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Taxonomy and Phylogenetic Relationships of Cyprinid Fish of Genus *Hemiculter* (Cyprinidae, Xenocypridinae): Sharpbellies of the Species Group *Hemiculter lucidus*

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Abstract—On the basis of a comparative morphological analysis, the multi-rakered sharpbellies were divided into four groups, differing in the number of branched rays in the anal fin, the relative length of the head, body depth, the length of the spine of the dorsal fin, and the color of the peritoneum: Ussuri sharpbelly *Hemiculter lucidus*; the Buir-Nuur sharpbelly *H. varpachovskii*; sharpbellies from the basin of the Yangtze River (it is shown, that *H. clupeoides* is an available name for them); the sharpbellies from the Lower Amur basin described as an independent species, the status of which is confirmed by its differences from *H. lucidus* and *H. clupeoides* in the composition of haplotypes of the mitochondrial cytochrome *b* gene. The phylogenetic relationships of the species of multi-rakered sharpbellies are discussed, some problems of synonymy are considered, and a key for diagnosing the species is given.

Keywords: multi-rakered sharpbellies *Hemiculter*, taxonomy, diagnostic features, phylogenetic relations, new species, identification keys

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INTRODUCTION

The present paper continues the study of cyprinids (Cypriniformes) of the g. *Hemiculter* Bleeker, 1860, which, according to the modern classification, is a member of the subfamily Xenocypridinae Günther, 1868 of the fam. Cyprinidae (Tan and Armbruster, 2018). It is also considered as an independent fam. Xenocyprididae (Fricke et al., 2021; Froese and Pauly, 2021). The so far accepted structure of the genus and the nomenclature of its representatives (Fricke et al., 2021; Froese and Pauly, 2021) are in conflict with the results of modern phylogeographic analysis of native populations (Chen et al., 2017; Wang et al., 2021; Vasil'eva et al., 2022; present paper). This study is devoted to a group of so-called multi-rakered sharpbellies, previously combined (Vasil'eva and Kozlova, 1988) into one species *H. lucidus* (Dybowski, 1872). It was erroneously reported in the papers by Berg (1909, 1949) and Nikolsky (1947, 1956) (Vasil'eva and Kozlova, 1988) as a subspecies belonging to the species *H. leucisculus* (Basilewsky, 1855). Unlike sharpbellies of the *H. leucisculus* species group, whose phylogenetic relationships and taxonomy were discussed earlier (Vasil'eva et al., 2022), the multi-rakered sharpbellies of the *H. lucidus* species group are characterized by a relatively large number of densely seated gill rakers on the 1st gill arch (18–30, on average 22–24), usually having at least 12 branched rays in the anal fin; the beginning of the dorsal fin, located, as a rule, closer to the end of the snout than to the beginning of the caudal fin; and a lateral line not sharply curving down at the pectoral fin in which there are 40–53 (42–46 on average) perforated scales (Vasil'eva and Kozlova, 1988; Vasil'eva, 2004). Currently, three species are recognized as valid in this group: Ussuri sharpbelly *H. lucidus* from the fresh waters of Russia and China, *H. bleekeri* Warpachowski, 1887 in the water bodies of China, and Buir-Nuur sharpbelly *H. varpachovskii* Nikolski, 1903 in the basin of the upper reaches of the Amur in Mongolia, Russia and China (Fricke et al., 2021; Froese and Pauly, 2021). The ranges of all these species need to be clarified.

The goal of the present paper is to assess the morphological variability and divergence of multi-rakered sharpbellies from different basins; find out the phylogenetic relationships of local groups of populations, taxonomic relationships and the nomenclature of the discovered phyletic lineages; identify diagnostic morphological characters of all taxa, determine their native ranges and develop identification keys.

MATERIALS AND METHODS

Morphological studies were carried out on materials from the collection of the Zoological Museum of Moscow State University (ZMMU); a total of 405 specimens were studied. Initially, all ZMMU samples collected before 1960, in accordance with the erroneous ideas of Berg (1949) and Nikolsky (1947, 1956) about the taxonomy and nomenclature of the sharpbellies, were identified by collectors or ZMMU staff members as *H. leucisculus* (including the fish from Lakes Buir-Nuur and Dalainor) or its subspecies *H. leucisculus lucidus* (Lake Khanka). All these samples, in accordance with the earlier revision of the genus (Vasil'eva and Kozlova, 1988) and the results of the present study, were reidentified and, together with our modern samples, were assigned to four different species, the taxonomic status of which is given below in the interpretation of the authors of the present paper.

***H. lucidus*, Lake Khanka basin**—78 ind., standard body length (*SL*) 55.0–172.5 mm and four juvenile ind. *SL* < 50 mm: P-7550—three ind., Astrakhanka, 24/06/1949, collector V.D. Lebedev; P-7557—one ind., 11/07/1948; P-7906—seven ind., Luzanova Hill, 19/07/1949; P-8343—14 ind., 1949; P-20064—one ind., rice paddy channels near Vladimiro-Petrovka Village, 20/09/1996, collector V.P. Vasil'ev; P-20066—one ind., Kamen'-Rybolov, TINRO base, 11/09/1996, collector V.P. Vasil'ev; P-20105—43 ind., Kamen'-Rybolov, TINRO base, 15/09/1996, collector V.P. Vasil'ev; P-21966—12 ind., Kamen'-Rybolov, TINRO base, 25–26/09/2007, collectors V.P. Vasil'ev, E.D. Vasil'eva, S. V. Shedko (include vouchers for DNA analysis).

***H. varpachovskii*, Lake *Buir-Nuur*, Mongolia**—82 ind. *SL* 85.5–129.0 mm: P-8041—three ind., summer 1948; P-8069—ten ind., July–August 1948; P-8375—16 ind., August 1948; P-8606—16 ind., in poor condition, 1948, collector A. Dashdorzh (on the labels hereinafter it is indicated: "coll. Anudarin"); P-8608—seven ind., summer 1948., collector A. Dashdorzh; P-8683—three ind., collector A. Dashdorzh; P-13018—27 ind. collector A. Dashdorzh.

Lake Dalainor basin, Mongolia – 106 ind. *SL* 77.0–119.0 mm. Samples by A.A. Svetovidova: P-8674—eight ind., Dalainor, 17/06/1957; P-8675—nine ind., Kerulen River, 17/06/1957; P-8699—one ind., Dalainor, turbid river branch, 13/06/1957; P-8700—21 ind., Urshun River (=Orshun-Gol), 07/06/1957; P-8701—20 ind., Urshun River, 28/06/1957; P-8702—three ind., Urshun River, 09/06/1957; P-8728—four ind., Dalainor, summer 1957; P-8729—29 ind., Dalainor, summer 1957; P-8730—ten ind., Dalainor, 16/06/1957; P-22031—one ind., Kerulen River, 47°01′ N, 109°08′ E, 28/08/2007, collector Yu.V. Slyn'ko.

H. clupeoides Nichols, 1925, **China**—44 ind. *SL* 71.0–118.0 mm: P-8638—one ind., gifted by the Institute of Hydrobiology, Chinese Academy of Sciences; P-9436—35 ind., Yangtse River ("collected from G-Chang"), 28/04/1958; P-22294—eight ind., Yangtse River, Jingzhou, Hubei Province, 31/10/2009, collectors E.D. Vasil'eva and V.P. Vasil'ev.

***Hemiculter* sp.**, described in the present paper at the state of new species, downstream Amur River basin—89 ind. Lake Bolon' basin—46 ind. *SL* 82.0–146.0 mm: P-6166—one ind., Cape Nergul', 01/08/1946, collector G.V. Nikolsky; P-6172—three ind., Cape Serebryanyi, 24/07/1946, collector G.V. Nikolsky; P-6174—two ind., Tuf Island, 06/07/1946, collector M.N. Lishev; P-6234—seven ind., June 1946, collector S.G. Soin; P-6506—ten ind., 20/06/1947, collector T.K. Sysoeva; P-6545—two ind., 28/05/1947; P-6600—three ind., Cape Serebryanyi, 10/07/1947, collector T.K. Sysoeva; P-6859—one ind., 28/06/1947, collector T.K. Sysoeva; P-6860—four ind., Tuf Island, 05/07/1947, collector T.K. Sysoeva; P-6867—six ind., 28/06/1947, collector T.K. Sysoeva; P-6880—three ind., 01/08/1946, collector T.K. Sysoeva; P-8432—three ind., Cape Serebryanyi, 03/08/1946; P-17128—one ind., selected from the sample P-6391 with four ind. *H. leucisculus*, Siy river branch, 30/07/1947, collector G. V. Nikolsky.

Amur River near Elabuga—12 ind. *SL* 99.0–142.0 mm: P-6405 – one ind., 19/06/1947, collector G.V. Nikolsky; P-7502—two ind., 24/07/1949, collector T.K. Sysoeva; P-7536—two ind., 12/07/1948, collector A.A. Svetovidova; P-7884—one ind., 30/07/1949; P-7885—three ind., 12/06/1949; P-7956—one ind., 01/08/1949; P-8574—two ind., Lake Medovoe, 20/06/1948, collector S. G. Soin.

Lower Amur River at various parts—29 ind. *SL* 61.0–115.0 mm: P-6082—seven ind., Lake Bol'shoye Kizi, 26/07/1946, collector M.N. Lishev; P-6098—three ind., Amur upstream Mogol'skoye Village, 23/08/1946, collector G.V. Nikolsky; P-6144—one ind., Lake Udyl', 29/07/1946, collector M.N. Lishev; P-6479—nine ind., Amur near Sikacha-Alyan, 12/06/1947, collector G.V. Nikolsky; P-7129—two ind., Amur near Dzhelinda, Bol'shoye Nevero mouth, 25/07/1948, collector V.D. Spanovskaya; P-7134—six ind., Amur, 7 km upstream Ol'gino, 07/08/1948, collector V.D. Spanovskaya; P-21562—one ind., Amur near Bezymyannoye (upstream Khabarovsk), 07/08/2004, collector E.D. Vasil'eva.

Sungari River (Amur basin) near Harbin (China): P-3513—two ind. *SL* 75.5 and 82.0 mm, 07/07/1932, collector A.S. Lukashkin.

In all individuals, the standard body length (*SL*) was measured and the features used in the differentiation and description of various nominal species of the g. *Hemiculter* and related taxa were analyzed (Bănărescu, 1968; Vasil'eva and Kozlova, 1988; Luo and Chen, 1998; Tan and Armbruster, 2018). First of all, these characteristics were revealing the greatest interpopulation variability within the *H. lucidus* group and were used by Chinese researchers to distinguish subspecies in the Amur River basin (Ching-Jiang and Be-Lu, 1959; Vasil'eva and Kozlova, 1989a): relative head length (*c*), the greatest depth of the body in front of the dorsal fin (*H*), the depth of the dorsal fin (*hD*), the length of the last unbranched ray (spine) of the dorsal fin (*Hsp*), the number of branched rays in the anal fin (*A*) (the last two closely spaced rays were counted as one ray), number of gill rakers on the 1st gill arch (*sp.br.*), number of scales in the lateral line (*ll*). The table does not include data on juvenile sharpbellies from Lake Khanka. At the analysis of the differentiation of fish from different basins and compiling the characteristics of taxa, we also used the previously obtained results of a study of the variability of a wide range of morphometric characteristics in sharpbellies of the *H. lucidus* species group at the intra- and interpopulation levels (Vasil'eva and Kozlova, 1989a). In some specimens from museum collections, the color of the peritoneum, the structure of the swim bladder, the formula of the pharyngeal teeth, and the relative length of the skin subclavian outgrowth (*flepl*—flesh slip at the pectoral fin base) were also analyzed (Dai and Yang, 2003, p. 78).

Statistical analysis was performed using the MS Excel software package; the magnitude of the differences between the compared samples for characteristics with identified significant differences (t_{st}) was estimated based on the values of the *CD* coefficient of differences (Mayr et al., 1956). At the assessment of the native ranges of species, materials from the museum collection, the results of the authors' own field work and molecular genetic studies, materials from the Genbank, as well as information from publications cited in the paper were used.

The full-length sequences of the mitochondrial cytochrome *b* gene (*cyt b*) were sequenced from 55 samples of multi-rakered sharpbellies (deposited to the GenBank under accession numbers MW508412–MW508458). In addition to the previously processed (Vasil'eva et al., 2022) materials of sharpbellies from the Yangtze River, Hubei Province (sample ZMMU P-22294, $n = 8$), *H. lucidus* specimens from Khanka Lake ($n = 20$, including specimens from sample ZMMU P-21966), as well as a new species of the g. *Hemiculter* described in the present paper, collected in 2006–2008 from the Sungari River near Harbin City (n = 8) and the Amur River near Khabarovsk ($n = 19$) were used. In addition to our own materials, we used data on the sequence of the *cyt b* gene KF760461 obtained from the sharpbely from South Korea, identified (Kim et al., 2014) as *H. leucisculus*, but attributed to *H. eigenmanni* (Jordan et Metz, 1913) in the GenBank.

DNA isolation, PCR amplification, DNA sequencing, and phylogenetic analysis were carried out in the same way as described previously (Vasil'eva et al., 2022). The only difference was that, due to the relatively low level of divergence of the *cyt b* gene within multi-rakered sharpbellies (maximum distances of about 2.5% of differing positions), the nucleotide sequence of this gene was not divided into partitions and the data matrix was analyzed using one optimal model of nucleotide substitutions (TN + F + G4) selected in the IQ-TREE v.1.6.12 program (Nguyen et al., 2015).

RESULTS AND DISCUSSION

Morphological Variability and Divergence of Multi-Rakered Sharpbellies of the Hemiculter Lucidus Group

A comparative morphological analysis of the variability of multi-rakered sharpbellies from local populations revealed that individuals from different basins differ quite clearly in the complex of the following characteristics: the number of branched rays in the anal fin, the relative length of the head, body depth and length of the last unbranched ray (spine) of the dorsal fin, and the color of the peritoneum.

Sharpbellies of the Lake Khanka basin exhibit the highest level of morphological divergence from populations of other basins. As a rule, they have at least 14 branched rays in the anal fin (Fig. 1): among the studied 78 ind. only one had 13 rays in this fin; individuals with 15–16 rays predominated (56.4%). According to Chinese authors (Ching-Jiang, Be-Lu, 1959), sharpbellies from Khanka rarely have 13 branched rays (2/28), usually 14–15 (17/28), and individuals with 19 rays occur as well (1/28). A large number of rays in the anal fin - from 14 to 18—are also indicated by other authors (Warpachowski, 1887; Warpachowski and Herzenstein, 1887; Lindberg and Taranets, 1929; Berg, 1949; Nikolsky, 1956; Bănărescu, 1968; Luo and Chen, 1998). The head of fish from Khanka is relatively small (Table), fits 4.2–5.4 times in *SL* (usually five or more times), as also indicated in the keys developed by Luo and Chen (Luo and Chen, 1998). According to Ching-Jiang and Be-Lu (1959), the head length of these sharpbellies varies from 17 to 20% *SL;* according to other authors, it is contains from 5.3 to 5.5 times in *SL* (Warpachowski, 1887; Warpachowski and Herzenstein, 1887; Berg, 1949).

The greatest body depth in the studied sharpbellies from Lake Khanka is always greater than the length of the head (table, Fig. 1d), which is also noted for them in the keys developed by Chinese authors (Luo and Chen, 1998); 3.3–4.0 times in *SL*, 3.8–4.0 times according to other authors (Warpachowski, 1887; Warpachowski and Herzenstein, 1887; Berg, 1949). The length of the spine of the dorsal fin is as a rule 75–85% *H*, usually exceeds 85% *c*, and is usually equal to or greater than the length of the head (Fig. 1b); according to Berg (1949), the length of the spine is greater than or equal to the length of the head; according to the keys by Chinese authors (Ching-Jiang and Be-Lu, 1959; Luo and Chen, 1998), it is usually greater than the length of the head. The peritoneum of all studied individuals from sample P-21966 (12 ind.) is black; in three ind. from sample P-8343—dark brown.

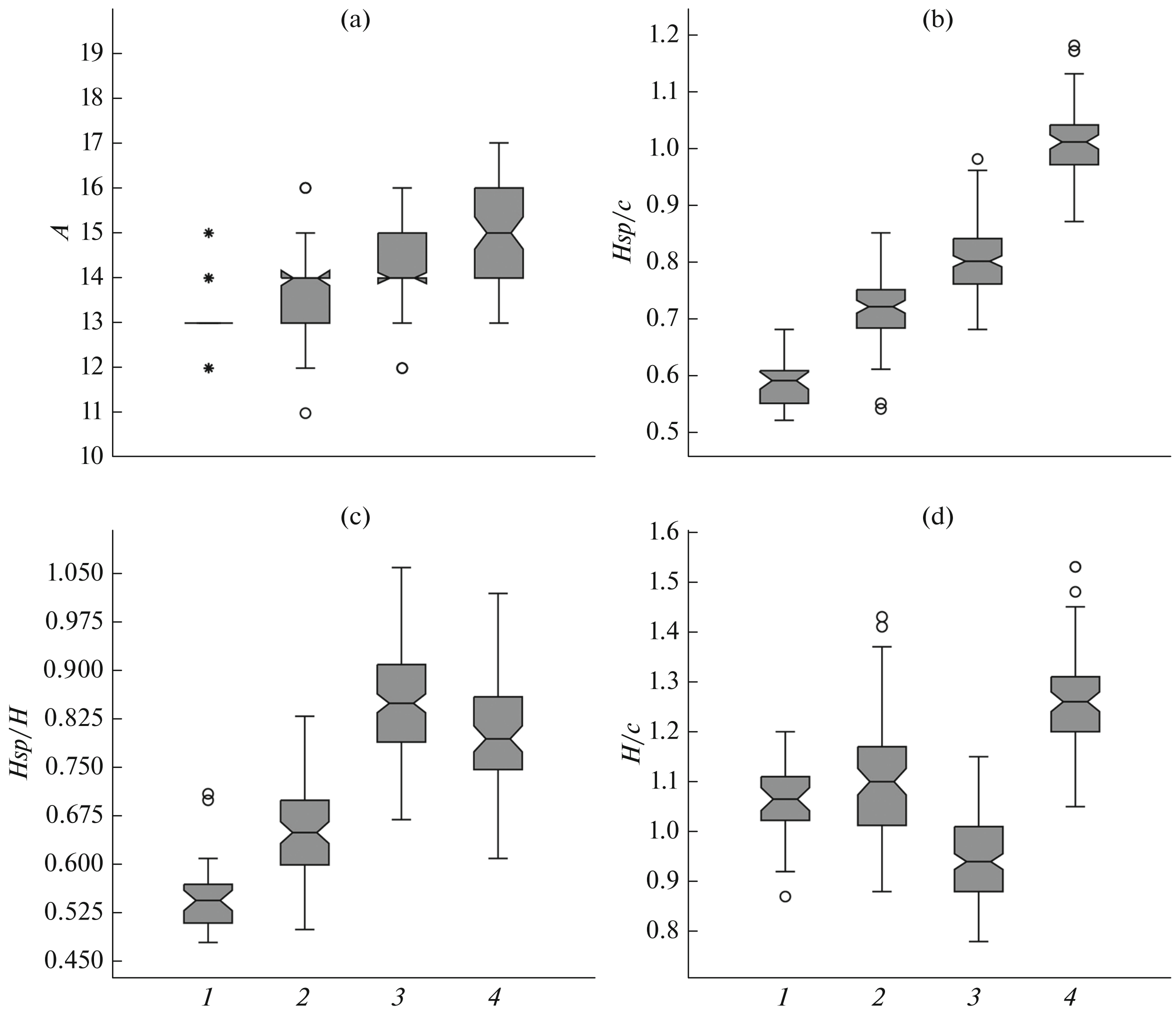

Fig. 1. Diagrams of the range of the main morphological characters used for the diagnosis of multi-rakered sharpbellies of the g. *Hemiculter* from different basins: (a) the number of branched rays in the anal fin (*A*), (b) the ratio of the length of the spine of the dorsal fin to the length of the head (*Hsp/c*), (c) the ratio of the length of the spine of the dorsal fin to the maximum body depth at the beginning of the dorsal fin (*Hsp/H*), (d) the ratio of the maximum body depth to the length of the head (*H/c*). Group samples: *1*—Yangtze River, *2*—Lower Amur basin, *3*—Upper Amur basin, *4*—Lake Khanka system; (I)—limits of variation of the indicator (from 25 to 75% of the data are enclosed in a gray-filled figure), (–)—median; (○), (*)—outliers.

Sharpbellies from the Yangtse River basin exhibit most striking differences in morphological characteristics from individuals from the Khanka basin (hereinafter, only characters for which statistically significant differences were found are considered). The studied fish have 12–15 branched rays in the anal fin, usually not more than 13 (27/37); other authors also indicate 12–13 rays for specimens from the Yangtze basin (Ching-Jiang and Be-Lu, 1959). Consequently, the length of the base of the anal fin in sharpbellies from the Yangtze is significantly less than in the Khanka ones (Table): the level of differences exceeds the formally subspecies level, *CD* = 1.48. Even lower mean *lA* values are reported for sharpbellies from the Yangtze by Chinese authors (Li et al., 2020): 13.9 ± 0.9% *SL*. The head length in the studied specimens from the Yangtze is greater than that in the sharpbellies from Khanka: 4.1–4.7 times in *SL*. The revealed differences are rather small (*CD* = 1.02) and, to a certain extent, may be determined by the smaller size of sharpbellies from the Yangtze, although similar mean head sizes, 21.2 ± 1.0% *SL*, are also reported by Chinese authors (Li et al., 2020).

The greatest body depth in sharpbellies from the Yangtze usually slightly exceeds the head length (Table, Fig. 1d), which is also noted for them in the keys developed by Chinese researchers (Luo and Chen, 1998)—3.4–4.8 times in *SL*. However, Chinese authors (Li et al., 2020) indicate a lower mean value of the characteristics than we: 20.2 ± 1.4% *SL*. The length of the dorsal fin spine is usually < 60% *c* and < 55% *H*. According to the *Hsp/c* index values, there is a hiatus between the distributions of the Yangtze and Khanka sharpbellies: *CD* = 3.70. According to the *Hsp/H* index

Table 1. Some morphometric characteristics of multi-rakered sharpbellies (*Hemiculter*) from various basins

Characteristic	Yangtse River	Lower Amur	Upper Amur	Khanka
n	37	88	170	78
SL, mm	71–118 / 88.1	56–146 / 99.4	77–129 / 98.6	55–172.5 / 119.0
A	12–15 / 13.1 ± 0.13	11–16 / 13.7 ± 0.12	12–16 / 14.1 ± 0.07	13–17 / 15.4 ± 0.12
Hsp/*H*	0.48–0.71 / 0.55 ± 0.009	0.50–0.83 / 0.66 ± 0.008	0.67–1.06 / 0.85 ± 0.006	0.61–1.02 / 0.80 ± 0.009
Hsp/*c*	0.52–0.68 / 0.59 ± 0.007	0.54–0.85 / 0.71 ± 0.006	0.68–0.96 / 0.80 ± 0.004	0.71–1.18 / 1.00 ± 0.008
H/*c*	0.87–1.20 / 1.07 ± 0.012	0.88–1.43 / 1.10 ± 0.013	0.78–1.15 / 1.00 ± 0.053	1.05–1.53 / 1.26 ± 0.010
*According to Vasil'eva and Kozlova, 1988, 1989a				
n	35	88	98	19
ll	40–47 / 43.0 ± 0.41	40–45 / 40.7–43.9	40–49 / 42.1–44.3	40–49 / 44.4 ± 0.48
In % *SL*				
aD	48.4–52.2 / 50.2 ± 0.16	46.0–54.2 / 49.6–51.9	46.6–54.4 / 49.3–50.8	47.8–53.6 / 50.3 ± 0.29
aV	46.0–50.7 / 48.3 ± 0.20	42.5–55.7 / 48.0–50.3	44.9–52.8 / 47.7–48.5	44.4–47.3 / 45.9 ± 0.21
lP	19.0–22.7 / 20.4 ± 0.12	17.8–27.2 / 21.0–25.4	21.4–26.4 / 23.5–24.2	22.2–24.6 / 23.4 ± 0.15
lV	13.4–16.0 / 14.7 ± 0.10	12.9–19.0 / 15.2–16.9	14.4–19.38 / 16.4–17.1	14.7–18.6 / 16.6 ± 0.27
lA	12.5–16.3 / 14.6 ± 0.15	11.6–20.5 / 14.2–15.6	12.0–17.8 / 14.8–15.4	15.4–18.7 / 17.2 ± 0.20
hD	15.5–18.3 / 16.8 ± 0.12	15.5–23.6 / 17.7–20.8	17.4–23.9 / 20.3–21.5	19.7–27.1 / 22.5 ± 0.47
Hsp	12.2–16.1 / 14.4 ± 0.15	13.7–20.8 / 15.2–17.6	16.3–22.7 / 19.2–20.4	18.5–23.6 / 20.5 ± 0.38
H	20.7–29.4 / 25.4 ± 0.27	19.0–30.9 / 22.5–26.6	19.8–28.0 / 23.1–23.3	25.3–30.4 / 27.2 ± 0.37
c	21.5–24.7 / 23.3 ± 0.13	20.4–27.4 / 22.0–24.5	21.3–27.1 / 23.3–24.6	18.6–23.8 / 21.0 ± 0.34

n—number of specimens; top—range of variability, bottom—mean and error of mean (*in the Lower and Upper Amur basins—variability of mean values in various group samples); *SL*—standard body length, *A*—number of branched rays in anal fin; *aD*, *aV*—predorsal and preventral distances; *lP*, *lV*—length of the pectoral and ventral fin, respectively, *lA*—length of the anal fin base, *hD*—depth of the dorsal fin, *Hsp*—length of the dorsal fin spine, *H*—maximum depth of the body at the beginning of the dorsal fin, *c*—length of the head, *ll*—the number of lateral line scales.

values (Fig. 1c), the magnitude of differences exceeds the formally subspecies level: *CD* = 1.57. In contrast to the studied sharpbellies from Khanka, in three ind. of the Yangtze from sample P-22294 and in an individual from China from sample P-8638, the peritoneum is light.

In addition to the characteristics noted above, sharpbellies from the Yangtze River differ significantly from the studied Khanka sample (Vasil'eva and Kozlova, 1989a) by a lower dorsal fin depth (a hiatus is observed between the distributions of the trait values, *CD* = 2.07), a shorter pectoral fin (*CD* = 2.20), as well as a shorter pelvic fin (Table 1). Chinese authors (Li et al., 2020) give the following mean values for these characteristics: 18.1 ± 1.2, 19.3 ± 0.8, and 14.7 ± 0.9% *SL*, respectively.

Sharpbellies from different populations of the Lower Amur basin demonstrate the greatest morphological similarity to those of the Yangtze basin, with a shift in the mean values towards the range of variation of sharpbellies from Khanka (Table 1). They have 11 to 16 branched rays in the anal fin (Fig. 1a), more often 13 (28/88) or 14 (30/88). Similar data are given for Amur populations from the territory of China (Ching-Jiang, Be-Lu, 1959): 12–16 rays, more often 13 (38/126) or 14 (56/126). According to Nikolsky (1947), sharpbellies from different water bodies of the Lower Amur basin have mean number of rays of 13.4–14.1. The length of the base of the anal fin varies in a wider range than in the fish from the Yangtze and Khanka, but the mean values in different Amur samples are closer to the mean value of the parameter in the sample from the Yangtze (Table), although their differences from the mean values in Khanka sharpbellies are small (*CD* value does not reach formally subspecific level of 1.28). Head length of Lower Amur sharpbellies fits 3.7–4.9 times in *SL*.

The greatest values of the body depth are usually greater than the length of the head (Table 1, Fig. 1d); in different local populations, the *H*/*c* ratio varies on average from 0.92 to 1.16; it fits 3.2–5.3 times in *SL*. In terms of the mean *H*/*c* value index, the Amur sharpbellies are similar to fish from the Yangtze and significantly differ from Khanka specimens, but these differences are rather small (Table 1). The length of the spine of the dorsal fin usually does not exceed 75% *c* and ranges from 60 to 70% *H* (Table 1, Fig. 1c). According to the mean values of the *Hsp*/*H* and *Hsp*/*c* indices, sharpbellies of the Lower Amur differ significantly from fish of the Yangtze and Lake Khanka, but, high differences are observed only in the *Hsp*/*c* index values between Amur and Khanka sharpbellies: *CD* = 2.32. At the same time, the average spine length in different Amur populations varies within 15.2–17.6% *SL*, and in the case of the sample from Lake Kabar with *Hsp* 17.3 ± 0.34% *SL*, the difference from sharpbellies of the Yangtze reaches *CD* = 1.29. In turn, the distribution of *Hsp* values in the sample of Amur sharpbellies from Lake Bol'shoye Kizi, 13.8–16.5 (mean 5.2) % *SL* (*n* = 7), does not overlap with the variation range of Khanka sharpbellies.

In terms of the depth of the dorsal fin, the studied populations of the Lower Amur occupy an intermediate position between the sharpbellies of the Yangtze and Khanka. All Amur samples significantly differ from the sample from the Yangtze, and in some cases these differences reach a significant value: for example, when compared with the Lake Kabar population with *hD* 20.4 ± 0.29% *SL CD* = 1.93, and with the sample from the Amur near the Elabuga Settlement with *hD* 20.3 ± 0.30% *SL CD* = 1.38. Differences of all Amur samples from Khanka sharpbellies are similarly significant, and in some cases they are enough high: versus a sample from Amur with *hD* 17.7 ± 0.20% *SL CD* = 1.60; Lake Bolon' with *hD* 18.6 ± 0.16 *CD* = 1.37, and the distribution of parameter values in the sample from Lake Bol'shoye Kizi *hD* 17.2–19.4% *SL* does not overlap with the Khanka sharpbellies variability range (Table 1).

The range of variability in the relative length of the pectoral and pelvic fins in Lower Amur sharpbellies exceeds the total variability of the Yangtze and Khanka specimens; the lowest mean values of the Amur samples are close to the mean values of features in the sample from the Yangtze; the highest, to the means of Khanka sharpbellies (Table 1).

Populations of the Argun River system (upper reaches of the Amur)—lakes Buir-Nuur (=Khulun-Buir) and Dalainor, the Urshun and Kerulen rivers. By most features these populations are more similar to sharpbellies from Lake Khanka than to individuals from the basins of the Lower Amur and the Yangtze River. As a rule, they have at least 13 branched rays in the anal fin (12 rays were found only in 6 out of 170 ind.), more often 14 (70/170) or 15 (51/170) rays. Chinese authors give similar data for the Buir-Nuur sharpbellies (Ching-Jiang, Be-Lu, 1959): 12–15 rays, more often 13 (12/40), 14 (10/40), or 15 (15/40); in the description of *H. varpachovskii*, compiled according to 8 ind., 15 rays are given (Nikolski, 1903). The mean values of the length of the anal fin base in different samples are similar to the mean values of this character in the sharpbellies from the Lower Amur basin (Table 1). The head length of the studied sharpbellies from the Upper Amur basin fits 3.7–4.7 times in *SL*, which is consistent with the characteristics of Buir-Nuur sharpbellies in the diagnostic key developed by Luo and Chen (1998) (<5.0 times in *SL*) and with the description of Nikolski (1903)—4½–4⅔. The mean head lengths in different populations are similar to those of sharpbellies from the Yangtze and the Lower Amur (Table 1). According to Ching-Jiang and Be-Lu (1959), the head length of these sharpbellies varies from 21 to 25% *SL* (mean 22.7%).

The greatest body depth usually does not exceed the length of the head (Table 1, Fig. 1d), it fits 3.6–5.1 times in *SL* (4–4½, according to the description by Nikolski (1903)). According to the identification keys developed by Chinese authors (Ching-Jiang and Be-Lu, 1959), the body depth of Buir-Nuur sharpbellies does not exceed 22% *SL*. In terms of the mean value of the *H/c* index, Upper Amur sharpbellies are similar to specimens from the Yangtze and from the Lower Amur basin, significantly differ from Khanka sharpbellies, but these differences are small. The length of the spine of the dorsal fin is usually greater than 75% but less than 90% *c* (shorter than the head: sensu Luo and Chen, 1998) and, as a rule, exceeds 80% *H* (Figs. 1b, 1c). According to the *Hsp/c* index value, the sharpbellies of the Upper Amur basin are significantly different from both the Yangtze sharpbellies (*CD* = 2.18, distributions of the parameter values in the samples practically do not overlap) and Lake Khanka sharpbellies (*CD* = 1.56). According to the *Hsp/H* index value, significant differences are observed between the sharpbellies of the Upper Amur and Yangtze: *CD* = 2.21. Mean *Hsp* values (in % *SL*) in Upper Amur sharpbellies are similar to the Khanka specimens; hiatus is observed with the distribution of parameter values in individuals from the Yangtze, and the differences with all Upper Amur samples reach a high level: *CD* = 2.26 with a sample from Lake Buir-Nuur with *Hsp* 19.2 ± 0.18% *SL*, *CD* = 3.15 with a sample from the Urshun River with *Hsp* 19.2 ± 0.13% *SL*, *CD* = 2.68 with sample from Lake Dalainor with *Hsp* 20.4 ± 0.26% *SL*. A high difference in the *Hsp* index values between the Upper and Lower Amur group samples with low mean values of the index is reached: when comparing the sample from the Lower Amur with *Hsp* 15.8 ± 0.25% *SL* with the sample from Lake Buir-Nuur *CD* = 1.40, with the sample from the Urshun River—1.85, with a sample from Lake Dalainor—1.80. At the same time, the differences from the Lower Amur samples with large mean *Hsp* values (for example, with the sample from Lake Kabar with *Hsp* 17.3 ± 0.34% *SL*) are significant, but small: *CD* value does not reach the level of 1.28. In two dissected specimens from sample P-8069, the peritoneum is dark.

In terms of the average depth of the dorsal, and pectoral, and pelvic fin lengths, sharpbellies from the Upper Amur basin waterbodies are most similar to Lake Khanka sharpbellies (Table 1).

Taxonomic Structure and Nomenclature Problems of Multi-Rakered Sharpbellies

Four groups of multi-rakered sharpbellies differentiated by morphological characters inhabit different basins. The differences between them in individual characteristics exceed formally the subspecific level of *CD* = 1.28, while in others there is a hiatus between the distributions of the parameter values, which corresponds to the species-rank morphological criterion. In any case, according to the complex of morphological characteristics that were previously used in identification keys, sharpbellies from different groups are clearly differentiated from each other (see the diagnostic key developed in this study below) and are accepted by us as independent taxa of the species rank. Sharpbellies from the Khanka basin and Lake Buir-Nuur were previously described as independent species, which are still recognized today: *H. lucidus* and *H. varpachovskii*, respectively (Fricke et al., 2021; Froese and Pauly, 2021). At the same time, the nomenclature of two other species, sharpbellies of the Yangtze River basin and sharpbellies of the lower reaches of the Amur, requires special analysis.

Yangtze River sharpbellies. Modern reports on the fish fauna for the Yangtze River specify two species of sharpbellies with *sp. br.* > 20: *H. tchangi* Fang, 1942 and already mentioned *H. bleekeri* (Luo and Chen, 1998; Fu et al., 2003; He, 2010). Our previous work (Vasil'eva et al., 2022) confirmed the conclusion of Bănărescu (1968) that *H. tchangi* was described from a hybrid individual, and therefore the name *tchangi* cannot be used as a valid for parental species of this hybrid (International Code of Zoological Nomenclature, 2000. Art. 23.8). The valid name for the species of the g. *Hemiculter* involved in hybridization is *nigromarginis*, proposed later (Yih and Wu, 1964). An endemic species of tributaries of the upper reaches of the Yangtze River, *H. nigromarginis*, belongs to the phylogenetic clade of low-rakered sharpbellies (Chen et al., 2017; Vasil'eva et al., 2022) and, alike these species, has a small number of branched rays in the anal fin (11 –12) and the beginning of the dorsal fin, located, as a rule, closer to the beginning of the caudal fin than to the end of the snout. It differs from other species of proper low-rakered sharpbellies in a larger number of gill rakers (25–28) and a relatively larger number of scales in the lateral line (49–53) (Bănărescu, 1968).

The species *H. bleekeri* was described by Warpachowski (1887) based on the description of two individuals from China (presumably from the Yangtze River), given by Bleeker (Bleeker, 1863–1864, 1871). Bleeker assigned it to the species *H. leucisculus*. Warpahowski's description repeats the following important characteristics from Bleeker publications: *D* II 7–8, *A* III 11–13, *P* I 13–14, *V* II 8, *ll* 40–42; *H* fits 4⅔–4¾ times in *SL*; *c*, 4⅓–4½ times in *SL*; the beginning of the dorsal fin is closer to the base of the caudal fin than to the end of the snout. However, it lacks the formula of three-row pharyngeal teeth given by Bleeker (2.4.5/5.4.2) and the fact that in the fish studied by Bleeker the 2nd unbranched ray of the dorsal fin is shorter than the head (Bleeker, 1871).

At that, Warpachowski indicated in the diagnosis that in *H. bleekeri* the belly is flattened in front of the pelvic fins, and behind them with a very blunt keel: "der Bauch ist vor den Ventralen abgeflacht, hinter denselben sehr stumpf gekielt" (Warpachowski, 1887. P. 702). Whereas Bleeker did not mention the presence/absence of a keel on the belly in the description,

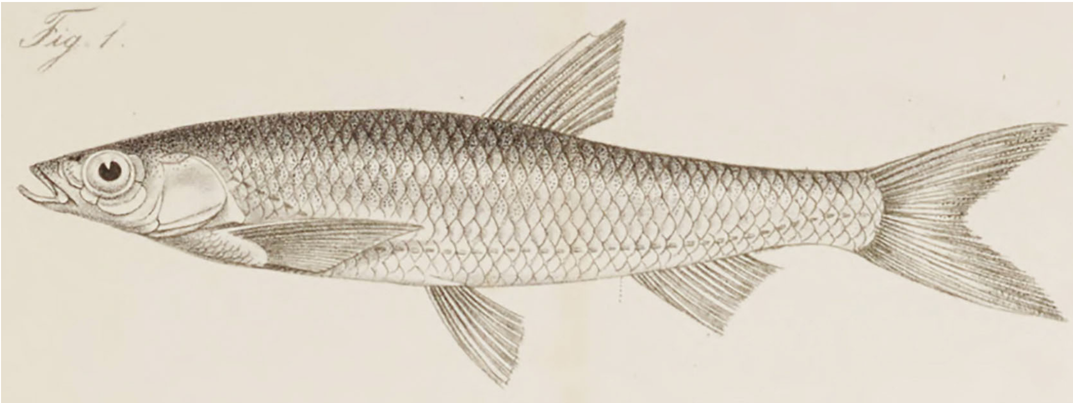

Fig. 2. Appearance of sharpbelly *Hemiculter leucisculus* according to: Bleeker, 1871. Tabl. 2. Fig. 1.

but in comparative remarks he indicated that in the g. *Hemiculter* (i.e., in the fish he studied, which he assigned to this genus), in contrast to the g. *Culter* Basilewsky, 1855, the belly is obtuse **even** behind the pelvic fins: "par le ventre qui est obtus même en arrière des ventrales" (Bleeker, 1871, p. 78). At the same time, Warpachowski, in the description of the g. *Hemiculter*, indicated that the belly of these fish **is mainly** with a keel: "Bauch meist gekielt" (Warpachowski, 1887, p. 693), while in the species keys for *H. bleekeri* he noted the absence of a keel ("nicht gekielt"—p. 694).

The absence of a keel in the fish studied by Bleeker (Bleeker, 1863–1864, 1871) was subsequently discussed by some authors. Thus, Peters (Peters, 1880, cited in: Warpachowski, 1887) believed that Bleeker had overlooked the keel because of the small size of the fish he studied. However, Warpachowski (1887) considered this very doubtful, since in a later paper, after the publication of the papers of Kner and Günther (Kner, 1867; Günther, 1868—cit. in: Warpachowski, 1887), Bleeker (1871) (who, by the way, cited the mentioned authors) should have reported his error. In connection with these statements, it should be noted, firstly, that Bleeker's description used individuals with a total body length (*TL*) of 136 and 143 mm (Bleeker, 1871), which are larger than the fish studied by us from sample P-22294 *TL* 101–129 mm, in which the keel is clearly visible from the pectoral fins to the anus. Second, as cited above, Bleeker (1871) noted the absence of a keel in species of the g. *Hemiculter* as distinct from fish of the g. *Culter*. Berg (1949), who erroneously attributed the multi-rakered sharpbellies to the species *H. leucisculus*, apparently guided by the description of Warpachowski (1887), and included *H. bleekeri* in the g. *Pseudohemiculter* Nichols et Pope, 1927, in which the keel is developed only in the rear part behind the pelvic fins. In his revision of the g. *Hemiculter,* Bănărescu (1968) noted the absence of a mention of the keel in the descriptions of Bleeker (Bleeker, 1863–1864, 1871), but considered it possible to adopt the species *H. bleekeri* on the grounds that the presence of "42 scales" indicated by Bleeker (Bănărescu, 1968. p. 526) is found only in this species.

Unfortunately, there are no type specimens of *H. bleekeri* (Bănărescu, 1968; Fricke et al., 2021), but there is an image of one of the fish on the basis of which this species was described (Bleeker, 1871. Table 2. Fig. 1). This individual (Fig. 2) noticeably differs from the sharpbellies from the Yangtze River studied by us (Figs. 3a, 3b) by the dorsal fin shifted to the rear of the body, the beginning of which, in accordance with the Bleeker's description, is closer to the base of the caudal fin (in the fish studied by us, as in all multi-rakered sharpbellies, it is closer to the end of the snout), a longer head, which fits no more than 4.5 times (in sharpbellies from the ZMMU collection, 4.1–4.7 times) in *SL*, and longer pectoral fins, almost reaching the bases of the ventral fins (far from reach the base of the ventral fins in multi-rakered sharpbellies from the Yangtze: *lP*/*P*–*V* 79.1% on average). The Bleeker fish shown in the figure also has a longer dorsal fin spine, >70% *H*, while the fish we studied have <55%.

If we not to consider the absence of a keel on the belly, then Bleeker's identification (Bleeker, 1863–1864, 1871) of the fish he studied from China as *H. leucisculus* is definitely more correct than their assignment to multi-rakered sharpbellies, which are currently identified in China as *H. bleekeri*. Indeed, in *H. leucisculus* widespread from the Amur basin to the mouth of the Mekong River, the beginning of the dorsal fin is closer to the beginning of the caudal fin than to the end of the snout, and in the lateral line sharply curving down at the pectoral fin there are 40–59 (on average 46–51) perforated scales, usually no more than 12 branched rays in the anal fin and long pectoral fins: *lP*/*P*–*V* 76.6–107.5 (on average 90.7 ± 0.68)% (Vasil'eva and Kozlova, 1988; Vasil'eva, 2004; Vasil'eva et al., 2022). However, the keel on the belly of *H. leucisculus* is well developed both behind and in front of the pelvic fins, as in all species of the g. *Hemiculter* in the modern sense.

The comparative analysis of our own and published data (Nichols, 1943; Berg, 1949; Chen et al., 1998;

Fig. 3. *Hemiculter clupeoides* from Yangtse River, ZMMU P-22294: (a) small specimen *SL* 81.5 mm, (b) larger specimen *SL* 103.0 mm, (c) opened (dissected) specimen *SL* 106.0 mm with light peritoneum, (d) right pharyngeal bone, pharyngeal teeth 2.4.5.

Kim and Park, 2002; Dai and Yang, 2003; Kottelat, 2006; Froese and Pauly, 2021) revealed that among known freshwater fish from China and its border countries there are no cyprinids lacking a keel on their belly, but possessing other features from the description of *H. leucisculus* by Bleeker (1871). In addition, there are no such species among fish in which the keel is developed only between the anus and ventral fins, which include representatives of the genera *Chanodichthys* Bleeker, 1860 and *Pseudohemiculter*. At the same time, the generic name *Hemiculter* appeared for the first time in the diagnostic keys compiled by Bleeker (1860) for cypriniforms. Following these keys, it may be argued that the genera *Hemiculter* and *Chanodichthys* are very similar in morphological features, and they are united by the presence of three-row pharyngeal teeth and spines in the dorsal fin. Bleeker differentiates them according to the following set of characters: in the g. *Chanodichthys* the body is not elongated, the snout is pointed, the scales are of moderate size, the lateral line is slightly curved, while in the g. *Hemiculter* the body is elongated, the snout is short, the scales are medium or small in size, the lateral line is strongly curved. In this connection, we are inclined to accept that Bleeker's (1871) remark about the keel in the fish he studied should be assessed as comparative with respect to species with a more pronounced sharp keel. According to other features of the description, they correspond to modern concept about the g. *Hemiculter* with a steeply curved lateral line ("la ligne latérale fortement et subetement courbée"—Bleeker, 1871. p. 78), *D* II–III (6)7–8 with a smooth spine, *A* III 10–19, *ll* 40–59 and three-row pharyngeal teeth.

However, as opposite to many other authors (Ching-Jiang, Be-Lu, 1959; Yih and Wu, 1964; Bănărescu, 1968; Luo and Chen, 1998; Fu et al., 2003; Jiang et al., 2008; He, 2010; Li et al., 2020; Fricke et al., 2021; Froese and Pauly, 2021), in accordance with the results of the above analysis, we consider *H. bleekeri* not an independent species or subspecies, but a junior synonym of *H. leucisculus*.

Among the names available for multi-rakered sharpbellies from the Yangtze River, *H. clupeoides* Nichols, 1925 was earliest described. The description is based on single specimen from Tungting Lake (=Dongting Hu) in Hunan Province, belonging to the Yangtze basin: a number of tributaries of the Yangtze flow into the lake, it is connected to the main course of the Yangtze by canals. The formulas of the fins and pharyngeal teeth given in the description, the shape of the lateral line, *ll* ~ 55, the presence of a keel on the belly extending forward beyond the ventral fins, as well as comparative remarks with respect to other species of the g. *Hemiculter* (Nichols, 1925, 1943) leave no doubt that this fish belongs to this genus. At the same time, the type specimen is certainly not conspecific with *H. leucisculus*, which is erroneously pointed out by a number of authors (Yih and Wu, 1964; Kottelat, 2006, 2013; Fricke et al., 2021). According to the description, it has 14 branched rays in the anal fin, and judging by the drawing (Nichols, 1943. Fig. 61, Pl. 4. Fig. 4), the dorsal fin begins much closer to the end of the snout than to the base of the caudal fin (*aD* ~ 48.4% *SL*), while in *H. leucisculus* the origin of the dorsal fin is strongly shifted to the rear of the body and usually there are no more than 12 branched rays in the anal fin. It should be noted that Bănărescu (1968), based on the description and comparative analysis of the holotype, considered *H. clupeoides* to be a synonym of *H. bleekeri*.

According to the main characteristics that differentiate the species in the multi-rakered sharpbellies group, the type specimen of *H. clupeoides* is fully consistent with the main characteristics of the sharpbellies from the Yangtze River studied by us. Its head length fits 4.6 times in *SL*, the maximum body depth exceeds the head length and fits 4.3 times in *SL*, the length of the spine of the dorsal fin, judging by the figure (Nichols, 1943), is noticeably less than the length of the head (~0.55) and <0.55 of the body depth. In this regard, we assign the sharpbellies of the Yangtze River to the species *H. clupeoides*, the validity of which is confirmed by the results of morphological analysis.

Sharpbellies of the Lower Amur basin. Among the nominal species described from water bodies of the territories north of the Yangtze basin and included by various authors (Ching-Jiang and Be-Lu, 1959; Bănărescu, 1968; Luo and Chen, 1998) into the list of multi-rakered sharpbellies as synonyms of *H. bleekeri*, there are *Toxabramis argentifer* Abbott, 1901, *Parapelecus elongatus* Mori, 1927, and *H. shibatae* Mori, 1933. *T. argentifer* is currently considered as an independent species of the g. *Toxabramis* (Fricke et al., 2021), which is unambiguously confirmed by its description (Abbott, 1901). It should be noted here that the species is described on the basis of a single specimen *SL* 130 mm, the holotype USNM 49545 (=CAS-SU 6299) (Abbott, 1901, Fricke et al., 2021), for which the presence of two-row pharyngeal teeth 5.3/3.4 and a serrated last unbranched ray in the dorsal fin "second spine rather stout, weakly serrated" are given (Abbott, 1901, p. 485). Two sharpbellies studied by Bănărescu (1968) from the collection of Stanford University (SU 6300) with three-row pharyngeal teeth are not listed in Abbott's description and cannot be considered paratypes of the indicated taxon: the error initially made by Bănărescu led to an incorrect conclusion.

The species *P. elongatus* was described from a single specimen *TL* 107 mm sampled in the Hun River, a tributary of the Liao River, which flows into the Liaodong Bay in South Manchuria. This specimen, whose current location is unknown, was characterized by the following main features: *D* II 7, *A* II 13, *ll* 48; the abdomen is pointed from the level of the pectoral fins to the anus, the beginning of the dorsal fin is much closer to the base of the caudal fin than to the end of the snout (at a distance equal to the distance from the end of the snout to the middle of the eye), the pectoral fins are long, pointed, reaching ¾ *P–V* (Mori, 1927). Based on these characteristics, it should be considered conspecific to *H. leucisculus* and, accordingly, *P. elongatus* should be included in the list of this species synonyms.

The species *H. shibatae* was described from one specimen sampled in Tsi-nan, (currently Jinan, center of the Shandong Province), the water bodies of which belong to the Yellow River basin of the Yellow Sea western coast. In the description (Mori, 1933) it is

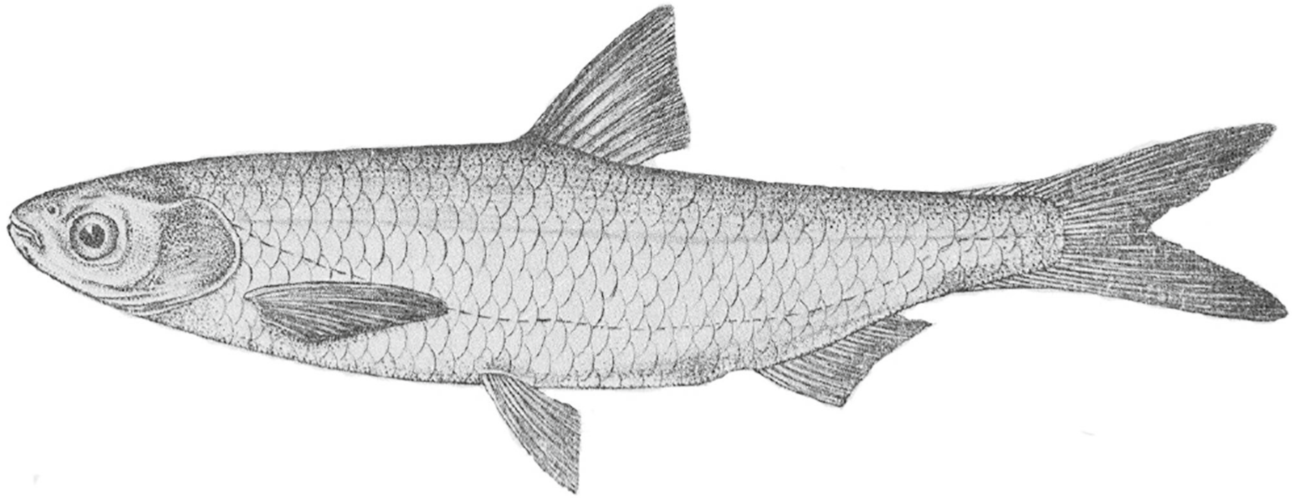

Fig. 4. Holotype of *Hemiculter shibatae* according to: Mori, 1933. P. 167. Fig. 2.

indicated that in this species *D* II 7, *A* II 13, *ll* 41, pharyngeal teeth are three-row 5.4.2/2.4.5; head length fits 4.5 times in *SL*; body depth, 4.3 times in *SL*; eyes small, fit1.3 times in snout length; on the belly, there is a keel stretching from the base of the pectoral fins to the anus; origin of dorsal fin equidistant from end of snout and base of caudal fin, slightly behind base of pelvic fins; 1st spine of dorsal fin ("nearly": Mori, 1933, p. 166) as long as 2nd; peritoneum is black. There is no information on the number of gill rakers in the description. It is noted that the new species is very close to *H. bleekeri* from the Yangtze and Shanxi, but differs by a noticeably taller body, smaller eyes, shorter pectoral fins, and a dorsal fin located more anteriorly.

The location of the type specimen of *H. shibatae*, which belongs to the g. *Hemiculter* is undoubtful, is unknown. Based on the description and its drawing (Fig. 4), it is not possible to determine the species status of the specimen. The low-rakered sharpbellies, which, according to genetic data (Chen et al., 2017; Vasil'eva et al., 2022), are represented in the type habitat of *H. shibatae* by the widespread species *H. leucisculus*, are similar in having small eyes (in multi-rakered sharpbellies, the horizontal diameter of the eye usually exceeds the length of the snout, in *H. leucisculus* it is noticeably shorter than the snout) and the position of the origin of the dorsal fin in relation to the ventral fins (in multi-rakered species, the origin of the dorsal fin is usually at the level of the base of the pelvic fins and *aV*/*aD* is usually >95%, while in *H. leucisculus* is usually <92%). At the same time, in low-rakered sharpbellies, as a rule, the beginning of the dorsal fin is closer to the base of the caudal fin than to the end of the snout, and *aD* exceeds 51.5% *SL*, while in multi-rakered sharpbellies, the beginning of the dorsal fin is usually closer to the end of the snout, but *aD* varies from 46.0 to 54.4% *SL* (Vasil'eva and Kozlova, 1988, 1989a, 1989b; Vasil'eva et al., 2022, present paper).

That is, according to the latter feature, the type of *H. shibatae* is similar to the multi-rakered species. However, among the multi-rakered sharpbellies, we found individuals with a black peritoneum only in *H. lucidus*, but in this species, according to our data, as a rule, there are at least 14 branched rays in the anal fin, the length of the head usually fits five or more times in *SL*; body depth no more than four times in *SL*. Among the dissected low-rakered sharpbellies, no individuals with black peritoneum were found: in the new species described by us from the Pearl River basin (Vasil'eva et al., 2022), the peritoneum is light, as in three individuals of *H. leucisculus* from the lower reaches of the Amur (samples ZMMU P-7795, P-6155); brown peritoneum is found in a single specimen of sample P-9188 from Vietnam. In relation with the above mentioned, we believe that until genetic and morphological studies of sharpbellies from the type habitat of *H. shibatae* are performed, the name *shibatae* should be considered *nomen dubium*. It is quite possible that an independent species lives in this area, but a hybrid origin of the type specimen may also be suggested.

In the present paper, multi-rakered sharpbellies of the Lower Amur basin are described as a species new to science. The description is given below, together with the diagnoses (compiled on the basis of our own data and the literature cited for synonymy), the main synonymy, and information on the distribution of other species of the multi-rakered sharpbellies group. The diagnoses do not include characteristics that are common to all species of the *lucidus* group: the origin of the dorsal fin is usually closer to the tip of the snout than to the base of the caudal fin, *aD* is usually < 50% *SL*; the swim bladder is two-chambered, the second chamber is elongated, with a narrow strip of connective tissue forming several turns of the spiral; the posterior end of the second chamber is pointed, with a short process; the eggs are pelagic.

(a)

(b)

Fig. 5. Khanka sharpbelly *Hemiculter lucidus SL* 150.0 mm from Lake Khanka, ZMMU P-8343: appearance (a) and abdominal part with opened (dissected) dark peritoneum (b).

Hemiculter lucidus (Dybowski, 1872)—Khanka sharpbelly

(Fig. 5)

Culter lucidus Dybowski, 1872. P. 214 (Chankasee—Lake Khanka).

Culter lucidus: Dybowski, 1877. P. 14.

Hemiculter lucidus: Warpachowski and Herzenstein, 1887. P. 46; Warpachowski, 1887. P. 704; Vasil'eva and Kozlova, 1988. P. 894 (partim); Vasil'eva and Kozlova, 1989a. P. 22 (partim); Bogutskaya and Naseka, 1996. P. 26 (partim); Naseka, 1998. P. 76 (partim); Bogutskaya and Naseka, 2004. P. 58 (partim); Vasil'eva, 2004. P. 151 (partim); Bogutskaya et al., 2008. P. 319.

Hemiculter leucisculus lucidus: Berg, 1909. P. 150; Nikolsky, 1947. P. 775, 776; Berg, 1949. P. 809; Nikolsky, 1956. P. 301.

Hemiculter bleekeri lucidus: Ching-Jiang and Be-Lu, 1959. P. 166; Yih and Wu, 1964. P. 88.

Hemiculter lucidus lucidus: Bănărescu, 1968. P. 526; Luo and Chen, 1998. P. 169.

D II–III 7, *A* III (13) 14–17, usually at least 14 branched rays, *V* II 7–8, ll 40–52, *sp.br.* 20–29; pharyngeal teeth three-row, 5.4.2/2.4.4, 5.4.1/1.3.4, 4.4.2/2.4.4; the keel on the belly is well defined, in the anterior part it reaches the throat; length of dorsal fin spine, as a rule, >0.85 *c*, usually nearly equal to or greater than head length; head relatively short, usually fits five or more times in *SL*; the body is deep, the depth of the body is always greater than the length of the head and usually noticeably greater than the length of the spine of the dorsal fin (the length of the latter is often 0.68–0.92 *H*); the peritoneum is dark; the dermal subclavian process is short, its length is equal to or slightly longer than the pupil diameter and ranges from 36.4 to 62.7% of the horizontal diameter of the eye (*o*). Distributed in the Lake Khanka basin, where it is sympatric with the low-rakered sharpbelly *H. leucisculus*.

Hemiculter varpachovskii Nikolski, 1903—Buir-Nuur sharpbelly

(Fig. 6)

Hemiculter varpachovskii Nikolski, 1903. P. 359 (Lac Buir-Nor—Lake Buir-Nuur).

(a)

(b)

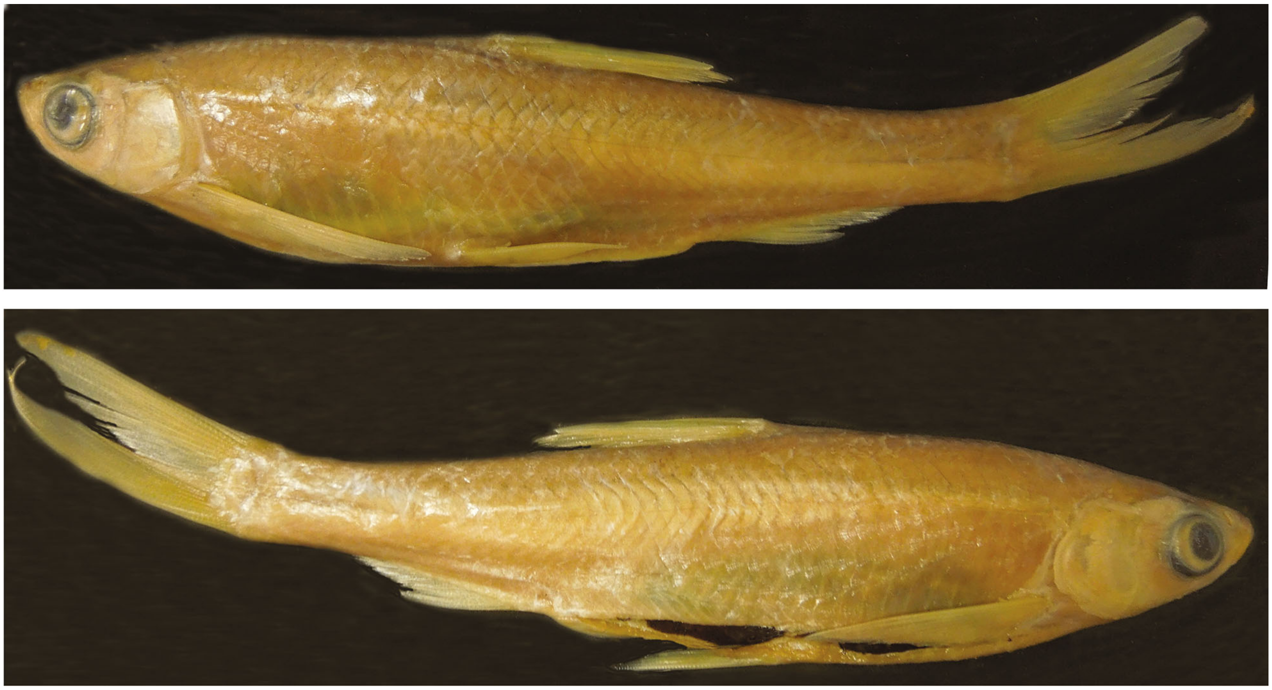

Fig. 6. Buirnuur sharpbelly *Hemiculter varpachovskii SL* 121.0 mm from lake Buir-Nuur (Mongolia), ZMMU P-8069: appearance (a) and abdominal part with opened (dissected) dark peritoneum (b).

Hemiculter leucisculus (non Basilewsky, 1855): Berg, 1909. P. 146 (partim); Nichols, 1943. P. 134 (partim); Nikolsky, 1947. P. 775 (partim); Berg, 1949. P. 808 (partim); Bogutskaya and Naseka, 1996. P. 25 (partim); Naseka, 1998. P. 75 (partim); Kottelat, 2006. P. 35 (partim); Ocock et al., 2006. P. 37.

Hemiculter varpachowskii (sic): Nikolsky, 1947. P. 774.

Hemiculter varpachovskii: Dashi-dorzhi, 1955. P. 571, 574; Kottelat, 2006. P. 36; Ocock et al., 2006. P. 13; Bogutskaya et al., 2008. P. 320.

Hemiculter leucisculus warpachowskii (sic): Nikolsky, 1956. P. 298; Baasanzhav et al., 1983. P. 194; Luo and Chen, 1998. P. 169.

Hemiculter bleekeri warpachowskii (sic): Ching-Jiang and Be-Lu, 1959. P. 166.

Hemiculter lucidus warpachowskii (*sic*): Bănărescu, 1968. P. 527.

Hemiculter lucidus (non Dybowski, 1872): Vasil'eva and Kozlova, 1988. P. 894 (partim); Vasil'eva and Kozlova, 1989a. P. 22 (partim); Bogutskaya and Naseka, 1996. P. 26 (partim); Naseka, 1998. P. 76 (partim); Vasil'eva, 2004. P. 151 (partim).

D II–III (6) 7 (8), *A* III (12) 13–16, more often 14 or 15 branched rays, *V* II 7–9, *ll* 40–55, *sp. br.* 20–28, pharyngeal teeth 4–5.3–4.1–2/2.4.4–5; the keel on the belly is well defined, reaching to the throat; length of dorsal fin spine always shorter than head length (usually greater than 0.75 but less than 0.9); head length fits less than five times in *SL*; body depth usually does not exceed the length of the head, but usually noticeably greater than the length of the spine of the dorsal fin, the length of which is from 0.67 to 1.06 *H*; the peritoneum is dark; the skin subclavian outgrowth is short, its length is noticeably less than the size of the pupil and is 44–51% *o*.

Inhabits the Argun' River basin, the upper reaches of the Amur: lakes Buir-Nuur, Dalaynor, rivers Khalkhin-gol, Urshun and Kerulen. The erroneous attribution of sharpbellies from this region by many authors to the low-rakered species *H. leucisculus* (this is how all ZMMU samples were initially identified, except for P-22031) served as the basis for the assertion that Lake Buir-Nuur is inhabited by two species of sharpbellies (Bogutskaya and Naseka, 1996; Naseka, 1998; Kottelat, 2006; Ocock et al., 2006). From this region, we studied a total of 17 samples, including 188 ind., and all of them belonged to the same species, while in samples from other basins, where species of the *H. lucidus* group are sympatric with species of low-rakered sharpbellies, there were always individuals of two species. This suggests that species from the low-rakered sharpbellies group do not occur in the basin of the upper reaches of the Amur, which corresponds to the earlier conclusion about their more southerly origin (Vasil'eva and Kozlova, 1988).

Hemiculter clupeoides Nichols, 1925— Chinese sharpbelly

(Fig. 3)

Hemicultur clupeoides (sic) Nichols, 1925. P. 7 (Tungting Lake, Hunan).

Hemiculter clupeoides: Nichols, 1943. P. 135; Bănărescu, 1968. P. 525, 526 (partim).

Hemiculter leucisculus (non Basilewski, 1855): Nichols, 1943. P. 134 (partim); Berg, 1949. P. 808 (partim); Kim and Park, 2002. P. 192 (partim); Kottelat, 2006. P. 35 (partim).

Hemiculter bleekeri bleekeri (non Warpachowski, 1888): Yih and Wu, 1964. P. 87; Jiang et al., 2008. P. 300.

Hemiculter bleekeri (non Warpachowski, 1888): Chin-Jiang and Be-Lu, 1959. P. 163 (partim); Bănărescu, 1968. P. 525 (partim); Luo and Chen, 1998. P. 167; Fu et al., 2003. P. 1669; He, 2010. P. 9; Li et al., 2020. P. 1.

Hemiculter jabouilei (*sic*) (non Chevey, 1936): Bănărescu, 1968. P. 525, 526 (partim).

Hemiculter lucidus (non Dybowski, 1872): Vasil'eva and Kozlova, 1988. P. 894 (partim); Vasil'eva and Kozlova, 1989a. P. 22 (partim); Bogutskaya and Naseka, 1996. P. 26 (partim); Naseka, 1998. P. 76 (partim).

D II–III 7, *A* III 12–14 (15), usually no more than 13 branched rays, *V* II 7–9, *ll* 40–51, *sp. br.* 20–30, pharyngeal teeth (4)5.(3)4.(1)2/(1)2.4.4(5); the keel on the belly extends from the anus to the throat, in the very anterior part it is sometimes poorly expressed; length of dorsal fin spine <0.7 *c* (usually <0.6); head length fits less than five times in *SL*; body depth commensurate with head length (0.87–1.20) and usually 1.5–2.0 times the length of the spine of the dorsal fin, usually not more than 0.55 *H*; the peritoneum is light; the skin subclavian outgrowth is small, its length is noticeably less than the pupil diameter and does not reach 40.0 (26.4–37.3)% *o*.

Dwells in the Yangtze basin. The only haplotype of the *cyt b* gene of an individual from Korea that we studied belongs to the same phyletic lineage with the Yangtze sharpbellies (see below), so the multi-rakered sharpbellies of Korea (sp.br. 26–32, ll 45–49), which Kim and Park (2002) identify as *H. leucisculus* should probably also be assigned to *H. clupeoides*. The conspecificity of populations from other river basins in China needs to be confirmed, in particular, this concerns the populations from the river systems of Shandong Province (the main river systems of the Huanghe and Weihe), whose similarity with the Yangtze fish fauna was noted earlier (Yang et al., 1994) and from where the species was described as *H. shibatae*. The presence of *H. clupeoides* in the waters of Vietnam, where it was recorded by Orsi (1974), is very doubtful. In tributaries of the upper Yangtze in the Sichuan region, *H. clupeoides* occurs sympatrically with an endemic species for which, according to our studies (Vasil'eva et al., 2022), the valid available name is *H. nigromarginis* and on a larger part of the river it lives together with *H. leucisculus* (Fu et al., 2003; He, 2010), another species of the low-rakered sharpbellies phyletic group, widely distributed in the waters of China and in the Amur basin.

Bănărescu (1968) included in synonyms of *H. bleekeri* (non Warpachowski, 1888) *H. jabouillei* Chevey, 1935, a species from the basin of the volcanic Lake Kouang-Tchéou-Wan, South China, Guangdong Province, based on its description (location of the holotype unknown). According to this description (Chevey, 1935), the species is characterized by *D* II 7, *A* II 14, *ll* 44; keel all over belly ("abdomen entirèment caréné"—Chevey, 1935. P. 431); head length is much greater than body depth and fits 3.56 times in *SL*; body depth fits 5.66 times in *SL*. Judging by the drawing (Chevey, 1935. Fig. 3), the origin of the dorsal fin is behind the base of the pelvic fins and much closer to the base of the caudal fin than to the end of the snout; dorsal fin spine length ~ 0.6 *c* and ~ 0.8 *H*. Kottelat (2013) includes *H. jabouillei* in the synonyms for *Pseudohemiculter hainanensis* (Boulenger, 1900), which is a mistake, since Chevey (Chevey, 1935) distinguished between proper *Hemiculter* and *Pseudohemiculter* and emphasized that the species described by him belongs to the first group of species, since its keel starts from the pectoral fins, and not from the ventral ones, as in the species of the *Pseudohemiculter* group. The species *H. jabouillei* differs from all multi-rakered sharpbellies in the position of the dorsal fin and does not match the diagnosis of *H. clupeoides* in terms of relative head length, body depth, and dorsal fin spine length. The characteristics of *H. jabouillei* also do not agree with the diagnosis of the low-rakered sharpbelly species described by us from the water bodies of Guangdong Province, in which *A* III 11–13, *ll* 49–56, the maximal body depth fits 4.0–4.7 times in *SL*; head length, 3.4–4.4, usually four, times in *SL* (Vasil'eva et al., 2022). It is therefore obvious that *jabouillei* must be considered a dubious name.

Hemiculter nikolskyi Vasil'eva, Vasil'ev et Shedko sp. nova—Nikolsky' sharpbelly

(Figs. 7–9)

Hemiculter leucisculus (non Basilewsky, 1855): Berg, 1909. P. 146 (partim); Nikolsky, 1947. P. 773 (partim); Berg, 1949. P. 808 (partim); Kim and Park, 2002. P. 192 (partim).

Hemiculter leucisculus leucisculus (non Basilewsky, 1855): Nikolsky, 1956. P. 290.

Hemiculter bleekeri (non Warpachowski, 1888): Chin-Jian and Be-Lu, 1959. P. 163 (partim); Bănărescu, 1968. P. 525 (partim).

Hemiculter lucidus (non Dybowski, 1872): Vasil'eva and Kozlova, 1988. P. 894 (partim); Vasil'eva and Kozlova, 1989a. P. 22 (partim); Bogutskaya and Naseka, 1996. P. 26 (partim); Naseka, 1998. P. 76 (partim); Bogutskaya and Naseka, 2004. P. 58 (partim); Vasil'eva, 2004. P. 151 (partim).

Hemiculter cf. *lucidus*: Bogutskaya et al., 2008. P. 320.

M a t e r i a l. Holotype P-21562—*TL* 128 mm, *SL* 102 mm, Amur near Bezymaynnyi (upstream

Fig. 7. Holotype of *Hemiculter nikolskyi* sp. nova *SL* 102 mm, ZMMU P-21562, Amur River near Bezymyannyi.

(a)

(b)

(c)

Fig. 8. Paratypes of *Hemiculter nikolskyi* sp. nova, ZMMU P-7502, Amur River near Elabuga: (a) swim bladder of specimen *SL* 142 mm, (b) the same in specimen *SL* 113 mm; (c) right pharyngeal bone, pharyngeal teeth 2.3.4.

Khabarovsk), August 7, 2004, collector E.D. Vasil'eva. Paratypes P-7502—two ind. *TL* 174 and 142 mm, *SL* 142 and 113 mm, Amur near Elabuga, July 24, 1949, collector T. K. Sysoeva. Additional materials are presented in the "Materials and Methods" section as *Hemiculter* sp.

D i a g n o s i s. *D* II (III) (6) 7 (8), *A* III (10, 11) 12–16 (17), usually 13–14 branched rays, *P* I (10) 11–14, *V* II 8–9, *ll* 40–52, *sp.br.* 20–30, pharyngeal teeth 4–5.3–4.1–2/1–2.3–4.4–5; belly with well-defined keel from throat to anus; the length of the dorsal fin spine is always less than the length of the head,

Fig. 9. *Hemiculter nikolskyi* sp. nova *SL* 98 mm from Amur River near Elabuga, ZMMU P-6405, opened (dissected) specimen with dark peritoneum.

usually not exceeding 0.75 *c*; head fits less than five times in *SL*; the body depth is usually greater than the length of the head (in different local populations, *H/c,* on average, 0.92–1.16) and is always noticeably greater than the length of the spine of the dorsal fin, the length of which ranges from 0.50 to 0.83 *H*; the skin subclavian outgrowth is small, its length is less than or equal to the diameter of the pupil and does not exceed 50.0 (29.0–50.0)% *o*; the peritoneum is dark.

Description of holotype. *D* II 7, *A* III 12, *P* I 14, *V* II 8, *ll* ~ 49 (scales are not completely preserved), *sp.br.* 29; the belly is pointed, the keel is pronounced from the anus to the end of the interbranchial space; the dorsal fin begins closer to the end of the snout than to the bases of the middle rays of the caudal fin; *aD* is 49.9% *SL*; head small, 22.8% *SL*; mouth superior; gill rakers short, dense; the eye is large, the horizontal diameter of the eye fits about four times in *c*; body is low, *H* 21.8% *SL*, body depth 0.95 *c*; lateral line descends not very steeply, reaching its lowest point before the end of the pectoral fins and again rises to the midline of the body behind the anal fin, making a sharp upward curve; the pectoral fins are elongated, 20.8% *SL*; the length of the pelvic fins is 14.7% *SL*; the last unbranched ray of the dorsal fin is spiny with a short soft part at the very apex, the length of the spine is 0.72 *c* and 0.76 *H*; the caudal fin is deeply notched. The skin subclavian outgrowth is small, poorly visible, its length is less than the pupil diameter and 29.0% *o*. Initially fixed in a 4% formaldehyde solution and transferred to 75% ethanol, the holotype has a brownish-yellow color of the belly, the back and upper part of the head are brown; from the upper edge of the gill cover along the entire body there is a longitudinal dark brown stripe separating the brown back from the lighter lower part, the dorsal and caudal fins are grayish, with noticeable dark specks along the rays; lower fins are light; eye blackish, with black border along lower margin (Fig. 7).

Brief characteristics of paratypes. *D* II 7, *A* III 13–14, *P* I 14, *V* II 8, *ll* 45–49, *sp.br.* 27, pharyngeal teeth 4.3.1–2/2.3.4 (Fig. 8c); dorsal fin begins closer to end of snout, keel reaches anteriorly to bases of pectoral fins, spine length 0.57–0.61 *H* and 0.66–0.82 *c*, *H* 1.16–1.33 *c*; the skin subclavian outgrowth is small, poorly visible, its length is less than the pupil diameter and is 31.9% *o* in the larger specimen and 46.4% in the smaller one. The peritoneum of a large specimen is dark brown, the swim bladder is two-chambered, of a typical shape: the second chamber is elongated, with a narrow strip of connective tissue forming several turns of a spiral; the posterior end of the second chamber is pointed, with a short process (Fig. 8a). In a smaller individual, the peritoneum is light brown, the swim bladder is atypical, with a curved second chamber (Fig. 8b). The pigmentation of the paratypes is not preserved, the whole body and fins are light brown.

Variability of morphological features. Previously, a detailed analysis of the interpopulation variability of morphometric characteristics in multirakered sharpbellies of the Lower Amur basin was carried out based on pairwise comparison of samples from Lake Bolon', the Amur channel in the Novogeorgievka Settlement area, Komsomolsk-on-Amur, Elabuga, and from Lake Kabar (Vasil'eva and Kozlova, 1989a). Significant differences were found in all plastic characteristics, except for the relative length of the dorsal spine, some of them are due to the size variability of characters and the heterogeneous quality of samples in terms of the body lengths of the individuals. Of the meristic characters, significant interpopulation differences were revealed only in the number of scales in the lateral line and branched rays in the pectoral fin, the number of the latter varies from 10 to 14; mean sample values range from 11.4 to 12.4.

However, these differences are rather small (*CD* varies from 0.20 to 1.12). No directional changes in morphometric characteristics were found in populations living in different hydrological conditions (lake and river), as well as the trend noted by Nikolsky (1947, 1956) of a decrease in the number of scales, rays in the anal fin and the relative length of the base of the anal fin and the length of the caudal peduncle in downstream direction. This made it possible to give a summary description of the plastic features of Lower Amur sharpbellies (Vasil'eva and Kozlova, 1989a). Based on these data, it was noted that Lower Amur sharpbellies significantly differ from the samples of three other species in a number of body proportions presented in the table according to the data from the cited publication. However, in most cases, the found differences are not high. The characters that turned out to be suitable for species diagnostics are discussed above (at the beginning of the "Results and Discussion" section).

Intravital coloring: the back is greenish-gray, the sides and belly are silvery; dorsal fin greenish gray; paired, anal and caudal fins yellowish gray (Nikolsky, 1956; our data).

Etymology. The species is named after the famous ichthyologist G.V. Nikolsky, the organizer and active participant of the Amur expeditions, the collections of which served as the basis for the present study.

Distribution. According to the present studies and data from Nikolsky (1956), the species is distributed in the Sungari River and the basin of the lower and middle reaches of the Amur from the Sverbeevo Settlement to Dayerga Village, and is most common from Dzhalinda Village to Lake Kizi (Bol'shoye Kizi). Throughout its range, *H. nikolskyi* is distributed sympatrically with the low-rakered sharpbely *H. leucisculus*, but it is much more numerous, as evidenced by both the species composition of the g. *Hemiculter* from the Lower Amur in the ZMMU collection and Nikolsky's data (1947) on the ratio of these species in catches: in small lake at Dayerga per a total catch of 160 specimens *H. nikolskyi* only one specimen of *H. leucisculus* was found; and in the catch in Lake Petropavlovsk, their ratio was 186 : 7. It is likely that the relative abundance of the species is determined by the characteristics of their reproduction: *H. nikolskyi* spawns pelagic eggs, and its spawning is not limited by the presence of a spawning substrate. As opposite, *H. leucisculus* glues the eggs to the substrate. It is also possible that the latter species stays in water bodies mainly along the current and avoids lake biotopes, where sharpbellies were often caught.

Phylogenetic Relationships of Multi-Rakered Sharpbellies of H. lucidus Group

Based on the results of sequencing of full-length sequences of the *cyt b* gene in 55 multi-rakered sharpbellies (GenBank: MW367253–MW367260, MW508412–MW508458), 34 different haplotype variants were identified. The *cyt b* sequence obtained from sharpbelly from South Korea (KF760461) was another unique variant. The phylogenetic tree constructed by the maximum likelihood method for these 35 unique haplotypes is shown in Fig. 10. The revealed haplotypes formed two clades, LA and LB, including 13 and 22 haplotypes, respectively. Mean TN distances (Tamura and Nei, 1993) are expressed as the number of nucleotide substitutions per position; the distances calculated using the SENDBS program (Nei and Jin, 1989) turned out to be 0.0027 ± 0.00071 and 0.0052 ± 0.00086, respectively, within clades. Mean interclade distance was 0.0179 ± 0.0037 (without correction) and 0.0139 ± 0.0036 (net, i.e., excluding variability within clades; distance calculated according to Nei's Equation 10.21 (Nei, 1987)). The mean TN distances between haplotypes from the LA and LB clades of multi-rakered sharpbellies turned out to be much smaller than the distances (total and net calculated by us) between the A, B, and C low-rakered sharpbellies clades from Chen et al. (2017): 2.5–2.7 times when compared with the distances between clades B and C, 3.4–3.8 times between clades A and B, 3.8–4.3 times between clades A and C.

Based on the calibration of the molecular clock performed for the *cyt b* gene in cyprinids (0.011 substitutions/site/million yr—Smith et al., 2002) and applying it to our net genetic distance estimate (0.0139 ± 0.0036), the evolutionary age of the clades LA and LB may be taken equal to 1.26 ± 0.33 million years.

Most specimens of the new species of multi-rakered sharpbellies *H. nikolskyi* contained haplotypes of the clade LA (21 out of 27, or 78.8%). On the contrary in Khanka sharpbelly *H. lucidus* samples, haplotypes of the LB clade prevailed (15 out of 20, or 75.0%). The differences between *H. nikolskyi* and *H. lucidus* in the ratio of haplotypes from the LA and LB clades are significant according to Fisher's exact test ($p = 0.0004$). In sharpbellies from the Yangtze River (*H. clupeoides*) and a specimen from the Korean Peninsula, only haplotypes from clade LB were found. Considering this picture, as well as the fact that the haplotypes occupying the basal position in the LB clade (Hp2, 4–8) belong to the specimens from the Yangtze River, we may propose the following phylogenetic hypothesis. The common ancestor of multi-rakered sharpbellies was divided into two groups: the Amur basin group and the group dwelling in water bodies located to the south of this basin. After some time, the southern lineage of multi-rakered sharpbellies again entered the Amur basin, bringing with it haplotypes from the LB clade. Over time, it disappeared here, remaining only in the form of the Khanka sharpbelly lineage. Reproductive isolation between the southern and aboriginal for the Amur basin lineages of multi-rakered sharpbellies was incomplete, which led to a partial mixing of their mitochondrial gene pools.

The net genetic distance between the group sample of multi-rakered sharpbellies from Khanka Lake and

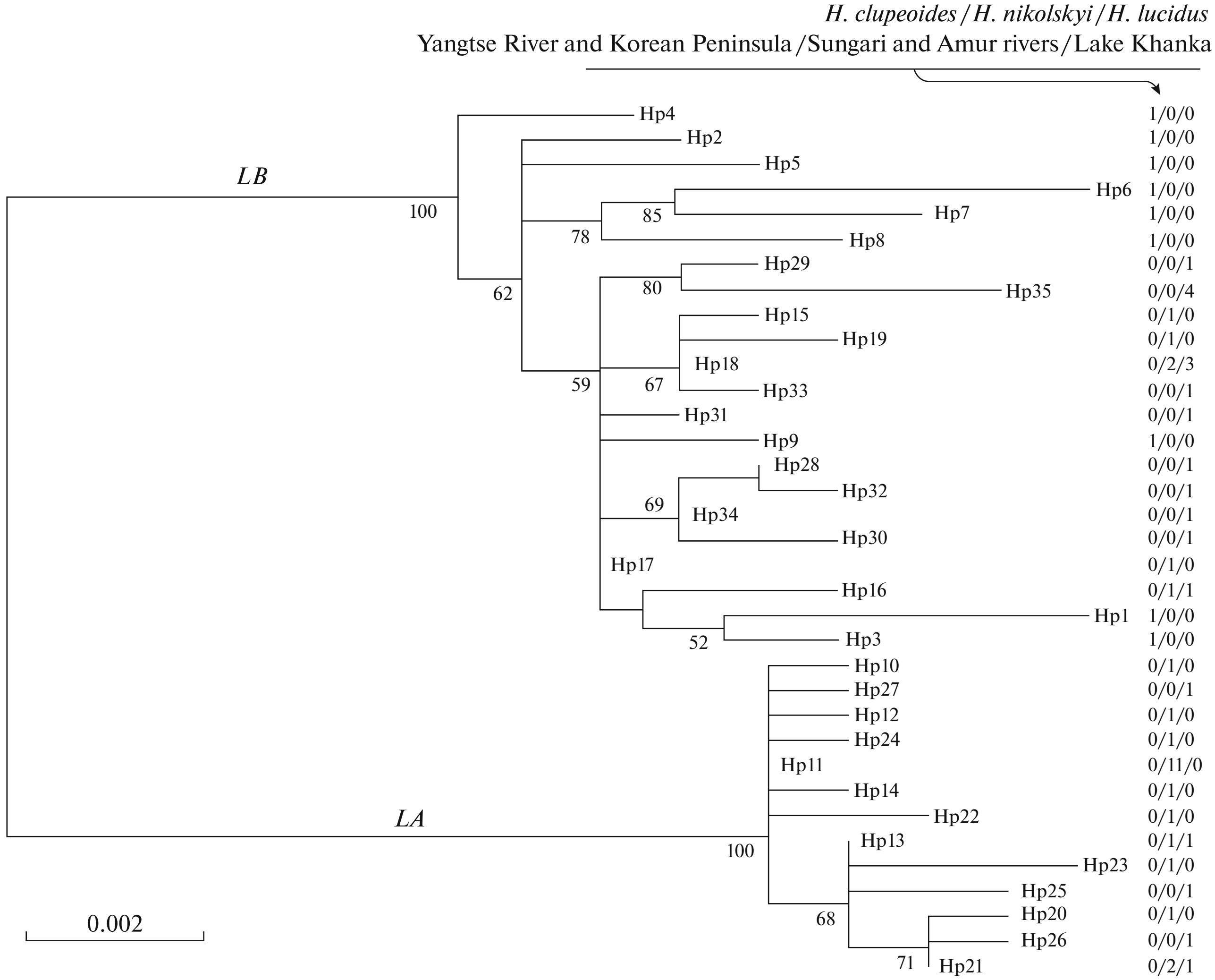

Fig. 10. The optimal ML tree (ln $L = -2118.5252$, model of nucleotide substitutions TN + F + G4), built for 35 haplotypes of the *cyt b* gene (Hp1–Hp35) revealed in multi-rakered sharpbellies *Hemiculter* spp. from three regions: the Yangtze River and the Korean Peninsula, the Sungari and Amur rivers, Lake Khanka. On the right, the numbers separated by a slash are the occurrence of haplotypes in samples of sharpbellies from the three indicated regions. The numbers at the base of the clades are estimates of bootstrap support (in % of 2000 cycles). The branch length scale is indicated at the bottom left in the number of replacements per site.

the sample from the Yangtze River and the Korean Peninsula is 0.0006 ± 0.0004 substitutions per position (the calculation was performed only for haplotypes from the LB clade). Then the time elapsed since the second invasion of the southern lineage into the Amur basin may be determined as 54 ± 33 thousand years. For the purpose of comparison, using data from a previous paper (Vasil'eva et al., 2022), the net genetic distance between a sample of *H. leucisculus* from the Amur basin ($n = 21$) and a pooled sample of sharpbellies of this species from Beijing and the Korean Peninsula was calculated ($n = 14$). Its value is 0.0007 ± 0.0007 substitutions per position that is close to the estimate obtained for the analogous case described above with multi-rakered sharpbellies. That is, the invasion of *H. leucisculus* and the ancestor *H. lucidus* into the Amur basin presumably occurred at the same time.

The genetic distances for the *cyt b* gene between multi-rakered sharpbellies are rather small (compared to low-rakered sharpbellies). However, the differences between *H. nikolskyi* and *H. lucidus* (and also from *H. clupeoides*) in terms of haplotype composition confirm its reproductive isolation and, therefore, an independent species status.

It is worth noting that despite significant morphological divergence, Khanka sharpbelly, as shown by our data, is a young species. Unfortunately, until now, *H. varpachovskii* has not been studied by genetic methods. The water bodies inhabited by Buir-Nuur sharpbelly are located in the East Mongolian steppe landscape-climatic region, characterized by an abundance of small drainless, saline and periodically drying lakes; Lake Buir-Nuur is the largest of the few freshwater lakes. The Late Pleistocene and Holocene in this area were characterized by significant fluctuations in moisture and discharge; lake levels close to modern date from the Middle Holocene (approximately 5000–4500 years ago) (Dorofeyuk, 2008). The small age of the lakes suggests that *H. varpachovskii* is also a young phyletic lineage, which was formed according to the same scenario as the Khanka sharpbelly lineage: the presence of a special niche (large lakes) triggered the process of differentiation. It should be emphasized that, for a more complete understanding of the evolutionary history of multi-rakered sharpbellies, it is essential to analyze populations both from the Upper Amur basin and from the southern part of the range of this species group.

In conclusion, we consider it necessary to give an identification key to the diagnosis of multi-rakered sharpbelly species.

KEY FOR IDENTIFICATION MULTI-RAKERED SHARPBELLIES SPECIES OF *HEMICULTER LUCIDUS* GROUP

1 (2) Head length usually fits five or more (4.2–5.4) times in body length; the length of the dorsal fin spine as a rule is equal to the length of the head; anal fin usually with at least 14 branched rays; Lake Khanka basin .... ***Hemiculter lucidus***

2 (1) Head length fits less than five times in body length; spine of dorsal fin shorter than head; anal fin contains 12–16 branched rays **3**

3 (4) The anal fin usually has no more than 13 branched rays; the length of the dorsal fin spine usually does not exceed 55% of the body depth; peritoneum is light............................ ***Hemiculter clupeoides***

4 (3) The anal fin usually has at least 13 branched rays; the length of the dorsal fin spine usually more than 60% of body depth; peritoneum is dark **5**

5 (6) The length of the dorsal fin spine is usually more than 80% of the body depth, averaging 19.2–20.4% *SL*; body depth is usually less than the head length (in different local populations, *H*/*c* averages 0.96–1.00); Upper Amur basin (lakes Buir-Nuur and Dalaynor)...........................***Hemiculter varpachovskii***

6 (5) The length of the dorsal fin spine usually less than 70% of body depth, 15.2–17.6% *SL* on average; the body depth is usually greater than the head length (in different local populations, *H*/*c* averages 0.92–1.16); Lower Amur basin ....***Hemiculter nikolskyi***

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