Japan, Chosen (= Korea)]; Berg 1948: 25, 29–34 [Arctic and Pacific Ocean basins]; Ivanova-Berg and Manteyfel' 1949:

- 18 [prespawning adults feed on blood and muscle of *Coregonus nasus* in Gulf of Ob' and Tazovskaya Bay and *Clupea pallasii* in Severnaya Dvina mouth and Pechorskaya Bay]; Birman 1950: 158–159 [common name: Pacific lamprey, lamprey marks on *Oncorhynchus gorbuscha* in the Amur River estuary and mouth of the Tumnin River, Russia, and less frequently on *O. keta*, in the Amur River estuary]; Walters 1955: 267, 272 [common name: Arctic lamprey, 355 mm TL adult, Point Barrow, Alaska, U.S.A.]; Morozova 1956: 149 [common name: Pacific lamprey, spawning run on Amur River near Elabuga and Malmyzh, Russia, 3 Dec. 1948 – 8 Jan. 1949, 6–30 Dec. 1949]; Nikol'sky 1956: 588–590 [common name: Pacific lamprey, 22 adults 147–293 mm TL, with a blue-gray dorsal aspect and silvery-white ventral aspect, except for the largest one in which the dorsal aspect is greenish and the ventral aspect yellowish, feeding on *Osmerus dentex* on 11 Aug. 1955 in marine waters two to three km off Ribnovsk, Sakhalin Island, Russia; their intestines contained *O. dentex* scales, muscle, intestine, gonad, and bones]; Heard 1966: 332, 334, 336, 338 [in part, common name: Arctic lamprey, presumed anadromous, parasitic on *Gasterosteus aculeatus*, *Prosopium coulterii*, *Oncorhynchus mykiss*, *O. nerka*, mature or spent adults 218–311 mm TL, Naknek River and Brooks River, Naknek River system, Alaska, U.S.A.]; Gritsenko 1968: 157 [lamprey marks on anadromous *Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. masou*, *Salvelinus alpinus* entering Tym' River, Sakhalin Island, Russia]; McPhail and Lindsey 1970: 50–55 [in part, common name: Arctic lamprey, adults from Alaska ca. 90–411 mm TL some feeding on *Oncorhynchus tshawytscha*, *Platichthys stellatus*; according to map, Alaskan waters of the Bering Sea basin from the Alaska Peninsula northwards to St. Lawrence Island, U.S.A., Beaufort Sea basin from near Barrow, Alaska, U.S.A. to Anderson River, Northwest Territories, Canada, Yukon River and off Herschel Island (feeding on *Osmerus dentex*, *Stenodus leucichthys*), Yukon, Canada, Great Slave Lake basin northward to Mackenzie River estuary, eastward to Artillery Lake and southward to Slave River at Fort Smith, Northwest Territories, Canada]; Savvaitova and Maksimov 1978: 556 [230–320 mm TL spawning individuals 17–21 June 1972 in the Levyi Kolkalvayam River, tributary to the Utkholok River, western Kamchatka, Russia]; Sato 1984: 2 [Japanese common name: Kawa-yatsume, parts of second dorsal and caudal fins blackish in adults, Japan]; Novomodnyy and Belyaev 2002: 81 [young lamprey adults  $\leq 210$  mm in length feed on *Oncorhynchus gorbuscha* and *O. keta* smolts  $\leq 85$  mm in length and *O. masou*  $\geq 120$  mm in length in the Amur River estuary and Sakhalin Bay, Russia]; Li et al. 2019: 1501–1502, 1505, 1507, 1509–1512 [Tumen and Amur rivers, People's Republic of China, early development].
- Lampetra mitsukurii* (non Hatta, 1901) – Jordan and Snyder 1901b: 734 [in part, 305–356 mm TL, Ishikari River, Sapporo, Hokkaido Island, Japan].
- Entosphenes camtschaticus* – Schmidt 1904: 336 [misspelling of *Entosphenus*, brackish-water form, Bering Sea off Kamchatka].
- Petromyzon dentex* Anikin, 1905: 15–17 [original description, mouth of the Yenisei River, near Gol'chikha, Russia].
- Lampetra fluviatilis* (non Linnaeus, 1758) – Berg 1906: 177, 179 [in part, ZIN 7814].

*Lampetra mitsukurii major* Hatta, 1911: 266–268, pl. IX, figs 1, 2, 5, 6 [original description, Sapporo, Hokkaido Island, Japan, spawning male and female].

*Entosphenus japonicus* – Regan 1911: 201–202 [comb. nov., Echigo Province (= Niigata Prefecture minus Sado Island), Tokyo, and Hokkaido Island, Japan; Archangelsk, Russia]; Jordan et al. 1913: 6 [Japanese common name: Kawayatsume, northern Japan]; Jordan and Hubbs 1925: 98 [supraoral lamina with a cusp at each end and at most a minute cusp on the bridge; infraoral lamina with six to eight teeth, the lateralmost bicuspid and the internal ones unicuspid; reported locality is Karafuto, near Otaru, Hokkaido Island, Japan, but this makes no sense as Karafuto is the former name of the southern part of Sakhalin Island].

*Lampetra fluviatilis japonica* – Berg 1911: 33–34 [comb. nov., ZIN 6308, 7814, 8545, 12159, 14371]; Ruzskiy 1920: 30 [common name: Siberian-Japanese lamprey, 389 mm TL adult, Tom' River near Tomsk, Russia]; Soldatov 1924: 16 [common name: River lamprey, 330 mm adult in a drift net at the freshwater/brackish water interface of the Pechora River mouth, Russia]; Knipovich 1926: 51 [common name: Siberian river lamprey].

*Entosphenus (Lethenteron) japonicus* – Creaser and Hubbs 1922: 3, 6–7, 11 [new subgenus based on *Lampetra wilderi* Gage in Jordan & Evermann, 1896; coasts and streams from Bering Sea west to the White Sea and south to the Sea of Japan].

*Lampetra borealis* – Jordan et al. 1930: 10 [comb. nov., common name: Arctic lamprey, streams of northern Alaska and Kamchatka].

*Lampetra (Lampetra) japonica septentrionalis* Berg, 1931: 93, 100–102, pl. V, fig. 4 [original description and key, Onega River at Podporozh'e, White Sea basin, Russia].

*Lampetra (Lampetra) japonica japonica* – Berg 1931: 93, 98 [nominative subspecies based on *Petromyzon Japonicus* von Martens, 1868].

*Lampetra (Lampetra) japonica kessleri* (non Anikin, 1905) – Berg 1931: 102 [Anadyr Liman (= Estuary), Russia; ZIN 23154, 258 mm TL spent female collected in brackish water attached to *Onchorhynchus keta*; ZIN 23158, two adults 135–138 mm TL with very sharp teeth collected in brackish water and attached to *O. keta*]; Berg 1948: 35 [Anadyr Estuary, Russia: two uncatalogued specimens with sharp teeth and thick intestines; one (155 mm TL) attached to a sculpin (Cottidae) and the other (144 mm TL) to *O. keta*].

*Lampetra (Lampetra) reissneri* (non Dybowski, 1869) – Berg 1931: 104 [Samarga (ZIN 15078) and Sedanka (ZIN 15747) rivers, Russia].

*Lampetra fluviatilis septentrionalis* (non Berg, 1931) – Ioganzen 1935a: 369 [comb. nov.].

*Lampetra japonica japonica* – Taranetz 1937: 47 [common names: Pacific lamprey, Japanese lamprey]; Shmidt 1950: 16, 232, 236 [Okhotsk Sea basin: mouth of Amur River, Gulf of Sakhalin, northern part of the Sea of Okhotsk, western coast of Kamchatka, eastern and northern coasts of Sakhalin Island, Russia].

*Entosphenus japonicus septentrionalis* – Rawson 1951: 208, 221 [comb. nov., common name: Northern lamprey, Great Slave Lake in Fort Resolution area, near town of Hay River and Gros Cap, Northwest Territories, Canada; the latter two in *Lota lota* and *Stenodus leucichthys* stomachs, respectively].

- Entosphenus lamottei japonicus* – Wilimovsky 1954: 281 [comb. nov., Arctic Alaska, Bering Sea, north and east Asia].
- Lampetra (Lethenteron) japonica* – Hubbs and Potter 1971: 51 [comb. nov., Varanger Fjord throughout Siberia, along the eastern Pacific coast, Japan, Alaska, and northern Canada].
- Lethenteron japonicum* – Nursall and Buchwald 1972: iv, 14, 18, 24 [comb. nov., common name: Arctic lamprey, adults 168 to > 300 mm TL; Great Slave Lake, Slave River, Hay River, Northwest Territories, Canada; host of *Catostomus catostomus*, *Coregonus artedii*, *C. clupeaformis*, *Lota lota*, *Salvelinus namaycush*, *Stenodus leucichthys* in fresh water]; Vladykov and Kott 1978a: 3, tables 9–10, 22 [MacKenzie River drainage, Northwest Territories, Canada; Beaufort Sea; Naknek River system, Nushagak and Yukon rivers, Alaska, U.S.A; Honshu and Hokkaido islands, Japan; Amur River, Russia]; Iwata et al. 1985: 185–186 [Saru, Mu, Ryukei rivers and Tofutsu Lake, Hokkaido Island, Japan]; Iwata and Hamada 1986: 17–20 [common name: Arctic lamprey, 197 mm TL adult male with fully pigmented caudal fin and blotch on second dorsal fin, Assabu River, Hokkaido Island, Japan; 153–228 mm TL young adults, Tofutsu Lake and Saru River, Hokkaido Island, Japan; 365–533 mm TL adult males, Assabu, Hime, Toshihetsu rivers, Hokkaido Island and Mabechi River, Honshu Island, Japan]; Yamazaki et al. 2001b: 1135 [Japan: Ishikari, Ohno, Saru, and Uzura rivers, Hokkaido Island, 215.2–478.0 mm TL adults; Mogami River, Honshu Island, 397.0–431.0 mm TL adults]; Martynov 2002: 145 [common name: Pacific lamprey, upstream migrants in the Vashka River, Mezen' River drainage, Russia, mean TL 417 mm for males and 424 mm for females, one out of 109 adults had a third cusp on the bridge of its supraoral lamina and two out of 111 adults had unicuspid instead of bicuspid lateralmost teeth on the infraoral lamina]; Gritsenko 2002: 13–21 [340–570 mm TL adults, Tym' River, and lamprey marks on anadromous *Oncorhynchus gorbuscha*, *O. keta*, *O. kisutch*, *O. masou*, *Salvelinus alpinus*, *S. leucomaenis* entering Tym' River and Nyyskiy Bay, Sakhalin Island, Russia]; Reshetnikov 2002: 28 [intestinal diameter in adult 4–20 mm].
- Lethenteron japonica* – Nikoforov et al. 1994: 26 [common name: Arctic lamprey, southern Sakhalin Island, Russia].
- Lampetra (Lethenteron) camtschatica* – Mecklenburg et al. 2002: 62 [comb. nov., common name: Arctic lamprey, Alaska and elsewhere in the northern hemisphere, but not Caspian Sea as erroneously stated].
- Lethenteron camtschaticum* – Sidorov and Pichugin 2005: 402–405 [common name: Japanese lamprey, silvery downstream migrants to the sea, 151–201 mm TL, feeding on *Oncorhynchus gorbuscha*, *O. nerka*, *Salvelinus malma*, Lake Sopochnoe basin, Iturup Island, Kuril Archipelago, Russia, 3–10 Aug. 2001]; Gritsenko et al. 2006: 16–17 [common name: Pacific lamprey]; Kucheryavii et al. 2007a: 41–44 [in part, Kolkavayam and Utkholok rivers, western Kamchatka, Russia, typically anadromous form, 174–350 mm mature individuals of both sexes combined]; Bugayev et al. 2007: 32–33 [common name: Pacific lamprey, 310–320 mm TL

adults, Kamchatka River estuary, Russia]; Sutton 2017: 1198 [anadromous, adults, 304–427 mm TL, Chatanika and Chena rivers, Yukon River drainage, Alaska, U.S.A.]; Chereshev 2008: 25–31 [common name: Pacific lamprey, 310 mm TL individual from the stomach of a burbot, *Lota lota*, in the middle reaches of the Anadyr River, Russia]; Shevlyakov and Parensky 2010: 396, 399 [common name: Kamchatka lamprey, lamprey wounds and scars 6–22 mm in diameter above the lateral line between the dorsal and adipose fins of *Oncorhynchus keta* in the lower Kamchatka River and Kamchatka Bay, Russia]; Novikov and Kharlamova 2018: 296, 298–301 [common name: Arctic lamprey, adults 230–480 mm TL, Barents Sea up to 76°N and White Sea at depths 10–131 m]; Siwicke and Seitz 2018: 111 [common name: Arctic lamprey, 28 feeding individuals collected using an epipelagic trawl in the eastern Bering Sea at depths < 100 m between mid-August and early October 2012]; Shink et al. 2019: 1993–1998 [common name: Arctic lamprey, feeding adults, 187–465 mm TL, on *Mallotus villosus*, *Clupea pallasii*, *Ammodytes hexapterus*, *Eleginus gracilis*, *Gadus chalcogrammus*, *Leptoclinus maculatus*, *Limanda aspera*, *Oncorhynchus gorbuscha*, *O. tshawytscha*, *Osmerus dentex*, Cottidae, Gasterosteidae, eastern Bering Sea, Alaska, U.S.A.].

*Lampetra camtschatica* – Sawatzky et al. 2007: 10, 12–13 [in part, common name: Arctic lamprey, Northwest Territories, Canada, including Horton River].

*Lethenteron reissneri* (non Dybowki, 1869) – Bugayev et al. 2007: 33–34 [two males, 185 mm TL, one from Lake Azabach'e and one from Lake Kurzin, both in the Kamchatka River drainage, Russia with half-digested fish flesh in their intestines].

### Synonymy of *Lethenteron mitsukurii* (Hatta, 1901), the Japanese brook lamprey

Synonyms, new combinations, and misidentifications are included.

*Lampetra mitsukurii* Hatta, 1901: 22–24 [original description, Hondo [= Honshu], Shikoku, Kyushu, and Hokkaido islands, Japan]

*Lampetra mitsukurii* – Jordan and Snyder 1901a: 126 [Japanese common name: Sunayatsume].

*Lampetra mitsukurii minor* Hatta, 1911: 263–266, 268, pl. IX, figs 3, 4, 7, 8 [trinomial based on *Lampetra mitsukurii* Hatta, 1901].

*Lampetra planeri* (non Bloch, 1784) – Regan 1911: 203 [misidentification based on synonymy with *Lampetra mitsukurii* Hatta, 1901]; Jordan et al. 1913: 6 [Japan]; Creaser and Hubbs 1922: 13 [Japan].

*Entosphenus appendix* (non DeKay, 1842) – Creaser and Hubbs 1922: 7, 12 [in part, eastern Asia, including Japan].

*Entosphenus mitsukurii* – Hubbs 1925: fig. 16, 589 [comb. nov., a degenerate, dwarf, brook lamprey derived from anadromous, parasitic *Entosphenus japonicus*]; Jordan and Hubbs 1925: 98–99 [in part, mature male, 147 mm TL, 67 trunk myomeres, mottled coloration and mature female, 142 mm TL, 63 trunk myomeres, plain coloration, Sapporo, Hokkaido Island, Japan].

- Lampetra (Lethenteron) mitsukurii* – Hubbs and Potter 1971: 52–53 [comb. nov., provisionally recognized, Japan].
- Lethenteron matsubarai* Vladyskov & Kott, 1978: 1792–1800 [original description, Shokotsu River, Hokkaido Island, Japan (44°22'N, 143°20'E)]; Vladyskov and Kott 1979c: 10 [common name: Japanese brook lamprey; we recommend this common name now be used for *Le. mitsukurii*].
- Lampetra reissneri* (non Dybowski, 1869) – Sato 1984: 2 [dorsal and caudal fins without blackish parts in adults, Japan].
- Lethenteron kessleri* (non Anikin, 1905) – Iwata et al. 1985: 186–188 [in part, Hokkaido Island, Japan, individuals with unpigmented second dorsal and caudal fins].
- Petromyzon mitsukurii* – Paepke and Schmidt 1988: 160 [comb. nov., Japan].

### Synonymy of *Lethenteron kessleri* (Anikin, 1905), the Siberian brook lamprey

Possible synonym, new combinations, and misidentifications are included.

- Petromyzon kessleri* Anikin, 1905: 10–15 [original description, Tom' River and at the mouth of its tributary the Kirgizka River, Ob' River drainage, near Tomsk, Russia].
- Lampetra planeri* (non Bloch, 1784) – Berg 1906: 180–182 [in part, ZIN 6174, 6307, 6310, 6311, 7815].
- Lampetra planeri reissneri* (non Dybowski, 1869) – Berg 1911: 42–43 [in part, ZIN 6174, 6307, 6310, 6311, 7815].
- Lampetra (Lampetra) japonica kessleri* – Berg 1931: 93, 102–103 [comb. nov., Ob' River drainage and Yenisei River, Siberia, Russia].
- Lampetra japonica kessleri* – Novikov 1966: 24–25 [Yakut common name: Bye-balyk, 134 mm TL female, July 1963, from Kolyma River, Russia]; Kuderskiy & Mel'nikova 1970: 16 [common name: Siberian lamprey, 139–173 mm TL spawning or spent adults, 13–16 June 1969, Yemtsa River, Severnaya Dvina River drainage, Russia]; Poltorkhina 1971: 281–285 [common name: Arctic brook lamprey, Bol'shoy and Malyy Krivoy channels of the Irtysh River, below Ust'-Kamenogorsk, Kazakhstan].
- Lampetra kessleri* – Poltorkhina 1974: 192–201 [common name: Siberian lamprey, side channel of the Irtysh River near Ust'-Kamenogorsk, Ul'ba and Cheremshanka rivers, upper Irtysh River system, Kazakhstan].
- Lampetra japonica* (non von Martens, 1868) – Savvaitova and Maksimov 1978: 556 [100–140 mm TL spawning individuals, 17–21 June 1972, Levyy Kolkalvayam River, tributary to the Utkholok River, western Kamchatka, Russia].
- ? *Lethenteron alaskense* Vladyskov & Kott, 1978: 7–9, fig. 3 [original description, West Creek, a tributary to Brooks Lake, Naknek River system, Alaska, U.S.A.]; Vladyskov and Kott 1979c: 10 [common name: Alaskan brook lamprey]; Sutton 2017: 1198 [Chena River, Yukon River drainage, Alaska, U.S.A.].
- Lethenteron kessleri* – Holčík 1986a: 197 [comb. nov.]; Holčík 1986b: 220–236; Sotnikov & Solov'ev 2002: 807–808 [common name: Siberian lamprey, 130–170 mm TL adults, 2 June 1993, Shipulovka River, Severnaya Dvina River drainage, Russia].

*Lethenteron camtschaticum* (non Tilesius, 1811) – Kucheryavyi et al. 2007a: 41–45, 47 [in part, Kolkavayam and Utkholok rivers, western Kamchatka, Russia, anadromous forma praecox, 145–220 mm mature individuals of both sexes combined, and resident form, 100–165 mm mature individuals of both sexes combined].

*Lethenteron reissneri* (non Dybowski, 1869) – Kottelat and Freyhof 2007: 43–44 [Svernaya Dvina and Pechora river drainages, Russia].

### **Partial synonymy of *Lethenteron reissneri* (Dybowski, 1869), the Far Eastern brook lamprey based on this study**

A more extensive synonymy is given in Renaud and Naseka (2015).

*Lampetra reissneri* – Mori 1936: 3, 6, 10, 15 [Maritime, Karafuto (= Sakhalin), Hokkaido, and Amur zoogeographical districts, Japan].

*Lethenteron japonica kessleri* (non Anikin, 1905) – Sato 1951: 58–59 [Shibechari River, now known as Shizunai River, Hokkaido Island, Japan, 26 spawning adults 144–193 mm TL].

*Lethenteron kessleri* (non Anikin, 1905) – Sato 1984: 2 [usually caudal fin but not dorsal fins with a blackish part in adults, Hokkaido Island, Japan]; Iwata et al. 1985: 186–188 [in part, Hokkaido Island, Japan, individuals with unpigmented dorsal fin, but pigmented caudal fin].

### **Generic assignment of *Lampetra* (*Eudontomyzon*) *morii***

When Berg (1931) described this new non-migratory species from the upper Yalu River, in what was then known as Manchuria, but now more or less follows the border of the People's Republic of China and North Korea, the only other members of the subgenus, *Lampetra danfordi* (Regan, 1911) and *La. mariae* Berg, 1931, were European in distribution. To explain the discontinuous distribution of the subgenus, he suggested two hypotheses: 1) the European and Asian species were relics of a former continuous distribution or 2) they arose independently, the former from *La. fluviatilis* and the latter from *La. japonica* (= *Le. camtschaticum*). However, in their cladistic study based on morphological characters Gill et al. (2003) showed that *Eudontomyzon danfordi* and *E. morii* constituted a clade supported by a single synapomorphy, the presence of alate rows of teeth in the laterals fields, and that this clade was sister to *La. fluviatilis*–*La. ayresii* rather than *Le. camtschaticum*. The four specimens of *E. morii* used in Gill (2003) included a syntype and three non-type adults from the upper Yalu River, People's Republic of China.

Later studies based on the mitochondrial DNA (Lang et al. 2009; White 2014; Pu et al. 2016; Ren et al. 2016) have suggested that *E. morii* should be assigned to the genus *Lethenteron*. However, the material used in these studies is of unconfirmed identity. In Lang et al. (2009) and White (2014) the specimen was a metamorphosing individual with exolaterals, but from the Liaohe River, west of the Yalu River. Although

Berg (1931) suggested that *La. morii* probably occurred in the Liao-ho (= Liaohe), he had only seen an ammocoete from that river. Additionally, exolaterals have occasionally been reported in *Lethenteron* species (see above 'Lethenteron species with exolaterals', page 23). The specimen was the same in Pu et al. (2016) and Ren et al. (2016) and came from the city of Dandong, at the Yalu River estuary, Yellow Sea basin, and may in fact have been *Le. camtschaticum*. Unfortunately, no morphological description of the specimen is provided. Given the uncertainty surrounding the identity of the specimens used in these molecular studies, we prefer to continue treating *E. morii* in the genus *Eudontomyzon*. According to Renaud (1982), who examined four adults from the type locality, including a syntype, *E. morii* possesses one or two exolateral rows on either side of the oral disc (Fig. 6) and this distinguishes it from members of the genus *Lethenteron* that usually have no exolateral teeth, rarely one or two teeth and exceptionally one row.

### Taxonomic key to adults of *Lethenteron*

*Lethenteron* adults are characterized by the presence of two dorsal fins; spade-like caudal fin; supraoral lamina with a wide bridge bearing a unicuspid (rarely bicuspid) tooth at each end and rarely one or two unicuspid teeth on the bridge; three (rarely four) endolateral bicuspid teeth on either side of the oral disc (rarely the third tooth may be unicuspid or tricuspid and the fourth tooth unicuspid); infraoral lamina usually with lateralmost bicuspid teeth and unicuspid teeth internally, but much variability exists within the genus (see Table 10); one or two (usually one) rows of posterial teeth; no exolateral teeth (rarely one or two teeth on one or both sides, and exceptionally, a complete row on both sides); transverse lingual lamina with an enlarged median cusp. The key was constructed based on the character matrix compiled in Table 10.

- 1 Caudal fin pigmentation absent to < 1% coverage (i.e., -) [Japan]..... ***Le. mitsukurii***
- Caudal fin pigmentation between 1% and 100% coverage (i.e., +, ++, +++) ... **2**
- 2 Trunk myomeres 58–62 [western Transcaucasia]..... ***Le. ninae***
- Trunk myomeres > 63..... **3**
- 3 Gular pigmentation between 75 and 100% coverage (i.e., +++) [eastern North America] ..... ***Le. appendix***
- Gular pigmentation absent to < 25% coverage (i.e., -, +) ..... **4**
- 4 Second dorsal fin unpigmented (no blotch at the apex) [Asia].... ***Le. reissneri***
- Second dorsal fin pigmented (blotch at the apex)..... **5**
- 5 Parasitic mode of life; individuals reaching up to 790<sup>1</sup> mm TL [Eurasia and North America] ..... ***Le. camtschaticum***
- Nonparasitic mode of life; individuals reaching ≤ 230 mm TL [Eurasia and western North America]..... ***Le. kessleri*, *Le. alaskense***

<sup>1</sup> Orlov et al. (2014).



**Figure 6.** Oral disc of syntype of *Lampetra morii*, CMNFI 1986–757 (formerly part of ZIN 23145), 171 mm TL. Photograph by George Ben-Tchavtchavadze, University of Ottawa, pre–1982.

### Phylogenetic considerations

The three phylogenetic studies that examined the most comprehensive sets of *Lethenteron* species (Yamazaki et al. 2006; Lang et al. 2009; White 2014) did not achieve any resolution among the species treated, and therefore their relationships cannot be established. The strict consensus tree generated from maximum parsimony in Yamazaki et al. (2006) was based on the partial mtDNA COI gene (1,009 bp) and that in Lang et al. (2009) on the partial mtDNA cyt b gene (1,133 bp). The tree generated from maximum-likelihood in White (2014) was based on the mtDNA ND3 gene (351 bp) and a portion of the mitochondrial control non-coding region I (340 bp). Additionally, Artamonova et al. (2015) examined nucleotide sequence diversity of the partial mtDNA COI gene (1,072 bp) in Eurasian *Lethenteron* using median joining network analysis and concluded that the heterogeneity in the distribution of the haplotypes does not give any grounds to assume that speciation has occurred. The four studies included material identified as *Le. camtschaticum*, *Le. reissneri* and/or *Le. kessleri*. Additionally, Lang et al.

**Table 10.** Character matrix of species of *Lethenteron*. Abbreviations: b, bicuspid; u, unicuspid. Pigmentation coverage as follows: -, absent to < 1%; +, 1% to < 25%; ++, 25% to < 75%; +++, ≥ 75%. Percentages in parentheses are percentages of occurrence of character states.

Species	Trunk Myomeres	Infraoral Lamina	Transverse Lingual Lamina	Pigmentation		
				Gular	Second Dorsal Fin	Caudal Fin
<i>Le. alaskense</i>	66–72 <sup>1</sup>	6–11 teeth (the lateralmost and sometimes an internal one bicuspid; the others unicuspid) <sup>1</sup>	9–15 teeth, the median one enlarged <sup>1</sup>	– <sup>1</sup>	with blotch (94%) <sup>1</sup> , no blotch (6%) <sup>1</sup>	+(17%) <sup>1</sup> , ++ (37%) <sup>1</sup> , +++ (46%) <sup>1</sup>
<i>Le. appendix</i>	64–70 <sup>2</sup> , 66–74 <sup>3</sup>	6–10 teeth (the lateralmost unicuspid or bicuspid; the others unicuspid) <sup>2,3</sup>	9–15 teeth, the median one enlarged <sup>2,3</sup>	+++ <sup>3</sup>	with blotch (38%) <sup>3</sup> , no blotch (62%) <sup>3</sup>	+(44%) <sup>3</sup> , ++ (26%) <sup>3</sup> , +++ (30%) <sup>3</sup>
<i>Le. camtschaticum</i>	65–73 <sup>4</sup> , 70–75 <sup>5</sup> , 72–77 <sup>6</sup>	1b4u1b <sup>5</sup> , 1b5u <sup>5</sup> , 6u1b <sup>6</sup>	6u–I–2u <sup>5</sup> , 3u–I–2u <sup>5</sup> , 4u–I–4u <sup>6</sup>	– <sup>4</sup>	with blotch (100%) <sup>4,15</sup>	+(27%) <sup>4</sup> , ++ (53%) <sup>4</sup> , +++ (20%) <sup>4,18</sup>
<i>Le. kessleri</i>	70–74 <sup>7</sup>	1b4u1b <sup>7</sup> , 1b5u1b <sup>7</sup>	5u–I–7u <sup>7</sup> , 7u–I–7u <sup>7</sup>	– <sup>12</sup> , + <sup>12</sup>	with blotch (100%) <sup>16</sup>	+++ (100%) <sup>19</sup>
<i>Le. mitsukurii</i>	66–70 <sup>8</sup>	6u <sup>8</sup>	2u–I–4u <sup>10</sup> , 3u–I–3u <sup>10</sup>	– <sup>13</sup>	no blotch (100%) <sup>17</sup>	– (100%) <sup>17</sup>
<i>Le. ninae</i>	58–62 <sup>9</sup>	7u <sup>9</sup> , 1b3u1b <sup>9</sup> , 5u1b <sup>9</sup> , 1b5u <sup>9</sup> , 6u1b <sup>9</sup> , 1b4u1b <sup>9</sup> , 3u1b3u <sup>9</sup> , 1b1u1b1u1b <sup>9</sup>	6u–I–5u <sup>9</sup> , 4u–I–4u <sup>9</sup> , 4u–I–5u <sup>9</sup> , 5u–I–5u <sup>9</sup> , 5u–I–6u <sup>9</sup> , 7u–I–7u <sup>9</sup> , 2u–I–2u <sup>9</sup> , 3u–I–2u <sup>9</sup> , 4u–I–3u <sup>9</sup> , 5u–I–4u <sup>9</sup> , 7u–I–5u <sup>9</sup> , 8u–I–7u <sup>9</sup>	– <sup>14</sup>	with blotch (100%) <sup>9</sup>	+(60%) <sup>20</sup> , ++ (33%) <sup>20</sup> , +++ (7%) <sup>20</sup>
<i>Le. reissneri</i>	70–72 <sup>6</sup>	1b5u <sup>6</sup> , 1b4u1b <sup>6</sup>	2u–I–2u <sup>11</sup>	– <sup>11</sup>	no blotch (100%) <sup>11</sup>	+++ (100%) <sup>11</sup>

<sup>1</sup> Vladyskov and Kott (1978a). <sup>2</sup> Vladyskov (1949) as *Entosphenus lamottenii* [Robins et al. (1980) state that *Petromyzon lamottenii* Lesueur, 1827 is unidentifiable and use the next available name *Lampetra appendix* (= *Lethenteron appendix*) for the American brook lamprey].

<sup>3</sup> Vladyskov and Kott (1978a as *Lethenteron lamottenii*, see note no. 2). <sup>4</sup> Vladyskov and Kott (1978a as *Lethenteron japonicum*). <sup>5</sup> this study, Table 2 (based on type material of *Petromyzon marinus camtschaticus* and *Petromyzon japonicus*). <sup>6</sup> Renaud and Naseka (2015).

<sup>7</sup> this study, Table 2 (based on type material of *Petromyzon kessleri*). <sup>8</sup> this study, Table 8 (based on type material of *Lampetra mitsukurii* and synonym *Lethenteron matsubara*). <sup>9</sup> Naseka et al. (2009), Tuniyev et al. (2016). <sup>10</sup> this study, Table 8 (based on type material of *Lethenteron matsubara*, synonym of *Lampetra mitsukurii*). <sup>11</sup> Renaud and Naseka 2015 (based on specimen from Shangshi River).

<sup>12</sup> this study, Table 6 (based on three specimens from the Ob' River identified by Berg (1931) as *Lampetra japonica kessleri*). <sup>13</sup> this study, Table 9 (based on type material of *Lethenteron matsubara*, synonym of *Lampetra mitsukurii*). <sup>14</sup> this study (based on CMNFI 2008–59, paratype of *Lethenteron ninae*). <sup>15</sup> this study, Table 3 (based on type material of *Petromyzon marinus camtschaticus* and *Petromyzon japonicus*). <sup>16</sup> Tilius 1811. <sup>17</sup> Anikin (1905). <sup>18</sup> this study, Table 9 (based on type material of *Lampetra mitsukurii* and synonym *Lethenteron matsubara*). <sup>19</sup> this study, Table 3 (based on type material of *Petromyzon marinus camtschaticus* and *Petromyzon japonicus*). <sup>20</sup> Tuniyev et al. (2016).

<sup>20</sup> Tuniyev et al. (2016).

(2009) and White (2014) included *Le. alaskense* and *Le. appendix*. None of the studies contained material identified as *Le. mitsukurii* or *Le. ninae*. According to Yamazaki and Goto (2016), the reason we do not see genetic differences between *Le. camtschaticum* and nonparasitic forms derived from it, is that the latter are the result of phenotypic plasticity rather than genetic polymorphism. However, Docker and Potter (2019) state that the lack of fixed differences in mtDNA sequences is not in itself evidence of phenotypic plasticity nor is demonstration of fixed genetic differences evidence of species-level differences. We do not treat *Lethenteron* sp. N and *Le.* sp. S here because neither have been formally described. We recognize that taxonomic changes will need to be made once they are. In order to achieve better resolution among the *Lethenteron* species that have been formally described, we suggest that a total evidence cladistic analysis which includes both morphological and molecular characters, including nuclear genes, be performed.

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# Redescription of *Stenothyra glabra* A. Adam, 1861 (Truncatelloidea, Stenothyridae), with the first complete mitochondrial genome in the family Stenothyridae

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## Abstract

In this study, *Stenothyra glabra* belonging to the truncatelloid family Stenothyridae is redescribed using morphological characters from the shell, operculum, and radula. The species is distinguished from other species in the group by its shell without spotted spiral lines and by its dome-shaped, mostly smooth, protoconch with some pits. Together with the morphological description, the complete mitogenome for the species is provided, which fill a knowledge gap in Stenothyridae. The mitogenome of *S. glabra* is 15,830 bp in length and has a circular structure. It contains 37 genes: 22 transfer RNA genes (tRNAs), two ribosomal RNA genes (rRNAs), and 13 protein-encoding genes (PCGs). The overall A+T content of the mitogenome is 68.9%. Molecular phylogenetic analysis and COI sequence divergence separate *S. glabra* from its congeners and show that *S. glabra* and *S. cf. divalis* form a sister clade.

## Keywords

Micromollusks, mitogenome, phylogeny, systematics

## Introduction

The Stenothyridae are a family of small to minute-sized gastropods found in intertidal, shallow-water aquatic habitats and brackish estuaries in Asia and Australia (Golding 2014). A preliminary investigation through the World Register of Marine Species (WoRMS) recovered 212 species-level names, belonging to ten genus-level groups, including approximately 80 extant species from four genera, while a previous estimate of stenothyrid diversity recognized approximately 60 species globally (Strong et al. 2008). Almost all recent species are placed in the genus *Stenothyra* Benson, 1856, involving approximately 75 extant species. Due to the groups being small in size and exhibiting relatively simple morphologies, only a few stenothyrids have been described in detail (Kosuge 1969; Davis et al. 1986, 1988; Golding 2014).

*Stenothyra glabra* A. Adam, 1861 is a brackish-water species, which is thought to be the only *Stenothyra* species distributed along the coast of north China (Zhang et al. 1964; Qi et al. 1989; Zhang et al. 2016). The brief original description (without illustration) by A. Adam (1861) is inadequate in that many features were not evaluated or included. On the other hand, stenothyrid species are so similar in morphology that it is relatively difficult to distinguish them with the naked eye, so it is important to obtain clear illustrations and to redescribe the species in detail. Moreover, the species have relatively little molecular data available at present, and not much is known about phylogenetic relationships within the family. The aims of this study were thus: (a) to redescribe *S. glabra* based on specimens collected from the coast of north China using Scanning Electron Microscope images of the shell, protoconch, operculum, and radula; (b) to sequence the complete mitogenome of *S. glabra* and fill a knowledge gap; and (c) to use molecular data to reconstruct phylogenetic relationships and clarify the position of *S. glabra*.

## Materials and methods

### Taxon sampling and processing

Samples were collected from a mud flat in the Yellow River estuary (37°49.3676'N, 119°09.0351'E), Shandong, China on 17 Sept. 2017 and Ganyu (34°51.9126'N, 119°12.681'E), Jiangsu, China on 16 Sept. 2018. All specimens were preserved in 95% non-denatured ethanol and deposited in the Laboratory of Shellfish Genetics and Breeding (**LSGB**), Fisheries College, Ocean University of China, Qingdao, China. The following standard measurements were taken using a stereomicroscope with an eyepiece micrometer. The number inside the brackets indicates the number of specimens in each lot. Total genomic DNA was extracted from entire animals with the TIANamp Marine Animals DNA Kit (Tiangen Biotech, Beijing, China) according to manufacturer's protocol, and stored at -4 °C for short-term use. The Scanning Electron Microscope (SEM) was used to examine shells, radulae, and opercula based on the methods

given by Geiger et al. (2007) and Geiger (2012). Briefly, for SEM studies of radula, the tissue surrounding the radula was dissolved by proteinase K when extracting DNA from entire animals using the TIANamp Marine Animals DNA Kit. The radula was precipitated to the bottom of the centrifugal tube after centrifuge separating, and was collected using a pipette. Then the radula was washed in drops of water or 10% KOH on a glass histology slide. Shells, radulae, and opercula were mounted on stubs, thinly coated with gold, and examined using a TESCAN VEGA3 SEM.

### Sequencing, assembly, and annotation

Library construction and sequencing were performed by Beijing Novogene Technology Co., Ltd (China) from total genomic DNA on the HiSeq X platform (Illumina Inc.) with 150-bp paired-end reads. Raw data were initially quality-trimmed using Trimmomatic v0.36 (Bolger et al. 2014). Resulting clean reads were assembled using the software SPAdes 3.13.0 (Bankevich et al. 2012) with default settings. The complete mitochondrial genome was identified using BLASTN (Altschul et al. 1997) and the previously published mitochondrial genome of *Oncomelania hupensis robertsoni* (EU079378.1) was used as the reference. The mitogenomes were annotated using MITOS WebServer (<http://mitos.bioinf.uni-leipzig.de/index.py>) (Bernt et al. 2013) to identify protein-coding genes (PCGs), ribosomal RNA (rRNAs), and transfer RNA (tRNAs) genes. Gene limits were refined by comparison with orthologous mtDNA sequences of closely related species of Truncatelloidea and using BLASTX (Altschul et al. 1997) against the non-redundant protein sequences database in GenBank. Two ribosomal RNA genes (rrnL and rrnS) were identified by alignment with published Truncatelloidea mitogenomes, and their ends were assumed to extend to the boundaries of their flanking genes. The tRNAs were also annotated with ARWEN v1.2 (Laslett and Canbäck 2008) and tRNAscan-SE v1.21 (Lowe and Eddy 1997) and manually curated when inconsistencies were detected between tools. Base composition and codon usage were analyzed with MEGA 6.0 (Tamura et al. 2013). The GC and AT skews were calculated using the formulae:  $AT\ skew = (A-T)/(A+T)$  and  $GC\ skew = (G-C)/(G+C)$  (Perna and Kocher 1995). The circular map of the *S. glabra* mitogenome was drawn with the mitochondrial visualization tool CGView (Stothard and Wishart 2005; [http://stothard.afns.ualberta.ca/cgview\\_server/](http://stothard.afns.ualberta.ca/cgview_server/)). In addition, contigs of 28S rRNA genes were identified using BLASTN with sequences from Golding (2014) serving as the reference against the assembled genomic data, followed by manual annotation of gene boundaries.

### Phylogenetic analysis

No mitochondrial genomes of stenothyrids were available from GenBank, so we reconstructed the phylogenetic trees of the genus *Stenothyra* using COI, 16S, and 28S fragments, combining our DNA sequences with sequences from GenBank that included eleven stenothyrid taxa and one anabathrid species, *Pisinna punctulum*, as the out-

group (Table 1). Alignment of all stenothyrid and outgroup sequences was performed using default parameters in MEGA 6.0 and proofread by eye. Aligned COI sequences were translated using the invertebrate mitochondrial code (NCBI translation code 5) to ensure stop codons or frameshift mutations were not present.

The best partition schemes and best-fit models of substitution for the data sets for phylogenetic analyses were identified using Partition Finder 2 (Lanfear et al. 2017) according to the Bayesian Information Criterion (BIC; Schwarz 1978). For the data sets analyzed at nucleotide levels, all genes were separated in the partitions (16S, 28S, COI). In addition, For the COI gene, these three partition schemes at nucleotide level were tested considering first, second and third codon positions separately.

Phylogenetic analyses were carried out using maximum likelihood (ML) and Bayesian Inference (BI) methods. ML analyses were performed with IQ-TREE (Nguyen et al. 2014) using the partition schemes and model (Table 2), and with 1000 Ultrafast bootstraps. The BI tree reconstruction was performed in MrBayes v3.2 (Ronquist and Huelsenbeck 2003) with two runs, each with four Markov Chain. All partitions were allowed to have their own set of parameters and to evolve under different rates. The analysis was run for ten million generations, sampling trees every 1000 generations. The initial 25% of the trees were discarded as burn-in and the remaining trees were used to generate a 50% majority rule consensus tree with nodal confidence assessed with posterior probabilities (BPP). Bayesian runs achieved sufficient convergence by ascertaining that the average standard deviation of split frequencies between chains was below 0.01 at the end of the runs and that the po-

**Table 1.** GenBank accession numbers for specimens included in the molecular analyses. For COI and 16S, see GenBank accession number of the mitochondrial genome (MN548735).

Family	Species	COI	16S	28S
Stenothyridae	<i>Stenothyra glabra</i>	–	–	MT090057
	<i>Stenothyra australis</i>	KC439692	KC439814	KC439915
	<i>S. gelasinosa gelasinosa</i>	KC439704	KC439826	KC439917
	<i>S. gelasinosa phrixa</i>	KC439717	KC439836	KC439920
	<i>S. gelasinosa apiosa</i>	KC439720	KC439842	KC439921
	<i>S. paludicola topendensis</i>	KC439731	KC439853	KC439922
	<i>S. paludicola timorensis</i>	KC439733	KC439855	KC439923
	<i>Stenothyra monilifera</i>	KC439735	KC439857	KC439924
	<i>Stenothyra</i> cf. <i>polita</i>	KC439737	KC439859	KC439926
	<i>Stenothyra</i> sp. ‘ <i>johor</i> ’	KC439740	KC439862	KC439927
	<i>Stenothyra</i> cf. <i>glabra</i>	KC439741	KC439863	KC439928
	<i>Stenothyra</i> cf. <i>divalis</i>	KC439744	KC439866	KC439929
	<i>Pisinna punctulum</i>	KC439794	KC109968	KC110020

**Table 2.** The best partition schemes and best-fit models of substitution for the data sets.

Data set	Set Partition	Best Model
Best Partition to rRNA genes	16s	GTR+I+G
	28s	GTR+I+G
Best Partition to COI gene at nucleotide level	cox1 1 <sup>th</sup>	GTR+I
	cox1 2 <sup>th</sup>	F81
	cox1 3 <sup>th</sup>	HKY+G

tential scale reduction factor of each parameter was 1.00. Trees were visualized using FigTree v1.3.1 and rooted using the outgroup species. Because these sequences are short and derived from closely related, so the *p*-distances are used as a simple measure of pairwise sequence divergences (Srivathsan and Meier 2012).

## Results

### Systematics

#### Stenothyridae Tryon, 1866

##### *Stenothyra* Benson, 1856

**Type species.** *Stenothyra delata* (Benson, 1837) from the delta of the Ganges (Benson 1837).

##### *Stenothyra glabra* A. Adams, 1861

Figures 1–3

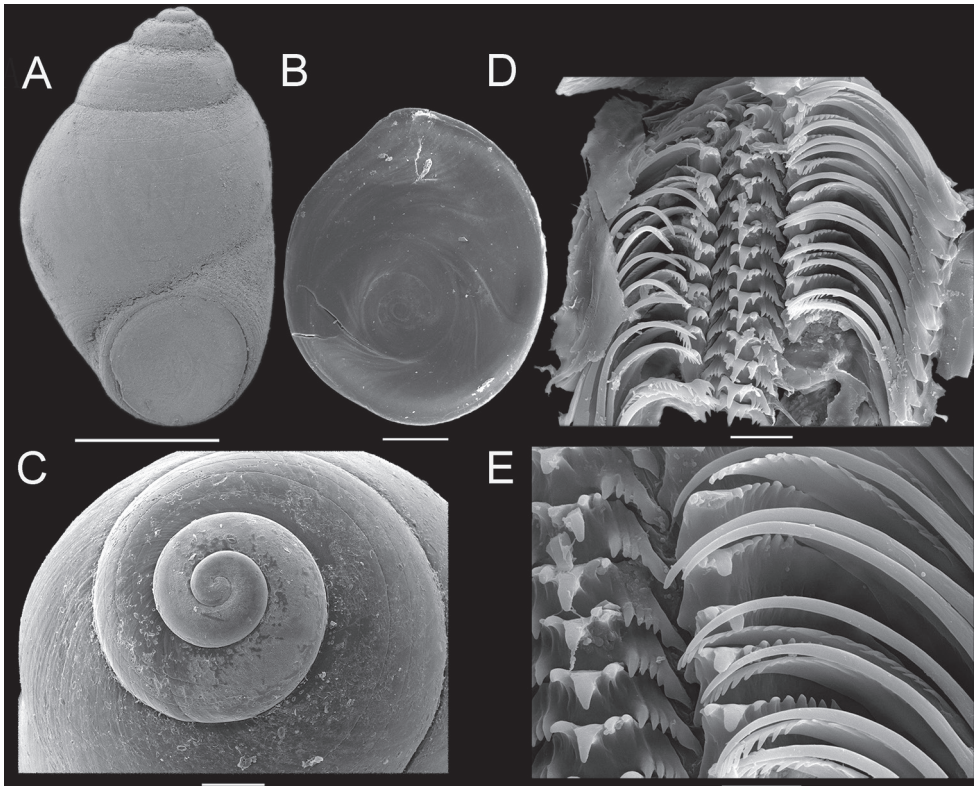
*Stenothyra glabra* A. Adam, 1861: 307; Yen 1939: 45, pl. 4, fig. 15; Yen 1942: 197, pl. 14, fig. 44; Zhang et al. 1964: 61; Qi et al. 1989: 32–33, fig. 30; Zhang et al. 2016: 60–61.

**Material examined.** CHINA • 4, specimens; Shandong province, Dongying, Yellow River estuary mud flat; 37°49.367'N, 119°09.035'E; 17 Sept. 2017; Lu Qi leg.; LSGB S1702; • 6, specimens; Jiangsu province, Ganyu beach; 34°51.912'N, 119°12.681'E; 16 Sept. 2018; LSGB G1801.

**Original description (verbatim).** “S. testa oblonga, laevi, polita, semipellucida, aurantiaca; anfractibus  $4\frac{1}{2}$ , convexis, supremis transversim obsolete striates; suturis marginatis; peritremate continuo; anfraetu ultimo ad aperturam concentrice striato” (A. Adams 1861).

**Diagnosis.** Shell ovate, dorso-ventrally compressed, with well-inflated body whorl and narrowly constricted aperture, without dotted spiral lines. Dome-shaped, smooth protoconch ( $1\frac{3}{4}$  whorls) with some pits. Posterior foot pointed, with metapodial tentacle.

**Description.** *Shell* minute ( $2.89 \pm 0.14$  mm in height;  $1.75 \pm 0.07$  mm in width), ovate-conic, rather thick, dorso-ventrally compressed, with rounded to angled inflation of last whorl; up to five whorls including protoconch, convex whorls, sutures moderately deep; Surface smooth, yellowish brown, sculpture not dotted lines but continuous spiral grooves (Fig. 1A). The aperture abruptly descending, contracted, and nearly circular; peristome continuous, showing a weak triangular area; outer lip with marked grooves (Fig. 1A).



**Figure 1.** *Stenothyra glabra* A. Adams, 1861 **A** shell LSGB-G1801-4 **B** exterior surface of operculum **C** protoconch **D, E** radula. Scale bars: 1 mm (**A**); 200 µm (**B**), 200 µm (**C**), 20 µm (**D**), 10 µm (**E**).

**Operculum** ovate, yellowish, translucence, with very weak angulation aligning with posterior apex of aperture; nucleus of the exterior surface is close to the inner lip, paucispiral (Fig. 1B).

**Protoconch** dome-shaped; smooth,  $1\frac{3}{4}$  to 2 whorls; Small pits apparently exist in a small central part of protoconch (Fig. 1C).

**Radula.** Radular teeth interlocked moderately in unfolded condition (Fig. 1D). Central tooth 1-2+1+1-2 (Fig. 1D, E); cusp with central denticle largest, 1–2 smaller ones on each side, basal denticles diminishing outwardly. Lateral teeth 2-3+1+6-8, apical ones largest, 2–3 denticles along inner edge of cusp, 6–8 along outer edge. Marginal teeth without groove; inner marginal teeth with ~20 cusps on tip and distal half of outer edge; outer marginal teeth with ~10 cusps on distal third of inner edge.

**Type locality.** Estuary of the Pei-ho River (also known as the Hai River in the current name), North China.

**Geographic distribution.** From Fujian to Hebei on coast of China (A. Adams 1861; Yen 1939; Qi et al. 1989; Yuan et al. 2002; Bao et al. 2007); Japan (Kuroda 1962).

**Ecology.** Inhabiting on the surface of mud flat or attaching to the under-surface of floating leaves in the freshwater estuary.

**Remarks.** The type locality of *Stenothyra glabra* A. Adams, 1861 is “estuary of the Pei-ho, North China”, which is on the coast of the Bohai Sea. One of the localities in this study, Yellow River estuary, is adjacent to the type locality. Moreover, the shells are very similar in size, shape, and microsculpture when compare with the descriptions (A. Adams 1861; Yen 1939; Yen 1942; Zhang et al. 1964), as well as with the figure of A. Adam’s type (Yen 1942: 197, pl. 14, fig. 44). We believe that specimens collected in this study belong to a common species along the coast of the Yellow and Bohai seas in China, and is conspecific with the type material.

The radular morphology is one of the diagnostic morphological characters, but the Rachidian tooth and general radular shape of *S. glabra* appear similar to that of other *Stenothyra* species. This may be due to similarities in habit, substrate, and diet, suggesting that species delimitation in micro-caenogastropods should not rely solely on radular morphology. In fact, recent work has shown that some microgastropods exhibit morphological stasis in response to environmental stability (e.g., Weigand et al. 2011). However, there are sufficient morphological grounds for separating this species, by the shell not having dotted spiral lines and by the dome-shaped, smooth protochonch bearing some pits.

**Sequence divergence.** The pairwise distance between species or non-conspecific subspecies ranged from 9.1% (*Stenothyra glabra* vs. *S. cf. divalis*) to 16.1% (*S. gelasinosa apiosa* vs. *S. monilifera*). COI sequence divergence between conspecific subspecies ranged from 3.0% (*Stenothyra paludicola timorensis* vs. *S. paludicola topendensis*) to 5.7% (*Stenothyra gelasinosa apiosa* vs. *S. gelasinosa gelasinosa*) (Table 3). Comparing the sequence divergences of within-taxon and between-taxon provided a sound basis for determining specific and subspecific-level differences. 3%-6% was evidence of sub-specific diversity and > 9% was found between species. In this study, the divergence between *S. glabra* and other species fell into the latter category, having a lowest divergence of 9.1%. Notably, the divergence between *Stenothyra glabra* and *S. cf. glabra* (KC439741) is 13.2%. *Stenothyra cf. glabra* was collected from Mai Po, Hong Kong, China (Golding 2014), and is likely a misidentified animal.

## Mitogenome architecture

### Genome organization and base composition

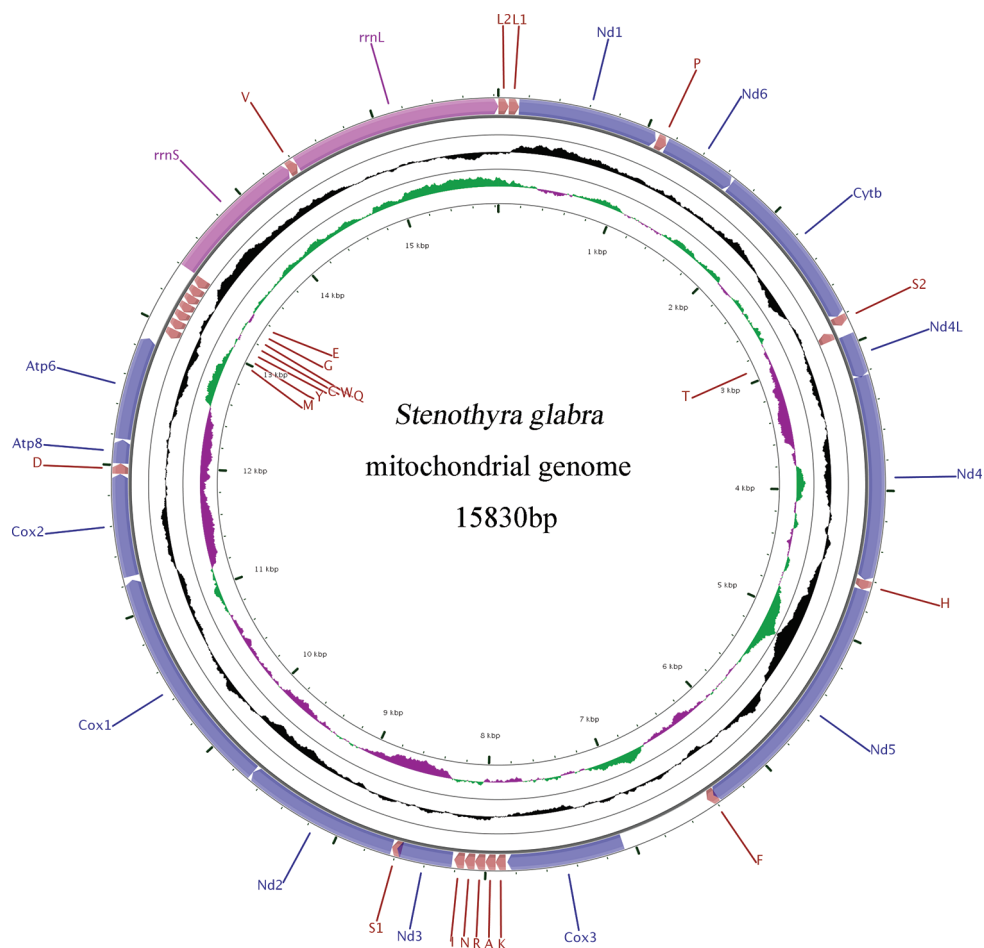
The circular mitogenome of *Stenothyra glabra* is 15,830 bp in size (GenBank accession number MN548735) and comprises 37 genes including 13 PCGs, 2 rRNAs genes, 22 tRNAs genes, and a putative control region (CR), typical of Gastropoda mitogenomes (Fig. 2). The CR is 633 bp and flanked by trnF and cox3.

### Protein-coding genes and codon usage

The total length of the concatenated 13 PCGs is 11271, with the average A+T content of 68.9%. ATG (for 12 PCGs) is the most commonly used start codon, whereas nad3

Table 3. Pairwise *p*-distance among species of *Stenothyra*.

	<i>S. australis</i>	<i>S. cf. divalis</i>	<i>S. cf. glabra</i>	<i>S. cf. polita</i>	<i>S. gelasinosa apiosa</i>	<i>S. gelasinosa gelasinosa</i>	<i>S. gelasinosa phrixia</i>	<i>S. glabra</i>	<i>S. monilifera</i>	<i>S. paludicola timorensis</i>	<i>S. paludicola topendensis</i>
<i>S. australis</i>											
<i>S. cf. divalis</i>	0.109										
<i>S. cf. glabra</i>	0.135	0.129									
<i>S. cf. polita</i>	0.135	0.138	0.152								
<i>S. gelasinosa apiosa</i>	0.126	0.132	0.141	0.149							
<i>S. gelasinosa gelasinosa</i>	0.105	0.109	0.126	0.146	0.057						
<i>S. gelasinosa phrixia</i>	0.121	0.120	0.141	0.155	0.049	0.052					
<i>S. glabra</i>	0.118	0.091	0.132	0.146	0.111	0.097	0.109				
<i>S. monilifera</i>	0.126	0.121	0.123	0.151	0.161	0.136	0.148	0.123			
<i>S. paludicola timorensis</i>	0.132	0.106	0.108	0.141	0.133	0.120	0.138	0.109	0.124		
<i>S. paludicola topendensis</i>	0.135	0.114	0.103	0.139	0.135	0.126	0.141	0.109	0.133	0.030	
<i>Stenothyra</i> sp. 'Johor'	0.117	0.118	0.118	0.129	0.136	0.115	0.126	0.115	0.112	0.120	0.114



**Figure 2.** Map of the complete mitochondrial genome of *Stenothyra glabra*.

used TTG. The most frequent terminal codons are TAA (for 11 PCGs), whereas *nad6* used a truncated T, *nad4L* used TAG, respectively (Table 4).

Codon usage, relative synonymous codon usage (RSCU), and codon family proportion (corresponding to the amino acids usage) of *S. glabra* is presented (Suppl. material 1). Serine (13.68%), phenylalanine (11.31%), leucine (11.15%) are the most frequent amino acids in the PCGs of *S. glabra*, whereas histidine (1.04%), glutamine (1.12%), arginine (1.12%) are relatively scarce.

### Transfer and ribosomal RNA genes

The sizes of 22 tRNA genes of *S. glabra* range from 37 bp to 69 bp, comprising 1447 bp (9.1%) of the total mitogenome (Table 5). All 22 tRNA genes were identified and the secondary structures were shown in Suppl. material 2.

**Table 4.** Annotated mitochondrial genome of *Stenothyra glabra*.

Gene	Direction	Position		Size	Intergenic Nucleotides	Condon		Anti-codon
		From	To			Start	Stop	
trnL2	F	1	68	68	–	–	–	TAA
trnL1	F	70	138	69	1	–	–	TAG
nad1	F	139	1080	942	0	ATG	TAA	–
trnP	F	1088	1156	69	7	–	–	TGG
nad6	F	1158	1659	502	1	ATG	T	–
cytb	F	1660	2799	1140	0	ATG	TAA	–
trnS2	F	2800	2865	66	0	–	–	TGA
trnT	R	2866	2932	67	0	–	–	TGT
nad4L	F	2937	3234	297	4	ATG	TAG	–
nad4	F	3228	4601	1374	-5	ATG	TAA	–
trnH	F	4603	4667	65	1	–	–	GTG
nad5	F	4668	6392	1725	0	ATG	TAA	–
trnF	F	6376	6443	68	-15	–	–	GAA
cox3	F	7077	7856	780	633	ATG	TAA	–
trnK	F	7868	7934	67	11	–	–	TTT
trnA	F	7935	8002	68	0	–	–	TGC
trnR	F	8004	8072	69	1	–	–	TCG
trnN	F	8073	8141	69	0	–	–	GTT
trnI	F	8143	8210	68	1	–	–	GAT
nad3	F	8224	8597	374	13	TTG	TAA	–
trnS1	F	8566	8633	68	-30	–	–	GCT
nad2	F	8634	9692	1059	0	ATG	TAA	–
cox1	F	9694	11229	1536	1	ATG	TAA	–
cox2	F	11256	11942	687	26	ATG	TAA	–
trnD	F	11944	12012	69	1	–	–	GTC
atp8	F	12013	12171	159	0	ATG	TAA	–
atp6	F	12177	12872	696	5	ATG	TAA	–
trnM	R	12930	12996	67	57	–	–	CAT
trnY	R	13002	13066	65	5	–	–	GTA
trnC	R	13071	13134	64	4	–	–	GCA
trnW	R	13136	13201	66	1	–	–	TCA
trnQ	R	13203	13264	62	1	–	–	TTG
trnG	R	13265	13331	67	0	–	–	TCC
trnE	R	13335	13403	69	3	–	–	TTC
rrnS	F	13404	14349	873	0	–	–	–
trnV	F	14349	14415	37	-1	–	–	TAC
rrnL	F	14416	15830	1415	0			

**Table 5.** The nucleotide composition of *Stenothyra glabra* mitogenome.

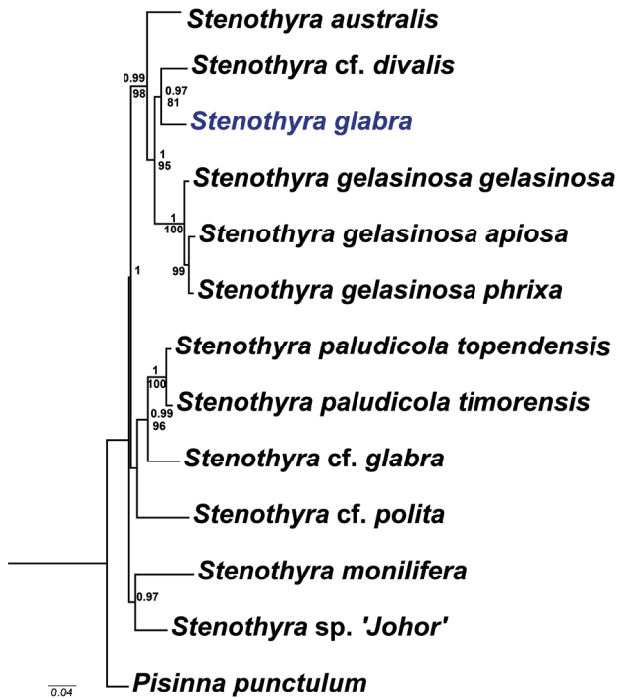
Genes or regions	Size	Nucleotides composition (%)				A+T (%)	AT Skew	GC Skew
		T	C	A	G			
Complete mitogenome	15830	41	12.5	28.7	17.8	69.7	-0.236	0.175
PCGs	11271	43	13	25.9	18.2	68.9	-0.248	0.167
tRNA genes	1447	33.7	13.5	34.7	18.1	68.4	0.014	0.144
rRNA genes	2361	35.6	10.9	36.1	17.4	71.7	0.0065	0.229
lrRNA	1415	36.7	10.7	35.9	16.7	72.6	0.0107	0.216
SrRNA	946	33.9	11.3	36.4	18.4	70.3	0.035	0.238
A+T-rich region	633	37.4	10	36.2	16.4	73.6	-0.017	0.246

The genes rrnL and rrnS are 1415 bp and 946 bp in size, with 72.6% and 70.3% A+T content, respectively (Table 5). The location of rrnS is between trnE and trnV, and rrnL is located between trnV and trnL2 (Table 4); this is the same arrangement reported for Littorinimorpha (Osca et al. 2015).

## Phylogenetic analysis

Phylogenetic reconstruction by BI and ML methods recovered mostly consensus trees with identical topologies, with the exception of one clade composed of *Stenothyra monilifera* and *S. sp. 'johor'*. Only the ML summary tree is shown here, labelled with both Bayesian posterior probabilities (BPP) and bootstrap support values (BS) generated by ML analysis (Fig. 3).

The phylogenetic analysis of stenothyrids, including most *Stenothyra* species with COI, 16S and 28S data in the NCBI, inferred the phylogenetic placement of *S. glabra*, and phylogenetic relationships of stenothyrids. *Stenothyra glabra* was recovered as the sister taxon to *S. cf. divalis*, and the COI divergence between them was 9.1%, the smallest value among those between *S. glabra* and other taxa of *Stenothyra* (Table 3). In the phylogeny, all *Stenothyra* taxa were split into three major clades. The basal clade included *S. monilifera* and *S. sp. 'johor'* with relatively strong support in the BI analysis (BPP = 0.97), but with weak support in the ML analyses (BS < 70). *Stenothyra australis*, *S. gelasinosa*, *S. cf. divalis*, and *S. glabra* formed a well-supported clade (BPP = 0.99; BS = 98), while the third clade was composed of *S. paludicola topendensis*, *S. paludicola timorensis*, *S. cf. glabra*, and *S. cf. polita*, with a high support by BPP (> 0.98) and ML bootstrap values (> 90), except for the branches of *Stenothyra cf. polita* (BPP < 0.90, BS < 70). Our results are almost congruent with those acquired in the previous study (Golding 2014).



**Figure 3.** Summary tree from Maximum Likelihood analysis of concatenated COI, 16S and 28S sequences. Support indices are BI posterior probabilities (above nodes, > 0.9) and ML bootstraps (below nodes, > 70).

## Conclusion

The redescription of *Stenothyra glabra* based on SEM examination shows more morphological details of the shell, protoconch, and operculum. Radulae are described and illustrated herein for the first time. Additionally, the first mitochondrial genome of Stenothyridae will provide reference data for subsequent phylogenetic studies.

## Acknowledgements

This research was supported by the National Natural Science Foundation of China (31772414), the Fundamental Research Funds for the Central Universities (201964001) and the National Infrastructure of Fishery Germplasm Resources (2019DKA30470). We thank Dr. Takenori Sasaki from the University of Tokyo, for his advices on the morphological research.

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## Supplementary material I

### Relative synonymous codon usage (RSCU) of each amino acid in the mitogenome of *S. glabra*

Authors: Lu Qi, Lingfeng Kong, Qi Li

Data type: image

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Link: <https://doi.org/10.3897/zookeys.991.51408.suppl1>

## Supplementary material 2

### Secondary structure of tRNA in *S. glabra* mitogenome

Authors: Lu Qi, Lingfeng Kong, Qi Li

Data type: doxc

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Link: <https://doi.org/10.3897/zookeys.991.51408.suppl2>



# Hidden in plain sight: two co-occurring cryptic species of *Supplanaxis* in the Caribbean (Cerithioidea, Planaxidae)

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<http://zoobank.org/9628FBDC-2F14-43D3-8102-AD7A6E606C30>

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## Abstract

The cerithioid *Supplanaxis nucleus* (Bruguière, 1789) is widespread in the Caribbean, where it lives in often dense aggregates on hard surfaces in the middle-high intertidal. Molecular evidence shows that it comprises two species that are in fact morphologically diagnosable. We fix the nomenclature of *Supplanaxis nucleus* by designating a sequenced neotype from Bruguière's historical locality of Barbados, and identify the second, cryptic species as *S. nancyae* (Petuch, 2013). The two live syntopically across the Caribbean and form a closely related species group with the Panamic *S. planicostatus* (G.B. Sowerby I, 1825). *Planaxis nucleola* Mörch, 1876, described from St Croix, in the Virgin Islands, never again recorded in the literature but listed as a synonym of *S. nucleus* in taxonomic authority lists, is recognized as a valid species of *Hinea* Gray, 1847. *Proplanaxis* Thiele, 1929 and *Supplanaxis* Thiele, 1929, are synonyms and the latter is given precedence over the former.

## Keywords

distribution, radular morphology, shell morphology, synonymy

## Introduction

*Supplanaxis nucleus* (Bruguière, 1789) (Cerithioidea, Planaxidae) is a small, gregarious gastropod that lives in moderate to large population densities in intertidal, well-oxygenated habitats throughout the Caribbean. It occurs on hard substrates, from small pebbles and cobbles to large boulders or massive bedrock (Vermeij 1973; Bandel 1976; Houbrick 1987), from which it presumably grazes the biofilm. Individuals remain concealed from the sun under spray-moistened rocks, but emerge to feed, migrating with the tide (Bandel 1976). Rather little has been published on its biology, despite its ubiquity in the Caribbean. Similar to other planaxids, the species broods its young in a sub-hemocoelic brood pouch (Simone 2001; Strong et al. 2011), which are released from a pore on the side of the neck at the veliger stage (Thorson 1940; Bandel 1976; Houbrick 1987). Bandel (1976) observed freshly collected females to release veligers throughout the year. Troschel (1858) and Bandel (1984) provided descriptions of the radula of the species, and Houbrick (1987) and Simone (2001) described the radula and anatomy.

Following the serendipitous discovery that syntopic specimens from Guadeloupe clustered in two molecular groups, freshly collected material from Curaçao and Barbados confirmed the existence of two molecular clades within *Supplanaxis nucleus*. Museum material was then examined to evaluate the global distribution of the two clades.

In the present paper, we re-assess the taxonomy of *Supplanaxis nucleus*; we stabilize its nomenclature through the fixation of a neotype and review the nominal planaxid species currently treated as synonyms; and we attribute the second, molecularly distinct taxon to the little-known *S. nancyae* (Petuch, 2013). Finally, we remove *Planaxis nucleola* Mörch, 1876 from the synonymy of *S. nucleus*, and revalidate it as a species of *Hinea* Gray, 1847.

## Materials and methods

Specimens for molecular and morphological study were collected intertidally from three sites in the Lesser Antilles (Guadeloupe, Curaçao, Barbados); tissues were separated from the shells following flash-boiling or microwaving (Fukuda et al. 2008; Galindo et al. 2014) and preserved in 95% EtOH.

Radulae were tissue digested overnight in 100 µl of ATL lysis buffer (Qiagen, Inc.) containing ~ 50 µg of Proteinase-K, sonicated and rinsed in de-ionized water (Holznagel 1997). Cleaned radulae were mounted on aluminum stubs using carbon adhesive tabs, then coated with 25–30 nm gold/palladium (60/40) and photographed using an Apreo scanning electron microscope (FEI Company) at the National Museum of Natural History. Shells were photographed using a Canon EOS 50D camera with a Canon EF 100 mm f/2.8 macro lens and Canon MT-24EX macro twin light flash (Canon USA, Inc.).

Whole genomic DNA was extracted from a ~ 1 mm<sup>3</sup> tissue clip of the foot using an Autogenprep965 (Autogen, Holliston, MA) automated phenol:chloroform extraction with a final elution volume of 50 µL. A 691 base pair (bp) fragment of cytochrome *c* oxi-

dase subunit I (COI) was amplified using the jgLCOI primer (Geller et al. 2013) in combination with Cerithioid\_COIR (Strong and Whelan 2019); a 509–511 bp fragment of 16S ribosomal DNA was amplified with the universal 16SAR/BR primers (Palumbi et al. 1991). PCR reactions were performed with 1 µL of undiluted DNA template in 20 µL reactions. Reaction volumes for COI consisted of 10 µL of Promega Go-Taq Hotstart Master Mix, 0.15 µM each primer, 0.25 µg/µL BSA, 1.25% DMSO and an amplification regime of an initial denaturation at 95 °C for 7 min, followed by 45 cycles of denaturation at 95 °C for 45 s, annealing at 42 °C for 45 s, extension at 72 °C for 1 min and a final extension at 72 °C for 3 min. Reaction volumes for 16S were 1x Biolase (Bioline, Taunton, MA) reaction buffer, 500 µM dNTPs, 3 mM MgCl<sub>2</sub>, 0.15 µM each primer, 0.25 µg/µL BSA, 1 unit Biolase DNA polymerase and an amplification regime of initial denaturation at 95 °C for 5 min, followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 48 °C for 30 s and extension at 72 °C for 45 s, followed by a final extension at 72 °C for 5 min. PCR products were purified using the Exo-SAP-IT protocol (GE healthcare, Piscataway, NJ). BigDye 3.1 (ABI, Foster City, CA) sequencing reactions and sequencing on an ABI 3730XL DNA analyzer capillary array were done following manufacturer's instructions.

Genes were sequenced in both directions to ensure accuracy. Chromatograms were visually inspected and corrected as necessary in Geneious Prime 2019 (Biomatters). COI alignments were translated into amino acids to check for stop codons and frameshift mutations, then trimmed to 658 bp representing the standard invertebrate barcoding region (Folmer et al. 1994). 16S sequences were aligned with MUSCLE (Edgar 2004) using default parameters as implemented in Geneious Prime. The final aligned length for the 16S dataset was 512 bp. All newly generated sequences have been deposited in GenBank (Table 1).

Sequences of additional planaxids [*Supplanaxis niger* (Quoy and Gaimard, 1833), *Planaxis planicostatus* G.B. Sowerby I, 1825] were downloaded from GenBank, including *Planaxis sulcatus* (Born, 1778), which was used to root the tree. Phylogenetic reconstruction was conducted using Maximum Likelihood (ML) in IQ-TREE ver. 1.6.12 (Nguyen et al. 2015) as implemented on the IQ-TREE web server (Trifinopoulos et al. 2016). The best-fit partitioning scheme and the most appropriate substitution model for each partition were estimated using ModelFinder (Kalyaanamoorthy et al. 2017) and partition models (Chernomor et al. 2016). Nodal support was estimated with 1,000 ultra-fast bootstrap replicates (Hoang et al. 2018).

## Repositories

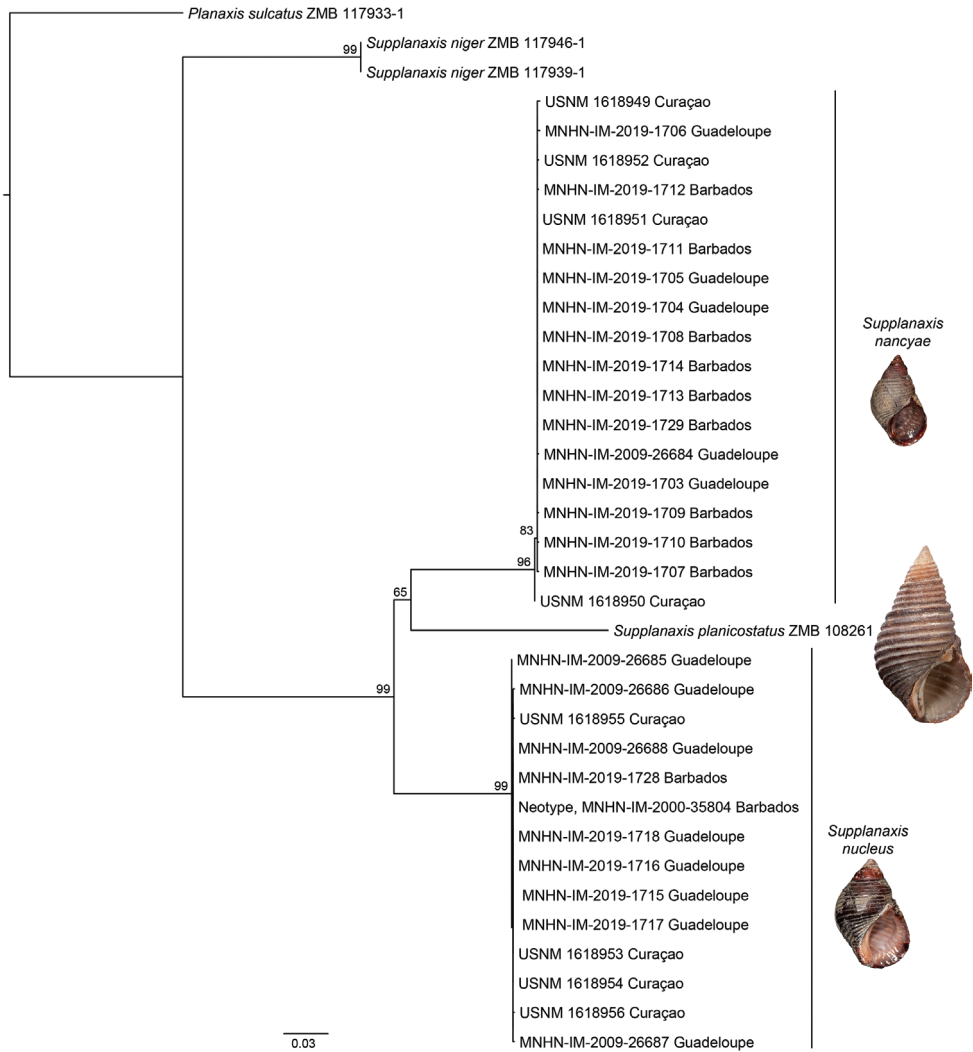
<b>FMNH</b>	Field Museum of Natural History;
<b>MNHN</b>	Muséum national d'Histoire naturelle, Paris;
<b>NHMK</b>	The Natural History Museum, London;
<b>USNM</b>	National Museum of Natural History, Smithsonian Institution (formerly U.S. National Museum), Washington DC;
<b>ZMB</b>	Museum für Naturkunde, Berlin;
<b>ZMK</b>	Statens Naturhistoriske Museum, Copenhagen.

**Table 1.** Voucher registration numbers and GenBank accession numbers for sequenced specimens of *Supplanaxis nucleus* and *S. nancyae*. Sequences for *Planaxis sulcatus*, *S. planicostatus*, and *S. niger* were downloaded from GenBank (source Wiggering et al. 2020).

Species	Voucher registration	Locality	COI	16S
<i>Planaxis sulcatus</i>	ZMB 117933-1	Egypt, Hurghada	MT593025	MT587883
<i>Supplanaxis planicostatus</i>	ZMB 108261-h1	Paitilla, Bay of Panama	–	MT621366
<i>Supplanaxis niger</i>	ZMB 117939-1	Madagascar, Southeast Island Ste Marie	MT587879	MT593021
	ZMB 117946-1	Indonesia, Sumatra, Aceh, Ule-le	MT587878	MT593020
<i>Supplanaxis nucleus</i>	MNHN-IM-2009-26685	Guadeloupe, Plage de Malendure	MT921856	MT921888
	MNHN-IM-2009-26686		MT921857	MT921889
	MNHN-IM-2009-26687		MT921858	MT921890
	MNHN-IM-2009-26688		MT921859	MT921891
	MNHN-IM-2019-1715		MT921860	MT921892
	MNHN-IM-2019-1716		MT921861	MT921893
	MNHN-IM-2019-1717		MT921862	MT921894
	MNHN-IM-2019-1718		MT921863	MT921895
	USNM 1618953	Curaçao, S shore, beach in front of CARMABI research station	MT921864	MT921896
	USNM 1618954		MT921865	MT921897
	USNM 1618955		MT921866	MT921898
	USNM 1618956		MT921867	MT921899
	MNHN-IM-2000-35804 (neotype)	Barbados, Hastings Rocks	MT921868	MT921900
	MNHN-IM-2019-1728		MT921869	MT921901
<i>Supplanaxis nancyae</i>	MNHN-IM-2009-26684	Guadeloupe, Plage de Malendure	MT921870	MT921902
	MNHN-IM-2019-1703		MT921871	MT921903
	MNHN-IM-2019-1704		MT921872	MT921904
	MNHN-IM-2019-1705		MT921873	MT921905
	MNHN-IM-2019-1706		MT921874	MT921906
	USNM 1618949	Curaçao, S shore, beach in front of CARMABI research station	MT921875	MT921907
	USNM 1618950		MT921876	MT921908
	USNM 1618951		MT921877	MT921909
	USNM 1618952		MT921878	MT921910
	MNHN-IM-2019-1729	Barbados, Hastings Rocks	MT921879	MT921911
	MNHN-IM-2019-1707		MT921880	MT921912
	MNHN-IM-2019-1708		MT921881	MT921913
	MNHN-IM-2019-1709		MT921882	MT921914
	MNHN-IM-2019-1710		MT921883	MT921915
	MNHN-IM-2019-1711		MT921884	MT921916
	MNHN-IM-2019-1712		MT921885	MT921917
	MNHN-IM-2019-1713		MT921886	MT921918
	MNHN-IM-2019-1714		MT921887	MT921919

Results

Thirty-two individuals from three sites in Guadeloupe, Curaçao and Barbados were sequenced for portions of the COI and 16S mitochondrial genes (Table 1). The concatenated dataset was 1170 bp in length. The best-fit partitioning scheme used distinct models for each locus, with the best-fit model being MGK+F3X4 and HKY+F+G4 for COI and 16S, respectively. The ML tree constructed from the concatenated dataset



**Figure 1.** Phylogenetic tree produced via Maximum Likelihood using a concatenated alignment composed of partial mitochondrial COI and 16S sequences. ML bootstrap values greater than 50 are shown at the nodes. Figured specimens: *Supplanaxis nancyae*, MNHN-IM-2019-1729; *S. planicostatus*, syntype, NHMUK 1966623; *S. nucleus*, neotype, MNHN-IM-2000-35804.

(Fig. 1) resolved two strongly supported clades among what has been traditionally recognized as a single species, *Supplanaxis nucleus*. Individuals collected in syntopy from all three sites occurred in both clades, which differed by 11.6–12.2% uncorrected pairwise sequence divergence in COI, with no geographic structuring among sites. Examination of the shells and radula revealed diagnostic morphological features consistent with the recognition of two species.

## Systematics

### Class GASTROPODA Cuvier, 1795

### Family PLANAXIDAE Gray, 1850

### Genus *Supplanaxis* Thiele, 1929

*Planaxis* (*Supplanaxis*) Thiele, 1929. Type species: *Buccinum nucleus* Bruguière, 1789, by monotypy.

*Planaxis* (*Proplanaxis*) Thiele, 1929. Type species: *Planaxis planicostatus* G.B. Sowerby I, 1825, by monotypy (syn. nov.).

**Remarks.** Thiele (1929: 203) established *Supplanaxis* as a subgenus of *Planaxis*, for planaxids with rather small, dark colored, largely smooth shells, with spiral grooves mostly on the base of the last whorl and under the suture; and with a radula characterized by a broad rachidian with two to four denticles on either side, the long lateral extensions of the lateral teeth, and the outer marginal with a very broad, finely toothed cutting edge. Based on the morphological differences in shell, radula, soft anatomy, and embryonic development, Houbbrick (1987) elevated *Supplanaxis* to full genus.

Thiele (1929: 203) also established *Proplanaxis* as a new subgenus of *Planaxis*, with *Planaxis planicostatus* G.B. Sowerby I, 1825, as type species by monotypy. Houbbrick (1987: 4) treated *Proplanaxis* as a synonym of *Planaxis*, but our molecular tree shows *P. planicostatus* to be nested within the *Supplanaxis* clade (see below), and not within *Planaxis* s.s., a taxonomic position in agreement with Laidre and Vermeij (2012), who had already used the combination *Supplanaxis planicostatus*. The names *Supplanaxis* and *Proplanaxis* having been published simultaneously, we act as First Revisers and, under Art. 24.2 of the ICZN Code, give precedence to the name *Supplanaxis* over *Proplanaxis*.

### *Supplanaxis nucleus* (Bruguière, 1789)

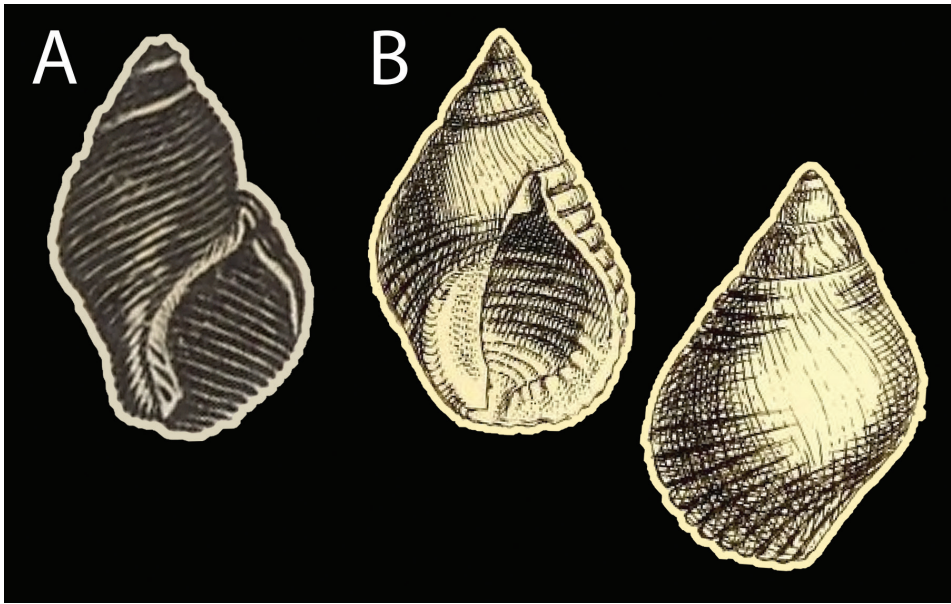
Figs 2, 3A, 4A–G, 5, 7A–L at right

*Buccinum nucleus* Bruguière, 1789: 211–212

*Planaxis semisulcatus* G.B. Sowerby I, 1823: [pl. 73] fig. 3

**Neotype.** BARBADOS • 16.9 mm in height; Hastings Rocks; 13°04'25"N, 59°35'39"W, Dec. 2018; P Bouchet leg.; MNHN-IM-2000-35804, here designated; GenBank: MT921868, MT921900 (Figs 3A, 4D, 7L at right).

Bruguière (1789: 254–255) based his description of *Buccinum nucleus* on three sources: (i) an illustration of a shell from Barbados published by Lister (1770: pl. 976 fig. 32) (Fig. 2A); (ii) specimens collected by himself at Foule-Pointe in Madagascar; (iii) shells used in a decorated garment brought back from New Zealand by Cook.



**Figure 2.** Original figures **A** *Buccinum nucleus* Bruguière, 1789 (Lister 1770: pl. 976, fig. 32) **B** *Planaxis semisulcatus* G.B. Sowerby I, 1823 ([pl. 73], fig. 3).

- (i) The shell from Barbados was accompanied by a non-binominal legend *Buccinum B.r.paruum nigrum, ex toto laeve* and the locality Barb., which was rendered by Bruguière as *Buccinum brevirostrum parvum nigrum extoto laeve Barbádense*. Some of the Lister collection was acquired by Sloane, and the Sloane collection was one of the founding collections of the British Museum (Natural History) [now The Natural History Museum], in London. However, there is no material in NHMUK corresponding to Lister's illustration (Wilkins 1953; and A. Salvador, pers. comm.), and this specimen is to be considered lost.
- (ii) Bruguière was a member of the second expedition (1773–1774) led by Kerguelen to the Subantarctic islands that were later to be called Kerguelen Is. On the return journey, his ship called in February–March 1774 at Foulpointe (or “Foule-Pointe” as spelled by Bruguière), now Mahavalona [district of Toamasina (Tamatave)] on the east coast of Madagascar. It is not known which, if any, natural history collections Bruguière brought back to France. He (Bruguière 1789: 255) used the past tense to refer to the specimens collected at Foul-Pointe “he had owned previously”. Regardless, there are no traces of this material in MNHN.
- (iii) Bruguière additionally recorded *Buccinum nucleus* based on specimens used for decoration on garments brought back by Cook from New Zealand, that Bruguière had seen in the cabinet of Mr Broussonet, then Secretary of the (French) Royal Society of Agriculture. Pierre Marie Auguste Broussonet (1761–1807) was a French scientist who was based in London in 1780, where he met such scientists

as Banks, Forster and Solander. It is therefore possible that Broussonet could have acquired Cook artifacts from this circle and brought them back with him to Paris. He took part in the French Revolution but, as a member of the “Girondins”, had to leave Paris in 1793 and his belongings were seized. However, Broussonet’s artifacts are not nowadays traceable in any French museum where they would have been deposited by the Revolutionary powers. Dr Adrienne Kaeppler, curator for the Pacific Islands in the Department of Anthropology at the Smithsonian’s National Museum of Natural History, has advised us that Maori cloaks from Cook’s voyage to New Zealand are not known to be decorated with shells, and a Tonga or Hawaii provenance for Broussonet’s artifacts would have been more likely.

There are thus no specimens left that could be considered a syntype of *Buccinum nucleus*. The specimens from Madagascar or the Pacific would not have been conspecific with the shell from the Caribbean illustrated by Lister; they might have been *Supplanaxis niger* (Quoy and Gaimard, 1833) (Fig. 3D), which bears a strong resemblance to *S. nucleus*—especially to the eye of an 18<sup>th</sup> century conchologist.

Because the description of *Buccinum nucleus* referred to more than one species, and because the Caribbean species designated under that name is a complex of two cryptic species, it is desirable to stabilize the nomenclature by the fixation of a neotype, which we designate herein.

*Planaxis semisulcatus* G.B. Sowerby I, 1823 (1823: [pl. 73], fig. 3) (Fig. 2B) was described from an unknown locality. It has been treated as a synonym of *Supplanaxis nucleus* since at least Smith (1872: 40), an opinion accepted by Sowerby II (1877: pl. 1, species no. 7; 1884: 177). There is no known type material in NHMUK (A. Salvador, pers. comm.). To stabilize the nomenclature, we are here designating the neotype of *Buccinum nucleus* also as the neotype of *Planaxis semisulcatus*.

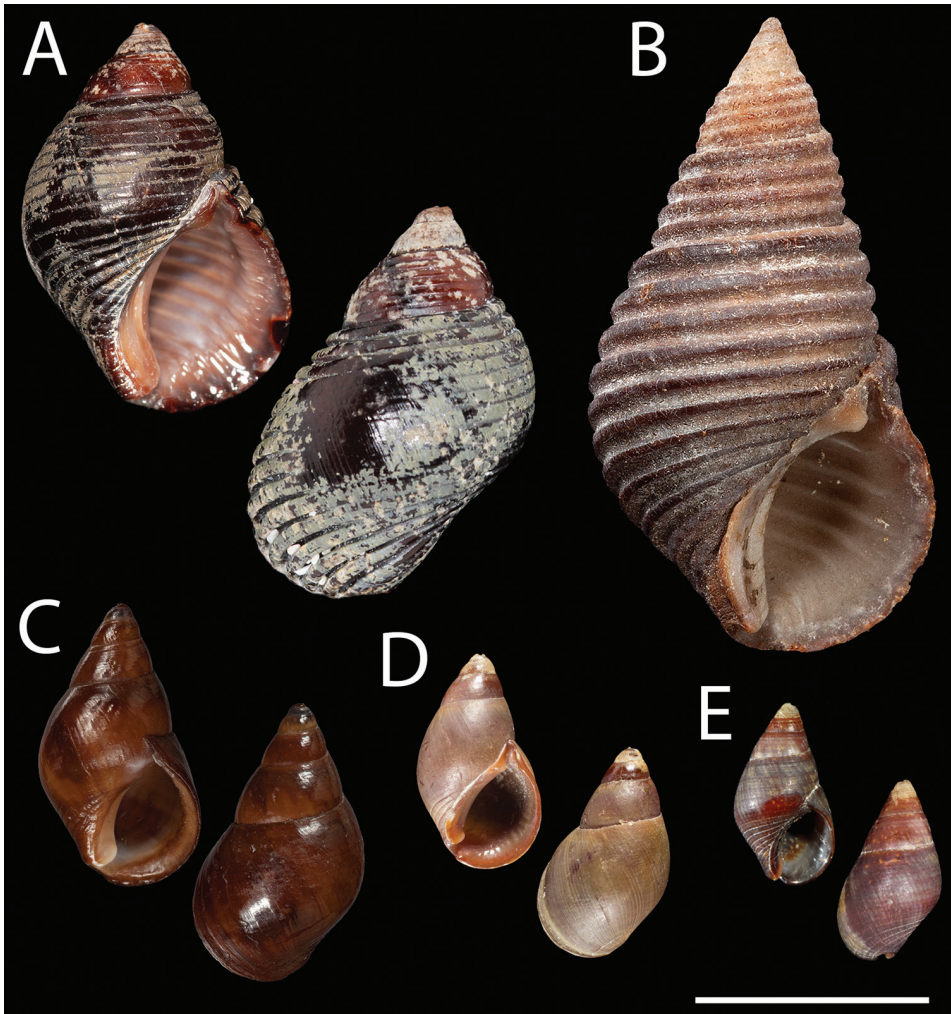
**Other material.** ANTIGUA AND BARBUDA • 1 spm; Antigua, Green Island; [17°04'12"N, 61°40'08"W]; 24 Apr. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; J Clarke leg.; USNM 738725.

BAHAMAS • 1 spm; Rawson leg.; USNM 54705; • 1 spm; New Providence, The Caves; [25°04'10"N, 77°27'02"W]; H Dodge leg.; USNM 603895.

BARBADOS • 1 spm; Hastings Rocks; 13°04'25"N, 59°35'39"W; Nov. 2018; P Bouchet leg.; GenBank: MT921869, MT921901; MNHN-IM-2019-1728.

BELIZE • 2 spms; Near Carrie Bow Cay; 27 Apr. 72; CCRE - Caribbean Coral Reef Ecosystems, Belize; RS Houbrick leg.; reef flat on algal covered rocks along shore; USNM 770861; • 18 spms; Carrie Bow Cay, NE Cay, Glover’s Reef; 15 Aug. 1973; CCRE - Caribbean Coral Reef Ecosystems, Belize; RS Houbrick leg.; intertidal on rocks; USNM 771083; • 5 spms; Carrie Bow Cay; depth 0.5 m; 12 Jan. 1976; CCRE - Caribbean Coral Reef Ecosystems, Belize; windward, reef crest, reef flat; USNM 828774.

BRITISH VIRGIN ISLANDS • 1 spm; Tortola, Newman Island, Treasure Point; 6 Apr. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; shore coll.; USNM 683319; • 1 spm; Guana Island, White Bay; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; W Schmitt leg.; from reefs in cove; USNM 735906.



**Figure 3.** Type specimens of *Supplanaxis nucleus* and relevant planaxids. **A** *Buccinum nucleus* Bruguière, 1789. Neotype, MNHN-IM-2000-35804 **B** *Planaxis planicostatus* G.B. Sowerby I, 1825. Syntype NHMUK 1966623 (© The Trustees of the Natural History Museum, London, <http://creativecommons.org/licenses/by/4.0/>; <https://data.nhm.ac.uk/object/4767541c-a5d1-41db-aa0c-0c03724e970a>) **C** *Planaxis* (*Supplanaxis*) *nancyae* Petuch, 2013. Holotype, FMNH 328402 (© Field Museum of Natural History—CC BY-NC; <https://collections-zoology.fieldmuseum.org/catalogue/2877223>) **D** *Planaxis niger* Quoy and Gaimard, 1833. Syntype, one of 22 specimens, MNHN-IM-2000-27769 **E** *Planaxis nucleola* Mörch, 1876. Probable holotype, ZMK 152749. Scale bar: 1 cm.

COLOMBIA • 3 spms; Cartagena; Chamberlain leg.; USNM 131448; • 1 spm; Vicinity of Cartagena; JA Link leg.; USNM 364399; • 1 spm; NE of Santa Marta; 12 Oct. 1977; M Jones leg.; assoc. with flat intertidal and barely subtidal rocks; USNM 770120.

COSTA RICA • 22 spms; Limón Province, Portete; 11 Jul. 1966; RS Houbriek leg.; common on rocks; USNM 702828; • 14 spms; Limón Province, Playa Bonita;

10 Mar. 1965; RS Houbbrick leg.; on rocks, low tide; USNM 702839; • 1 spm; Limón Province, Cahuita, Portete; 13 Jul. 1964; D Hucklebey leg.; USNM 702859; • 19 spms; Limón Province, Portete; 11 Jul. 1966; RS Houbbrick leg.; USNM 706451.

CUBA • 1 spm; Guantanamo, Cable House; Tomas Barrera Expedition; Schooner Tomas Barrera; J Henderson and P Bartsch leg.; shore; USNM 450605; • 3 spms; Cardenas, Peninsula de Hicacos; V Conde leg.; USNM 599927; • 2 spms; Punta de Maya, in front of lighthouse; 13 Nov. 80; Cuba Expedition 1980; J Rosewater leg.; dogtooth coral; USNM 803412; • 1 spm; Veradero, La Conchito; 14 Nov. 80; Cuba Expedition 1980; J Rosewater leg.; USNM 803413; • 1 spm; Cojimar; 15 Nov. 80; J Rosewater leg.; USNM 807614.

CURAÇAO • 1 spm; S shore, beach in front of CARMABI research station; 12°07'20"N, 68°58'08"W; 18 May 2015; E Strong leg.; among cobbles; GenBank: MT921864, MT921896; USNM 1618953; • 1 spm; *ibid*; GenBank: MT921865, MT921897; USNM 1618954; • 1 spm; *ibid*; GenBank: MT921866, MT921898; USNM 1618955; • 1 spm; *ibid*; GenBank: MT921867, MT921899; USNM 1618956.

DOMINICAN REPUBLIC • 2 spms; Oro Oro Beach [*sic*, possibly Playa Dorada], S. shore; [19°46'27"N, 70°38'30"W]; H Dodge leg.; USNM 603900.

GUADELOUPE • 1 spm; Aug. 1946; on rocks; USNM 487939; • 1 spm; Plage de Malendure; 16°10'28"N, 61°46'47"W; 7 May 2012; KARUBENTHOS Expedition stn. GM7; GenBank: MT921856, MT921888; MNHN-IM-2009-26685; • 1 spm; *ibid*; GenBank: MT921857, MT921889; MNHN-IM-2009-26686; • 1 spm; *ibid*; GenBank: MT921858, MT921890; MNHN-IM-2009-26687; • 1 spm; *ibid*; GenBank: MT921859, MT921891; MNHN-IM-2009-26688; • 1 spm; Plage de Malendure; 16°10'28"N, 61°46'47"W; 1 Apr. 2017; D Lamy leg.; GenBank: MT921860, MT921892; MNHN-IM-2019-1715; • 1 spm; *ibid*; GenBank: MT921861, MT921893; MNHN-IM-2019-1716; • 1 spm; *ibid*; GenBank: MT921862, MT921894; MNHN-IM-2019-1717; • 1 spm; *ibid*; GenBank: MT921863, MT921895; MNHN-IM-2019-1718.

HAITI • 130 spms; Orcutt leg.; USNM 383065; • 6 spms; Anse à Cochons; R/V Eolis; J Henderson leg.; shore; USNM 434880; • 150 spms; Département de l'Ouest, Saltron; Orcutt leg.; USNM 439970; • 11 spms; Département du Sud, Port-Salut; Orcutt leg.; USNM 440004; • 2 spms; Forban; A Curtiss leg.; USNM 518264.

HONDURAS • 26 spms; Swan Island; Townsend leg.; USNM 83649; • 41 spms; Utila Island; [16°05'47"N, 86°55'44"W]; Simpson leg.; USNM 434879; • 2 spms; Webb leg.; USNM 434885.

JAMAICA • 28 spms; St. Thomas, Morant Bay; Orcutt leg.; USNM 401450; • 4 spms; Pt. Antonio; CWJ leg.; USNM 434882; • 24 spms; Annotta Bay; Orcutt leg.; USNM 440695; • 17 spms; Portland, Port Antonio; Orcutt leg.; USNM 440864; • 15 spms; Portland, near Buff Bay; Orcutt leg.; USNM 441213; • 2 spms; Montego Bay; Mrs LS McLean leg.; USNM 464162; • 8 spms; Portland, Port Antonio; Vendeyes, Orcutt leg.; USNM 518050; • 1 spm; Montego Bay Area, Doctor's Cave Pier; 26 Nov. 1976; Paul and Sharon Greenhall leg.; USNM 767665; • 6 spms; St. Mary, 2 mi. N Port Maria; 18°24'19"N, 76°53'18"W; JI McCurkin leg.; 1 ft above splash line under cobbles; USNM 770590.

MEXICO • 79 spms; Quintana Roo, Mujeres Island, 0.5 mi. S of village; 29 Mar. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; E Bousfield, H Rehder and W Schmitt leg.; rocky open ocean shore; USNM 662233; • 27 spms; Cozumel, 1 mi. N of San Miguel, in front of Cabanas del Caribe property; [20°31'59"N, 86°56'21"W]; 3 Apr. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; H Rehder, W Schmitt and E Bousfield leg.; on rocks from above high tide to below water line; USNM 662773; • 3 spms; 100 km. SSE Tampico, Lobos Reef; depth 0-6 ft; 5 Jun. 1973; JW Tunnell leg.; coral spoil, along ship channel; USNM 710350; • 4 spms; Quintana Roo, Cozumel Island, San Miguel, along shore 0.25 NE of pier; 29 Apr. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; W Schmitt leg.; on rocks; USNM 736539; • 1 spm; Quintana Roo Ids., Cozumel, N Pt., nr. Lighthouse; depth 6 ft; 9 Apr. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; H Rehder and E Bousfield leg.; coral rocks, splash pools; USNM 736750.

MONTSERRAT • 3 spms; Fox Bay, just N of Plymouth; 20 Apr. 1959; Smithsonian - Bredin Caribbean Expedition; R/V Caribee; black sand beach; USNM 682493.

NETHERLANDS ANTILLES • 6 spms; St. Martin; Ford leg.; USNM 434878.

PANAMA • 4 spms; Colón; Stearns leg.; USNM 54700; • 10 spms; San Blas; TG Thompson leg.; USNM 597416; • 33 spms; Puerto Perme, NW of Cape Tiburon; [8°44'13"N, 77°32'41"W]; 14 Mar. 1953; RH Stewart leg.; USNM 664216; • 11 spms; 3rd cove SW of Buenaventura; 19 Apr. 1971; Smithsonian STRI Panama Survey; on cobbles on cobble beach with coral heads and tide pools; USNM 732810; • 30 spms; 1.7 km WSW of Portobelo, on bay side of Coral Pt.; 11 Nov. 1971; Smithsonian STRI Panama Survey; large cobbles, boulders; USNM 734007; • 1 spm; 1.7 km WSW of Portobelo, on bay side of Coral Pt.; 11 Nov. 1971; Smithsonian STRI Panama Survey; fauna assoc. with rocks; USNM 734020; • 1 spm; Canal Zone, Ft. Sherman, Toro Pt., outside base of jetty; 13 Nov. 1971; Smithsonian STRI Panama Survey; under cobbles; USNM 734070; • 5 spms; Canal Zone, Galeta Island; 23 Apr. 1972; Smithsonian STRI Panama Survey; varied habitat; USNM 734717; • 1 spm; Canal Zone, Ft. Sherman, Punta De Toro; 25 Apr. 1972; Smithsonian STRI Panama Survey; *Thalassia* and hard limestone substrate with potholes; USNM 734763; • 1 spm; Canal Zone, Gatun Locks, lower W chamber; Intertidal; 20 Mar. 1972; Smithsonian STRI Panama Survey; at water edge outside of casson; USNM 742409; • 5 spms; San Blas, Pico Feo; 8 Nov. 1972; Smithsonian STRI Panama Survey; USNM 743277.

PUERTO RICO • 11 spms; Fajardo; 10 Dec. 1951; J Weber leg.; USNM 663091; • 3 spms; USNM 1291138.

ST. VINCENT AND THE GRENADINES • 6 spms; St. Vincent; Chamberlain leg.; USNM 131804.

TRINIDAD AND TOBAGO • 1 spm; Trinidad, Chaguaramas Bay; SP Archino leg.; USNM 518500; • 5 spms; Trinidad, N.A.S., Macqueripe Beach; CI Aslaksan leg.; USNM 608788; • 1 spm; Tobago; 5 Nov. 1953; J Weber leg.; USNM 663352; • 2 spms; Tobago, Buccoo Reef; 5 Apr. 1959; Smithsonian - Bredin Caribbean Expedition; R/V Caribee; USNM 682203.

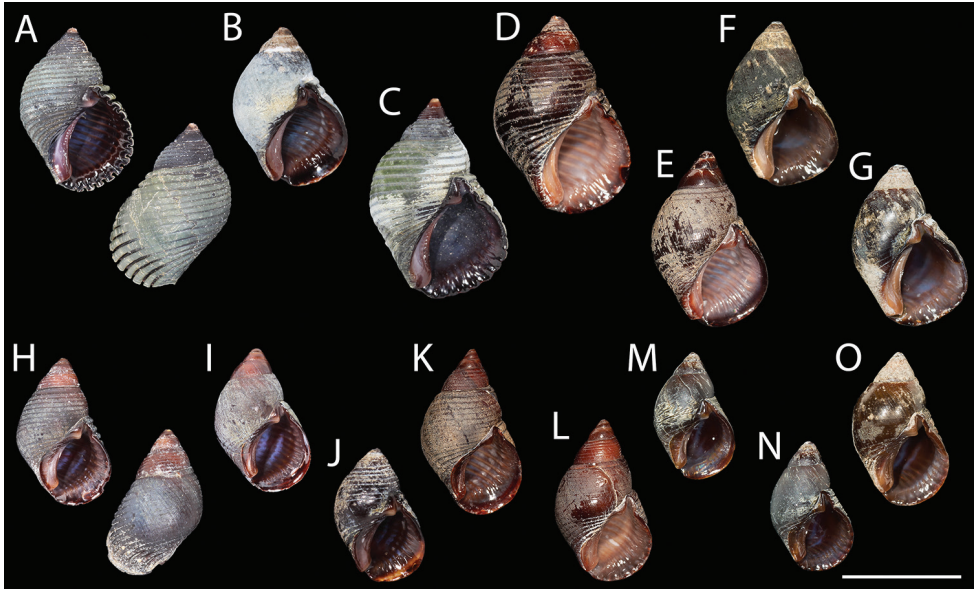
U.S. VIRGIN ISLANDS • 3 spms; St. Thomas; CB Adams leg.; USNM 6419; • 213 spms; St. Thomas, edge Magens Bay; Shoemaker leg.; rocks; USNM 214816; • 3 spms; Water Island, Drift Bay; Shoemaker leg.; USNM 214882; • 5 spms; St. Thomas; M Petit leg.; USNM 250143; • 143 spms; St. Thomas; Petit leg.; USNM 530351; • 2 spms; St. Croix; 10 Sep. 1956; J Weber leg.; USNM 663480; • 5 spms; St. Thomas, S side Carreen Hill; M Jones leg.; rocky intertidal; USNM 666124; • 1 spm; St. Thomas, S end Magens Bay; M Jones leg.; rocks adjacent to beach; USNM 666146; • 58 spms; St. Thomas, S end Magens Bay; M Jones leg.; rocks adjacent to beach; USNM 666148; • 2 spms; St. John, Francis Bay, McCauley beach; 28 Mar. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; from rocks; USNM 683466; • 2 spms; St. Croix; W Old leg.; USNM 714103; • 11 spms; St. John, Caneel Bay; [18°20'34"N, 64°47'13"W]; 25 Mar. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; C Shuster and J Finlay leg.; USNM 738775.

UNITED STATES • 6 spms; Miami; Offer leg.; USNM 159423; • 2 spms; Palm Beach Inlet; Ted Bayer leg.; under jetty rocks; USNM 513679; • 1 spm; Tortugas, S of Long Key; USNM 780137; • 27 spms; Miami Beach, South Beach, jetty at inlet; 21 Apr. 82; RS Houbrick leg.; in rubble at intertidal zone; USNM 809779; • 30 spms; Miami Beach, S Miami Beach, jetties; 16 Mar. 83; RS Houbrick leg.; intertidal, on and under rocks.; USNM 809780; • 4 spms; Miami Beach, South Beach, at jetty; [25°45'48"N, 80°07'45"W]; 12 Aug. 84; RS Houbrick leg.; intertidal rock and boulders; USNM 842270; • 18 spms; Miami Beach, South Beach, at jetty; [25°45'48"N, 80°07'45"W]; 5 Sep. 83; RS Houbrick leg.; among intertidal boulders, high tide mark; USNM 842271; • 12 spms; Miami Beach, South Beach, at jetty; [25°45'48"N, 80°07'45"W]; 20 Nov. 83; RS Houbrick leg.; intertidal, on rocks and boulders; USNM 842272; • 20 spms; South Miami Beach; 16 Jan. 1984; RS Houbrick leg.; USNM 858456; • 17 spms; Palm Beach Inlet, South jetty; 14 Jan. 39; F Bayer leg.; under stones; USNM 889605; • 14 spms; offshore rocks off south central edge of Boca Chica Key; 26 Feb. 1975; P Poland leg.; under intertidal rocks near low water mark; USNM 1446615.

VENEZUELA • 31 spms; Macuto; Lyon and Robinson leg.; rocks along shore; USNM 170221; • 6 spms; Sucre, Pena, Manacuare; Arnold leg.; USNM 252635.

**Description.** *Shell.* Shell (Figs 3A, 4A–G, 7A–L at right) large for the genus, solid, littoriniform, medium high-spined, consisting of 5+ (apex generally broken or corroded in adults) moderately convex whorls separated by impressed suture, last whorl occupying ca 75–82% of total shell height. Shell surface usually covered with 15–17 even, deeply incised spiral grooves extending over all shell height, especially well marked adapically and on base behind outer lip. Aperture ovoid, expanding abaxially at mid-height, occupying ca 50% of total shell height, with 7–10 sharp internal lirae, columellar pillar extending almost to the abapical point of the aperture, delimiting a narrow siphonal notch, callus adpressed to parietal and columellar areas, parietal tooth strong, blunt. *Color* uniformly reddish brown to dark violet, parietal tooth and columellar callus orange violet. *Height* 11–18 mm.

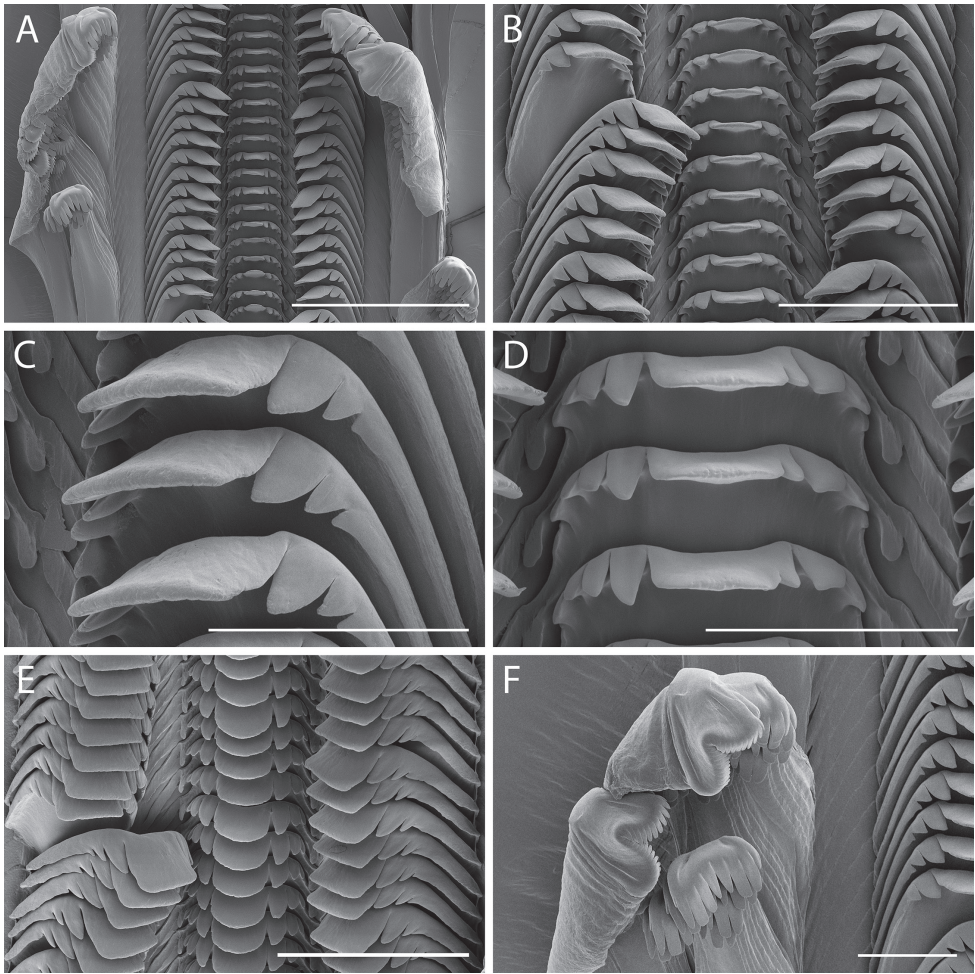
*Neotype* (Figs 3A, 4D, 7L at right) reddish brown, with weak parietal tooth, height 16.9 mm.



**Figure 4.** Shell morphology of *Supplanaxis* from the Caribbean. Sequenced vouchers **A–G** *S. nucleus* **H–O** *S. nancyae* **A–C** Guadeloupe, Plage de Malendure **A** MNHN-IM-2019-1716 **B** MNHN-IM-2009-26686 **C** MNHN-IM-2009-26687 **D–E** Barbados, Hastings Rocks. **D** Neotype, MNHN-IM-2000-35804 **E** MNHN-IM-2019-1728 **F–G** Curaçao, S shore, beach in front of CARMABI research station **F** USNM 1618956 **G** USNM 1618953 **H–J** Guadeloupe, Plage de Malendure **H** MNHN-IM-2019-1703 **I** MNHN-IM-2019-1704 **J** IM MNHN-2009-26684 **K–L** Barbados, Hastings Rocks **K** MNHN-IM-2019-1729 **L** MNHN-IM-2019-1711 **M–O** Curaçao, S shore, beach in front of CARMABI research station **M** USNM 1618949 **N** USNM 1618951 **O** USNM 1618952. Scale bar: 1 cm.

*Radula*. Radula taenioglossate (Fig. 5A). Rachidian pentagonal, with broad basal plate, long basolateral extensions, and short, rounded, median basal projection (Fig. 5B, D). Upper lateral part of basal plate with narrowly rectangular basal denticle. Rachidian cutting edge broad, comprising two-thirds width of tooth. Cutting edge shallowly and smoothly concave with large, squarish, spatulate median cusp, flanked by three to four smaller pointed denticles on each side. Lateral tooth with broad, high basal plate with central supporting ridge, rounded margins, and long lateral basal extension (Fig. 5C). Cutting edge broad with large, squarish, central cusp flanked by three to four inner and two to three sharp outer denticles. Marginal teeth elongate with curved paw-like tips (Fig. 5A, F). Inner marginal tooth with narrow flange along length of shaft outer edge, and with concave, rake-like tip with nine to ten rounded denticles. Outer marginal tooth with broad, membranous flange along distal outer edge, and with broad, bilobed tip bearing approximately 28 to 30 small, rounded denticles.

**Distribution and ecology.** Throughout the Caribbean in high energy, intertidal environments, on hard substrates, from large boulders to small cobbles and pebbles, in populations of moderate to large size (Vermeij 1973; Bandel 1976; Houbrick 1987). Its range extends from Palm Beach Inlet, Florida, in the north, to the northern coast



**Figure 5.** Radular morphology of *Supplanaxis nucleus* (MNHN-IM-2019-1716) **A** Radular ribbon **B** Rachidian and lateral teeth **C** Detail of lateral teeth **D** Detail of rachidian **E** Rachidian and lateral teeth viewed at a  $\sim 45^\circ$  angle from above, showing detail of cutting edge. **F** Internal and external lateral teeth. Scale bars: 200  $\mu\text{m}$  (**A**), 100  $\mu\text{m}$  (**B**, **E**), 50  $\mu\text{m}$  (**C**, **D**, **F**).

of South America, from Veracruz, Mexico in the west (Tunnell 1974) and as far east as Trinidad and Tobago off Venezuela, including the Gulf of Mexico, Caribbean Sea and the Antillean Arc (Fig. 7). It is “rare” in Bermuda (Sterrer and Schoepfer-Sterrer 1986: 413), which may indicate that it only forms pseudopopulations there, and is absent from the Guyanas and Brazil.

**Remarks.** It is evident, from the morphology of the rachidian, that the radular descriptions of Troschel (1858: pl. 12, fig. 9A–D), Houbrick (1987: fig. 18A–E) and Simone (2001: fig. 88) were based on *S. nucleus*. Houbrick (1987: figs 19A, B, 20A–I, 21A–G, 22A–F) described the external anatomy and gross morphology of the mantle cavity, alimentary tract, and excretory, reproductive and nervous systems based on

specimens from the same lot that yielded the radula (USNM 809780). Examination of the shells from this lot confirmed them all to be *S. nucleus*, although other lots collected from the same site at subsequent occasions comprised mixtures of the two species. Simone (2001: figs 56, 74, 88, 189–206) also provided a detailed description of the anatomy based on material obtained from several sites in Venezuela. The figured shells (figs 17–19) are *S. nucleus*, but both species occur in Venezuela and it is possible the anatomical descriptions are composite.

Despite its abundance in modern-day Caribbean faunas, *Supplanaxis nucleus* is surprisingly recorded as a fossil only in the Upper Pleistocene of Venezuela (Weisbord 1962: 168, pl. 14, figs 17, 18; and B. Landau, pers. comm.). It is not known from the well-preserved horizons of Florida.

***Supplanaxis nancyae* (Petuch, 2013) comb. nov.**

Figs 3C, 4H–O, 6, 7A–L at left

*Planaxis* (*Supplanaxis*) *nancyae* Petuch, 2013: 193, fig. 6.13A, B

**Holotype.** HAITI • 11 mm in height; off southern Gonave Island; depth 2 m; under rocks; FMNH 328402 (Fig. 3C)

**Other material.** ANGUILLA • 6 spms; 29 Apr. 1958; Smithsonian - Bredin Caribbean Expedition; USNM 738885?

ANTIGUA AND BARBUDA • 9 spms; Antigua, Shell Beach; CI Aslaksen leg.; USNM 608782; • 2 spms; Antigua, Nonsuch Bay, N side of Bird Island; depth 4 ft; 24 Apr. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; shore coll.; USNM 683510; • 21 spms; Redonda Island, lee side; 10 Apr. 1956; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; W Schmitt leg.; wave washed rocks; USNM 714035; • 67 spms; Antigua, Green Island; [17°04'12"N, 61°40'08"W]; 24 Apr. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; J Clarke leg.; USNM 1620283 (ex USNM 738725).

BAHAMAS • 5 spms; Rawson leg.; USNM 1620260 (ex USNM 54705); • 2 spms; New Providence, The Caves; [25°04'10"N, 77°27'02"W]; H Dodge leg.; USNM 1620274 (ex USNM 603895).

BARBADOS • 1 spm; USNM 19768; • 1 spm; EW Williams, CB Lungren leg.; USNM 341803; • 4 spms; beach; USNM 459982; • 32 spms; off Needham Pt.; low tide; USNM 459983; • 1 spm; Hastings Rocks; 13°04'25"N, 59°35'39"W; Nov. 2018; P Bouchet leg.; GenBank: MT921879, MT921911; MNHN-IM-2019-1729; • 1 spm; *ibid*; GenBank: MT921880, MT921912; MNHN-IM-2019-1707; • 1 spm; *ibid*; GenBank: MT921881, MT921913; MNHN-IM-2019-1708; • 1 spm; *ibid*; GenBank: MT921882, MT921914; MNHN-IM-2019-1709; • 1 spm; *ibid*; GenBank: MT921883, MT921915; MNHN-IM-2019-1710; • 1 spm; *ibid*; GenBank: MT921884, MT921916; MNHN-IM-2019-1711; • 1 spm; *ibid*; GenBank: MT921885, MT921917; MNHN-IM-2019-1712; • 1 spm; *ibid*; Gen-

Bank: MT921886, MT921918; MNHN-IM-2019-1713; • 1 spm; *ibid*; GenBank: MT921887, MT921919; MNHN-IM-2019-1714.

BELIZE • 4 spms; Carrie Bow Cay, NE Cay, Glover's Reef; 15 Aug. 1973; CCRE - Caribbean Coral Reef Ecosystems, Belize; RS Houbrick leg.; intertidal on rocks; USNM 1620286 (ex USNM 771083).

BRITISH VIRGIN ISLANDS • 5 spms; Tortola; Kjaer leg.; USNM 6488; • 4 spms; Jost Van Dyke Island, Little Harbour; Apr. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; shore coll.; USNM 683404.

COLOMBIA • 4 spms; New Grenada, Sabanilla; USNM 103165; • 11 spms; "Albatross", Sabanilla; USNM 193614; • 7 spms; New Grenada, Sabanilla; USNM 224969.

CURAÇAO • 5 spms; Slangenbaai; 1 Dec. 1971; KB Meyer leg.; on rocks just above tide; USNM 702302; • 1 spm; Willemstad; 23 Jun. 1925; J Eldred leg.; tide pools just above high tide; USNM 889594; • 1 spm; Willemstad; 23 Jun. 1925; J Eldred leg.; tide pools just above high tide; USNM 889598; • 1 spm; S shore, beach in front of CARMABI research station; 12°07'20"N, 68°58'08"W; 18 May 2015; E Strong leg.; among cobbles; GenBank: MT921875, MT921907; USNM 1618949; • 1 spm; *ibid*; GenBank: MT921876, MT921908; USNM 1618950; • 1 spm; *ibid*; GenBank: MT921877, MT921909; USNM 1618951; • 1 spm; *ibid*; GenBank: MT921878, MT921910; USNM 1618952.

DOMINICA • 11 spms; Marigot; RG Fennah leg.; USNM 513253; • 3 spms; Scotts Head, windward coast; 27 Feb. 1966; Manning and Hobbs leg.; among rocks above or at high tide level; USNM 678753; • 1 spm; Prince Rupert Bayat Cabrits; 9 Mar. 1966; Hobbs and Manning leg.; rocky; USNM 678763; • 1 spm; W of Portsmouth; 19 Apr. 1939; Smithsonian - Bredin Caribbean Expedition; Nicholson, et al leg.; among boulders and off shingle beach; USNM 682469; • 81 spms; Berekua; 8 Feb. 1965; Smithsonian - Bredin Caribbean Expedition; WW Wirth leg.; on rocks on beach; USNM 709072.

DOMINICAN REPUBLIC • 1 spm; Oro Oro Beach [sic, possibly Playa Dorada], S. shore; [19°46'27"N, 70°38'30"W]; H Dodge leg.; USNM 1620275 (ex USNM 603900).

GRENADA • 5 spms; Saline Point; 14 Mar. 1956; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; W Schmitt and F Chace leg.; USNM 714033.

GUADELOUPE • 46 spms; Aug. 1946; on rocks; USNM 1620270 (ex USNM 487939); • 1 spm; Plage de Malendure; 16°10'28"N, 61°46'47"W; 7 May 2012; KARUBENTHOS Expedition stn. GM7; GenBank: MT921870, MT921902; MNHN-IM-2009-26684; • 1 spm; Plage de Malendure; 16°10'28"N, 61°46'47"W; 1 Apr. 2017; D Lamy leg.; GenBank: MT921871, MT921903; MNHN-IM-2019-1703; • 1 spm; *ibid*; GenBank: MT921872, MT921904; MNHN-IM-2019-1704; • 1 spm; *ibid*; GenBank: MT921873, MT921905; MNHN-IM-2019-1705; • 1 spm; *ibid*; GenBank: MT921874, MT921906; MNHN-IM-2019-1706.

HAITI • 3 spms; Orcutt leg.; USNM 1620262 (ex USNM 383065); • 166 spms; Département de l'Ouest, Saltron; Orcutt leg.; USNM 1620267 (ex USNM 439970); • 6 spms; Département du Sud, Port-Salut; Orcutt leg.; USNM 1620268 (ex USNM 440004).

HONDURAS • 34 spms; Utila Island; [16°05'47"N, 86°55'44"W]; Simpson leg.; USNM 1620264 (ex USNM 434879); • 1 spm; Webb leg.; USNM 1620266 (ex USNM 434885).

JAMAICA • 1 spm; St. Mary, Markham Hill; Orcutt leg.; USNM 377918; • 1 spm; Pt. Antonio; CWJ leg.; USNM 1620265 (ex USNM 434882); • 4 spms; Portland, near Buff Bay; Orcutt leg.; USNM 1620269 (ex USNM 441213); • 1 spm; Portland, Port Antonio; Vendeyes, Orcutt leg.; USNM 1620271 (ex USNM 518050); • 8 spms; St. Mary, 2 mi. N Port Maria; 18°24'19"N, 76°53'18"W; JI McCurkin leg.; 1 ft above splash line under cobbles; USNM 1620285 (ex USNM 770590).

MEXICO • 2 spms; Quintana Roo, Mujeres Island, Naval Station; 29 Mar. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; W Schmitt leg.; USNM 662200; • 2 spms; Cozumel, 1 mi. N of San Miguel, in front of Cabanas del Caribe property; [20°31'59"N, 86°56'21"W]; 3 Apr. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; H Rehder, W Schmitt and E Bousfield leg.; on rocks from above high tide to below water line; USNM 1620276 (ex USNM 662773); • 1 spm; Quintana Roo, Cozumel Island; 9 Apr. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; H Rehder and E Bousfield leg.; splash pool high up; USNM 735218; • 1 spm; Quintana Roo, Ascension Bay, Suliman Pt. to 300 yds. to SW shore; 19 Apr. 1960; Smithsonian - Bredin Caribbean Expedition; R/V Blue Goose; W Schmitt, F Daiber, E Bousfield, J Clarke, H Rehder, Haynes and Harvey leg.; reef to sand flats; USNM 736379.

MONTSERRAT • 24 spms; Fox Bay, just N of Plymouth; 20 Apr. 1959; Smithsonian - Bredin Caribbean Expedition; R/V Caribee; black sand beach; USNM 1620281 (ex USNM 682493).

NETHERLANDS ANTILLES • 12 spms; St. Martin; Ford leg.; USNM 1620263 (ex USNM 434878).

PANAMA • 1 spm; San Blas; TG Thompson leg.; USNM 1620273 (ex USNM 597416); • 3 spms; Puerto Perme, NW of Cape Tiburon; [8°44'13"N, 77°32'41"W]; 14 Mar. 1953; RH Stewart leg.; USNM 1620279 (ex USNM 664216).

PUERTO RICO • 1 spm; Culebra, Ensenada Honda; USNM 161343; • 15 spms; E of Guanica, Tamarindo Beach; 23 Feb. 1958; GL Warmke leg.; under rocks; USNM 655599; • 2 spms; Fajardo; 10 Dec. 1951; J Weber leg.; USNM 1620277 (ex USNM 663091).

ST. LUCIA • 3 spms; Pigeon Island, N of Pigeon Island Club; 15 Apr. 1959; Smithsonian - Bredin Caribbean Expedition; R/V Caribee; sand and boulder flats around breakwater; USNM 682400.

ST. VINCENT AND THE GRENADINES • 9 spms; St. Vincent; Chamberlain leg.; USNM 1620261 (ex USNM 131804).

U.S. VIRGIN ISLANDS • 3 spms; St. Thomas; CB Adams leg.; USNM 1620259 (ex USNM 6419); • 1 spm; St. Croix; Helen F Dunn leg.; USNM 363994; • 9 spms; St. Croix, Davies Bay; Jan. 1936; HA Beatty leg.; from rocks; USNM 423961; • 12 spms; St. Thomas; Petit leg.; USNM 1620272 (ex USNM 530351); • 2 spms; St. Thomas, S end Magens Bay; M Jones leg.; rocks adjacent to beach; USNM 1620280

(ex USNM 666148); • 4 spms; St. John, Caneel Bay; [18°20'34"N, 64°47'13"W]; 25 Mar. 1958; Smithsonian - Bredin Caribbean Expedition; R/V Freelance; C Shuster and J Finlay leg.; USNM 1620284 (ex USNM 738775).

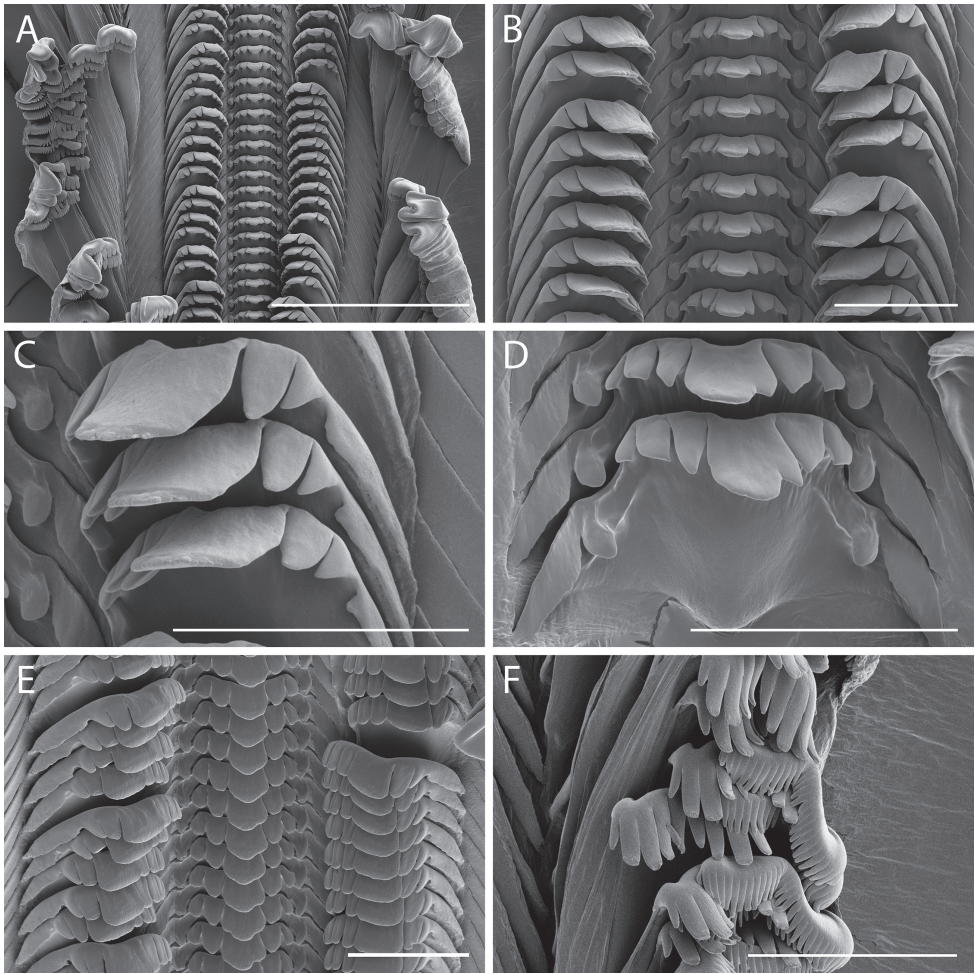
UNITED STATES • 2 spms; Miami Beach, South Beach, at jetty; [25°45'48"N, 80°07'45"W]; 12 Aug. 84; RS Houbrick leg.; intertidal rock and boulders; USNM 1620287 (ex USNM 842270); • 5 spms; Miami Beach, South Beach, at jetty; [25°45'48"N, 80°07'45"W]; 20 Nov. 83; RS Houbrick leg.; intertidal, on rocks and boulders; USNM 1620288 (ex USNM 842272); • 2 spms; South Miami Beach; 16 Jan. 1984; RS Houbrick leg.; USNM 1620289 (ex USNM 858456).

VENEZUELA • 5 spms; Cubagua Island; WL Schmidt leg.; low cliffs just back of sand beach; USNM 604065; • 1 spm; La Orchila Island; Sep. 1950; S Arias-Carbonell leg.; USNM 656012.

**Description.** *Shell.* Shell (Figs 3C, 4H–O, 7A–L at left) medium-sized for the genus, solid, littoriniform, high-spired, consisting of 5+ (apex generally broken or corroded in adults) weakly convex whorls separated by impressed suture, last whorl occupying ca 75–80% of total shell height. Shell surface rarely smooth, usually covered with 15–17 even, incised spiral grooves extending over all shell height, especially well marked on base. Aperture ovoid, occupying ca 50% of total shell height, with or without sharp internal lirae, 7–11 in number, outer lip regularly convex, columellar pillar truncated above broad siphonal notch, callus adpressed to parietal and columellar areas, particularly expanded adapically, its outer edge thickened and slightly raised, parietal tooth strong, blunt. *Color* uniformly reddish brown to dark violet, parietal tooth and columellar callus often lighter. *Height* 11–13.5 mm.

*Radula.* Radula taenioglossate (Fig. 6A). Rachidian pentagonal, with broad basal plate, long basolateral extensions, and short, rounded, median basal projection (Fig. 6B, D). Upper lateral part of basal plate with robust, rounded basal denticle. Rachidian cutting edge rather narrow, comprising one-half width of tooth, but thick and heavily buttressed. Cutting edge sharply concave at midline, with narrowly rectangular, pointed median cusp, flanked by two to four smaller, robust, pointed denticles on each side. Lateral tooth with broad, high basal plate with central supporting ridge, rounded margins, and long lateral basal extension (Fig. 6C). Cutting edge broad with large, squarish, central cusp flanked by three to four inner and two to three sharp outer denticles. Marginal teeth elongate with curved paw-like tips (Fig. 6A, F). Inner marginal tooth with narrow flange along length of shaft outer edge, and with concave, rake-like tip with nine to ten rounded denticles. Outer marginal tooth with broad, membranous flange along distal outer edge, and with broad, bilobed tip bearing approximately 32 to 34 small, rounded denticles.

**Distribution and ecology.** The range of *Supplanaxis nancyae* extends from Miami Beach, Florida, in the north, to the northern coast of South America, from Veracruz, Mexico in the west (Tunnell 1974) and as far east as Trinidad and Tobago off Venezuela, including the Gulf of Mexico, Caribbean Sea and the Antillean Arc (Fig. 7). This species can occur in syntopy with *Supplanaxis nucleus* (Fig. 8) and museum lots across its range may comprise mixtures of the two species; ~ 30% of museum lots in the USNM with more than a single specimen included both species. Guadeloupe

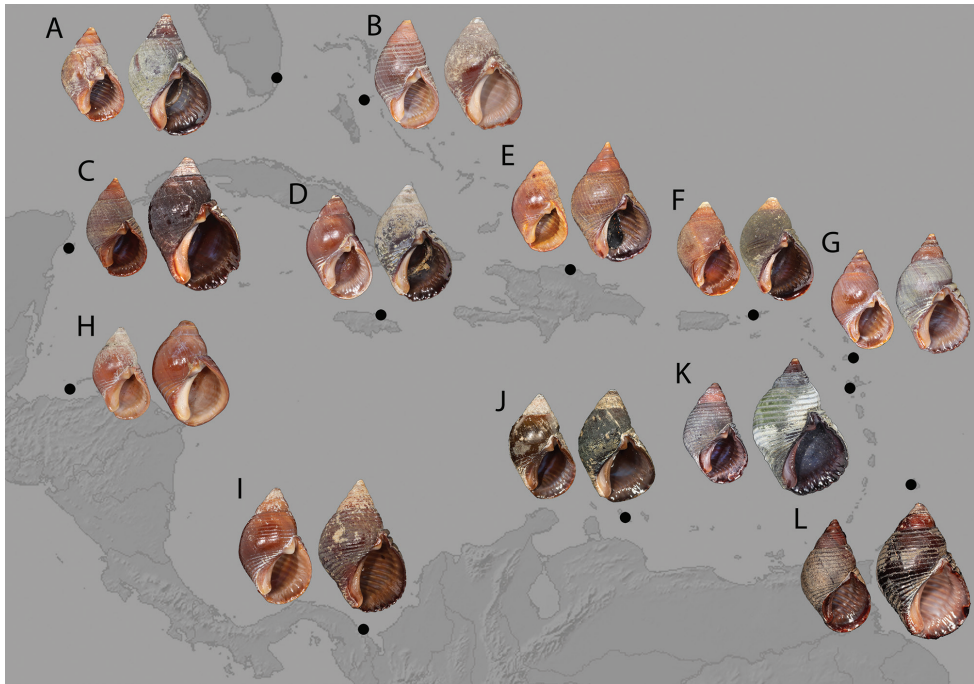


**Figure 6.** Radular morphology of *Supplanaxis nancyae* (MNHN-IM-2019-1703, except as noted) **A** Radular ribbon **B** Rachidian and lateral teeth **C** Detail of lateral teeth **D** Detail of rachidian. Note fusion of innermost denticle with central cusp **E** Rachidian and lateral teeth viewed at a  $\sim 45^\circ$  angle from above, showing detail of cutting edge **F** Internal and external lateral teeth (MNHN-IM-2019-1704). Scale bars: 200  $\mu\text{m}$  (**A**), 50  $\mu\text{m}$  (**B, C, D, E, F**).

specimens of the two species are illustrated by Lamy and Pointier (2017: pl. 40, fig. 6A, B [*nucleus*], 6C–E [*nancyae*], both as *S. nucleus*). It is unknown whether this species also occurs in Bermuda.

**Remarks.** Petit (2013: 9) questioned the precision of the type locality and presented circumstantial evidence that Petuch's original material consisted of shells occupied by hermit crabs.

*Planaxis nancyae* was described based on two specimens, both unusually smooth and reddish for the species. In the absence of sequenced topotypic material, we are confident of the identity of the holotype based on our examination of more than 2,100



**Figure 7.** Comparative shell morphology of *Supplanaxis* around the Caribbean. *Supplanaxis nancyae* is shown at left, and *S. nucleus* is at right, for each pair. The individuals from each pair were sampled from the same site and were originally part of the same lot **A** Florida, Miami Beach, South Beach, at jetty (at left, USNM 1620287; at right, USNM 842270) **B** Bahamas, New Providence, The Caves (at left, USNM 1620274; at right, USNM 603895) **C** Mexico, Cozumel, 1 mi. N of San Miguel (at left, USNM 1620276; at right, USNM 662773) **D** Jamaica, St. Mary, 2 mi. N Port Maria (at left, USNM 1620285; at right, USNM 770590) **E** Dominican Republic, Oro Oro Beach [sic, possibly Playa Dorada], S. shore (at left, USNM 1620275; at right, USNM 603900) **F** Virgin Islands, St. John, Caneel Bay (at left, USNM 1620284; at right, USNM 738775) **G** Antigua and Barbuda, Antigua, Green Id. (at left, USNM 1620283; at right, USNM 738725) **H** Honduras, Utila Id. (at left, USNM 1620264; at right, USNM 434879) **I** Panama, Puerto Perme, NW of Cape Tiburon (at left, USNM 1620279; at right, USNM 664216) **J** Curaçao, S shore, beach in front of CARMABI research station (at left, USNM 1618952; at right USNM 1618956; sequenced vouchers) **K** Guadeloupe, Plage de Malendure (at left, MNHN-IM-2019-1703; at right MNHN-IM-2009-26687; sequenced vouchers) **L** Barbados, Hastings Rocks (at left, MNHN-IM-2019-1729; at right, neotype, MNHN-IM-2000-35804; sequenced vouchers). Base map: Wikimedia Commons contributors (2017).

specimens of *Supplanaxis* from all over the Caribbean, and particularly material from Jamaica and the Virgin Islands that conforms with both our sequenced material from the Lesser Antilles and the Haiti holotype. The shell of *S. nancyae* differs from that of *S. nucleus* in its generally smaller size and lighter color, the regularly convex shape of the aperture, and its adapically expanded callus.

The protoconch figured by Houbbrick (1987: fig. 17H) for *S. nucleus* may be that of *S. nancyae*, as all the adult shells in that lot (USNM 714035) represent the latter spe-



**Figure 8.** Habitat **A** Curaçao, S shore, beach in front of CARMABI research station **B** *Supplanaxis nucleus* and *S. nancyae* individuals among cobbles.

cies. The radula of *S. nancyae* was described and figured as *S. nucleus* by Bandel (1984: fig. 59; pl. 2 figs 6, 8), as is evident from the morphology of the rachidian. Indeed, Bandel (1984) mistook the comparatively short lateral extensions of the rachidian described by Troschel (1858) as erroneous, but the latter were based on *S. nucleus* which has a broader cutting edge and comparatively shorter lateral extensions. The radular morphology of *S. nancyae* differs from that of *S. nucleus* primarily in its narrower and thicker cutting edge of the rachidian, the robustness and shape of the rachidian basal denticle, the narrower and more pointed rachidian central cusp, and the slightly greater number of denticles on the outer marginal tooth. There may be fewer flanking denticles on the rachidian in *S. nancyae* caused by fusion of the innermost denticles with the central cusp, as seen in the specimens examined herein from Guadeloupe (Fig. 6B, D), but the range of variation overlaps in the two species. These differences in tooth morphology strongly suggest the two species differ in trophic ecology, but this deserves further research. Regardless, in addition to features of the aperture of the shell, the characteristic rachidian provides diagnostic characters sufficient to separate *S. nancyae* from its co-occurring congener.

We note a strong resemblance with the fossil *Planaxis ame* Woodring, 1928 (342, pl. 25, fig. 16), known from the Upper Pliocene of Jamaica (type locality) and from the Upper Miocene Cercado Formation of the Dominican Republic (Landau, pers. comm.). Woodring compared *Planaxis ame* with *P. nucleus*, then the only known Recent Caribbean planaxid species, but the smooth forms of *Supplanaxis nancyae* are a better match, and we do not rule out that *P. ame* might turn out to be a senior synonym of *S. nancyae*.

### Genus *Hinea* Gray, 1847

**Type species.** *Planaxis mollis* G.B. Sowerby I, 1823 [= *Buccinum brasilianum* Lamarck, 1822], by monotypy.

***Hinea nucleola* (Mörch, 1876), comb. nov.**

Fig. 3E

*Planaxis nucleola* Mörch, 1876: 126

**Holotype.** U.S. VIRGIN ISLANDS • 7.8 mm in height; St Croix; 1849; Ørsted leg.; ZMK 152749 (Fig. 3E).

**Other material.** U.S. VIRGIN ISLANDS • 1 spm; St. John, Caneel Bay; USNM 1620829.

**Description.** *Shell.* Shell small for the genus, solid, littoriniform, high-spired, consisting of 5+ (apex broken or corroded in the two known specimens) weakly convex whorls separated by impressed suture, last whorl occupying ca 80% of total shell height. Shell surface smooth, except incised spiral grooves, 0–2 adapically below suture and 2–8 on shell base. Aperture ovoid, occupying ca 40% of total shell height, with 0–4 low internal lirae, with distinct siphonal notch, narrow callus adpressed to parietal and columellar areas, parietal tooth strong, blunt. *Color* dark brown olive in holotype, to light orange brown with white parietal tooth and columellar callus. *Height* 7.8–8.4 mm.

**Remarks.** *Planaxis nucleola* was described based on a single specimen, and the “probable holotype” (Fig. 3E) is in the Statens Naturhistoriske Museum [formerly Naturhistorisk Museum], Copenhagen. The type locality was St Croix, then in the Danish Virgin Islands [currently U.S. Virgin Islands].

*Planaxis nucleola* was explicitly separated from *P. nucleus* by Mörch (1876) by its much less acutely pointed shell and spiral grooves restricted to the base. It had never been illustrated, and we have not traced any citation of that species since Mörch (1876). It is currently indexed in MolluscaBase in the synonymy of *S. nucleus* based on Rosenberg (2009).

The genus-group name *Angiola* Dall, 1926, has long been in use for Caribbean planaxids (Houbrick 1987; Rosenberg 2009), but was synonymized with *Hinea* by Ponder (1988).

**Discussion.** The sympatry and syntopy of *Supplanaxis nucleus* and *S. nancyae* raise the question of the evolutionary mechanism that might have led to the emergence of two species. Unexpectedly, the phylogenetic tree did not resolve *S. nucleus* and *S. nancyae* as sister taxa. A specimen of the Panamic *Supplanaxis planicostatus* (G.B. Sowerby I, 1825) from Panama City [type locality: Galapagos Is; Fig. 3B], sequenced only for the 16S gene, is placed as sister to *S. nancyae*, albeit with no support. A further eastern Pacific *Supplanaxis* species is *S. obsoletus* (Menke, 1851) [type locality: Mazátlan, Pacific coast of Mexico]. The Caribbean and the Panamic species of *Supplanaxis* have obviously shared a long part of their evolutionary history, and more phylogenetic work needs to be done to properly assess their relationship.

**Acknowledgments**

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funding from Fonds Européen de Développement Régional (FEDER) and Port Autonome de la Guadeloupe, and subsequently in 2017 by Dominique Lamy; in Curaçao as part of the Bivalve Assembling the Tree-of-Life project and supported by the U.S. National Science Foundation (NSF) Assembling the Tree of Life (AToL) program (award DEB-0732854 to Rüdiger Bieler, FMNH, and colleagues); and in Barbados with the assistance of Nadeshinie Parasram and Henri Valles (University of the West Indies, Barbados). Bernard Landau shared with us his knowledge of fossil Caribbean planaxids.

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# Redescription of *Pseudopoda taibaischana* (Araneae, Sparassidae), with the first description of the female

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## Abstract

*Pseudopoda taibaischana* Jäger, 2001 (Sparassidae) is redescribed based on new material from the type locality in Taibaishan Nation Forest Park of Shaanxi Province, China. The female is described and illustrated for the first time, and a redescription is provided for the male.

## Keywords

Biodiversity, huntsman spiders, Shaanxi, taxonomy

## Introduction

The genus *Pseudopoda* was established by Jäger (2000) to include nine species previously assigned to *Heteropoda*: *P. casaria* (Simon, 1897), *P. exigua* (Fox, 1938), *P. exiguoides* (Song & Zhu, 1999), *P. grahami* (Fox, 1936), *P. lushanensis* (Wang, 1990), *P. prompta* (O. Pickard-Cambridge, 1885), *P. virgata* (Fox, 1936), *P. zhangmuensis* (Hu & Li, 1987), and *P. zhejiangensis* (Zhang & Kim, 1996). Currently, *Pseudopoda* is the third largest genus of the subfamily Heteropodinae, and includes 142 species. Members of this genus are known from Bhutan, China, India, Indonesia, Japan, Laos, Myanmar, Nepal, Pakistan, Thailand, and Vietnam (World Spider Catalog 2020). From China,

63 species are known; among them, seven species are only known from females and eleven only from males (World Spider Catalog 2020). *Pseudopoda taibaischana* Jäger, 2001 was first described based on one male specimen from Taibaishan National Forest Park of Shaanxi Province, China (Jäger 2001). Recently, new material of both sexes was collected from the type locality of this species, enabling us to describe the female for the first time in this paper.

## Materials and methods

Specimens were examined and measured with a Leica M205C stereomicroscope. The points arising from the tegular appendages are listed as clock-positions from the left bulb in ventral view. Male palps were examined after dissection and detachment. The epigynes were examined and illustrated after dissection: they were removed and cleared in warm lactic acid before illustration. The vulva was photographed after being embedded in Arabic gum. All photographs were taken with a Leica DFC450 digital camera attached to a Leica M205C stereomicroscope, with 10–20 photographs taken in different focal planes and combined using the image stacking software Leica LAS. Images were edited using Adobe Photoshop CC 2015.

Leg measurements are listed as: total length (femur, patella, tibia, metatarsus, tarsus). The number of spines is listed for each segment in the following order: prolateral, dorsal, retrolateral, ventral (in femora and patellae, ventral spines are absent, and the fourth digit is omitted in the spination formula).

Abbreviations used in the text and figures are given below:

**SMF** Senckenberg Research Institute and Museum, Frankfurt, Germany (P. Jäger);  
**HUST** School of Nuclear Technology and Chemistry & Biology, Hubei University of Science and Technology, Xianning, Hubei, China (Y. Zhong);

<b>ALE</b>	anterior lateral eye;	<b>OW</b>	opisthosoma width;
<b>AME</b>	anterior median eye;	<b>Pa</b>	patella;
<b>AW</b>	anterior width of carapace;	<b>PI</b>	posterior incision of LL;
<b>C</b>	conductor;	<b>PL</b>	carapace length;
<b>CO</b>	copulatory opening;	<b>PLE</b>	posterior lateral eyes;
<b>CH</b>	clypeus height;	<b>PME</b>	posterior median eyes;
<b>E</b>	embolus;	<b>Pp</b>	palp;
<b>EP</b>	embolic projection;	<b>PP</b>	posterior part of spermathecae;
<b>FD</b>	fertilization duct;	<b>PW</b>	carapace width;
<b>FE</b>	femur;	<b>RTA</b>	retrolateral tibial apophysis;
<b>FW</b>	first winding;	<b>S</b>	spermathecae;
<b>LL</b>	lateral lobes;	<b>T</b>	tegulum;
<b>Mt</b>	metatarsus;	<b>Ta</b>	tarsus;
<b>OL</b>	opisthosoma length;	<b>Ti</b>	tibia. I, II, III, IV—legs I to IV.

## Taxonomy

Family Sparassidae Bertkau, 1872

Subfamily Heteropodinae Thorell, 1873

Genus *Pseudopoda* Jäger, 2000

**Type species.** *Sarotes promptus* O. Pickard-Cambridge, 1885.

**Diagnosis.** See Jäger (2000) and Jiang et al. (2018).

**Composition.** *P. daliensis*-group (*P. anguilliformis* Zhang et al., 2017, *P. peronata* Zhang et al., 2017, *P. sicyoidea* Zhang et al., 2017, *P. daliensis* Jäger & Vedel, 2007, *P. kunmingensis* Sun & Zhang, 2012), *P. diversipunctata*-group (*P. diversipunctata* Jäger, 2001, *P. intermedia* Jäger, 2001, *P. marsupia* (Wang, 1991)), *P. latembola*-group (*P. albolineata* Jäger, 2001, *P. alta* Jäger, 2001, *P. chauki* Jäger, 2001, *P. everesta* Jäger, 2001, *P. latembola* Jäger, 2001, *P. monticola* Jäger, 2001, *P. sinopodoides* Jäger, 2001), *P. martensi*-group (*P. chulingensis* Jäger, 2001, *P. dhulensis* Jäger, 2001, *P. gogona* Jäger, 2001, *P. hyatti* Jäger, 2001, *P. kalinchoka* Jäger, 2001, *P. khimtensis* Jäger, 2001, *P. martensi* Jäger, 2001, *P. martinae* Jäger, 2001, *P. megalopora* Jäger, 2001, *P. platembola* Jäger, 2001, *P. tinjura* Jäger, 2001, *P. varia* Jäger, 2001, *P. virgata* (Fox, 1936)), *P. parvipunctata*-group (*P. biapicata* Jäger, 2001, *P. dao* Jäger, 2001, *P. jirensis* Jäger, 2001, *P. parvipunctata* Jäger, 2001, *P. schawalleri* Jäger, 2001, *P. thorelli* Jäger, 2001, *P. triapicata* Jäger, 2001, *P. lushanensis* (Wang, 1990)), *P. prompta*-group (*P. brauni* Jäger, 2001, *P. cuneata* Jäger, 2001, *P. grasshoffi* Jäger, 2001, *P. huberti* Jäger, 2001, *P. marmorea* Jäger, 2001, *P. trisuliensis* Jäger, 2001, *P. casaria* (Simon, 1897), *P. prompta* (O. Pickard-Cambridge, 1885), *P. zhangmuensis* (Hu & Li, 1987)), *P. schwendingeri*-group (*P. hirsuta* Jäger, 2001, *P. schwendingeri* Jäger, 2001), and *P. signata*-group (*P. bibulba* (Xu & Yin, 2000), *P. physematosa* Zhang et al., 2019, *P. semilunata* Zhang et al., 2019, *P. signata* Jäger, 2001, *P. wu* Jäger, Li & Krehenwinkel, 2015, *P. yinae* Jäger & Vedel, 2007, *P. yunnanensis* (Yang & Hu, 2001)) and 88 other species that have not yet been grouped.

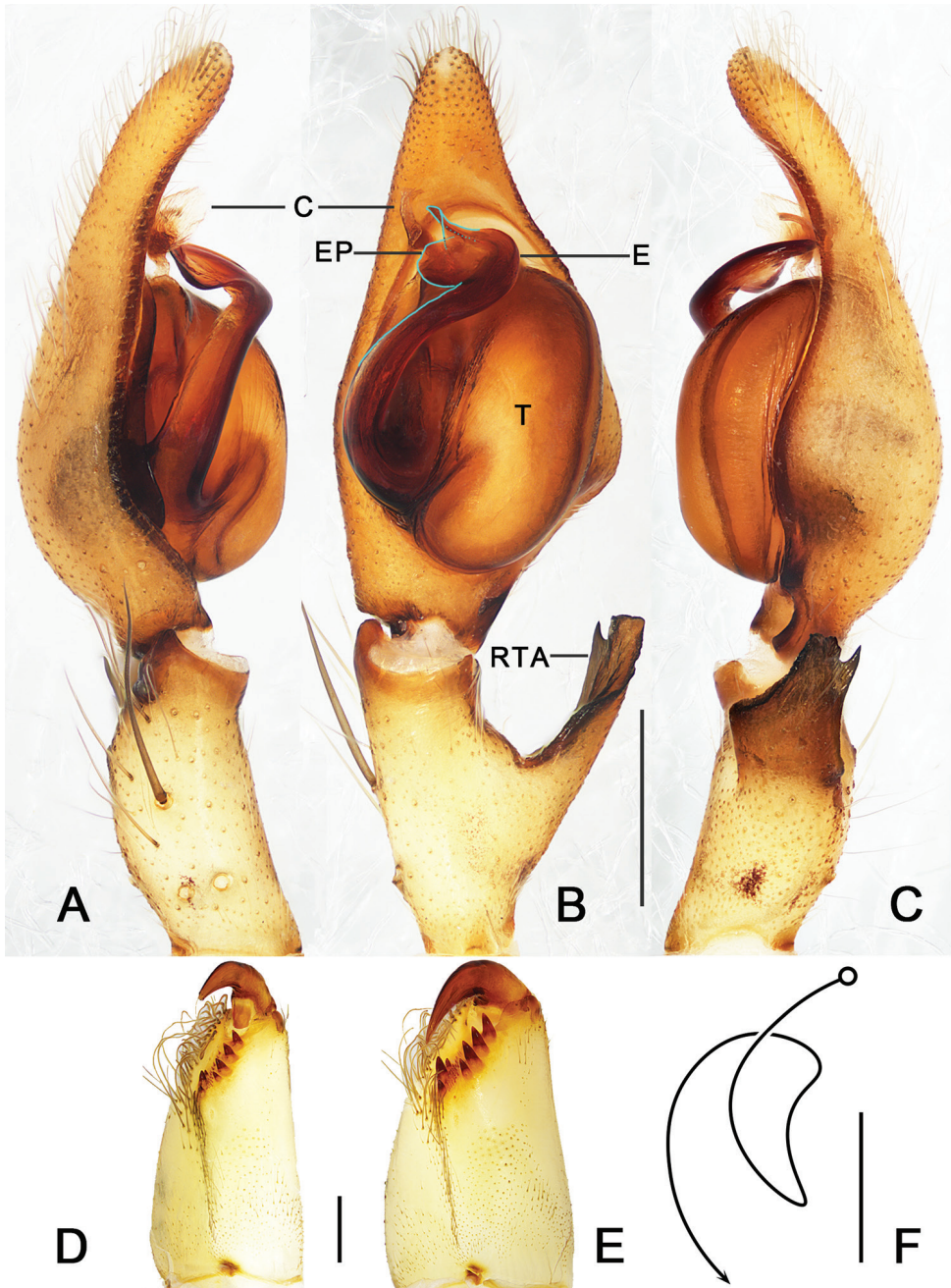
*Pseudopoda taibaischana* Jäger, 2001

Figures 1–4

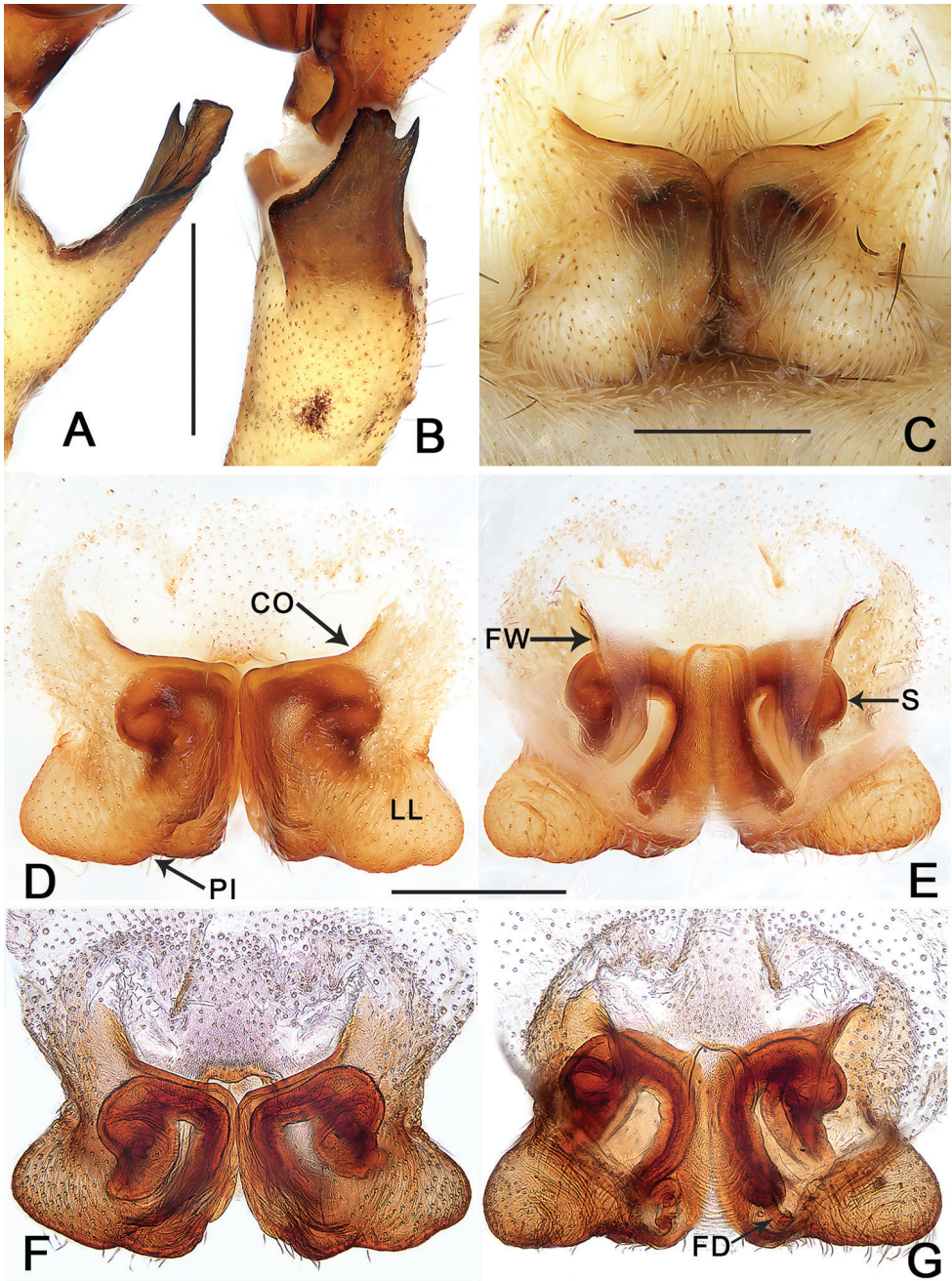
*Pseudopoda taibaischana* Jäger, 2001: 86, figs 47a–e (holotype male from Taibaishan National Forest Park of Shaanxi Province, deposited in SMF PJ1056)

**Material examined.** 2♂, 10♀ (HUST 0001), Shaanxi Province, Baoji City, Taibaishan National Forest Park; 34.05°N, 107.87°E; alt. 1438 m; 20.VII. 2019, Y. Zhong leg.

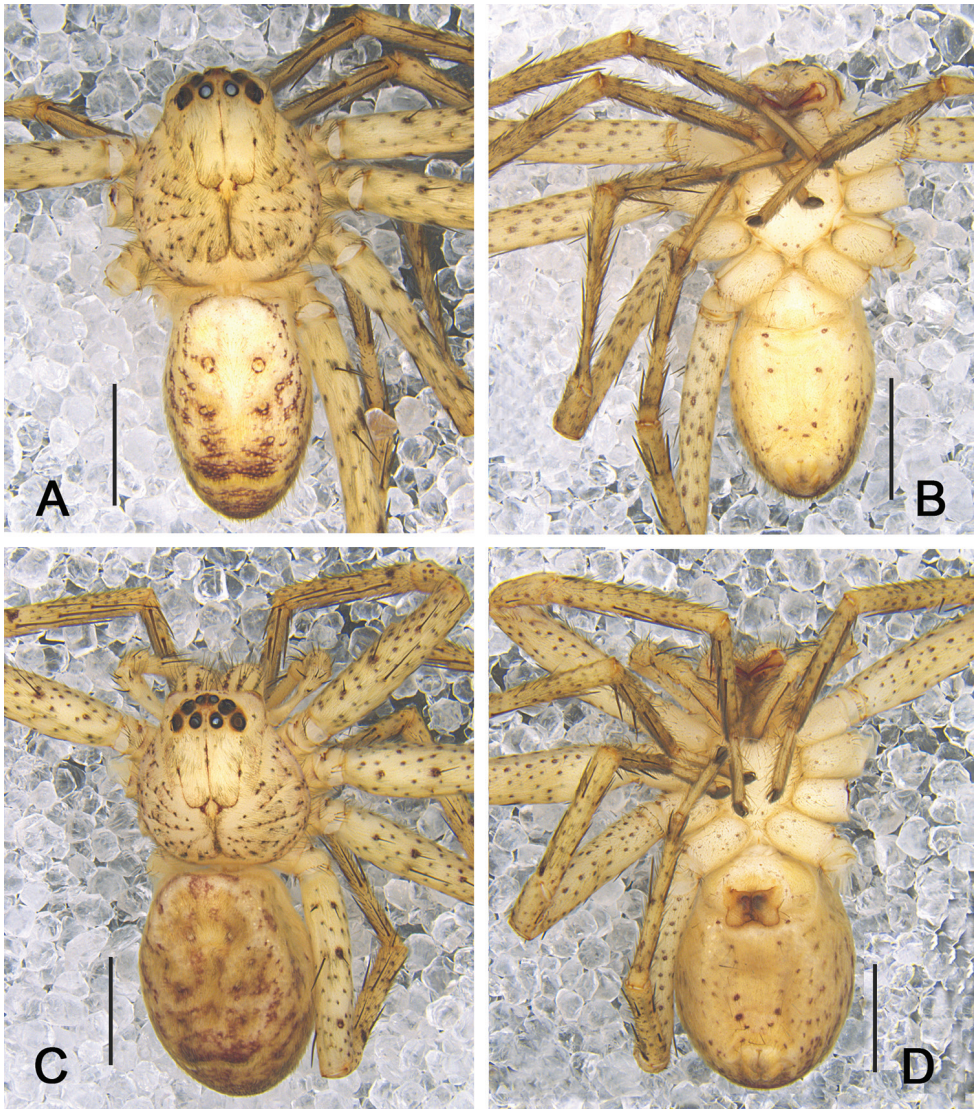
**Diagnosis.** This species resembles *Pseudopoda cangshana* Jäger & Vedel, 2007 (Jäger and Vedel 2007: figs 66–68, 70–72) in having the embolus strongly S-shaped, proximal part of embolus visible, and lateral loops of internal duct system extending laterally beyond its first winding, but can be distinguished from the latter by the



**Figure 1.** *Pseudopoda taibaischana* Jäger, 2001 **A–C** left male palp (**A** prolateral view **B** ventral view **C** retrolateral view) **D, E** cheliceral dentition, ventral view (**D** male **E** female) **F** schematic course of internal duct system. Abbreviations: C–conductor, E–embolus, EP–embolic projection, RTA–retrolateral tibial apophysis, T–tegulum. Scale bars: 0.5 mm.



**Figure 2.** *Pseudopoda taibaischana* Jäger, 2001 **A, B** Left male palpal tibia (**A** ventral view **B** retrolateral view) **C** epigyne, intact **D** epigyne, cleared **E** vulva, cleared **F** epigyne, cleared and embedded in Arabic gum **G** vulva, cleared and embedded in Arabic gum (**C, D, F** ventral view **E, G** dorsal view). Abbreviations: CO—copulatory opening, FD—fertilization duct, FW—first winding, LL—lateral lobes, PI—posterior incision of LL, S—spermathecae. Scale bars: 0.5 mm.



**Figure 3.** *Pseudopoda taibaischana* Jäger, 2001 **A,B** male habitus (**A** dorsal view **B** ventral view) **C,D** female habitus (**C** dorsal view **D** ventral view). Scale bars: 2 mm.

following characters: 1, male palp with laminar and rounded embolic projection (absent in *P. cangshana*); 2, tip of RTA with distinct triangular extension dorsally (absent in *P. cangshana*); 3, female epigyne with converging part of anterior margins of lateral lobes T-shaped (Y-shaped in *P. cangshana*); 4, female vulva with loops of internal duct system distinctly curved in ventral view (not curved in *P. cangshana*) (Figs 1, 2).

**Description. Male.** PL 3.7, PW 2.8, AW 2.0, OL 4.0, OW 3.2. Eyes and interdistances: AME 0.20, ALE 0.25, PME 0.21, PLE 0.27, AME–AME 0.18, AME–ALE 0.07, PME–PME 0.24, PME–PLE 0.30, AME–PME 0.32, ALE–PLE 0.27,



**Figure 4.** Collection localities of *Pseudopoda taibaischana* in Shaanxi Province, China.

CH AME 0.30, CH ALE 0.28. Spination: Palp: 131, 101, 2101; Fe: I–III 323, IV 331; Pa: I–IV 001; Ti: I–II 2026, III–IV 2126; Mt: I–II 2024, III 3024, IV 3036. Measurements of palp and legs: Palp 6.3 (2.0, 1.1, 1.2, –, 2.0), I 17.9 (4.7, 2.0, 5.4, 4.2, 1.6), II 19.4 (5.4, 2.1, 5.8, 4.3, 1.8), III 14.9 (4.4, 1.6, 4.2, 3.3, 1.4), IV 18.2 (5.2, 1.7, 4.7, 4.9, 1.7). Leg formula: 2-4-1-3. Cheliceral furrow with three anterior and four posterior teeth, each tooth with 22 denticles (Fig. 1D). Carapace yellowish brown, with fovea slightly darker and bearing more spots. Chelicerae deep reddish brown. Sternum pale yellow, with small and irregular spots. Legs yellowish brown, with medium-sized spots and slightly larger spine patches. Abdomen yellowish brown dorsally, with three pairs of dark patches laterally and an irregular pattern in posterior half; ventrally yellowish brown with small and irregular patches (Fig. 3A, B).

Palp as in diagnosis. Cymbium longer than tibia. Embolus arising from tegulum at 8 o'clock position, embolic projection making the tip of embolus look somewhat incised. Conductor curved, arising from an 11 o'clock position. Spermathorax visible and slightly curved in retrolateral view. RTA arising medially from tibia, with only one apex, broad in retrolateral view (Figs 1, 2A, B).

**Female.** PL 3.6, PW 3.2, AW 2.3, OL 4.7, OW 3.4. Eyes and interdistances: AME 0.17, ALE 0.23, PME 0.20, PLE 0.26, AME–AME 0.16, AME–ALE 0.10, PME–PME 0.23, PME–PLE 0.30, AME–PME 0.33, ALE–PLE 0.28, CH AME 0.35, CH ALE 0.31. Spination: Palp: 131, 101, 1014, 2121; Fe: I–III 323, IV 331; Pa: I–IV 001; Ti: I 2026, III–IV 2126; Mt: I–II 2024, III 3025, IV 3036. Measurements of palp and legs: Palp 4.9 (1.6, 0.7, 1.0, –, 1.6), I 12.8 (3.8, 1.7, 3.3, 2.8, 1.2), II 14.0 (4.3, 1.3, 3.7, 3.4, 1.3), III 11.6 (3.5, 1.4, 2.8, 2.9, 1.0), IV 13.3 (4.0, 1.3, 3.3, 3.5, 1.2). Leg formula: 2-4-1-3. Cheliceral furrow with three anterior and four posterior teeth, each tooth with 32 denticles (Fig. 1E).

Epigynal field only slightly wider than long, with very short anterior bands or without such bands. Anterior margins of lateral lobes bent anteriorly at their lateral ends. Posterior incision of lateral lobe distinct, near the posterior meeting point of lateral lobes. Base of internal duct system distinctly extending laterally beyond first winding (Fig. 2C–G).

Coloration in ethanol: as in male, but generally darker, abdomen with more spots ventrally (Fig. 3C, D).

**Distribution.** China (Shaanxi Province) (Fig. 4).

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# Description of a new species of *Aleuroclava* Singh, 1931 (Hemiptera, Aleyrodidae) infesting *Schima superba* from China

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## Abstract

A new whitefly species, *Aleuroclava schimae* Wang, **sp. nov.** infesting leaves of *Schima superba* (Parietales, Theaceae) is described and illustrated from Zhejiang, China. Puparia of the new species are elliptical, broad at the transverse molting suture region and broadly truncate posteriorly. Thoracic and caudal tracheal pores are discernible. In life, the puparia are covered by a thin layer of white wax.

## Keywords

*Aleuroclava schimae* sp. nov., instar, morphology, new species, puparia, taxonomy, whitefly

## Introduction

The whitefly genus *Aleuroclava* Singh, 1931 is represented by 124 species worldwide, of which 38 species are from China (Evans 2007; Wang et al. 2014; Wang and Du 2016), including *A. schimae* sp. nov.. *Aleuroclava* species occur predominantly in the Oriental and Austro-Oriental Regions and feed on a wide range of host plants (Evans 2007).

Wang and Du (2016) provided a diagnostic key to *Aleuroclava* species including those of Hong Kong and Taiwan. *Aleuroclava schimae* sp. nov. found densely infesting leaves of *Schima superba* Gardner & Champ. at Thousand Island Lake (TIL), Gutianshan Nature Reserve, Shuangxikou village, Zhejiang, China is described herein. Morphological characteristics of puparia and immatures of the new species are described with images of habitus, holotype, line drawings and SEM images.

*Schima superba* (Parietales, Theaceae) is an economically and ecologically important woody tree of China. It is a dominant tree species in the subtropical evergreen broad-leaved forests of southern China (Zhang et al. 2019), and commercially used for timber, furniture and construction purposes, and also as fire breaks to prevent forest fires (Yang et al. 2017).

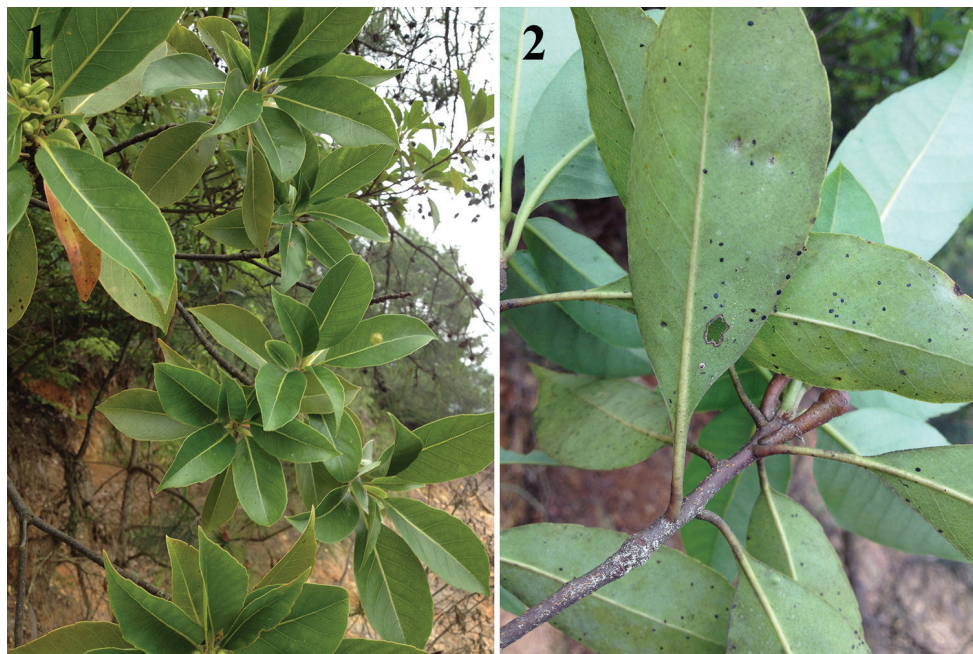
## Material and methods

Puparia of the new species were collected on leaves of *Schima superba* from Zhejiang, Thousand Island Lake (hereafter TIL) and Gutianshan Nature Reserve, Shuangxikou village, China. No adult emergence was noticed during rearing of puparia for two weeks. Puparia were mounted following Dubey and David (2012). The terminology for morphological structures follows Bink-Moenen (1983), Martin (1985) and Gill (1990). Habitus images were taken using a digital camera Canon IXUS 105 and a camera DFC 290 (Leica, Wetzlar, Germany) attached to a Leica stereomicroscope M 125 (Leica, Wetzlar, Germany). Puparial measurements and microphotographs were taken using a compound microscope (Carl Zeiss, Gottingen, Germany) from Zhejiang Agriculture and Forestry University (ZAFU). The scanning electron microscope images were taken by Hitachi TM-1000 Scanning Electron Microscope (Hitachi, Japan) from the Center of Electron Microscopy, Zhejiang University (Life Sciences Division). Adobe Photoshop 7 software was used for figure preparation. The holotype is deposited in the Insect Collections of Zhejiang Agriculture and Forestry University, Lin'an, China (ZAFU). One paratype will be deposited in the Shanghai Entomological Museum, Chinese Academy of Sciences (SEM-CAS) and the remainder in ZAFU.

## Taxonomy

### *Aleuroclava* Singh

**Diagnosis.** Puparia small in size, elliptical or subelliptical. Margin with one row of teeth. Submarginal area not separated from dorsal disc, with papillae-like markings in some species, dorsum generally with tubercles. Thoracic tracheal folds and pores not discernible; caudal furrow and pore distinct. Vasiform orifice generally notched posteriorly; operculum cordate, nearly filling orifice; lingual hidden.



**Figures 1–2.** Leaves of host plant *Schima superba* infested by *A. schimae* sp. nov.

***Aleuroclava schimae* Wang, sp. nov.**

<http://zoobank.org/2A18B6BA-16DC-41CD-834F-FCE9AA22EDB5>

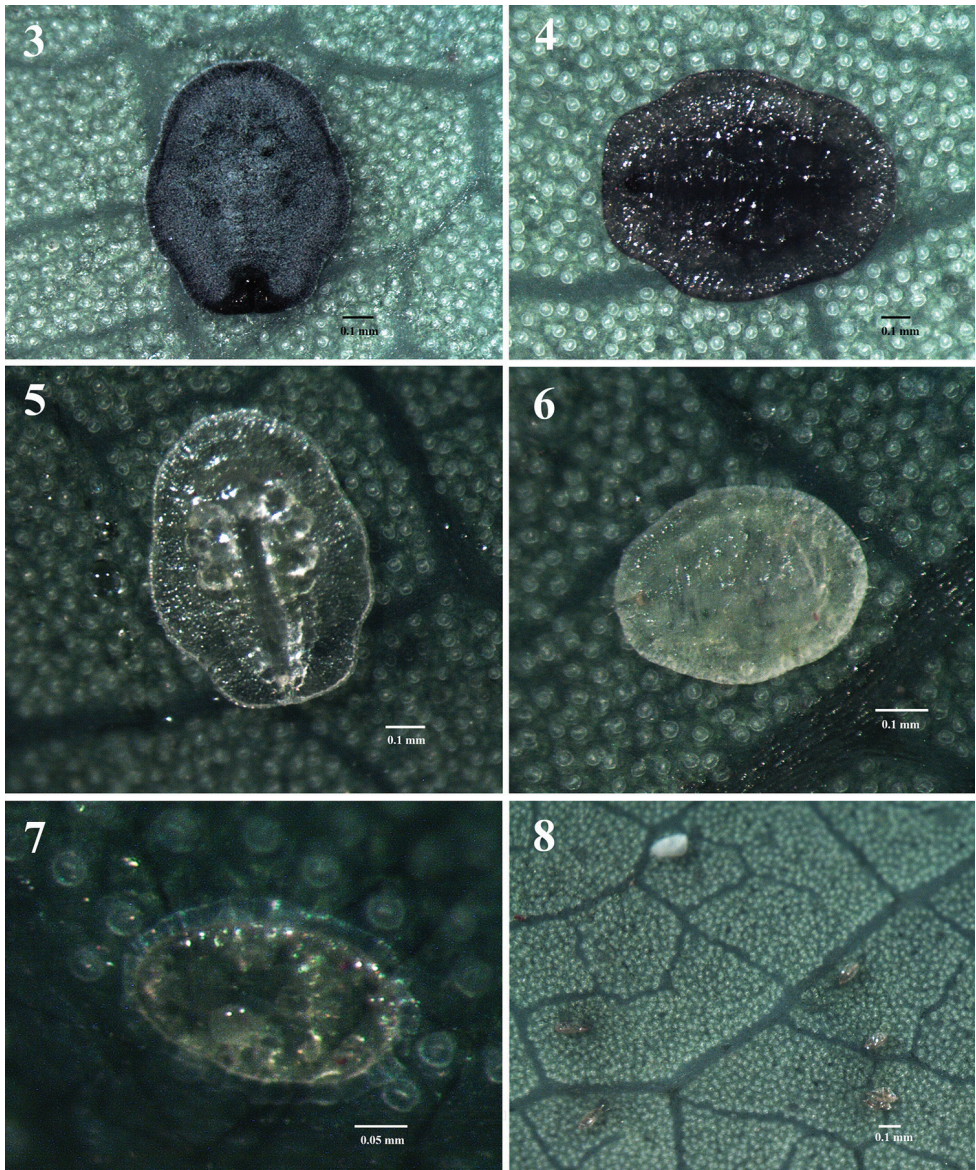
Figs 3–18

**Type material.** *Holotype*: China, Zhejiang, Zhejiang, Chun'an, Thousand Island Lake, 1 puparium on slide, on *Schima superba*, 6. vi. 2016, 29°31.21'N, 118°52.41'E, leg. JR Wang. Deposited in the Insect Collections of ZAFU, Lin'an, China. *Paratypes*: Fifty-six, of which 30 puparia on 21 slides, data same as for holotype; Gutianshan Nature Reserve, Zhejiang, Kaihua, 15 puparia on 12 slides, on *Schima superba*, 28.xiii.2018, 29°15.12'N, 118°06.42'E, leg. AQ Dai; Zhejiang, Jiangshan, Shuangxikou village, 11 puparia on 10 slides, 30. xiii. 2018, 28°23.12'N, 118°41.15'E, leg. AQ Dai. (SEM-CAS 1 paratype, ZAFU 55 paratypes and dry collection).

**Description.** *Egg* (Fig. 8). Fusiform; yellowish, gradually becoming dark brown over time; about 152 µm long, 69 µm wide, found deposited randomly on lower surface of leaves.

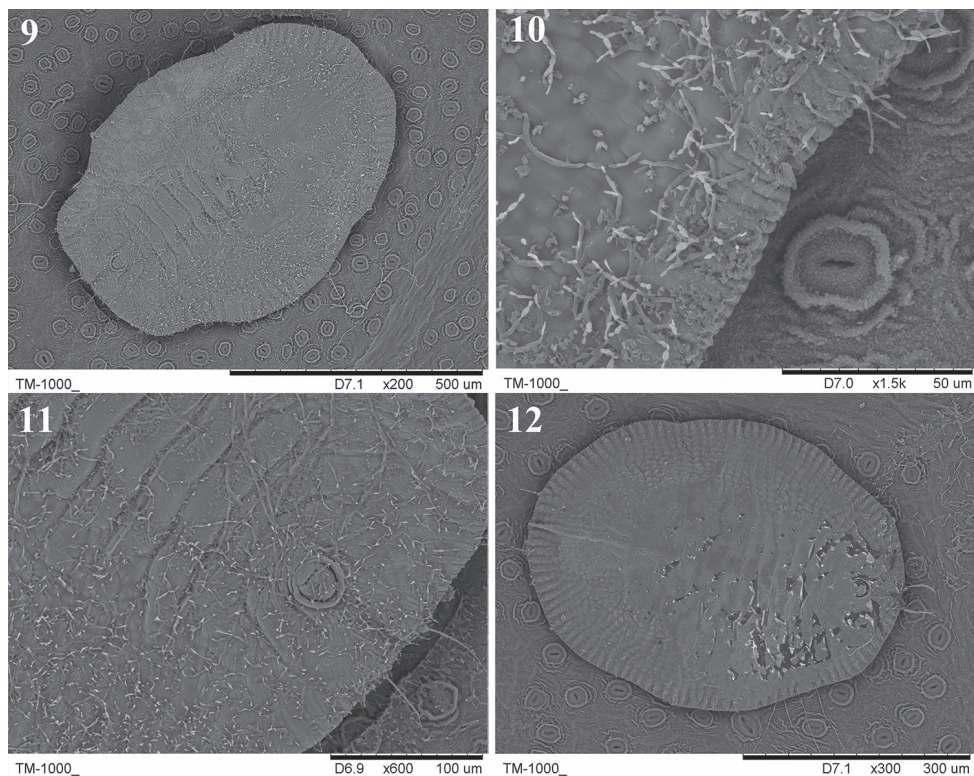
**Puparium.** Covered by a thin layer of white wax (Fig. 3); puparium in early stage white (Fig. 5), gradually turns black (Figs 3, 4), about 926–1120 µm long, 763–832 µm wide; elliptical, broadest at the transverse molting suture region; posteriorly horizontal.

**Margin** (Figs 10, 14, 17). Crenulate, 0.1 mm wide, 23–28 crenulations. Paired anterior and posterior marginal setae 27 and 16 µm long, respectively. Thoracic tracheal pore area slightly recessed and emarginated at margin. **Dorsum.** Almost flat,



**Figures 3–8.** Habitus, developmental stages of *A. schimae* sp. nov., on *S. superba*. **3, 4** puparium, late stage **5** puparium, early stage **6** third instar **7** second instar **8** eggs.

slightly raised on abdomen; without tubercles. Submargin demarcated from the dorsal disc by a faint line. Longitudinal moulting suture reaching anterior margin and the transverse moulting suture reaching submargin (Figs 13, 16). Thoracic and abdominal segment sutures well defined. Middle length of abdominal segment I 53  $\mu$ m; segment II 47  $\mu$ m; segments III–VI subequal, 37  $\mu$ m; segment VII 28  $\mu$ m

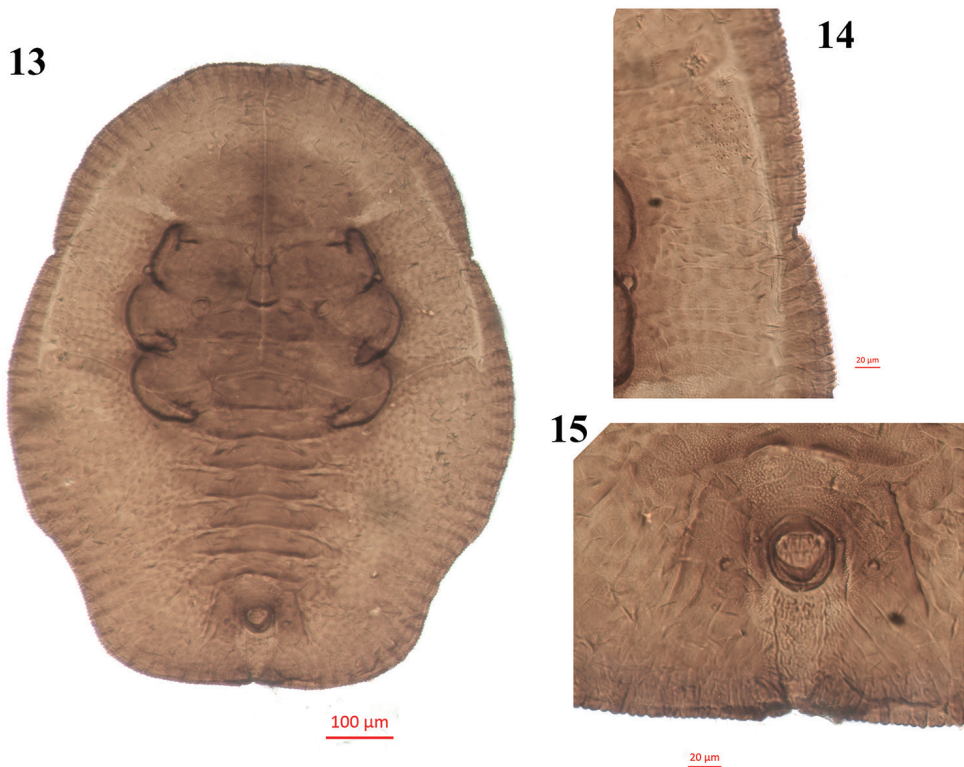


**Figures 9–12.** Scanning electron microscope (SEM) photographs of *A. schimae* sp. nov. **9** puparium, dorsal view **10** margin **11** vasiform orifice and operculum **12** third instar nymph.

long. Geminate pores present (Figs 9, 13, 16). **Chaetotaxy.** Cephalic, first, eighth abdominal and caudal setae 9, 13, 4 and 47  $\mu\text{m}$  long, respectively. Eighth abdominal setae located below the base of orifice. Caudal furrow 68  $\mu\text{m}$  long. **Vasiform orifice** (Figs 11, 15, 18). Cordate to subcircular, slightly longer than wide, 48  $\mu\text{m}$  long, 44  $\mu\text{m}$  wide, lateral margins rounded, basal ends being curved to meet basal margin; operculum cordate, 33  $\mu\text{m}$  long, 29  $\mu\text{m}$  wide, almost covering the orifice and obscuring the lingula. **Venter.** Thoracic and caudal tracheal folds discernible (Fig. 16). Ventral abdominal setae placed on anterior to vasiform orifice, 6  $\mu\text{m}$  long, 49  $\mu\text{m}$  apart. Antennae extending near the base of prolegs. **Third instar nymph** (Figs 6, 12). Light yellow, body transparent, elliptical, about 720  $\mu\text{m}$  long, 540  $\mu\text{m}$  wide; eye spots obvious. **Second instar nymph** (Fig. 7): yellowish, elongate-elliptical, about 290  $\mu\text{m}$  long, 170  $\mu\text{m}$  wide; transparent wax secretion along the body margin, about 11  $\mu\text{m}$  wide; eye spots red.

**Host plant.** *Schima superba* Gardner & Champ (Parietales, Theaceae) (Figs 1, 2).

**Distribution.** China: Zhejiang.



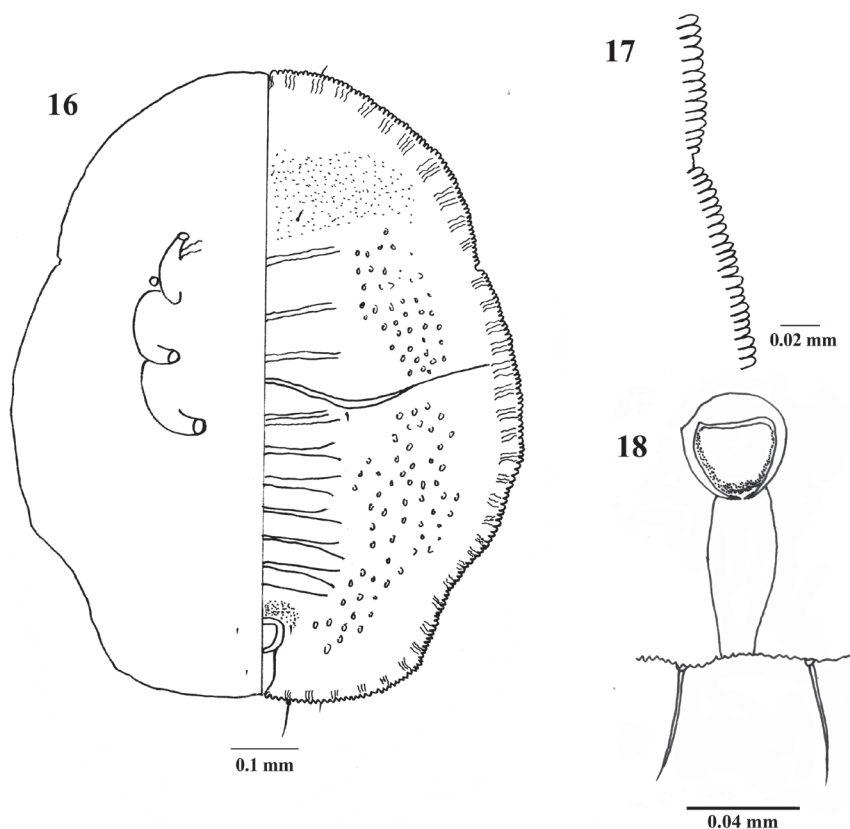
**Figures 13–15.** *Aleuroclava schimae*, sp. nov., slide mounted specimen. **13** puparium, dorsal view **14** margin **15** vasiform orifice and operculum.

**Biology.** Puparia were found on the lower surface of leaves; 10–40 per leaf (Figs 2–4); covered by a thin layer of white wax (Fig. 5). Exuviae of previous instars were present. No parasitoids and ants were observed.

**Etymology.** The species is named after the host plant, *Schima superba*.

**Remarks.** Puparia of the new species are elliptical in outline, broad at the transverse moulting suture region, truncate posteriorly (Figs 3, 4, 9, 13, 16), thoracic tracheal pores recessed, emarginated (Figs 10, 14, 17), transverse moulting suture reaching submargin (Figs 13, 16), and vasiform orifice cordate to subcircular, slightly longer than wide.

Puparium of *A. schimae* sp. nov. resembles that of *A. tianmuensis* in body shape, size and colour, but differs in having horizontal posterior end (curved in *A. tianmuensis*), and in lacking median tubercles on abdominal segments II–VI. It differs from *Aleuroclava similis* (Takahashi) in colour of puparium, and from *A. trivandricus* Dubey & Sundararaj in colour and thoracic tracheal pores not deeply inset at the margin. It also differs from *A. hikosanensis* (Takahashi) from the characteristic of the median area of each abdominal segment.



**Figures 16–18.** *Aleuroclava schimae* sp. nov., holotype puparium, China, Zhejiang. **16** puparium, dorsal (right) and ventral (left) views **17** margin **18** vasiform orifice.

## Acknowledgements

We express our deep gratitude to Dr Anil Kumar Dubey (Zoological Survey of India) for editing and helpful suggestions for improvement of the manuscript. The comments by the other two reviewers, Chiun-Cheng KO (Department of Entomology, National Taiwan University) and Maurice Jansen (Netherlands Food and Consumer Product Safety Authority) are also appreciated. This research was supported by grants from the National Natural Science Foundation of China (31930073, 31601884) and the Research and Development Fund of Zhejiang A&F University (2017FR041), China.

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# New record of the genus *Typhlocolenis* Hoshina, 2008 (Coleoptera, Leiodidae) from South Korea with a key to the species

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<http://zoobank.org/5C93E895-370A-4998-B47A-3B504ABFC84B>

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## Abstract

This is the first record of the genus *Typhlocolenis* Hoshina, 2008 (Coleoptera, Leiodidae, Leiodinae, Pseudoliadini) in South Korea. Two new Korean species are described, under the names *T. sillaensis* **sp. nov.** and *T. jejudensis* **sp. nov.** As a result of this study, the number of *Typhlocolenis* species is now five. A key to the species of the genus is provided.

## Keywords

Blind beetle, East Asia, Leiodinae, new species, Pseudoliadini, wingless beetle

## Introduction

The genus *Typhlocolenis* belongs to the tribe Pseudoliadini Portevin, 1926 of the subfamily Leiodinae Fleming, 1812 of the family Leiodidae (Perreau 2015) and was established based on three Japanese species by Hoshina (2008). Since then, no species have been added to this genus; therefore, *Typhlocolenis* was considered to be endemic to Japan (Perreau 2015). *Typhlocolenis* is a blind and wingless genus that can be distinguished from the blind genus *Zelodes* Leschen, 2000 of Pseudoliadini by its metaventrite with a median carina. In contrast, *Zelodes* has no median carinae on its metaventrite (Leschen 2000; Hoshina 2008).

In South Korea, three species of two genera of Pseudoliadini, *Dermatohomoeus terrenus* (Hisamatsu, 1985), *Pseudocolenis hilleri* Reitter, 1885, and *P. hoshinai* Park & Ahn, 2007, have been recorded (Park and Ahn 2007; National Institute of Biological Resources 2019). Recently, we studied approximately 20 previously unidentified Korean specimens of Pseudoliadini in the collection of the National Institute of Biological Resources, Incheon. The specimens were collected from forest litter layers by sifting. After careful examination, we discovered that the specimens represented two new species of *Typhlocolenis*. In this paper, we record the genus for the first time in South Korea, describe these new species, and provide a key to the species of the genus.

## Materials and methods

All specimens used in this study were deposited in the National Institute of Biological Resources (NIBR), Incheon, South Korea.

The methods were the same as those described in Hoshina (2012). Length and width of head, pronotum, and elytra are measured as follows: length of head is from anterior margin of clypeus to basal margin of head; width of head is between external margins of both eyes; length and width of pronotum and elytra are vertical and horizontal maximum.

## Key to the species of the *Typhlocolenis* genus

- 1 Elytra not strigose, bearing large punctures (Fig. 5)..... *Typhlocolenis uenoi* Hoshina
- Elytra densely and transversely strigose, bearing minute punctures (Fig. 6)....2
- 2 Median lobe of aedeagus broadly rounded at apex in dorsal view (Fig. 12).... *Typhlocolenis furunoi* Hoshina
- Median lobe of aedeagus with a nipple at apex in dorsal view (Figs 7, 9, 11) .....3
- 3 Median lobe of aedeagus relatively slender and bearing a relatively large nipple at apex in dorsal view (Fig. 11); distribution: Japan (Honshu) (Fig. 15)..... *Typhlocolenis fusca* Hoshina
- Median lobe of aedeagus relatively thick and bearing a relatively small nipple in dorsal view (Figs 7, 9); distribution: South Korea (Fig. 15) .....4
- 4 Median lobe of aedeagus feebly curved at lateral margins in dorsal view (Fig. 7); distribution: mainland of South Korea (Fig. 15) ..... *Typhlocolenis sillaensis* sp. nov.
- Median lobe of aedeagus strongly expanded at about middle of lateral margins in dorsal view (Fig. 9); distribution: Jeju Island (Fig. 15) ..... *Typhlocolenis jejuensis* sp. nov.

## Taxonomy

Leiodidae Fleming

Leiodinae Fleming

Pseudoliodini Portevin

*Typhlocolenis* Hoshina

*Typhlocolenis sillaensis* Hoshina & Park, sp. nov.

<http://zoobank.org/12717A0F-5DAB-4B5C-AE91-0625B08AC153>

Figures 1, 3, 6–8, 13, 15

**Type locality.** SOUTH KOREA, Gangwon-Prov., Pyeongchang-Gun, Mt. Odaesan.

**Material examined.** *Holotype*, ♂ (NIBR): KOREA, Gangwon-Prov. Pyeongchang-Gun, Mt. Odaesan, 22. vii. 2004, S.-J. Park leg. *Paratypes*, 2♂ 1♀ (NIBR): 16. v. 2005, same data as holotype except for the date; 1♂ (NIBR): 21. ix. 2006, same data as holotype except for the date.

**Diagnosis.** Body length approximately 1.3–1.4 mm. Dorsum almost concolorous, brown, or dark brown. Head and pronotum strongly microreticulate, sparsely and very minutely punctate. Elytra almost smooth, sparsely and very minutely punctate, and densely and transversely strigose. The median lobe of aedeagus relatively thick and feebly curved at lateral margins and bearing a relatively small nipple at apex in dorsal view.

**Description. Measurement of holotype.** Body length: 1.39 mm; head length: 0.26 mm, width: 0.39 mm; pronotum length: 0.45 mm, width: 0.83 mm; elytron length: 0.81 mm, width: 0.83 mm.

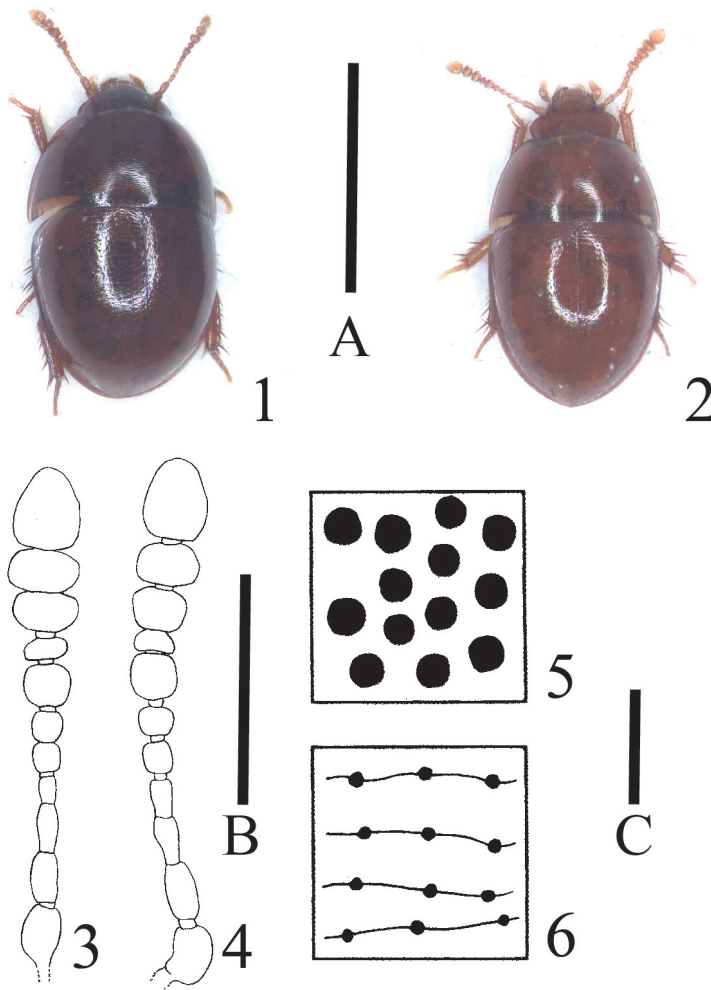
**Coloration.** Dorsum of body shiny and almost concolorous, brown or dark brown; antennae light brown; mesoventrite brown or dark reddish brown with a black median carina; metaventrite brown or dark reddish brown with a dark brown median carina; abdominal ventrites brown or dark reddish brown; legs brown with light brown tarsi.

Body 1.31–1.39 mm in length, approximately 1.8 times as long as wide (Fig. 1).

Head approximately 1.6 times as wide as long, strongly microreticulate, sparsely and very minutely punctate; head length approximately 0.54 times pronotum length; head width approximately 0.48 times pronotum width; antennomeres 1–4 and 11 longer than wide; antennomere 5–7 almost as long as wide; other antennomeres wider than long; antennomere 11 approximately 1.3 times as long as wide (Fig. 3).

Pronotum approximately 1.8 times as wide as long, strongly microreticulate, sparsely and very minutely punctate; pronotum length approximately 0.58 times elytron length; pronotum width almost same as elytron width.

Scutellum weakly microreticulate and almost impunctate or sparsely and very minutely punctate.



**Figures 1–6.** *Typhlocolenis sillaensis* sp. nov. (1, 3, 6). *T. jejudoensis* sp. nov. (2, 4). *T. uenoi* Hoshina (5) 1, 2 habitus (paratypes) 3, 4 antenna 5, 6 elytral punctures. Scale A: 1 mm (1, 2). Scale B: 0.2 mm (3, 4). Scale C: 0.02 mm (5, 6).

Elytra almost as long as wide or slightly wider than long, widest at approximately basal 1/6, almost smooth, sparsely and very minutely punctate, and densely and transversely strigose (Fig. 6).

Legs show no sexual dimorphism on protarsi and normal shape for *Typhlocolenis*.

Meso- and metaventrites strongly microreticulate, almost impunctate, and glabrous; abdominal ventrites strongly microreticulate, almost impunctate, and bearing sparse and very fine pubescences.

Male. Aedeagus generally thick (Figs 7, 8); median lobe of aedeagus feebly curved at lateral margins and bearing a relatively small nipple at apex in dorsal view (Fig. 7) and weakly curved in lateral view (Fig. 8); parameres almost symmetrical and bearing several apical setae (Figs 7, 8).

**Female.** Spermatheca generally crescent shaped (Fig. 13).

**Etymology.** The specific name is derived from an ancient Korean kingdom, *Silla*, where is the type locality of the present new species.

**Distribution.** South Korea (Gangwon-Prov.) (Fig. 15).

**Differential diagnosis.** The genus *Typhlocolenis* is here first recorded in South Korea and is the only blind genus in the Korean Pseudoliadini. Therefore, *T. sillaensis* sp. nov. can be easily separated from *Dermatohomoeus* Hlisenkovský, 1963 and *Pseudcolenis* Reitter, 1885 of the tribe by the lack of eyes. Moreover, *T. sillaensis* sp. nov. can be distinguished from *Dermatohomoeus* and *Pseudcolenis* by having a metaventrite with a distinct median carina. In contrast, *Dermatohomoeus* and *Pseudcolenis* have no median carinae on the metaventrites.

*Typhlocolenis sillaensis* sp. nov. is similar to *T. fusca* Hoshina, 2008 in appearance but can be distinguished by the relatively thick median lobe of aedeagus (Fig. 7) that has a relatively small nipple at the apex in dorsal view (Fig. 7). In contrast, *T. fusca* has a relatively slender median lobe that has a relatively large nipple at the apex in dorsal view (Fig. 11).

**Natural history.** The life history of *Typhlocolenis sillaensis* Hoshina & Park, sp. nov. is not known.

***Typhlocolenis jejuensis* Hoshina & Park, sp. nov.**

<http://zoobank.org/D9611B36-5743-4E22-A247-69B106BF4C5F>

Figures 2, 4, 9, 10, 14, 15

**Type locality.** SOUTH KOREA, Jeju Is., Jeju-City, Goepyeongioreum

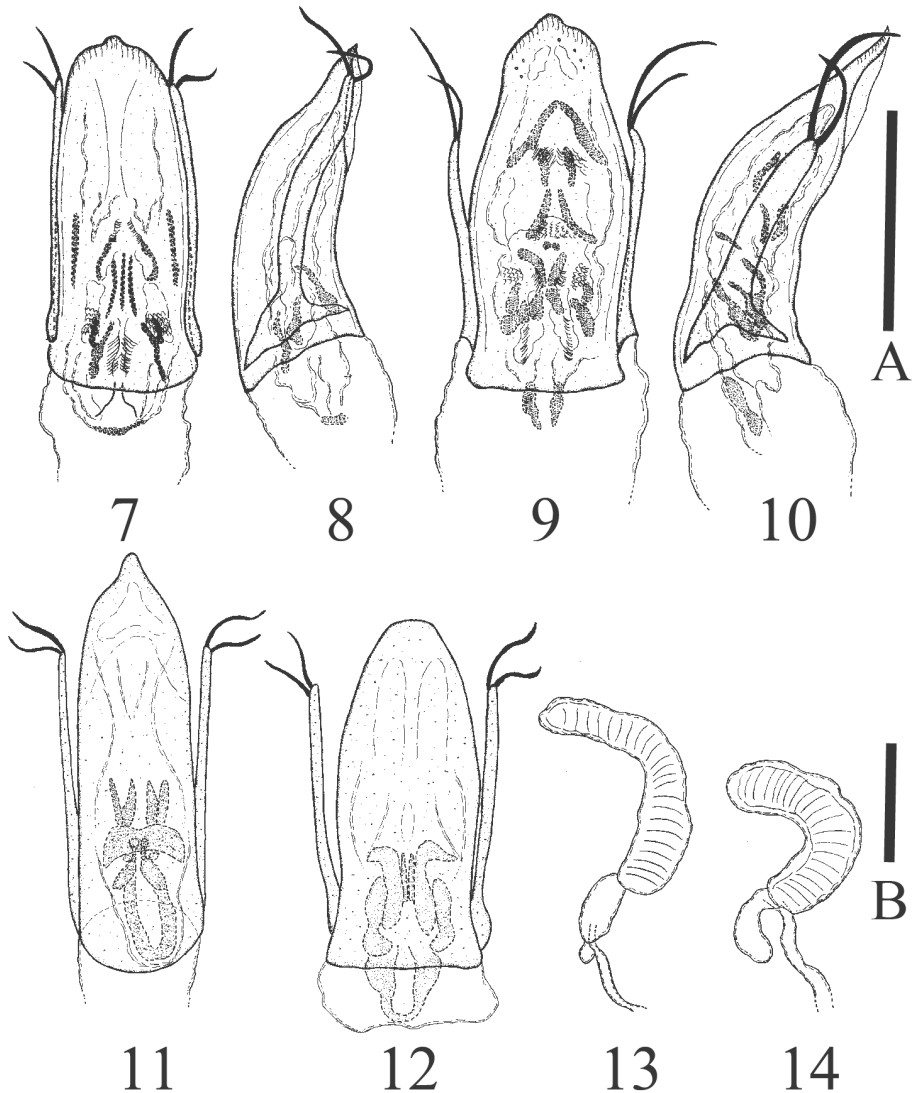
**Material examined.** *Holotype*, ♂ (NIBR): KOREA, Jeju Is., Jeju-City, Goepyeongioreum, 13. vi. 2005, S.-I. Lee leg. *Paratypes*, 3 ♀ (NIBR): same data as holotype; 1 ♂ 5 ♀ (NIBR): Jeju Is., Jeju-City, Bijarium, 12. vi. 2005, S.-J. Park leg.; 2 ♂ 2 ♀ (NIBR): Jeju Is., Jeju-City, Dongbaekdongsan, 13. vi. 2005, S.-I. Lee leg.; 2 exs. (NBIR): Jeju Is., Jeju-City, Dongbaekdongsan, 22. v. 2006, S.-I. Lee & Y.-H. Kim leg.

**Diagnosis.** The present species very similar to *Typhlocolenis sillaensis* Hoshina & Park, sp. nov. Body length approximately 1.3–1.4 mm. Dorsum almost concolorous, brown to blackish brown. Head and pronotum strongly microreticulate, sparsely and very minutely punctate. Elytra almost smooth, sparsely and very minutely punctate, and densely and transversely strigose. The median lobe of aedeagus relatively thick, strongly expanded at about middle of lateral margins, and bearing a small nipple at apex in dorsal view.

**Description.** *Measurement of holotype.* Body length: 1.30 mm; head length: 0.24 mm, width: 0.35 mm; pronotum length: 0.40 mm, width: 0.71 mm; elytron length: 0.73 mm, width: 0.73 mm.

**Coloration.** Dorsum of body shiny and almost concolorous, brown to blackish brown; mesoventrite brown or dark reddish brown with a black median carina; metaventrite brown or dark reddish brown with a dark brown median carina; abdominal ventrites brown or dark reddish brown; legs brown with light brown tarsi.

Body 1.28–1.42 mm in length, approximately 1.7 times as long as wide (Fig. 2).



**Figures 7–14.** *Typhlocolenis sillaensis* sp. nov. (7, 8, 13). *T. jejudoensis* sp. nov. (9, 10, 14). *T. fusca* Hoshina (11). *T. furunoi* Hoshina (12) 7, 9, 11, 12 aedeagus, dorsal view 8, 10 ditto, lateral view 13, 14 spermatheca. Scale A: 0.2 mm (7–12). Scale B: 0.05 mm (13, 14).

Head approximately 1.5 times as wide as long, strongly microreticulate, sparsely and very minutely punctate; head length approximately 0.61 times pronotum length; head width approximately 0.48 times pronotum width; antennomeres 1–4 and 11 longer than wide; antennomere 5–7 almost as long as wide; other antennomeres wider than long; antennomere 11 approximately 1.3 times as long as wide (Fig. 4).

Pronotum approximately 1.8 times as wide as long, strongly microreticulate, sparsely and very minutely punctate; pronotum length approximately 0.52 times elytron length; pronotum width almost same as or slightly narrower than elytron width.



**Figure 15.** Distribution map of *Typhlocolenis*. Double circle: *Typhlocolenis sillaensis* sp. nov. Square: *T. jejudoensis* sp. nov. Circle: *T. fusca* Hoshina. Star: *T. uenoi* Hoshina. Triangle: *T. furunoi* Hoshina.

Scutellum weakly microreticulate and almost impunctate or sparsely and very minutely punctate.

Elytra almost as long as or slightly longer than wide, widest at approximately basal 1/6, almost smooth, sparsely and very minutely punctate, and densely and transversely strigose (Fig. 6).

Legs show no sexual dimorphism on protarsi and normal shape for *Typhlocolenis*.

Meso- and metaventrites strongly microreticulate, almost impunctate, and glabrous; abdominal ventrites strongly microreticulate, almost impunctate, and bearing sparse and very fine pubescence.

**Male.** Aedeagus generally thick (Figs 9, 10); median lobe of aedeagus strongly expanded at about middle of lateral margins, and bearing a small nipple at apex in dorsal view (Fig. 9), slightly, and weakly curved in lateral view (Fig. 10); parameres almost symmetrical and bearing several apical setae (Figs 9, 10).

**Female.** Spermatheca generally C-shaped (Fig. 14).

**Etymology.** The specific name is derived from the type locality, Jeju Island.

**Distribution.** South Korea (Jeju Island) (Fig. 15).

**Differential diagnosis.** *Typhlocolenis jejudoensis* sp. nov. is similar to *T. sillaensis* sp. nov. in appearance but can be distinguished by being strongly expanded at about middle of lateral margins in dorsal view (Fig. 9). In contrast, *T. sillaensis* sp. nov. has a very feebly curved median lobe in dorsal view (Fig. 7).

Moreover, *T. jejudoensis* sp. nov. resembles *T. furunoi* Hoshina, 2008 in appearance but can be distinguished by median lobe of aedeagus with a small nipple at the apex in dorsal view (Fig. 9). In contrast, *T. furunoi* has a median lobe broadly rounded at the apex (Fig. 12).

**Natural history.** The life history of *Typhlocolenis jejudoensis* Hoshina & Park, sp. nov. is not known.

### Notes of the distribution of *Typhlocolenis*

The genus *Typhlocolenis* is distributed only in East Asia (Fig. 15). Among all five species of *Typhlocolenis*, *T. uenoi* Hoshina, 2008 has been collected only in caves (Hoshina 2008). Others have generally been collected in litter layers of forests, although *T. fusca* specimens have sometimes been found in caves (Hoshina 2008). Currently, the two species of *Typhlocolenis* have not been concurrently collected at one location. It is possible that the two Korean species, *T. sillaensis* sp. nov. and *T. jejudoensis* sp. nov. are endemic to the mainland of South Korea and Jeju Island, respectively (Fig. 15).

### Acknowledgments

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# The Stoor Hobbit of Guangdong: *Goniurosaurus gollum* sp. nov., a cave-dwelling Leopard Gecko (Squamata, Eublepharidae) from South China

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## Abstract

A new species of the genus *Goniurosaurus* is described based on three specimens collected from a limestone cave in Huaiji County, Guangdong Province, China. Based on molecular phylogenetic analyses, the new species is nested within the *Goniurosaurus yingdeensis* species group. However, morphological analyses cannot ascribe it to any known species of that group. It is distinguished from the other three species in the group by a combination of the following characters: scales around midbody 121–128; dorsal tubercle rows at midbody 16–17; presence of 10–11 precloacal pores in males, and absent in females; nuchal loop and body bands immaculate, without black spots; iris orange, gradually darker on both sides. The discovery of yet another limestone-adapted species of *Goniurosaurus* in Guangdong Province underscores a growing body of evidence for the high biodiversity of limestone habitats and brings into sharp focus the urgent need for their conservation.

## Keywords

*Goniurosaurus gollum* sp. nov., karst, limestone cave, taxonomy, systematics

\* Contributed equally as the first authors.

## Introduction

The eublepharid genus *Goniurosaurus* Barbour, 1908, currently contains 22 species that are scattered throughout much East and northern Southeast Asia (Uetz et al. 2020; Zhu et al. 2020; Qi et al. 2020). All species of *Goniurosaurus* have generally restricted, circumscribed ranges and many are restricted to habitats with either granite or limestone (karst) rock (Wang et al. 2014; Liang et al. 2018; Qi et al. 2020). Recent molecular phylogenetic analyses resulted in the partitioning of *Goniurosaurus* into four monophyletic species groups (Liang et al. 2018 ; Qi et al. 2020; Zhu et al. 2020), namely the *G. kuroi* group, *G. lichtenfelderi*, *G. lui* and, *G. yingdeensis* groups. The morphological comparisons also sustain the recognition of the *G. kuroi* and *G. yingdeensis* groups, however, the definitions of the *G. lichtenfelderi* and *G. lui* groups still require clarification (Qi et al. 2020).

Currently, three narrowly distributed species within the *Goniurosaurus yingdeensis* group are known from the karst environments of northern Guangdong, China: *G. yingdeensis* Wang, Yang & Cui, 2010, *G. zhelongi* Wang, Jin, Li & Grismer, 2014 and *G. varius* Qi, Grismer, Lyu, Zhang, Li & Wang, 2020. These three species share consistent morphological features that differentiate them from species of the other groups: (1) base of claws sheathed by four scales, two lateral scales of claw short and shell-shaped; (2) precloacal pores fewer than 15 in males and absent in most females (precloacal pores present in females in *G. yingdeensis* only); precloacal pores form a continuous transverse series not extending onto the femora; (3) enlarged row of supraorbital tubercles indistinct or absent; (4) nuchal loop rounded posteriorly; and (5) four body bands between the nuchal loop and the caudal constriction.

During our herpetological surveys in Guangdong Province, China, three specimens of *Goniurosaurus* were collected from a new locality during May 2020. Morphological and molecular analyses place this new population within the *Goniurosaurus yingdeensis* group but cannot ascribe them to any of the known species. We therefore describe this population as a new species.

## Materials and methods

### Sampling

Three specimens of the undescribed species were collected from Huaiji County, Guangdong Province, China. Following euthanasia, all specimens were fixed in 10% formalin and transferred to 75% alcohol. Tissue samples were preserved in 99% alcohol and stored at -40 °C. All specimens are deposited in The Museum of Biology, Sun Yat-sen University (SYS). Sequences of other species of *Goniurosaurus* generated by Qi et al. (2020) were accessed from GenBank.

## Morphological characters

Measurements were taken following Ziegler et al. (2008) using digital calipers (Neiko 01407A Stainless Steel 6-Inch Digital Caliper, USA) to the nearest 0.1 mm. Abbreviations of morphological characters are as follows: **SVL** snout-vent length (from tip of snout to vent); **TaL** tail length (from vent to tip of tail); **HL** head length (from tip of snout to posterior margin of ear opening); **HW** maximum head width; **SE** snout-to-eye distance (measured from tip of snout to the boney anterior margin of the orbit); **EE** eye-to-ear distance (from the boney posterior margin of the orbit to posterior margin of ear opening); **SPL** supralabials; **IFL** infralabials; **N** nasal scales surrounding nare; **IN** internasals; **PostIN** granular scales bordering the internasals; **PM** postmentals; **GP** gular scales bordering postmentals; **CIL** eyelid fringe scales or ciliaria; **PO** preorbital scales (number of scales in a line from posterior margin of external naris to anterior margin of the boney orbit); **GST** granular scales surrounding dorsal tubercles; **PTL** paravertebral tubercles between limb insertions; **DTR** longitudinal dorsal tubercle rows at midbody; **MB** scales around midbody; **PP** preloacal pores; **PAT** postloacal tubercles. Bilateral scale counts are given as left/right.

Morphological character data of known congeners were taken from the literature (Grismer et al. 1999, 2002; Orlov et al. 2008; Ziegler et al. 2008; Blair et al. 2009; Wang et al. 2010, 2013, 2014; Yang and Chan 2015; Zhou et al. 2018; Qi et al. 2020; Zhu et al. 2020) and from 34 examined museum specimens of the eight species listed in the Appendix.

## DNA Extraction, Polymerase Chain Reaction (PCR), and sequencing

Genomic DNA was extracted from muscle tissue samples, using a DNA extraction kit from Tiangen Biotech (Beijing) Co., Ltd. Partial segments of the mitochondrial genes 16S ribosomal RNA gene (16S) and Cytochrome b gene (Cytb) were amplified. Primers used for 16S were r16S-5L (5'-GGTMMYGCCTGCCCAGTG-3') and 16sbr-H (5'-CCGGTCTGAACTCAGATCACGT-3') (Palumbi et al. 1991) and for Cytb the primers were L14731 (5'-TGGTCTGAAAAACCATTGTTG-3') (Honda et al. 2014) and H15149m (5'-GCMCCTCAGAAKGATATTTGYCCTCA-3') (Chambers and MacAvoy 1999). The PCR procedure was performed with an initial denaturation at 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 55 °C for 30 s and 72 °C for 1 min, followed by a final extension at 72 °C for 10 min (Liang et al. 2018). PCR products were purified with spin columns and then sequenced with forward primers using BigDye Terminator Cycle Sequencing Kit as per the guidelines on an ABI Prism 3730 automated DNA sequencer by Shanghai Majorbio Bio-pharm Technology Co., Ltd.

## Phylogenetic analysis

Fifty-one sequences from 13 known *Goniurosaurus* species plus one outgroup sequence from the eublepharid *Hemitheconyx taylori* Parker, 1930, which was used to root the

**Table 1.** Localities, voucher information, and GenBank accession numbers for all specimens used in this study.

Species name	Locality	Specimen voucher	16S	Cytb	References
<b>Ingroup: <i>Goniurosaurus</i></b>					
<b><i>Goniurosaurus yingdeensis</i> species group</b>					
(1) <i>Goniurosaurus gollum</i> sp. nov.	Huaiji, Guangdong, China	SYS r002420	MT995784	MT995787	This study
(2) <i>Goniurosaurus gollum</i> sp. nov.	Huaiji, Guangdong, China	SYS r002421	MT995785	MT995788	This study
(3) <i>Goniurosaurus gollum</i> sp. nov.	Huaiji, Guangdong, China	SYS r002422	MT995786	MT995789	This study
(4) <i>G. varius</i>	Yangshan, Guangdong, China	SYS r002330	MT995753	MT995768	Qi et al. 2020
(5) <i>G. varius</i>	Yangshan, Guangdong, China	SYS r002331	MT995754	MT995769	Qi et al. 2020
(6) <i>G. varius</i>	Yangshan, Guangdong, China	SYS r002333	MT995755	MT995770	Qi et al. 2020
(7) <i>G. varius</i>	Yangshan, Guangdong, China	SYS r002362	MT995756	MT995771	Qi et al. 2020
(8) <i>G. varius</i>	Yangshan, Guangdong, China	SYS r002363	MT995757	MT995772	Qi et al. 2020
(9) <i>G. yingdeensis</i>	Yingde, Guangdong, China	SYS r001271	MT995759	MT995774	Qi et al. 2020
(10) <i>G. yingdeensis</i>	Yingde, Guangdong, China	SYS r001272	MT995760	MT995775	Qi et al. 2020
(11) <i>G. yingdeensis</i>	Yingde, Guangdong, China	SYS r001493	MT995761	MT995776	Qi et al. 2020
(12) <i>G. yingdeensis</i>	Yingde, Guangdong, China	SYS r002115	MT995762	MT995777	Qi et al. 2020
(13) <i>G. zhelongi</i>	Yingde, Guangdong, China	SYS r000816	KJ423105	MT995778	Wang et al. 2014; Qi et al. 2020
(14) <i>G. zhelongi</i>	Yingde, Guangdong, China	SYS r001491	MT995763	MT995779	Qi et al. 2020
(15) <i>G. zhelongi</i>	Yingde, Guangdong, China	SYS r001492	MT995764	MT995780	Qi et al. 2020
(16) <i>G. zhelongi</i>	Yingde, Guangdong, China	SYS r002108	MT995765	MT995781	Qi et al. 2020
<b><i>Goniurosaurus luei</i> species group</b>					
(17) <i>G. huiliensis</i>	Vietnam	N/A	AB853453	AB853479	Honda et al. 2014
(18) <i>G. liboensis</i>	Libo, Guizhou, China	SYS r000217	KC900230	N/A	Wang et al. 2013
(19) <i>G. luei</i>	Jingxi, Guangxi, China	SYS r000255	KC765083	N/A	Wang et al. 2013
(20) <i>G. luei</i>	Jingxi, Guangxi, China	SYS r000256	KC765084	N/A	Wang et al. 2013
(21) <i>G. luei</i>	Cao Bang, Vietnam	ZFMK 87057	EU499391	N/A	Ziegler et al. 2008
<b><i>Goniurosaurus lichtenfelderi</i> species group</b>					
(22) <i>G. bawanglingensis</i>	Bawangling, Hainan, China	SYS r002162	MT995758	MT995773	Qi et al. 2020
(23) <i>G. bawanglingensis</i>	Bawangling, Hainan, China	BL-RBZ-021	MH247190	MH247201	Liang et al. 2018
(24) <i>G. hainanensis</i>	Jianfengling, Hainan, China	SYS r000349	KC765080	N/A	Wang et al. 2013
(25) <i>G. zhoui</i>	Central area, Hainan, China	SYS r002213	MT995766	MT995782	Qi et al. 2020
(26) <i>G. zhoui</i>	Central area, Hainan, China	SYS r002214	MT995767	MT995783	Qi et al. 2020
(27) <i>G. zhoui</i>	Central area, Hainan, China	BL-RBZ-001	MH247196	MH247207	Liang et al. 2018
<b><i>Goniurosaurus kuroiwae</i> species group</b>					
(28) <i>G. kuroiwae</i>	Northern Okinawajima Island, Japan	N/A	AB853448	AB853473	Honda et al. 2014
(29) <i>G. orientalis</i>	Iejima Island, Japan	N/A	AB853446	AB853467	Honda et al. 2014
(30) <i>G. splendens</i>	Tokunoshima Island, Japan	N/A	AB853451	AB853477	Honda et al. 2014
(31) <i>G. yamashinae</i>	Kumejima Island, Japan	N/A	AB853442	AB853460	Honda et al. 2014
<b>Outgroup</b>					
(32) <i>Hemitheconyx taylori</i>	East Africa	N/A	AB308457	N/A	Jonniaux and Kumazawa 2008

tree, were obtained from GenBank and composed the dataset (Table 1). DNA sequences were aligned by the Clustal W with default parameters (Thompson et al. 1997) and trimmed with gaps partially deleted in MEGA 6 (Tamura et al. 2013). Two gene segments, with 486 base pairs (bp) of 16S and 396 bp of Cytb, were concatenated seriatim into an 882 bp sequence, and further divided into two partitions based upon each gene. The partitions were tested in jmodeltest v2.1.2 with Akaike and Bayesian information criteria, all resulting the best-fitting nucleotide substitution models of GTR+I+G. Sequence data were analyzed using Bayesian inference (BI) in

MrBayes 3.2.4 (Ronquist et al. 2012), and maximum likelihood (ML) in RaxmlGUI 1.3 (Silvestro and Michalak 2012). Two independent runs were conducted in the BI analysis with 10,000,000 generations each and sampled every 1000 generations with the first 25% of samples discarded as burn-in, resulting in a potential scale reduction factor (PSRF) of  $< 0.005$ . In the ML analysis, a bootstrap consensus tree inferred from 1000 replicates was generated. Nodes with Bayesian posterior probabilities (BPP)  $\geq 0.95$  and ML support values of  $\geq 70$  were considered strongly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002). Uncorrected pairwise sequence divergences utilizing the 16s gene were calculated using MEGA 6.

## Results

The ML and BI analyses resulted in identical topologies (Fig. 1) and maintained a high degree of consistency with recent molecular phylogenetic analyses (Liang et al. 2018; Qi et al. 2020). Uncorrected pairwise sequence divergences are reported in Table 2. The phylogenetic analyses support previous analyses indicating that *Goniurosaurus* can be divided into four strongly supported clades, namely the *G. kuroiwa* group, *G. lichtenfelderi* group, *G. luii* group and the *G. yingdeensis* group. The *Goniurosaurus yingdeensis* group is composed of four species with genetic differences among them ranging from 5.5–5.9%. Three of the species are *G. varius*, *G. yingdeensis* and *G. zhelongi* and the fourth species is composed of the individuals of the new population from Guangdong Province. All specimens were recovered as monophyletic with a high nodal support (1.00 in BI and 100 in ML) and low intrapopulation genetic differentiation (0.0–0.5%; Table 2). But due to low nodal support, the phylogenetic relationships among *G. varius*, *G. yingdeensis* and *G. zhelongi* are still unclear. Additionally, the Guangdong population has a combination of morphological characteristics distinguishing it from other species in the *G. yingdeensis* group as well as showing significant morphological differences from all known congeners. Thus, we hereby describe the specimens from Guangdong Province as a new species.

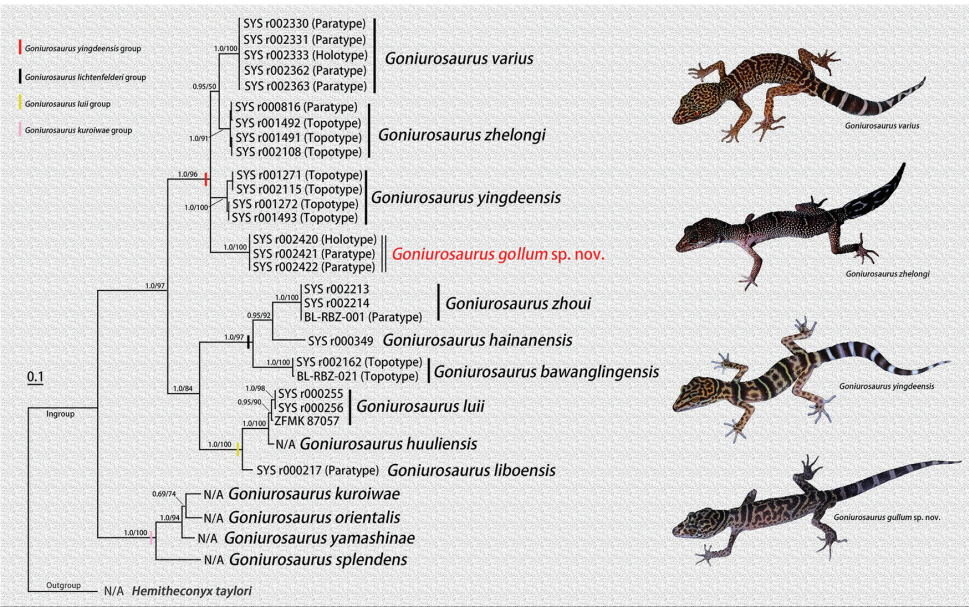
### *Goniurosaurus gollum* Qi, Wang, Grismer, Lyu & Wang, sp. nov.

<http://zoobank.org/C1369EA0-37AB-457C-89C8-E98ED643E1E4>

Figs 2, 3, 4A, 5

**Material examined.** *Holotype*. SYS r002420, adult male (Figs 2, 3A, 4A, 5), collected by Shuo Qi, Jian Wang and Hong-Hui Chen on 21 May 2020 from Huaiji County, Zhaoqing City, Guangdong Province, China. Exact locality available to only qualified researchers upon request. *Paratypes*. One adult male (SYS r002421) and one adult female (SYS r002422) share the same collection information as the holotype.

**Diagnosis.** *Goniurosaurus gollum* sp. nov. can be distinguished from all other congeners by the following combination of characters: (1) adult body size moderate, 91.0–93.4 mm

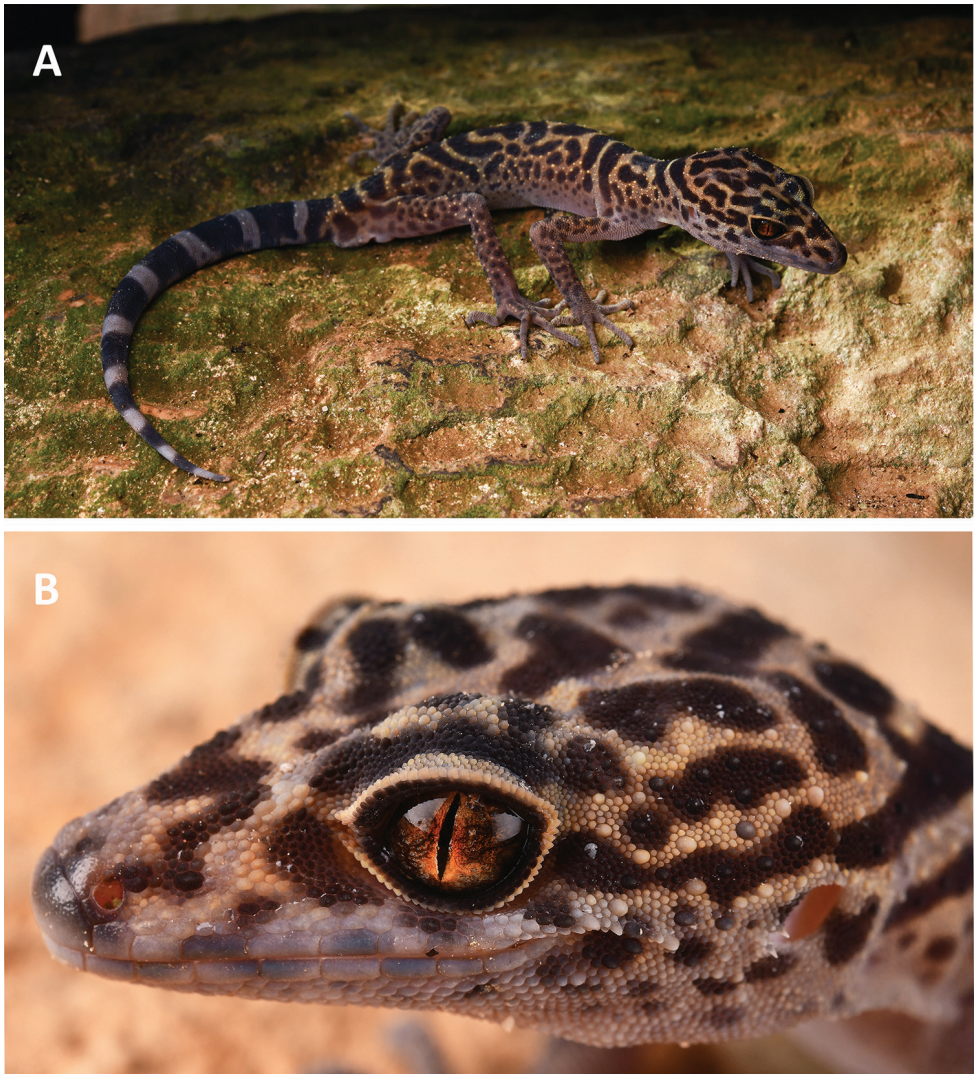


**Figure 1.** Bayesian inference tree of 14 species of *Goniurosaurus*, based on the partial DNA sequences of the mitochondrial 16S rRNA and Cytb genes. *Hemitheconyx taylori* is the outgroup. Numbers before slash indicate Bayesian posterior probabilities (BPP) and numbers after slash are bootstrap support for ML (1000 replicates) analyses.

**Table 2.** Uncorrected *P*-distance of 16S gene among 14 *Goniurosaurus* species used in this study.

ID		1–3	4–8	9–12	13–16	17	18	19–21	22–23	24	25–27	28	29	30	31
1–3	<i>Goniurosaurus gollum</i> sp. nov.	0–0													
4–8	<i>G. varius</i>	5.6	0–0.1												
9–12	<i>G. yingdeensis</i>	5.9	4.2	0–0.3											
13–16	<i>G. zhelongi</i>	5.5	3.3	4.7	0–0.2										
17	<i>G. huuliensis</i>	17.4	12.9	15.5	14.5	/									
18	<i>G. liboensis</i>	15.7	13.1	13.4	13.5	6.1	/								
19–21	<i>G. luii</i>	16.4	13.9	14.5	14.7	1.4	5.9	0–0.5							
22–23	<i>G. bawanglingensis</i>	17.3	15.9	16.8	15.8	17.4	14.5	17.3	0–0.3						
24	<i>G. hainanensis</i>	17.3	16.6	16.6	17.9	14.8	14.5	15.3	8.3	/					
25–27	<i>G. zhoui</i>	16.7	16.3	18.1	17.3	16.1	16.5	17.2	7.0	7.5	0–0				
28	<i>G. kuroiwae</i>	22.7	21.2	20.3	22.4	22.2	23.4	21.5	18.7	18.9	18.9	/			
29	<i>G. orientalis</i>	21.3	18.5	18.2	19.6	21.3	22.2	21.3	19.6	19.8	18.8	3.6	/		
30	<i>G. splendens</i>	21.9	19.7	19.0	21.8	22.9	23.3	22.2	19.8	18.1	20.2	7	7.9	/	
31	<i>G. yamashinae</i>	22	18.5	18.8	19.9	21.4	22.9	22	20.3	19.1	19.2	3.7	3.1	7	/

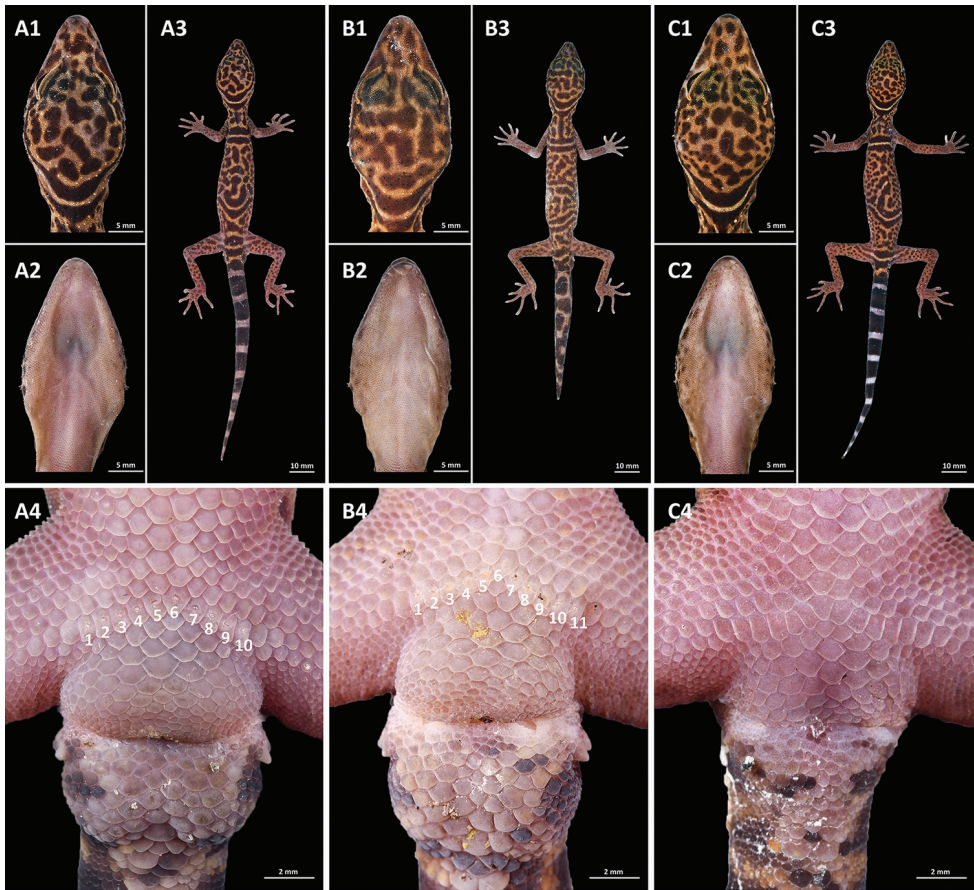
SVL; (2) nasal scales surrounding nares seven or eight; (4) internasal single; (5) eyelid fringe scales 59–63; (6) granular scales of upper eyelids similar in size to those on top of head; (7) scales around midbody 121–128; (8) longitudinal dorsal tubercle rows at midbody 16 or 17; (9) paravertebral tubercles between limb insertions 25 or 26; (10) claws sheathed by



**Figure 2.** **A** The general aspect of the adult male holotype of *Goniurosaurus gollum* sp. nov. (SYS r002420) in life **B** scalation and coloration characters of the head of the holotype. Photographs by Shuo Qi.

four scales, dorsal claw scales small, two lateral claw scales short and shell-shaped; (11) axillary pockets deep; (12) presence of 10 or 11 precloacal pores in males and absent in females; (13) dorsal ground color of head, body, and limbs in adults yellowish brown and mottled with irregularly shaped dark-brown blotches; (14) nuchal loop complete, rounded posteriorly; (15) presence of three or four thin dorsal body bands between nuchal loop and caudal constriction, with black anterior and posterior borders, bands usually irregularly shaped; (16) iris orange, gradually darker on both sides.

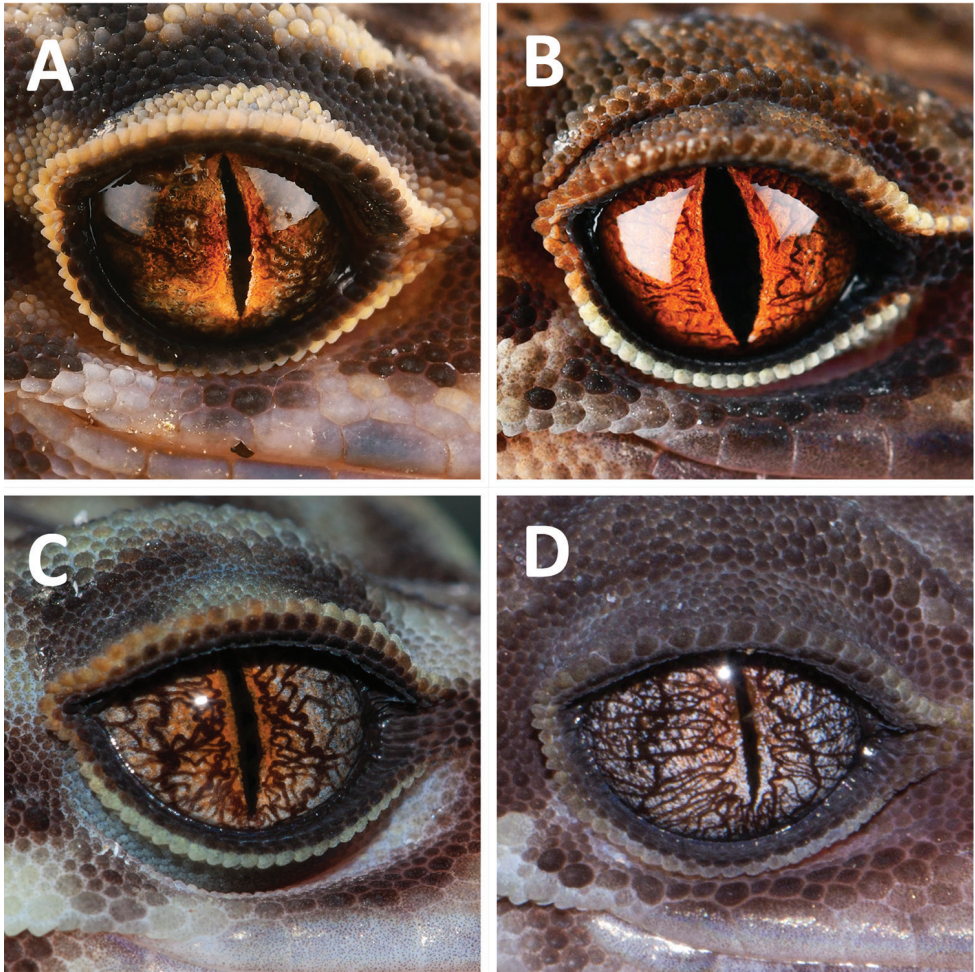
**Comparisons.** *Goniurosaurus gollum* sp. nov. can be distinguished from the other 21 known species in the genus by the following combination of characters: base of



**Figure 3.** Type series of *Goniurosaurus gollum* sp. nov. **A** holotype, male, SYS r002420 **B** paratype, male, SYS r002421 **C** paratype, female, SYS r002421; (1) dorsal view; (2) dorsal view of head; (3) ventral view of head; (4) close-up of the precloacal region, the Arabic number refer to the number of precloacal pores. Photographs by Shuo Qi.

claws being sheathed by four scales, two lateral claw scales short and shell-shaped (vs. claws sheathed by four scales, two lateral scales of claw long, curved in *G. lichtenfelderi* group and *G. luii* group, and not sheathed in *G. kuroiwa* group); having 10 or 11 precloacal pores in males (vs. 17–46 in *G. lichtenfelderi* group, 16–33 in *G. luii* group and absent in *G. kuroiwa* group); and lacking an enlarged row of supraorbital tubercles (present in *G. lichtenfelderi* group and *G. luii* group).

*Goniurosaurus gollum* sp. nov. can be distinguished from its closest relatives in the *Goniurosaurus yingdeensis* group by the following combination of characters: scales around midbody 121–128 (vs. 101–110 in *G. varius*, 101–116 in *G. yingdeensis*, 99–109 in *G. zhelongi*); longitudinal dorsal tubercle rows at midbody 16 or 17 (vs. 21–24 in *G. varius*, 20–25 in *G. yingdeensis*, 23–28 in *G. zhelongi*); absence of ten precloacal pores in females (vs. present in *G. yingdeensis*); nuchal loop and body bands im-



**Figure 4.** Comparisons of iris color with three closely related congeners **A** *Goniurosaurus gollum* sp. nov. (holotype, SYS r002420) **B** *Goniurosaurus varius* (holotype, SYS r002333) **C** *Goniurosaurus yingdeensis* (holotype SYSr000504) **D** *Goniurosaurus zhelongi* (holotype, SYS r000770). Photographs by Shuo Qi and Ying-Yong Wang.

maculate (vs. having black spots in *G. varius*); iris orange, gradually darker on both sides (vs. iris orange-red in *G. varius*, iris gray and becoming orange near the pupil in *G. yingdeensis*, iris gray-white and tinged with orange in *G. zhelongi*). Additional comparisons of morphological characteristics are provided in Table 4 and Figure 4.

**Description of holotype.** Adult male with original tail; SVL 93.4 mm; HL 24.2 mm; HW 16.2 mm; SE 9.3 mm; EE 9.3 mm; SVL:HL 3.9; HL:HW 1.5; SE:EE 1. Head triangular, wider than neck, covered with granular scales, densely interspersed with tubercles in the temporal and occipital regions; area between orbits uniformly covered by small granular scales; supraorbital tubercles nearly uniform in size; scales of

rostrum slightly larger than those in between orbits; rostral convex and hemi-elliptic, 1.8 times as broad as high, middorsal portion of rostral partially sutured dorsomedially, bordered laterally by first supralabial and prenasal, dorsolaterally by supranasal, dorsally by one internasal; external nares oval, surrounded by 8/9 nasals each, anteriorly by prenasal and supranasal, dorsally by supranasal and a granular scale, posteriorly by 7/8 smaller granular scales, and ventrally by the prenasal; prenasal with long recurved ventral portion; supranasals large, separated by one internasals; supralabials rectangular, 10/10; preorbital scales 16/17; eyes relatively large, pupils vertical; eyelid fringe scales 59/60; outer surface of upper eyelid composed of granular scales of about same size of those on top of head; external auditory meatus circular, tympanum deeply recessed; mental triangular, bordered laterally by first infralabial and posteriorly by three postmentals; infralabials rectangular, 10/10; gular scales juxtaposed uniform granular, abruptly into flat juxtaposed pectoral scales, and grading posteriorly imbricated larger ventral scales. Tongue with a small notch at tip. Crowns of teeth expanded, occlusal margins bearing multiple ridges.

Dorsal surface of neck and body covered with uniform granular scales, interspersed with densely sharply pointed conical tubercles; scales around midbody 125; longitudinal rows of dorsal tubercles at midbody 16; vertebral row of scales indistinct; paravertebral tubercles between limb insertions 25; dorsal body tubercles surrounded by 9–10 granular scales; dorsal scales grading ventrally into larger flattened imbricate ventral scales; ten precloacal pores in a transverse series; postcloacal region greatly swollen, covered with imbricate flattened scales, containing 2/2 postcloacal tubercles laterally at level of the vent.

Tail original, long and thin, thickest at base, bearing whorls anteriorly, gradually narrowing to the tip; composed of nine recognizable annuli anteriorly that are 8–9 scales wide, annuli fade abruptly posteriorly into flat juxtaposed scales; incorporating 2–8 sharply pointed conical tubercles in a transverse row, tubercles do not encircle the tail; ventral caudals larger and more nearly square than dorsal caudals.

Limbs relatively long and slender; dorsal surface covered with granular scales, densely interspersed with tubercles; ventral surface covered by flat scales, juxtaposed, subimbricate or imbricate; dorsal surface of pes and manus covered with granular scales, interspersed with several conical tubercles on top of pes, lacking tubercles on top of manus; hind limbs slightly larger than forelimbs; ventral surfaces of pes and manus covered with large granular scales; axillary pockets deep; subdigital lamellae wide, 10/10 on Finger I, 12/14 on Finger II, 15/16 on Finger III, 16/14 on Finger IV, 13/14 on Finger V, 12/12 on Toe I, 15/ 16 on Toe II, 20 / 19 on Toe III, 22 / 23 on Toe IV, and 18 / 20 on Toe V; fingers laterally compressed, relative finger lengths  $I < V < II < IV < III$ ; toes laterally compressed, third toe nearly as long as the fourth toe, relative toe length  $I < II < V < III < IV$ ; base of claws sheathed by four scales, two lateral scales of claw short, asymmetrical shell-shaped.

**Coloration in life.** Dorsal ground color of head, neck, body, and limbs yellowish brown, mottled with irregularly shaped dark-brown blotches; nuchal loop complete and rounded posteriorly, anterior ends terminating at posterior margins of ear openings,

**Table 3.** Mensural (mm) and meristic diagnostic characters (minimum/maximum) of type series of *Goniurosaurus gollum* sp. nov. See Materials and methods for abbreviations. \* holotype, # paratype.

Morphological character	SYS r002420 *	SYS r002421 #	SYS r002422 #
Sex	male	male	female
SVL	93.4	93.3	91.0
TaL	83.5	Regenerated	76.0
HL	24.2	24.0	23.3
HW	16.2	15.3	14.8
SE	9.3	9.3	9.1
EE	9.3	9.4	8.6
SPL	10/10	10/10	10/10
IFL	10/10	10/10	10/10
N	8/9	9/8	8/9
IN	1	1	1
PostIN	2	2	2
PM	2	3	3
GP	7	8	8
CIL	59/60	59/61	63/63
PO	16/17	15/15	16/17
GST	9–10	9–10	9–11
PTL	25	26	25
DTR	16	16	17
MB	125	121	128
PP	10	11	Absent
PAT	2	2	2

edged dorsally and ventrally by wide dark-brown margin, yellow. Only two complete body bands can be recognized between nuchal loop and caudal constriction: first band located posterior to axilla; second band inserts onto dorsal surface of thigh, bands on limbs dirty yellow, lacking dark spots, edged by broad dark-brown borders anteriorly and posteriorly, other blotches incomplete, not forming a complete bands. Supralabials and infralabials grayish brown; pupils vertical and appear black; iris orange, gradually darkening on both sides; dorsal surface of limbs light grayish brown with dark brown and dirty yellow tubercles and dark spots and blotches; chin, throat, thorax, and ventral surfaces of body pink, tinged brownish, with dark-brown lateral spots; ventral surface of limbs pink, tinged brownish, without dark-brown spots; digits light grayish brown; ground color of original tail dark brown with nine immaculate white caudal bands completely encircling the tail, and a white tip. Body color becomes darker after capture.

**Coloration in preservative.** Dorsal ground color of head, body, and limbs become darker; ventral surface faded to grayish white; all darker spots, blotches and bands on dorsal surface blurred.

**Variations.** Measurements of type series specimens are shown in Table 3. Two paratypes have same approximate measurements as holotype, but have significant variations in coloration. Male paratype (SYS r002421, Fig. 3B) has four body bands, the second band extending a three forked branch connecting with third band. Female paratype (SYS r002422, Fig. 3C) has three complete body bands, second band extending a branch forward to middle of body, original tail has ten immaculate white caudal bands completely encircling tail, and dark-brown tip.



**Figure 5.** The holotype of *Goniurosaurus gollum* sp. nov. (SYS r002420) at its habitat: a barren limestone cave of Guangdong, China. Photograph by Shuo Qi.

**Table 4.** Diagnostic characters distinguishing *Goniurosaurus gollum* sp. nov. from all other known species of *Goniurosaurus*. Data come from Grismer et al. 1999, 2002; Orlov et al. 2008; Ziegler et al. 2008; Blair et al. 2009; Wang et al. 2010, 2013, 2014; Yang and Chan 2015; Zhou et al. 2018; Qi et al. 2020; Zhu et al. 2020.

Character	<i>G. yingdeensis</i> group (4 species)						
	<i>G. kuvoivae</i> group (5 spp.)	<i>G. lichtenfelderi</i> group (5 spp.)	<i>G. luii</i> group (7 spp.)	<i>Goniurosaurus gollum</i> sp. nov.	<i>G. varius</i>	<i>G. yingdeensis</i>	<i>G. zhelongi</i>
Scales of upper eyelid one-half the size of scales on the top of head or equal in size	Equal	Equal	Equal or 1/2	Equal	Equal	Equal	Equal
Enlarged row of supraorbital tubercles	Absent	Absent or present	Absent or present	Absent	Absent	Absent or indistinct	Absent or indistinct
Eyelid fringe scales	<52	43–77	41–67	59–63	50–56	46–64	42–53
No. of paravertebral tubercles	Unknown	23–36	27–38	25–26	27–29	22–33	28–33
Dorsal tubercle rows at midbody	Unknown	19–22	20–25	16–17	21–24	20–25	23–28
Scales around midbody	Unknown	95–140	112–147	121–128	101–110	101–116	99–109
Nasal scales surrounding nares	Unknown	8–9	5–9	7–8	7–9	7–11	6–8
Internasals	Unknown	1	0–3	1	1–2	1–3	1–2
Tubercles between orbits	Present or absent	Present or absent	Present or absent	Absent	Present	Present	Absent
Claws sheathed by scales	Absent	Present	Present	Present	Present	Present	Present
Lateral scales of claw sheaths	Absent	Long, curved	Long, curved	Short, shell-shaped	Short, shell-shaped	Short, shell-shaped	Short, shell-shaped
No. of preloatal pores in males	0	17–46	16–33	10–11	10	10–13	9–12
Posterior shape of nuchal loop	Rounded	Protracted or rounded	Protracted	Rounded	Rounded	Rounded	Rounded
No. of body bands between nuchal loop and the caudal constriction	3 or 4	3 or 4	3, 4 or 5	2, 3 or 4	4	4	4
Dark spotting in body bands	Present or absent	Present or absent	Present or absent	Absent	Present or absent	Absent	Absent
Lateral spotting on belly present or absent	Absent	Absent	Present or absent	Present	Present	Present	Present

**Etymology.** The specific epithet “*gollum*” is named after the fictional character, Gollum, from J.R.R. Tolkien’s *The Lord of the Rings* book series. This new species and Gollum have similar cave-dwelling habit and emaciated body. We suggest the common name as “Gollum Leopard Gecko”, and according to the type locality, we suggest the Chinese formal name as “guǎng dōng jiǎn hǔ” (广东睑虎).

**Distribution and ecology.** Currently, *Goniurosaurus gollum* sp. nov. is known only from Huaiji County, Guangdong Province, China. All individuals were found within a barren limestone cave approximately 50 m from the cave entrance at night after 2130 hrs (Fig. 5). The surface of the cave is covered with bat (unidentified) and bird (*Apus pacificus*) droppings. Stalactites are suspended from the roof and there is no vegetation. *Duttaphrynus melanostictus* was observed in the same area.

## Discussion

With the description of *Goniurosaurus gollum*, there are now 23 known species in the eublepharid genus *Goniurosaurus*, 15 of which occur in China. The *G. yingdeensis* group is endemic in Guangdong Province, with only two species recognized previously, but the discoveries of *G. varius* (Qi et al. 2020) and *G. gollum* adds to this and indicates there might be more new species yet to be discovered.

Although the species of *Goniurosaurus* are also called “cave geckos”, they prefer inhabiting the forest floor, limestone cliffs, rocky and cement drains along the road, and near the entrances of caves. However, the cave-dwelling species *G. gollum* appears to be a true cave dweller as opposed to other *Goniurosaurus*. The fact that all three specimens were found at least 50 m inside the cave from its entrance supports this hypothesis.

These results support the growing body of evidence from China (Luo et al. 2016) and elsewhere (Grismer et al. 2016 and references therein) that karstic habitats not only provide a substrate for the evolution of new species—especially gekkotan lizards—but maintain levels of biodiversity that rival that of other tropical habitats. Yet they are some of the most imperiled and least protected habitats in the world (Day and Urich 2000; Gillieson 2005). The discovery of yet another new species in the vast karstic landscape of northern Guangdong underscores this fact and brings into sharp focus the urgent need to protect these unique landscapes. We aim to protect *G. gollum* from the pet trade, by withholding its precise locality. However, these data are available to qualified researchers upon official request to The Museum of Biology, Sun Yat-sen University.

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## Appendix

### Examined specimens

*Goniurosaurus bawanglingensis* ( $N = 3$ ): China: Hainan Province: Bawangling National Nature Reserve: SYS r001075, 1670, 2162.

*Goniurosaurus hainanensis* ( $N = 2$ ): China: Hainan Province: Jianfengling National Forest Park: SYS r000349; Baoting County: SYS r001270.

*Goniurosaurus liboensis* ( $N = 3$ ): China: Guizhou Province: Libo County: Maolan National Nature Reserve: SYS r000217, 854, 855.

*Goniurosaurus luii* ( $N = 4$ ): China: Guangxi Zhuang Autonomous Region: Jingxi City: SYS r000255, 256, 859, 860.

*Goniurosaurus varius* ( $N = 5$ ): China: Guangdong Province: Yangshan County: SYS r002330, 2331, 2333, 2362, 2363.

*Goniurosaurus yingdeensis* ( $N = 10$ ): China: Guangdong Province: Yingde City: SYS r000501, 503, 504, 535, 536, 550, 1271, 1272, 1493, 2115.

*Goniurosaurus zhelongi* ( $N = 5$ ): China: Guangdong Province: Yingde City: SYS r000816, 1491, 1492, 2011, 2108.

*Goniurosaurus zhoui* ( $N = 2$ ): China: Hainan Province: SYS r002213, 2214.

