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Source: Zoological Science, 40(6) : 486-496

Published By: Zoological Society of Japan

URL: <https://doi.org/10.2108/zs230067>

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Systematics and Distributions of Upper Bathyal Species in *Bathyancistrolepis*, a Deep-Sea Whelk Genus Endemic to the Northwest Pacific (Gastropoda: Buccinidae)

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The deep-sea buccinid snail genus *Bathyancistrolepis* is redefined based on the reconstruction of a molecular phylogeny and morphological examination of shell and radular characters. This genus is distinguished from other genera of the subfamily Parancistrolepidinae with a combination of shell traits, including (1) a low spire, (2) sharp, carinate spiral cords or keels and (3) a long, curved siphonal canal, but not with a difference in radular morphology as suggested by previous authors. Three allopatric or parapatric species are recognized in the upper bathyal (447–2057 m) waters around Japan and Taiwan: *B. tokoyodaensis* from off Hokkaido to Sagami Bay in the Northwest Pacific, *B. trochoidea* off Kumano-nada to Miyazaki in the Northwest Pacific and along Nansei Islands in the East China Sea, and *B. taiwanensis* sp. nov. in the South China Sea. These species bear large paucispiral protoconchs that are indicative of benthic early development without a pelagic larval period, and hence low dispersal capability. Seafloor topography seems to have acted as a barrier for their dispersal; the range of *B. tokoyodaensis* supports the previous finding that Izu Peninsula delimits westward distribution of bathyal gastropod species of boreal origins.

Key words: Buccinoidea, dispersal, distribution, molecular phylogeny, Parancistrolepidinae, radula, shell, taxonomy, whelk

INTRODUCTION

The Buccinidae (true whelks) constitute one of the most diverse families of marine gastropods, with a worldwide distribution from the tropics to polar regions (Bouchet and Warén, 1986; Harasewych and Kantor, 2002). They occur on all types of seafloor, ranging from intertidal rocky shores to hadal trenches (Kantor et al., 2020, 2022). Buccinids are particularly abundant and diverse in the shelf and bathyal depth zones of the Northwest Pacific (Kosyan and Kantor, 2009), where they are widely harvested for food (e.g., Fujinaga et al., 2006; Yamakami and Wada, 2021) and have served as suitable model organisms for studying the biogeography of deep-sea benthos (e.g., Amano, 2004; Iguchi et al., 2007; Azuma et al., 2015). The latest molecular phylogeny of the superfamily Buccinoidea (Kantor et al., 2022) has provided the basis for the current classification of the family, encompassing eight subfamilies and 34 extant genera (MolluscaBase, 2023).

Bathyancistrolepis Habe and Ito, 1968 is a buccinid genus endemic to deep waters around Japan and adjacent areas (Okutani and Iwahori, 1992; Tsuchida, 1993; Noda and Kikuchi, 2001; Hasegawa, 2005, 2009; Fukumori et al.,

2018, 2019). This genus was established for *Chrysodomus trochoideus* Dall, 1907, which had long been placed in *Ancistrolepis* Dall, 1895 (e.g., Dall, 1919; Kuroda, 1931; Okutani, 1964; Habe and Ito, 1965a). The basis for the proposal of *Bathyancistrolepis* was a slight difference in the shape of the radula, a feeding apparatus of mollusks. The lateral tooth of the radula bears three cusps with the middle one smallest in both *Ancistrolepis* and *Bathyancistrolepis* (Azuma, 1965: text-fig. 1; Okutani, 1966: text-fig. 10; Habe and Ito, 1972: fig. 3), while the size difference among the cusps seemed more conspicuous in the latter, whose outer cusp was found to be very large and central cusp minuscule (Habe and Ito, 1968).

The type species *B. trochoidea* was described from bathyal depths of 805–1097 m off Cape Shiono-misaki, Wakayama Prefecture, Honshu, Japan (Hasegawa, 2009). Its subspecies, *Ancistrolepis trochoidea ovoidea* Habe and Ito, 1965, was later proposed (as *A. trochoideus ovoideus*; see Systematics) for specimens from “off Choshi, Chiba Prefecture” (Habe and Ito, 1965a). This subspecies was distinguished from the nominotypical form in having a larger shell with thicker, rounder spiral ribs (Habe and Ito, 1965b: 20). However, succeeding authors have considered the shell forms to be continuous and thus recognized only one taxon for extant individuals of the genus (e.g., Okutani, 1966, 2017; Tiba and Kosuge, 1981; Bouchet and Warén, 1986; Kantor and Sysoev, 2006; Hasegawa, 2009). Hasegawa and

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doi:10.2108/zs230067
<https://zoobank.org/4730D513-5B22-46B9-BF31-444BE0790666>

Okutani (2011: 136) argued the possibility of their independent species status, partly based on differences in geographic and bathymetric ranges, although without a formal nomenclatural act. *Ancistrolepis trochoidea tokoyodaensis* Ozaki, 1958, a fossil subspecies from an uplifted Pleistocene deposit at Tokoyoda, Choshi, has also been considered synonymous with the nominotypical form (Okutani, 1966; Egorov and Barsukov, 1994; Noda and Kikuchi, 2001; Kantor and Sysoev, 2006; Amano and Oleinik, 2016).

The aforementioned phylogeny of Buccinoidea, however, has suggested the presence of more than one extant species in *Bathyancistrolepis* (Kantor et al., 2022). An unidentified specimen of the genus from southwest off Taiwan formed a clade with *B. "trochoideus"* from off Kesenuma, Miyagi Prefecture, northeastern Japan, albeit with very long branches leading to them (Kantor et al., 2022: fig. 2), which are suggestive of substantial genetic differentiation and reproductive isolation. This study aims to (1) examine the validity of the genus *Bathyancistrolepis* as an entity independent from *Ancistrolepis* in both phylogenetic and morphological points of view, (2) revise its species tax-

onomy with reference to the type specimens and topotypic material of the previously named taxa, and (3) provide an overview of species' geographic and bathymetric ranges.

MATERIALS AND METHODS

Sampling

A total of 16 buccinid specimens were collected and analyzed for our molecular phylogenetic reconstruction (Table 1). Of these, eight specimens of *Bathyancistrolepis* were accumulated during eight deep-sea expeditions to the Pacific slope of the mainland Japan, East China Sea, and South China Sea (Fig. 1). Five other specimens were included to represent *Clinopegma* Grant and Gale, 1931, *Japelion* Dall, 1916, *Parancistrolepis* Azuma, 1965, *Pseudoliomesus* Habe and Sato, 1973, and *Thalassoplanes* Dall, 1908, all of which belong to the same subfamily with *Bathyancistrolepis* (Parancistrolepidinae Habe, 1972; see Kantor et al., 2022: 819). Three outgroup taxa belong to genera in other subfamilies, namely *Metajapelion* Goryachev, 1987 of Beringiinae and Starobogatov, 1975, *Buccinum* Linnaeus, 1758 of Buccininae Rafinesque, 1815, and *Neptunea* Röding, 1798 of Neptuneinae Stimpson, 1865.

The sampling was made using Oregon-type beam trawls of 3 m

Table 1. Buccinid specimens used in phylogenetic reconstruction with voucher ID, locality information, date of sampling and DDBJ/EMBL/GenBank accession numbers.

Species	Voucher ID	Locality	Coordinates	Depth (m)	Date (M/D/Y)	Cruise and station nos.	COI	28S
Parancistrolepidinae								
<i>Bathyancistrolepis trochoidea</i>	NSMT-Mo 119134* ¹	Off Tanabe, Wakayama	33°33'N, 135°07'E	646–752	04/23/2019	Seisui-maru SS-19-2B	OR438942	OR482187
	AORI_YK#3380	Off Cape Toi, Miyazaki	31°07'N, 131°39'E	1063–1082	06/23/2011	Tansei-maru KT-11-12, st. T10-2	OR438939	OR482188
	AORI_YK#3399	W of Takara Is.	29°19'N, 127°41'E	1017	11/30/2008	Nagasaki-maru N275, st. Q	OR438940	OR482189
	MNHN-IM-2013-78089* ²	NE of Taiwan	25°19'N, 122°37'E	755–988	06/28/2018	Ocean Researcher I Kavalan 2018, CP4117	OR438941	–
<i>Bathyancistrolepis tokoyodaensis</i>	NSMT-Mo 117206* ³	Off Kushiro, Hokkaido	42°11'N, 144°11'E	1134–1219	09/18/2001	Hakuho-maru KH-01-2, st. KC-0	OR438938	–
	AORI_YK#3374	Off Kamaishi, Iwate	39°02'N, 142°32'E	1019–1041	07/23/2012	Tansei-maru KT-12-18, st. 15	OR438936	OR482186
	AORI_YK#4480	Off Kashima, Ibaraki	35°57'N, 141°12'E	627–629	07/18/2021	Shinsei-maru KS-21-14, st. IB2	OR438937	OR482185
<i>Bathyancistrolepis taiwanensis</i> sp. nov.	MNHN-IM-2013-59628* ⁴	SW of Taiwan	22°03'N, 119°04'E	1306–1756	08/01/2015	Ocean Researcher I ZhongSha 2015, CP4167	OR438935	OR482190
<i>Ancistrolepis grammata</i>	Bu-OS-1188	W of Onokotan Is., Kuril	49°31'N, 154°25'E	571–580	2019	Akademik Oparin 56, st. 68	MW429804	–
<i>Clinopegma magnum unicum</i>	AORI_YK#3403	Off Onagawa, Miyagi	38°25'N, 142°00'E	342–343	08/07/2015	Shinsei-maru KS-15-10, st. ON5	OR438944	OR482192
<i>Japelion hirasei</i>	AORI_YK#3449	Off Otsuchi, Iwate	39°21'N, 142°19'E	470–487	08/04/2015	Shinsei-maru KS-15-10, st. OT4-2	OR438945	OR482193
<i>Parancistrolepis fujitai</i>	AORI_YK#3401	Off Namie, Fukushima	37°29'N, 141°59'E	531–540	05/02/2014	Shinsei-maru KS-14-6, st. NO4	MW751549	OR482191
<i>Pseudoliomesus canaliculatus</i>	AORI_YK#4141	Off Tokachi, Hokkaido	42°28'N, 143°54'E	298–303	08/17/2020	Shinsei-maru KS-20-18, st. T1	MW751550	–
<i>Thalassoplanes moerchii</i>	AORI_YK#3404	S of Kamchatka	47°01'N, 160°02'E	5179–5223	05/27/2014	Hakuho-maru KH-14-2, st. NBD1	OR438947	–
Outgroup taxa								
<i>Buccinum lamelliferum</i>	AORI_YK#3407	Off Otsuchi, Iwate	39°26'N, 143°44'E	3370–3547	08/01/2017	Shinsei-maru KS-17-6, st. KANO6	OR438943	OR482194
<i>Metajapelion pericochlion</i>	AORI_YK#4152	Off Otsuchi, Iwate	39°23'N, 142°05'E	144–145	10/03/2020	Shinsei-maru KS-20-15, st. OT130-2	MW751551	–
<i>Neptunea fukueae</i>	AORI_YK#3658	SW of Nagasaki	32°10'N, 129°31'E	470–487	11/14/2006	Nagasaki-maru N226, st. A	OR438946	–

Voucher ID for extracted DNA: *¹AORI_YK#4129, *²#3660, *³#3474, *⁴#3505

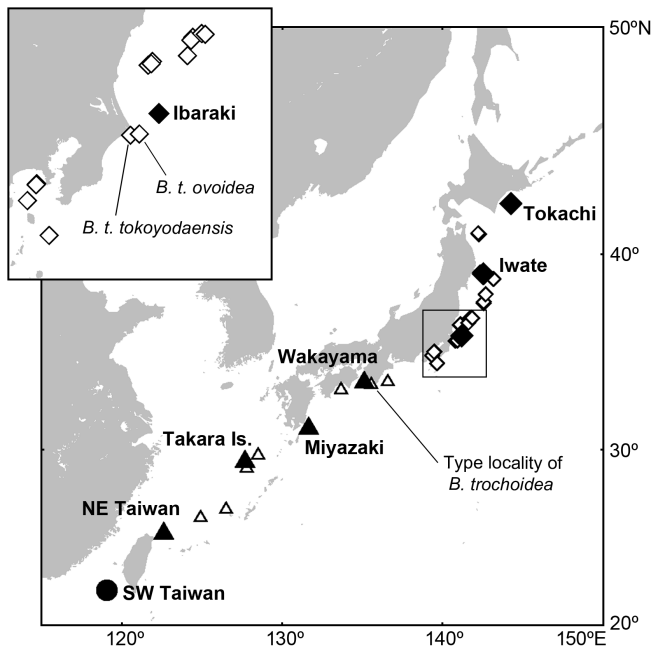


Fig. 1. Geographic distributions of three *Bathyancistrolepis* species. Filled symbols represent sampling sites of specimens used in molecular phylogenetic analysis (triangles: *B. trochoidea*, diamonds: *B. tokoyodaensis*, circle: *B. taiwanensis* sp. nov.). Open triangles and diamonds denote verified occurrence records of *B. trochoidea* and *B. tokoyodaensis*, respectively. Type localities are also shown for three nominal taxa.

span (on R/V *Tansei-maru*, R/V *Shinsei-maru*, R/V *Seisui-maru*, and T/V *Nagasaki-maru*) or 4 m span (on R/V *Hakuho-maru*), or an otter trawl of 16.4 m backstroke (on R/V *Ocean Researcher 1*). All but one individual were preserved in 95–100% ethanol; a specimen of *Bathyancistrolepis* (NSMT-Mo 117206) was fixed in 10% seawater-diluted formalin and preserved in 75% ethanol. The specimens are deposited in Atmosphere and Ocean Research Institute, The University of Tokyo (AORI), Muséum national d'Histoire naturelle, Paris (MNHN), and National Museum of Nature and Science, Tokyo (NSMT or NMNS; Table 1).

Molecular analysis

Total DNA was extracted from the foot tissue using a DNeasy Blood and Tissue Kit (Qiagen) and then treated with GeneReleaser (Bioventures). Partial fragments of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene were amplified with Folmer et al.'s (1994) universal LCO1490 and HCO2198 primers. Amplification for all except the formalin-fixed specimen was conducted in a total volume of 25 μ l, including 16.0 μ l DDW, 4.0 μ l DNA solution, 0.1 μ l Ex Taq HS (TaKaRa Bio), 2.5 μ l Ex Taq Buffer, 2.0 μ l dNTP mixture (2.5 mM each), and 0.3 μ l forward and reverse primers (20 μ M each). Polymerase chain reactions were carried out with an initial denaturation at 94.5°C (2 min), followed by 35 cycles of denaturation at 94.5°C (30 s), annealing at 42°C (40 s) and extension at 72°C (1 min), and final extension at 72°C (5 min). For the formalin-fixed specimen, amplification was performed in a reaction mixture of 7.25 μ l DDW, 4.0 μ l DNA solution, 0.5 μ l MightyAmp DNA Polymerase Ver.2 (TaKaRa Bio), 12.5 μ l MightyAmp Buffer, 0.375 μ l of each primer, with an initial denaturation at 98°C (2 min), followed by 30 cycles of denaturation at 98°C (10 s), annealing at 50°C (30 s) and extension at 68°C (1 min).

Successful amplicons were purified with ExoSAP-IT (Thermo Fisher Scientific) following the manufacturer's protocol and then sequenced using a BigDye Terminator Cycle Sequence Kit v3.1

(Thermo Fisher Scientific) and amplification primers LCO1490 and HCO2198. After purification with a BigDye XTerminator Purification Kit (Thermo Fisher Scientific), the reaction mixtures were analyzed on an ABI 3130xl sequencer at AORI. Resulting sequences from both strands were edited and assembled in AliView 1.25 (Larsson, 2014). The final dataset consisted of 658 characters and 17 operational taxonomic units, including another parancistrolepidine species, *Ancistrolepis grammata* (Dall, 1907), with a sequence in the DDBJ/EMBL/GenBank databases (MW429804; Kantor et al., 2022).

The phylogenetic analysis of the dataset was performed using the maximum likelihood approach in a GUI version (raxml-GUI 2.0) of RAXML v. 8.2.12 (Stamatakis, 2014; Edler et al., 2021). The substitution model HKY + G + I was selected with ModelTest-NG 0.1.6 (Darrriba et al., 2020) implemented in raxmlGUI 2.0; each codon position was allowed to have its own parameter estimates. Nodal support was evaluated with 1000 bootstrap replications using the rapid bootstrapping option (Stamatakis et al., 2008). The obtained tree was edited in FigTree 1.4.3 (available at: <http://tree.bio.ed.ac.uk/software/figtree/>). Finally, pairwise Kimura 2-parameter (K2P) distances were calculated among the eight individuals of *Bathyancistrolepis* in MEGA v.10.2.4 (Kumar et al., 2018).

Ten individuals, including six from the ingroup and four from the outgroup taxa, were selected based on this mitochondrial COI-gene tree to reconstruct a nuclear 28S rDNA phylogeny for the species of *Bathyancistrolepis*. Polymerase chain reactions were carried out as described above for Ex Taq HS with an annealing temperature of 50°C and primers LSU5 (Littlewood et al., 2000) and ECD2S (Williams and Ozawa, 2006). Resulting sequences from both strands were edited in AliView, aligned using the online version of MAFFT with the L-INS-I strategy (Kato et al., 2019), and then masked to remove alignment ambiguous sites in Gblocks 0.91b with the default parameters except "Allowed gap positions" set to "With half" (Castresana, 2000). Phylogenetic reconstruction was performed with the substitution model GTR + G + I as selected by ModelTest-NG in RAXML.

Morphology and distribution records

The shells of the buccinid specimens used in the phylogenetic reconstruction were all photographed from a frontal view. Five of *Bathyancistrolepis* were dissected to extract the radula for scanning electron microscopy. The extracted radula was soaked in sodium hypochlorite for 10–60 min, washed in distilled water, dried, mounted on a stub and coated with platinum for observation under Hitachi S-4800 at AORI or TeScan TS5130MM at MNHN. The shells of primary types were also examined for all taxa currently allocated to the extant *Bathyancistrolepis*, namely *Chrysodomus trochoideus* Dall, 1907, *Ancistrolepis trochoidea tokoyodaensis* Ozaki, 1958 and *Ancistrolepis trochoidea ovoidea* Habe and Ito, 1965, either through the loan of the specimens from NSMT or examination of photographs in the digitized specimen records of the Smithsonian National Museum of Natural History (USNM).

Previous occurrence records of *Bathyancistrolepis* were also investigated through a critical review of the following papers: Okutani (1966), Okutani and Iwahori (1992), Hasegawa (2005, 2009), Hasegawa and Okutani (2011), Zhang et al. (2015) and Kantor et al. (2022). The localities of the previous samples were plotted on the distribution map (Fig. 1) when species identity was determined from photographs in the literature or examination of actual specimens deposited in NSMT.

RESULTS

Partial sequences of the mitochondrial COI gene, 658 bp long excluding the primer regions, were successfully determined for eight individuals of *Bathyancistrolepis* and eight other buccinid species. The sequences were newly

deposited in the DDBJ/EMBL/GenBank databases with the accession numbers OR438935–OR438947 (Table 1), except three that were published in a previous paper (Kantor et al., 2022). The maximum-likelihood analysis supported the monophyly of the subfamily Parancistrolepidinae, albeit with a moderate bootstrap proportion (BS) value of 78% (Fig. 2A). The eight individuals of *Bathyncistrolepis* were found to be monophyletic (BS = 97%) and sister to the remaining six genera of Parancistrolepidinae (BS = 88%). Relationships among the latter six were unresolved with insufficient BS values ($\leq 59\%$) except for the monophyly of *Ancistrolepis* + *Clinopegma* (BS = 99%).

Bathyncistrolepis consisted of three clades. An individual from southwest off Taiwan in the South China Sea, representing *B. taiwanensis* sp. nov. (see Systematics), was recovered as sister to the remaining seven individuals from the Pacific and East China Sea with a moderate BS value (78%). The latter individuals formed two robust clades, one from off the northeastern coasts of Japan (Hokkaido, Iwate and Ibaraki; BS = 93%) and the other from southwestern Japan and East China Sea (Wakayama, Miyazaki, Tokara and northeast off Taiwan; BS = 99%). Within the northeastern clade (hereafter called *B. tokoyodaensis*), two individu-

als from off Honshu appeared closer to each other than to the one from Hokkaido (BS = 50%). The southwestern clade (*B. trochoidea*) also showed a topology concordant with the geographic origins of the individuals; those from off mainland Japan were paraphyletic to a subclade from the East China Sea (BS = 99%), with the easternmost Wakayama being the first offshoot (BS = 96%; see Fig. 1). Pairwise K2P distances were 11.2–13.2% between *B. taiwanensis* sp. nov. and others, 8.1–10.3% between *B. tokoyodaensis* and *B. trochoidea*, 0.5–2.5% within *B. tokoyodaensis*, and 1.1–4.4% within *B. trochoidea*. All substitutions within *Bathyncistrolepis* were silent except for one at a second codon position (at position 318 in 658 bp): C in *B. taiwanensis* (GCA alanine) and T in *B. trochoidea* and *B. tokoyodaensis* (GTA valine).

Nuclear 28S rDNA sequences were determined for 10 individuals representing the three species of *Bathyncistrolepis* and four species of other buccinid genera. The sequences ranged from 769 to 779 bp in length excluding the primers and were deposited in the DDBJ/EMBL/GenBank databases (OR482185–OR482194). Sequence alignments had 781 and 765 sites before and after the Gblocks masking, respectively. The maximum-likelihood

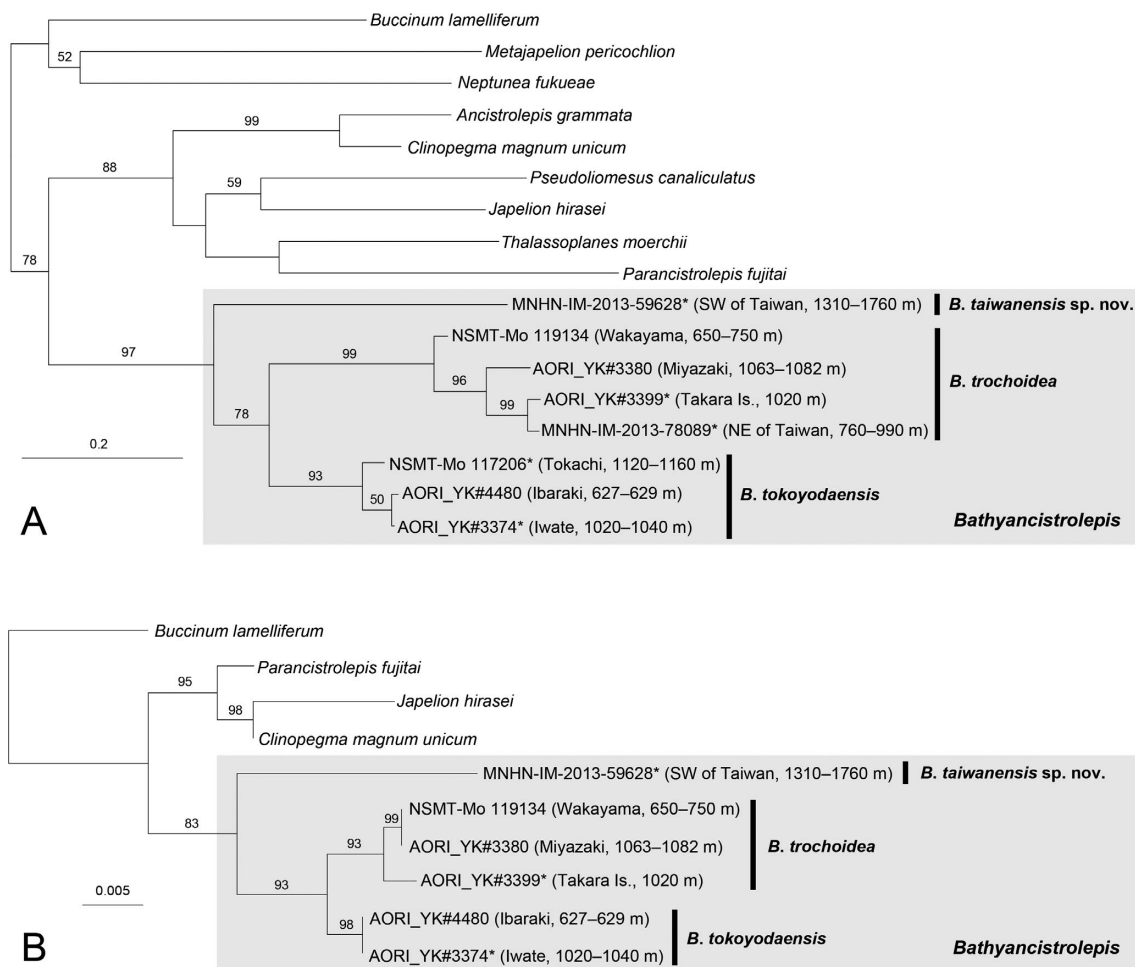


Fig. 2. Maximum likelihood trees of *Bathyncistrolepis* inferred from 658-bp dataset of mitochondrial COI gene (**A**) and masked 765-site alignment of nuclear 28S rDNA sequences (**B**). Numerals on branches denote bootstrap proportion values in %. All individuals of *Bathyncistrolepis* are shown in Figs. 3 and 4; asterisks denote those examined for radulae shown in Fig. 5.

analysis of the masked 28S dataset corroborated the monophyly of each of *Bathyancistrolepis* (BS = 83%), *B. trochoidea* (93%) and *B. tokoyodaensis* (98%; Fig. 2B). The latter two species formed reciprocal sisters as in the COI tree with a higher BS value (93%). Two individuals of *B. trochoidea* from off mainland Japan (Wakayama and Miyazaki) had the exact same 28S sequence that resulted in a very high BS value for their monophyly (99%); this was the only incongruence between the mitochondrial and nuclear gene trees with meaningful support indices (see Fig. 2).

SYSTEMATICS

Family **Buccinidae** Rafinesque, 1815

Subfamily **Parancistrolepidinae** Habe, 1972

Genus ***Bathyancistrolepis*** Habe and Ito, 1968

Type Species. *Chrysodomus trochoideus* Dall, 1907 by original designation.

Diagnosis. Shell small for subfamily, rhomboid to elliptical in outline; spire relatively low; teleoconch surface bearing sharp, carinate spiral cords or keels with secondary spiral striae in between; outer lip of aperture simple, thin; siphonal canal long, strongly curved to left; central and lateral teeth of radula tricuspid or each with up to seven cusps.

Remarks. Habe and Ito (1968) established this genus by separating its type species, *B. trochoidea*, from the species of *Ancistrolepis* Dall, 1895, based solely on a subtle difference in the shape of the radula. They noted that the lateral tooth was tri-cuspid in both genera with the middle cusp being the smallest (Azuma, 1965: text-fig. 1; Okutani, 1966: text-fig. 10; Habe and Ito, 1972: fig. 3), whereas *Bathyancistrolepis* appeared to have a particularly conspicuous size difference, with the outer cusp being very large and central one minuscule (Habe and Ito, 1968: 3).

The present molecular phylogenetic reconstruction shows that *B. trochoidea* is indeed distantly related to six other genera of the subfamily Parancistrolepidinae, including *Ancistrolepis* (Fig. 2). Although its type species, *A. eucosmia* (Dall, 1891), could not be incorporated in the analysis, diagnostic shell traits seem to further warrant the independent status of *Bathyancistrolepis* (see below). The depths of splits among three major clades or species of *Bathyancistrolepis* were comparable to or even greater than those among other parancistrolepidine genera. We attribute this to finer taxonomic sampling in *Bathyancistrolepis*, and/or the need of taxonomic relocation in (or synonymization of) other genera, rather than the need of establishing a new genus or genera for the studied taxa.

The inclusion of *B. taiwanensis* sp. nov., however, invalidates the use of the subtle difference in the radular teeth as the differential diagnosis of *Bathyancistrolepis*. This new species bears a highly apomorphic radula that resembles those of some unrelated parancistrolepidine taxa (see Discussion). We instead propose that *Bathyancistrolepis* can be distinguished from other genera with a combination of the following conchological traits. (1) The siphonal canal of the aperture is long and curved to left, not short and straight as in other genera (Habe and Ito, 1968: 7). (2) The spire is relatively low with the aperture occupying half the shell height, in contrast with a higher spire and a smaller aperture in many others (Egorov and Barsukov, 1994; Amano and Oleinik,

2016). (3) The teleoconch surface is ornamented with sharp, carinate spiral cords or keels, rather than thick, round spirals found in *A. eucosmia* and other species of *Ancistrolepis* (e.g., Egorov and Barsukov, 1994).

The specific and subspecific names in this genus have long been spelled incorrectly with a masculine epithet (i.e., *B. trochoideus* and *B. t. ovoideus*), as pointed out by Habe (1977, 2001) and Petit and Bieler (1996). A genus-group name that ends in a Greek word, including “-lepis,” is feminine (International Code of Zoological Nomenclature, Article 30.1.2), and thus the two names above should be spelled *B. trochoidea* and *B. t. ovoidea*.

***Bathyancistrolepis trochoidea* (Dall, 1907)**

(Figs. 3A–D; 5A, B)

Chrysodomus trochoideus Dall, 1907: p. 156; Kosuge, 1972, pl. 15, fig. 7 (lectotype).

Ancistrolepis trochoideus — Dall, 1919, p. 313; Dall, 1921, pl. 9, fig. 5 (lectotype); Kuroda, 1931, p. 230, fig. 5 [reproduction of Dall (1921: pl. 9, fig. 5)]; Habe and Ito, 1965a, p. 46, no. 17, pl. 13, fig. 17; Okutani, 1966, p. 19 (in part), text-fig. 9A; Tsuchida, 1985, p. 101, fig. 9.

Bathyancistrolepis trochoideus — Habe and Ito, 1968, p. 4, 7; Bouchet and Warén, 1986, p. 460 (in part), fig. 34 (lectotype); Okutani and Iwahori, 1992, p. 248, figs. 30 (shell), 31, 32 (radulae); Tsuchida, 1993, pl. 1, fig. 9; Higo et al., 2001, fig. G2550 (lectotype); Zhang et al., 2015, fig. 1; Kitagawa, 2017, fig. 117-30; Okutani, 2017, p. 254 (in part), pl. 210, fig. 8a.

Bathyancistrolepis trochoidea — Habe and Sato, 1973, p. 3. *Ancistrolepis (Bathyancistrolepis) trochoideus* — Tiba and Kosuge, 1981, p. 12 (in part), fig. 1; Egorov and Barsukov, 1994, p. 9, fig. 18F (lectotype); Hasegawa, 2005, p. 159, fig. 8H.

Bathyancistrolepis trochoideus trochoideus — Okutani and Habe, 1983, p. 292, 120 (text-fig.); Okutani, 2000, p. 463, pl. 20, fig. 43.

Type specimens. Lectotype by present designation: USNM 110494, dried shell from Albatross station (st.) 4972, off Cape Shiono-misaki (33°25'45"N, 135°33'00"E), 440 fathoms (805 m), 30 August, 1906 (see Hasegawa, 2009: 285) (<http://n2t.net/ark:/65665/301a2bfa9-2b7d-404a-8aa7-8b371df46013>). Paralectotypes by present designation: four dried shells from Albatross st. 4973, off Cape Shiono-misaki (33°24'15"N, 135°30'30"E), 600 fathoms (1097 m), 30 August, 1906, three specimens USNM 110495 (<http://n2t.net/ark:/65665/36bfae4f0-d2b2-4340-b1d9-72f50b81fdae>), one specimen NSMT-Mo 49774 (Habe and Ito, 1965a: pl. 13, fig. 17; K. Hasegawa, pers. comm.).

Redescription. Shell up to 22.6 mm high and 15.5 mm wide (19.5 mm and 14.2 mm in lectotype) with a rhomboid outline. Protoconch paucispiral, smooth, 2.2 mm in maximum dimension. Teleoconch with up to six whorls, covered with a thin, lamellose periostracum of yellowish color. Penultimate whorl with up to three spiral cords above a strong spiral keel on shoulder. Last whorl occupying $\geq 70\%$ of shell height, marked with two prominent spiral keels near periphery, ornamented with several weaker spiral cords (up to four above, and five to seven below, keels); surface between

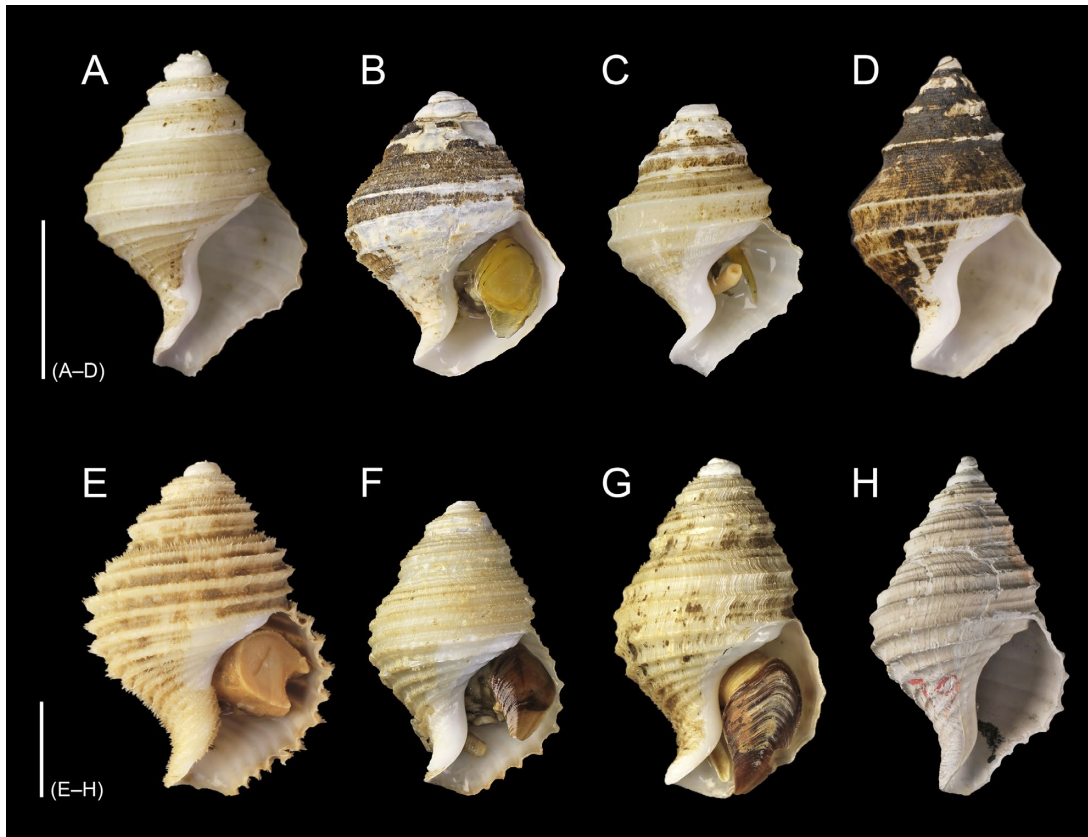


Fig. 3. *Bathyancistrolepis trochoidea* (A–D) and *B. tokoyodaensis* (E–H). (A) NSMT-Mo 119134 from off Wakayama, 646–752 m deep. (B) AORI_YK#3380, off Miyazaki, 1063–1082 m. (C) AORI_YK#3399, off Takara Is., 1017 m. (D) MNHN-IM-2013-78089, northeast off Taiwan, 755–988 m. (E) NSMT-Mo 117206, off Tokachi, 1134–1219 m. (F) AORI_YK#3374, off Iwate, 1019–1041 m. (G) AORI_YK#4480, off Ibaraki, 627–629 m. (H) NMNS PM 4446, holotype of *Ancistrolepis trochoideus tokoyodaensis* Ozaki, 1958 from Iioka Formation, Tokoyoda, Choshi, Chiba. Scale bars: 10 mm.

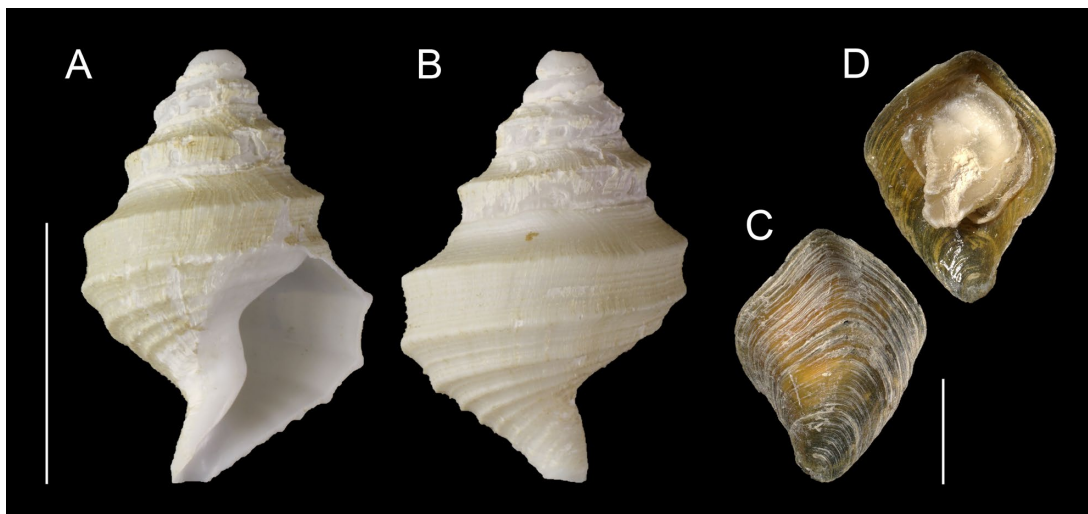


Fig. 4. *Bathyancistrolepis taiwanensis* sp. nov., holotype, MNHN-IM-2013-59628 from southwest off Taiwan, 1306–1756 m deep. (A, B) Apertural and abapertural views of shell. Scale bar: 10 mm. (C, D) Exterior and interior views of operculum, respectively. Scale bar: 2 mm.

keels and cords with secondary spiral striae and fine growth lines. Aperture rhomboid to obovate, up to 12.1 mm high and 8.0 mm wide (10.6 mm and 6.6 mm in lectotype), occupying 50–58% of shell height and 49–52% of shell width; siphonal

canal long, wide, strongly curved to left. Central tooth of radula rectangular with three to five cusps; central cusp(s) larger than others. Lateral tooth with three curved cusps; outer cusp very large, twice as high as inner cusp; central

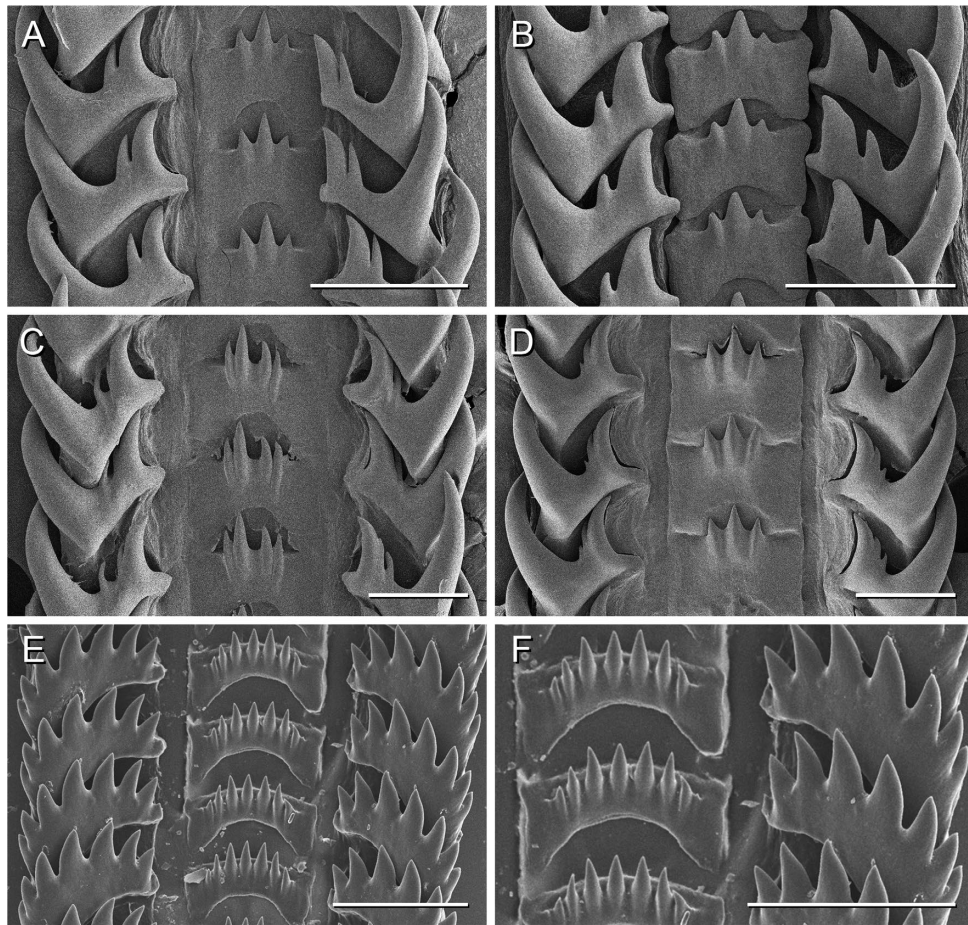


Fig. 5. Radulae of three *Bathyancistrolepis* species, scanning electron microscopy. **(A, B)** *B. trochoidea*. **(A)** AORI_YK#3399 from off Takara Is., 1017 m deep. **(B)** MNHN-IM-2013-78089, northeast off Taiwan, 755–988 m. **(C, D)** *B. tokoyodaensis*. **(C)** NSMT-Mo 117206, off Tokachi, 1134–1219 m. **(D)** AORI_YK#3374, off Iwate, 1019–1041 m. **(E, F)** *B. taiwanensis* sp. nov., holotype, MNHN-IM-2013-59628 from southwest off Taiwan, 1306–1756 m deep. Scale bars: 100 μ m.

cusps smallest, often located closer to inner cusp.

Distribution. From off Kumano-nada to Miyazaki in the Northwest Pacific and along Nansei Islands in the East China Sea, 646–2050 m deep.

Remarks. The original description of *Chrysodomus trochoideus* was based on multiple syntypes from two sampling stations off Cape Shiono-misaki (Dall, 1907; see Hasegawa, 2009: 285). It was not accompanied by an illustration, but a line drawing of a single shell was later provided by the same author (Dall, 1921: pl. 9, fig. 5). This particular shell from the Albatross station 4972 (USNM 110494) was photographed and shown as “type” by Kosuge (1972: pl. 15, fig. 7) and Tiba and Kosuge (1981: fig. 1). Habe and Ito (1965a) apparently considered this to be the holotype of the species when they showed a syntype from station 4973 as a “paratype” (pl. 13, fig. 17; a specimen donated and relocated from USNM 110495 to NSMT-Mo 49774). These apparently led many subsequent authors to more explicitly indicate USNM 110494 as the holotype (e.g., Bouchet and Warén, 1986; Egorov and Barsukov, 1994; Higo et al., 2001; Noda and Kikuchi, 2001; Hasegawa, 2009). Kantor and Sysoev (2006: 155) instead considered this specimen as a lectotype designated by Tiba and Kosuge (1981). However, Tiba and Kosuge’s (1981: 12) reference to the specimen as “type,” not

“the type,” did not make an unambiguous selection of a particular syntype and is therefore deemed an invalid designation (see International Code of Zoological Nomenclature, Article 74.5). Here, the same specimen is formally designated as the lectotype of *C. trochoideus* to ensure nomenclatural stability.

This species has been considered the only extant taxon of *Bathyancistrolepis* with a widespread distribution from Kuril Islands to East China Sea (e.g., Okutani, 1966; Okutani and Iwahori, 1992; Tsuchida, 1993; Kantor and Sysoev, 2006; Hasegawa, 2009; Okutani, 2017; Fukumori et al., 2018, 2019). Hasegawa and Okutani (2011) argued the possibility of independent species statuses of “*trochoideus* and *ovoideus* forms”, but without a formal nomenclatural act. The present study shows that the two subspecies or morphotypes indeed represent different species (Fig. 2; see below), with *B. trochoidea* occurring only on upper bathyal floors off southwestern Japan in the Pacific Ocean and East China Sea. The sampling site of one of our sequenced specimens (NSMT-Mo 119134 from off Tanabe, Wakayama, 646–752 m deep) is very close, both geographically and bathymetrically, to the type locality of the species (off Shiono-misaki, Wakayama, 805 m; Fig. 1). This sequenced specimen (Fig. 3A) is also very similar conchologically to the

lectotype (e.g., Kosuge, 1972: pl. 15, fig. 7; Bouchet and Warén, 1986: fig. 34), thus warranting the nomenclatural identity of the species. The occurrence record from off Kumano-nada, Mie Prefecture by Okutani (1966: text-fig. 9A) represents the easternmost known distribution of the species (Fig. 1).

***Bathyncistrolepis tokoyodaensis* (Ozaki, 1958)**

(Figs. 3E–H; 5C, D)

Ancistrolepis trochoideus (Dall, 1907) — Suzuki, 1935, p. 187–194, figs. 1–9; Ozaki, 1958, p. 149, pl. 15, figs. 14, 15; Okutani, 1964, p. 410, pl. 2, figs. 9, 10; Okutani, 1966, p. 19 (in part), text-fig. 9C–G; Baba, 1990, p. 162, pl. 10, fig. 13.

Ancistrolepis trochoideus tokoyodaensis Ozaki, 1958: p. 150, pl. 15, figs. 16, 17 (holotype); Shikama, 1970, p. 108, pl. 31, fig. 27.

Ancistrolepis trochoideus ovoideus Habe and Ito, 1965a, p. 46, pl. 13, fig. 18; Habe and Ito, 1965b, p. 20, 33, 34, pl. 2, fig. 13.

Bathyncistrolepis trochoidea ovoidea — Habe and Sato, 1973, p. 3, 6, pl. 1, fig. 11 (radula).

Ancistrolepis (*Bathyncistrolepis*) *trochoideus* — Tiba and Kosuge, 1981, p. 11 (in part), figs. 2–9.

Bathyncistrolepis trochoideus ovoideus — Okutani and Habe, 1983, p. 232, text-fig. in p. 120; Okutani, 1986, p. 149 with a color figure; Okutani, 2000, 463, pl. 230, fig. 44; Kitagawa, 2017, fig. 117–29.

Bathyncistrolepis trochoideus — Bouchet and Warén, 1986, p. 460 (in part), pl. 2, fig. 7 (radula), pl. 6, fig. 35 (shell); Watanabe and Naruke, 1988, p. 49, pl. 7, fig. 5; Okutani et al., 1988, p. 110, fig. 78; Noda and Kikuchi, 2001, p. 103–111, figs. 2–7; Kantor and Sysoev, 2006, pl. 70, fig. A, A'; Hasegawa, 2009, p. 284 (in part), fig. 170; Okutani, 2017, p. 254 (in part), pl. 210, fig. 8b; Kantor et al., 2022, p. 820, fig. 12H.

Ancistrolepis (*Bathyncistrolepis*) *trochoideus ovoideus* — Egorov and Barsukov, 1994, p. 9, fig. 2B.

Ancistrolepis (*Bathyncistrolepis*) *trochoideus tokoyodaensis* — Egorov and Barsukov, 1994, p. 9, fig. 2A.

Type specimens. Holotype: NMNS PM 4446, fossil shell from Iioka Formation (= Early Pleistocene Obama Formation: T. Haga, pers. comm.), Inubo Group, Tokoyoda, Choshi, Chiba Prefecture, 1951 by T. Imazeki. Type specimens of *Ancistrolepis trochoidea ovoidea* Habe and Ito, 1965: “off Choshi, Chiba Prefecture, Japan, about 200 m deep,” holotype NSMT-Mo 54874, paratype NSMT-Mo 54875.

Redescription. Shell up to 38.4 mm high, up to 26.9 mm wide (36.5 mm and 21.4 mm in holotype) with an elliptical or spindle-shaped outline. Protoconch paucispiral, smooth, ca. 2.6 mm in maximum dimension. Teleoconch with up to five round whorls, covered with a thick, hairy periostracum of greenish yellow color. Penultimate whorl with five or six spiral cords. Last whorl occupying $\geq 75\%$ of shell height, bearing 12–17 spiral cords, which are strongest near periphery with wider interspaces, weaker and denser toward suture and base, each equipped with a line of periostracal hairs on ridge; surface between cords with secondary spiral

striae and fine growth lines. Aperture rhomboid to obovate, up to 21.2 mm high and 14.1 mm wide (21.5 mm and 8.3 mm in holotype), occupying 49–56% of shell height and 49–53% of shell width; siphonal canal long, wide to relatively narrow, strongly or slightly curved to left. Central tooth of rectangular, tri- or tetracuspid with inner cusp(s) larger than others. Lateral tooth with three or four curved cusps; outer cusp very large, twice as high as inner cusp; central cusp(s) very small and slender, located closer to or often almost integrated to inner cusp.

Distribution. From off Hokkaido to Sagami Bay in the Northwest Pacific, 447–2057 m deep.

Remarks. This species can be distinguished from the allopatric *B. trochoidea* in having a larger shell with more round whorls. Its spiral cords are more regularly sized and spaced than those of the former species, and each cord bears a line of periostracal hairs on the ridge only in *B. tokoyodaensis* (Fig. 3). These two species formed reciprocal sisters in both of our mitochondrial COI and nuclear 28S gene trees (Fig. 2).

Ozaki (1958) described this as a fossil subspecies (*Ancistrolepis trochoidea tokoyodaensis*) from an uplifted Pleistocene deposit at Tokoyoda, Choshi, Chiba Prefecture (0.9–1.2 million years ago: T. Haga, pers. comm.). The holotype of *B. tokoyodaensis* is a somewhat atypical form of the species with a slender outline and a weakly curved siphonal canal (Fig. 3H), but shells from the same Iioka Formation are variable in these characters (Noda and Kikuchi, 2001: figs. 2–6) and agree well with extant shells from off the nearby Ibaraki (Fig. 3G) and Sagami Bay (Okutani, 1966: text-fig. 9C–G; Okutani et al., 1988: fig. 78). Another subspecies name, *Ancistrolepis trochoideus ovoideus*, was proposed 7 years later by Habe and Ito (1965a) for an extant shell with a much broader outline (Habe and Ito, 1965b: pl. 2, fig. 13). Such broad shells with thick, evenly spaced spiral cords and conspicuous periostracal hairs are typically found from off Iwate, Miyagi, and Fukushima Prefectures (Fig. 3E; Hasegawa, 2009: fig. 170; Kantor et al., 2022: fig. 12H). Although this holotype was recorded from “off Choshi, Chiba Prefecture, Japan, about 200 m deep,” which could be very close to the type locality of the Pleistocene fossil form (Fig. 1), it was probably a fishing bycatch landed at Choshi and the actual sampling might have been made at a deeper site off Fukushima or further up north (see Hasegawa and Okutani, 2011: 135, 136). Regardless, these slender and broad shells are continuous with intermediate phenotypes and well within the variation of a single species, and at the same time discernible from the specimens of *B. trochoidea* as diagnosed above. *Bathyncistrolepis tokoyodaensis* based on the Pleistocene fossil thus precedes as the senior synonym of this species.

***Bathyncistrolepis taiwanensis* sp. nov.**

(Figs. 4; 5E, F)

Bathyncistrolepis n. sp. — Kantor et al., 2022: fig. 2 (molecular tree).

Type specimen. Holotype: MNHN-IM-2013-59628, dried shell, operculum and extracted head-foot from st. CP4167, ZhongSha 2015, 1306–1756 m deep, southwest off

Taiwan, South China Sea (22°03'N, 119°04'E), 1 August, 2015.

Etymology. The name refers to the type locality, off Taiwan.

Diagnosis. Shell small, last whorl with two spiral keels, one on shoulder and another on periphery, supplemented with six weaker spirals below periphery; siphonal canal long, narrow; central and lateral teeth of radula oblong comb-like, each bearing seven cusps.

Description. Shell 16.6 mm high, 11.2 mm wide with a rhomboid outline. Protoconch paucispiral, smooth, ca. 2.2 mm in maximum dimension. Teleoconch with five whorls, covered with a thin yellowish periostracum. Penultimate whorl with a strong spiral keel on shoulder. Last whorl occupying ca. 75% of shell height, marked with two prominent spiral keels, one on shoulder and another on periphery, supplemented with six weaker spiral cords below periphery; surface between keels and cords ornamented with secondary spiral striae and fine growth lines. Aperture rhomboid, 8.6 mm high and 7.6 mm wide, occupying 52% of shell height and 68% of shell width; siphonal canal long, narrow and tapering, strongly curved to left. Operculum 4.6 mm high, 3.5 mm wide, pale brown, rhomboid with a terminal nucleus. Central and lateral teeth of radula oblong, comb-like and slightly curved, each bearing seven cusps with decreasing sizes toward edges; cusps acute in central tooth while large and stout in lateral tooth.

Distribution. Known only from the type locality, southwest off Taiwan in the South China Sea, 1306–1756 m deep.

Remarks. Although represented by a single holotype, this new species is distinguished from the two preceding species in having entirely different morphology of the radula (Fig. 5; see Discussion). Conchologically, this resembles the type species, *B. trochoidea*, in sharing two spiral keels on the shoulder–periphery area of the last whorl. These keels make the shell outline sharp, contrasting to the round outline of *B. tokoyodaensis* (Figs. 3, 4). The long, narrow, and tapering siphonal canal is a shell trait unique to *B. taiwanensis*. The molecular phylogenetic reconstruction also supports its independent status (Fig. 2).

DISCUSSION

Our independent mitochondrial and nuclear gene phylogenies support the validity of the buccinid genus *Bathyancistrolepis* as an entity independent from *Ancistrolepis* and other genera in the subfamily Parancistrolepidinae (Fig. 2). Three Recent species are recognized, namely *B. trochoidea*, *B. tokoyodaensis*, and *B. taiwanensis* sp. nov. (Figs. 3, 4), as independent clades with diagnostic morphological characters. The genus is now distinguished from other genera with a combination of shell traits, including (1) a low spire, (2) sharp, carinate spiral cords or keels and (3) a long, curved siphonal canal, but not with a difference in radular morphology as suggested by the original authors (Habe and Ito, 1968).

The radulae of *B. trochoidea* and *B. tokoyodaensis* resemble those of many other buccinid taxa, particularly the species of *Clinopegma* and *Ancistrolepis*, in sharing a very large outer cusp of the lateral tooth (Fig. 5A–D; see Habe and Ito, 1972; Habe and Sato, 1973; Tiba and Kosuge, 1981; Bouchet and Warén, 1986). However, *B. taiwanensis* sp.

nov. has a markedly different radula, where central and lateral teeth are oblong comb-like with seven cusps (Fig. 5E, F). Similar lateral teeth have been reported for unrelated parancistrolepidine species, *Thalassoplanes moerchii* (Dall, 1908) and *Parancistrolepis kinoshitai* (Kuroda, 1931) (Azuma, 1965: text-fig. 2; Kantor et al., 2022: fig. 11E; see Fig. 2). These apomorphic radulae seem to have been acquired in parallel, potentially reflecting similar feeding ecology (see Radwin and Wells, 1968 for the cases of another gastropod family Muricidae).

The three species of *Bathyancistrolepis* live allopatrically or parapatrically in the upper bathyal (447–2057 m) zone around Japan and Taiwan: *B. tokoyodaensis* from off Hokkaido to Sagami Bay in the Northwest Pacific, *B. trochoidea* off Kumano-nada to Miyazaki in the Northwest Pacific and along Nansei Islands in the East China Sea, and *B. taiwanensis* sp. nov. in the South China Sea (Fig. 1). The large paucispiral protoconchs seen in *Bathyancistrolepis* indicate that they hatch directly as benthic juveniles without a pelagic larval period, as in the case of all other deep-sea buccinids (Bouchet & Warén, 1986; P. Bouchet, pers. comm.). The dispersal capability of an individual would therefore be very low—presumably much lower than individuals of other direct-developing invertebrates, including amphipod and isopod crustaceans, which may disperse as juveniles and adults with bottom currents and turbidity currents (Weisshappel, 2001; Brix and Svavarsson, 2009).

The distribution range of *B. tokoyodaensis* is delimited to the west by a saddle (with depth of ca. 400–600 m) between the Izu Peninsula and the northern Izu Islands, which is known to act as a dispersal barrier for bathyal gastropod species with boreal distributions (Okutani, 1972; Hasegawa and Okutani, 2011: fig. 59). This barrier appears particularly impermeable for direct-developing buccinids. Hasegawa (2009) has pointed out that none among dozens of boreal buccinid species occur on the western side of the saddle but with “*B. trochoidea*” as a single possible exception. The present study shows that Hasegawa’s rule applies to all buccinid species by discriminating *B. tokoyodaensis* from *B. trochoidea*. The Taiwan and Luzon Straits that connect the East and South China Seas might have similarly been acting as a dispersal barrier for *B. trochoidea* and *B. taiwanensis* sp. nov. (see Xu et al., 2018; Gu et al., 2021). Their non-sister relationship (Fig. 2) and boreal distributions of most parancistrolepidine taxa, however, imply independent southern migration rather than vicariant speciation around Taiwan.

The present study recognizes three species of *Bathyancistrolepis* in the upper bathyal zone of Japan and adjacent areas. Previous faunistic studies have reported occurrences of this group from deeper bathyal and abyssal zones from 2700 to 5500 meters, either as *B. trochoidea* or *Bathyancistrolepis* sp. (Hasegawa, 2009; Hasegawa and Okutani, 2011; Fukumori et al., 2018, 2019). Another taxonomic work is underway to describe several new species from the deeper waters and to elucidate the geographic and bathymetric distributions for the entire genus (Ishiyama et al., in preparation).

ACKNOWLEDGMENTS

We are indebted to the captains and crews of R/V *Tansei-maru*,

R/V *Shinsei-maru*, R/V *Hakuho-maru*, R/V *Seisui-maru*, R/V *Ocean Researcher I* and T/V *Nagasaki-maru* for managing deep-sea cruises, and to chief scientists and all other participants of the cruises for collecting, sorting and processing the samples. Two specimens from off Taiwan, including the holotype of *B. taiwanensis*, were collected during the ZhongSha 2015 and Kavalan 2018 expeditions organized by P. Bouchet, W.-J. Chen and S. Samadi. We are also grateful to B. Buge, T. Haga, K. Hasegawa and N. Puillandre for the loan of the specimens. Invaluable comments were provided by P. Bouchet, T. Haga, and K. Hasegawa for the improvement of the manuscript. Financial support was provided by the Research Institute of Marine Invertebrates and the Japan Society for the Promotion of Science (KAKENHI grant nos 19H00999, 19KK0385, 20J22102 and 22H02681).

COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

GI and Y Kano conceived and designed the study. All authors collected and prepared the materials. GI performed molecular analyses. GI and Y Kano wrote the original draft of the manuscript. All authors read and approved the final manuscript.

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(Received July 6, 2023 / Accepted September 19, 2023 /
Published online November 29, 2023)