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Overview of Antarctic icefish species of the genus *Channichthys* Richardson, 1844 (Notothenioidei: Channichthyidae) based on morphological studies

Ekaterina Nikolaeva

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab., 1, Saint Petersburg, 199034, Russian Federation

Address correspondence and requests for materials to Ekaterina Nikolaeva, Ekatherina.Nikolaeva@zin.ru

Abstract

The study presents the results of a most recent comprehensive review of the morphology of little-studied endemic Antarctic icefishes of the genus *Channichthys* Richardson, 1844 (family Channichthyidae). It aims at a detailed taxonomic revision in order to analyze their general similarity and relationships and to conclude on the exact species composition of this genus. Previously, there was reported from 1 polymorphic to 9 separate sympatrically widespread species within the genus *Channichthys*, while the validity of most species remained questionable up to date. In this study, the structure of the gill apparatus and the seismosensory system have been studied along with the up-to-date methods of digital microfocus radiography and statistical methods accompanied by conventional methods of analyzing the external morphology of fish. The representatives of all nine species listed previously in different publications were analyzed with strict reference to museum collections. As a result, the validity of only four out of nine nominal species of the genus *Channichthys* was confirmed: *Ch. rhinoceratus, Ch. rugosus, Ch. velifer,* and *Ch. panticapae.* The validity of five other species has not been confirmed: three species (*Ch. aelitae, Ch. mithridatis,* and *Ch. richardsoni*) are conspecific with *Ch. rhinoceratus,* while two species (*Ch. bospori* and *Ch. irinae*) with *Ch. panticapae.* Most of their distinctive morphological characters, identified previously as indicators of the species level, overlap with those of valid species. Improved differential diagnoses of valid species of the genus *Channichthys* have been compiled, including key features that make it possible to identify the species of this genus correctly.

Keywords: Antarctic icefishes, morphology, taxonomy, validity, review, Notothenioidei, Channichthyidae.

Introduction

Antarctic icefishes of genus *Channichthys* Richardson, 1844 belong to the family Channichthyidae, representing one of the largest and evolutionarily advanced branches of notothenioids (suborder Notothenioidei, order Perciformes) (Balushkin, 1996). According to various authors, this family includes from 15 to 24 species belonging to 11 genera. This discrepancy in the number of icefish species is associated with the differences in the interpretation of the genus *Channichthys*, or crocodile icefishes, whose species composition still remains controversial (Gon and Heemstra, 1990; Iwami and Kock, 1990; Kock, 2005; Duhamel, Gasco, and Davaine, 2005; Eastman and Eakin, 2021; Manilo, 2021).

Crocodile icefishes are demersal species endemic to the Kerguelen zoogeographical province. The genus range covers the shelves of islands and seamounts (banks) of the Kerguelen Ridge from its northern tip (Kerguelen Islands) to the southern end (Heard Island and McDonald Islands), located in the Indian

Citation: Nikolaeva, E. 2024. Overview of Antarctic icefish species of the genus *Channichthys* Richardson, 1844 (Notothenioidei: Channichthyidae) based on morphological studies. Bio. Comm. 69(3): 162–173. https://doi.org/10.21638/spbu03.2024.304

Author's information: Ekaterina Nikolaeva, Junior Researcher, orcid.org/0000-0003-2156-1862

Manuscript Editor: Pavel Skutschas, Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Saint Petersburg, Russia

Received: February 17, 2024;

Revised: March 28, 2024;

Accepted: April 10, 2024.

Funding: The study was supported by the Russian State Task of the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) No. 122031100285-3 "Systematics, Phylogeny, and Biogeography of Fishes of the Far Eastern Seas, the Arctic, Antarctic, and Fresh Waters of Russia", based on the collections of the Laboratory of Ichthyology of ZIN RAS, and using the ZIN RAS scientific equipment, including that of the Centre of Collective Use "TAXON" ZIN RAS.

Ethics statement: This paper does not contain any studies involving human participants or animals performed by any of the authors.

Competing interests: The authors have declared that no competing interests exist.

Ocean sector of the Southern Ocean (Andriashev, 1986; Balushkin, 1992; Iwami and Kock, 1990; Kock, 2005). These fishes are found in coastal waters at relatively shallow depths from 95 to 361 m. They are actively moving predators (Nelson, Grande and Wilson, 2016).

Initially, the genus *Channichthys* was monotypic, consisting of single type species (unicorn icefish *Ch. rhinoceratus* Richardson, 1844), described by the Scottish naturalist and ichthyologist J. Richardson from the northeastern tip of Kerguelen Island at a depth of 91 m. The original species description included only the data on the number of rays in the first and second dorsal, pectoral, anal, and caudal fins (Richardson, 1844; 1844–1848).

Subsequently, the British scientist C. T. Regan described red icefish *Ch. rugosus* Regan, 1913, from the same area; this species differed from the type species by the smaller eyes, the height of the dorsal fin, as well as by characteristic reddish colour of the body (Regan, 1913). However, at the same time, the original description was so brief that it did not allow for clear differentiation of these two species.

In 1972, in the area of Kerguelen Island, the Yugrybpromrazvedka expedition (organized by the former USSR on board research vessel (RV) "Kara-Dag") discovered six specimens of fish of the genus *Channichthys*, partially different from those known already. As a result, another new species was discovered: sail icefish *Ch. velifer* Meissner, 1972, named for the unique sail-like shape of the first dorsal fin (Meisner, 1974). The original detailed description was made by a Ukrainian ichthyologist E. E. Meisner (Meisner and Kratkii, 1978).

Later, a Ukrainian ichthyologist G. A. Shandikov conducted a series of even more detailed morphological studies based on material obtained during the expedition performed in 1990 on board RV "Professor Mesyatsev" in the shelf zone of the Kerguelen Island. He presented the first species revision of the genus *Channichthys,* where he described six new species (Shandikov, 1995a; 1995b; 1996; 2008; 2011). In addition to the species listed above, the genus was supplemented by the charcoal icefish *Ch. panticapae* Shandikov, 1995, externally different from other species by the darkest black-brown, charcoal colour (Shandikov, 1995a); the big-eyed icefish *Ch. bospori* Shandikov, 1995, distinguished by relatively large eyes (Shandikov, 1995b); the pygmy icefish *Ch. irinae* Shandikov, 1995, characterized by the smallest size in the genus (Shadikov, 1995b); as well as by three species that differ from the others only in some morphometric characters: the Aelita icefish *Ch. aelitae* Shandikov, 1995 (Shandikov, 1995b), the green icefish *Ch. mithridatis* Shandikov, 2008 (Shandikov, 2008), and the robust icefish *Ch. richardsoni* Shandikov, 2011 (Shandikov, 2011).

However, the validity of a number of species included in the genus was questioned by many experts (Hureau, 1964; 1985; Meisner, 1974; Andriashev, 1986; Iwami and Kock, 1990; Balushkin, 1996; Balushkin and Fedorov, 2002; Voskoboinikova, 2001; Duhamel, Gasco and Davaine, 2005; Nikolaeva, 2016; 2017; 2019; 2020; 2021; Nikolaeva and Balushkin, 2019). First of all, this was due to the lack of a clear methodological approach to the development of morphological criteria and the assessment of significance of the described characters, as well as the incompleteness or unreliability of differential diagnoses of species.

The need for revision of the genus *Channichthys* was raised repeatedly by J. C. Hureau (1985), A. P. Andriashev (1986), G. A. Shandikov (1995), A. V. Balushkin (1996), and E. A. Nikolaeva (2016; 2017; 2019; 2020; 2021). Obviously, there is a need to reconsider the composition of the genus *Channichthys,* using all possible classical and modern comprehensive research methods to establish the exact composition of the genus and the validity of its species. We have carried out such a series of studies.

First of all, we have identified two groups of species within the genus *Channichthys*: "single-rowed gill rakers" and "double-rowed gill rakers" (Nikolaeva, 2016; 2017). Then, when reviewing a group of species, characterized by a specific structure of the gill apparatus, i. e., by the presence of two rows (external and internal) of gill rakers on the gill arches, we showed that only a single species of the three of them is valid (*Ch. panticapae, Ch. bospori,* and *Ch. irinae)*. In particular, this is *Ch. panticapae,* which was described the first; the species *Ch. bospori* and *Ch. irinae* were then reduced to its synonyms (Nikolaeva, 2019). Further, during the review and redescription of the six species carrying one row of gill rakers on the gill arches, only three of them were confirmed valid: namely, *Ch. rhinoceratus, Ch. rugosus,* and *Ch. velifer* (Nikolaeva and Balushkin, 2019; Nikolaeva, 2020; 2021). The remaining species (*Ch. aelitae, Ch. mithridatis* and *Ch. richardsoni*) turned out to be morphologically similar to *Ch. rhinoceratus*, so they are conspecific with it and therefore should be considered as junior synonyms (Nikolaeva, 2020).

Aim and tasks

This is a review paper. The study aims to summarize and generalize all our morphological studies of fishes of the genus *Channichthys,* carried out on the basis of an analysis of their external morphology, the structure of the axial skeleton, gill apparatus, and seismosensory system.

Materials and methods

All the specimens of fishes of the genus *Channichthys* available for analysis (from 2013 to 2023) were the material for this study. The specimens have been analyzed from the collections of three museums depositing type specimens of the studied species: the Zoological Institute of the Russian Academy of Sciences (ZIN), the National Scientific and Natural History Museum of the National Academy of Sciences of Ukraine (IZANU), and the Natural History Museum, London (BMNH). A total of 280 specimens of nine species were studied, including available holotypes (7 out of 9).

Channichthys velifer (45 ind.): *SL* from 134 to 490 mm, Kerguelen Island, depth from 130 to 157 m. ZIN: Nos. 53005, 54807, 56271, 56273–56290. For more details, see research by Nikolaeva and Balushkin (2019).

Channichthys rugosus (10 ind., including holotype): *SL* from 215 to 370 mm, Kerguelen Island, depth from 64 to 120 m. Holotype BMNH No. 1876.3.23.4 *SL* 370 mm. BMNH No. 1937.9.21.95. ZIN: Nos. 53007, 56291–56994. For more details, see: Nikolaeva (2021).

Channichthys rhinoceratus (160 ind.): *SL* from 150 to 395 mm, Kerguelen Island, depth from 140 to 420 m. ZIN: Nos. 53006, 55586, 55587, 56631–56644. For more details, see research by Nikolaeva (2020).

Channichthys aelitae (1 ind.): holotype IZANU No. 4575A *TL* 375 mm, *SL* 334 mm, Kerguelen Island, 49°54′ S 70°16′ E, FV "Aelita", cruise no. 2, trawl no. 119, 25.02.1969, depth 161 m, collector N. V. Kononov.

Channichthys mithridatis (1 ind.): holotype IZANU No. 5111 *TL* 371 mm, *SL* 332 mm, Kerguelen Island, 47°44′4 S 71°31′6 E, RV "Professor Mesyatsev", cruise no. 23, trawl no. 91, 10.08.1990, depth 270–310 m, collector G. A. Shandikov.

Channichthys richardsoni (1 ind.): holotype IZANU No. 5116 *TL* 355 mm, *SL* 316 mm, Kerguelen Island, 48°22′5 S 70°44′ E, RV "Professor Mesyatsev", cruise no. 23, trawl no. 6, 19.07.1990, depth 126 m, collector G. A. Shandikov.

Channichthys panticapaei (61 ind., including holotype): *SL* from 138 to 398 mm, Kerguelen Island, depth from 80 to 380 m. Holotype IZANU No. 5109 *SL* 348 mm, Kerguelen Island, FV "Skyf", cruise no. 21, trawl no. 8, 18.02.1987, depth 120 m, collector A. N. Todiev. ZIN: Nos. 56520–56538. For more details, see research by Nikolaeva (2019).

Channichthys bospori (1 ind.): holotype IZANU № 5106 *SL* 350 mm, o. Kerguelen, RV "Professor Mesyatsev", cruise no. 23, trawl no. 6, 19.07.1990, depth 126 m, collector G. A. Shandikov.

Channichthys irinae (1 ind.): holotype IZANU № 5103 *SL* 209 mm, o. Kerguelen, RV "Professor Mesyatsev", cruise no. 23, trawl no. 91, 10.08.1990, depth 270–310 m, collector G. A. Shandikov.

The work used a technique developed by A. V. Balushkin (1996) and adapted for the study of Kerguelen icefish (Balushkin and Nikolaeva, 2015; Nikolaeva, 2016; 2017; 2019; 2020; 2021; Nikolaeva and Balushkin, 2019). For each specimen, 50 different morphological characters and indices were recorded (10 morphometric characters, 19 meristic characters, and 21 indices). The features of the gill apparatus, seismosensory system, skin granulation (the degree of its development), and coloration were also examined.

The axial skeleton was studied using a digital microfocus X-ray diagnostic unit "PRDU-02" ("ELTECH-MED", Saint Petersburg, Russia) in the Centre of Collective Use "TAXON" ZIN RAS. Statistical processing of the obtained data was carried out using Microsoft Excel 2010 and STATISTICA (Version 10) software packages.

Symbols and abbreviations:
SL — standard body length; *c* — head length; *hD*1 — maximum height of the 1st dorsal fin; lP_l and lP_d — length of the left and right pectoral fins; *ho* — head height through the middle of the eye; *lmx* — length of the upper jaw; *lmd* — length of the lower jaw; *ao* — snout length; *o* — longitudinal diameter of the eye orbit; *io* — interorbital space; *D*1, *D*2, *A* — number of rays in the 1st dorsal, 2nd dorsal and anal fins, respectively; P_l and P_d — number of rays in the left and right pectoral fins; *sp.br.* — total number of gill rakers on the first gill arch; *sp.br.a* — number of gill rakers on the outer side of the first gill arch; *sp.br.b* — number of gill rakers on the inner side of the first gill arch; Dll_l and Dll_d — number of pores and scales in the left and right dorsal lateral lines of the seismosensory system; Mll_l and Mll_d — number of pores and scales in the left and right medial lateral lines of the seismosensory system; *vert.* — the total number of vertebrae in the spine.

For all meristic characters, the following basic statistical features were calculated: min–max — limits of variation, M — mean, m — error of the mean.

Results

A comprehensive morphological study of all species of the genus *Channichthys* was carried out resulting in their redescription; the general differential diagnosis of the genus was clarified and supplemented; differential diagnoses of the species were compiled, highlighting the most significant diagnostic features (Nikolaeva, 2016; 2017; 2019; 2020; 2021; Nikolaeva and Balushkin, 2019; present study).

Diagnosis of genus *Channichthys*

*D*1 5–12, *D*2 29–35, *P* 17–23, *A* 28–34, *Dll* 56–88, *Mll* 4–45, *sp.br.* 6–32, *vert.* 54–58. The head with an elongated dorsoventrally flattened snout, slightly larger than half the head length, rounded in front and having at the end a well-developed rostral spine with 4–6 separate apical tubercles. The eye size is relatively small. The outer edges of the frontalia above the eyes are slightly raised. The posterior edge of the maxillare usually reaches a vertical line

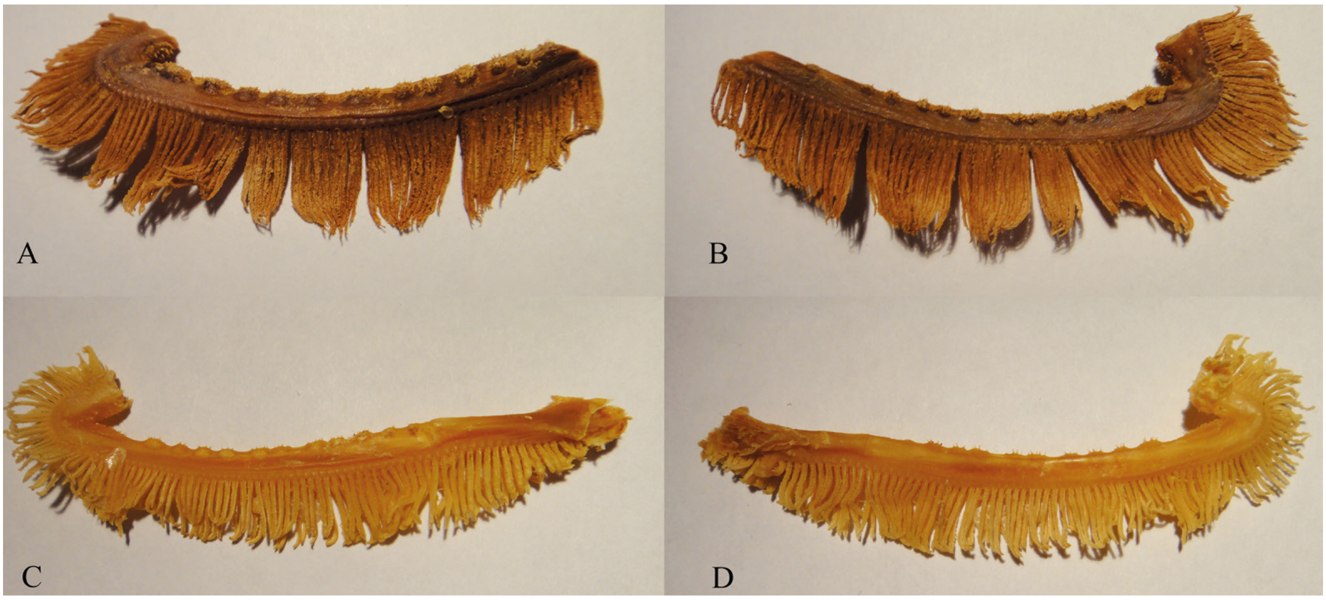

Fig. 1. Gill arches (*sp.br.*): outer side (A) and inner side (B) of "double-rowed gill rakers"; outer side (C) and inner side (D) of "single-rowed gill rakers".

passing through ½ of the diameter of the eye orbit. The upper and lower jaws are approximately equal in length, they are covered with 3–10 rows of small, sharp, bristle-like teeth. The 1st and 2nd dorsal fins are well separated; the inter-dorsal space is often relatively wide; the posterior edge of the fin fold of the last ray of the 1st dorsal fin does not reach the base of the 1st ray of the 2nd dorsal fin. The pectoral fins reach the anus. The pelvic fins are wide, slightly shorter or approximately equal to the length of the pectoral fins; they do not reach the anus or end at the level of the anal fin origin. The caudal fin is slightly rounded. There are two lateral lines (dorsal and medial) on the left and right sides along the body.

As a result of a comparative analysis of all the data obtained, only four out of nine species of the genus may be considered valid: *Ch. panticapae, Ch. rhinoceratus, Ch. rugosus,* and *Ch. velifer,* differing from each other in a set of main characters (Table 1).

First of all, all species of the genus *Channichthys* according to the structure of the gill apparatus can be divided into 2 non-taxonomic groups: (1) "double-rowed gill rakers", having two rows of gill rakers on the gill arches (*sp.br.*) on the outer side of the ceratobranchiale (*sp.br.a*) and on the inner side of the hypobranchiale (*sp.br.b*) (Fig. 1A, B); and (2) "single-rowed gill rakers", having only one row of gill rakers on the gill arches on the outer side of the ceratobranchiale (*sp.br.a*), while on the inner side of the hypobranchiale (*sp.br.b*) there are no gill rakers at all (Fig. 1C, D) (Nikolaeva, 2019, 2020). At the same time, in our opinion, «single-rowed gill rakers» species are evolutionarily more advanced than "double-rowed gill rakers", since the partial simplification of the gill apparatus of icefishes is most likely a progressive feature, as an adaptation to living in cold Antarctic waters saturated with oxygen. Only single species belongs to the "double-rowed gill rakers" group (*Ch. panticapaei*), while the "single-rowed gill rakers" group includes three species (*Ch. rhinoceratus, Ch. rugosus* and *Ch. velifer*).

Main differential characteristics

Channichthys panticapae (Fig. 2). The main species-specific feature that distinguishes *Ch. panticapaei* from all other species of the genus is the presence of two rows of rakers on the gill arches (*sp.br.*): one on the outer side (*sp.br.a*) — 16 rakers on average, and one on the inner side (*sp.br.b*) — 10 rakers on average; the total average number of rakers is 26. The first dorsal fin (*D*1) is high, of normal shape, relative average height (*hD*1/*SL*) is 24.6 %; the average number of rays is 7, the first three rays (usually the 2nd or 3rd) are the longest; the fin membrane between the rays *D*1 is low, does not reach the tips of the longest rays (Fig. 6,A). The inter-dorsal space is relatively wide, *D*1 and *D*2 are well separated. The eye size (*o*) is slightly larger than in the other species, averaging 18.3 % of the head length (*c*) or averaging 39.3 % of the snout length (*ao*). The interorbital space (*io*) is wide, flat, but more often equal to the eye diameter (*o*), averaging 16.9 % of the head length (*c*). The snout length (*ao*) is slightly less than that of other species, averaging 46.8 % of the head length (*c*). Along the entire medial lateral lines (*Mll*), including their posterior end, there are bone scales developed very strongly. Granulation is generally highly developed. The body colour is very characteristic, it is darker than in other species: brown-black, especially the upper part of the head and body, the back is covered with even darker spots, merging into a marble pattern (Nikolaeva, 2019).

Table 1. Main characteristics of valid species of the genus *Channichthys* (Nikolaeva and Balushkin, 2019; Nikolaeva, 2019; 2020; 2021)

Species (number of specimens studied)	*Ch. panticapae* (61 ind.)	*Ch. rhinoceratus* (160 ind.)	*Ch. rugosus* (10 ind.)	*Ch. velifer* (45 ind.)
Meristic characters				
Gill rakers on the first gill arch: on the inner side of the hypobranchiale (*sp.br.b*)	4–14 (10 ± 0.2)	—	—	—
on the outer side of the ceratobranchiale (*sp. br.a*)	12–20 (16 ± 0.3)	6–19 (12 ± 0.2)	9–15 (12 ± 0.8)	10–17 (13 ± 0.3)
Number of rays of the 1st dorsal fin (*D*1)	6–8 (7 ± 0.1)	5–9 (7 ± 0.05)	7–9 (8 ± 0.4)	9–12 (10 ± 0.1)
Number of rays of the 2nd dorsal fin (*D*2)	30–34 (32 ± 0.1)	29–35 (32 ± 0.1)	29–33 (31 ± 0.5)	29–33 (31 ± 0.1)
Number of rays in pectoral fins (*P*)	17–22 (20 ± 0.2)	18–23 (20 ± 0.1)	18–20 (19 ± 0.2)	18–21 (21 ± 0.1)
Number of rays in anal fin (*A*)	28–32 (30 ± 0.2)	18–34 (31 ± 0.07)	29–31 (30 ± 0.2)	28–32 (29 ± 0.1)
Dorsal lateral lines (*Dll*), bony scales	63–82 (72 ± 0.8)	56–87 (72 ± 0.6)	63–70 (68 ± 0.8)	60–75 (67 ± 0.5)
Medial lateral lines (*Mll*), bony scales	4–44 (21 ± 1.8) always along the entire sideline, including on the back; developed strongly	5–39 (15 ± 0.6) usually present along the entire lateral line, including on the back; developed moderately	15–42 (30 ± 4.1) always along the entire sideline, including on the back; developed well	8–38 (13 ± 0.8) none on the back; developed poorly
Total number of vertebrae (*vert.*)	55–57 (56 ± 0.1)	55–58 (56 ± 0.1)	52–56 (55 ± 0.1)	54–56 (55 ± 0.1)
Morphometric characters				
Relative head length, % of standard body length (*c/SL*)	35.2–40.2 (37.6 ± 0.2)	33.3–41.4 (37.3 ± 0.1)	36.9–41.8 (39.4 ± 0.7)	33.2–40.4 (36.3 ± 0.03)
Relative head height, % of standard body length (*ho/SL*)	9.0–15.8 (11.6 ± 0.2)	7.2–16.6 (10.8 ± 0.1)	11.6–16.7 (14.2 ± 0.6)	11.1–18.4 (13.7 ± 0.03)
Head height, % of head length (*ho/c*)	24.4–42.6 (30.8 ± 0.5)	18.9–43.8 (29.0 ± 0.3)	29.5–39.6 (35.9 ± 1.3)	30.9–52.6 (37.9 ± 0.7)
Snout length, % of head length (*ao/c*)	42.9–51.2 (46.8 ± 0.3)	44.9–54.3 (49.3 ± 0.1)	45.5–51.6 (48.2 ± 0.9)	46.6–51.1 (48.6 ± 0.2)
Eye, % of head length (*o/c*)	14.9–23.0 (18.3 ± 0.3) relatively small eye size	12.9–21.7 (16.6 ± 0.1) relatively small eye size	14.3–18.2 (15.6 ± 0.5) relatively small eye size	14.1–19.3 (16.4 ± 0.2) relatively small eye size
Eye, % of snout length (*o/ao*)	30.8–53.5 (39.3 ± 0.8)	25.0–46.4 (33.7 ± 0.3)	27.9–40.0 (32.4 ± 1.4)	28.6–40.0 (33.7 ± 0.4)
Interorbital space, % of head length (*io /c*)	11.6–22.4 (16.9 ± 0.5), flat, wide	9.7–22.4 (16.4 ± 0.2), flat, wide	13.1–19.5 (16 ± 0.7), concave, narrow	13.9–21.3 (17.5 ± 0.3), flat, wide
Interorbital space, % of snout length (*io/ao*)	22.7–47.6 (36.1 ± 0.1)	18.7–45.5 (33.3 ± 0.4)	25.6–41.7 (33.3 ± 1.9)	28.0–41.8 (35.9 ± 0.5)
io/o	0.6–1.4 (1.0 ± 0.04), often smaller than eye diameter	0.5–1.6 (1.1 ± 0.02), slightly larger than eye diameter	0.9–1.3 (1.1 ± 0.05), often smaller than eye diameter	0.7–1.4 (1.1 ± 0.02), slightly larger than eye diameter

o/io	0.7–1.7 (1.1 ± 0.04)	0.6–2.0 (1.0 ± 0.02)	0.8–1.1 (0.9 ± 0.04)	0.7–1.3 (0.9 ± 0.02)
Upper jaw length, % of head length (*lmx/c*)	46.3–55.7 (52.1 ± 0.3)	48.7–64.6 (55.3 ± 0.2)	52.3–58.6 (54.6 ± 0.8)	51.5–59.3 (55.4 ± 0.3)
Lower jaw length, % of head length (*lmd/c*)	65.7–76.8 (68.8 ± 0.3)	63.6–89.3 (69.6 ± 0.2)	67.4–71.1 (69.2 ± 0.4)	65.1–72.3 (68.5 ± 0.3)
Shape of the 1st dorsal fin (*D*1)	high, regular form	low, regular form	high, regular form	high, sail-shaped
Relative height of the 1st dorsal fin, % of standard body length (*hD*1/ *SL*)	17.0–31.1 (24.6 ± 0.5)	7.5–28.1 (19.6 ± 0.3)	13.3–29.2 (20.6 ± 2.4)	18.0–29.6 (22.7 ± 0.3)
Longest rays *D*1	3 rays (1–3, usually 2nd or 3rd)	2–3 rays (from 1st to 3rd)	4 rays (2nd to 5th)	2–5 rays (3rd to 7th, usually 4th or 5th)
Fin membrane *D*1	does not reach the tips of the largest rays	does not reach the tips of the largest rays	reaches the tips of the largest rays	reaches the tips of the largest rays
Inter-dorsal gap	wide, *D*1 and *D*2 are well separated	wide, *D*1 and *D*2 are well separated	wide, *D*1 and *D*2 are well separated	very narrow, *D*1 and *D*2 almost touching
Relative length of pectoral fins, % of standard body length (*lP/SL*)	16.0–20.9 (18.6 ± 0.2) reach the anus	13.7–26.2 (17.8 ± 0.1) reach the anus	17.0–18.2 (17.6 ± 0.2) reach the anus	15.2–20.5 (17.6 ± 0.02) reach the anus
Body granulation (degree of development)	strong	weak or moderate	well	weak or moderate
Body coloration	darker than other species, brown-black	usually dark with numerous dark spots merging into a marble pattern	plain, reddish	lighter than other species, with numerous small rounded dark spots

Note: Values are given as *min–max (M±m)*, where: *min–max* — limits of variation, *M* — mean, *m* — error of mean.

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Fig. 2. *Channichthys panticapaei*, photo (A) and X-ray (B) (IZANU 5109 Holotype, *SL* 348 mm, formalin preserved specimen).

Fig. 3. *Channichthys rhinoceratus*, photo (A) and X-ray (B) (ZIN 56633, *SL* 346 mm, formalin preserved specimen).

Channichthys rhinoceratus (Fig. 3). There is only single row of gill rakers (12 on average) on the gill arches (*sp.br.*). The first dorsal fin (*D*1) is low, the average relative height (*hD*1/*SL)* is 19.6 %; it carries 7 rays on average, of which 2–3 rays (1^{st} to 3^{rd}) are the longest; the fin membrane does not reach the tips of the longest rays (Fig. 6B). The inter-dorsal space is wide, the first and second dorsal fins (*D*1 and *D*2) are well separated. The eye size (*o*) is on average 16.6 % of the head length (*c*) or 33.7 % of the snout length (*ao*) on average. The interorbital space (*io*) is wide, flat, 16.4 % of the head length (*c*) on average; it is often greater than or equal to the eye diameter (*o*). The snout length (*ao*) is slightly less than or approximately equal to half the head length (*c*), averaging 49.3 % *c*. The posterior part of the medial lateral lines (*Mll*) usually has moderately developed bony scales. In general, granulation is poorly or moderately developed. The body coloration is usually dark, with numerous dark spots merging into a marbled pattern (Balushkin and Nikolaeva, 2015; Nikolaeva, 2020).

Channichthys rugosus (Fig. 4). In this species, there is also a single row of gill rakers (12 on average) on the gill arches (*sp.br.*). The first dorsal fin (*D*1) is of normal shape, high (a relative height *hD*1/*SL* is 20.6 % on average); it includes 8 rays on average, the longest ray is usually the fourth one (from the 2^{nd} to the 5^{th}); the fin membrane of *D*1 reaches the tips of the longest rays (Fig. 6C). The inter-dorsal space is wide, *D*1 and *D*2 are well separated. The eye diameter (*o*) is on average 15.6 % of the head length (*c*) or 32.4 % of the snout length (*ao*).

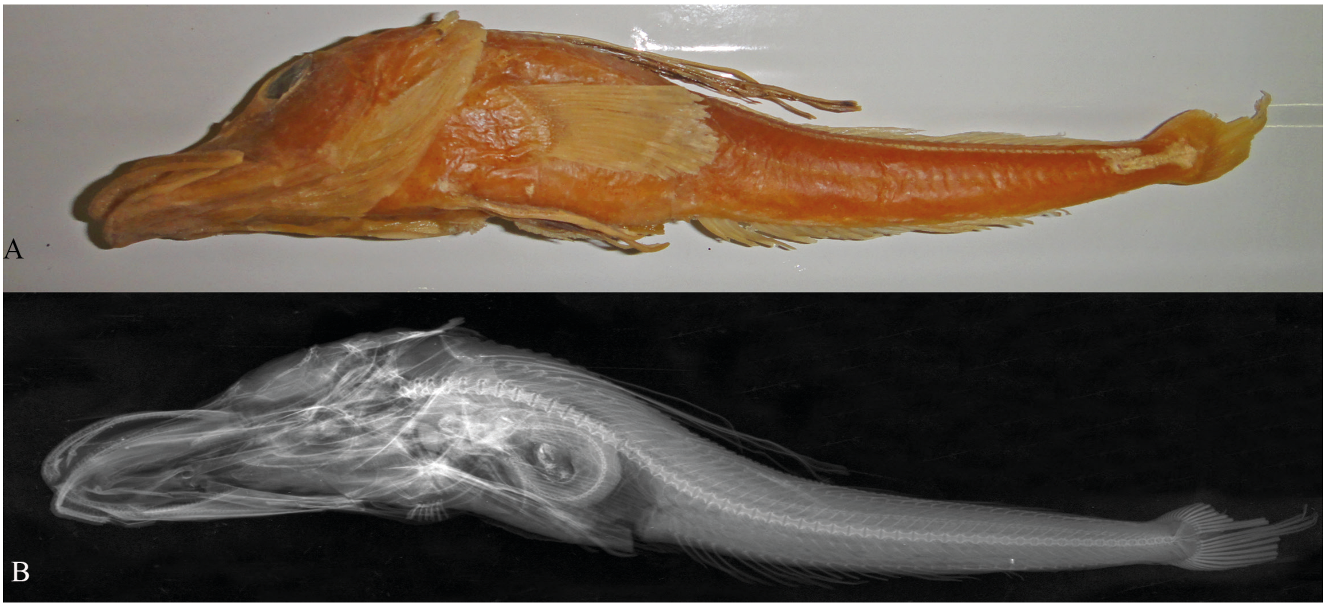

Fig. 4. *Channichthys rugosus*, photo (A) and X-ray (B) (ZIN 53007, *SL* 360 mm, formalin preserved specimen).

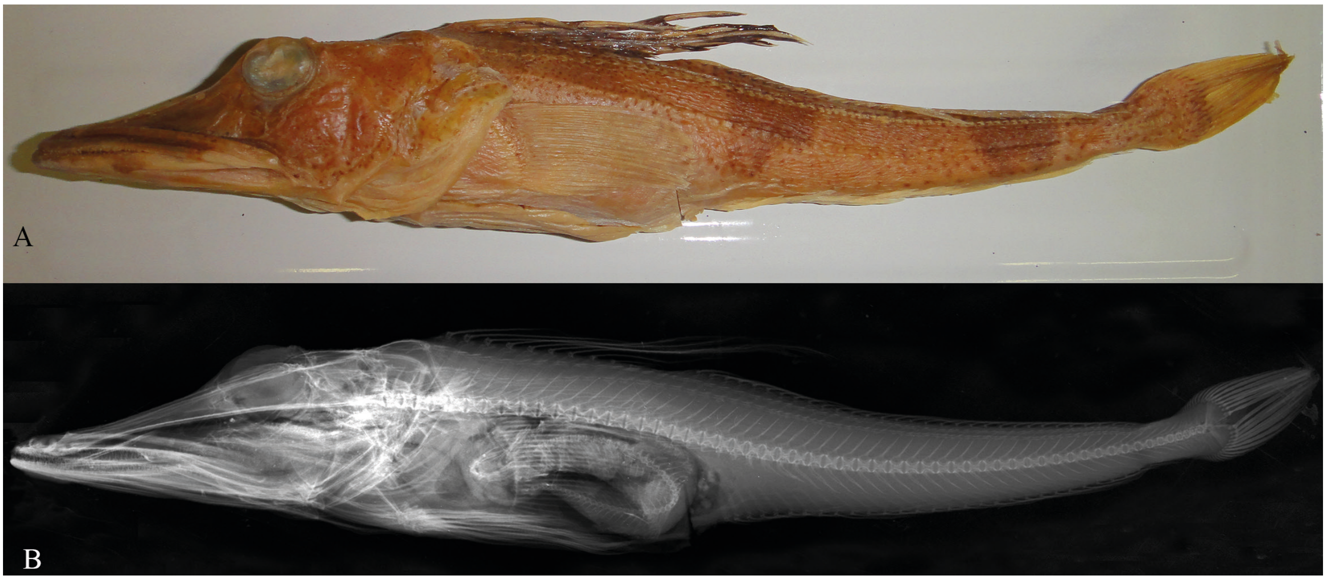

Fig. 5. *Channichthys velifer*, photo (A) and X-ray (B) (ZIN № 56275, *SL* 300 mm, formalin preserved specimen).

The interorbital space (*io*) is concave and narrow, averaging 16 % of the head length (*c*), it is smaller than the eye diameter (*o*). The snout length (*ao*) is on average 48.2 % of the head length (*c*). There are well-developed bony scales along the entire medial lateral lines (*Mll*), including their posterior end. Skin granulation is well developed. The colour of the body and dorsal fins is uniform, species-specific reddish (Nikolaeva, 2021).

Channichthys velifer (Fig. 5). In this species, there is also a single row of gill rakers (13 on average) on the gill arches (*sp.br.*). The first dorsal fin (*D*1) is unique, species-specific (high sail-shaped), with a relative average height (*hD*1/*SL*) of 22.7 %; the average number of rays is 10, which is always more than in all other species. The fin membrane between the *D*1 rays is high, reaching the tips of the longest rays, 2–5 rays are the longest (from the 3^{rd} to the 7^{th}, usually the 4^{th} or 5^{th}) (Fig. 6D). The inter-dorsal space is very narrow, unlike in other species; the posterior edge of the fin fold of the last ray of *D*1 almost reaches the base of the 1^{st} ray of *D*2, so *D*1 and *D*2 almost touch each other. The eye diameter (*o*) is on average 16.4 % of the head length (*c*) or 33.7 % of the snout length (*ao*). The interorbital space (*io*) is flat, wide, averaging 17.5 % of the head length (*c*); it is usually larger than the eye diameter (*o*). The snout length (*ao*) is on average 48.6 % of the head length (*c*). There are usually no bone scales in the posterior part of the medial lateral lines (*Mll*). In general, granulation is poorly or moderately developed. The colour of the body, including the first dorsal fin, is usually lighter than in other spe-

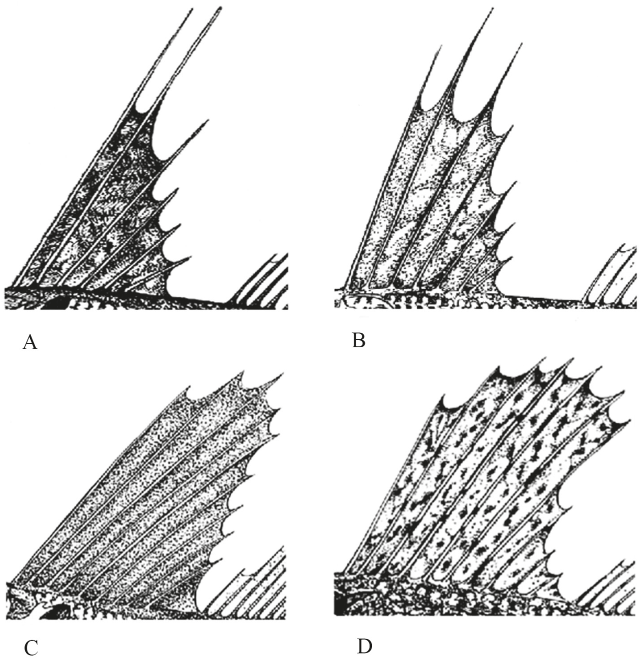

Fig. 6. First dorsal fins (*D*1): A — *Ch. panticapaei*, B — *Ch. rhinoceratus*, C — *Ch. rugosus*, D — *Ch. velifer* (modified from (Shandikov, 2008)).

cies, with numerous scattered small rounded dark spots (Nikolaeva and Balushkin, 2019).

According to our studies (Nikolaeva, 2016; 2017; 2019; 2020), the remaining nominal species of the genus, recognized by G. A. Shandikov (1995b, 2008, 2011), turn out to be invalid since all their main diagnostic features partially or completely overlap with those of previously described valid species.

It should be noted also that G. A. Shandikov described new species and redescribed already known ones from relatively small samples: *Ch. panticapae* (24 ind.), *Ch. bospori* (5 ind.), *Ch. irinae* (20 ind.), *Ch. rhinoceratus* (24 ind.), *Ch. aelitae* (3 ind.), *Ch. mithridatis* (29 ind.), *Ch. richardsoni* (18 ind.), *Ch. velifer* (9 ind.), and no indication was made for the number of specimens studied for *Ch. rugosus* (Shandikov, 1995a; 1995b; 1996; 2008; 2011).

According to the description of G. A. Shandikov, *Ch. aelitae* differs from other species by the following diagnostic characters: wide interorbital space (*io*) 20.2–22.1 % of the head length (*c*), exceeding the eye diameter (*o*); medium-sized eye (18.2–18.9 % *c* or 37.9–38.9 % *ao*); the first dorsal fin (*D*1) has 7–8 rays; its membrane does not reach the tips of the longest rays (Shandikov, 1995b). *Ch. mithridatis* is characterized by a narrow interorbital space (*io* 13–16 % *c* or 60–82 % *o*), less than the eye diameter; large eye (18–22 % *c* or 37–47 % *ao*), which is always greater than *io;* the first dorsal fin (*D*1) has 6–9 rays, and a fin membrane does not reach the tips of the longest rays (Shandikov, 2008). *Ch. richardsoni* is distinguished by a narrow interorbital space (*io* 13–17 % *c* or 72–98 % *o*), which is less than the eye diameter; average eye size (16–19 % *c* or 33–39 % *ao*) is usually larger than *io;* the first dorsal fin (*D*1) has 7–8 rays, and a fin membrane does not reach the tips of the longest rays (Shandikov, 2011).

According to our data (Table 2), obtained on representative samples (160 ind. of *Ch. rhinoceratus)* and after applying various methods of statistical analysis (including methods of principal component analysis PCA and multidimensional scaling MDS), the values of the above-listed distinctive features of nominal species *Ch. aelitae, Ch. mithridatis,* and *Ch. richardsoni* fall within the range of variation for similar characters of *Ch. rhinoceratus.*

According to the description given by G. A. Shandikov, *Ch. bospori* is characterized by moderate interorbital space (*io* 17.1–19.6 % *c*), slightly smaller than the eye diameter (85.3–95.8 % *o*)*;* large eyes (18.8–20.7 % *c* or 41.7–45.7 % *ao*)*;* the first dorsal fin (*D*1) has 6–7 rays, and a fin membrane does not reach the tips of the longest rays (Shandikov, 1995b). *Ch. irinae* differs from others by its smallest size, as well as by narrow interorbital space (*io*), smaller than the eye diameter (13.3–14.1 % *c* or 46.3–68 % *ao*)*;* large eyes (21.4–24.8 % *c* or 45.9–56 % *ao*)*;* the first dorsal fin (*D*1) has 5–8 rays, and *D*1 membrane does not reach also the tips of the longest rays (Shandikov, 1995b). However, according to our data (Table 2), also obtained on representative sample (61 ind. of *Ch. panticapaei)*, the indicators of all diagnostic characters of the nominal species *Ch. bospori* and *Ch. irinae* are within the range of variation of similar characters of *Ch. panticapaei.*

We have found that *Ch. aelitae, Ch. mithridatis,* and *Ch. richardsoni* are conspecific with *Ch. rhinoceratus* (Nikolaeva, 2020); *Ch. bospori* and *Ch. irinae,* with *Ch. panticapaei* (Nikolaeva, 2019). As a result, currently there are only four valid species in the genus *Channichthys*: *Ch. rhinoceratus, Ch. rugosus, Ch. velifer,* and *Ch. panticapaei.*

Based on all our research, a key to four valid species of the genus *Channichthys* was compiled and published, based on exclusively significant diagnostic characters that allow to identify icefish species reliably (Nikolaeva, 2020).

The main key differences between valid species of the genus *Channichthys* are presented in a brief diagram (Fig. 7).

As a corollary, the genus *Channichthys* is still considered monotypic in a number of recent studies (Iwami and Kock, 1990; Kock, 2005; Eastman and Eakin, 2021), with a single species *Channichthys rhinoceratus* Richardson, 1844. However, our results do not support this idea. Obviously, a final solution to the issue of the species composition of this genus is possible by comparing the morphological data we obtained with the results of molecular genetic studies. The newly obtained genetic data, based on a comparison of the mitochondrial genomes of *Ch. rhinoceratus* and

Table 2. Diagnostic characters of nominal *Channichthys* species conspecific with *Ch. rhinoceratus* and *Ch. panticapaei* (highlighted in background)

Characters (number of specimens studied)	*Ch. aelitae* (3 ind. / 1 holotype ind.)	*Ch. mithridatis* (29 ind. / 1 holotype ind.)	*Ch. richardsoni* (18 ind. / 1 holotype ind.)	*Ch. rhinoceratus* (24 ind. / 160 ind.)	*Ch. bospori* (5 ind. / 1 holotype ind.)	*Ch. irinae* (20 ind. / 1 holotype ind.)	*Ch. panticapae* (24 ind. / 61 ind.)
	Shandikov, 1995b / Our data (holotype)	Shandikov, 2008 / Our data (holotype)	Shandikov, 2011 / Our data (holotype)	Shandikov, 1995b / Our data	Shandikov, 1995b / Our data (holotype)	Shandikov, 1995b / Our data (holotype)	Shandikov, 1995b / Our data
Interorbital space (*io*) % *c*	"wide, flat" 20.2–22.1 / 19.8	"narrow" 13–16 / 13.9	"narrow" 13–17 / 15.7	"wide, flat" 18.6–20.8 / 9.7–22.4	"moderately wide, concave" 17.1–19.6 / 22.4	"very narrow, concave" 13.3–14.1 / 14.3	"wide, flat" 18.7–22.7 / 11.6–22.4
io % o	– / 117.3	60–82 / 81.7	72–98 (104) / 102.1	– / 50–155	85.3–95.8 (104.4) / 104.6	46.3–68.0 / 63.4	– / 58.3–142.9
io/o	"larger than eye diameter" – / 1.2	"less than eye diameter" – / 0.8	"less than eye diameter" – / 1	"larger than eye diameter" – / 0.5–1.6	"usually smaller than the diameter of the eye" – / 1.1	"less than eye diameter" – / 0.6	"noticeably larger than the diameter of the eye" – / 0.6–1.4
Eye (*o*) % *c*	"of medium size" 18.2–18.9 / 16.9	"big" 18.0–22.0 / 17.1	"of medium size" 16.0–19.0 / 15.4	"small" 14.8–16.1 / 12.9–21.7	"big" 18.8–20.7 / 21.4	"very big" 21.4–24.8 / 22.6	"small" 15.4–18.5 / 14.9–23
o % ao	37.9–38.9 / 34.8	37–47 / 36.5	33–39 / 31.9	28.0–31.6 / 25–46.4	41.7–45.7 / 45.4	45.9–56.0 / 52.2	32.0–38.2 / 30.8–53.5
o/io	– / 0.9	– / 1.2	– / 1.0	– / 0.6–2.0	– / 1.0	– / 1.6	0.7–1.0 / 0.7–1.7
Rays *D*1	7–8 / 8	6–9 / 8	7–8 / 7	6–7 (8) / 5–9	6–7 / 7	5–8 / 7	6–8 / 6–8
Fin membrane in regard to the tips of largest rays	"does not reach" / does not reach	"does not reach" / does not reach	"does not reach" / does not reach	"does not reach" / does not reach	"does not reach" / does not reach	"does not reach" / does not reach	"does not reach" / does not reach

Note: The values given left to the slash (/) refer to the original descriptions by G. A. Shandikov (text citations are given in quotation marks); right to the slash (/) — our data (where indicated, according to holotype); "–" — no data.

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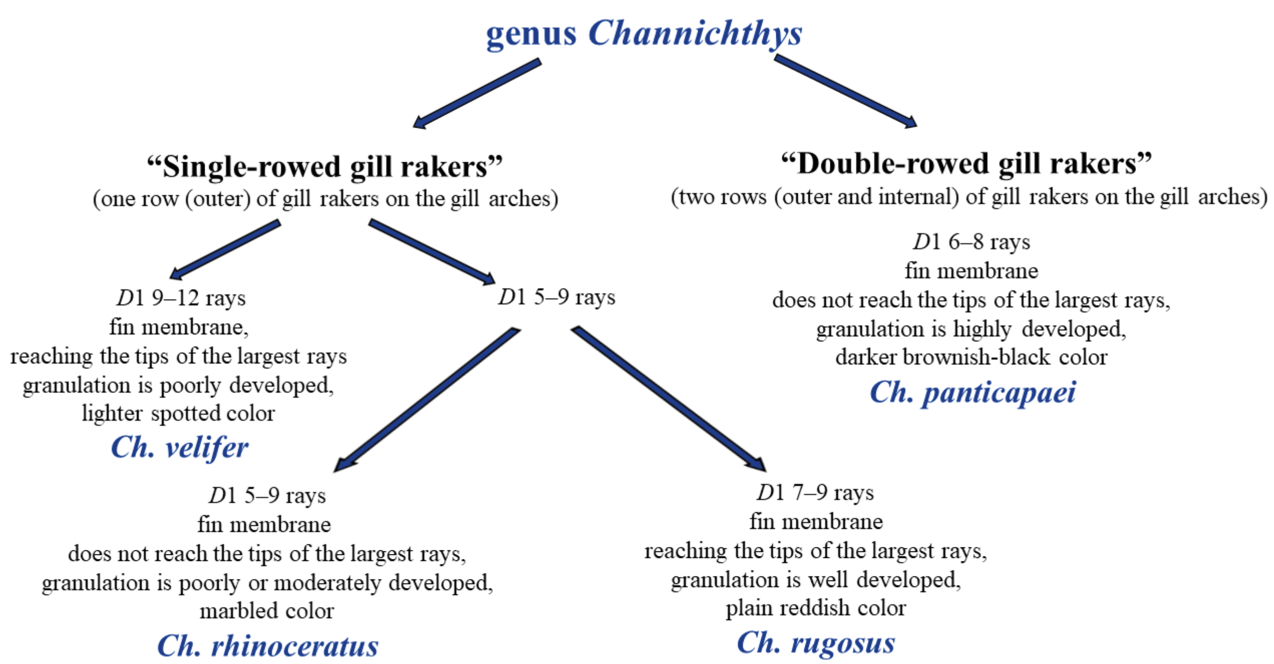

Fig. 7. Main differences between the valid species of the genus *Channichthys* and their main diagnostic characters.

Ch. rugosus, testify to conspecificity of these species (Muschick, Nikolaeva, Rüber, and Matschiner, 2022). However, we tend to consider them preliminary until more detailed information about the genetic differences between these species will be received. Undoubtfully, detailed genetic studies using both mitochondrial and nuclear markers are required to confirm the species status of the valid species of the genus *Channichthys* isolated in the present study.

Conclusions

1. Most of the morphological characters (morphometrics and meristics, indices) used in the previous revision to identify five new species of the genus *Channichthys* (Shandikov, 1995a; 1995b) have low value for taxonomic identification since they overlap significantly and do not show significant differences between the species, which is confirmed by statistical methods of analysis.
2. The most important for diagnosis meristic characters are: the number of rays in the first (*D*1) and second (*D*2) dorsal fins, pectoral fins (*P*), anal fin (*A*), the number of gill rakers on the first gill arches (*sp.br.)*, the number of scales in the dorsal (*Dll*) and medial (*Mll*) lateral lines; as well as some head measurements: head length (*c*), head height through the middle of the eye (*ho)*, snout length (*ao)*, longitudinal diameter orbit of the eye (*o)*, interorbital space (*io)*, length of the upper (*lmx)* and lower (*lmd)* jaws, and some indices.
3. The validity of four out of nine nominal species of the genus, namely *Channichthys rhinoceratus, Ch. rugosus, Ch. velifer* and *Ch. panticapaei,* has been confirmed.
4. The validity of five nominal species was not confirmed: three species (*Ch. aelitae, Ch. mithridatis,* and *Ch. richardsoni)* are conspecific with *Ch. rhinoceratus,* and two species (*Ch. bospori, Ch. irinae)*, with *Ch. panticapaei.* Relatively minor morphological differences noted for *Ch. aelitae, Ch. mithridatis, Ch. richardsoni, Ch. bospori,* and *Ch. irinae,* reflect intraspecific and ontogenetic variability.
5. Based on a detailed morphological analysis of the gill apparatus, two groups of species of the genus *Channichthys* can be distinguished*:* "double-rowed gill rakers", having two rows (outer and internal) of gill rakers on the gill arches (*Ch. panticapaei)* and "single-rowed gill rakers", having only single (outer) row of gill rakers on the gill arches (*Ch. rhinoceratus, Ch. rugosus,* and *Ch. velifer)*.

Acknowledgments

The author is grateful to her first supervisor A. V. Balushkin (ZIN RAS) for providing and teaching the methodology used in this paper and for guidance in the first stages of the work. The author also expresses special gratitude to N. V. Chernova and K. E. Nikolaev (ZIN RAS) for invaluable assistance and valuable comments during the manuscript preparation.

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