

A review of species of the genus *Theodoxus* (Gastropoda: Neritidae) of the Ponto-Caspian region, with considerations on available type materials

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ABSTRACT. An illustrated overview of the type series of nominal taxa of the gastropod genus *Theodoxus* (Neritidae) inhabiting the Ponto-Caspian region is presented. It is based on a revision of large European malacological collections and includes descriptions of the type specimens of 16 taxa of different rank (species, variety, morph). Apart of these, the “type” specimens of four taxa with unavailable names have been traced in ZIN collection; we illustrate them to show the variability of Ponto-Caspian *Theodoxus*. In most cases, the photographs of the type specimens are published for the first time. We provide a taxonomic analysis of all studied type series, with comments on the nomenclature, systematic position and taxonomic rank of all nominal taxa of *Theodoxus* recorded from the Ponto-Caspian area.

Обзор видов рода *Theodoxus* (Gastropoda: Neritidae) Понто-Каспийского региона с рассмотрением доступного типового материала

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РЕЗЮМЕ. На основе ревизии крупных европейских коллекций представлен иллюстрированный обзор типовых серий 16 номинальных таксонов рода *Theodoxus* (Neritidae) ранга вида и ниже, обитающих в Понто-Каспийском регионе. Иллюстрации большинства типовых экземпляров публикуются впервые. Использованы коллекции Зоологического института РАН (Санкт-Петербург), Института зоологии НАН Украины (Киев), Зоологического музея Львовского национального университета и некоторые другие. В том числе в коллекции ЗИН обнаружены «типовые» экземпляры четырех таксонов, имеющих непригодные названия; мы также приводим их изображения, чтобы дополнить картину изменчивости понто-каспийских *Theodoxus*. Изученные материалы проанализированы с таксономической точки зрения, также приводятся комментарии по номенклатуре, систематическому положению и рангу всех таксонов, отмеченных в регионе.

Introduction

The neritid genus *Theodoxus* Montfort, 1810 is widely distributed in fresh- and brackishwater

streams and reservoirs of the Western Palearctic, including such large basins as the Caspian Sea and (formerly) the Aral Sea [Starobogatov, 1970; Bandel, 2001; Welter-Schultes, 2012; Eichhorst, 2016; Wesselingh *et al.*, 2019]. Despite a long history of investigations, the actual species richness of this genus is still unclear, and many nominal species of *Theodoxus* need a revision based on a thorough molecular and morphological analysis. It may be estimated roughly that the overall species richness of this genus is around 20 valid species [e.g. Sands *et al.*, 2019a].

According to different authors, the malacofauna of the Ponto-Caspian region contains three [Golikov, Starobogatov, 1966, 1972], five [Zhadin, 1952; Wesselingh *et al.*, 2019] or even seven [Welter-Schultes, 2012; Vinarski, Kantor, 2016] species and subspecies of *Theodoxus*. However, the systematics and nomenclature of these taxa are highly tangled, and sometimes different authors have applied the same name for designation of two apparently distinct species, and *vice versa* [see review in Anistratenko *et al.*, 1999]. The validity of some nominal species described from the Ponto-Caspian region [such as *Theodoxus subthermalis* Issel, 1865 and *Th. euxinus* (Clessin, 1886)] is also still ambiguous [e.g. Bandel, 2001]. Although the genetic data published to present day [Bunje, 2006; Bunje, Lindberg, 2007; Mezherin *et al.*, 2011; Sands *et al.*, 2019a, b, 2020] are quite comprehensive, the current knowledge of systematics, phylogeny, and distribution of the Ponto-Caspian *Theodoxus* is not deficient yet. Some important works on taxonomy of this group have appeared recently [Anistratenko *et al.*, 1999, 2017; V. Anistratenko, O. Anistratenko, 2001; Bandel, 2001; Zettler, 2007, 2008; Neubauer *et al.*, 2018], many questions remain open though. One of the main causes for this is that the type series of the nominal *Theodoxus* species have rarely been examined and discussed. Although the type specimens of some species have been illustrated in the literature [V. Anistratenko, O. Anistratenko, 2001; Kantor, Sysoev, 2006; Sitnikova *et al.*, 2012], the rest of the type materials remains not characterized or even not discovered.

The aim of this paper is to present an illustrated overview of all available type series of nominal taxa (species, subspecies) of *Theodoxus* of the Ponto-Caspian region. We provide the images of the type specimens of 16 taxa as well as taxonomic and nomenclatural considerations about their identity and status.

Material and Methods

We managed to examine the extant type series of almost all nominal species of the Ponto-Caspian

Theodoxus included in the most comprehensive check-lists and catalogues [Kantor, Sysoev, 2006; Vinarski, Kantor, 2016; Wesselingh *et al.*, 2019]. The only exception was *Theodoxus major* Issel, 1865, whose type series is extant but currently inaccessible [Wesselingh *et al.*, 2019], though we were able to study probable topotypes of this species. The types of *Th. fluviatilis* var. *abrauensis* (Milaschewitsch, 1914), suspected to be stored in Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg (ZIN, hereafter), could be traced neither in the catalogue nor in the collection. The types of *Neritina euxina* Clessin, 1886 described from Romania are presumably lost since Clessin's collection was destroyed during WWII [Dance, 1986].

The type series of *Theodoxus* described in the present paper are deposited in collections of ZIN, I.I. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev, B. Dybowski Zoological Museum of Lviv University, Ukraine and in the Linnaean Collection, London, UK. In addition, few samples recently collected in various parts of the Ponto-Caspian region have been examined by us (Table 1). Images of the specimens were taken with a Leica M165C stereomicroscope equipped with a digital camera. The higher taxa systematic classification follows Bouchet *et al.* [2017]. The species are presented herein in the following order: the accepted names for taxa of the Caspian Sea are listed first and then follow the freshwater species, all ordered alphabetically. A following subchapter lists available but not valid taxa names.

Abbreviations used:

IZAN – I.I. Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev.

LSL – Linnaean Collection of the Linnean Society, London, UK.

MHNG – Muséum d'Histoire Naturelle, Geneva, Switzerland.

NMNH – National Museum of Natural History of the National Academy of Sciences of Ukraine, Kiev.

ZIN – Zoological Institute of the Russian Academy of Sciences, St. Petersburg.

ZB-M W.Dyb. – Zoological Museum Depository of Invertebrates, W. Dybowski collection in the ZMD.

ZMD – B. Dybowski Zoological Museum of Lviv University, Ukraine.

Systematic part

Class Gastropoda Cuvier, 1795

Subclass Neritimorpha Golikov et
Starobogatov, 1975

Order Cycloneritida Frýda, 1998

Superfamily Neritoidea Rafinesque, 1815

Table 1. Collection data of illustrated specimens of *Theodoxus* from the Ponto-Caspian region. The numbers of locations refer to the text and figures. Coordinates of collecting sites sampled prior to 2003 are given approximately, based on data in museum catalogue cards, labels and corresponding publications.

#	Taxon name	Location	Date	Latitude (N)	Longitude (E)	Leg.	Collection and lot#
1	<i>Th. pallasi</i>	Caspian Sea coast, ?Derbent, Dagestan, Russia	? 1825	44°01'12"	50°52'01"	E. Eichwald	ZIN, 54547/63
2	<i>Th. schultzi</i>	Caspian Sea, eastern part, station 124, Kazakhstan	02.07.1876	43°17'00"	51°03'00"	O.A. Grimm	ZIN, 6214/5; ZMD, ZB-M W.Dyb.71
3	<i>Th. fluviatilis</i>	Dnieper River, Kherson Region, Ukraine	08.10.2013	46°39'01.43"	32°39'52.84"	T.L. Alexenko	IZAN, HBS 390-391
4	<i>Th. velox</i>	Dnieper River delta, Zburjevskiy liman, Kherson Region, Ukraine	06.10.1982	46°28'21"	32°24'03"	unknown	IZAN, unnumbered
5	<i>Th. sarmaticus</i>	Oskol River near Golubino, Belgorod Region, Russia	1897–1898	50°49'33"	37°47'35"	W.A. Lindholm	ZIN, 6099/24
6	<i>Th. ater</i>	Oskol River near Novyi Oskol, Belgorod Region, Russia	1897–1898	50°44'31.73"	37°51'16.50"	W.A. Lindholm	ZIN, 6102/1
7	<i>Th. tanaiticus</i>	Voronezh River near Voronezh City, Russia	no date	51°43'12.53"	39°15'24.94"	K.O. Milaschewitsch	ZIN, 6104/1
8	<i>Th. caucasicus</i>	Sochi, Krasnodar Krai, Russia	no date	43°35'07"	39°43'13"	K.O. Milaschewitsch	ZIN, 6054/1
9	<i>Th. cereoflavus</i>	Psyrtskha River near Novyi Afon monastery, Abkhazia	26.05.1910	43°05'07.40"	40°47'42.52"	W.A. Lindholm	ZIN, 6055/1
10	<i>Th. "subthermalis"</i>	Psyrtskha River, Gudauta district, Abkhazia	02.02.2012	43°05'30"	40°48'52"	D.M. Palatov	IZAN, Pal-370K
11	<i>Th. "subthermalis"</i>	Besletka River near Veneto bridge, not far from Sukhum, Abkhazia	05.08.2010	43°01'49"	41°04'35"	R.S.Vargovitsh	IZAN, 391
12	<i>Th. "fluviatilis"</i>	Duab River, vicinity of Mokva village, Abkhazia	30.08.2003	42°50'07.43"	41°30'23.99"	V.V. & O.Yu. Anistratenko	IZAN, 231
13	<i>Th. subthermalis</i>	Paleostomi Lake, near Poti, Georgia	?1865	42°07'09.51"	41°43'41.37"	unknown	MHNG, Bourguignat coll., No. 11737
14	<i>Th. "subthermalis"</i>	Gabistskali River, vicinity of Ianeti vil., Imereti, Georgia	16.04.2016	42°10'26"	42°25'43"	A.V. Martynov	IZAN, 516
15	<i>Th. major</i>	Arax River, Azerbaijan	09–10.1979	39°49'35.21"	48°02'20.95"	A.R. Aliev	ZIN, 47267/1
16	<i>Th. brauneri</i>	?Black Sea near Odessa, Ukraine	28.12.1902	46°31'40.44"	30°43'18.74"	A. Brauner	ZIN, 6046/1
17	<i>Th. alboguttatus</i>	?Black Sea near Odessa, Ukraine	no date	46°31'40.44"	30°43'18.74"	A. Brauner	ZIN, 6051/1
18	<i>Th. lacrymans</i>	?Black Sea near Odessa, Ukraine	no date	46°31'40.44"	30°43'18.74"	A. Brauner	ZIN, 6052/1
19	<i>Th. pulcherrimus</i>	?Black Sea near Odessa, Ukraine	no date	46°31'40.44"	30°43'18.74"	A. Brauner	ZIN, 6053/1
20	<i>Th. danasteri</i>	Dniester liman near Belgorod-Dnestrovskiy, Odessa region, Ukraine	no date	46°11'53.42"	30°20'10.36"	A. Brauner	ZIN, 5910/3
21	<i>Th. obliteratus</i>	Dniester River near Rybnitsa, Moldova	no date	47°47'26.59"	28°59'25.44"	A. Brauner	ZIN, 5912/1
22	<i>Th. lamelliferus</i>	Black Sea near Alushta, Crimea	15.08–15.09.1909	44°40'01.35"	34°25'30.01"	S.A. Zernov	ZIN, 6119/1
23	<i>Th. milachevitchi</i>	Black Sea near Chauda Cape, Crimea	15.08–15.09.1909	44°47'15"	35°50'20"	S.A. Zernov	ZIN, 6134/1

Family Neritidae Rafinesque, 1815
 Subfamily Neritinae Poey, 1852
 Genus *Theodoxus* Montfort, 1810

Type species: *Theodoxus lutetianus* Montfort, 1810 (= *Nerita fluviatilis* Linnaeus, 1758)

Accepted names

Theodoxus pallasii Lindholm, 1924
 (Fig. 1A)

Nerita pupa. – Pallas, 1771: 435 (non Linné, 1767).

Nerita fluviatilis. – Ménétries, 1832: 270, no. 1299 (non Linnaeus, 1758).

Neritina serratilinea. – Hohenacker, 1837: 147 (non Rossmässler, 1835).

Neritina liturata Eichwald, 1838: 156–157 (non Schultzze, 1826).

Neritina danubialis. – Siemaschko, 1847: 102 (non C. Pfeiffer, 1828).

Theodoxus pallasii Lindholm, 1924: 33 (nom. nov. pro *Neritina liturata* Eichwald, 1838, non Schultzze, 1826).

Theodoxus astrachanicus Starobogatov in Starobogatov *et al.*, 1994: 8–9, figs 1, 2.

Theodoxus astrachanicus. – V. Anistratenko, O. Anistratenko, 2001: 112, fig. 74.

Theodoxus (Theodoxus) pallasii. – Eichhorst, 2016: 942, pl. 294.

Type material. The lectotype of *Neritina liturata* Eichwald, 1838 and *Theodoxus pallasii* Lindholm, 1924 [designated by Starobogatov *et al.*, 1994]: ZIN, catalogue #54547/63; label by Eichwald: Dagestan; Eichwald [1838]: amongst *Fucus* in the littoral of Derbent (Dagestan, Caspian Sea).

Type locality. Shore of Derbent, Dagestan, Russia.

Other material. Hundreds of specimens stored in the IZAN collection, catalogue ##228, 244, 364, 418 and 428. Several specimens of *Th. pallasii* are stored in the NMNH, catalogue ##3498, 530, 1068 and 5571.

Remarks. The name *Theodoxus pallasii* has been in common use for designation of a Caspian neritid snail, originally recorded by Pallas [1771] as *Nerita pupa*. Since true *Nerita pupa* Linné, 1767 (now *Puperita pupa*) is a Western Atlantic species, Eichwald [1838] introduced for the Caspian one the name *Neritina liturata*. However this name was pre-occupied by *Neritina liturata* Schultzze, 1826, so eventually Lindholm [1924] erected *Th. pallasii* as a replacement name for *N. liturata* Eichwald, 1838 non Schultzze. Starobogatov *et al.* [1994: 8] designated one of Eichwald's specimens as the lectotype of *Th. pallasii*, which is therefore also the lectotype for *Neritina liturata* Eichwald, 1838.

Theodoxus pallasii is characterized by enormous intraspecific variation both in shell shape and shell colour pattern. Some morphs of *Th. pallasii* resemble externally another species of *Theodoxus*, namely

Th. danubialis (C. Pfeiffer, 1828), which lives in the Danube basin as well as in the southern Alpine region [e.g. Zettler, 2008]. However, *Th. danubialis* has a more convex whorl profile [see Glöer, 2002; Zettler, 2008], and the operculum in *Th. danubialis* differs from that of *Th. pallasii* by the presence of an additional knob at the base of the apophysis. The radula of *Th. danubialis* also differs considerably by having the central tooth wider than in *Th. pallasii* and the marginal teeth smoother [Zettler, 2008: fig. 25g, h]. *Theodoxus pallasii* is the most common neritid species living under fresh- and brackishwater conditions in the entire Black Sea and the Caspian Sea basins [e.g. Zhadin, 1952; Akramovski, 1976]. *Theodoxus astrachanicus*, a species described from the Volga delta [Starobogatov *et al.*, 1994], was once considered a distinct taxon, occurring, besides its type locality, in some sites in the Sea of Azov [e.g. Anistratenko *et al.*, 1999; 2011]. Recently, it was demonstrated that the ranges of morphological variation of *Th. pallasii* and *Th. astrachanicus* are similar, and thus the two taxa have to be regarded conspecific [Anistratenko *et al.*, 2017].

Ecologically, *Th. pallasii* is restricted to shallow waters, including desalinated areas of the Volga Delta. We registered this species in different points in the lower courses of the Volga and Don Rivers as well as from its tributaries and the Volga-Don canal (M. Vinarski, pers. observations, 2015–2017). In the Caspian Sea, *Th. pallasii* forms dense aggregations in the shallow zone on hard substrates (up to 250 individuals per m² in the vicinity of Aktau; V. Anistratenko and O. Anistratenko, pers. observations).

Theodoxus schultzei (Grimm, 1877)
 (Fig. 1 B, C)

Neritina schultzei Grimm, 1877: 77–78, pl. 7, fig. 5 (radula), pl. 8, fig. 16 (shell).

Neritina (Ninnia) schultzei [sic]. – Andrusov, 1909: 106–107, pl. 6, fig. 38.

?*Theodoxus (Ninnia) schultzei* [sic] var. *jukovi* Kolesnikov, 1947: 106, 110.

Theodoxus (Ninnia) schultzei [sic]. – Kolesnikov, 1950: 215–216, pl. 26, figs 12–13.

Theodoxus schultzei [sic]. – Logvinenko, Starobogatov, 1969: 344, fig. 357.

Neritina (Ninnia) schultzei [sic]. – Ali-Zade, 1973: 161–162, pl. 47, figs 4–6.

Theodoxus (Theodoxus) schultzei. – Eichhorst, 2016: 952, pl. 299.

Type material. Lectotype (here designated) and 19 paralectotypes (including 17 alcohol-preserved specimens) are in ZIN, #6214/5 in systematic catalogue. One paralectotype in ZMD (ZB-M W.Dyb. 71; von Baer collection; see Anistratenko *et al.* [2018, 2019]).

Type locality. East part of the central Caspian Sea, ca. 50 km south of Aktau (see Table 1).

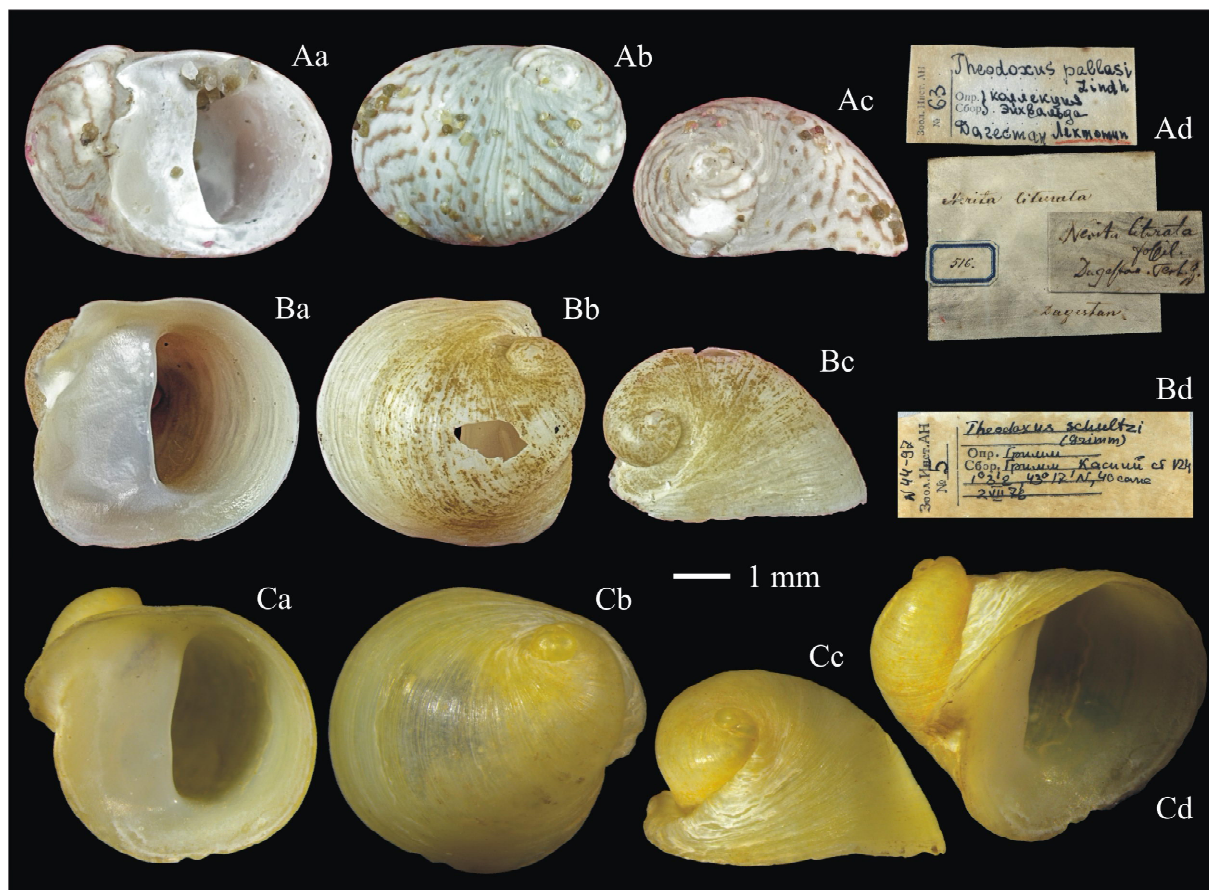


FIG. 1. A. *Theodoxus pallasi*, ZIN #54547/63, lectotype, locality 1. B, C. *Th. schultzi*: B. ZIN #6214/5, lectotype, locality 2; C. ZB-M W.Dyb. 71, paralectotype, locality 2. Ad, Bd – the original labels.

РИС. 1. A. *Theodoxus pallasi*, ZIN 54547/63, лектотип, локалитет 1. B, C. *Th. schultzi*: B. ZIN 6214/5, лектотип, локалитет 2; C. ZB-M W.Dyb. 71, паралектотип, локалитет 2. Ad, Bd – оригинальные этикетки.

Other material. Two specimens (empty shells) of *Th. schultzi* are deposited in the NMNH, catalogue # 538, Caspian Sea, square 6575, depth 42 m, 24.06.1956, coll. and det. B.M. Logvinenko.

Remarks. Originally Grimm [1877] described this species based on clear differences from *Th. pallasi* in shell shape, colour pattern and radula morphology. He also stressed the deeper occurrence of *Th. schultzi* as compared to *Th. pallasi*, which is shallow-water inhabitant. Interestingly, the epithet '*schultzi*' was given by Grimm in honour of G.F. Schultz, the captain of schooner "Persiyanin", on the board of which Grimm collected material in the Caspian Sea in 1876 [Grimm, 1877: 77, footnote 1]. However, some authors [e.g. Andrusov, 1909; Ali-Zade, 1973] used a different spelling '*schultzei*' likely referring to F.T.S. Schultze who erected the name *Neritina liturata* for the first time [Schultze, 1826].

The very fact that *Th. schultzi* is represented in the studied collections by a very small amount of specimens convinces us that it was, and remains, one of the rarest gastropod species of the Caspian

Sea. On the other hand, observations of Grimm [1877] and Karpinsky [2002] show that it might be more common in a deeper zone (45–90 m) in the middle and southern sectors of the sea. At least all known living specimens of *Th. schultzi* were found at depths below 45 m [see Zettler, 2007], while *Th. pallasi* occurs in shallow water. Since K. von Baer sampled molluscs mainly from the shoal this would be a cause of scarcity of *Th. schultzi* in his collection (kept in ZMD). W. Dybowski noted [1887: 60, footnote] that *Neritina schultzi* is represented in Baer's collection by a single specimen, donated by Dr. O.A. Grimm. Indeed the specimen, kept in the lot # ZB-M W.Dyb. 71, is of perfect preservation, demonstrates the most characteristic conchological feature of *T. schultzi*, namely the conspicuous elongation of the upper and lower apertural edge (Fig. 1C), fits the drawings of Clessin [Dybowski, 1888: Tab. 2, fig. 9], and, most likely, served as the original for these drawings. Thus, this specimen was considered a syntype [Anistratenko *et al.*, 2019]; the rest of the syntypes are deposited in ZIN. We designate here as the lectotype of *Neritina schultzi*

one of specimens from ZIN collection (Fig. 1B); apparently the radula of this specimen was studied and illustrated by Grimm [1877: pl. 7, fig. 5].

We provisionally include *Theodoxus jukovi* Kolesnikov, 1947 in the synonymy of *Th. schultzi* though the status of the former remains uncertain since its type series is still unknown. The probable identity between *Th. jukovi* and *Th. schultzi* is based on a similar shell outline presented in Kolesnikov's drawing [1947: 107, pl. 1, fig. 4] as well as on distribution of *Th. jukovi* in the middle and southern Caspian Sea basins. The ranges of shell variation of the two species overlap [see also Weslingh *et al.*, 2019].

The problem of taxonomic relationships between *Th. schultzi* and *Th. pallasii* needs a special consideration. Most authors traditionally distinguished the former species from *Th. pallasii* by its rounder shell, heavily expanded aperture and citreous shell colouration [Grimm, 1877; Logvinenko, Starobogatov, 1969; Zettler, 2007]. The most characteristic feature of *Th. schultzi* shell is the conspicuous elongation of the upper and lower aperture edges. The radulae of these two species morphologically are also quite different [see Zettler, 2007 and compare Anistratenko *et al.*, 2017]. The usage of the molecular genetic approach has recently led to suggestion for synonymization of these species [Sands *et al.*, 2019a, b], however, this needs to be confirmed that material, which was used for DNA study, accorded to conception of species under discussion. The problem is that, in the middle and southern sectors of the Caspian Sea, specimens morphologically intermediate between typical *pallasii* and typical *schultzi* can be found. Such shells are globular-shaped (what is characteristic to *pallasii*), but have more or less massively expanded aperture, thus resembling shells of *schultzi*.

Theodoxus abrauensis
(Milaschewitsch, 1914)

Neritina fluviatilis L. var. *abrauensis* Milaschewitsch, 1914: 429–430.

Type material. Not studied. The type series was thought to be stored in ZIN, though it could be traced neither in the catalogue nor in the collection.

Type locality. Lake Abrau, Krasnodar Krai, Russia.

Remarks. According to the original description, this taxon is characterized by small shells, whose colour surface pattern is “resembling the Caspian *Neritina liturata* Eichwald” [Milaschewitsch, 1914: 430]. We consider it is similar to *pallasii*-like *Theodoxus* from others fluvial locations in Caucasus (see below), but the true taxonomic identity and status of this variety require further study.

Theodoxus fluviatilis (Linnaeus, 1758)
(Fig. 2 A–C)

Nerita fluviatilis Linnaeus, 1758: 777.

Theodoxus fluviatilis. – Issel, 1865: 22; Issel, 1866: 406.

Theodoxus fluviatilis. – Zhadin, 1952: 206–207, fig. 121.

?*Theodoxus dniestroviansis* Put', 1972: 80–82, textfig. 5.

Th.[eodoxus] fluviatilis. – Anistratenko *et al.*, 1999: 13, figs 2, 3, 4, 1.

Theodoxus fluviatilis. – V. Anistratenko, O. Anistratenko, 2001: 109–110, figs. 68–69.

Theodoxus (Theodoxus) fluviatilis. – Eichhorst, 2016: 913, pl. 279–280; Vinarski, Kantor, 2016: 154–155.

Type material. The lectotype of *Nerita fluviatilis* Linnaeus, 1758 was designated by Anistratenko *et al.* [1999], the images of the lectotype and five paralectotypes are given in this as well as in a later published work [Anistratenko, 2005]. Type specimens of *Nerita fluviatilis* Linnaeus, 1758 deposited in LSL (Box number: LSL.566) and can be seen on the Linnean Collections site: <http://linnean-online.org/17145/>.

Type locality. Near Uppsala, Sweden.

Other material. IZAN collection, catalogue ##231, 242, 319, 384, HBS 390–391.

Remarks. Although the species is widely distributed all over Europe (except its northern part), Anatolia, and Northern Africa it does not occur in the Caspian Sea (except the Volga delta). We provide here some illustrations of *Th. fluviatilis* shells (Fig. 2 A–C) in order to facilitate the discrimination among species having similar shell shape and colour pattern. The applicability of the name *Theodoxus fluviatilis* is clearly determined by its lectotype [Anistratenko *et al.*, 1999; Anistratenko, 2005] though the shells of this species demonstrate a considerable variation in their colour pattern and shape [e.g. Zettler, 2008; Glöer, Pešić, 2015]. The status of a number of nominal taxa, such as *Theodoxus braueri* (with variants), *Th. cereoflavus*, *Th. danasteri* and *Th. sarmaticus* is here considered as synonyms of *Th. fluviatilis* (see below). However, it needs to be confirmed by an analysis of variation in characters other than shell shape and/or colour pattern. A superficial similarity in shell habitus may lead to wrong conclusions about their identity. For instance, a similar zigzag-like pattern of shell surface colouration occurs occasionally in *Th. fluviatilis* and some populations of *Th. danubialis* inhabiting the upper part of the Danube basin [see Zettler, 2008] as well as in *Th. pallasii* from the Caspian Sea [Anistratenko *et al.*, 2017]. In freshwater waterbodies of Abkhazia were recorded snails with typical *fluviatilis*-like pattern (Fig. 2 B, C) as well as with colouration similar to *pallasii* (Fig. 2E). At the same time, Glöer and Pešić [2015: 90] stated that colour patterns are likely influenced by the environmental conditions.

The taxonomic status of *Th. dniestroviansis* Put', 1972, described from the Dniester River (Rukhotyn village, Khotyn district, Chernivtsi region, Ukraine),

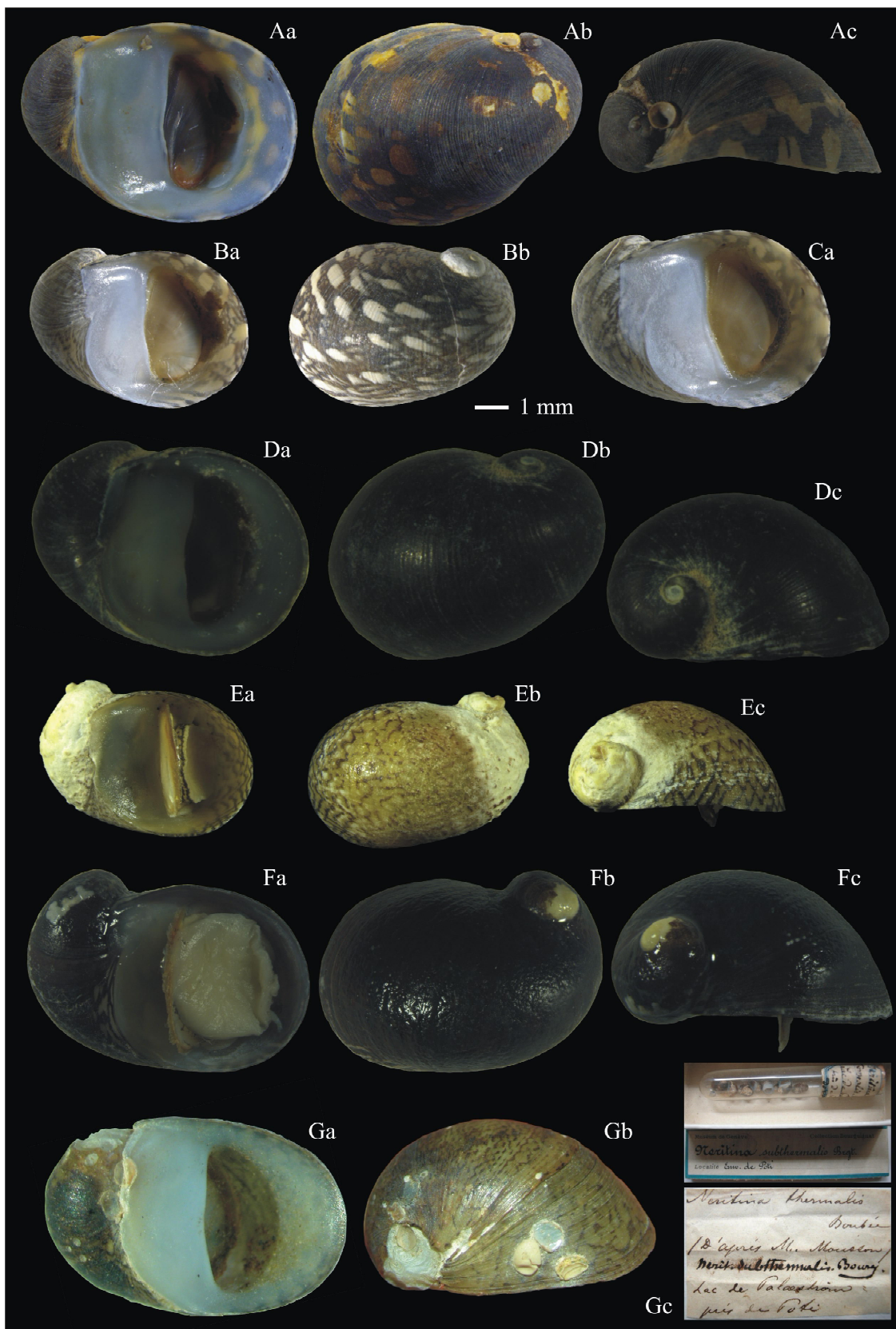


FIG. 2. **A–C.** *Theodoxus fluviatilis*: **A.** IZAN HBS390-391, locality 3; **B, C.** IZAN 231, locality 12. **D–G.** *Th. subthermalis*: **D.** IZAN 516, locality 14; **E.** IZAN 391, locality 11; **F.** IZAN Pal-370K, locality 10; **G.** MHNG, Bourguignat collection, No. 11737 lectotype and general view of the lot and its labels.

РИС. 2. **A, B.** *Theodoxus fluviatilis*: **A.** IZAN HBS390-391, локалитет 3; **B.** IZAN 231, локалитет 12. **D–G.** *Th. subthermalis*: **D.** IZAN 516, локалитет 14; **E.** IZAN 391, локалитет 11; **F.** IZAN Pal-370K, локалитет 10; **G.** MHNG, коллекция Бургинья, No. 11737 лектотип и общий вид лота и этикеток.

is not absolutely clear at the moment. We were unable to trace the type specimens of this species (they are apparently lost) though basing on the original description and illustration [Put', 1972] it may be regarded as a junior synonym of *Th. fluvialtilis* having an unusual colour pattern [Anistratenko *et al.*, 1999].

Theodoxus lamelliferus
(Milaschewitsch, 1912)
(Fig. 3E)

Neritina lamellifera Milaschewitsch, 1912: 521–522, unnumbered text-figure.

Theodoxus pilidei lamelliferus (Milaschewitsch, 1912). – Golikov, Starobogatov, 1972: 86, tab. 1, fig. 16a, b.

Type material. ZIN, catalogue #6119/1, lectotype (here designated); ##6120/2–6124/6, 14 paralectotypes; see Table 1.

Type locality. Black Sea near Alushta (Crimea).

Remarks. This species has been described on the basis of empty shells dredged from the Black Sea phaseoline silt at depths between 80 and 160 m; it clearly differs from all known neritids of the region by shell sculpture ornamented with 15–20 distinct axial lamellae arranged at regular intervals. The specimen illustrated here (Fig. 3E) was already depicted in the original description [Milaschewitsch, 1912], and we designate it here as the lectotype of *Neritina lamellifera* Milaschewitsch, 1912. Since alive snails have never been found, *N. lamellifera* is an apparently extinct neritid species that once inhabited the Black Sea basin. This name was used by Golikov and Starobogatov [1972] in combination ‘*Theodoxus pilidei lamelliferus*’ because these authors have considered Milaschewitsch’s species as almost identical to *Theodoxus pilidei* (Tournouër, 1879). *Theodoxus lamelliferus* can be considered either a distinct species or subspecies of the *Th. pilidei* described from Romanian deposits of Rumania [Tournouër, 1879]. These fossil neritids (*Th. pilidei* and *Th. lamelliferus*) are extremely similar in shell shape and sculpture to the specimens of supposedly extant *Theodoxus gloeri* Odabaşı et Arslan, 2015 recently described from the Balikdami Wetland located on the Sakarya River in the Eskişehir Province, Turkey [Odabaşı, Arslan, 2015]. The shell of *Th. gloeri* is smaller than those of both *Th. pilidei* and *Th. lamelliferus*, relatively thin and translucent with no pigmentation [Odabaşı, Arslan, 2015]. Although all the samples of *Th. gloeri* contain only empty shells without opercula, the authors suggested this species is a locally endemic snail living as subterranean form.

Theodoxus major Issel, 1865
(Fig. 3 A–D)

Theodoxus schirazensis var. *major* “Bourguignat” Issel, 1865:

24; Issel, 1866: 408.

Theodoxus pallasii morpha *major*. – Akramowski, 1976: 88, textfig. 23, pl. 1, fig. 2.

Type material. Not studied. According to Wesselingh *et al.* [2019], the types of *Theodoxus major* are kept in the Museo Regionale di Scienze Naturali, Torino, Italy, though these are currently inaccessible due to museum renovation.

Type locality. Lake Sevan in Armenia [= “Lago Goktscha”, see Issel, 1865: 24]. Akramowski [1976] declared that the indication of locality is erroneous and the true *locus typicus* should be “Yerevan in Armenia”. Neither in the Lake Sevan nor in the adjacent area of the lake the species was found [Akramowski, 1976].

Other material. Three illustrated shells (Fig. 3 A–D) come from a lot containing 24 alcohol-preserved specimens collected in Arax River within Azerbaijan, ix–x 1979, coll. A.R. Aliev (ZIN catalogue #47267/1, det. Ya.I. Starobogatov). As these specimens were collected close to the region from where the type material originates, we consider them as probable topotypes.

Remarks. Since Bourguignat proposed the name for ‘*major*’ in a letter, he is not the author of this taxon and the authorship should be given as “Issel, 1865”.

The true identity of *Theodoxus major* Issel, 1865 is difficult to determine due to the inaccessibility of the type series. However, judging from the data given in the original description [Issel, 1865: 24], shells of this variety have a colour pattern similar to that of typical *Th. pallasii* occurring in the Caspian Sea. The examination of the probable topotypes of ZIN collection (Fig. 3 A–D) confirms it: the specimens collected from the Arax River in Azerbaijan resemble *Th. pallasii* from Meghri River (tributary of Arax) illustrated by Akramowski [1976: pl. 1, fig. 1] and look similar to *Th. pallasii* from the Caspian Sea (Fig. 1A). Given the probable topotypes and individuals from Meghri River occurred in montane riverine conditions their identity with Caspian’s *Th. pallasii* is biologically surprising. According to Akramowski [1976], in Armenia *Th. pallasii* may co-occur with *Th. pallasii* morpha *major*. However, the Armenian specimens of *Th. major* resemble freshwater *Th. subthermalis* s.l. from other regions of Caucasus where snails with black (Fig. 2 D, F) and variegated shells (Fig. 2E) can be found. Thus, the status of black-coloured *Theodoxus* from Armenia (as well as from whole Caucasian area) designated by Akramowski [1976: pl. 1, fig. 2] as *Th. pallasii* morpha *major* remains unclear. In the meantime Sands *et al.* [2019a, b] concluded that *Th. pallasii* and *Th. schultzei* are conspecific with *Th. major*.

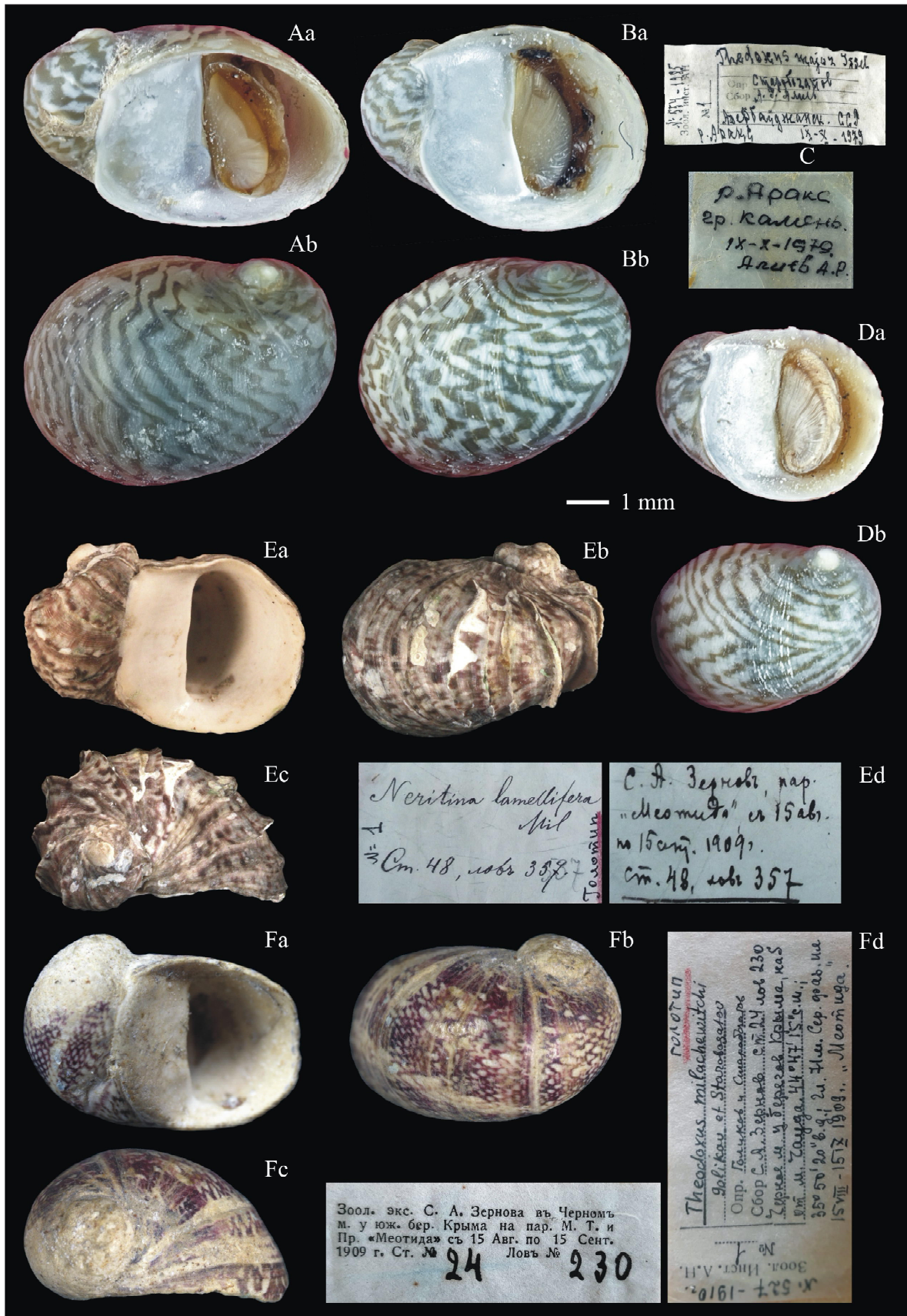


FIG. 3. A–D. *Theodoxus major*, ZIN #47267/1, three of 24 probable topotypes, locality 15. E. *Th. lamelliferus*, ZIN #6119/1, lectotype, locality 22. F. *Th. milachevitchi*, ZIN #6134/1, holotype, locality 23. C, Ed, Fd – the original labels.

РИС. 3. A–D. *Theodoxus major*, ZIN #47267/1, три из 24 возможных топотипов, локалитет 15. E. *Th. lamelliferus*, ZIN #6119/1, 1 лектотип, локалитет 22. F. *Th. milachevitchi*, ZIN #6134/1, голотип, локалитет 23. C, Ed, Fd – оригинальные этикетки.

Theodoxus milachevitchi Golikov et
Starobogatov, 1966
(Fig. 3F)

Theodoxus milachevitchi Golikov, Starobogatov, 1966: 352–353, fig. 1, 1a, 1b.

Type material. ZIN, catalogue #6134/1, holotype; ##6135/2–6141/8, 21 paratypes.

Type locality. Black Sea near Chauda Cape, off Crimea.

Remarks. This fossil species has been described on the basis of empty shells dredged from the Black Sea phaseoline silt at depths between 20 and 160 m. Shells of *Th. milachevitchi* clearly differ from all known extant neritid species of the region by three wide coloured spiral stripes on the body whorl. A taxonomic relationship of this species with other extinct neritids requires study of additional Quaternary/Pliocene material.

Theodoxus subthermalis Issel, 1865
(Fig. 2 D–G)

Theodoxus fluviatilis var. *subthermalis* “Bourguignat” Issel, 1865: 22–23; Issel, 1866: 406–407.

Th.[eodoxus] subthermalis. – Anistratenko *et al.*, 1999: 17, fig. 4, 5; Kantor, Sysoev, 2006: 45–46, pl. 21, A.

Theodoxus subthermalis. – V. Anistratenko, O. Anistratenko, 2001: 111, fig. 73.

Theodoxus fluviatilis subthermalis. – Bank, Neubert, 2017.

Type material. Lectotype (here designated) and six paralectotypes of *Theodoxus fluviatilis* var. *subthermalis* Issel, 1865 are deposited in MHNG, Bourguignat collection, No. 11737. The shell of lectotype was illustrated by Sitnikova *et al.* [2012]; this illustration is reproduced here (Fig. 2G).

Type locality. Lake Paleostomi near Poti, Georgia [“Lago di Paleaston”, see Issel, 1865: 22–23].

Other material. IZAN collection, catalogue ##516, 391, Pal-370K, see Tab. 1.

Remarks. Since Bourguignat proposed the name for ‘*subthermalis*’ in a letter, he is not the author of this taxon and the authorship should be given as “Issel, 1865”.

There is no widely accepted concept of *Th. subthermalis*. In the Russian literature, *Th. subthermalis* is usually considered as a distinct species with black-coloured shell [Zhadin, 1952; Anistratenko *et al.*, 1999; Kantor, Sysoev, 2006; Vinarski, Kantor, 2016] occurring in Iran and Transcaucasia. Akramowski [1971] suggested that *Th. subthermalis* from Armenia (sensu Zhadin, 1952 but not sensu Issel, 1865) represents a black-coloured morph of *Th. pallasi*. Later on, this author [Akramowski, 1976] treated the black-coloured *Theodoxus* from Armenia as an intraspecific variety of *Th. pallasi major* Issel, 1865, which inhabits springs. Bank and Neubert [2017] accepted *subthermalis* as a subspecies of *Th. fluviatilis*. Given the black colour being

a key diagnostic character for *Th. subthermalis* (see photo in the catalogue by Kantor and Sysoev [2006: pl. 21, fig. A]), the status of this species is not clear because specimens of *Theodoxus* with typical *subthermalis*-like pattern (Fig. 2 D, F) may be found in waterbodies of Caucasus alongside with relatively smaller individuals resembling *pallasi* (e.g. Fig. 2E). Sands *et al.* [2019a] molecularly assessed the specimens identified as *subthermalis* and they group with *fluviatilis* in the phylogenetic tree; the authors concluded that it is a junior synonym of *Th. fluviatilis*.

The shell of *Th. subthermalis* illustrated by Sitnikova *et al.* [2012] has a variegated surface colouration resembling that of *Th. pallasi*, but its zigzag-like pattern is of smaller size than in the latter species (Fig. 2G). The shell shape of this type specimen is more similar to shells of *Th. fluviatilis* (Fig. 2 A, B) than to typical shells of *Th. pallasi* (Fig. 1A). Sitnikova *et al.* [2012] have showed that the shells of ZIN collection, labeled as *Th. subthermalis*, differ from the types by their shell shape (Fig. 2G). Moreover, the majority of published records of this taxon [Zhadin, 1952; Anistratenko, 1998; Anistratenko *et al.*, 1999] refers also to a different species having a shell rather squarish in the frontal plane, not rhomboidal as in the types of *Th. subthermalis* [Sitnikova *et al.*, 2012: pl. 1, fig. A, B]. In order to define the species more clearly, here we fix the illustrated specimen (MHNG, Bourguignat collection, No. 11737, Fig. 2G) as the lectotype of the species.

Basing on a general shell outline and index of aperture width plus columellar shield/shell width in the type series, Sitnikova *et al.* [2012] suggested that specimens from lakes and rivers of Caucasus, determined earlier as *Th. subthermalis*, might represent a distinct, new species, whereas the validity of *Th. subthermalis* and its actual range require an additional study. According to this point of view, the genuine *Th. subthermalis* might be considered as a local endemic of western Georgia while *Th. subthermalis* auct. is probably a distinct pan-Caucasian species, not named yet.

Theodoxus velox V. Anistratenko
in O. Anistratenko, Starobogatov et
V. Anistratenko, 1999
(Fig. 4 A–C)

Th.[eodoxus] velox V. Anistratenko in O. Anistratenko *et al.*, 1999: 17–18, fig. 4, 7.

Theodoxus fluviatilis. – Zettler, 2008: 16, pl. 19, figs e–f (non Linnaeus, 1758).

Theodoxus velox. – V. Anistratenko, O. Anistratenko, 2001: 113–114, fig. 75.

Theodoxus (Theodoxus) fluviatilis. – Vinarski, Kantor, 2016: 154–155 (non Linnaeus, 1758).

Theodoxus (Theodoxus) velox. – Eichhorst, 2016: 965, pl. 308.

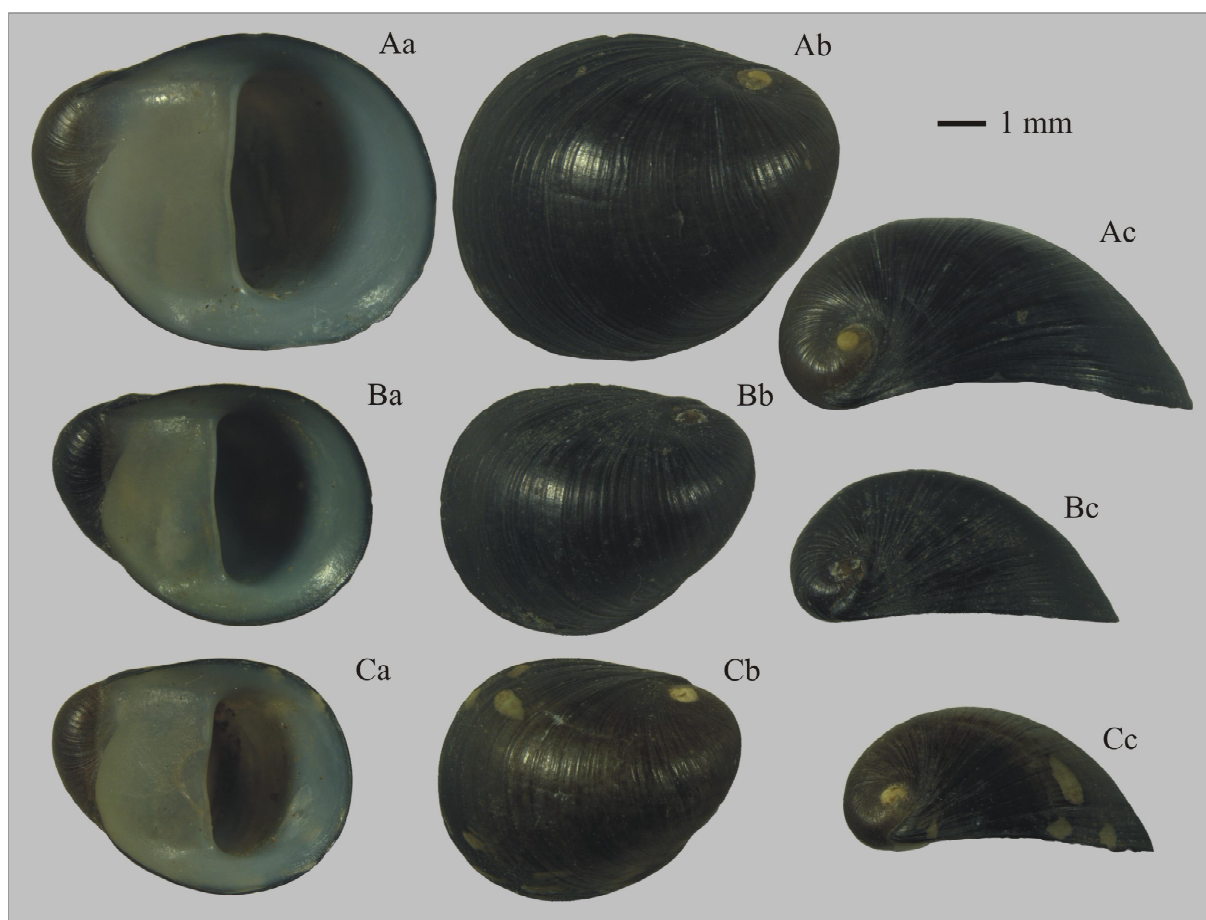


FIG. 4. Type specimens of *Theodoxus velox*, IZAN, unnumbered, locality 4. A. The holotype. B–C. Paratypes.

РИС. 4. Типовые экземпляры *Theodoxus velox*, IZAN, без номера, локалитет 4. А. Голотип. В–С. Паратипы.

Type material. The holotype and five paratypes, IZAN, unnumbered (see Tab. 1).

Type locality. Dnieper delta, Zburievskiy liman, Kherson Region, Ukraine.

Other material. About 10 specimens from the Dnieper delta, IZAN, catalogue #384.

Remarks. In the original description [Anistratenko *et al.*, 1999], only an outline drawing of the *Th. velox* holotype was given to illustrate the shell of this species. Later, the holotype was figured in the catalogue of Kantor and Sysoev [2006; pl. 21, fig. B], which we reproduce here (Fig. 4A). The shells of the paratypes of this species are very similar to *Th. fluviatilis* and differ from the latter by faster expanding of spire whorls (see Fig. 4 A–C). Type specimens of *Th. velox* resemble very much the “holotype” of *Neritina fluviatilis* var. *sarmatica* f. *atra*, which apparently represents a form of variation of *Th. velox* (see below). The distribution area of *Th. velox* lies largely within the range of *Th. fluviatilis*. This might be evidence they are conspecific as it was suggested basing on DNA analysis [e.g. Bunje, 2006]. However, recent molecular data

argue that *Th. velox* represent a genetically distinct clade [e.g. Sands *et al.* 2019a, b, 2020].

Available but not valid names

“*Theodoxus alboguttatus* (Lindholm, 1908)” (Fig. 5B)

Neritina brauneri f. *alboguttata* Lindholm, 1908: 217.

Th.[eodoxus]fluviatilis. – Anistratenko *et al.*, 1999: 13, figs 2, 3, 4, 1.

Theodoxus fluviatilis. – V. Anistratenko, O. Anistratenko, 2001: 109, figs. 68–69.

Type material. ZIN, catalogue #6051/1, holotype; see Table 1.

Type locality. [Black Sea] near Odessa (Ukraine).

Remarks. *Theodoxus alboguttatus* is usually considered as an intraspecific variant of *Th. fluviatilis* differing by its colour pattern [Anistratenko *et al.*, 1999; V. Anistratenko, O. Anistratenko, 2001]. The type series of this variety contains only one specimen (holotype by monotypy [ICZN, 1999]) of perfect preservation; shell morphology of this type

specimen corresponds well with the *Th. fluviatilis* variability range, and these taxa are to be considered synonyms.

“*Theodoxus brauneri* (Lindholm, 1908)”

(Fig. 5A)

Neritina brauneri Lindholm, 1908: 217.

Theodoxus fluviatilis var. *brauneri*. – Zhadin, 1952: 207.

Th.[*eodoxus*]*fluviatilis*. – Anistratenko *et al.*, 1999: 13, figs 2, 3, 4, 1.

Theodoxus fluviatilis. – V. Anistratenko, O. Anistratenko, 2001: 109, figs. 68–69.

Theodoxus brauneri. – Welter-Schultes, 2012: 27, textfig.

Type material. ZIN, catalogue #6046/1, lectotype (here designated) and two paralectotypes; see Table 1.

Type locality. [Black Sea] near Odessa (Ukraine).

Remarks. In the Russian literature, *Th. brauneri* is considered as an intraspecific variation of *Th. fluviatilis* [Zhadin, 1952; Anistratenko *et al.*, 1999; V. Anistratenko, O. Anistratenko, 2001] having a relatively smaller and thin-walled shell. On the other hand, Welter-Schultes [2012] accepts it as a valid species, distinct from *Th. fluviatilis*. One of three syntypes stored in ZIN (catalogue #6046/1) is designated here as the lectotype of *Neritina brauneri* Lindholm, 1908 (Fig. 5A). Shell morphology of the studied type specimens of *Th. brauneri* accords well with the variability range of *Th. fluviatilis*, and these taxa are most likely conspecific. Lindholm (1908: 217–218) established three intraspecific forms within the *Neritina brauneri*, based on specimens collected at the same locality (see below).

“*Theodoxus cereoflavus* (Lindholm, 1913)”

(Fig. 6, A–D)

Neritina fluviatilis L. var. *cereoflava* Lindholm, 1913: 68.

Type material. ZIN, catalogue #6055/1, lectotype (here designated) and four paralectotypes.

Type locality. Psyrtskha River near Novyi Afon monastery, Abkhazia [“Im Fluss Psirssa beim Kloster Nowyi Afon (westl. Transcaucasien)”].

Remarks. Lindholm [1913: 68] differentiated this form from the typical *fluviatilis* by the monochrome waxy yellow colour of the shell surface. Two of three type specimens (Fig. 6 B, C) show a clear similarity in pattern and/or shape to the shells we found in Besletka River near Veneto bridge, not far from Sukhum, Abkhazia (compare Fig. 2E). On the other hand, some specimens collected in locality 10 (see Table 1), i.e. very close to the type locality, look like typical “*subthermalis*”, i.e. having completely black-coloured shell (Fig. 2F). One of the syntypes is designated here as the lectotype (Fig. 6A) of *Neritina fluviatilis* var. *cereoflava* Lindholm, 1913. Conchologically, Lindholm’s specimens

from Psyrtskha River probably represent a local variation of *Th. fluviatilis*, and the name *Neritina cereoflava* can be considered as the junior synonym of *Th. fluviatilis*.

In ZIN collection the “type” specimens have been traced of two names that were only introduced by Milaschewitsch in the collection labels representing “catalogue names”. The names *Neritina fluviatilis* L. var. *tanaitica* Milaschewitsch and *Neritina fluviatilis* L. var. *caucasica* Milaschewitsch were never established in the ICZN sense, so they are not available and represent “collection, label or catalogue names”. Apart of the three “types” of “*Theodoxus tanaiticus*” from Voronezh City, Russia (ZIN, catalogue #6104/1; see Table 1), ZIN collection contains 106 specimens sampled in different regions of south Russia, Ukraine and Moldova (ZIN, catalogue ##6105/2, 6106/3, 6107/4, 58872/5) and determined as ‘*Neritina fluviatilis* L. var. *tanaitica* Milaschewitsch’. The shells of “*Th. tanaiticus*” (Fig. 6E) fit well to those of *Th. fluviatilis* occurring in the same region and should be considered as its variations. Six “type” specimens of “*Theodoxus caucasicus*” from Sochi (North Caucasus, Krasnodar Krai, Russia) (Fig. 6F) are housed in ZIN collection (catalogue #6054/1; see Table 1). They fit well to the shells of *Th. subthermalis* occurring in rivers of the adjacent regions of the Caucasus, which have relatively smaller shells with colour patterns like in *Th. pallasi* (compare Fig. 2E).

“*Theodoxus danasteri* (Lindholm, 1908)”

(Fig. 7 A–D)

Neritina danubialis Pfeif. var. *danasteri* Lindholm, 1908: 215–216.

Theodoxus donasteri (sic!). – Anistratenko, 1998: 72, pl. 1, fig. 2 (incorrect subsequent spelling).

Th.[*eodoxus*]*danasteri*. – Anistratenko *et al.*, 1999: 16, fig. 4, 2.

Theodoxus danasteri. – V. Anistratenko, O. Anistratenko, 2001: 110, fig. 70.

Type material. ZIN, catalogue #5910/3, lectotype (here designated) and two paralectotypes; #5911/4, seven paralectotypes; see Table 1.

Type locality. Dniester liman near Akkerman (nowadays Belgorod-Dnestrovskiy), Odessa region (Ukraine) and Dniester River near Rybnitsa (Moldova).

Remarks. In the Russian literature, *Th. danasteri* is usually considered as an intraspecific variation of *Th. fluviatilis* [e.g. Vinarski, Kantor, 2016] or *Th. danubialis* (C. Pfeiffer, 1828) having a slightly more elongated shell [e.g. Zhadin, 1952], however sometimes it has been treated as a distinct species [e.g. Anistratenko *et al.*, 1999: fig. 4, 2]. One of the three type specimens from Dniester liman stored in ZIN (catalogue #5910/3; see Table 1) is designated

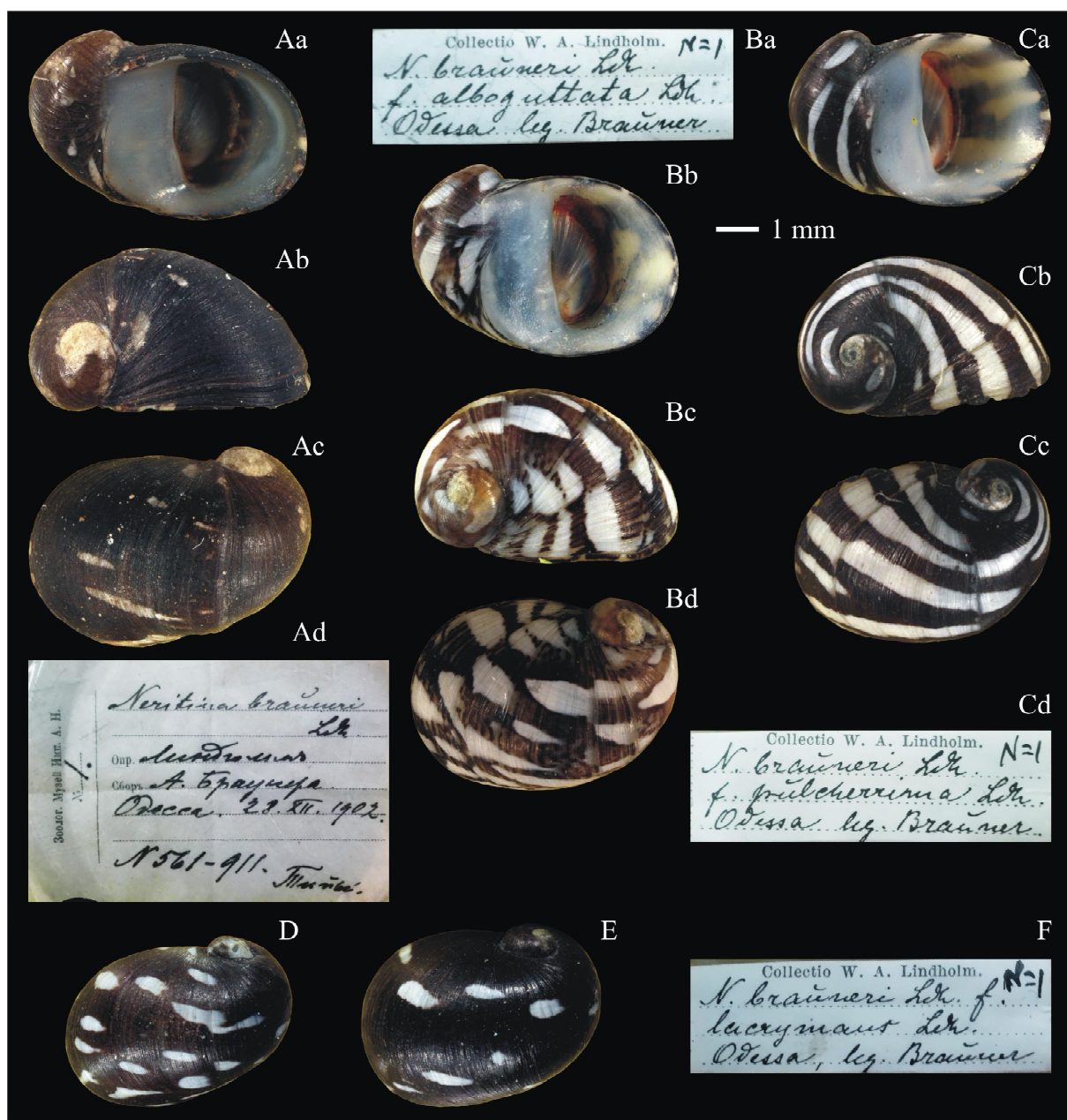


FIG. 5. A. “*Theodoxus brauneri*”, ZIN #6046/1, lectotype, locality 16. B. “*Th. alboguttatus*”, ZIN #6051/1, holotype, locality 17. C. “*Th. pulcherrimus*”, ZIN #6053/1, holotype, locality 19. D–F. “*Th. lacrymans*”: D. ZIN #6052/1, lectotype, locality 18; E. ZIN #6052/1, paralectotype, locality 18. Ad, Ba, Cd, F – the original labels.

РИС. 5. А. “*Theodoxus brauneri*”, ZIN #6046/1, лектотип, локалитет 16. В. “*Th. alboguttatus*”, ZIN #6051/1, голотип, локалитет 17. С. “*Th. pulcherrimus*”, ZIN #6053/1, голотип, локалитет 19. D–F. “*Th. lacrymans*”: D. ZIN #6052/1, лектотип, локалитет 18; E. ZIN #6052/1, паралектотип, локалитет 18. Ad, Ba, Cd, F – оригинальные этикетки.

here as the lectotype for *Neritina danubialis* var. *danasteri* Lindholm, 1908 (Fig. 7A). This specimen accords to the shell drawing given by Anistratenko *et al.* [1999, fig. 4, 2]. Shell morphology of the studied type specimens of *Th. danasteri* falls into the morphological range of *Th. fluviatilis*, and these taxa are most likely conspecific.

Apart this, Lindholm [1908: 217] described *Neritina danubialis* Pfeif. var. *danasteri* Ldh. f. *obliter-*

ata from the Dniester River near Rybnitsa (Moldova). The name “*Th. obliteratus*” has never been applied to a distinct taxon of species or subspecies rank [e.g. Anistratenko *et al.*, 1999; V. Anistratenko, O. Anistratenko, 2001; Vinarski, Kantor, 2016] and is also unavailable. The “type series” of *Neritina danubialis* var. *danasteri* f. *obliterata* consists of a single specimen (ZIN, catalogue #5912/1; see Table 1) morphologically matching well to the typi-

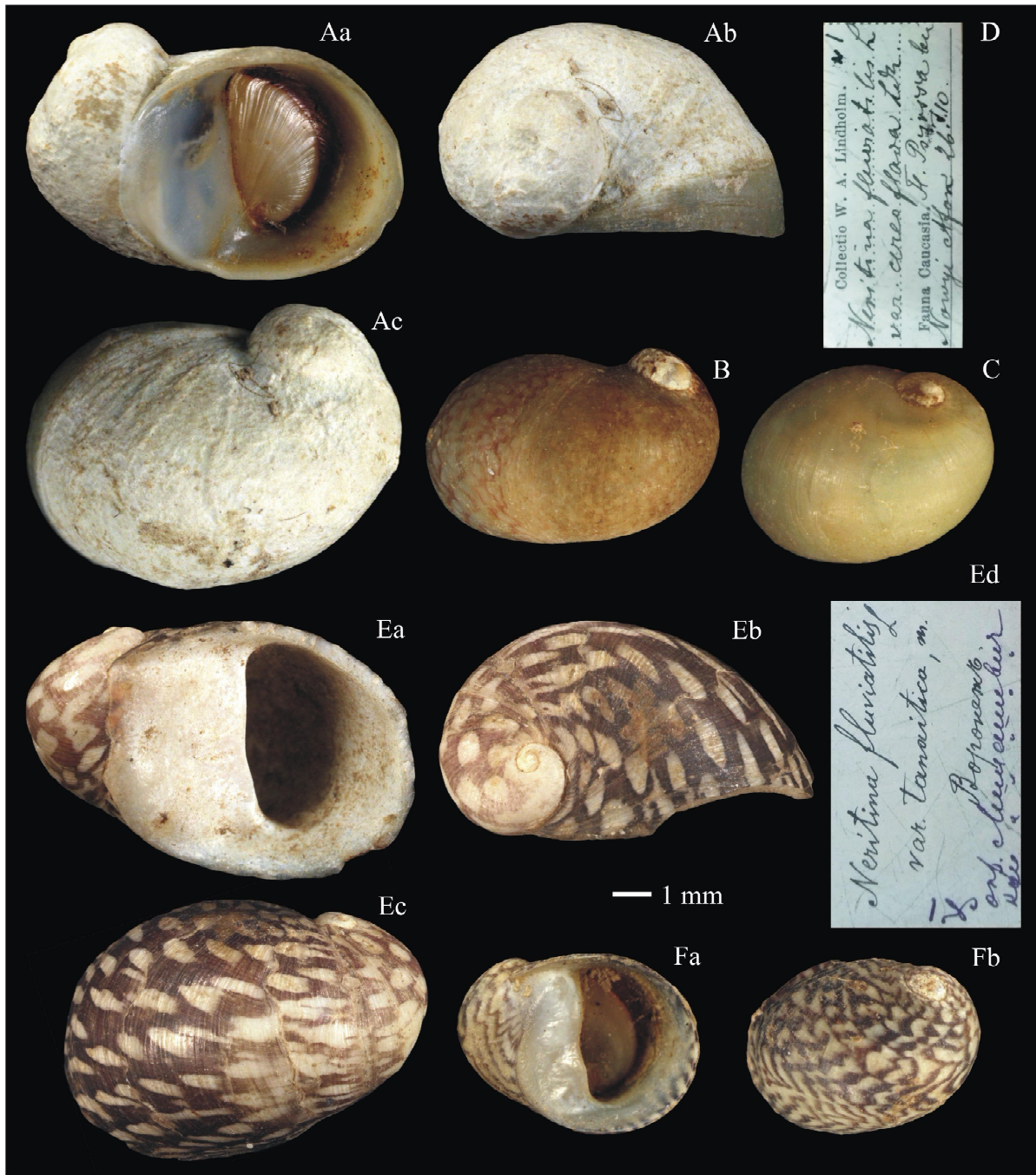


FIG. 6. A–D. “*Theodoxus cereoflavus*”: A. ZIN #6055/1, lectotype, locality 9; B, C. ZIN #6055/1, paralectotypes, locality 9. E. “*Th. tanaiticus*”, ZIN #6104/1, locality 7. F. “*Th. caucasicus*”, ZIN #6054/1, locality 8. D, Ed – the original label.

РИС. 6. А–Д. “*Theodoxus cereoflavus*”: А. ZIN #6055/1, лектотип, локалитет 9; В, С. ZIN #6055/1, паралектотипы, локалитет 9. Е. “*Th. tanaiticus*”, ZIN #6104/1, локалитет 7. F. “*Th. caucasicus*”, ZIN #6054/1, локалитет 8. D, Ed – оригинальная этикетка.

cal *Th. fluviatilis* in shape, proportions as well as colour pattern (Fig. 7E).

“*Theodoxus lacrymans* (Lindholm, 1908)”
(Fig. 5 D–F)

Neritina braueri f. *lacrymans* Lindholm, 1908: 217.
Th.[eodoxus] fluviatilis. – Anistratenko *et al.*, 1999: 13 (partim).

Theodoxus fluviatilis. – V. Anistratenko, O. Anistratenko, 2001: 109 (partim).

Type material. ZIN, catalogue #6052/1, lectotype (here designated) and one paralectotype; see Table 1.

Type locality. [Black Sea] near Odessa (Ukraine).

Remarks. Like the previous, *Th. lacrymans* is

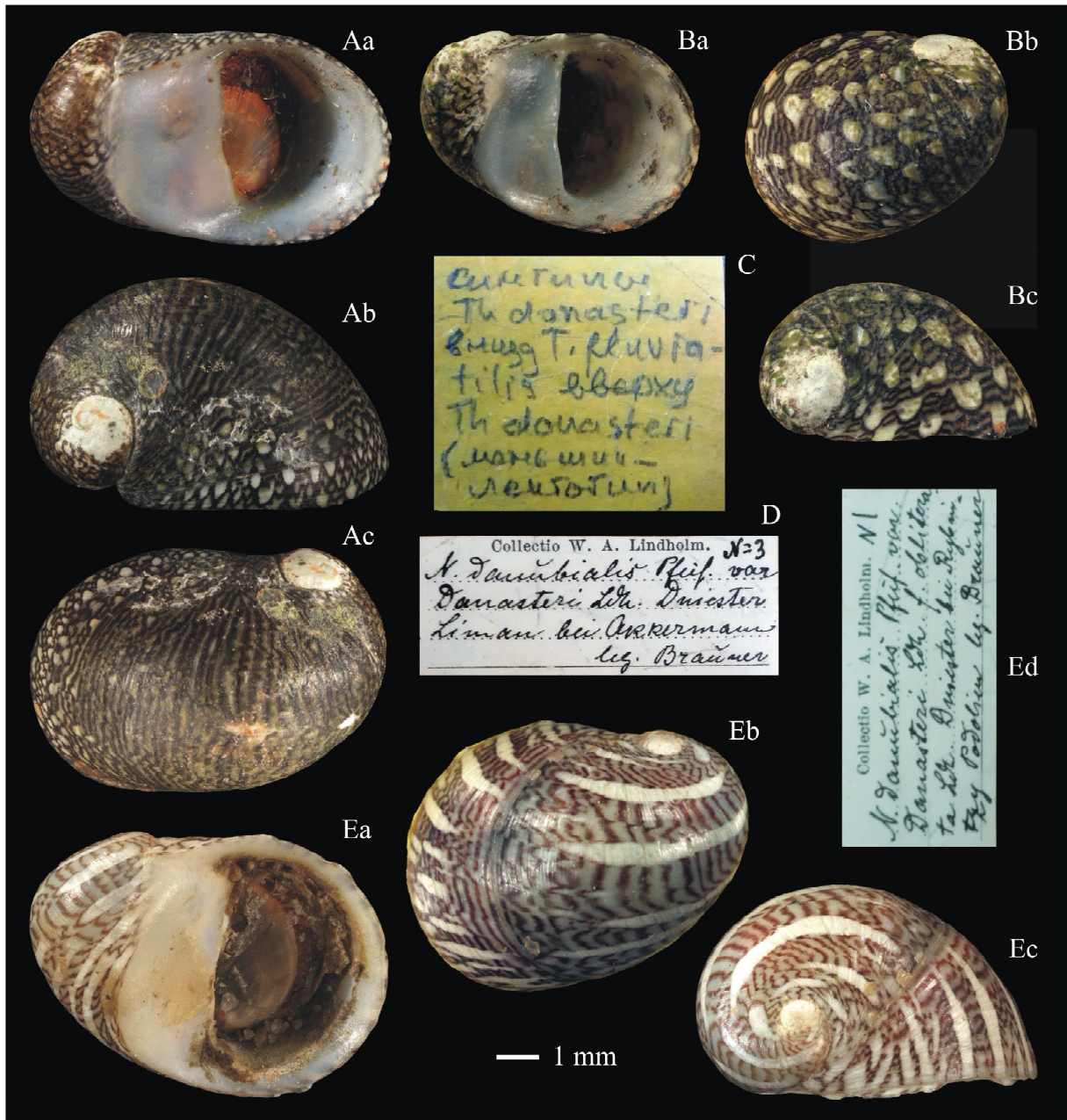


FIG. 7. A–D. “*Theodoxus danasteri*”: A. ZIN #5910/3, lectotype, locality 20; B. ZIN #5910/3, paralectotype, locality 20. E. “*Th. obliteratedus*” ZIN #5912/1, locality 21. C, D, Ed – the original labels.

РИС. 7. A–D. “*Theodoxus danasteri*”: A. ZIN #5910/3, лектотип, локалитет 20; B. ZIN #5910/3, паралектотип, локалитет 20. E. “*Th. obliteratedus*” ZIN #5912/1, локалитет 21. C, D, Ed – оригинальные этикетки.

regarded as an intraspecific colour variation of *Th. fluviatilis* [Anistratenko *et al.*, 1999; V. Anistratenko, O. Anistratenko, 2001]. The type series of this taxon contains two perfectly preserved specimens, one of which we designate here as the lectotype of *Neritina braueri* f. *lacrymans* Lindholm, 1908 (Fig. 5D). The shell morphology of type specimens accords well with the *Th. fluviatilis* variability range, and these taxa are considered synonyms.

“*Theodoxus pulcherrimus* (Lindholm, 1908)”
(Fig. 5C)

Neritina braueri f. *pulcherrima* Lindholm, 1908: 217–218.
Th.[eodoxus] fluviatilis. – Anistratenko *et al.*, 1999: 13 (partim).

Theodoxus fluviatilis. – V. Anistratenko, O. Anistratenko, 2001: 109 (partim).

Type material. ZIN, catalogue #6053/1, holotype; see Table 1.

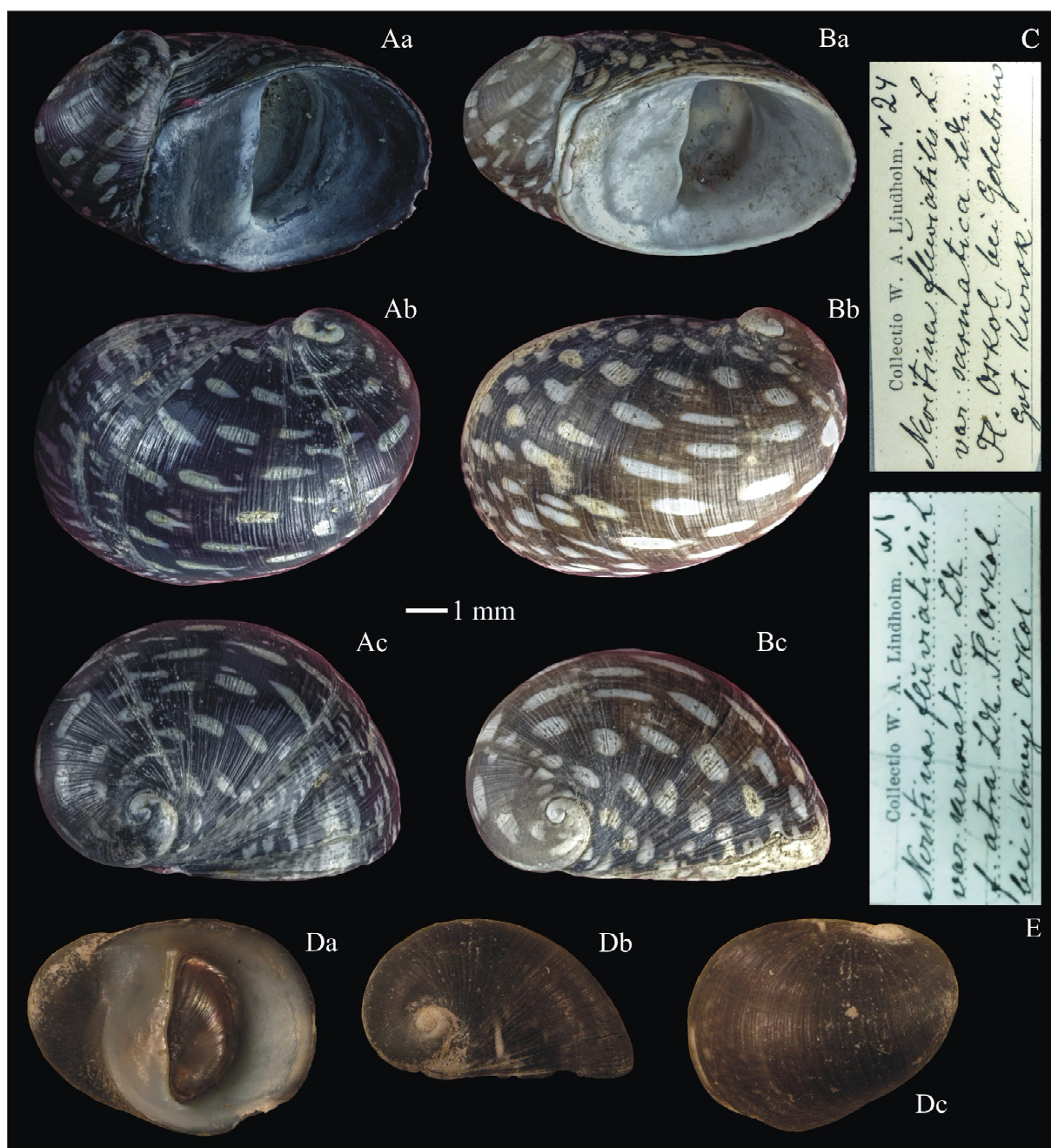


FIG. 8. A–C. “*Theodoxus sarmaticus*”: A. ZIN #6099/24, paralectotype, locality 5; B. ZIN #6099/24, lectotype, locality 5. D, E. “*Th. ater*”, ZIN #6102/1, locality 6. C, E – the original labels.

РИС. 8. A–C. “*Theodoxus sarmaticus*”: A. ZIN #6099/24, паралекотип, локалитет 5; B. ZIN #6099/24, лекотип, локалитет 5. D, E. “*Th. ater*”, ZIN #6102/1, локалитет 6. C, E – оригинальные этикетки.

Type locality. [Black Sea] near Odessa (Ukraine).

Remarks. The name *Th. pulcherrimus* has been considered a synonym of *Th. fluviatilis*, representing an intraspecific variation of colour pattern [Anistratenko *et al.*, 1999; V. Anistratenko, O. Anistratenko, 2001]. A single well preserved specimen forms the type series of this taxon and is the holotype by monotypy [ICZN, 1999]; shell mor-

phology of this type specimen accords well with the *Th. fluviatilis* variability range.

“*Theodoxus sarmaticus* (Lindholm, 1901)”
(Fig. 8 A–C)

Neritina fluviatilis (L.) var. *sarmatica* Lindholm, 1901: 181–182.

Theodoxus fluviatilis (L., 1758) var. *sarmatica*. – Zhadin, 1952: 207.

Th.[eodoxus] sarmaticus. – Anistratenko *et al.*, 1999: 16, fig. 4, 4.

Theodoxus sarmaticus. – V. Anistratenko, O. Anistratenko, 2001: 111, fig. 72.

Theodoxus (Theodoxus) fluviatilis. – Kantor, Sysoev, 2006: 45, pl. 20 B (non Linnaeus, 1758).

Theodoxus (Theodoxus) sarmaticus. – Eichhorst, 2016: 948, pl. 297.

Type material. ZIN, catalogue #6099/24, lectotype (here designated) and 16 paralectotypes (see Tab. 1); #6098/23, four paralectotypes; #6100/25, 18 paralectotypes.

Type locality. Oskol River, near Golubino, Govern. Kursk (nowadays Belgorod Region), Russia.

Other material. ZIN, catalogue #6076/1, eight specimens.

Remarks. In the Russian literature, *Th. sarmaticus* is usually considered as an intraspecific variation of *Th. fluviatilis* having the dark-coloured shell [e.g. Zhadin, 1952] though sometimes it has been treated as a distinct species [e.g. Anistratenko *et al.*, 1999: fig. 4, 4; Eichhorst, 2016]. We have studied a series of 17 syntypes stored in ZIN (catalogue #6099/24) and designate here one of them as the lectotype of *Neritina fluviatilis* var. *sarmatica* Lindholm, 1901 (Fig. 8B). The comparison of the types of *Th. sarmaticus* with illustrations of the type specimens of *Th. fluviatilis* given by Anistratenko *et al.* [1999: figs 2 and 3] shows that both shell shape and colour pattern, which are observed in *Th. sarmaticus*, fall into the range of *Th. fluviatilis* variability. The distribution of the former species lies within the range of *Th. fluviatilis* what convinces us these two taxa are conspecific.

Lindholm [1901: 181–182] described *Neritina fluviatilis* (L.) var. *sarmatica* forma *atra* from Oskol River, near Novyi Oskol, Belgorod Region (Russia). The name “*Theodoxus ater*” is never mentioned in literature among accepted neritid taxa of species or subspecies rank [e.g. Anistratenko *et al.*, 1999; V. Anistratenko, O. Anistratenko, 2001; Vinarski, Kantor, 2016] and is unavailable [ICZN, 1999: Art. 45.5]. There is only a single specimen (ZIN, catalogue 6102/1; see Table 1) on which Lindholm based this taxon. Comparison of this specimen (Fig. 8 D, E) with the types of *Th. velox* (see above) demonstrates their clear similarity in shape, proportions and colour patterns. This finding expands the area of geographic distribution of *Th. velox* at least from the Dnieper delta up to the SW part of Russia.

Discussion

At present, there is no consensus on the taxonomy and nomenclature of the neritids of the Ponto-Caspian region including its rivers basins. The presented review of the type series is mainly limited to

the study of empty shells or shells with dried body inside and is insufficient for an unambiguous conclusion about the taxonomic validity of the taxa under discussion. However, it contributes some new information that can be used to test taxonomic hypotheses based on morphological and/or molecular studies of newly collected samples. For example, the examined material shows that *Th. fluviatilis* comprises many different variations of shell shape and colour pattern in the fresh water bodies of the region. An overview of the collections studied demonstrates that in the rivers and lakes of the Caucasian region *Theodoxus* with shells that look like typical “*pallasi*”, “*subthermalis*” or “*fluviatilis*” occur. Some variations of “*fluviatilis*” are registered also in the rivers of Ponto-Caspian area. The present study suggests that either several separate species exist (overlapping in many features though) or, alternatively, these forms can be interpreted as local variants of one or few polymorphic species. Some of these morphotypes may represent hybrids that evolved in the intergradation zone of freshwater *Th. fluviatilis* and brackish-water *Th. pallasi*. A further study that would combine all available data on morphology, genetics, distribution (including depth ranges of species), and ecology is required to determine how many valid species of the genus *Theodoxus* exist in the Ponto-Caspian region and what are the proper names for their designation.

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