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Taxonomic status of genera of Buccininae (Neogastropoda, Buccinidae) updated based on molecular data with description of new species and corrections of nomenclature of *Buccinum*

Yuri KANTOR [1,*], Boris SIRENKO [2], Sofya S. ZVONAREVA [3] & Alexander FEDOSOV [4]

[1,3,4] A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Leninsky prospect, 33, Moscow, 119071, Russia.
[2] Zoological Institute of Russian Academy of Sciences, Universitetskaya nab.1, St. Petersburg, 199034, Russia.

[*] Corresponding author: kantor.yuri1956@gmail.com
[2] Email: marine@zin.ru
[3] Email: sonyazv@mail.ru
[4] Email: FedosovAlexander@gmail.com

[1] urn:lsid:zoobank.org:author:48F89A50-4CAC-4143-9D8B-73BA82735EC9
[2] urn:lsid:zoobank.org:author:3646D12C-2475-403A-8EA7-4F2F1D5924EE
[3] urn:lsid:zoobank.org:author:EC81D276-0242-4B9F-AE04-A669D413B7FF
[4] urn:lsid:zoobank.org:author:22DD5413-60EF-4FBB-B78A-8C4950E84EFF

Abstract. The status of five genera recognized within subfamily Buccininae (Buccinidae) is critically re-assessed based on the molecular phylogenetic analysis of the *cox-1*, 16S, and 28S gene fragments. Our results suggest restoring *Volutharpa* P. Fischer, 1856 from synonymy of *Buccinum* and we also consider *Plicibuccinum* Golikov & Gulbin, 1977 as valid genus. New molecular data provide further support for the synonimization of *Bathybuccinum* Golikov & Sirenko, 1988 with *Buccinum* Linnaeus, 1758. Furthermore, our data demonstrate that *Thysanobuccinum* Golikov & Gulbin in Golikov, 1980 and *Ovulatibuccinum* Golikov & Sirenko, 1988 as currently construed are nested within *Buccinum* and their subgeneric rank is not confirmed. Therefore, we synonymize these genera with *Buccinum*. In the absence of molecular data the monotypic genus *Corneobuccinum* Golikov & Gulbin, 1977 is provisionally considered valid. Two new species, *Buccinum hasegawai* sp. nov. and *B. bizikovi* sp. nov. are described from the Kurile Islands; these species were previously erroneously identified as *Bathybuccinum bombycinum* (Dall, 1907) and *Ovulatibuccinum ovulum* (Dall, 1907), respectively. New replacement names are proposed for the secondary junior homonym *Buccinum perlatum* (Fraussen & Chino, 2009) and the primary junior homonyms *Buccinum coronatum* Golikov, 1980 and *Buccinum costatum* Golikov 1980.

Keywords. *cox-1*, 28S, 16S, Buccinoidea, deep-water species, Kurile Islands, Japan Sea.

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Introduction

The genus *Buccinum* Linnaeus, 1758 is one of the largest in the Neogastropoda Wenz, 1938 and currently encompasses more than 130 accepted recent species (MolluscaBase 2021). It is broadly distributed in the northern Hemisphere in temperate and Arctic waters from intertidal to abyssal depths and is characterized by high conchological variability, including adult size, shell shape, spiral and axial sculpture. Together with other recognized genera *Buccinum* comprises the subfamily Buccininae Rafinesque, 1815, and the subfamily was recovered as monophyletic within the family Buccinidae Rafinesque, 1815 in the recent multigene phylogeny of Buccinoidea Rafinesque, 1815 (Kantor *et al*. 2022). One of the characteristic features of *Buccinum* and of the subfamily Buccininae in general, is the oval concentric operculum with the nucleus situated usually sub-centrally, or rarely close to the operculum's edge, but never terminally.

In addition to *Buccinum* at least one genus, *Volutharpa* P. Fischer, 1856 has usually been included in the subfamily Buccininae, sometimes at the rank of a subgenus (Yamazaki *et al*. 2018). The taxonomic complexity of subfamily was recognized by Golikov & Gulbin (1977), who proposed new monotypical genera *Corneobuccinum* Golikov & Gulbin, 1977 for *Colus lepidus* Dall, 1918 and *Plicibuccinum* Golikov & Gulbin, 1977 for *Plicibuccinum plicatum* Golikov & Gulbin, 1977 (= *Buccinum ochotense declivis* Habe & Ito, 1976). Later Golikov (1980) in his comprehensive revision of the subfamily erected the subgenus *Buccinum* (*Thysanobuccinum*) Golikov & Gulbin in Golikov, 1980 for two species from the Kurile Islands and Okhotsk Sea and ranked *Volutharpa* as a subgenus of *Buccinum*. Further development of the system of the subfamily was proposed by Golikov & Sirenko (1988). They described the new genus *Bathybuccinum* Golikov & Sirenko, 1988, which, in addition to the nominotypical subgenus, included a new subgenus *Bathybuccinum* (*Ovulatibuccinum*). Furthermore, they introduced 22 subgenera of *Buccinum*. Later Golikov *et al*. (2001) considered *Volutharpa*, *Plicibuccinum*, *Corneobuccinum*, *Thysanobuccinum* Golikov & Gulbin in Golikov, 1980, and *Bathybuccinum* as genera and this ranking was followed by later authors (e.g., Kantor & Sysoev 2006; Hasegawa 2009). Fraussen & Chino (2009) revised the taxonomy of *Bathybuccinum* and *Ovulatibuccinum* Golikov & Sirenko, 1988, elevated *Ovulatibuccinum* to the full genus rank, and described two new species of *Bathybuccinum* and one new species of *Ovulatibuccinum*.

Molecular phylogenetic studies on the Buccininae are scarce. In several published papers that had a broader taxonomic focus and targeted the family Buccinidae in its traditional scope (before Kantor *et al*. 2022), a limited set of species or even single species of *Buccinum* were representing the subfamily (Hayashi 2005; Zhang & Zhang 2017). Using portions of the *cox-1* and 28S genes Vendetti (2009) performed an analysis of Buccinoidea from the Japan area, which included 11 species of *Buccinum* s.s. Most recently, ten species of Buccininae, including representatives of *Bathybuccinum*, *Ovulatibuccinum*, *Volutharpa*, *Thysanobuccinum*, and *Buccinum*, were included in the multigene analysis of buccinoidean phylogeny (Kantor *et al*. 2022). As a result of this analysis, *Volutharpa* and *Bathybuccinum* were synonymized with *Buccinum.* Yet, this work did not deal with the phylogeny and taxonomy of the Buccininae at the species level.

Recently new gastropod specimens collected off the Kurile Islands and the Japan Sea were made available to us through the courtesy of Drs Anastassya Maiorova and Alexei Chernyshev from the A.V. Zhirmunsky National Scientific Center of Marine Biology. This material represented several specimens of Buccinoidea, including type species of the genera *Volutharpa*, *Thysanobuccinum*, and *Plicibuccinum* as well, as several additional species that share diagnostic characters of *Ovulatibuccinum*. Therefore, we conducted a more detailed analysis of the subfamily based on the partial sequences of mitochondrial *cox-1,* 16S rRNA, and nuclear 28S rRNA genes in order to clarify the status and relationships of the previously and currently recognized genera of Buccininae.

Material and methods

Sampling

The crucial new samples were collected during the research cruises of R/V Akademik Oparin, 56th off the Kurile Islands in 2019, and 64th in the Japan Sea in 2021 (Table 1). The coding "Buc***" refers to the database of the specimens temporarily stored in IEE RAS and used for molecular phylogenetic studies.

We generated original sequences for 13 specimens of Buccininae in addition to ten specimens previously included in the analysis by Kantor *et al.* (2022), resulting in a final dataset with a total of 21 species based on conchological characters. Most of the specimens were identified to species level by comparison with the photographs of the relevant type specimens and original species descriptions. Holotypes of the new species are deposited in the Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russia (ZIN).

Additional non-sequenced material stored in the collections of ZIN was used to supplement descriptions of new species. This material was collected by four Russian expeditions off southeastern Sakhalin and the southern Kuril Islands: the Kuril-Sakhalin expedition on the F/T Toporok in 1949, on the R/V Odyssey in cruises 33 and 34 in 1984 and 1984–1985 respectively, and on the R/V Tikhookeanskiy in 1987. Bathymetric ranges are reported as inner values of the shallowest and deepest stations as suggested by Bouchet *et al*. (2008).

DNA extraction and PCR

Total DNA was extracted from small samples of foot muscle using Investigator Kit (Qiagen), following the manufacturer's recommendations. The barcode fragment of the Cytochrome Oxidase subunit I (*cox-1*) gene (658 bp) and standard fragments of 16S rRNA (~550 bp) and 28S rRNA (~715 bp) were amplified using the universal primer pairs LCO1490 – HCO2198 (Folmer *et al.* 1994), 16SH – 16LC (Palumbi et al. 1996) and C1 – D2 (Jovelin & Justine 2001) respectively. PCRs were performed in 20 µl final volume containing approximately 3 ng template DNA, 1.5 mM $MgCl_2$, 0.26 mM of each nucleotide, 0.3 µl of each primer, 5% BSA and 0.75 µl of BioHYTaq DNA polymerase (Dialat).

The PCR profile for *cox-1* started with 5 min at 95 °C followed by 40 cycles with denaturation at 95 °C (35 s), annealing at 50 °C (35 s) and elongation at 72 °C (1 min), with a final elongation phase at 72 °C (10 min). A similar PCR profile was set for 16S and 28S (annealing at 55 °C and 56 °C respectively). All amplicons were sequenced in both directions to confirm accuracy of each sequence. The sequencing was performed in the IEE RAS molecular facility on an ABI 3500 Genetic analyser or at Eurogen (Moscow).

Phylogenetic analysis

Novel nucleotide sequences of *cox-1*, 16S and 28S were first aligned using ClustalW implemented in BioEdit ver. 7.0.9.0 (Hall 1999), and then manually aligned to the single-gene datasets of Kantor *et al.* (2022). Then a ML analysis using IQtree ver. 2.1.1 (Nguyen *et al.* 2015) with the option -MFP-MERGE enabled for model selection, and with 1000 ultrafast Bootstrap iterations to evaluate nodal support (Minh *et al.* 2013) was performed for each single-gene data set and the resulting trees compared to ensure that they do not contain supported conflicting topologies. Then the three fragments were concatenated, the dataset comprised 237 taxa and 1964 nucleotide positions, which were coded as five ulinked partitions: three for each codon position of *cox-1*, and one for each, 16S, and 28S). For the

Table 1. List of examined material included in the molecular phylogenetic analysis. GB = GenBank. New sequences are highlighted in bold typeface. Abbreviations: see Material and methods.

IEE tissue clips numbers	Depository / GenBank (GB)	Catalog_N	Genus	species	Expedition, station	Locality	Coordinates	depth (m)	GB *cox-1*	GB 16S	GB 28S
Buc165	MSU	WS5301	*Buccinum* Linnaeus, 1758	*glaciale* Linnaeus, 1761		White Sea, Kandalaksha Bay	66°32′28″ N, 33°16′25″ E	30–35	MN752199	MN756789	MN756773
Buc175	AORI	AORI_YK#3402	*Buccinum* Linnaeus, 1758	sp. 2	KS-15-10, stn ON9-2	Off Onagawa, Miyagi, Honshu I., Japan	38°16′ N, 143°32′ E	3302–3311	MW181886	MW174105	MW174152
Buc187	AORI	AORI_YK#3989	*Buccinum* Linnaeus, 1758	*nipponense* Dall, 1907	KS-15-10, stn. OT4-2	Off Otsuchi, Iwate, Honshu Is., Japan	39º22′ N, 142°15′ E	479–484	MW181889	MW174109	MW174156
Buc188	AORI	AORI_YK#3992	*Buccinum* Linnaeus, 1758	*bicordatum* (Golikov & Sirenko, 1988)	KS-15-10, stn ON5	Off Onagawa, Miyagi, Honshu Is., Japan	38°25′ N, 142°00′ E	342–343	MW181888	MW174108	MW174155
Buc189	IEE		*Buccinum* Linnaeus, 1758	sp. 1	KS-15-1, stn 0 ON5	Off Onagawa, Miyagi, Honshu Is., Japan	38°25′ N, 142°00′ E	342–343	MW181887	MW174106	MW174153
Buc190	AORI	AORI_YK#3993	*Buccinum* Linnaeus, 1758	*chinoi* nom. nov.	KS-15-10, stn. ON5	Off Onagawa, Miyagi, Honshu I., Japan	38°25′ N, 142°00′E	342–343	MW181885	MW174104	MW174151
Buc206	MNHN	IM-2013-78012	*Buccinum* Linnaeus, 1758	*hydrophanum* Hancock, 1846	A13-2017, stn. 560	Iceland	67°41,5′ N, 23°01′ W	730–737	MW076988	MW067233	MW067164
Buc264	IEE		*Buccinum* Linnaeus, 1758	*tenuisulcatum* Golikov & Gulbin, 1977	R/V Oparin, cr.56, stn 68	Okhotsk Sea, Kurile Is., Onekotan I.	49°31.3′ N, 154°25.0′ E	571–580	**OM791438**	**OM778265**	**OM778274**
Buc265	IEE		*Buccinum* Linnaeus, 1758	*tunicatum* Golikov & Gulbin, 1977	R/V Oparin, cr.56, stn 7	Okhotsk Sea, Kurile Is., Urup I.	45°52.2′ N, 149°37.0′ E	142	**OM791440**	**OM778266**	**OM778275**
Buc266	IEE		*Buccinum* Linnaeus, 1758	*unicordatum* (Golikov &Sirenko, 1988)	R/V Oparin, cr.56, stn 28	Kurile Is., Iturup I., Prostor Bay	45°44.6′ N, 148°34.0′ E	264–270	**OM791441**	**OM778267**	**OM778276**
Buc269	IEE		*Buccinum* Linnaeus, 1758	cf. *tunicatum* Golikov & Gulbin, 1977	R/V Oparin, cr.56, stn 26	Okhotsk Sea, Kurile Is., Urup I.	45°51.59′ N, 149°47′ E	2	**OM791442**	**OM778268**	**OM778277**
Buc273	MIMB	MIMB 42300	*Buccinum* Linnaeus, 1758	*hasegawai* sp. nov.	R/V Oparin, cr.56, stn 24	Okhotsk Sea, Kurile Is., Urup I.	46°15.9′ N, 150°15.4′ E	450–460	**OM791443**	–	**OM778278**
Buc274	ZIN	ZIN 62775	*Buccinum* Linnaeus, 1758	*hasegawai* sp. nov.	R/V Oparin, cr.56, stn 19	Kurile Is., Simushir I.	46°40.6′ N, 151°58.4′ E	436	**OM791444**	**OM778269**	**OM778279**
Buc275	IEE		*Buccinum* Linnaeus, 1758	*fimbriatum* (Golikov et Sirenko, 1988)	R/V Oparin, cr.56, stn 19	Kurile Is., Simushir I.	46°40.6′ N, 151°58.4′ E	436	**OM791446**	**OM778270**	**OM778280**
Buc276	ZIN	ZIN 62902	*Buccinum* Linnaeus, 1758	*hasegawai* sp. nov.	R/V Oparin, cr.56, stn 19	Kurile Is., Simushir I.	46°40.6′ N, 151°58.4′ E	436	**OM791445**	–	–
Buc278	IEE		*Buccinum* Linnaeus, 1758	cf. *kobjakovae* Golikov & Gulbin, 1977	R/V Oparin, cr.56, stn 19	Kurile Is., Simushir I.	46°40.6′ N, 151°58.4′ E	436	**OM791448**	–	**OM778281**
Buc281	IEE		*Buccinum* Linnaeus, 1758	*cyaneum* Bruguière, 1789		Barents Sea, Teriberka Inlet	69°11.3′ N, 35°09.9′ E	10–17	**OM791449**	**OM778272**	**OM778282**

Table 1. continued.

IEE tissue clips numbers	Depository/ GenBank (GB)	Catalog_N	Genus	species	Expedition, station	Locality	Coordinates	depth (m)	GB *cox-1*	GB 16S	GB 28S
Buc283	IEE		*Buccinum* Linnaeus, 1758	*percrassum* Dall, 1883	R/V Oparin, cr.56, stn 23	Kurile Is., Simushir I.	47°07.4′ N, 152°09.6′ E	1–6	**OM791450**	**OM778273**	–
Buc284	IEE		*Buccinum* Linnaeus, 1758	*tenuisulcatum* Golikov & Gulbin, 1977	R/V Oparin, cr.56, stn 68	Okhotsk Sea, Kurile Is., Onekotan I.	49°31.3′ N, 154°25.0’ E	571–580	**OM791439**	–	–
Buc289	IEE		*Plicibuccinum* Golikov & Gulbin, 1977	*declivis* (Habe & Ito, 1976)	R/V Oparin, cr. 64, stn 73	Japan Sea, Primorje	43°43.5′ N, 135°22.9’ E	45–49	–	**OM832587**	**OM832649**
Buc277	IEE		*Volutharpa* P. Fischer, 1856	*ampullacea* (Middendorff, 1848)	R/V Oparin, cr.56, stn 14	Kurile Is., off Chir-poi I.	46°21.5′ N, 150°53.4′ E	148–147	**OM791447**	**OM778271**	–
	GB	LSGB23204	*Volutharpa* P. Fischer, 1856	*perryi* (Jay, 1857)		China	35°05′ N, 119°20′ E		HQ834060		FJ710108
	GB	BMNH-20070640	*Buccinum*	*undatum* Linnaeus, 1758		Reykjanes, Iceland			MK558051		KT753764

data on the specimens and GenBank accession numbers other than belonging to subfamily Buccininae, please refer to supplementary table_S1 in Kantor *et al.* (2022).

Maximum likelihood based tree reconstruction was performed using IQtree with the same parameters as those used for the single-gene phylogenies. The Bayesian analyses were performed using MrBayes (Huelsenbeck & Ronquist 2001) running two parallel analyses, each consisting of six Markov chains of 25 000 000 generations with sampling frequency of one tree each 1000 generations, chain temperature set to 0.02. Parameters of the substitution model were estimated during the analysis (6 substitution categories, a gamma–distributed rate variation across sites approximated in four discrete categories and a proportion of invariable sites). Trees from the first 6 250 000 generations (25% of total number of generations) were discarded as burn in prior to the construction of consensus trees. Convergence of Bayesian analysis was evaluated using Tracer ver. 1.4.1 (Rambaut *et al.* 2014) by checking that all Efficient Sample Size (ESS) values exceeded 200 (default burning). We ran IQtree locally, and Bayesian analysis was performed on the Cipres Science Gateway (http://www.phylo.org/portal2), using MrBayes on XSEDE ver. 3.2.7 (Miller *et al.* 2010). The Dolicholatiridae-Belomitridae clade recovered by Kantor *et al*. (2022) as the sister group of all other buccinoideans, was used to root the trees.

Nodes with Bootstraps values (B, in percent) lower than 70 and Posterior Probabilities (PP) lower than 0.90 are considered non-supported; B values between 70 and 90 and PP values between 0.90 and 0.95 are regarded as weakly supported; and B > 90 and PP > 0.95 as well-supported.

Institutional abbreviations

AORI = Atmosphere and Ocean Research Institute, University of Tokyo, Japan
IEE RAS = A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow, Russia
MIMB = Museum of A.V. Zhirmunsky, National Scientific Center of Marine Biology of the Far Eastern Branch, Russian Academy of Sciences, Vladivostok, Russia
MNHN = Muséum national d’Histoire naturelle, Paris, France
MSU = Pertsov Biological Station, Moscow State University, Moscow, Russia
RNC = collection of R.N. Clark
SPSU = St. Petersburg State University, St. Petersburg, Russia
ZIN = Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.
ZSM = Zoologische Staatssammlung München, München, Germany

Abbreviations for morphological terms and measurements

AL = aperture length
B = Bootstrap values
BA = Bayesian analysis
F/T = fish trawler
dd = dead collected specimen
I. = island
Is = islands
LW = last whorl length
lv = live collected specimen
PP = posterior probability value
R/V = research vessel
stn = station
SL = shell length
SW = shell width

Results

Phylogenetic analysis

The analyses of the concatenated dataset generated trees that were highly congruent with the multilocus tree of Kantor *et al*. (2022) (Supp. file 1). Because topologies of the trees based on the IQtree and BA were virtually identical, we here only provide the Buccinidae segment of the Bayesian tree (Fig. 1), however discuss the support values obtained by both analyses. The subfamily Buccininae is recovered monophyletic (PP = 0.95; B = 100). Within the Buccininae the first offshoot combines the maximally supported *Volutharpa* clade [including the type species *V. ampullacea* and *V. perryi* (Jay, 1857)] and *Buccinum chishimanum* Pilsbry, 1904, albeit this relation is weakly supported only in the IQ tree. The second offshoot is *Plicibuccinum declivis* (Habe & Ito, 1976), the type species of monotypical *Plicibuccinum* Golikov & Gulbin, 1977. The remaining species form a weakly supported clade in BA and a highly supported one in IQ trees (PP = 0.91; B = 93), referred to as "*Buccinum*" clade in Fig. 1 with many unresolved polytomies.

The *Buccinum* clade in addition to species traditionally attributed to *Buccinum* s.s. includes species of the three previously recognized (sub)genera of Buccininae (*Thysanobuccinum* – highlighted in red in Fig. 1, *Bathybuccinum* – highlighted in green, and *Ovulatibuccinum* – highlighted in blue). We accept the generic rank of this clade and therefore the name *Buccinum* can be applied to the entire clade. Hence, full genus rank cannot be applied to any of the aforementioned (sub)genera. Similarly, their subgeneric rank cannot been accepted on several grounds. First, the monophyly of the subgenera is not supported and therefore their diagnostic characters are homoplastic (see Discussion for more details). Second, recognition of any of these subgenera as valid will necessitate placing remaining species into the nominotypical subgenus *Buccinum* s.s., while they do not constitute a supported clade. Alternatively, to avoid paraphyly the genus *Buccinum* should be split in numerous subgenera, corresponding to supported subclades. This is definitely untimely and presently unjustified since the examined dataset represents only a fraction of the known diversity of the genus (140 accepted species according to MolluscaBase), internal nodes are not fully resolved and this splitting is not supported by morphological characters. Therefore, we synonymize *Thysanobuccinum*, *Bathybuccinum*, and *Ovulatibuccinum* with *Buccinum*.

Within *Buccinum* several highly supported subclades are recovered in all analyses. *Buccinum tunicatum* Golikov & Gulbin, 1977 (type species of *Thysanobuccinum*) is clustering with maximal support with *B.* cf. *tunicatum* (red in Fig. 1). *B. chinoi* nom. nov. is clustering with maximal support with *B. fimbriatum* Golikov & Sirenko, 1988. Both species were previously referred to the (sub)genus *Ovulatibuccinum* (blue in Fig. 1). The third maximally supported clade comprises *Buccinum* sp. 1, *Buccinum* sp. 2, and three specimens of *B. hasegawai* sp. nov. *Buccinum* sp. 1 (Fig. 2I) corresponds to the morphological characterization of *Bathybuccinum, Buccinum* sp. 2 (Fig. 2C) conchologically is similar to *Thysanobuccinum,* while *B. hasegawai* sp. nov. was referred to *Ovulatibuccinum* by Golikov & Sirenko (1988) under the name *Bathybuccinum* (*Ovulatibuccinum*) *bombycinum* Dall 1907.

Three morphologically strongly heterogeneous species [*Buccinum* cf. *kobjakovae* Golikov & Sirenko, 1988: Fig. 3G–H; *B. niponense* Dall, 1907: Fig. 3E; *B. bicordatum* (Golikov & Sirenko, 1988): Fig. 2E–E'] form a highly supported subclade in all analyses. Two former species of this subclade have been previously attributed to *Buccinum* s.s., while *B. bicordatum* is the type species of the formerly recognized *Bathybuccinum*.

The remaining two subclades include species, always attributed to *Buccinum* – *B. hydrophanum* Hancock, 1846 + *B. glaciale* Linnaeus, 1761 + *B. tenuisulcatum* Golikov & Gulbin, 1977; and *B. undatum* Linnaeus, 1758 + *B. cyaneum* Bruguière, 1789.

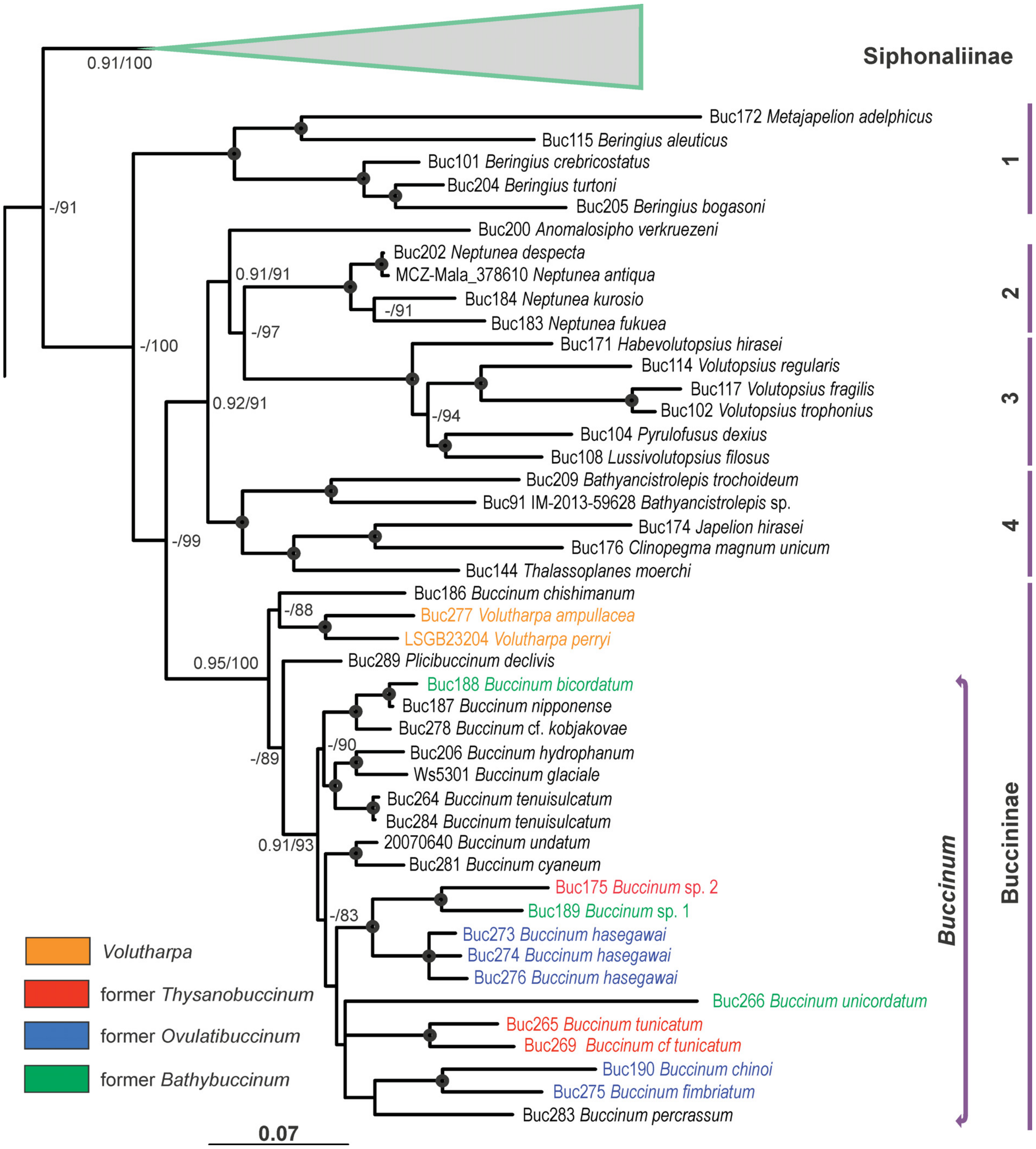

Fig. 1. Part of the Bayesian phylogenetic tree of Buccinoidea Rafinesque, 1815 obtained with the *cox-1,* 16S and 28S concatenated dataset representing family Buccinidae Rafinesque, 1815. The full tree is available as supplementary material (Supplementary file 1). Subfamily Siphonaliinae Finlay, 1928 is collapsed. Vertical numbered lines on the right mark the subfamilies of Buccinidae: 1 = Beringiinae Golikov & Starobogatov, 1975; 2 = Neptuneinae Stimpson, 1865; 3 = Volutopsinae Habe & Sato, 1973; 4 = Parancistrolepidinae Habe, 1972. Posterior probabilities and bootstrap values are shown for each medium supported node. Highly supported nodes are marked with black dots. The colors of the text refer to valid genus (orange = *Volutharpa* P. Fischer, 1856) and species referred to or morphologically attributable to formerly recognized (sub)genera of Buccininae: red = *Thysanobuccinum* Golikov & Gulbin in Golikov, 1980; blue = *Ovulatibuccinum* Golikov & Sirenko, 1988; green = *Bathybuccinum* Golikov & Sirenko, 1988.

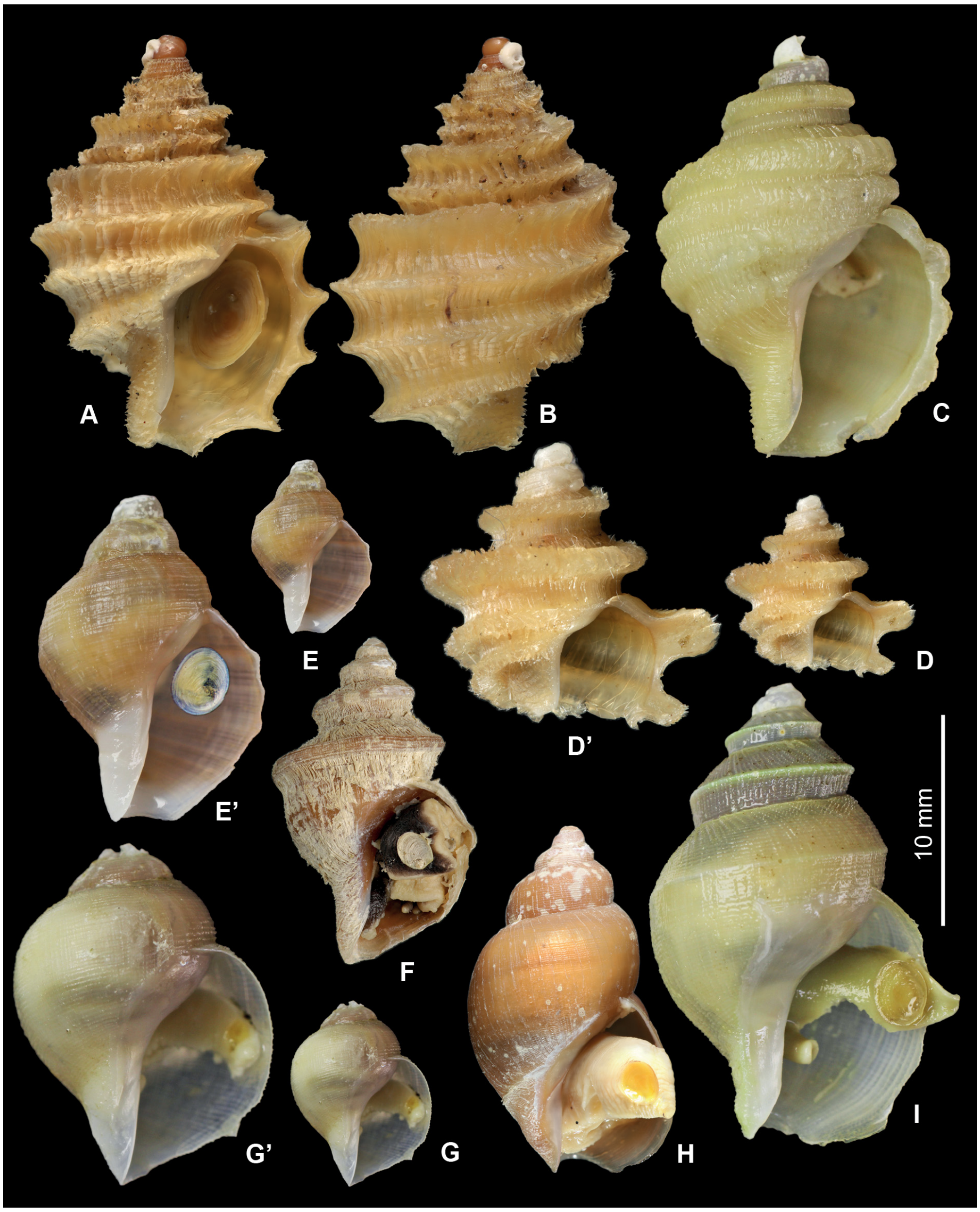

Fig. 2. Sequenced species of *Buccinum* Linnaeus, 1758 previously attributed to *Thysanobuccinum* Golikov & Gulbin in Golikov, 1980*, Bathybuccinum* Golikov & Sirenko, 1988 and *Ovulatibuccinum* Golikov & Sirenko, 1988. **A–B**. *Buccinum tunicatum* Golikov & Gulbin, 1977 (Buc265), Okhotsk Sea, off Urup I., depth 142 m, R/V Akademik Oparin, 56 cr., sta 7, SL 20.4 mm. **C**. *Buccinum* sp. 2 (Buc175), off Onagawa, Miyagi, Honshu I., Japan, depth 3302–3311 m, SL 20.3 mm. **D–D'**. *Buccinum* cf. *tunicatum* (Buc269), Okhotsk Sea coast of Urup I., 2 m, R/V Akademik Oparin, 56 cr., sta 26, SL 8.7 mm. D = at the same scale as others; D' = enlarged. **E–E'**. *Buccinum bicordatum* (Golikov & Sirenko, 1988) (Buc188), off Onagawa, Miyagi, Honshu I., Japan, depth 342–343 m, SL 8.4 mm. E = at the same scale as others; E' = enlarged. **F**. *Buccinum unicordatum* (Golikov & Sirenko, 1988) (Buc266), Kurile Is, Iturup I., Prostor Bay, depth 264–270 m, SL 15.9 mm. **G**. *Buccinum chinoi* nom. nov. (Buc190), off Onagawa, Miyagi, Honshu I., Japan, depth 342–343 m, SL 9.0 mm. **H**. *Buccinum fimbriatum* (Golikov & Sirenko, 1988) (Buc275), Kurile Is, Simushir I., depth 436 m, R/V Akademik Oparin, 56 cr., stn 19, SL 16.6 mm. **I**. *Buccinum* sp. 1 (Buc189), off Onagawa, Miyagi, Honshu I., Japan, depth 342–343 m, SL 22.4 mm. All shells (except D', E') at the same scale.

The new phylogenetic data and a detailed analysis of the taxonomy of species treated herein required some taxonomic revisions. For four species included in our phylogenetic analysis no valid names were available and they appeared to be new for science. Three of them were represented by inadequate or

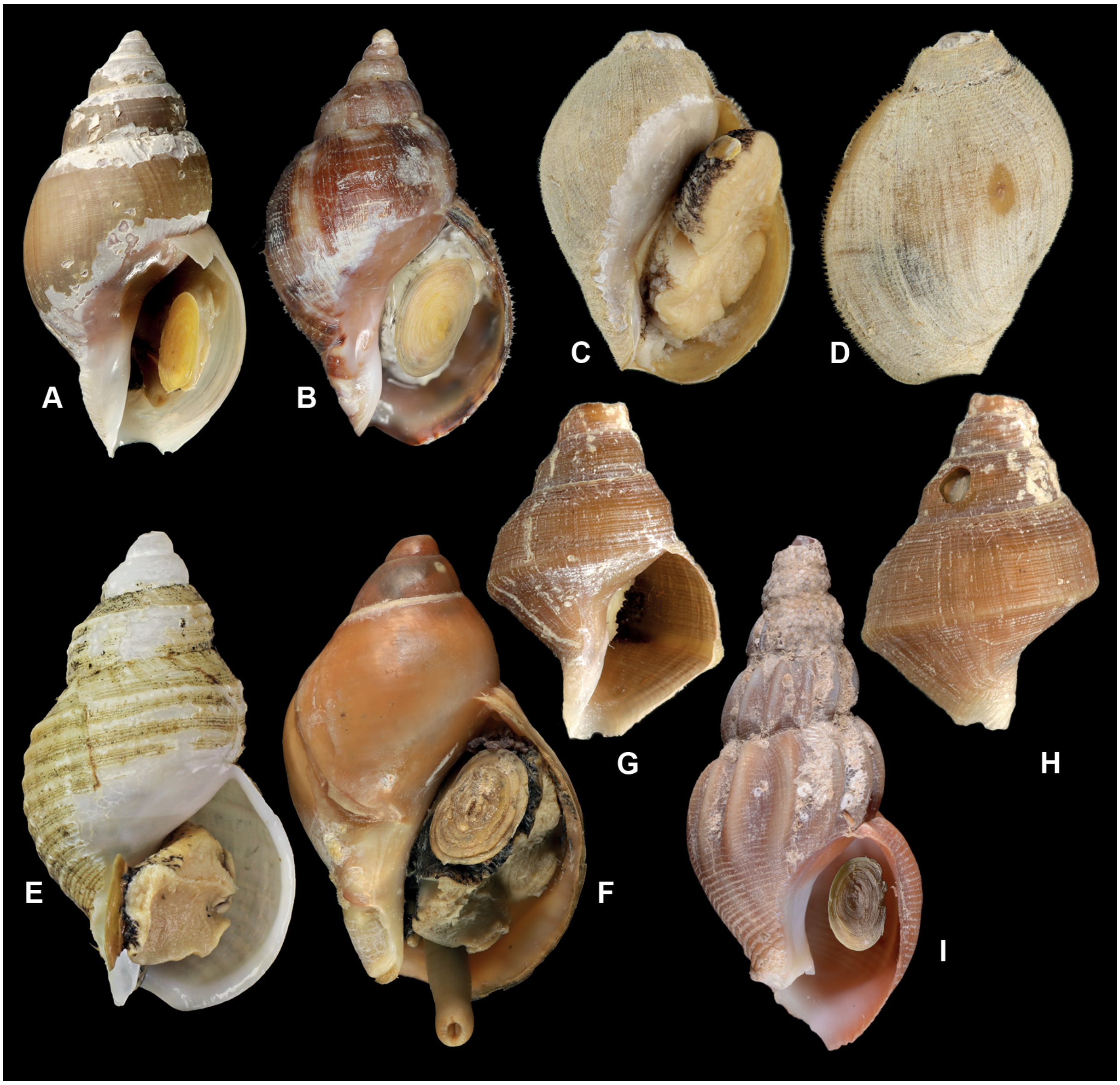

Fig. 3. Sequenced species of *Buccinum* Linnaeus, 1758, *Volutharpa* P. Fischer, 1856, and *Plicibuccinum* Golikov & Gulbin, 1977. **A**. *Buccinum tenuisulcatum* Golikov & Gulbin, 1977 (Buc264), Okhotsk Sea, Kurile Is, Onekotan I., depth 571–580 m, R/V Akademik Oparin, 56 cr., stn 68, SL 29.4 mm. **B**. *Buccinum cyaneum* Bruguière, 1789 (Buc281), Barents Sea, Teriberka Inlet, depth 10–17 m, SL 18.1 mm. **C–D**. *Volutharpa ampullacea* (Middendorff, 1848) (Buc277), Kurile Is, off Chirpoi I., depth 148–147 m, SL 14.1 mm. **E**. *Buccinum nipponense* Dall, 1907 (Buc187), off Otsuchi, Iwate, Honshu I., Japan, depth 479–484 m, SL 40.8 mm. **F**. *Buccinum percrassum* Dall, 1883 (Buc283), Kurile Is, Simushir I., 1–6 m, SL 33.5 mm. **G–H**. *Buccinum* cf. *kobjakovae* Golikov & Gulbin, 1977 (Buc278), Kurile Is, Simushir I., R/V Akademik Oparin, 56 cr., stn 19, 46°40.6′ N, 151°58.4′ E, depth 436 m, SL 12.1 mm. **I**. *Plicibuccinum declivis* (Habe & Ito, 1976) (Buc289), Japan Sea, Primorje, R/V Akademik Oparin, 64 cr., stn 73, 43°43.5′ N, 135°22.9′ E, depth 45–49 m, SL 36.2 mm. Shells not to scale.

unavailable for the study material (only tissue clips and photographs of specimens from AORE were available to us for *Buccinum* sp. nov. and *Buccinum* sp. nov.; *Buccinum* cf. *tunicatum* was represented by incomplete shell) and therefore they are left unnamed. One species, previously erroneously identified as *Buccinum bombycinum* Dall, 1907 by Golikov (1990) and by Golikov & Sirenko (1998) and included in our analysis (as *B. hasegawai* sp. nov.) remains formally undescribed. We also find the present work a good opportunity to address the incorrect identification of the type species of *Ovulatibuccinum* – *Buccinum ovulum* sensu Golikov, non Dall, and to correct the primary homonymy of two species of *Buccinum*.

Taxonomy

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Neogastropoda Wenz, 1938
Superfamily Buccinoidea Rafinesque, 1815
Family Buccinidae Rafinesque, 1815
Subfamily Buccininae Rafinesque, 1815

Genus ***Buccinum*** Linnaeus, 1758

Buccinum (*Thysanobuccinum*) Golikov & Gulbin in Golikov, 1980, syn. nov.

Bathybuccinum Golikov & Sirenko, 1988.

Bathybuccinum (*Ovulatibuccinum*) Golikov & Sirenko, 1988, syn. nov.

Buccinum hasegawai sp. nov.
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Figs 4, 6A–C; Table 1

Buccinum (*Buccinum*) *bombycinum* – Golikov 1980: 327, figs 85, 183, 391, *1* pl. XXXI, 1a–1k (part.) (non Dall 1907).

Bathybuccinum (*Ovulatibuccinum*) *bombycinum* – Golikov & Sirenko 1988: 87 (non Dall 1907).

Bathybuccinum bombycinum – Golikov & Sirenko 1998: 122, fig. 12b; Kantor & Sysoev 2006:160, pl. 74c (non Dall, 1907).

?*Buccinum* sp. cf. *bulimuloideum* – Okutani 1964: 414, pl. II fig.12 (non Dall 1907).

Bathybuccinum sp.1 — Sirenko *et al*. 2013:159.

Diagnosis

Shell reaching 18.5 mm in length, thin, oval to elongate-oval, smooth. Axial sculpture only of thin growth lines, spiral sculpture absent. Operculum thin, small, less than ¼ of AL, with nucleus notably shifted towards lower outer edge.

Etymology

Named in honour of Dr Kazunori Hasegawa, Japanese malacologist whose studies made a significant contribution to the systematics of the deep-sea gastropods of Japan and the Pacific.

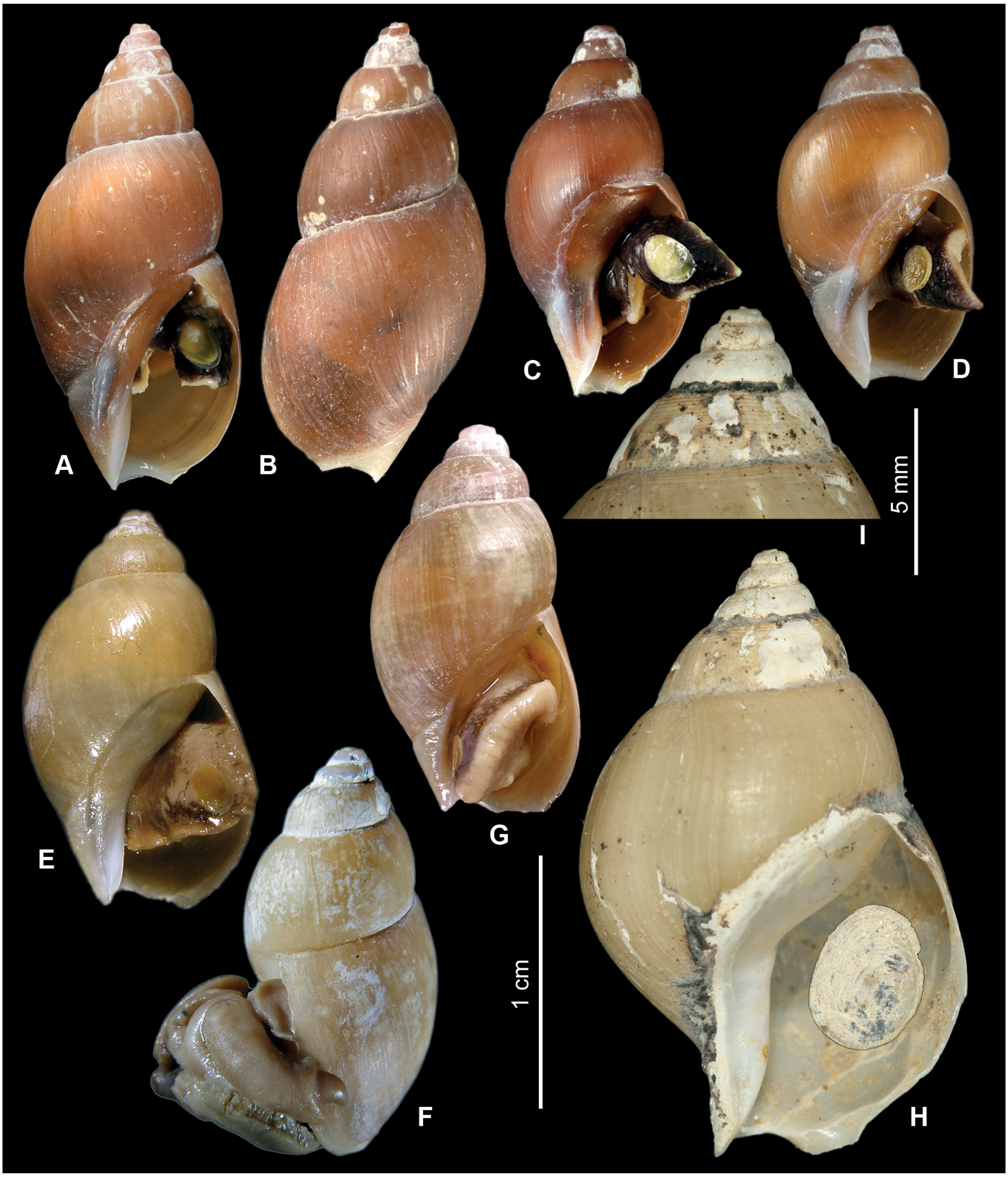

Fig. 4. *Buccinum hasegawai* sp. nov. **A–B**. Holotype (ZIN 62775 (Buc274)), SL 18.5 mm. **C**. Paratype 1 (ZIN 62902 (Buc276)) from the type locality, SL 14.8 mm. **D**. Paratype 2 (MIMB 42300 (Buc273)), Urup I., 450–460 m, SL 14.7 mm. **E**. Paratype (ZIN 26228), Iturup I., 414 m, SL 16.1 mm. **F**. Paratype (ZIN 26228), Iturup I., 414 m, SL 16.2 mm, lateral view to show the penis. **G**. *Buccinum bombycinum* Dall, 1907 (ZIN 48100) Iturup I., 910–920 m, SL 15.3 mm. **H–I**. Syntype (USNM 1105311), Japan, Honshu I., Suruga Bay, 536 m, SL 23.9 mm. I = enlarged upper part of the shell to show the sculpture. Scale bars: A–H = same scale; I = 5 mm. Photos H–I: courtesy of USNM.

Type material

Holotype

KURILE ISLANDS • lv; South-east of Simushir I.; 46°40.6′ N, 151°58.4′ E; depth 436 m; R/V Akademik Oparin*,* cruise 56, stn 19; ZIN 62775, Buc274.

Paratypes

KURILE ISLANDS • 1 lv (paratype 1, SL 14.8 mm); same collection data as for holotype; ZIN 62902, Buc276 • 1 lv (paratype 2, SL 14.7 mm); Okhotsk Sea, Urup I.; 46°15.9′ N, 150°15.4′ E; depth 450–460 m; R/V Oparin, cruise 56, stn 24; MIMB 42300, Buc273 • 8 lv (SL 9.0–16.2 mm); Iturup I.; 44°20.8′ N, 148°24.0′ E; depth 414 m; Kurile-Sakhalin Expedition, F/T Toporok, stn 101; 14 Sep 1949; ZIN 26228 • 7 lv; Iturup I.; 44°52′ N, 149°27.7′ E; depth 910–920 m; R/V Odyssey; 25 Jul. 1984; ZIN 48100.

Other material examined

Sequenced material

Holotype, paratypes 1, 2 (see above on localities).

Not-sequenced material

KURILE ISLANDS • 1 lv (SL 16.5 mm); Shikotan I.; 43°37′ N, 147°19′ E; depth 400 m; R/V Tikhookeanskyi; 11 Jul. 1987; ZIN 62780 • 1 lv (SL 16.0 mm); Iturup I.; 44°05.7′ N, 148°05.4′ E; depth 500 m; R/V Tikhookeanskiy; 10 Aug. 1987; ZIN 62779.

SEA OF OKHOTSK • 3 lv (SL 15.0–16.0 mm); Southern Sakhalin, 47°50.4′ N, 142°53.5′ E; depth 78 m; Kurile-Sakhalin Expedition; F/T Toporok; stn 145; 30 Sep.–1 Oct. 1949; ZIN 26226.

Description

Measurements (holotype, largest specimen). SL 18.5 mm, AL 9.2 mm, SW 8.6 mm.

Shell. Thin, fragile, oval to elongate-oval, smooth, with short siphonal canal, chocolate-brown in fresh specimens to brownish and olive with lighter convex strongly demarcated fasciole. Protoconch eroded in available material, rendering exact whorl count impossible. Teleoconch whorls up to 4+. Suture distinct, adpressed at periphery of previous whorl. SW/SL ratio 0.48 (holotype) to 0.58, LW/SL ratio 0.75 (holotype) to 0.84. Axial sculpture of thin prosocline growth lines, spiral sculpture absent. Aperture large, semi-oval. Outer lip thin, slightly pressed adapically. Columella smooth, nearly straight, sometimes weakly concave, lighter than shell. AL/SL ratio 0.51 (holotype) to 0.63. Siphonal notch wide and rather shallow. Periostracum very thin, smooth, tightly adhering. Operculum (Fig. 6B) small, thin, yellowish, transparent, oval, with nucleus strongly displaced to lower edge, spanning about 0.25 of AL.

Radula (n = 1). Rachidian tooth with rectangular basal plate and three equal, short cusps. Lateral tooth with three cusps, outer cusp longest, intermediate shortest and most narrow (Fig. 6A).

Penis (n = 1). Distal part with large hook-shaped papilla, surrounded by circular fold (Fig. 6C).

Head-foot. Characteristically strongly pigmented on the dorsal side, nearly black in fresh specimens, fading with time in alcohol.

Remarks

The species is variable in shell shape and coloration (Fig. 4). The shell can range from oval, with a protruded basal edge of the outer apertural lip (Fig. 4E, G) to narrowly oval with non-protruded lip (Fig. 4A–D). Shell color varies from brown to olive, although it is possible that the color fades over time in alcohol, since lightest shells were collected in 1949, while most dark specimens were collected in 2019.

The size of the operculum varies significantly, constituting from 1/6 to ¼ of AL.

Golikov (1980) identified this species (together with *B. bizikovi* sp. nov.) as *Buccinum bombycinum* based on Dall's (1907) incorrect report of the type locality for this species (east coast of Sakhalin, in 53 m). However, it turned out that the type locality was Suruga Bay, Japan in 527 m (Kuroda 1950; Hasegawa & Okutani 2011). Later, when examining the samples in which both new species were sympatric, Golikov & Sirenko (1998) recognized the presence of two species and identified the specimens with a narrow shell as *Bathybuccinum bombycinum*, and those with a wider shell (*B. bizikovi* sp. nov.) as *B. ovulum*. Kantor & Sysoev (2006: 160) pointed out that the specimens identified as *B. bombycinum* by Golikov and Golikov & Sirenko belong to a different, possibly undescribed species.

The new species is clearly different from *Buccinum bombycinum* (Fig. 4H–I) in having a much narrower, smooth shell with a smaller operculum. Furthermore, in *B. bombycinum* the upper whorls bear distinct spiral cords (Fig. 4I). Hasegawa & Okutani (2011: fig. 26) illustrated a specimen of *B. bombycinum* from Sagami Bay with even better developed spiral sculpture, covering the entire shell surface. *B. bombycinum* is probably endemic of Honshu. For the comparison with *B. bizikovi* sp. nov. see under remarks of the latter species.

In the molecular phylogeny, the new species is clustering with maximal support with two morphologically very different species, *Buccinum* sp. 1 and *Buccinum* sp. 2. From the former (Fig. 2I) it differs in much narrower shell and absence of the distinct spiral keel on the shoulder. From the latter (Fig. 2C) the new species differs in much narrower shell, higher spire, lack of spiral cords, and smooth and thin periostracum vs thick and leathery one.

Distribution

Kurile Is (Iturup I., Shikotan I., Simushir I.), Sea of Okhotsk, South Sakhalin, depth 78–910 m.

Buccinum bizikovi sp. nov.

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Figs 5, 6D–F

Buccinum (Buccinum) bombycinum – Golikov 1980: 327, figs 85, 183, 391, *1* pl. XXXI, 1a–1k (part.) (non Dall 1907).

Bathybuccinum (Ovulatibuccinum) ovulum – Golikov & Sirenko 1988: 93, figs 13–15 (non Dall, 1895).

Bathybuccinum ovulum – Golikov & Sirenko 1998: 122, fig. 12c; Kantor & Sysoev 2006: 160, pl. 74i (non Dall, 1895).

Bathybuccinum bombycinum – Kantor & Sysoev 2006: pl. 74d (non Dall 1907).

Bathybuccinum sp. 2 — Sirenko *et al*. 2013:159.

Diagnosis

Shell reaching 29.5 mm in length, thin, broadly oval, smooth except inconspicuous, irregularly spaced, sometimes oblique spiral cords. Axial sculpture only of thin growth lines. Operculum thin, small, less than 1/5 of AL, brown, with terminal nucleus notably shifted to lower outer operculum edge.

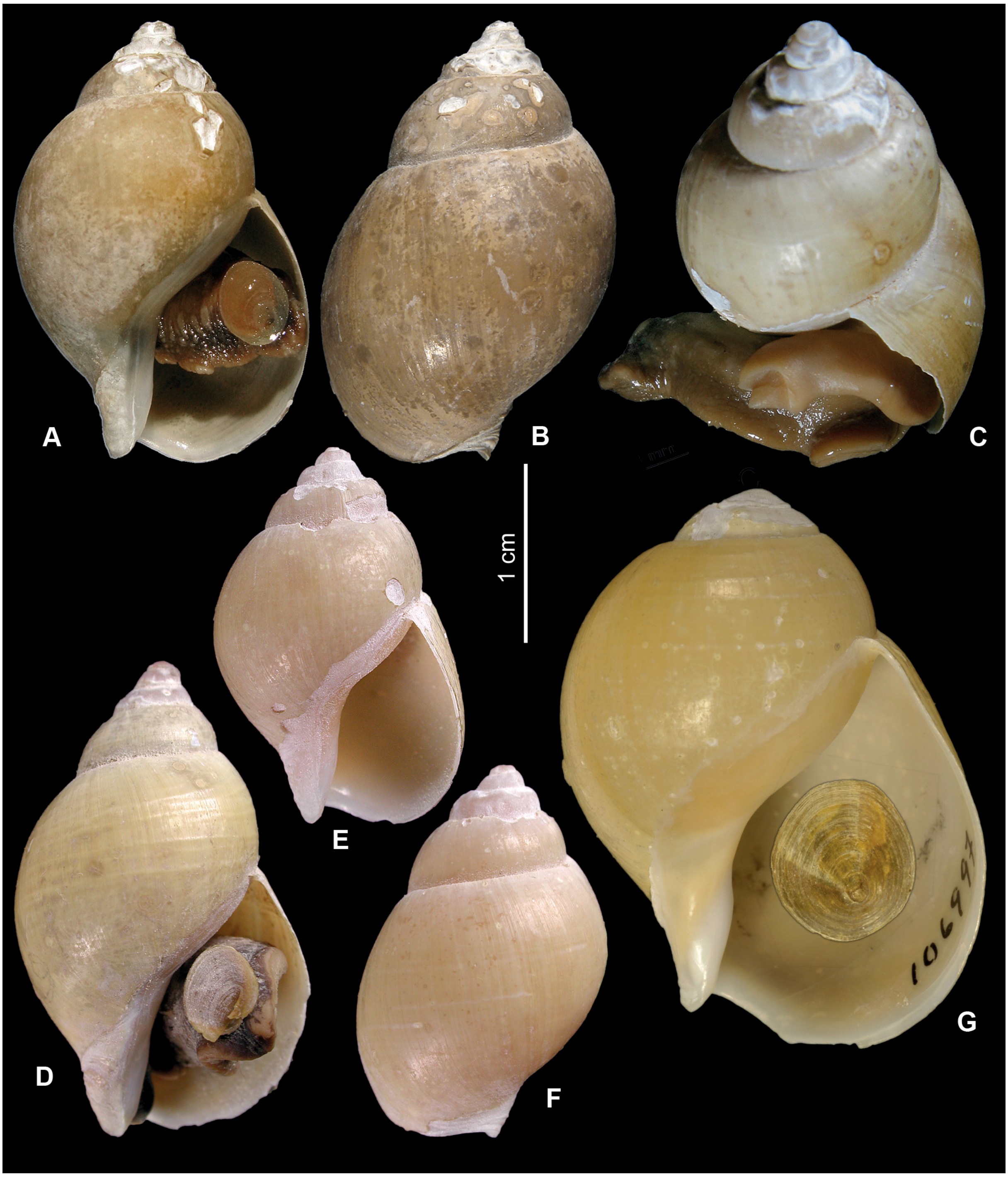

Fig. 5. *Buccinum bizikovi* sp. nov. **A–B**. Holotype (ZIN 62781), SL 20.0 mm. **C**. Paratype (ZIN 62782), SL 20.0 mm, lateral view to show the penis. **D**. South-eastern Sakhalin, depth 78 m, SL 21.5 mm, ZIN 62783. **E–F**. *Buccinum ovulum* Dall, 1895 (ZIN 48103), Kurile Is, Iturup I., depth 605–620 m, SL 16.9 mm. **G**. Holotype (USNM 106997), Aleutian Is, Andreanof Is, Amukta Pass, depth 454 m, SL 25.6 mm. Photo G: courtesy of USNM.

Etymology

Named in honour of Vyacheslav Bizikov, Soviet and Russian malacologist, who collected deep-water gastropods, including this species, near the Kurile Islands.

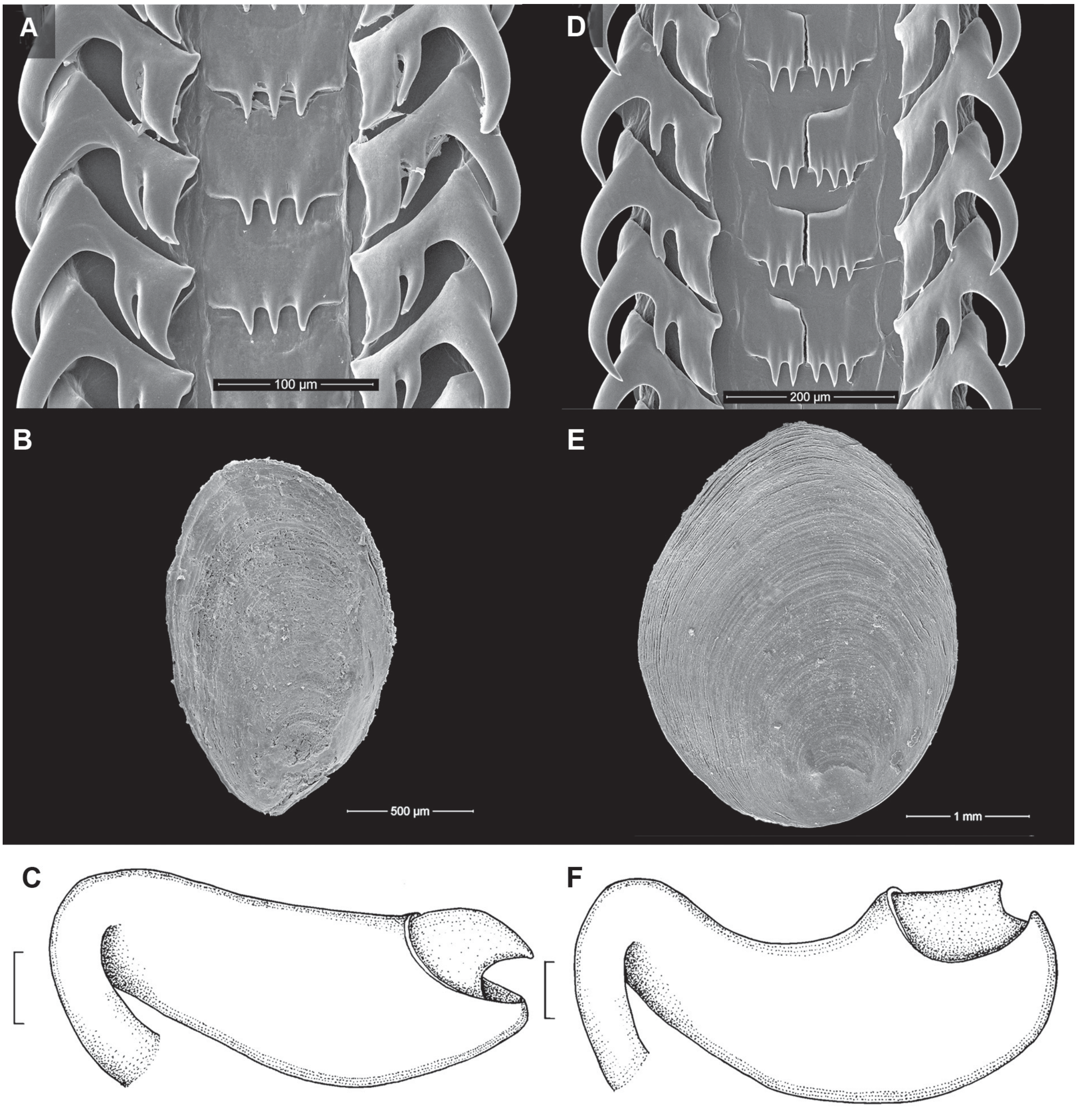

Fig. 6. *Buccinum hasegawai* sp. nov. (A–C) and *Buccinum bizikovi* sp. nov. (D–F). **A–B**. Paratype (ZIN 62777), SL 16.5 mm. **A**. Radula. **B**. Operculum. **C**. Paratype (ZIN 62782), penis. **D**. Paratype (ZIN 62782), SL 16.5 mm, radula. **E.** Paratype (ZIN 62782), SL 19.1 mm, operculum. **F**. Paratype (ZIN 62782), SL 16.5 mm, penis. Scale bars: C, F = 1 mm.

Type material

Holotype

KURILE ISLANDS • lv; Iturup I., 44°20.8′ N, 148°24.0′ E; depth 414 m; Kurile-Sakhalin Expedition, F/T Toporok, stn 101; 14 Sep. 1949; ZIN 62781.

Paratypes

KURILE ISLANDS • 4 lv; same collection data as for holotype; ZIN 62782.

Other material examined

KURILE ISLANDS • 1 lv (SL 19.1 mm); Shikotan I.; 44°08.1′ N, 147°57.0′ E; depth 285–286 m; Kurile-Sakhalin Expedition, F/T Toporok, stn 93; 13 Sep. 1949; ZIN 62788 • 1 lv (SL 16.9 mm); Iturup I.; 44°58.2′ N, 149°19.0′ E; depth 605–620 m; R/V Odyssey; 25 Jul. 1984; ZIN 48103 • 1 lv (SL 18.0 mm); Simushir I.; depth 450–480 m; R/V Odyssey; 30 Dec. 1984; ZIN 62787 • 1 lv (SL 29.5 mm); Polonskogo I.; 43°19′ N, 146°37′ E; depth 500 m; R/V Tikhookeanskiy, stn 10, sample 26; 9 Jul. 1987; ZIN 62785 • 1 lv (SL 14.0 mm); Shikotan I.; 43°37′ N, 147°19′ E; depth 400 m; R/V Tikhookeanskiy; 11 Jul. 1987; ZIN 62783 • 1 lv (SL 18.0 mm); Iturup I.; 44°49.5′ N, 149°01.7′ E; depth 650 m; R/V Tikhookeanskiy; 13.08.1987; ZIN 62786.

SEA OF OKHOTSK • 3 lv (SL 15.0–23.1 mm); South-eastern Sakhalin, 47°50.4′ N, 142°53.5′ E; depth 78 m; Kurile-Sakhalin Expedition; F/T Toporok; stn 145; 30 Sep.–1 Oct. 1949; ZIN 62783.

Description

Measurements (holotype). SL 20.0 mm, AL 13.6 mm, SW 13.1 mm. Largest available specimen attains 29.5 mm.

Shell. Thin, fragile, oval, smooth, with short siphonal canal, pale-brownish to rose- brownish. Protoconch of about 1.5 low, convex whorls, strongly eroded. Teleoconch whorls 3+, suture distinct, adpressed at periphery of previous whorl. SW/SL ratio 0.62–0.67 (0.65 in holotype), LW/SL ratio 0.80–0.81 (0.80 in holotype). Axial sculpture of thin, weakly prosocline growth lines. Spiral sculpture of low, indistinct irregularly spaced, sometimes oblique cords. Aperture large, semi-oval. Outer lip thin, slightly adpressed adapically. Columella straight, smooth. Siphonal notch wide and rather shallow. AL/SL ratio 0.64–0.70 (0.68 in holotype). Periostracum thin, smooth, yellowish brown. Operculum (Fig. 6E) small, spanning less than 0.25 of AL, thin, brownish, translucent, oval, with nucleus shifted to lower edge,.

Radula (n = 1). Rachidian tooth with broad rectangular basal plate and five short cusps nearly equal in length. Lateral tooth with three cusps, outer cusp longest, intermediate shortest and most narrow (Fig. 6D).

Penis (n = 1). Distal end of the penis with cone-shaped papilla, surrounded by circular fold (Fig. 6F).

Remarks

Specimens of this new species were previously identified as *Buccinum bombycinum* (Golikov 1980) or *Bathybuccinum ovulum* (Golikov & Sirenko 1988, 1998). Kantor & Sysoev (2006) suggested that the specimens, identified by Golikov & Sirenko are not conspecific with *B. ovulum.*

The new species differs from *B. ovulum* (Fig. 5G) in having a higher spire (LW/SL ratio is 0.92 in *B. ovulum* vs 0.80–0.81 in *B. bizikovi*) and a smaller operculum (less than 0.25 of AL in *B. bizikovi* and typically around 0.4 in *B. ovulum*) with nucleus situated much closer to the edge. The new species differs from *B. hasegawai* in having a broader shell (SW/SL ratio 0.48–0.58 in *B. hasegawai* and 0.62–0.67 in *B. bizikovi*) and a lower aperture (AL/SL ratio 0.51–0.63 in *B. hasegawai* and 0.64–0.70 in *B. bizikovi*).

Buccinum ovulum sensu Golikov & Sirenko 1988 (non Dall 1907) was designated as the type species of *Bathybuccinum (Ovulatibuccinum).* Therefore, it is a case of misidentified type species and it is now fixed (under Article 70.3 of the Code) as *Buccinum bizikovi* sp. nov. misidentified as *Buccinum ovulum* Dall, 1907 in the original designation by Golikov & Sirenko (1988).

Distribution

Kurile Islands: Simushir, Iturup, Shikotan and Polonskogo Islands, depth 285–650 m; Okhotsk Sea, south-eastern Sakhalin, depth 78 m.

Buccinum chinoi nom. nov.
Fig. 2G; Table 1

Ovulatibuccinum perlatum – Fraussen & Chino, 2009: 152, 154, figs. 7–8, 17–18. — Hasegawa 2009: 289, fig. 183.

Etymology

Named in honour of Mr Mitsuo Chino, citizen scientist in malacology, who co-authored the description of *Ovulatibuccinum perlatum.*

Type material

Holotype

JAPAN • lv (SL 8.4 mm); northeastern Honshu, off Iwate Prefecture; depth 900–1000 m; NSMT-Mo 76771.

Distribution

Known from the slope of the Japan Trench (type locality), off northeastern Honshu (350–480 m; Hasegawa 2009) and Kurile-Kamchatka Trench. Bathymetric range: the lower continental plateau from 300 m down to abyssal depth of at least 2700 m. Inhabiting muddy and silty bottoms (after Fraussen & Chino, 2009).

Remarks

After synonimization of *Ovulatibuccinum* with *Buccinum* the new combination *Buccinum perlatum* (Fraussen & Chino, 2009) is becoming the junior secondary homonym of *Buccinum perlatum* Conrad, 1833 and *Buccinum perlatum* Küster, 1858 (= *Engina natalensis* Melvill, 1895). Since there is no known available and potentially valid synonym, according to art. 60.3 of ICZN the name *Buccinum perlatum* must be replaced by a new substitute name proposed herein.

Buccinum golikovi nom. nov.

Buccinum coronatum Golikov, 1980: 359–360, fig. 407 (2) pl. 34 (2a, 2b). — Kantor & Sysoev 2006:163, pl. 76b (holotype).

Etymology

Named in honour of late Dr Alexander Golikov, outstanding Soviet and Russian malacologist who among other works produced a comprehensive revision of *Buccinum.*

Type material

Holotype

NEWFOUNDLAND BANK • lv (SL 42.2 mm); ZIN 26156/1.

Distribution

Newfoundland Bank, western Laptev Sea; depth 46–55 m (Golikov 1980).

Remarks

The name *Buccinum coronatum* Golikov, 1980 is a junior primary homonym of *Buccinum coronatum* Bruguière, 1789 [= *Nassarius coronatus* (Bruguière, 1789)], *Buccinum coronatum* Quoy & Gaimard, 1833 [= *Nassarius distortus* (A. Adams, 1852)] and *Buccinum coronatum* Gmelin, 1791[= *Nassa serta* (Bruguière, 1789)]. Since there is no known available and potentially valid synonym, according to art. 60.3 of ICZN the name *Buccinum coronatum* Golikov, 1980 must be replaced by a new substitute name proposed herein.

Buccinum gulbini nom. nov.

Buccinum costatum Golikov, 1980: 338–340, figs. 90, 187, 397 pl. 32 (2a, 2b). — Kantor & Sysoev 2006:164, pl. 78f (holotype).

Etymology

Named in honour of Dr Vladimir Gulbin, Soviet and Russian malacologist, who studied gastropods of the Far East seas and Kurile Islands.

Type material

Holotype

BERING SEA • lv (SL 88.5 mm); Bristol Bay; 54°20′7″ N, 166°58′8″ W; depth 600–760 m; F/T Adler, stn 90; 1 Oct. 1964; ZIN 15778/1.

Distribution

Bristol Bay of the Bering Sea and northern Kurile Islands; depth 250–820 m (Golikov 1980).

Remarks

The name *Buccinum costatum* Golikov, 1980 is a junior primary homonym of *Buccinum costatum* Linnaeus, 1758 [= *Harpa costata* (Linnaeus, 1758)] and *Buccinum costatum* Quoy & Gaimard, 1833 [=*Cominella eburnea* (Reeve, 1846)]. Since there is no known available and potentially valid synonym, according to art. 60.3 of ICZN the name *Buccinum costatum* Golikov, 1980 must be replaced by a new substitute name proposed herein.

Discussion

Relationships of the genera of Buccininae

Contrary to the molecular phylogenetic analysis of Kantor *et al.* (2022) that addressed the relationships of family-group taxa of Buccinoidea, the present one is focusing on the species and genus level and includes new data on the type species of three (sub)genera of Buccininae – *Volutharpa*, *Plicibuccinum* and *Thysanobuccinum* in addition to the previously sequenced type species of *Bathybuccinum*. Besides, the present analysis includes 21 species of Buccininae vs ten in Kantor *et al.* (2022). The extended dataset allowed to re-evaluate relationships and ranks of previously recognized (sub)genera of Buccininae.

The genus *Volutharpa* is represented in the analysis by two species [*V. ampullacea* (Middendorff, 1848), the type species, and *V. perryi* (Jay, 1857)] forming a maximally supported clade. This genus includes three species and two subspecies, according to the latest account (Yamazaki *et al*. 2018). The shared features of the genus are the characteristic oval shell with a very high last whorl, broad aperture, well developed periostracum and a vestigial operculum with a nearly terminal nucleus, sometimes missing. *Volutharpa* together with *B. chishimanum* is the first offshoot of Buccininae. The sister position of *B. chishimanum* to *Volutharpa* is weakly supported in the present IQ tree analysis (B = 88), and this species clustered with the clade *B. nipponense* – *B. bicordatum* in the analysis of Kantor *et al.* (2022). Conchologically, there is no similarity between *Volutharpa* spp. and *B. chishimanum*, and the latter also possesses a very large operculum spanning most of aperture (Kantor *et al.* 2022: fig. 10a). Therefore because of both, contradictory placements in the phylogenetic trees, and notable morphological differences with *Volutharpa*, *B. chishimanum* cannot be included in this genus, and its position requires further studies. Nevertheless, the position of *Volutharpa* as a sister clade to remaining Buccininae and its characteristic morphology support its generic rank and so, we re-instate the genus, previously synonymized with *Buccinum* by Kantor *et al.* (2022).

The monotypic genus *Plicibuccinum* is a sister to *Buccinum* clade. The only known species, *P. declivis* possesses an unusual and so far, unique for Buccininae shell character – a short but distinctive siphonal canal, rather than a siphonal notch. Our sequenced specimen (Fig. 3I) unfortunately lacks the lower part of the shell, but the comparison of the remaining whorls with the photo of the *P. declivis* holotype (Habe & Ito 1976: pl. 1, fig. 1) and with the holotype of *P. plicatum* (illustrated in Kantor & Sysoev 2006: pl. 87c) suggests that they are conspecific. We retain the full genus rank for *Plicibuccinum* based on its inferred position in the Buccininae phylogeny, supported by its characteristic shell morphology.

Discordance of phylogenetic and morphological concepts of *Buccinum* subgenera

Subgenera *Thysanobuccinum, Bathybuccinum* and *Ovulatibuccinum* were erected on the basis of combination of shell and opercular characters, but according to the molecular analysis some of the characters appeared to be homoplastic.

Thysanobuccinum Golikov & Gulbin in Golikov, 1980 originally included two species, the type species *Buccinum tunicatum* Golikov & Gulbin, 1977 from southern Kurile Is (Fig. 2A–B) and *B. pilosum* Golikov & Gulbin, 1977 from Moneron I. in the Okhotsk Sea. The diagnostic character of the genus is the "periostracum constituting most of shell wall, overlying sutures and forming strong spiral cords and axial lamellae" (Golikov 1980: 162). Operculae of the mentioned species are oval, concentric and span more than half aperture length.

In addition to *B. tunicatum* (Buc265), collected in the type locality (Urup I., Kurile Is), two additional species that fit the diagnosis of the genus were included in the analysis (Fig. 2C–D). The incomplete juvenile specimen (Buc269, Fig. 2D), *Buccinum* cf. *tunicatum* is morphologically similar to *B. tunicatum*, and clusters with it in the molecular tree. One more specimen of still new for science species (Buc175, *Buccinum* sp. 2, shell in Fig. 2C) and collected off Honshu I., Japan at abyssal depths (3302–3311 m) has an oval shell with a very strong periostracum, forming spiral cords, similar to the *B. tunicatum* shell. In the tree, it forms a highly supported cluster with another single specimen, which matches the diagnosis of *Bathybuccinum* (Buc189, *Buccinum* sp. 1, shell in Fig. 2I). Remarkably *Buccinum* sp. 2 has a very small operculum, which was considered a character typical for *Bathybuccinum* and *Ovulatibuccinum* but not for *Thysanobuccinum*. Thus, the three sequenced species that share the major morphological character of the (sub)genus, i.e., a well-developed periostracum, are not closely related, and such periostracum was developed at least in two separate lineages.

The genus *Bathybuccinum* (type species *B. bicordatum* Golikov & Sirenko, 1988) containing the nominotypical subgenus and the subgenus *Ovulatibuccinum* (type species *Buccinum ovulum* sensu Golikov & Sirenko, 1988, non Dall, 1895 = *Buccinum bizikovi* sp. nov.) was erected for several small species (SL less than 25 mm) of Buccininae lacking axial ribs and possessing a very small operculum. The operculum is oval with the nucleus located at the lower edge of the operculum in species of

Bathybuccinum, and it spans less than 30% of the aperture length. *Bathybuccinum* (*Bathybuccinum*) originally included two species, the type species and *B. unicordatum* Golikov & Sirenko, 1988; two more species were described later (Fraussen & Chino 2009). Both species originally placed in *Bathybuccinum* were included in our analysis, and they do not cluster together. *Buccinum bicordatum* (Buc188, shell in Fig. 2E) forms a fully supported cluster with *Buccinum nipponense*, a conchologically very different species, which possesses a large operculum (Fig. 3E). Sister to it with high support (PP = 1, B = 100) is *Buccinum* cf. *kobjakovae*, which is also conchologically different from *Buccinum bicordatum* and possesses a large operculum. *Buccinum unicordatum* (Buc266, shell in Fig. 2F) forms a long branch with an unresolved position in our tree. One more still unnamed species, *Buccinum* sp. 1 shares with *Bathybuccinum* the small shell with a well-developed keel and a very small operculum (Buc189; Fig. 2I). This species was illustrated by Hasegawa (2009) as *Ovulatibuccinum* sp. 2. Thus, three species possessing diagnostic characters of *Bathybuccinum* are scattered across the tree, and two of them show highly supported relationships with species of very different morphology, suggesting that the diagnosis of *Bathybuccinum* is based on homoplastic characters.

Bathybuccinum (*Ovulatibuccinum*) differs from the nominotypical subgenus by the "weak development of spiral sculpture, rounded and not angular whorls and the absence of keels" (Golikov & Sirenko, 1988: 86). Originally also *Bathybuccinum* (*Ovulatibuccinum*) *fimbriatum* Golikov & Sirenko, 1988 was included in this subgenus. Later few more species were added to the genus – *Bathybuccinum* (*Ovulatibuccinum*) *clarki* Kantor & Harasewych, 1998 from the Aleutian Islands (although it has a much larger shell, up to 60 mm, and prominent, fine spiral sculpture), *Buccinum bombycinum* sensu Golikov & Sirenko (1998), non Dall, 1907 (= *B. hasegawai* sp. nov., part.), and *Ovulatibuccinum perlatum* Fraussen & Chino, 2009. *Ovulatibuccinum* was raised to genus rank by Fraussen & Chino (2009).

Three species referable to *Ovulatibuccinum* are included in our analysis (Fig. 1): *Buccinum* "*bombycinum*" sensu Golikov & Sirenko (1998) as *Buccinum hasegawai* sp. nov. (Buc273, Buc274, Buc276, shells in Fig. 4), *Bathybuccinum* (*Ovulatibuccinum*) *fimbriatum* (Buc275, shell in Fig. 2H), *Ovulatibuccinum perlatum* (Buc190, shell in Fig. 2G, as *Buccinum chinoi* nom. nov.). Based on our analysis, the species that were previously included in *Ovulatibuccinum* group in two subclades, and the relationships between them remain unresolved.

Thus, the small shell and operculae (less than 0.3 of the aperture length), i.e., the main diagnostic characters of the formerly accepted *Bathybuccinum* and *Ovulatibuccinum* are homoplastic characters, found in several unrelated lineages within *Buccinum* and in *Volutharpa* as well. Also, the small operculae and high intraspecific size variation are found in some species that are classified in *Buccinum* s.s. For instance, according to our data the ratio of operculum length/AL ranges from 0.26 to 0.37 in *Buccinum ciliatum sericatum* Reeve, 1845; from 0.33 to 0.55 in *B. pemphigus* Dall, 1907, and from 0.19 to 0.36 in *B. micropoma* Jensen, 1944, it constitutes 0.19 in *B. sigmatopleura* Dall, 1907, and 0.22 in *B. kashimanum* Okutani, 1964.

One more previously recognized genus group taxon attributed to Buccininae – monotypical *Corneobuccinum* Golikov & Gulbin, 1977 [TS *Colus* (*Latisipho*) *lepidus* Dall, 1918; OD], was not included in the present molecular study. It is characterized by a very thin shell, mostly consisiting of an smooth, orange-brown conchioline layer (Kantor & Sysoev 2006: pl. 87d) and by a large oval opercuum with central nucleus. In the absence of the molecular data we presently consider it as valid.

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Supplementary file

Supp. file 1. Bayesian phylogenetic tree of Buccinoidea Rafinesque, 1815 obtained with the *cox-1,* 16S and 28S concatenated dataset. https://doi.org/10.5852/ejt.2022.817.1759.6627