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Cambaloid millipedes of Tasmania, Australia, with remarks on family-level classification and descriptions of two new genera and four new species (Diplopoda, Spirostreptida)

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Abstract

The Southern Hemisphere cambaloid millipede genera are here assigned or re-assigned to the families Cambalidae Bollman, 1893 and Iulomorphidae Verhoeff, 1924. *Tasmanocambala* is erected for the three Tasmanian cambalids, *T. greeni* **gen. n., sp. n.** (type species), *T. tasmanica* **sp. n.** and *T. taylori* **sp. n.** The new genus is distinguished by a thin, transverse tab at the tip of the anterior gonopod telopodite with a comb of setae immediately behind the tab. The iulomorphid *Talomius weldensis* **gen. n., sp. n.** is described from a single site in Tasmania's southern mountain district. The new species is unusual among the Australian Iulomorphidae in having a fully-developed, ambulatory leg 1 in the male, and small, compact gonopods.

Keywords

Diplopoda, Spirostreptida, Cambalidae, Iulomorphidae, Tasmania, Australia

Introduction

The classification of the cambaloid spirostreptidans has long been unsettled:

> "*Suborder Cambalidea. The systematics of this group are, and will for a long time remain, in a state of particular confusion...*" (Hoffman 1980: 82).
> "*Throughout this century great confusion has reigned regarding the classification of the 'Cambalida'...*" (Jeekel 1985: 101)
> "*Having had very little experience with cambalidans, I am not in a position to resolve this chaos...*" (Shelley 2003: 191).
> "*Confusion still reigns in the various classification databases available on the WWW, and the position of all the "cambalidan" families are chaotic...*" (Korsós and Johns 2009: 2).

Especially confusing has been the systematics of the Australasian cambaloid genera, which have even been placed in different orders (Mauriès 1987). In his classification of the Diplopoda, Hoffman (1980) placed three of the Australasian cambaloid genera in Cambalidae Bollman, 1893 and the rest in Iulomorphidae Verhoeff, 1924, which he described as "an assemblage of incongruities" (Hoffman 1980: 84). The 10 Southern Hemisphere iulomorphid genera were "provisionally referred here pending revisionary studies" (Hoffman 1982: 699).

Jeekel (1985) accepted Hoffman's grouping as a working classification, and drew a tentative distinction between Cambalidae and Iulomorphidae. In both families the anterior gonopods are thought to deliver sperm, but the posterior gonopods are better developed in Cambalidae. Twenty years later, after examining the eastern Australian cambaloids he had collected in 1980, Jeekel retained the two-family classification and offered another diagnostic character:

> "*The main character used for distinguishing the Cambalidae from the Iulomorphidae is the presence of a well developed flagellum in the anterior gonopods. It remains to be seen if this character is of sufficient importance to separate the two groups. In the family Julidae genera with and without a flagellum may be quite closely related.*" (Jeekel 2006: 65)

Korsós and Read (2012) decided that presence/absence of a flagellum was not of sufficient importance, and placed all Southern Hemisphere cambaloid genera in Iulomorphidae:

> "*...we prefer here to consider all the following 15 genera in the family Iulomorphidae. The only diagnostic difference for separating Iulomorphidae from Cambalidae was the absence of a flagellum in the anterior gonopods (Jeekel 2006a) but this can be a homoplastic, convergent character state as has been shown for the family Julidae (Enghoff 1981, Read 1990). Given this situation, we think it is plausible to combine the very similar Southern Hemisphere (i.e. Gondwanan) elements into one family.*" (Korsós and Read 2012: 44)

Since "Gondwanan" and "Southern Hemisphere (-dwelling)" are not synapomorphies, this action left Iulomorphidae sensu Korsós & Read, 2012 not diagnosable on morphology. I accepted Iulomorphidae sensu Korsós & Read, 2012 for *Amastigogonus* Brölemann, 1913, *Atelomastix* Attems, 1911 and *Equestrigonus* Mesibov, 2017 (Mesibov 2017a). However, like Jeekel I have examined two distinct groups of Australian cambaloids: flagella-bearing taxa with relatively well-developed posterior gonopods and non-flagella-bearing taxa with greatly reduced posterior gonopods. The two groups differ ecologically as well, at least in southeast mainland Australia and Tasmania. The first group is most abundant in leaf litter and is common in dry forest and woodland, while the second is mainly associated with rotting wood in higher rainfall areas.

The higher classification of Australasian cambaloids may be resolved in future with the inference of a molecular phylogeny of the group. In the meantime, although I do not wish to further confuse the already muddled classification of the cambaloids, I would like to formalise the distinction between the two Australasian cambaloid groups. I am therefore restoring the Southern Hemisphere genera to the families in which they were placed by Hoffman (1980), with the addition of new Australian genera as assigned by Jeekel (2006, 2009) and Mesibov (2017a), and with species numbers from MilliBase (http://www.millibase.org/; accessed 2 January 2019) amended following Korsós and Read (2012) and Mesibov (2017a, 2017b) as follows:

Southern Hemisphere genera of Cambalidae Bollman, 1893:

Apocoptogonus Jeekel, 2006 (2 spp; eastern Australia)
Dimerogonus Attems, 1903 (1 Australian sp; eastern Australia)
Eumastigogonus Chamberlin, 1920 (11 spp; New Zealand)
Euryischiogonus Jeekel, 2009 (1 sp; eastern Australia)
Proscelomerion Verhoeff, 1924 (1 sp; eastern Australia)
Stenischiogonus Jeekel, 2009 (1 sp; eastern Australia)
Zinagon Chamberlin, 1957 (1 sp; southern Chile)

Genera of Iulomorphidae Verhoeff, 1924:

Amastigogonus Brölemann, 1913 (11 spp; Tasmania)
Atelomastix Attems, 1911 (30 spp; western and eastern Australia, including Tasmania)
Dinocambala Attems, 1911 (1 sp; western Australia)
Equestrigonus Mesibov, 2017 (1 sp; Tasmania)
Iulomorpha Porat, 1872 (ca 18 spp; southern Africa; excluding the three Australian "*Iulomorpha*" of Silvestri (1897), which may be cambalids)
Merioproscelum Verhoeff, 1924 (1 sp; eastern Australia)
Podykipus Attems, 1911 (3 spp; western Australia)
Samichus Attems, 1911 (2 spp; western Australia)
Thaumaceratopus Verhoeff, 1924 (2 spp; eastern Australia)
Victoriocambala Verhoeff, 1944 (2 spp; eastern Australia)

Cambalidae as recognised here and by Hoffman (1980, 1982) and Jeekel (2006, 2009) is a temporary, place-holding taxon and may not be a natural group. It can be distinguished from Iulomorphidae within the Australasian cambaloids by the much greater development of the posterior gonopods and by the presence of a long, very slender flagellum arising medially near the base of the anterior gonopod coxa.

In this paper I describe a new genus and three new species of Cambalidae from Tasmania. I also describe an interesting new species of Tasmanian Iulomorphidae and erect for it a new genus.

Materials and methods

All specimens are preserved in 80% ethanol in their respective repositories.

Photomicrographs were taken with a Canon EOS 1000D digital SLR camera mounted on a Nikon SMZ800 binocular dissecting microscope equipped with a beam splitter. Measurements were made to the nearest 0.1 mm with the same microscope using an eyepiece grid and a reference scale. Photomicrographs used in the figures are focus-stacked composites prepared with Zerene Stacker 1.04. Scanning electron microscope images were acquired digitally using an Hitachi SU-70; specimens were examined after air-drying and sputter-coating with a minimal layer of platinum, then removed from stubs and returned to alcohol. The gonopods of the iulomorphid holotype were temporarily mounted in 1:1 glycerine:water and imaged using an eyepiece video camera mounted on an Amscope binocular microscope. Preliminary drawings of the gonopods were traced from printed copies of images, and drawings were then edited by reference to the actual specimens. Images and drawings were prepared for publication using GIMP 2.8.

Maps were drawn with QGIS 2.4. Latitude/longitude figures in the text (all based on the WGS84 datum) are given in decimal degrees to four decimal places, together with a spatial uncertainty. In some cases, collecting site locations have been upgraded from UTM grid references (on original labels, with the AGD66 datum), based on advice from collectors and the latest digital mapping of Tasmania. The spatial uncertainty figure covers the likely error in the location upgrade as well as my estimate of the likely error in the original location. All specimen records referred to in the text are in Supplement 1.

I follow Enghoff et al. (1993) in counting trunk rings by excluding the telson and giving podous + apodous ring counts, e.g. "(55+1) rings", and I give the upper limits of the count ranges I observed rather than count frequencies.

Abbreviations:

QVMAG	Queen Victoria Museum and Art Gallery, Launceston, Australia
TMAG	Tasmanian Museum and Art Gallery, Hobart, Australia
ZMUC	Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark

Results

Order Spirostreptida Brandt, 1833
Family Cambalidae Bollman, 1893

Tasmanocambala gen. n.

http://zoobank.org/667CC914-B9F5-4489-9DEB-747074BC19E1

Type species. *Tasmanocambala greeni* sp. n., by present designation.

Name. "Tasmano", combining form of Tasmania + *Cambala*, type genus of Cambalidae; feminine gender.

Diagnosis. Differs from the other seven Southern Hemisphere cambalid genera by the anterior gonopod telopodite ending in a thin tab just anterior to an apical, transverse comb of setae; from *Dimerogonus* and *Eumastigogonus* in having a smoothly rounded apex of the coxal process, without a medial extension; from *Proscelomerion* in lacking a pseudoflagellum and in having a rounded rather than acuminate tip on the coxal process; from *Apocoptogonus* and *Euryischiogonus* by the flagellum not having a bifurcate tip; from *Stenischiogonus* by the lack of a distinct medial lobe on the tip of the anterior gonopod telopodite; and from *Zinagon* by the male leg 1 femur being much wider than the more distal three podomeres and by the anterior section of the posterior gonopod lacking a needle-like extension.

Description. Living animals grey-black, in life with lighter-coloured annular band at rear of metazonite. Male/female midbody diameters to ca 2.5/2.9 mm; trunk ring counts to 55/56.

Head smooth apart from sparse setae on clypeus. Antenna reaching ring 2 dorsally when extended, relative antennomere lengths (3,6)>(2,4,5), 6th antennomere widest, 4 apical cones. Ocelli of older individuals in 3 or 4 rows, posterior row longest with 7+ ocelli. Collum half-moon-shaped in dorsal view; corners broadly rounded. Gnathochilarium (Fig. 1A) with gnathochilarial stipetes well separated posteriorly by wide mentum; a broad medial depression in the mentum, deepest posteriorly, with anteriorly concave posterior margin; promentum triangular with base of triangle convex. Trunk rings (Fig. 2A-C) smooth, shiny; prozonite demarcated from metazonite by shallow constriction containing suture dorsally; suture turning posteriorly just ventral to ozopore, becoming dorsalmost of parallel series of horizontal striae on lateral and ventral portions of metazonite; limbus short, lamellar. Ozopores beginning on ring 6 at ca 1/2 ring height, slightly higher on subsequent rings; ozopores very small, round, in small, slight depressions at slightly less than 1/2 the distance between suture and posterior metazonite margin. Telson with dorsal margin of preanal ring only slightly produced, not forming distinct epiproct; hypoproct margin broadly paraboloid. Midbody legs ca 1/2 ring diameter in length; relative podomere lengths (prefemur=tarsus) >femur>postfemur>tibia; claw ca 1/2 as long as tarsus.

Male leg 1 (Fig. 1B) on undivided sternite; coxae fused with sternite but demarcation clearly visible; coxa mediolaterally widened and anteroposteriorly flattened, a few long setae in 1 or2 transverse rows on distolateral margin of coxa; prefemur very short, wide, subcylindrical; femur wide, tapering distally, extended basally on anterior surface as bluntly rounded process overlapping both prefemur and coxa; postfemur and tibia subcylindrical; tarsus subcylindrical and tapering distally, with deep, narrow groove medially (Fig. 1C); claw absent (or in some specimens small, malformed, on one leg of a pair); a few very small setae on distalmost 4 podomeres; relative widths prefemur > femur >> postfemur > tibia > tarsus; relative lengths (femur = tarsus) > postfemur > tibia > prefemur.

Aperture on ring 7 (Fig. 2D-F) cordate (apex to rear), the lateral margins slightly raised. Anterior and posterior gonopods forming small, compact structure, tilted posteriorly in ring 7. Coxa of anterior gonopod (Figs 1D, E; 2) about as long as telopodite or a little shorter, anteroposteriorly flattened and with large posterior concavity holding telopodite; apex rounded and very thin, directed distomedially; flagellum not bifurcate, arising medially on coxal base and curving first posterobasally, then distally, then anteriorly. Telopodite of anterior gonopod (Fig. 1D, E) not as wide as coxa, tapering distally, posterolaterally slightly excavate with a few very short setae in deepest portion of excavation near base ("rudimentary terminal podomere" of Korsós and Read (2012)); telopodite ending in translucent, rounded tab with comb of setae just posterior to tab, the setae shorter than tab. Posterior gonopods (Fig. 1F) reaching ca 2/3 height of anterior gonopods; anteriorly divided by deep, oblique groove into anterolateral and posteromedial sections, subequal in height; anterolateral section tapering at ca 1/2 section height from wide base to apically rounded lamina; posteromedial section with apex stout, bluntly rounded and tipped with sparse brush of short setae, and with row of very short setae along anteromedial margin of section.

Females like males in overall appearance but noticeably stouter; vulvae not examined.

Distribution. So far known only from Tasmania, Australia.

Remarks. Males of *Tasmanocambala* gen. n. species are identifiable by examination of the tip of the anterior gonopod, even with the gonopods lying in situ in ring 7: there is a terminal fringe of setae apparent behind a thin, translucent, anterior tab. The type species is likely to be a species complex (see Remarks on the type species) and the taxonomy of this genus would greatly benefit from genetic analysis.

The deep medial groove on the male leg 1 tarsus (Fig. 1C) is hard to detect with optical microscopy. It may be an autapomorphy for the genus, or it may be present in other cambaloid millipedes but overlooked by describers.

Tasmanocambala greeni sp. n.

http://zoobank.org/AE0BA87A-060C-405A-818A-CD30E374AB9E
Figs 1A, B, D, F; 2A, D

Holotype. Male in pieces, gonopod complex in genitalia vial, Maggs Mountain Road, Tasmania, -41.6908, 146.2075 ±2 km, ca 450 m a.s.l., 8 October – 6 November 1979, R.H. Green, QVMAG QVM:2017:23:0006.

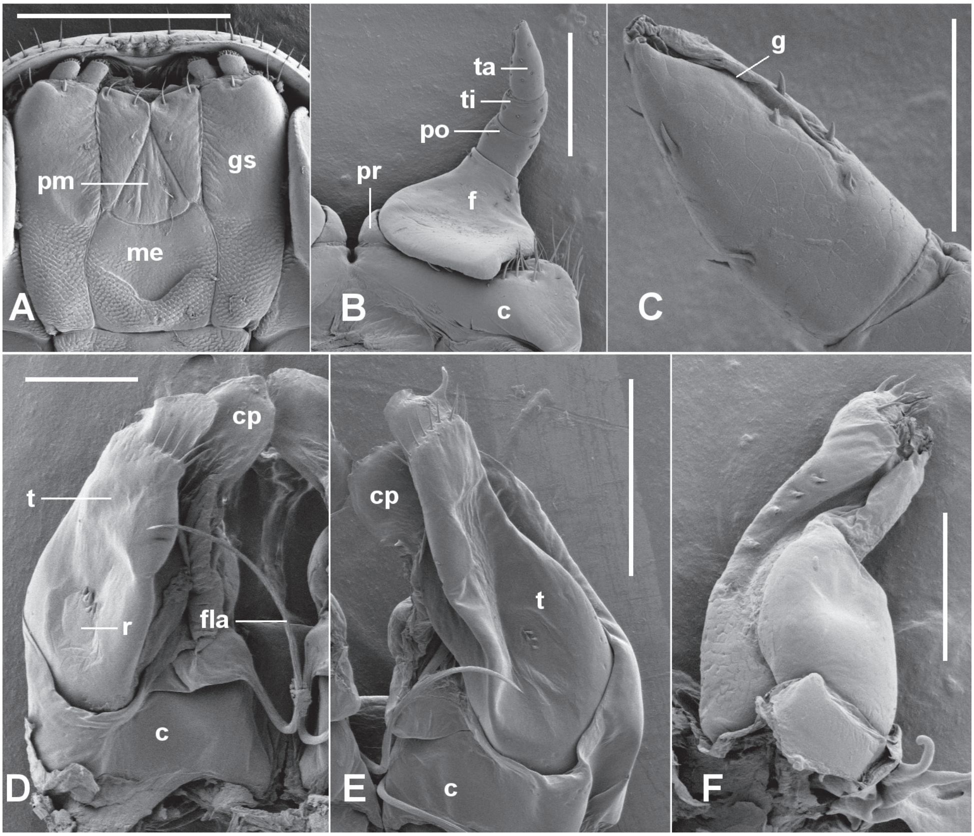

Figure 1. *Tasmanocambala greeni* gen. n. et sp. n. (**A, B, D, F**) and *T. tasmanica* sp. n. (**C, E**). **A** gnathochilarium; QVM:2017:23:0028 **B** left leg 1, anterior view; QVM:2017:23:0034 **C** tarsus of right leg 1, anterior view; QVM:2017:23:0091 **D** right anterior gonopod, posterior view; QVM:2017:23:0028 **E** left anterior gonopod, posterior view; QVM:2018:23:0075 **F** left posterior gonopod, anterior view; QVM:2017:23:0028. **c** = coxa, **cp** = coxal process, **f** = femur, **fla** = flagellum, **g** = medial groove on tarsus, **gs** = gnathochilarial stipes, **me** = mentum, **pm** = promentum, **po** = postfemur, **pr** = prefemur, **r** = "rudimentary terminal podomere" of Korsós and Read (2012), **t**= telopodite, **ta**= tarsus, **ti** = tibia. Scale bars: 0.5 mm (**A**); 0.25 mm (**B, E**); 0.1 mm (**C, D, F**).

Paratypes. In QVMAG: 1 female, same general locality and collector as holotype but compartment 2 turnoff, -41.7264, 146.1872 ±1 km, ca 880 m a.s.l., 17 May 1979, QVM:2017:23:0005; 2 females, same details but 4 February 1980, QVM:2017:23:0007; 1 male, 6 females, same details but from "tussock corner", -41.6908, 146.2075 ±2 km, 18 March 1980, QVM:2017:23:0008; 2 males, same details but from "plateau rainforest", 3 December 1980, QVM:2017:23:0009; 1 female, same details but from "site F", -41.7269, 146.1878 ±1 km, ca 880 m a.s.l., 14 January 1981, QVM:2017:23:0010; 1 male, same details but 23 September 1981, QVM:2017:23:0277; 1 female, same details but 20 February 1989, QVM:2017:23:0020; 3 females, same details but from "site E", -41.7258, 146.1867

±1 km, ca 800 m a.s.l., 9 February 1982, QVM:2017:23:0011; 2 females, same details but 21 February 1984, QVM:2017:23:0012.

Other material. 89 males and 76 females from 44 sites other than the type locality, in QVMAG, TMAG and ZMUC; see Supplement 1 for details.

Description. As for the genus, with the following details: male/female to 55+1/56+1 rings, 1.9/2.3 mm in midbody diameter. Anterior gonopod tip with 3–5 setae behind apical tab, on medial side (Fig. 1D).

Distribution. Widespread in Tasmania but not yet recorded from the Midlands or the Northeast (Fig. 5A).

Name. In honour of Robert “Bob” Green (1925–2013), Tasmanian zoologist and former Curator of Zoology at QVMAG. Green collected the type specimens of *T. greeni* sp. n. during his 15-year study of the impact of logging operations at Maggs Mountain in northwest Tasmania.

Remarks. This species is likely to be a species complex, as there are geographically correlated variations in body size and in the length, position and distinctiveness of the horizontal striae on the trunk rings. However, I have not been able to observe any consistent, corresponding differences in gonopod structure. I chose the type specimens from the largest form in the putative species complex; this larger form mainly occurs in mid – to high-elevation areas in northwest and central Tasmania.

***Tasmanocambala tasmanica* sp. n.**

http://zoobank.org/F5885BDE-74BE-4A88-8CDF-B6DEE34D488B
Figs 1C, E; 2B, E

Holotype. Male, Mt Gnomon, Tasmania, -41.1777, 146.0289 ±25 m, 290 m a.s.l., 16 April 2016, R. Mesibov, QVMAG QVM:2018:23:0116.

Paratypes. In QVMAG: 2 males, 4 females, details as for holotype, QVM:23:54461; 1 male, same locality and collector, -41.1739, 146.0344 ±100 m, 14 February 1996, QVM:2017:23:0057; 3 males, 3 females, same locality and collector, -41.1775, 146.0285 ±25 m, 300 m a.s.l., 5 February 2017, QVM:2017:23:0091.

Other material. 53 males, 47 females from 42 sites other than the type locality, in QVMAG; see Supplement 1 for details.

Name. This species appears to be endemic to Tasmania.

Diagnosis. Distinguished from *T. greeni* n. sp. and *T. taylori* n. sp. by the annular striae on the prozonite and by the larger number of setae in the apical comb on the anterior gonopod telopodite.

Description. As for the genus, with the following details: in life, legs distinctly red-coloured in life (colour fades in alcohol) and strongly contrasting light-coloured annular band at rear of metazonite; male/female to 52+1/56+1 rings, 2.5/2.9 mm in midbody diameter. Trunk rings with variable number of annular striae on prozonite anterior to suture, most obvious ventrally (Fig. 2B). Anterior gonopod coxa (Figs 1E, 2E) with broad tip, usually wider than in *T. greeni* n. sp., usually shorter than telopodite; setal comb behind apical tab extending full width

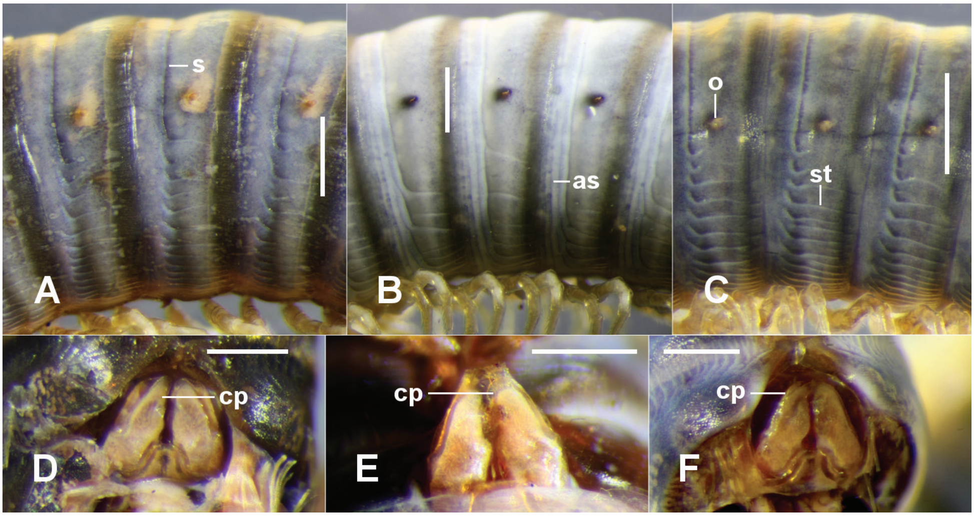

Figure 2. A–C Left lateral views of midbody rings of *Tasmanocambala greeni* gen. n. et sp. n. (**A** holotype), *T. tasmanica* sp. n. (**B** paratype ex QVM:23:54461) and *T. taylori* sp. n. (**C** holotype). **D–F** Ventral views of gonopod complex in situ of *T. greeni* gen. n. et sp. n. (**D** QVM:2018:23:0080), *T. tasmanica* sp. n. (**E** paratype ex QVM:23:54461) and *T. taylori* sp. n. (**F** paratype ex QVM:2017:23:0057). **as** = annular stria, **cp** = coxal process, **o** = ozopore, **s** = suture, **st** = horizontal stria. Scale bars: 0.5 mm (**A–E**), 0.25 mm (**F**).

of telopodite tip and with 7-10 setae; tab sometimes with small finger-like projection laterally.

Distribution. East of Tyler's Line (Mesibov 1994) in the Northwest, but apparently absent from the northeast of the main island and from islands in Bass Strait (Fig. 5B). The polydesmidan *Tasmanodesmus hardyi* Chamberlin, 1920 is similarly distributed (Mesibov 2004).

Remarks. *Tasmanodesmus tasmanica* n. sp. is the largest cambalid species in Tasmania and could be confused at first glance with the similar-sized iulomorphid *Equestrigonus tasmaniensis* Mesibov, 2017. The two spirostreptidans have not yet been found to co-occur, but their ranges may overlap in wet forest south of Wynyard and near Blessington.

Tasmanodesmus tasmanica sp. n. is very abundant in the Dial Range south of Penguin (i.e., around the type locality), where it can readily be found in and under damp leaf litter in wet eucalypt forest at any time of year.

Tasmanocambala taylori sp. n.

http://zoobank.org/3E485A0D-02E3-4948-BF3B-ADD70407500E
Fig. 2C, F

Holotype. Male in 3 pieces, anterior portions in genitalia vial, Badgers Hill, Flinders Island, **Tasmania**, – 40.0275 148.0233 ±100 m, ca 200 m a.s.l., 31 August 1993, R.J. Taylor, QVMAG QVM:2018:23:0115.

Paratypes. In QVMAG: 2 females, details as for holotype, QVM:2017:23:0041.

Other material. 18 males, 41 females and 3 juveniles from 11 other sites on Flinders Island and 4 sites on Prime Seal Island, in QVMAG and TMAG; see Supplement 1 for details.

Name. In honour of Robert Taylor, collector of the type specimens. During his 13 years in Tasmania, Taylor instigated and managed a number of forest conservation projects that employed the author and other local zoologists as field workers and specimen processors. Material collected for those projects has been a valuable taxonomic resource for the author and others, and will continue to be valuable for years to come.

Diagnosis. Distinguished from *T. tasmanica* n. sp. by the absence of annular prozonite striae and from *T. greeni* n. sp. by the strong mediad curvature and greater narrowing of the tip of the anterior gonopod coxa.

Description. As for the genus, with the following details: male/female to 55+1/52+1 rings, 1.4/1.8 mm in midbody diameter. Anterior gonopod with tip of coxa curving strongly medially and narrowing (Fig. 2F); 3-4 apical telopodite setae behind tab on medial side.

Distribution. So far known from Flinders and Prime Seal Islands at the eastern end of Bass Strait between Tasmania and Victoria (Fig. 5A).

Remarks. *Tasmanodesmus taylori* sp. n. is not greatly different from central Tasmanian forms of *T. greeni* n. sp., and the narrowing of the tip of the anterior gonopod coxa is variable from specimen to specimen.

Suborder Epinannolenidea Chamberlin, 1922
Family Iulomorphidae Verhoeff, 1924

Talomius gen. n.

http://zoobank.org/670C1ED1-7903-481B-B3E4-2249DEE9641C

Type species. *Talomius weldensis* sp. n., by present designation.

Name. Anagram of "tasm" from "Tasmania" and "iulo" from "Iulomorphidae"; masculine gender.

Diagnosis. Distinguished from all other genera of Iulomorphidae by the male first legs having a reduced prefemur, but with the four more distal podomeres appearing as in normal walking legs, including a normal claw on the tarsus; and distinguished from the other nine Australian iulomorphid genera by the small size of the gonopods relative to ring 7 diameter, by the strong medial curvature of the coxal process on the anterior gonopod, and by the bare, posteriorly curving apex of the anterior gonopod telopodite terminating in the opening of the prostatic groove.

Description and distribution. As for the type species.

Talomius weldensis sp. n.

http://zoobank.org/8137B3A4-3385-4A1A-9E83-7F07B8427957
Figs 3, 4

Holotype. Male, dissected, with pieces in genitalia vials (see Remarks), Mt Weld altitudinal transect, **Tasmania**, – 42.9981 146.6167 ±100 m (originally UTM 55G “468762 5239322”, GDA94 datum), ca 600 m a.s.l., pitfall 5U emptied 28 March 2012, M. Driessen and N. Doran, QVMAG QVM:2018:23:0118.

Paratypes. In QVMAG: 2 males, dissected and without gonopods (see Remarks), details as for holotype, QVM:23:54522.

Other material. None.

Name. For the type locality, Mt Weld.

Description. In alcohol, specimens grey-brown with lighter annular band at rear of metazonite. Largest male (paratype) with 36+4 body rings, 1.9 mm midbody diameter. Head smooth, clypeus moderately setose. Ocellar area lenticular; ca 20 ocelli in 4 rows in largest male (paratype), dorsal > ventral 6,6,5,3. Antennae short, just reaching rear of ring 2 when extended dorsally; relative antennomere lengths (2=3=6)>(4=5); antennomere 6 widest; 4 apical cones. Gnathochilarium (Fig. 3A) with lateral edges of mentum slightly convex; mentum wider than combined lingual plates, anterior edge strongly concave, posteriorly with wide medial depression, the posterior lip of the depression sharply defined, broadly “U”-shaped; promentum triangular with base of triangle convex. Collum strongly convex, almost symmetrical around transverse axis, the corners bluntly acuminate. Ring 2 with ventrolateral margin slightly produced, rings 3 and 4 similarly produced but less so. Prozonites and metazonites (Fig. 3C) smooth, shiny; shallow waist with weakly defined suture line, most distinct dorsally; indistinct, fine horizontal striae in lower 1/3 of trunk rings, anteriorly bending upwards and extending anteriorly onto the prozonite, past an imaginary continuation of the suture. Limbus lamellar, undivided. Ozopore on ring 6 at ca 1/2 ring height, slightly higher on subsequent rings; ozopores small, round, located ca 1/3 the distance between suture and posterior metazonite margin. Telson with preanal ring smooth; posterior margin only slightly extended over anal valves medially, not forming distinct epiproct; hypoproct with gently convex dorsal margin. Midbody legs ca 2/3 ring diameter in length; relative podomere lengths (prefemur=femur=tarsus)>postfemur>tibia.; claw ca 1/2 as long as tarsus. No prefemoral tab on any legs.

Leg 1 (Fig. 3B) with coxa laterally produced, anteroposteriorly flattened, with a few setae on distal margin lateral to prefemur; prefemur reduced, with normally long setae; distal podomeres as in walking legs, with normally long setae; relative podomere lengths femur>tarsus>postfemur>tibia>>prefemur; claw ca 1/2 tarsus length. Leg 2 with penis forming a small plate at posterodistal end of elongated coxa.

Aperture (Fig. 3D) V-shaped (apex to rear), the margin thickened and slightly raised posteriorly. Gonopods (Figs 3D, 4) in situ forming small, compact complex strongly tilt-

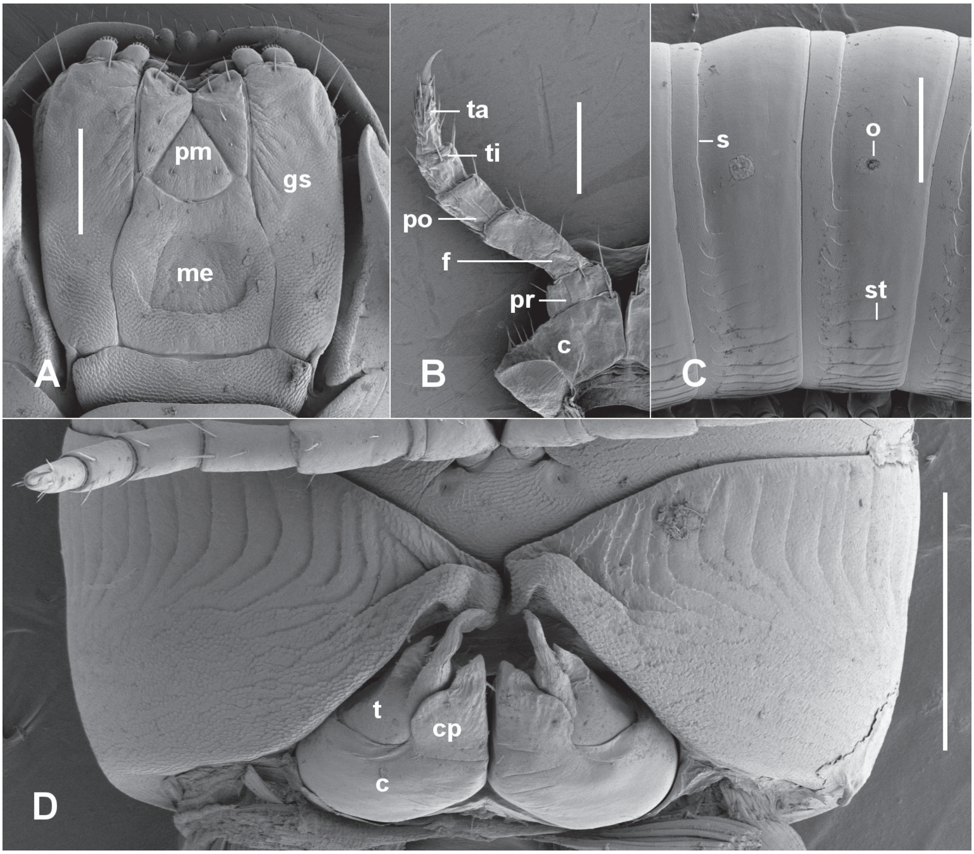

Figure 3. *Talomius weldensis* gen. n. et sp. n. , holotype. **A** gnathochilarium **B** right leg 1, anterior view (leg shrivelled due to drying) **C** midbody ring, left lateral view **D** ring 7, ventral view. **c** = coxa, **cp** = coxal process, **gs** = gnathochilarial stipes, **me** = mentum, **pm** = promentum, **o** = ozopore, **s** = suture, **st** = horizontal stria, **t** = telopodite. Scale bars: 25 mm (**A**); 0.5 mm (**B–D**).

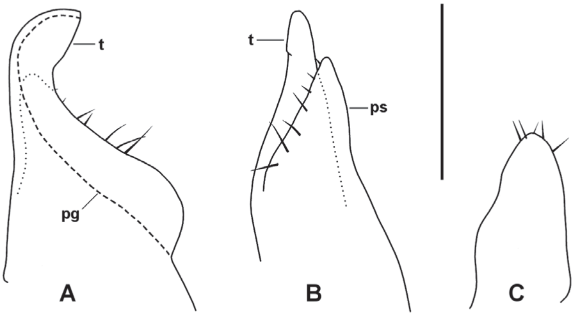

Figure 4. *Talomius weldensis* gen. n. et sp. n., holotype. Left anterior gonopod, medial (**A**) and posterior (**B**) views, and right posterior gonopod (**C**), posterior view. Dashed line (**pg**) indicates course of prostatic groove, dotted lines indicate outline of hidden structure. **pg** = prostatic groove, **ps** = pseudoflagellum, **t** = telopodite. Scale bar: 0.25 mm (approximate).

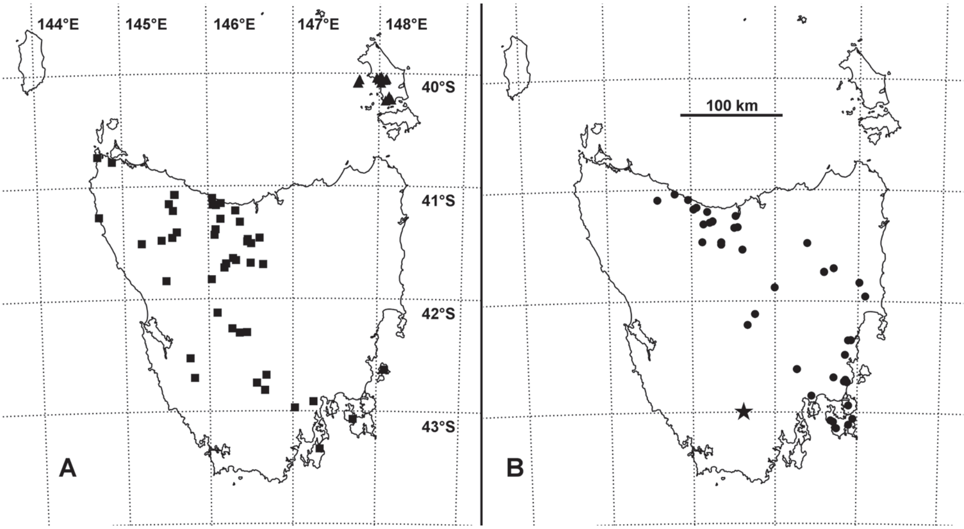

Figure 5. Known localities as of 31 December 2018 for *Tasmanocambala greeni* gen. n. et sp. n. (**A** squares), *T. tasmanica* sp. n. (**B** circles), *T. taylori* sp. n. (**A** triangles) and *Talomius weldensis* gen. n. et sp. n. (**B** star). Mercator projection; distance scale approximate.

ed posteriorly. Anterior gonopod coxa short, bulbous, cradling base of telopodite laterally; coxal process arising distomedially and extending as flattened tab curving posteriorly and partly sheltering telopodite medially. Telopodite (Fig. 4A, B) erect, taller than coxal process, broad basally and strongly tapered. the tip curving posteriorly; pseudoflagellum wide, branching off medially at ca 2/3 telopodite height, paralleling telopodite but not as high, broadly rounded at apex; posterior surface of telopodite with narrow, flattened ridge bearing a few setae, continuing distally on pseudoflagellum; prostatic groove running along posteromedial surface of telopodite base, curving anterodistally and following outer margin of telopodite, terminating at posteriorly directed telopodite tip.

Posterior gonopods (Fig. 4C) separate, less than 1/2 anterior gonopod height; cradled within coxal recess and partly sheltered distally by telopodite base; fingertip-shaped with flattened anteromedial surface distally and with 5 or 6 short apical setae.

Distribution. Known only from the type locality (Fig. 5B).

Remarks. When sorting spirostreptidan millipedes for an article on Tasmanian Iulomorphidae (Mesibov 2017a), I set aside the three Mt Weld males as “Cambalidae”, because the males had a small, compact gonopod complex like the Tasmanian cambalids described above, and the legs lacked the prefemoral tabs found in Australian Iulomorphidae. The males also had apparently ambulatory first legs, which so far as I am aware have not been reported before in any iulomorphids. When preparing the current article, I removed the gonopods of two of these “cambalids” and cleared and imaged one of the undissected complexes. Unfortunately, I then lost the two gonopod complexes, leaving only one of the three males intact. Rings 7 and 8 of that male were removed for SEM imaging of the gonopod complex (Fig. 3D), but with only a very thin coat of metal applied. The rings were returned to alcohol and the gonopods dissected and illustrated here; this specimen has been designated the holotype.

I regret not having additional material of *T. weldensis* n. sp. for study and description, but the type locality is in Tasmania's southern mountain district, which in 2019 remains a remote and little-sampled wilderness area. The three known specimens of *T. weldensis* n. sp. were in pitfall traps emptied on 28 March 2012 at 600 m on Mt Weld, during a biological monitoring study along an altitudinal transect. They were among ca 50 *Amastigogonus verreauxii* (Gervais, 1847) (Iulomorphidae) in pitfalls emptied on the same day at the same elevation (*A. verreauxii* records in Mesibov (2006-2019)). The Mt Weld study generated its invertebrate samples in 2001-2002 and again in 2011-2012. I did not observe any other *T. weldensis* n. sp. specimens among the millipedes pitfall-trapped in the two sampling periods.

Discussion

There are far fewer specimens of Cambalidae in Tasmanian museum collections than of Iulomorphidae. My field experience over 45 years in Tasmania is that this difference is not due to sampling bias, but reflects the patchy distribution of Cambalidae. Where they occur, however, Cambalidae are often abundant. This "abundant but patchy" distribution is also characteristic of procyliosomatid Sphaerotheriida in Tasmania. Hundreds of pill millipedes can be found in small patches of richly organic forest soil in some areas, while none are seen in apparently identical macro – and microhabitats nearby.

The patchiness of cambalids in Tasmania accords with what Jeekel (2006) observed on the Australian mainland: "During a collecting trip through New South Wales by the author and his wife between 27.X. and 12.XI.1980 only five sites out of 32 yielded representatives of the family. Since each sample consisted of a different species, it is obvious that Cambalidae are quite local in their occurrence. Possibly also their appearance in the upper layers of the soil is restricted to periods of favourable weather conditions. Under such conditions populations may be quite numerous" (Jeekel 2006, p. 65).

Jeekel found no Cambalidae in Victoria or Tasmania (Jeekel 2009, p. 83), but I have observed specimens of Victorian Cambalidae in Museums Victoria and have also collected cambalids in South Australia (specimens deposited in the South Australian Museum).

The almost complete lack of cambalid records in northeast Tasmania is curious, as the region has been intensively sampled for millipedes over many years and hundreds of iulomorphid Spirostreptida have been collected there (see fig. 7 in Mesibov (2017a)). Two, possibly introduced, cambalid species are known from Cuckoo Plantation, which is a long-established *Pinus* and *Eucalyptus* plantation near Scottsdale in northeast Tasmania (QVMAG specimen lots QVM:2017:23:0054 and QVM:2018:23:0003). These two species, one of which appears to be a *Dimerogonus*, may have been carried to Tasmania from mainland Australia on forestry equipment. I have not found additional specimens of either of these species in the Plantation or elsewhere in northeast Tasmania, despite careful recent searching. A third QVMAG specimen lot (QVM:2017:23:0016) contains a female and a juvenile of a possible cambalid from a logged forest area northeast of Goulds Country in the Northeast.

Talomius n. gen. is the fourth iulomorphid genus to be recognised in Tasmania. Like the two Tasmanian *Atelomastix* species, *T. weldensis* n. sp. may have a restricted distribution, but it also possible that the three spirostreptidans will be found to have substantial ranges when Tasmania's southern and southwestern wilderness areas are carefully sampled for millipedes in future.

Acknowledgements

I thank Henrik Enghoff (ZMUC), David Maynard and Tammy Gordon (QVMAG) and Kirrily Moore (TMAG) for the loan of specimens and assistance with registrations, and Sandrin Feig (Central Science Laboratory, University of Tasmania) for operating the Hitachi SEM. I am also very grateful to reviewer Sergei Golovatch for helpful suggestions on improving the manuscript.

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Supplementary material 1

Specimen data for Tasmanian Spirostreptida

Authors: Robert Mesibov

Data type: occurrence

Explanation note: Data file *Specimen_data_Mesibov_Tasmanian_Spirostreptida_2019.tsv* for 123 museum specimen lots of *Tasmanocambala greeni* n. gen. n. sp., *T. tasmanica* n. sp., *T. taylori* n. sp. and *Talomius weldensis* n. gen. n. sp. The file is a tab-separated table in UTF-8 encoding with the following 27 Darwin Core fields: institutionCode, catalogNumber, phylum, class, order, family, genus, specificEpithet, scientificName, typeStatus, organismRemarks, locality, country, stateProvince, decimalLatitude, decimalLongitude, geodeticDatum, coordinateUncertaintyInMeters, georeferenceSources, georeferencedBy, georeferenceRemarks, verbatimCoordinates, verbatimSRS, minimumElevationInMeters, recordedBy, eventRemarks and eventDate

Link: https://doi.org/10.3897/zookeys.827.32969.suppl1

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RESEARCH ARTICLE

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The complete mitogenome of *Helix pomatia* and the basal phylogeny of Helicinae (Gastropoda, Stylommatophora, Helicidae)

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Abstract

A complete mitochondrial genome of the Roman snail *Helix pomatia* Linnaeus, 1758 has been sequenced. The length and gene order correspond to that of other available helicid mitogenomes. We used the mitogenome sequence to reappraise the relationships among the four presumed principal groups of the helicid subfamily Helicinae. The results support the idea that the subfamily is divided between two western Palaearctic diversification centres: Iberian Peninsula and western Maghreb in the west, and Anatolia, the Aegean and Caucasus in the east. One group, the tribe Helicini, diversified in the east and the remaining three currently recognised tribes in the west. However, the exact relationships among lineages of the non-Helicini tribes could not be resolved.

Keywords

Allognathini, biogeography, Helicini, land snail, Mediterranean, mitochondrial genome, Otalini, phylogeny, Thebini

Introduction

Phylogenetic research on land snails has been thus far dominated by studies based on mitochondrial markers, mostly partial sequences of the *cox1* (COI) and *rrnL* (16S rRNA) genes, not exceeding 2000 bp in total. These genes dominate not only in terms of the amount of sequences generated, but usually also by the variability of the sequences used if combined with sequences of nuclear loci. Although modern techniques targeting many loci simultaneously begin to advance also into the phylogenetics of pulmonate land snails (Teasdale et al. 2016), the mitochondrial markers will likely continue to be used not only due to relatively low costs and accessibility of the methods, but especially thanks to the wealth of previously published data. Mitochondrial genome sequences may then become handy for primer design, to facilitate assembly of further mitochondrial genomes from outputs of high-throughput sequencing, or directly as the data for phylogenetic analyses. In fact, one of the best resolved backbone phylogenies of Stylommatophora to date was reconstructed from mitochondrial genome sequences (Groenenberg et al. 2017).

We sequenced a complete mitogenome of *Helix pomatia* Linnaeus, 1758, a large and common European edible land snail species, to provide a reference for further work focused on the family Helicidae Rafinesque, 1815. We then used other helicid mitogenomic sequences to evaluate the support for the basal branching order in the subfamily Helicinae, which was reported by Neiber and Hausdorf (2015) from analyses based on partial sequences of *rrnL* and *cox1* genes along with part of the nuclear rRNA gene cluster (5.8S rRNA, internal transcribed spacer 2, 28S rRNA).

The subfamily Helicinae includes several charismatic species, which are large, common, and edible. As the most prominent, we may mention *Cepaea nemoralis* (Linnaeus, 1758), famous for evolutionary studies of its colour polymorphism (e.g. Cain and Sheppard 1950, Jones et al. 1977, Silvertown et al. 2011), *Cornu aspersum* (Müller, 1774), the most commonly reared and consumed helicid species which became a pest in several regions around the globe (e.g. Rees 1955, Ansart et al. 2009), and *Helix pomatia*, a characteristic snail of Central Europe and the type species of the family's type genus. Each of these three species represents a different lineage of the three presumed clades constituting the Helicinae, which were proposed and assigned a tribe status in the first comprehensive molecular phylogenetic study of Helicoidea by Razkin et al. (2015). *Cepaea* represents Allognathini Westerlund, 1902, *Helix* Helicini Rafinesque, 1815, and *Cornu* Otalini Pfeffer, 1930. Razkin et al. (2015) also recognized a fourth tribe, the monotypic Thebini Wenz, 1923 represented by *Theba* Risso, 1826. The phylogenetic position of *Theba* has been contentious (Perrot 1939, Gittenberger and Ripken 1987, Bouchet and Rocroi 2005, Schileyko 2013, Razkin et al. 2015), but *Helix*, *Cornu* and *Cepaea* were generally considered closer to each other than to *Theba*, for which a separate tribe or even subfamily has been erected.

Neiber and Hausdorf (2015) used a more informative dataset than Razkin et al. (2015) and found *Cepaea, Cornu* and *Theba* to be more closely related to each other than to *Helix* and some other eastern Mediterranean genera. Their results suggest a principal biogeographic division within Helicinae, running approximately along the Apennine Peninsula and separating two equally old clades with centre of diversification in the western (*Cornu, Cepaea* and *Theba,* with their respective relatives) and the eastern (*Helix* and relatives; Korábek et al. 2015) Mediterranean basin, respectively. Considering the Paleogene/Neogene palaeogeographic evolution of the western Mediterranean (Giusti and Manganelli 1984, Rosenbaum et al. 2002, Advokaat et al. 2014, van Hinsbergen et al. 2014), it may be expected that the western taxa are indeed more closely related to each other.

Alternatively, the eastern group may be an offshoot of the western diversity, if the western group is paraphyletic. The systematic concept and monophyly of Otalini remains an open issue, as they (in the sense of Neiber and Hausdorf 2015) may be paraphyletic to both Thebini and Allognathini, and the east-west divide has not been unambiguously supported. The absence of an east-west divide in the phylogeny would lend support to a Western European origin of the whole subfamily Helicinae and to the north-western Maghreb being a refugium of its oldest and perhaps phylogenetically most distinctive lineages. Apart from biogeographic implications, the branching order at the base of the Helicinae has for us also a practical significance for the selection of appropriate outgroup taxa for analyses of relationships between *Helix* and related genera.

There are already published complete mitochondrial genome sequences of *Ce. nemoralis* (Terrett et al. 1996; NCBI accession number NC_001816), *Co. apersum* (Gaitán-Espitia et al. 2013; NCBI accession number NC_021747) and *Theba pisana* (Müller, 1774) (Wang et al. 2018b; Genbank accession number MH362760), as well as of a convenient outgroup species *Cylindrus obtusus* (Draparnaud, 1805) (Groenenberg et al. 2012; NC_017872). Combined with the newly sequenced mitogenome of *Helix pomatia* they offered an opportunity to verify the relationships between the four Helicinae tribes.

Methods

Sequencing and annotation

As a starting point we utilised mitochondrial sequences obtained from transcriptome sequencing (mRNA-Seq) performed for a different project, which included also a single *H. pomatia* individual (from Rožmitál pod Třemšínem, Czechia). In detail, 20 mg of foot tissue was homogenised with MagNA Lyser (Roche) and total RNA was extracted using the standard Trizol reagent protocol (Thermo Fisher Scientific). The barcoded and stranded mRNA-sequencing libraries were prepared using the Illumina TruSeq mRNA v2 sample preparation kit (Illumina, San Diego, CA, USA). The libraries were loaded on an Illumina NextSeq 500 sequencer and 75 bp were sequenced uni-directionally, resulting in approx. 87 million reads. The raw Illumina reads were trimmed for adapters and low-quality bases in GENEIOUS R7.1 (Kearse et al. 2012) with the trim utility using default parameters. Reads with a length of less than 50 bp were removed from the dataset. The trimmed reads were checked for quality in FASTQC (Andrews 2010) and MULTIQC (Ewels et al. 2016), and mapped with GENEIOUS R7.1 to the mitogenome of *Co. aspersum*. The partial sequences of 12 protein coding genes (all but *atp8*) of *H. pomatia* (GenBank acc. nos. MK400678-MK400689) were extracted from the alignment and were used to design primers for PCR amplification of the mitogenome of *H. pomatia* in few long overlapping fragments.

For amplification we used another individual sharing an identical *cox1* sequence with the transcriptome data. The sample originated from Huldsessen, Bavaria, Germany (48.3978N, 12.7084E) and the shell voucher is deposited in the National Museum, Prague, lot P6M 29637. We designed specific primers with Primer BLAST (Ye et al. 2012) based on the transcriptome sequences and previous 16S data. Then, we amplified the mitogenome in several overlapping segments of ca. 4000–6000 bp with Platinum SuperFi proof-reading DNA polymerase (Invitrogen, Carlsbad, CA, USA) and sequenced ends of the fragments using the primers used for PCR. Resulting gaps were iteratively filled in further rounds of sequencing using new individual-specific primers flanking the gaps. The reads were aligned to the *Co. aspersum* sequence as reference and combined into a single 14070 bp contig. The sequence is available at GenBank (MK347426).

We used MITOS (Bernt et al. 2013b) to annotate the genome sequence, which identified the full set of the expected 2 rRNA, 22 tRNA, and 13 protein-coding genes (Table 1). However, we made manual adjustments to the MITOS output regarding the limits of rRNA and protein-coding genes, which were inconsistent between the MITOS annotation and the *Ce. nemoralis*, *Co. aspersum*, and *Cy. obtusus* RefSeq entries. To be more specific, we looked for start- and stop-codons whose positions would be compatible between *H. pomatia* and the other three species, and considered also the positions of adjacent genes. However, as gene overlap and alternative start- and incomplete stop-codons may occur in invertebrate mitogenomes (Bernt et al. 2013a) including land snails (Gaitán-Espitia et al. 2013), the start and end positions of the genes remain tentative until sequences of the coded proteins and rRNAs are known. The 16S gene was not recovered in one piece by MITOS, probably because the structure towards the 3' end was too variable; so we combined the two fragments.

Phylogenetic analyses

For the phylogenetic analysis we used a concatenated alignment of 12 protein-coding genes, excluding the short and fast evolving *atp8*. From annotated, previously published sequences (accession numbers NC_001816, NC_021747 and NC_017872), we extracted the individual genes following the annotation in the NCBI RefSeq database. However, previous studies, which used the sequence of *Ce. nemoralis* in mitogenomic phylogenetic analyses, repeatedly resulted in a spuriously long branch for this species (Knudsen et al. 2006, González et al. 2016, Minton et al. 2016, Groenenberg et al. 2017). A closer examination of the mitogenome sequence and translation of its protein coding regions revealed a very low quality of the sequence (see also White et al. 2011). Compared to newer *Ce. nemoralis* sequences there seemed to be frequent indels and suspect amino-acid changes were found in translated sequences. The very high number of errors in the sequence probably stems from the complex way it was obtained, which involved two rounds of cloning, and generally the immature methods of that time (Terrett et al. 1996). Therefore, we replaced the sequences of protein-coding genes of *Ce. nemoralis* by data retrieved from a transcriptome shotgun assembly (TSA) (Kerkvliet et al. 2017; NCBI BioProject PRJNA377398; see Table 1). To extract the mitochondrial genes from the transcriptome data, we performed for each gene a BLASTn search limited to *Ce. nemoralis* with the respective part of NC_001816 as the query in the NCBI TSA database. The sequence of *T. pisana* (MH362760) was not

Table 1. NCBI Transcriptome Shotgun Assembly database accession numbers of the *Cepaea nemoralis* sequences used in analysis.

cox1	GFLU01084822
nd6	GFLU01007552
nd5	GFLU01092360
nd1	GFLU01092360
nd4L	GFLU01092360
cyb	GFLU01076837
cox2	GFLU01076837
atp6	GFLU01122686
nd3	GFLU01014131
cox3	GFLU01122685
nd4	concatenated from GFLU01122684, GFLU01122687, GFLU01122688

annotated, so we identified the individual genes by alignment with the extracted gene sequences of the other four species.

We performed the phylogenetic analyses in three stages, staring with the analysis of the nucleotide sequences. The protein coding genes were aligned with TRANSLATORX (Abascal et al. 2010), which aligns nucleotide sequences based on their amino acid translations. TRANSLATORX was run with the MAFFT 5 aligner (Katoh et al. 2005) and the invertebrate mitochondrial genetic code; other settings were left at their defaults. The resulting alignments were trimmed to a common length of the sequences. We specified a partitioning scheme consisting of the three codon positions and used IQTREE 1.6.5 to test the scheme against simpler scenarios, select substitution models (Kalyaanamoorthy et al. 2017) and to perform a maximum likelihood phylogenetic analysis (Nguyen et al. 2015, Chernomor et al. 2016). The model selection suggested the TIM2+F+I+Γ4, TVM+F+Γ4, and TIM2+F+Γ4 models for the three partitions. We used standard bootstrap and Shimodaira-Hasegawa-like approximate likelihood ratio tests (SH-aLRT; Guindon et al. 2010; both with 1000 replicates) to calculate branch supports. Then we translated the alignment into amino acid sequences, leaving it a single partition with 417 parsimony informative sites out of the total of 3489 sites, and run the model selection (selecting mtZoa+F+Γ4 as the best fit substitution model; Rota-Stabelli et al. 2009) and phylogenetic analysis as above.

The resulting topologies showed substantial differences in branch lengths between taxa. To explore if the resulting topology was influenced by long-branch attraction (LBA), we employed a site-heterogeneous mixture model using posterior mean site frequencies (PMSF; Wang et al. 2018a). This approach has been shown to effectively overcome LBA, and even to be somewhat prone to long-branch repulsion. Thus, if a grouping is due to LBA, this approach is likely to reveal that. We calculated the PMSF under the mtZoa+C60+F+Γ4 mixture model. As a guide tree we used successively all the three alternative topologies in the western group: *Cornu*+(*Theba*+*Cepaea*), (*Cornu*+*Theba*)+*Cepaea*, and (*Cornu*+*Cepaea*)+*Theba*.

Finally, to account for differences in nucleotide composition, we performed a Bayesian phylogenetic analysis of the nucleotide data with a branch-heterogeneous model allowing branches to have distinct compositions as implemented in P4 1.0 (Foster 2004; http://p4.nhm.ac.uk/). We performed the analysis in two runs of 1,000,000 generations with four heated chains each, using the same partitioning scheme as with IQTREE and the closest possible substitution models. For each data partition we allowed for three different nucleotide compositions to be assigned to tree branches randomly. We sampled each 1000th generation and discarded the first 20% of samples of each run as burn-in. To account for differences in results caused by the use of different inference algorithms in the methods, we repeated the analysis in P4 also assuming composition homogeneity.

Table 2. Annotation of the mitogenome of *Helix pomatia*. The plus/minus strand refers to the position of the *cox1* gene.

Gene	Start position	Start codon	End position	Stop codon	Strand
cox1	1	ATG	1530	TAA	plus
trnV	1527		1589		plus
rrnL (16S)	1657		2555		plus
trnL1	2566		2626		plus
trnA	2630		2691		plus
nd6	2692	TTG	3180	TAA	plus
trnP	3177		3239		plus
nd5	3285	ATG	4955	TAA	plus
nd1	4970	ATA	5842	TAG	plus
nd4L	5842	GTG	6118	T--	plus
cyb	6119	ATG	7190	T--	plus
trnD	7234		7285		plus
trnC	7286		7345		plus
trnF	7346		7404		plus
cox2	7405	ATG	8071	T--	plus
trnY	8073		8119		plus
trnW	8121		8180		plus
trnG	8186		8233		plus
trnH	8237		8296		plus
trnQ	8296		8355		minus
trnL2	8356		8411		minus
atp8	8405	ATA	8578	TAG	minus
trnN	8579		8638		minus
atp6	8637	ATG	9290	T--	minus
trnR	9291		9349		minus
trnE	9349		9411		minus
rrnS (12S)	9479		10173		minus
trnM	10173		10235		minus
nd3	10241	TTG	10581	T--	minus
trnS2	10579		10629		minus
trnT	10632		10693		minus
cox3	10693	ATG	11472	TAA	minus
trnS1	11664		11719		plus
nd4	11720	ATA	13027	TAA	plus
trnI	13030		13090		plus
nd2	13091	GTG	14021	T--	plus
trnK	14022		14070		plus

Results

We have sequenced a complete mitogenome of *H. pomatia*, from a specimen representative of a common central-European lineage (Korábek et al. 2018) of this broadly distributed snail species. The length and gene content and order (Table 2) correspond with those of mitogenomes of *Ce. nemoralis*, *T. pisana* and *Co. aspersum*, the other Helicinae species with available mitogenome sequences.

The phylogenetic analyses in all cases recovered the expected split between the eastern *Helix* and the western group of *Theba*, *Cepaea*, *Cornu*, assuming *Cylindrus* as an outgroup (Figure 1). This grouping received equivocal support in the analysis based on the nucleotide data, but it increased with amino acid data and further when using site-heterogeneous model. The support thus increased as the analyses got less sensitive to substitution saturation and among site heterogeneity. In the western group, the results united *Theba* and *Cepaea* to the exclusion of *Cornu*, but this branch received positive support only from bootstrap with the nucleotide data. Especially analyses of the amino-acid alignment with the site-heterogeneous model based on alternative guide trees resulted in very low support for the branch uniting *Cepaea* and *Theba*. The Bayesian analysis of nucleotide data with P4 recovered the same topology as the maximum likelihood analysis but with full support, regardless whether homo- or heterogeneous model was used.

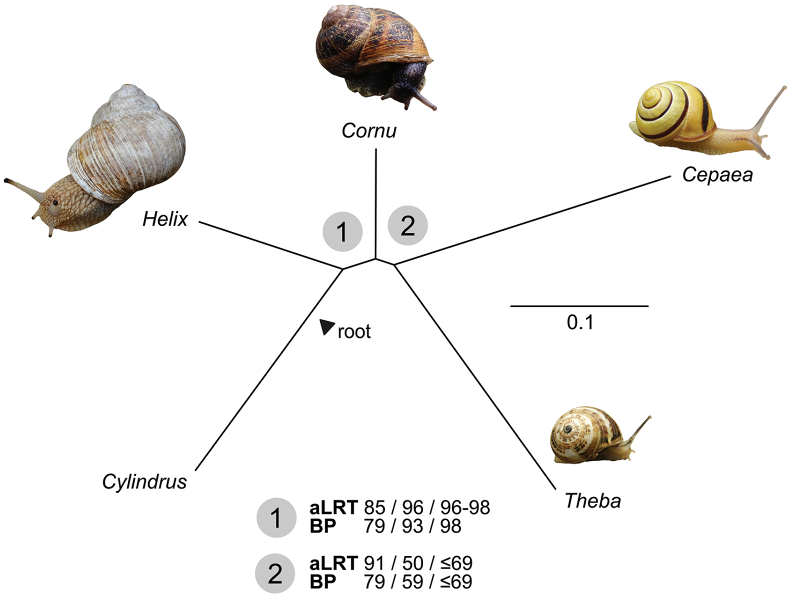

Figure 1. The inferred phylogenetic relationships between the five helicid mitogenomes available. Branch supports are given for maximum likelihood analyses based on nucleotide data, amino acid data under homogeneous model, and amino acid data under site-heterogeneous model (in this order). The latter was run under alternative settings, see details in the text. Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT) and standard bootstrap percentages (BP) are reported. Values of SH-aLRT >90 % and BP >75 % are considered positive support. *Cylindrus* is included as an outgroup.

Discussion

Because *Theba* and *Cepaea* had the longest branches in the tree, which had short internal branches, and there is no independent indication of the relationship between *Theba* and *Cepaea*, we suspected the result to be caused by the LBA (Bergsten 2005). *Theba* is annual to biannual and semelparous (Heller 1982, Cowie 1984), unlike the other helicids, which are more long-lived (Pollard 1975, Bisenberger et al. 1999; Ansart et al. 2009). The genus may generally cause problems in phylogenetic inference if the difference in life history results in differece in substitution rate (Thomas et al. 2010; cf. Saclier et al. 2018). In addition, analysis of the nucleotide composition of the five taxa revealed substantial differences, where *Cornu* (GC 30.5%) and *Cepaea* (GC 41.6%) differed the most, which could obscure potential relationship between the two species. The low support with presumably more robust methods suggests that the relationship between *Cepaea* and *Theba* could be an artefact.

Our results are consistent with the hypothesis that Helicinae are principally divided into a western (mainly Iberia, western Maghreb, Macaronesia) and an eastern (Caucasus, Anatolia, Greece) group (Neiber and Hausdorf 2015). The split between these two lineages probably occurred no later than during the Late Eocene−Early Oligocene (Neiber and Hausdorf 2015), but the east-west pattern in the distribution of the two lineages persists despite 30 million years having elapsed since the split. Only two *Helix* species naturally represent the eastern group west of ca 9°E (one in Europe, one in Africa; Neubert 2014, Korábek et al. 2018), and two species of *Cepaea* (Europe; Welter-Schultes 2012) and few species of *Eremina* Pfeiffer, 1855 (northern Africa; Ali et al. 2016) represent the western group east of 18°E.

Despite analysing a substantially higher number of genes than Razkin et al. (2015) and Neiber and Hausdorf (2015), we also could not resolve the relationships between *Cornu*, *Cepaea* and *Theba*. We assume that additional lineages should be analysed in order to resolve all the major phylogenetic and biogeographic problems within the western branch of Helicinae. These include *Macularia* Albers, 1850, whose phylogenetic position is equally problematic as that of *Theba* (Nordsieck 1987; Schileyko 2006; Neiber and Hausdorf 2015), the closest relative of *Theba* (perhaps *Eremina*, but see Holyoak et al. 2018), and the type genera of the tribes Otalini and Allognathini. Nevertheless, it is likely that only analyses of multiple nuclear loci will yield robust estimates of the basal relationships of Helicinae due to high and lineage-specific evolutionary rates of the mtDNA and the saturation of nucleotide substitutions.

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Mollusc species from the Pontocaspian region – an expert opinion list

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Abstract

Defining and recording the loss of species diversity is a daunting task, especially if identities of species under threat are not fully resolved. An example is the Pontocaspian biota. The mostly endemic invertebrate faunas that evolved in the Black Sea – Caspian Sea – Aral Sea region and live under variable salinity conditions are undergoing strong change, yet within several groups species boundaries are not well established. Collection efforts in the past decade have failed to produce living material of various species groups whose taxonomic status is unclear. This lack of data precludes an integrated taxonomic assessment to clarify species identities and estimate species richness of Pontocaspian biota combining morphological, ecological, genetic, and distribution data. In this paper, we present an expert-working list of Pontocaspian and invasive mollusc species associated to Pontocaspian habitats. This list is based on published and unpublished data on morphology, ecology, anatomy, and molecular biology. It allows us to (1) document Pontocaspian mollusc species, (2) make species richness estimates, and (3) identify and discuss taxonomic uncertainties. The endemic Pontocaspian mollusc species richness is estimated between 55 and 99 species, but there are several groups that may harbour cryptic species. Even though the conservation status of most of the species is not assessed or data deficient, our observations point to deterioration for many of the Pontocaspian species.

Keywords

Aral Sea, bivalves, Black Sea, Caspian Sea, conservation, gastropods, nomenclature, taxonomy

Introduction

The aquatic Pontocaspian (or Ponto-Caspian) biota is constituted by taxa that evolved in saline water bodies in the Caspian Sea – Black Sea – Aral Sea region and surrounding rivers in the past few million years. They include diverse groups such as diatoms, dinoflagellates, foraminiferans, crustaceans, molluscs, as well as fish and the Caspian seal. Major Pontocaspian habitats are located in the northern coastal zone of the Black Sea (mostly confined to the Romanian and Ukrainian coasts) and the Sea of Azov (mostly in the Taganrog Bay), cover the entire Caspian Sea and, until recently, the Aral Sea (Fig. 1). However, Pontocaspian habitats are impacted by human activities such as pollution, habitat modification and introduction of invasive species (Bologa et al. 1995, Zolotarev 1996, Zaitsev and Mamaev 1997, Gomoiu et al. 2002, Grigorovich et al. 2003, Occhipinti-Ambrogi and Savini 2003, Barannik et al. 2004, Shalovenkov 2005, UNEP 2006, Stolberg et al. 2006, Selifonova 2008a, b, Popa et al. 2009), as well as the entire obliteration of environments in the case of the Aral Sea in the second half of the 20th century (Mainguet and Létolle 1997, Andreeva and Andreev 2003, Plotnikov et al. 2016).

Faunas in the Pontocaspian region have strongly changed in the past century. Pontocaspian species that were abundant only a century ago, such as *Dreissena elata* and *D. caspia* in the Caspian Sea, have vanished in the mid-20th century (Kosarev and Yablonskaya 1994). For the Aral Sea, the faunas appear to have largely disappeared with the demise of the lake system since the 1950s (Andreeva and Andreev 2003). Abundances of several other species in the Caspian Sea and Black Sea Basin have severely declined (Bologa et al. 1995, Zaitsev and Mamaev 1997, Barannik et al. 2004, Popa et al. 2012).

Figure 1. Map of the Pontocaspian region with the indication of major basins, rivers, regions, and cities referred to in the text.

However, we cannot evaluate the extent or nature of biodiversity loss as there is no general agreement on the species that it might concern. Much of the diversity in Pontocaspian mollusc groups is contained within a limited number of genera. Changing taxonomic approaches through time (e.g., Zhadin 1952, Logvinenko and Starobogatov 1969, Alexenko and Starobogatov 1987, Sitnikova and Starobogatov 1999, Munasypova-Motyash 2006a, b, Anistratenko 2007b, Kijashko in Bogutskaya et al. 2013, Vinarski and Kantor 2016, Neubauer et al. 2018) combined with large morphological variability and few diagnostic characters in certain groups, as well as the paucity of living material and partial disappearance of type material, has precluded critical reassessment of species boundaries and thus species richness. For the Caspian Sea, multiple efforts to collect fresh material in the past decade failed to produce sufficient living material to elucidate these taxonomic matters for most of the groups. Sampling efforts include coastal sampling around Turali, Russia (FW, 2003); northern Azerbaijan (FW, 2016), middle and southern Azerbaijan (VA, ML, AFS, TW, 2017); Mangyshlak region coastal areas, Kazakhstan (OA, VA, 2016, 2017); the transition of the northern to middle Caspian Sea Basin in Kazakhstan (PRIDE expedition, 2017); and the Gorgan Bay in Iran (AFS, 2018). A faunal inventory of the deep-water southern Caspian Sea Basin (> 200 m water depth) of southern Azerbaijan was published lately by Mirzoev and Alekperov (2017). We are uncertain whether it concerns living material nor can we assess the species identities. Their records are mentioned below but require further confirmation. We did find some living endemic species ourselves, and from coastal areas low numbers of such species have been reported elsewhere (e.g., Latypov 2015). Yet, many species and even groups of species (e.g., *Turricaspia* species) have not been encountered alive despite our attempts. Our inability to collect life specimens for several groups has made a combined molecular-morphological approach to delineate species impossible. As a result, a reliable estimate of the number of species involved is lacking, and therefore the potential magnitude of the biodiversity decline is speculative. Hence, we need an alternative approach to outline the species boundaries and estimate the numbers affected.

By pooling all insights, data (published and unpublished) and expert opinions on the Pontocaspian mollusc species through taxonomists we aim to provide a list of Pontocaspian mollusc species that can serve as a base for further research. We use molluscs as a model group since they are (1) an important, representative and well-known part of the Pontocaspian fauna, (2) have a number of taxonomic specialists available, and (3) can often be identified based on their shell characters even when living populations have vanished. The Pontocaspian aquatic mollusc species list will highlight uncertainties in species complexes as to give guidance to further research in resolving taxonomic matters. The aim of this work is to compile a list of Pontocaspian mollusc species with the underlying arguments why we consider these species as (likely) valid species, to outline taxonomic uncertainties and to provide an updated estimate of species richness.

Materials and methods

A preliminary Pontocaspian mollusc species list was assembled during a PRIDE program workshop in Giessen, Germany, in May 2018. The PRIDE ("Drivers of Pontocaspian Rise and biodiversity Demise") program is an EU funded Innovative Training Network that studies the drivers of the rise and demise of Pontocaspian faunas. Using listings in Vinarski and Kantor (2016) supplemented with further information from the participants, this initial list was then circulated among a wider community of taxonomic workers for further updates and comments. Data on distribution and type material were derived from Vinarski and Kantor (2016) and further completed and amended. The systematic order above the species level follows Bouchet et al. (2017) and MolluscaBase (2018a). In cases where we deviate from the supraspecific classification, arguments are discussed below.

The list comprises aquatic Holocene Pontocaspian mollusc faunas. A substantial number of Pontocaspian species has been described from empty shells from beach material or derive from grab samples. Such samples typically are dominated by time-averaged Holocene shell assemblages, which may or may not yield living specimens and in very rare occasions also contain older (Pleistocene) material (see, e.g., Leroy et al. 2018). For the Black Sea Basin, the Holocene time interval largely coincides with the date of the marine flooding through the Bosphorus and subsequent marginalisation of Pontocaspian species to the NW coastal zone (Danube Delta to Dnieper Estuary) and the Sea of Azov (Mordukhay-Boltovskoy 1960). For the Caspian Sea, the time interval corresponds to the so-called Novocaspian period that started after the very deep Mangyshlak regression 8 ka (Fedorov 1953, Nevesskaja 1958, 2007, Yanina 2005). The time interval contains the earliest impact of humans on native faunas, such as the introduction of *Cerastoderma glaucum* in the Caspian Basin during the early Holocene (Fedorov 1957, Yanina 2009). It also contains the large faunal changes of the 20th century related to pollution, invasive species, and obliteration of habitats (Kosarev and Yablonskaya 1994).

Table 1. Definitions we use to characterise the status of species.

Pontocaspian	Centre of evolutionary history in Pontocaspian lakes
Native	Present in the Pontocaspian region today and in the Quaternary (not introduced by man) but centre of evolution not necessarily in that region: e.g., planorbid species with a Palearctic distribution, *Cerastoderma glaucum*.
Introduced	Species introduced in the Pontocaspian from elsewhere, usually anthropogenic: some Pontocaspian species have migrated between Pontocaspian basins and their status is explained in detail there (e.g., *Monodacna colorata/Dreissena bugensis*: introduced in Caspian from natural ranges in Black Sea Basin).
Invasive	Species that have become disruptive in the ecosystem after introduction.

One of the greatest difficulties is to establish the identities of taxa reported as geographic subspecies. Many species have forms, varieties, and subspecies described from the Aral Sea, the Caspian Sea Basin, and the Black Sea Basin (including the Azov Sea). Often, such distinctions are made based on the geographical isolation alone or on a range of morphological characters whose variation seems to be overlapping in geographical subpopulations. In order to assess whether the geographical populations are indeed species, we need combined morphological, ecological, and molecular data, but only few studies produced this information to date (e.g., Popa et al. 2012 for Black Sea Basin *Monodacna*). For the Aral Sea, we expect difficulties to obtain fresh material of almost all species for molecular analyses due to the obliteration of most of the lake and its fauna in the 20th century (Andreeva and Andreev 2003, Plotnikov et al. 2016). To date, hardly any molecular data on closely related species that are (potentially) shared between the Caspian and Black Sea have been published with the exceptions of *Dreissena grimmi/D. bugensis* (e.g., Therriault et al. 2004, Stepien et al. 2013) and *Ecrobia maritima/E. grimmi* (Haase et al. 2010). For several potentially shared species, ecological tolerances and preferences between Caspian and Black Sea Basin populations are overlapping, but in some cases (like for *D. grimmi/D. bugensis*) they are not. We have adopted a conservative approach, and as long as no additional arguments (morphological, ecological, or genetic differences) were found, we consider the Aral, Caspian and Black Sea varieties/subspecies synonyms. Another difficulty in especially Caspian taxa is the erection of so-called "bathymetric" subspecies, which seem to be distinguished mostly based on their depths of occurrence. As long as no other (morphological, genetic) arguments are available, we synonymise such bathymetrical forms.

A listing of synonyms and important past misidentifications from the literature is given. The list is not exhaustive and intended to show major shifts in taxonomic thinking about Pontocaspian and invasive species. The format of synonymy lists follows mostly suggestions of Matthews (1973). Asterisks in front of a record indicate valid first descriptions, a superscript "o" a prior yet invalidly introduced synonym. The status of each species is defined according to criteria outlined in Table 1.

As for the conservation status we have indicated the IUCN Red List status as of July 2018 from [www.iucnredlist.org] and added our own observations. For updated stratigraphic terminology and age estimates we refer to Krijgsman et al. (2019).

Abbreviations used are:

ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.
RGM	Naturalis Biodiversity Center, collections of fossil Mollusca, Leiden, The Netherlands.

For personal observations of the various authors we used the following abbreviations:

FW	Frank P. Wesselingh,	**AFS**	Arthur F. Sands,
TN	Thomas A. Neubauer,	**MV**	Maxim V. Vinarski,
VA	Vitaliy V. Anistratenko,	**TW**	Thomas Wilke.
OA	Olga Anistratenko,		

Finally, with the long literature record and various languages involved we came across some problems in spellings of geographical names and authors that we could not always resolve. Often, the transliteration of Russian names into French, German, and English literature resulted in different spellings, for example Ostroumoff/Ostroumov, Andrussoff/Andrussow/Andrusoff/Andrusov, and Apsheron/Absheron. We have followed the translations that are used by most the Russian-language authors of this paper but in some cases denote the different available spellings.

Systematic catalogue

Bivalvia

Remarks. Within the endemic bivalve species groups, a general lack of combined molecular, morphological, and ecological approaches has led to partially unresolved taxonomy, especially within the genera *Monodacna* and *Dreissena*. Much of the bivalve taxonomy follows the latest review of Caspian bivalves by Kijashko in Bogutskaya et al. (2013), and we discuss deviations from his schedule. The list of Aral bivalves published by Vinarski and Kantor (2016) is based chiefly on Andreeva and Andreev (2003), and it is used here as a base with appropriate changes in nomenclature.

Family Mytilidae Rafinesque, 1815

Mytilaster minimus (Poli, 1795)

*1795 *Mytilus minimus* Poli: 209–210, pl. 32, fig. 1.
1932 *Mytilaster lineatus* (Gmelin, 1790). – Bogachev: 38, pl. 1, figs 5–11 [**non** *Mytilus lineatus* Gmelin, 1791].
1952 *Mytilaster lineatus* (Gmelin, 1789). – Zhadin: 285, fig. 248 [**non** Gmelin, 1791].

1969 *Mytilaster lineatus* (Gmel.). – Logvinenko and Starobogatov: 311–312, figs 339a, b, pl. 5, figs 1, 2 [**non** Gmelin, 1791].
1969 *Mytilaster lineatus* (Gmelin, 1790). – Vekilov: 155–157, pl. 35, figs 1–25 [**non** Gmelin, 1791].
2013 *Mytilaster lineatus* (Gmelin, 1791). – Kijashko in Bogutskaya et al.: 316, fig. 104 [**non** Gmelin, 1791].

Status. Native to Black Sea Basin, invasive in Caspian Sea, introduced in Aral Sea but extinct there.

Type locality. Sicily, Italy.

Distribution. Native to the Mediterranean and Black Sea. Introduced in the Caspian Sea between 1917 and 1919 (Grigorovich et al. 2003).

Taxonomic notes. This species has commonly been mentioned as *Mytilaster lineatus* (Gmelin, 1791), but the Caspian-Aral species lacks the ribbing typical for that species. The attribution to *M. minimus* is based on shell morphology but confirmation from molecular analyses is required.

Remarks. *Mytilaster minimus* has successfully replaced *Dreissena caspia* and *D. elata* between 1938 and 1957 (Kostianoy and Kosarev 2005) in the Caspian Sea. Logvinenko and Starobogatov (1969) reported this species from the southern areas of the northern Caspian Sea, in the middle and the southern Caspian Sea down to 35–50 m water depth. Rarely, small individuals were found at depths down to 100 m. The species does not tolerate salinities below 7–8‰. This species was mentioned from depths between 200 and 600 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *M. lineatus*). These deep records are unusual given other records and will require confirmation.

Conservation status. Not assessed.

Family Cardiidae Lamarck, 1809

Remarks. For the genus *Cerastoderma*, the species status of Pontocaspian material is subject of debate where morphological and increasingly molecular arguments show the possibility of sibling species occurrences (Sromek et al. 2016). The genus *Didacna* is relatively well established, however much uncertainty exists over distinction between the genera *Monodacna*, *Adacna*, and *Hypanis*. The generic concepts have shifted through time. Only lately, Kijashko in Bogutskaya et al. (2013) treated *Monodacna* as a subgenus of *Adacna*. Büyükmeriç and Wesselingh (2018) discussed the distinction between the three genera and considered *Monodacna*, *Adacna*, and *Hypanis* as valid.

Adacna laeviuscula (Eichwald, 1829)

*1829 *G.*[*lycymeris*] *laeviuscula* Eichwald: 279, pl. 5, fig. 1a, b.
1838 *Adacna Laeviuscula* m. – Eichwald: 170–171.
1841 *Adacna laeviuscula*. – Eichwald: 281–282, pl. 39, fig. 1a–d.

1905 *Adacna laeviuscula* (Eichwald, 1829). – Ostroumov: pl. 2, fig. E.
1907 *Adacna laeviuscula*. – Ostroumov: 25, text fig., pl. 4, figs 6–8.
1952 *Adacna* (*Adacna*) *laeviuscula* (Eichwald, 1829). – Zhadin: 353–354, pl. 9, fig. 331.
1958 *Adacna* (*Adacna*) *laeviuscula* (Eichwald), 1829. – Nevesskaja: 49–50, pl. 9, figs 15–18.
1969 *Hypanis laeviuscula laeviuscula* (Eichw.). – Logvinenko and Starobogatov: 337, fig. 353(5).
1973 *Hypanis laeviuscula laeviuscula* Eichwald, 1829. – Grossu: 144–145, text fig. 29.
2013 *Adacna laeviuscula* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 377, fig. 154, photo 48.
2016 *Adacna* (*Adacna*) *laeviuscula* (Eichwald, 1829). – Vinarski and Kantor: 64.

Status. Pontocaspian species, endemic to Caspian Sea and possibly Black Sea Basin.

Type locality. Azerbaijan, Caspian Sea, Gulf of Baku is the type locality given by Vinarski and Kantor (2016) and this is written on the label of the type material. However, the type description reads "Hab. australem ripam maris caspii, in sinu Astrabadensi" [southern border of the Caspian Sea, in bight of Astrabad (= Gorgan, Iran)]. Further research on the labels and documentation is required to assess whether a new lectotype or even neotype must be assigned for *Adacna laeviuscula*.

Distribution. Caspian Sea; limans, coastal lakes, and Danube Delta in Black Sea Basin (in case *A. fragilis* will be shown to be a synonym of *A. laeviuscula*).

Taxonomic notes. See discussion under *A. fragilis*.

Remarks. Kijashko in Bogutskaya et al. (2013) list the presence of this species at 30–60 m water depth in the Caspian Sea from muddy, sandy-mud, and rarely sandy bottoms. Logvinenko and Starobogatov (1969) reported the species from the northern, middle, and southern Caspian Sea basins down to 80–85 m water depth. In the Caspian Sea, the species has not been found in areas with salinities below 4‰. However, the common occurrence of fresh (paired) specimens on beaches seen at Turali (Dagestan, Russia) and northern Azerbaijan indicates this species maintains viable populations in foreshore and possibly even shoreface habitats.

Conservation status. Not assessed.

Adacna fragilis Milaschewitsch, 1908

*1908 *Adacna fragilis* Milaschewitch: 992–993.
1973 *Hypanis laeviuscula fragilis* Milaschevitsch, 1916. – Grossu: 145.
?2006b *Hypanis* (*Adacna*) *laeviuscula fragilis* (Milachevitch, 1908). – Munasypova-Motyash: 522.
2009 *Adacna (Adacna) fragilis* Milaschevich, 1908. – Popa et al.: 13, fig. 5.
2016 *Adacna* (*Adacna*) *fragilis* Milaschewitsch, 1908. – Vinarski and Kantor: 64.

Status. Pontocaspian species, Black Sea Basin, status uncertain.

Type locality. Odessa region, Dniester liman and Katlabhuk Lake (Ukraine: Vinarski and Kantor 2016).

Distribution. Danube Delta region and NW Black Sea Basin coastal areas of Ukraine.

Taxonomic notes. We are uncertain about the status of *Adacna fragilis* Milaschewitch, 1908. The Black Sea Basin material has a wide variety of shapes and often is thinner and sometimes more elliptical than the Caspian *A. laeviuscula*. Both forms were synonymised by Graf and Cummings (2018) and indicated as a possible synonym in MolluscaBase (2018b). However, the Black Sea Basin occurrences are recorded from (coastal) lakes and small rivers suggesting little or only partial overlap in the ecological (and especially salinity) preferences of *A. laeviuscula* (e.g., Munasypova-Motyash 2006a, b, Popa et al. 2009). We are uncertain if *A. fragilis* might constitute a geographical subspecies (a status advocated by Grossu 1973), and further molecular analyses are needed to clarify the status of the Black Sea taxon.

Remarks. The species has been reported alive by Popa et al. (2009) from the Razim Lake complex on the Romanian Black Sea coast.

Conservation status. Not assessed.

Adacna minima Ostroumov, 1907

*1907 *Adacna minima* Ostroumov: 23, text fig., pl. 4, figs 1–5.
1952 *Adacna* (*Adacna*) *vitrea* var. *minima* (Ostroumoff, 1907). – Zhadin: 353.
1967 *Hypanis minima ostroumovi* Logvinenko and Starobogatov: 233.
1969 *Hypanis minima ostroumovi* Logv. et Star. – Logvinenko and Starobogatov: 338, fig. 354(3).
1973 *Hypanis minima ostroumovi* Logvinenko et Starobogatov, 1968. – Grossu: 146, text fig. 31.
?1974 *Hypanis minima sidorovi* Starobogatov: 246, fig. 213.
2003 *Hypanis minima minima* (Ostroumov, 1907). – Andreeva and Andreev: 88, fig. 5.1(3, 4).
?2009 *Hypania* [sic] *minima* (Ostroumoff, 1907). – Filippov and Riedel: 75, fig. 4s, t.
2013 *Adacna minima ostroumovi* (Logvinenko et Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 378, fig. 146.
2016 *Adacna* (*Adacna*) *minima minima* (Ostroumov, 1907). – Vinarski and Kantor: 64.
2016 *Adacna* (*Adacna*) *minima ostroumovi* Logvinenko et Starobogatov, 1967. – Vinarski and Kantor: 64.

Status. Pontocaspian species, endemic to Caspian Sea and Aral Sea; likely disappeared from the latter.

Type locality. The northern Caspian Sea and the Aral Sea (Vinarski and Kantor 2016).

Distribution. Aral Sea (probably extinct there; Andreeva and Andreev 2003), Caspian Sea.

Taxonomic notes. Graf and Cummings (2018) consider this species as a synonym of *A. vitrea*, but Kijashko in Bogutskaya et al. (2013) regards it as a valid species. The latter considers *A. minima minima* from the Aral Sea and *A. minima ostroumovi* syn. n. from the Caspian Sea as distinct geographical subspecies. The likely disappearance of the species from the Aral Sea makes a molecular assessment of their distinctness very difficult and given the lack of other arguments we synonymise both. Furthermore, we are uncertain about the status of the subspecies *Hypanis minima sidorovi* Starobogatov, 1974 from the western Aral Sea. Without further data we assume it concerns a form that falls within the wide morphological variation of *A. minima*. We moreover are very uncertain as to the status of *Hypanis minima* from Holocene deposits of Aral Sea as illustrated by Filippov and Riedel (2009, fig. 4s, t). The juvenile specimen has relatively strong cardinal teeth, onset of clear ribs, and a general shape that more resembles *Monodacna caspia*.

Remarks. The species has been recorded mostly from the middle and southern Caspian Sea and more rarely from the eastern areas in the northern Caspian Sea down to 35 m water depth (Logvinenko and Starobogatov 1969) as well as from the Aral Sea from where it may have disappeared.

Conservation status. Not assessed.

Adacna vitrea (Eichwald, 1829)

*1829 *G.*[*lycymeris*] *vitrea* Eichwald: 279, pl. 5, fig. 3.
1838 *Adacna vitrea* m. – Eichwald: 172–173.
1841 *Adacna vitrea*. – Eichwald: 282–283, pl. 39, fig. 2a, b.
1905 *Adacna glabra* Ostroumov: 18–19.
1932a *Adacna vitrea* (Eichwald, 1829). – Bogachev: pl. 1, figs 3, 4, 11.
1932b *Adacna vitrea* (Eichwald, 1829). – Bogachev: 33, pl. 3, figs 13–16, 28–29.
1952 *Adacna* (*Adacna*) *vitrea* (Eichwald, 1829). – Zhadin: 352–353, fig. 330.
1958 *Adacna* (*Adacna*) *vitrea* (Eichwald), 1838. – Nevesskaja: 47–48, pl. 9, figs 19–22.
1969 *Hypanis vitrea vitrea* (Eichw.). – Logvinenko and Starobogatov: 337, fig. 354(1), pl. 5, fig. 11.
1969 *Hypanis vitrea glabra* (Ostr.). – Logvinenko and Starobogatov: 338, fig. 354(2).
1973 *Hypanis vitrea vitrea* Eichwald, 1829. – Grossu: 145–146, text fig. 30A.
1973 *Hypanis vitrea glabra* Ostroumoff, 1905. – Grossu: 146, text fig. 30B.
2003 *Hypanis vitrea bergi* Starobogatov, 1974. – Andreeva and Andreev: 86, fig. 5.1(1, 2).
2013 *Adacna* (*Adacna*) *vitrea vitrea* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 378, fig. 148.
2013 *Adacna* (*Adacna*) *vitrea glabra* Ostroumoff, 1905. – Kijashko in Bogutskaya et al.: 379, fig. 149.
2016 *Adacna* (*Adacna*) *vitrea vitrea* (Eichwald, 1829). – Vinarski and Kantor: 65.
2016 *Adacna* (*Adacna*) *vitrea glabra* Ostroumov, 1905. – Vinarski and Kantor: 65.
2016 *Adacna* (*Adacna*) *vitrea bergi* (Starobogatov, 1974). – Vinarski and Kantor: 65.

Status. Pontocaspian species, endemic to Caspian Sea Basin, Black Sea Basin, and Aral Sea Basin.

Type locality. “Australem oram caspii maris, Astrabadensem” [southern coast of Caspian Sea, near Astrabad (= Gorgan, Iran)].

Distribution. Black Sea Basin (also in Azov Sea and adjacent lower Don River), Caspian Sea Basin, and Aral Sea (including delta of Amu-Darya River). The Aral populations may have gone extinct in the 1980s (Andreeva and Andreev 2003).

Taxonomic notes. The species has been subdivided into three geographical subspecies which were not recognised by Graf and Cummings (2018). It concerns a species with thin shells that yield very few diagnostic characters that show overlap. Here, we synonymise the subspecies pending molecular assessments of their status.

Conservation status. Not assessed.

Cerastoderma glaucum (Bruguière, 1789) s.l.

*1789 *Cardium glaucum* Bruguière: 221–222.
1789 *Cardium Glaucum* Poiret: 13–15.
1869 *Cardium isthmicus* Issel: 74–76.
1952 *Cardium edule* L., 1758. – Zhadin: 344–345, fig. 318 [**non** *Cardium edule* Linnaeus, 1758].
2003 *Cerastoderma isthmicum* (Issel, 1869). – Andreeva & Andreev: 54, 62, figs 6.1(b), 6.7.
2013 *Cerastoderma glaucum* (Poiret, 1789). – Kijashko in Bogutskaya et al.: 342, fig. 126, photo 39.
2016 *Cerastoderma glaucum* (Bruguière, 1789). – Vinarski and Kantor: 69.
2016 *Cerastoderma isthmicus* (Issel, 1869). – Vinarski and Kantor: 70.

Status. Native Pontocaspian species (Black Sea Basin), Holocene invasive in Caspian Sea and Aral Sea.

Type locality. French Mediterranean.

Distribution. NE Atlantic, Baltic Sea, Mediterranean, Black Sea Basin, Caspian Sea Basin, Aral Sea, isolated Saharan lakes (Plaziat 1991).

Taxonomic notes. DNA studies have shown a strong structuring between Atlantic–western Mediterranean, Ionian, and Aegean-Pontocaspian populations of *C. glaucum* (Nikula and Väinölä 2003, Sromek et al. 2016). According to Sromek et al. (2016: 515), the "strong genetic differentiation and the occurrence of private alleles may hint at the presence of cryptic species within *C. glaucum*". For a discussion on the authority of *C. glaucum*, see Vinarski and Kantor (2016: 69–70).

Remarks. The arrival of *Cerastoderma glaucum* in the Caspian Sea circa 8000 years ago has been linked to human settlement expansion through the Manych corridor (Fedorov 1957, Yanina 2009). It would be among the earliest human-mediated dispersal events for invertebrate species known to date.

Conservation status. Not assessed.

Cerastoderma sp. A [non *C. rhomboides* (Lamarck, 1819)]

1916 *Cardium edule* var. *nuciformis* Milaschewitch: 257–259, pl. 7, figs 7, 8 [**non** *Cardium nuciforme* d'Orbigny, 1850].

2003 *Cerastoderma rhomboides rhomboides* (Lamarck, 1819). – Andreeva and Andreev: 93, fig. 6.1(A) [**non** *Cardium rhomboides* Lamarck, 1819].
2013 *Cerastoderma rhomboides* (Lamarck, 1819). – Kijashko in Bogutskaya et al.: 343, fig. 127, photo 40 [**non** Lamarck, 1819].
2016 *Cerastoderma rhomboides* (Lamarck, 1819). – Vinarski and Kantor: 70 [**non** Lamarck, 1819].

Status. Native Pontocaspian species (Black Sea Basin), introduced to Caspian Sea and Aral Sea.

Distribution. Black Sea (including Sea of Azov), Caspian Sea, Aral Sea, Aegean.

Taxonomic notes. This concerns a common rhomboid-shaped species in the Pontocaspian region whose name is uncertain. It has a short ligament in common with *C. glaucum* and the persistent occurrence of ribs on the posterior margin, the well-defined character of the ribs and the regular occurrence of scales in common with western European *C. edule*. This form has been often referred to as *C. rhomboides* (Lamarck, 1819) that has been described from the Italian Pliocene but that concerns a typical *glaucum* form (Fig. 2), not the rhomboid form of the Pontocaspian *Cerastoderma*. The species has been named *Cardium edule* var. *nuciformis* by Milaschewitch (1916), but that name is a junior primary homonym of *Cardium nuciforme* d'Orbigny, 1850. Even though some morphological features mentioned in the description of *C. lamarcki* (Reeve, 1845) may resemble those of the Pontocaspian species, the former has been traced to southern Great Britain from where molecular analyses only show the presence of *C. glaucum* (Nikula and Väinölä 2003).

Conservation status. Not assessed.

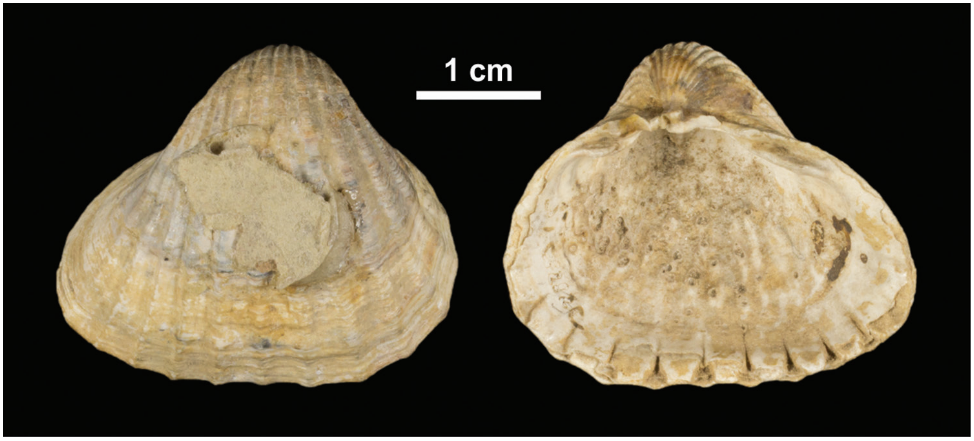

Figure 2. Syntype of *Cerastoderma rhomboides* (Lamarck, 1819), stored in the Muséum national d'Histoire naturelle Paris (MNHN.F.A50142), Pliocene, Tuscany, Italy. Photograph by E Porez. https://science.mnhn.fr/institution/mnhn/collection/f/item/a50142?lang=fr_FR

Didacna baeri (Grimm, 1877)

Fig. 3a

*1877 *Cardium Baeri* Grimm: 51–54, pl. 8, figs 2, 3.
1914 *Didacna Baeri* (Grimm, 1877). – Nalivkin & Anisimov: 4, pl. 1, figs 4, 5.
1932 *Didacna Baeri* (Grimm, 1877). – Bogachev: 29, pl. 3, figs 1–7.
1933 *Didacna Baeri* (Grimm, 1877). – Zhizhchenko: 34, pl. 2, figs 5–8.
1952 *Didacna baeri* (Grimm, 1877). – Zhadin: 347–348, figs 321, 322.
1953 *Didacna baeri* (Grimm, 1877). – Fedorov: 129, pl. 20, figs 10, 11.
1968 *Didacna baeri* (Grimm, 1877). – Gadzhiev: 76–77, pl. 1, figs 1, 2.
1969 *Didacna baeri* (Grimm). – Logvinenko & Starobogatov: 324, fig. 344(2).
1969 *Didacna baeri* (Grimm, 1877). – Vekilov: 139–144, pl. 25, figs 1–8.
1973 *Didacna baeri* Grimm, 1877. – Grossu: 131, text fig. 7.
1983 *Didacna baeri* (Grimm, 1877). – Popov: 180, pl. 16, figs 20–23.
1988 *Didacna baeri* (Grimm, 1877). – Yanina & Svitoch: 129, pl. 3, figs 7–13.
2005 *Didacna baeri* (Grimm, 1877). – Yanina: 242–244, pl. 14, figs 12–15.
2007 *Didacna baeri* (Grimm, 1877). – Nevesskaja: 940–941, pl. 23, figs 11–17.
2013 *Didacna baeri* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 352, fig. 136, photo 41 [pars, excluding synonymy of *Didacna crassa*].
2016 *Didacna baeri* (Grimm, 1877). – Vinarski & Kantor: 71 [pars, excluding synonymy of *Didacna crassa*].

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, offshore Turkmenistan, station 132, 40°32'N, 52°23'E.

Distribution. Logvinenko and Starobogatov (1969) reported *Didacna baeri* from the southern basin (mostly on the eastern side) and from the middle basin down to 60 m water depth.

Taxonomic notes. In recent works (e.g., Kijashko in Bogutskaya et al. 2013), the species *Didacna crassa* (Eichwald, 1829) [= *D. eichwaldi* (Krynicki, 1837)] has been considered a synonym of *D. baeri*. However, both species can be distinguished. *Didacna baeri* has a less extended, more roundish shell, a less developed keel, and a low top with less projecting beak and in general more ribs than *D. eichwaldi* (Fig. 3). *Didacna baeri* occurred for the first time in the Novocaspian transgressive deposits whereas *D. crassa* already occurred in the late Khvalynian (Late Pleistocene). Both became very common during the Novocaspian.

Conservation status. Not assessed.

Didacna barbotdemarnii (Grimm, 1877)

*1877 *Cardium Barbot-de-Marnii* Grimm: 56–58, pl. 8, figs 5, 6.
1952 *Didacna barbot-de-marnyi* [sic] (Grimm, 1877). – Zhadin: 348, fig. 323.
1969 *Didacna barbotdemarnyi* [sic] (Grimm). – Logvinenko and Starobogatov: 326–327, fig. 346, pl. 5, fig. 8.

1973 *Didacna barbotdemarnyi* [sic] Grimm, 1877. – Grossu: 133, text fig. 10.
2007 *Didacna barbotdemarnyi* [sic] (Grimm, 1877). – Nevesskaja: 941–943, pl. 24, figs 10–14.
2013 *Didacna barbotdemarnii* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 353, fig. 139, photo 42.
2016 *Didacna barbotdemarnii* (Grimm, 1877). – Vinarski and Kantor: 71.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, station 116, 44°17'N, 50°22'E.

Distribution. Southern, middle, and southern part of the northern Caspian Sea down to 40 m water depth, preferentially on sandy sediments (Logvinenko and Starobogatov 1969).

Conservation status. Not assessed.

Didacna eichwaldi (Krynicki, 1837)

Fig. 3b

°1829 *C.*[*ardium*] *crassum* Eichwald: 283 [**non** *Cardium crassum* Gmelin, 1791].
*1837 *Cardium Eichwaldi* Krynicki: 61 [**nom. nov.** pro *C. crassum* Eichwald, 1829, **non** Gmelin, 1791].
1841 *Didacna crassa*. – Eichwald: 273, pl. 39, fig. 6a, b.
1876 *Cardium crassum* Eichwald, 1829. – Grimm: 136–138, pl. 6, fig. 3.
1905 *Didacna crassa* (Eichwald, 1829). – Ostroumov: 15, 69, pl. 2(A).
1932 *Didacna* aff. *crassa* (Eichwald, 1829). – Bogachev: 27, pl. 2, figs 11–14.
1952 *Didacna crassa* Eichwald, 1841. – Zhadin: 349, fig. 325.
1953 *Didacna crassa* (Eichwald, 1829). – Fedorov: 130, pl. 20, figs 8, 9, 12, 13.
1958 *Didacna crassa crassa* Eichwald, 1829. – Nevesskaja: 39–40, pl. 7, figs 8, 9.
1969 *Didacna crassa* (Eichwald, 1829). – Vekilov: 134–139, pl. 24, figs 1–6, pl. 27, figs 1, 2.
1988 *Didacna crassa crassa* (Eichwald, 1829). – Yanina and Svitoch: pl. 12, figs 8, 9, pl. 13, figs 1–5.
2005 *Didacna crassa* (Eichwald, 1829). – Yanina: 242, pl. 14, figs 3–6.
2007 *Didacna crassa* (Eichwald, 1829). – Nevesskaja: 939–940, pl. 23, figs 1–5.
2013 *Didacna baeri* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 352 [pars, non fig. 136, photo 41, **non** *Cardium baeri* Grimm, 1877].
2016 *Didacna baeri* (Grimm, 1877). – Vinarski and Kantor: 71 [pars, **non** Grimm, 1877].

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. “Caspium mare” (Caspian Sea) (for *C. crassum* Eichwald, 1829).

Distribution. Caspian Sea. *Didacna eichwaldi* is known from the middle and southern Caspian Sea basins down to 35 m water depth and cannot tolerate lowered salinities.

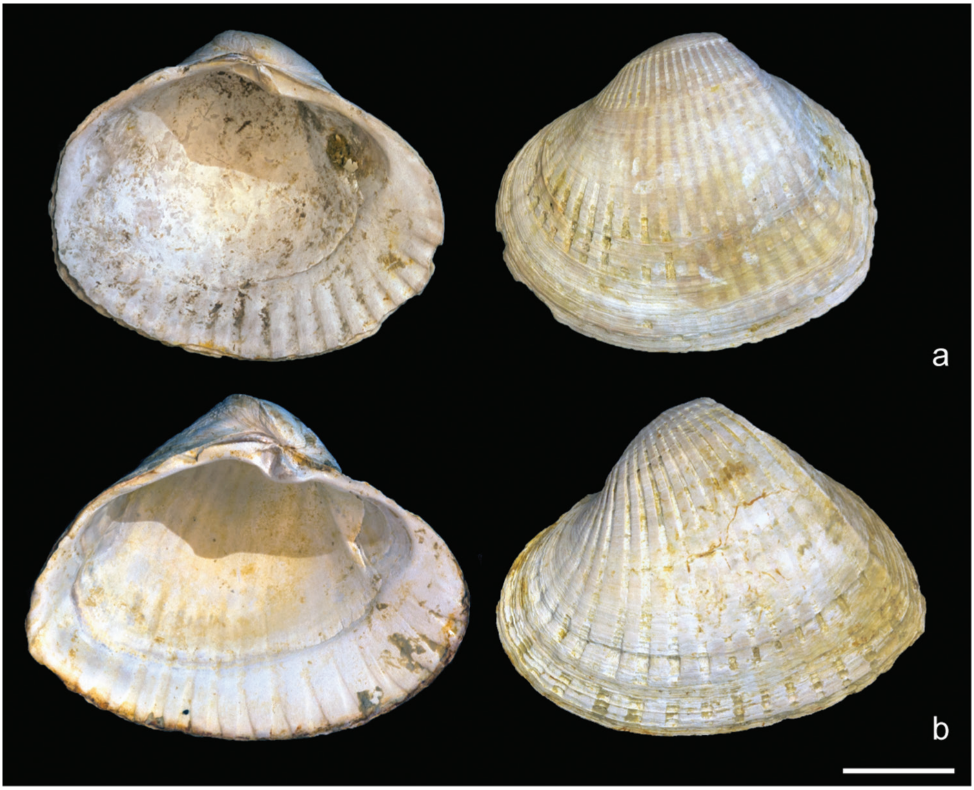

Figure 3. *Didacna baeri* versus *D. eichwaldi* from Holocene (Novocaspian) deposits of Turali Lagoon (Dagestan, Russia). **a** RGM.961899, *Didacna baeri* (Grimm, 1877) **b** RGM.961900, *Didacna eichwaldi* (Krynicki, 1837), same locality. Scale bar: 1 cm.

Taxonomic notes. In recent works (Kijashko in Bogutskaya et al. 2013), the species *Didacna crassa* (Eichwald, 1829) [= *D. eichwaldi* (Krynicki, 1837)] has been considered a synonym of *D. baeri*. However, we see morphological discontinuities in our extensive material from the northern Caspian Sea Basin that implies that *D. eichwaldi* with its protruding umbo and shouldered appearance is distinct from *D. baeri* that is characterised by a rounded umbo (see discussion above under *D. baeri*). Despite being in common usage, the name *Didacna crassa* is invalid as it is a junior homonym of *Cardium crassum* Gmelin, 1791; Krynicki (1837) introduced *Cardium eichwaldi* as replacement name.

Conservation status. Not assessed.

Didacna longipes (Grimm, 1877)

*1877 *Cardium longipes* Grimm: 54–56, pl. 8, fig. 4a–c.
1952 *Didacna longipes* (Grimm, 1877). – Zhadin: 349–350, fig. 326.
1969 *Didacna longipes* (Grimm). – Logvinenko and Starobogatov: 326, fig. 345.

1973 *Didacna longipes* Grimm, 1877. – Grossu: 132, text fig. 9, pl. 1, fig. 2.
?2007 *Didacna carinata* Nevesskaja: 943, pl. 24, figs 15–19.
2013 *Didacna longipes* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 354, fig. 137, photo 43.
2016 *Didacna longipes* (Grimm, 1877). – Vinarski and Kantor: 71.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, offshore Azerbaijan, approximately 40°39'N, 50°26'E.

Distribution. Southern and middle Caspian Sea basins and southern part of the northern Caspian Sea down to 30–40 m water depth. The species often co-occurs with *D. barbotdemarnii*.

Remarks. We are uncertain about the status of *Didacna carinata* Nevesskaja, 2007. The overall outline resembles that of *D. barbotdemarnii*, but the former species appears smaller and thinner. Kijashko in Bogutskaya et al. (2013) considered *D. carinata* as a synonym of *D. longipes*.

Conservation status. Not assessed.

Didacna parallela Bogachev, 1932

*1932a *Didacna parallela* Bogachev: pl. 2, figs 2, 3.
1932b *Didacna parallela* Bogachev: 44, pl. 5, figs 1–7, 9.
1953 *Didacna parallella* [sic] Bogatchev, 1932. – Fedorov: 126, pl. 17, figs 1–11.
1969 *Didacna parallella* [sic] Bog. – Logvinenko and Starobogatov: 324–325, fig. 344(3).
1969 *Didacna parallella* [sic] Bogatchev, 1932. – Vekilov: 117–120, pl. 21, figs 1–8.
1973 *Didacna parallella* [sic] Bogatchev, 1922 [sic]. – Grossu: 131, text fig. 8, pl. 1, fig. 4.
2005 *Didacna parallella* [sic] Bogatchev, 1932. – Yanina: 237–238, pl. 12, figs 1–8.
2007 *Didacna parallella* [sic] Bogatchev, 1932. – Nevesskaja: 933–935, pl. 21, figs 1–5.
2013 *Didacna parallela* Bogachev, 1932. – Kijashko in Bogutskaya et al.: 355–356, fig. 138.
2016 *Didacna parallela* Bogachev, 1932. – Vinarski and Kantor: 72.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Khala, Apsheron Peninsula, Azerbaijan (early Khvalynian, Late Pleistocene).

Distribution. Caspian Sea, southern basin and western part of middle basin between 50–85 m water depth (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017), but we are not certain whether it concerns living specimens.

Remarks. *Didacna parallela* has been considered as extinct by Nevesskaja (2007) but was nevertheless treated in Kijashko in Bogutskaya et al. (2013). Live records are known at least until 1986 and we have no particular reason to assume it is extinct.

Conservation status. Not assessed.

Didacna praetrigonoides Nalivkin & Anisimov, 1914

*1914 *Didacna praetrigonoides* Nalivkin & Anisimov: 5–6, 16–17, pl. 1, figs 1, 2.
1932a *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Bogachev: pl. 2, fig. 1.
1932b *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Bogachev: 42, pl. 4, figs 1–8, pl. 5, fig. 8.
1948 *Didacna praetrigonoides* Nal. – Fedorov: pl. 2, figs 10–13.
1953 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Fedorov: 128, pl. 18, figs 1–6, pl. 19, figs 1–6.
1958 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Nevesskaja: 17–20, pl. 1, figs 1–14.
1969 *Didacna trigonoides praetrigonoides* Nal. & Anis. – Logvinenko and Starobogatov: 324, fig. 343(2).
1969 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Vekilov: 120–128, pl. 22, figs 1–9.
1973 *Didacna trigonoides praetrigonoides* Nalivkin & Anisimov, 1915. – Grossu: 129, text fig. 5.
1983 *Didacna praetrigonoides praetrigonoides* Nalivkin & Anisimov, 1914. – Popov: 195, pl. 15, figs 1, 2.
1988 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Yanina and Svitoch: pl. 8, figs 4–7.
2005 *Didacna praetrigonoides* Nalivkin & Anisimov, 1914. – Yanina: 241, pl. 14, figs 1, 2.
2007 *Didacna praetrigonoides praetrigonoides* Nalivkin & Anisimov, 1914. – Nevesskaja: 927, pl. 19, figs 9, 10.

Status. Pontocaspian species, endemic to Caspian Sea. Possibly extinct.

Type locality. Apsheron Peninsula, Azerbaijan, Quaternary.

Distribution. Caspian Sea. Logvinenko and Starobogatov (1969) reported the species from the southern Caspian Sea Basin and the southern part of the middle Caspian Sea Basin down to 60 m water depth. The species has been collected from Holocene deposits and beach occurrences the western part of the middle Caspian Sea Basin as well (FW, pers. obs.). The species is reportedly extinct, not mentioned in Kijashko in Bogutskaya et al. (2013).

Remarks. The first appearance of *Didacna praetrigonoides* is in lower Khvalynian deposits, it became widespread during the late Khvalynian and was rare during the Novocaspian.

Conservation status. Not assessed. *Didacna praetrigonoides* has been reported to occur 'rarely in the modern Caspian Sea' (Nevesskaja 2007: 927), but material from recent assemblages has not been found.

Didacna profundicola Logvinenko & Starobogatov, 1966

*1966a *Didacna profundicola* Logvinenko & Starobogatov: 13–14, fig. 1.
1969 *Didacna profundicola* Logv. & Star. – Logvinenko and Starobogatov: 328–329, fig. 349.

1973 *Didacna profundicola* Logvinenko & Starobogatov, 1966. – Grossu: 134, text fig. 13.
2007 *Didacna profundicola* Logvinenko & Starobogatov, 1966. – Nevesskaja: 944, pl. 20, fig. 28a–c.
2013 *Didacna profundicola* Logvinenko & Starobogatov. – Kijashko in Bogutskaya et al.: 356, fig. 140, photo 45.
2016 *Didacna profundicola* Logvinenko & Starobogatov. – Vinarski and Kantor: 72.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Central part of the Caspian Sea, 39°38'N, 52°02'E(offshore Turkmenistan).

Distribution. Middle and southern basins of Caspian Sea between 75 and 409 m water depth (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 600 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Conservation status. Not assessed.

Didacna protracta (Eichwald, 1841)

*1841 *Adacna protracta* Eichwald: 280, pl. 40, figs 10, 11 [non figs 9, 10 as indicated in the text].
1877 *Cardium catillus* Eichw. – Grimm: 58, pl. 8, figs 7, 8 [**non** *Monodacna catillus* Eichwald, 1841].
1910 *Didacna protracta* (Eichwald, 1841). – Andrusov: 67, pl. 8, figs 22, 33, pl. 9, figs 1–9.
1952 *Didacna protracta* (Eichwald, 1841). – Zhadin: 348–349, fig. 324.
1953 *Didacna protracta* (Eichwald, 1829). – Fedorov: 127, pl. 14, figs 12–15, pl. 15, figs 1–16.
1967 *Didacna protracta* Eichwald, 1841. – Svitoch: 42–43, pl. 6, figs 6–9, pl. 7, figs 1, 2.
1969 *Didacna protracta protracta* (Eichw.). – Logvinenko and Starobogatov: 327, fig. 347.
1973 *Didacna protracta protracta* Eichwald, 1841. – Grossu: 133, text fig. 11.
1973 *Didacna protracta submedia* Andrusov, 1911. – Grossu: 133–134, text fig. 12.
1999 *Didacna protracta* (Eichwald, 1829). – Fedorov: pl. 12, figs 4–7.
2005 *Didacna protracta* (Eichwald, 1829). – Yanina: 238–239, pl. 12, figs 9–19.
2007 *Didacna protracta protracta* (Eichwald, 1829). – Nevesskaja: 938–939, pl. 22, figs 4–13.
2013 *Didacna protracta* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 356, fig. 141.
2013 *Didacna protracta submedia* Andrusov, 1910. – Kijashko in Bogutskaya et al.: 356, fig. 142.
2016 *Didacna protracta* (Eichwald, 1841). – Vinarski and Kantor: 72.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. The type series (?Recent, Caspian Sea) was reported as lost by Nevesskaja (2007) who introduced a neotype from the Elton Lake surroundings in the northern Caspian plains, Russia (early Khvalynian, Late Pleistocene).

Distribution. Middle and southern Caspian Sea basins; it is most common in the middle basin at 25–85 m water depth (Logvinenko and Starobogatov 1969).

Taxonomic notes. According to Logvinenko and Starobogatov (1969), two subspecies occur in the Caspian Sea at different depth ranges: *D. protracta protracta* at 25–50 m and *D. protracta submedia* Andrusov, 1910 at 50–85 m. The latter differs from *D. p. protracta* by the relative posterior location of the umbo that is furthermore subdued. Both forms of *Didacna protracta* are widespread in the Khvalynian deposits of the Caspian Sea and Manych depression. According to Kijashko in Bogutskaya et al. (2013) morphological differences characteristic for the subspecies of *Didacna protracta* are due to allometric growth. The mere difference in depth distribution, with overlapping depths and intermediate forms, does not provide any argument to maintain these subspecies. *Didacna protracta* is the type species of the subgenus *Protodidacna* Logvinenko & Starobogatov, 1966.

Remarks. The authorship attribution of this species to Eichwald (1829) as proposed by several authors was rejected in Vinarski and Kantor (2016). According to them, *Cardium protractum* Eichwald, 1829, described from the western Ukraine, probably refers to a different species.

Conservation status. Not assessed.

Didacna pyramidata (Grimm, 1877)

*1877 *Cardium pyramidatum* Grimm: 46–49, pl. 8, fig. 1a–d.
1932 *Didacna pyramidata* (Grimm, 1877). – Bogachev: 28–29, pl. 2, figs 15, 16.
1952 *Didacna pyramidata* (Grimm, 1877). – Zhadin: 347, fig. 320.
1969 *Didacna pyramidata* (Grimm). – Logvinenko and Starobogatov: 324, fig. 344(1).
1969 *Didacna pyramidata* (Grimm, 1877). – Vekilov: 144–147, pl. 26, figs 1–5.
1973 *Didacna pyramidata* Grimm, 1877. – Grossu: 130, text fig. 6, pl. 1, fig. 1.
2007 *Didacna pyramidata* (Grimm, 1877). – Nevesskaja: 940, pl. 23, figs 6–10.
2013 *Didacna pyramidata* (Grimm, 1877). – Kijashko in Bogutskaya et al.: 357, fig. 135, photo 47.
2016 *Didacna pyramidata* (Grimm, 1877). – Vinarski and Kantor: 73.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, offshore Azerbaijan, 39°47'N, 49°59'30"E (Kijashko in Bogutskaya et al. 2013).

Distribution. Caspian Sea: southern basin and southern part of the middle basin at depths between 30–100 m (Logvinenko and Starobogatov 1969).

Conservation status. Not assessed.

Didacna trigonoides (Pallas, 1771)

*1771 *Cardium trigonoides* Pallas: 478.
1831 *Cardium trigonoides* (Pallas, 1771). – Eichwald: 282.

1838 *Didacna trigonoides* n. – Eichwald: 166–167.
1841 *Didacna trigonoides*. – Eichwald: 271–272, pl. 39, fig. 5a–c.
1876 *Cardium trigonoides*, Pall. – Grimm: 138–140, pl. 6, fig. 2.
1914 *Didacna trigonoides* (Pallas, 1771). – Kalitskiy: pl. 3, figs 1, 2.
1914 *Didacna trigonoides* (Pallas, 1771). – Nalivkin and Anisimov: 6, pl. 1, fig. 3.
1932a *Didacna trigonoides* (Pallas, 1771). – Bogachev: pl. 1, figs 5, 6.
1932b *Didacna trigonoides* (Pallas, 1771). – Bogachev: 25, pl. 2, figs 1–9.
1933 *Didacna trigonoides* (Pallas, 1771). – Zhizhchenko: 35–36, pl. 2, figs 9, 10.
1950 *Didacna trigonoides* (Pallas, 1771). – Pravoslavlev: 21–22, figs 1–4.
1952 *Didacna trigonoides* (Pallas, 1771). – Zhadin: 346, fig. 319.
1953 *Didacna trigonoides* (Pallas, 1771). – Fedorov: 129, pl. 20, figs 7–9.
1969 *Didacna trigonoides trigonoides* (Pall.). – Logvinenko and Starobogatov: 323, fig. 343(1), pl. 5, fig. 7.
1969 *Didacna trigonoides* (Pallas, 1771). – Vekilov: 128–134, pl. 23, figs 1–9, pl. 27, fig. 6.
1973 *Didacna trigonoides trigonoides* Pallas, 1771. – Grossu: 129, text fig. 4, pl. 1, fig. 3.
1977 *Didacna trigonoides tuzetae* Tadjalli-Pour: 97, pl. 1, fig. 3.
1983 *Didacna trigonoides* (Pallas, 1771). – Popov: 204, pl. 16, fig. 19.
1986 *Didacna trigonoides* (Pallas, 1771). – Yakhimovich et al.: 79, pl. 10, fig. 1.
1988 *Didacna trigonoides* (Pallas, 1771). – Yanina and Svitoch: pl. 9, figs 7–12.
2005 *Didacna trigonoides* (Pallas, 1771). – Yanina: 244–245, pl. 14, figs 7–11.
2007 *Didacna trigonoides* (Pallas, 1771). – Nevesskaja: 941, pl. 24, figs 1–9.
2013 *Didacna trigonoides* (Pallas, 1771). – Kijashko in Bogutskaya et al.: 358, fig. 134.
2016 *Didacna trigonoides* (Pallas, 1771). – Vinarski and Kantor: 70.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Caspian Sea, a neotype has been designated based on a specimen from Chechen Island by Nevesskaja (2007, pl. 24, fig. 4).

Distribution. Caspian Sea, mostly eastern part of northern Caspian Sea Basin (Logvinenko and Starobogatov 1969). Furthermore found in living position in Novocaspian deposits near Turali, Dagestan (western part middle basin; FW).

Remark. Genetic data are available through Albrecht et al. (2014).

Conservation status. Not assessed.

Hypanis plicata (Eichwald, 1829)

*1829 *G.*[*lycymeris*] *plicata* Eichwald: 279, pl. 5, fig. 2a, b.
1838 *Adacne* [sic] *plicata* m. – Eichwald: 171–172.
1916 *Adacna relicta* Milaschewitch: 274–276, pl. 8, figs 10–13 [non figs 10–12 as indicated in the text].
1926 *Adacna relicta* var. *dolosmiana* Borcea: 468–469, pl. 18, figs 156–158, pl. 21, fig. 2.
1952 *Adacna* (*Hypanis*) *plicata* (Eichwald, 1829). – Zhadin: 354–355, fig. 332.
1958 *Adacna* (*Hypanis*) *plicata* (Eichwald), 1829. – Nevesskaja: 50–51, pl. 9, figs 9–14.
1969 *Hypanis plicata plicata* (Eichw.). – Logvinenko and Starobogatov: 331–332, fig. 350.

1973 *Hypanis plicata plicata* Eichwald, 1829. – Grossu: 136, text fig. 14, pl. 1, fig. 5.
1973 *Hypanis plicata relicta* Milaschevitsch, 1916. – Grossu: 136, text fig. 15, pl. 1, figs. 6, 20–23.
1973 *Hypanis dolosmaniana* [sic] Borcea, 1826. – Grossu: 136, text fig. 16, pl. 1, figs 16–19.
1977 *Hypanis plicata golbargae* Tadjalli-Pour: 99, pl. 1, fig. 5.
2006a *Hypanis plicata relicta* (Milachevitch, 1916). – Munasypova-Motyash: 45–46.
2009 *Adacna (Hypanis) plicata relicta* Milaschevich, 1916. – Popa et al. 12, fig. 4.
2013 *Hypanis plicata* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 387, fig. 164, photo 56.
2016 *Hypanis plicata plicata* (Eichwald, 1829). – Vinarski and Kantor: 73.
2016 *Hypanis plicata relicta* (Milaschewitsch, 1916). – Vinarski and Kantor: 74.

Status. Pontocaspian species, endemic to Caspian Sea Basin and Black Sea Basin.

Type locality. “Sinum Astrabadensem” [Caspian Sea near Astrabad (= Gorgan, Iran)].

Distribution. Caspian Sea, western liman coast Black Sea Basin.

Taxonomic notes. The Black Sea populations of *H. plicata* show a large range of morphological variation with elongated specimens that cannot be distinguished from Caspian *H. plicata* to severely stunted and irregularly shaped specimens that have been considered as a subspecies (*H. plicata relicta*) or as distinct species (*H. dolosmiana*) (e.g., Munasypova-Motyash 2006a). These forms have intermediates indicating that the Black Sea Basin specimens are a single species that should be attributed to *H. plicata* even though the latter appear to have lived under lower salinities than their Caspian counterparts. Molecular studies are required to elucidate the status of the Black Sea Basin material.

Conservation status. Not assessed. Fresh shells (including paired specimens) have been found at several beaches around the Caspian Sea (Turali, Dagestan, Russia; Şuraabad, Azerbaijan; FW). The species has been reported alive from the Razim lake complex of the Romanian Black Sea coast by Popa et al. (2009).

Monodacna acuticosta (Logvinenko & Starobogatov, 1967)

*1967 *Hypanis acuticosta* Logvinenko & Starobogatov: 232.
1969 *Hypanis angusticostata acuticosta* Logvinenko & Starobogatov: 334, fig. 353(1).
1973 *Hypanis angusticostata acuticosta* Logvinenko et Starobogatov, 1967. – Grossu: 141, fig. 23.
2013 *Adacna* (*Monodacna*) *acuticosta* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 379, fig. 160, photo 50.
2016 *Adacna* (*Monodacna*) *acuticosta* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 66.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. “Northern Caspian Sea on the central part of the slope” (Vinarski and Kantor 2016: 66), which likely refers to northern slope of the middle Caspian Sea Basin.

Distribution. Caspian Sea (middle Caspian Sea Basin).

Conservation status. Not assessed.

Monodacna albida (Logvinenko & Starobogatov, 1967)

*1967 *Hypanis albida* Logvinenko & Starobogatov: 232.
1969 *Hypanis albida* Logv. & Star. – Logvinenko and Starobogatov: 336, fig. 353(3).
1973 *Hypanis albida* Logvinenko & Starobogatov, 1967. – Grossu: 144, text fig. 28.
2013 *Adacna* (*Monodacna*) *albida* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 380, fig. 162, photo 51.
2016 *Adacna* (*Monodacna*) *albida* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 66.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. "Western Caspian Sea southeastwards from Derbent" (Vinarski and Kantor 2016: 66).

Distribution. Caspian Sea (middle and southern Caspian Sea Basin). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Hypanis albida*).

Taxonomic notes. This species is part of a group of Caspian *Monodacna* with relative flat and wedge-shaped shells with low and sometimes poorly defined ribs (*M. albida, M. polymorpha*). Like for the *Monodacna caspia* group (see below), we are in need of studies to assess whether these taxa might form ecomorphs of a single species.

Conservation status. Not assessed.

Monodacna caspia (Eichwald, 1829)

*1829 *C.*[*orbula*] *caspia* Eichwald: 281, pl. 5, fig. 6a, b.
1841 *Monodacna caspia*. – Eichwald: 274, pl. 39, fig. 4a–c.
1905 *Monodacna caspia* (Eichwald, 1829). – Ostroumov: pl. 3, fig. C.
1932a *Monodacna caspia* (Eichwald, 1829). – Bogachev: pl. 1, figs 10, 13.
1932b *Monodacna caspia* (Eichwald, 1829). – Bogachev: 30, pl. 3, figs 21–27.
1952 *Monodacna edentula* (Pallas, 1771) var. *caspia* Eichwald, 1841. – Zhadin: 350, fig. 327B.
1958 *Monodacna caspia* (Eichwald), 1829. – Nevesskaja: 44–46, pl. 9, figs 1–8.
1963 *Monodacna caspia caspia* (Eichwald, 1829). – Nevesskaja: 66, pl. 8, figs 1–4.
1965 *Monodacna caspia caspia* (Eichwald). – Nevesskaja: 187–198, pl. 9, figs 6–15, 17–19, 23–26, 29.
1969 *Monodacna caspia* (Eichwald, 1829). – Vekilov: 147–150, pl. 31, figs 9–11.
1973 *Hypanis caspia caspia* Eichwald, 1829. – Grossu: 139, text fig. 19B.
1977 *Hypanis caspia assalae* Tadjalli-Pour: 99, pl. 1, fig. 4.
1977 *Hypanis caspia nahali* Tadjalli-Pour: 99, pl. 1, fig. 6.

2013 *Adacna* (*Monodacna*) *caspia caspia* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 380, fig. 154.
2016 *Adacna* (*Monodacna*) *caspia caspia* (Eichwald, 1829). – Vinarski and Kantor: 67.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. "Caspium mare" [Caspian Sea].

Distribution. Caspian Sea.

Taxonomic notes. The *Monodacna caspia* group (*M. caspia*, *M. filatovae*, and *M. knipowitschi*) comprises three (sub-) species that all share the relatively convex and rounded shell and well-defined ribbing. These species have been described from different areas and habitats in the Caspian Sea and have been morphologically characterised by Kijashko in Bogutskaya et al. (2013). However, neither morphological analyses of intermediate populations nor genetic analyses have been performed to clarify if the three taxa are distinct or ecomorphs of a single species. We are therefore uncertain whether *M. filatovae* and *M. knipowitschi* should be maintained.

Conservation status. Not assessed.

Monodacna colorata (Eichwald, 1829)

*1829 *G.*[*lycymeris*] *colorata* Eichwald: 279–280, pl. 5, fig. 4a, b.
1838 *Adacna colorata* m. – Eichwald: 169–170.
?1838 *Monodacna pontica* Eichwald: 168–169.
1926 *Monodacna colorata* var. *ialpugensis* Borcea: 452, pl. 15, fig. 16.
1926 *Monodacna colorata* var. *angusticostata* Borcea: 452–453, pl. 15, figs 27, 28, pl. 16, figs 90, 91, pl. 18, figs 143, 169, 173, pl. 21, fig. 7.
1926 *Adacna Luciae* Borcea: 469–471, pl. 18, figs 146, 148–149, 151–153, pl. 21, figs 8, 9.
1952 *Monodacna colorata* (Eichwald, 1829). – Zhadin: 351, fig. 328.
?1972 *Hypanis caspia grossui* Scarlato and Starobogatov: 214, pl. 4, fig. 1a, b.
1973 *Hypanis caspia grossui* Scarlato & Starobogatov, 1971. – Grossu: 140, text fig. 21, pl. 1, fig. 8.
1973 *Hypanis angusticostata angusticostata* Borcea, 1926. – Grossu: 141, pl. 1, fig. 12.
1973 *Hypanis luciae* Borcea, 1926. – Grossu: 138, text fig. 18.
1973 *Hypanis ialpugensis* Borcea, 1926. – Grossu: 142, fig. 24, pl. 1, figs 9, 10.
1973 *Hypanis colorata* Eichwald, 1829. – Grossu: 142–143, fig. 25, pl. 1, figs 13–15.
1973 *Hypanis pontica* Eichwald, 1838. – Grossu: 143, fig. 26, pl. 1, fig. 11.
2006a *Hypanis colorata* (Eichwald, 1829). – Munasypova-Motyash: 42–43.
?2006a *Hypanis pontica* (Eichwald, 1838). – Munasypova-Motyash: 43–44.
?2006a *Hypanis angusticostata angusticostata* (Borcea, 1926). – Munasypova-Motyash: 44.
2009 *Monodacna pontica* Eichwald, 1838. – Popa et al.: 10, text fig. 2.
2009 *Monodacna colorata* Eichwald, 1829. – Popa et al.: 10–11, text fig. 3.
2012 *Hypanis colorata* (Eichwald, 1829). – Popa et al.: 153, 154.
2012 *Hypanis angusticostata* (Borcea, 1926). – Popa et al.: 153, 154.

2013 *Adacna* (*Monodacna*) *colorata* (Eichwald, 1829). – Kijashko in Bogutskaya et al.: 383, fig. 158.
2016 *Adacna* (*Monodacna*) *angusticostata* (Borcea, 1926). – Vinarski and Kantor: 66.
2016 *Adacna* (*Monodacna*) *grossui* (Scarlato et Starobogatov, 1972). – Vinarski and Kantor: 67.
2016 *Adacna* (*Monodacna*) *ialpugensis* (Borcea, 1926). – Vinarski and Kantor: 68.

Status. Pontocaspian species, native to Black Sea Basin (including lower Danube River), invasive in Caspian Sea and Volga River.

Type locality. "Hypanin fluvium, ad nigrum usque mare" [Lower course of the Yuzhnyi Bug River, all the way to the Black Sea, Ukraine].

Distribution. Native to all Black Sea Basin Pontocaspian habitats and lower courses of adjacent rivers such as the Danube, Dnieper, and Dniester; invasive in Caspian Sea Basin and lower Volga, as well as Lake Balkhash (Kazakhstan). Occurs hundreds of kilometres upstream in major tributaries (Danube: Popa et al. 2009; recent observations in Volga River upstream Volgograd by MV and AFS).

Taxonomic notes. *Monodacna colorata* appears to be a morphologically very variable species. Here, we propose to synonymise several local Black Sea species with this taxon. Given the difficulty to distinguish relatively flat shells typically associated with *M. colorata* from the more convex shells typically associated with *M. pontica* in, e.g., Lake Razim (Romania) and the apparent lack of genetic differentiation of convex specimens from *M. colorata* we assume that *M. pontica* is a synonym of *M. colorata*. Shell differences have been attributed to substrate differences. Further investigations to confirm the synonymy are required. *Monodacna angusticostata* was synonymised by Popa et al. (2012) based on molecular evidence, even though some morphological distinction was reported from *M. colorata*, which they attributed to differential habitat preference (sediment type).

Conservation status. Not assessed.

Monodacna filatovae (Logvinenko & Starobogatov, 1967)

1876 *Cardium caspium*, Eichw. – Grimm: 134–136 [pars].
*1967 *Hypanis caspia filatovae* Logvinenko and Starobogatov: 231.
1973 *Hypanis caspia filatovae* Logvinenko & Starobogatov, 1967. – Grossu: 139, text fig. 19a.
2013 *Adacna* (*Monodacna*) *caspia filatovae* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 381, fig. 155, photo 52.
2016 *Adacna* (*Monodacna*) *caspia filatovae* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 67.

Status. Pontocaspian species, endemic to Caspian Sea. Uncertain whether it concerns a morph of *M. caspia*.

Type locality. Gulf of Baku, Caspian Sea, Azerbaijan.

Distribution. Southern Caspian Sea Basin.

Taxonomic notes. See remarks under *Monodacna caspia* above for uncertain status of *M. filatovae*.

Conservation status. Not assessed.

Monodacna knipowitschi (Logvinenko & Starobogatov, 1966)

*1966a *Hypanis caspia knipowitschi* Logvinenko & Starobogatov: 15, fig. 2.
1973 *Hypanis caspia knipowitschi* Logvinenko & Starobogatov, 1967. – Grossu: 140, text fig. 20.
2013 *Adacna* (*Monodacna*) *caspia knipowitschi* (Logvinenko & Starobogatov, 1966). – Kijashko in Bogutskaya et al.: 381–382, figs 152, 153, photo 53.
2016 *Adacna* (*Monodacna*) *caspia knipowitschi* (Logvinenko & Starobogatov, 1966). – Vinarski and Kantor: 67.

Status. Pontocaspian species, endemic to Caspian Sea. Uncertain whether it concerns a morph of *M. caspia*.

Type locality. Middle Caspian Sea Basin.

Distribution. Caspian Sea (middle and southern basins). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Hypanis caspia knipowitchi*).

Taxonomic notes. See remarks under *Monodacna caspia* above for uncertain status of *M. knipowitschi*.

Conservation status. Not assessed.

Monodacna polymorpha (Logvinenko & Starobogatov, 1967)

*1967 *Hypanis angusticostata polymorpha* Logvinenko & Starobogatov, 1967: 232.
1973 *Hypanis angusticostata polymorpha* Logvinenko & Starobogatov, 1967. – Grossu: 141, fig. 22, pl. 1, fig. 7.
2013 *Adacna* (*Monodacna*) *polymorpha* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 383–384, fig. 159, photo 54.
2016 *Adacna* (*Monodacna*) *polymorpha* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 68.

Status. Pontocaspian species, endemic to Caspian Sea. Status uncertain.

Type locality. Central part of northern Caspian Sea.

Distribution. Northern Caspian Sea.

Taxonomic notes. See remarks under *M. albida* for uncertain species status.

Conservation status. Not assessed.

Monodacna semipellucida (Logvinenko & Starobogatov, 1967)

*1967 *Hypanis semipellucida* Logvinenko & Starobogatov: 232–233.

1973 *Hypanis semipellucida* Logvinenko & Starobogatov, 1967. – Grossu: 144, text fig. 27.
2013 *Adacna* (*Monodacna*) *semipellucida* (Logvinenko & Starobogatov, 1967). – Kijashko in Bogutskaya et al.: 384, fig. 161, photo 55.
2016 *Adacna* (*Monodacna*) *semipellucida* (Logvinenko & Starobogatov, 1967). – Vinarski and Kantor: 68–69.

Status. Pontocaspian species, endemic to Caspian Sea.

Type locality. Off Tokmak Cape (also as Toqmaq Müyis), southern Kazakhstan, Caspian Sea.

Distribution. Middle Caspian Sea.

Conservation status. Not assessed.

Family Semelidae Stoliczka, 1870

Abra segmentum (Récluz, 1843)

°1836 *Erycina ovata* Philippi: 13, pl. 1 fig. 13 [**non** *Erycina ovata* Gray, 1825].
*1843 *Syndosmya segmentum* Récluz: 365–366.
1969 *Abra ovata* (Phil.). – Logvinenko and Starobogatov: 339, fig. 355, pl. 5, fig. 12.
2013 *Abra segmenta* (Récluz, 1843). – Kijashko in Bogutskaya et al.: 391, fig. 165.
2015 *Abra ovata* (Philippi, 1836). – Latypov: 240.

Status. Invasive Pontocaspian species.

Type locality. Mediterranean coast near Taranto (Italy).

Distribution. Mediterranean, Black Sea coastal regions, Sea of Azov, Caspian Sea, Aral Sea.

Taxonomic notes. This species has been reported in much of the 20th century literature as *Abra ovata* (Philippi, 1836), which is invalid since the original name (*Erycina ovata* Philippi, 1836) represents a junior primary homonym of *Erycina ovata* Gray, 1825.

Remarks. The first transfer of *Abra segmentum* into the Caspian Sea occurred in 1947–1948, and the species has not been detected since 1955 (Latypov, 2015).

Conservation status. Not assessed.

Family Cyrenidae Gray, 1840

Corbicula fluminalis (Müller, 1774)

*1774 *Tellina fluminalis* Müller: 205–206.
1952 *Corbicula fluminalis* (Müller, 1774). – Zhadin: 317, fig. 283.
2012 *Corbicula fluminalis* (Müller, 1774). – Welter-Schultes: 15, unnumbered text figures.

2016 *Corbicula fluminalis* (O.F. Müller, 1774). – Nabozhenko and Nabozhenko: 62, text fig. 1(3, 4).
2016 *Corbicula fluminalis* (O.F. Müller, 1774). – Vinarski and Kantor: 80.

Status. Native/Invasive Pontocaspian species.

Type locality. Euphrates River.

Distribution. Native to large parts of western Asia (including southern Caspian river systems) and northern Africa, introduced in 1939 to southern North America and in 1980 from there to Europe (Seddon and Van Damme 2016). The species has been recently recorded from the Caspian Dagestan coast (Nabozhenko and Nabozhenko 2016).

Remarks. This species has been native to south Caspian rivers including the Kura river system (Zhadin 1952) and has expanded several times in the Late Pleistocene into the Caspian Sea, where in time intervals it survived in proximal lacustrine habitats. A recent introduction and expansion of the species has been recorded in the Kizlyarsky Gulf in Dagestan (Nabozhenko and Nabozhenko 2016) and the strong increase in fresh material found around the gulf in subsequent years, including whole specimens (AS Gasanova, Makhachkala, pers. comm.) suggests the species may have established there.

Conservation status. Least Concern (Seddon and Van Damme 2016).

Family Dreissenidae Gray, 1840

Remarks. Pontocaspian dreissenid taxonomy suffers from a lack of coordinated shell and DNA analyses. A large part of our considerations relies on the work of Rosenberg & Ludyanskiy (1994) who examined and illustrated all type material of Pontocaspian *Dreissena*.

Dreissena bugensis Andrusov, 1897

*1897 *Dreissensia bugensis* Andrusov: 285–286, pl. 15, figs 31–37.
1972 *Dreissena rostriformis bugensis* (Andrusov, 1897). – Scarlato and Starobogatov: 232–233, pl. 6, fig. 16.
1994 *Dreissena bugensis* (Andrusov, 1897). – Rosenberg and Ludyanskiy: 1479–1480, fig. 1a–e.
2013 *Dreissena bugensis* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 331, fig. 119.
2016 *Dreissena bugensis* (Andrusov, 1897). – Vinarski and Kantor: 78.

Status. Until mid-20th century endemic to northern Black Sea liman coast, since then invasive elsewhere in Black Sea Basin, Volga catchment, western Europe, and North America.

Type locality. Bug Liman near Nikolaev, Ukraine.

Distribution. Endemic to western Ukrainian liman coast, introduced in Danube Delta, Azov Sea, Volga catchment, western and central Europe, and North America (Orlova et al. 2005, Coughlan et al. 2017).

Taxonomic notes. This species has been considered as a subspecies of *D. rostriformis* (Deshayes, 1838) by some authors (e.g., Orlova et al. 2005), yet we follow the argumentation of Kijashko in Bogutskaya et al. (2013) to consider it as a distinct species. The proposed synonymy of Caspian *D. rostriformis* (= *D. grimmi*) and Black Sea *D. bugensis* by Stepien et al. (2013) is discussed below under *D. grimmi*.

Conservation status. Least Concern (von Rintelen and Van Damme 2011a).

Dreissena caspia Eichwald, 1855

*1855 *Dreissena caspia* Eichwald: 311–312, pl. 10, figs 19–21.
1969 *Dreissena caspia* (Eichw.). – Logvinenko and Starobogatov: 316–318, fig. 341(2).
1994 *Dreissena caspia* Eichwald, 1855. – Rosenberg and Ludyanskiy: 1482, fig. 3e, f.
2013 *Dreissena caspia* Eichwald, 1855. – Kijashko in Bogutskaya et al.: fig. 109.
2016 *Dreissena* (*Dreissena*) *caspia caspia* Eichwald, 1855. – Vinarski and Kantor: 76.

Status. Caspian endemic, probably extinct.

Type locality. Chistyi Bank and Cheleken Island, Caspian Sea, Russia.

Distribution. Caspian Sea and Aral Sea, probably extinct.

Taxonomic notes. The species is commonly subdivided into a Caspian subspecies (*D. caspia caspia*) and an Aral Sea subspecies (*D. caspia pallasi* Andrusov, 1897). However, syntypes of the latter illustrated in Rosenberg and Ludyanskiy (1994, fig. 3f) show a broad and keeled *Dreissena* that has major morphological characters in common with *D. polymorpha*/*elata* rather than *D. caspia*. Filippov and Riedel (2009) reported *Dreissena caspia* from Holocene core deposits of Aral Sea, but given the juvenile status of their material they noted they were uncertain whether it might comprise *D. polymorpha*. *Dreissena caspia* was reported alive from the remaining "small Aral Sea" by Plotnikov et al. (2016). However, this latter record concerns more likely *D. polymorpha* and needs confirmation. Andreeva and Andreev (2003) mentioned that this subspecies has not been found in the Aral Sea since 1989.

Conservation status. Critically endangered, possibly extinct (von Rintelen and Van Damme 2011b).

Dreissena elata Andrusov, 1897

*1897 *Dreissensia polymorpha* var. *elata* Andrusov: 353, pl. 20, fig. 25.
1969 *Dreissena elata* (Andr.). – Logvinenko and Starobogatov: 316, fig. 341(1).
1994 *Dreissena elata* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1482, fig. 3g.
2013 *Dreissena elata* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: fig. 108.
2016 *Dreissena* (*Dreissena*) *elata* (Andrusov, 1897). – Vinarski and Kantor: 76.

Status. Pontocaspian species, endemic to the Caspian Sea, probably extinct. Species status uncertain.

Type locality. Kuuli Cape, Dazmyk, Apsheron Peninsula, Azerbaijan (Vinarski and Kantor 2016).

Distribution. Caspian Sea. Probably extinct.

Taxonomic notes. *Dreissena elata* has morphological features in common with *D. polymorpha*, including a relatively wide shell and a well-pronounced keel located close to the ventral margin. However, the *D. elata* shell is in general wider, flatter, and has a more rounded abapical margin even though shell characters are higly variable. *Dreissena elata* has been reported from areas in the Caspian Sea with salinities well above 5 ‰, which is unusual for *D. polymorpha* elsewhere. We are uncertain whether *D. elata* might be a sibling species. Its apparently distinct morphology and autecological preferences suggest it is different from *D. polymorpha*, but it will require molecular comparison to investigate whether it concerns a mere morph that has undergone "ecological release" (Kohn 1972) or is a different species. However, no living specimens of *D. elata* have been recorded since 1957 (Kostianoy and Kosarev 2005) when its Caspian habitats were invaded by *Mytilaster minimus*.

Conservation status. Not assessed. It was reported as extinct by Kostianoy and Kosarev (2005, and references therein). If *D. elata* is accepted as a valid species, it might qualify for the same conservation status as *D. caspia* (critically endangered, possibly extinct; von Rintelen and Van Damme 2011b).

Dreissena grimmi **(Andrusov, 1890)**

Fig. 4b

1877 *Dreyssena Brardii* var. *caspia* Grimm: 74–75 [**non** *Dreissena caspia* Eichwald, 1855].
*1890 *Dr.*[*eissena*] *Grimmi* Andrusov: 233 [**nom. nov.** pro *Dreissena caspia* Grimm, 1877, **non** Eichwald, 1855].
1897 *Dreissensia Grimmi* Andrus. – Andrusov: 279–282, pl. 16, figs 16–18.
1897 *Dreissensia rostriformis* var. *distincta* Andrusov: 273–278, pl. 14, figs 18–24.
1897 *Dreissensia Tschaudae* var. *pontocaspica* Andrusov: 294–297, pl. 9, figs 27–32, pl. 15, figs 29, 30.
1966a *Dreissena rostriformis compressa* Logvinenko and Starobogatov: 15–16, fig. 3.
1969 *Dreissena rostriformis grimmi* Andr. – Logvinenko and Starobogatov: 318, fig. 341(3).
1969 *Dreissena rostriformis pontocaspica* (Andr.). – Logvinenko and Starobogatov: 319, fig. 341(6).
1994 *Dreissena rostriformis* (Deshayes, 1838). – Rosenberg and Ludyanskiy: 1477–1479, figs 1f, 2a–j [**non** *Mytilus rostriformis* Deshayes, 1838].
2013 *Dreissena rostriformis* (Deshayes, 1838). – Kijashko in Bogutskaya et al.: 330 [**non** Deshayes, 1838].
2013 *D.*[*reissena*] *rostriformis compressa* Logvinenko & Starobogatov, 1966. – Kijashko in Bogutskaya et al.: 331, fig. 117a, photo 38.
2013 *D.*[*reissena*] *rostriformis distincta* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 331, fig. 117c.
2013 *D.*[*reissena*] *rostriformis grimmi* (Andrusov, 1890). – Kijashko in Bogutskaya et al.: 331, fig. 117b.
2013 *D.*[*reissena*] *rostriformis pontocaspica* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 331, fig. 117d.

Figure 4. Lectotype *Dreissena rostriformis* versus *D. grimmi*. **a** *D. rostriformis* Deshayes, 1838. Lectotype. Pliocene, Crimea. Reproduced from Archambault-Guezou (1976, pl. 6, fig 2a-2c) **b** RGM.961901, *D. grimmi* (Andrusov, 1890). Caspian Sea offshore Aktau, Kazakhstan, sample KAZ17-21, depth 44.3 m. Scale bar: 1 cm.

Status. Caspian Sea endemic.

Type locality. Caspian Sea.

Distribution. Middle to southern Caspian Sea basins. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *D. rostriformis compressa*) and found living offshore Aktau (Kazakhstan) in 2017 below 20 m water depth.

Taxonomic notes. This Caspian species is very often cited as *Dreissena rostriformis*. Rosenberg and Ludyanskiy (1994: 1497) discuss the uncertainties of this attribution but state that "*D. pontocaspica, D. distincta, D. compressa*, and *D. grimmi* are synonyms of *D. rostriformis*" even though they find "some justification for maintaining a distinction between an extinct subspecies, *D. rostriformis rostriformis* and a living one, for which *D. rostriformis grimmi* is the oldest name". Their figure of the lectotype of *D. rostriformis* (Rosenberg and Ludyanskiy 1994: fig. 2a), which derives from Pliocene deposits of the Black Sea Basin, concerns a relative small, thick-shelled, and low *Dreissena* with a pointed beak and lacking a keel. On interior view, the shell area outside the pallial line is thick. Deshayes's lectotype has several characters in common with modern Caspian *D. rostriformis* and the closely related Black Sea Basin *D. bugensis*. Yet, the Pliocene form has a broader umbonal area that results in a more subquadrangular shape, which is different from the modern Caspian *Dreissena* that have tear-drop to pear-shaped shells. The subquadrangular shape of Deshayes's material is even more pronounced in the pallial line on the shell's interior, a feature not seen in any modern Caspian material. The Pliocene Black Sea *D. rostriformis* has its general shape in common with Apsheronian (Early Pleistocene) Caspian dreissenids referred to as *D. carinatocurvata* as illustrated in Kolesnikov (1950, pl. 14, figs 14–16). Hence, we conclude that the recent Caspian species should be treated different from Pliocene *D. rostriformis* and the name *D. grimmi* should be applied instead.

Various subspecies have been attributed to Caspian *Dreissena rostriformis* (see, e.g., Kijashko in Bogutskaya et al. 2013 for a synonymy list). Even though morphological differences appear to be large, intermediates are known between the morphs. Stepien et al. (2013) reviewed molecular evidence for species boundaries within *Dreissena*. They concluded that (1) all Caspian Sea forms that have been mentioned in literature as (sub-) species of *D. rostriformis* (= *D. grimmi*) are one and the same species and (2) there is not enough molecular evidence and great difficulty in morphology to separate the Caspian species from the Black Sea Basin *D. bugensis*. We agree with the first point made by Stepien et al. (2013); all forms reported from the middle and southern Caspian Sea basins appear to be mere morphs of a single species, a feature also noted by Rosenberg and Ludyanskiy (1994). However, we disagree with their second proposal. *Dreissena bugensis* and *D. grimmi* have non-overlapping ecological tolerances and are separated geographically (Rosenberg and Ludyanskiy 1994). This fact together with the very limited but consistent genetic differentiation suggests that it may concern very recently evolved sister species. In the early 1980s, *D. bugensis* was introduced in the Volga (Zhulidov et al. 2005) and since then spread from there to central and western Europe and North America. So far, *Dreissena bugensis* has only been reported from the Volga itself and its delta but not from the northern Caspian Sea Basin. If it would be conspecific with the middle-southern Caspian species, which lives at higher salinities and deeper habitats, we would expect that the invasive populations in the north would have been blended with the Caspian population in the south. With no such intermediate populations found so far we consider both taxa as viable species.

Conservation status. Least Concern (for *Dreissena rostriformis*; von Rintelen and Van Damme 2011c).

Dreissena polymorpha (Pallas, 1771) s.l.

*1771 *Mytilus polymorphus* Pallas: 368, 435, 478.
1897 *Dreissensia Andrusovi* Andrusov: 374–376 pl. 18, figs 21–23.
1897 *Dreissensia Pallasi* Andrusov: 671–672, pl. 20, figs 33–35.
1897 *Dreissensia polymorpha* var. *aralensis* Andrusov: 354–355.
1897 *Dreissensia polymorpha* var. *obtusecarinata* Andrusov: 354.
1994 *Dreissena polymorpha* (Pallas, 1771). – Rosenberg and Ludyanskiy: 1480–1482, fig. 3a, b.
1994 *Dreissena polymorpha aralensis* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1480, fig. 3c.
1994 *Dreissena polymorpha obtusecarinata* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1481, fig. 3d.
1994 *Dreissena caspia pallasi* Andrusov, 1897. – Rosenberg and Ludyanskiy: 1482, fig. 3f.
2003 *Dreissena caspia pallasi* (Andrusov, 1897). – Andreeva and Andreev: 80, fig. 4.1(7–9).
2003 *Dreissena polymorpha aralensis* (Andrusov, 1897). – Andreeva and Andreev: 79, fig. 4.1(1–3).

2003 *Dreissena obtusecarinata* (Andrusov, 1897). – Andreeva and Andreev: 80, fig. 4.1(4–6).
2013 *Dreissena* (*Dreissena*) *polymorpha* (Andrusov, 1897). – Kijashko in Bogutskaya et al.: 328, fig 118a [pars, status fig. 118b uncertain].
2016 *Dreissena* (*Dreissena*) *polymorpha polymorpha* (Andrusov, 1897). – Vinarski and Kantor: 75.
?2016 *Dreissena* (*Dreissena*) *polymorpha andrusovi* (Brusina in Andrusov, 1897). – Vinarski and Kantor: 75.
?2016 *Dreissena* (*Dreissena*) *polymorpha aralensis* (Andrusov, 1897). – Vinarski and Kantor: 75.
?2016 *Dreissena* (*Dreissena*) *polymorpha obtusecarinata* (Andrusov, 1897). – Vinarski and Kantor: 76.
?2016 *Dreissena* (*Dreissena*) *caspia pallasi* (Andrusov, 1897). – Vinarski and Kantor: 7.

Status. Native Pontocaspian species.

Type locality. Volga and Yaik (Ural) rivers, Caspian Sea.

Distribution. Eurasian (native and invasive), North America (invasive) rivers, lakes, estuaries, deltas (Rosenberg and Ludyanskiy 1994, Cummings and Graf 2015, Coughlan et al. 2017). Several unique forms/species within this group reported from the Pontocaspian region.

Taxonomic notes. *Dreissena polymorpha* has been subject of intense DNA and ecological studies, but rarely were Caspian communities involved. Combined insights into the shell morphology, ecology, and molecular biology has to date not fully resolved several aspects of Pontocaspian records of this species. Occurrences in rivers and deltas of the Pontocaspian region are consistently attributed to *Dreissena polymorpha*. However, slightly deviating morphs exist(ed) in salinities typically not favoured by *D. polymorpha* elsewhere in the Caspian and Aral seas. A particular form of *Dreissena polymorpha*, documented by Kijashko in Bogutskaya et al. (2013), viz. *D. polymorpha andrusovi* (his figure 118b) will need further study as it has many morphological similarities with *D. caspia* (including general shape, location of semidiameter, and broad flat shape of hinge platform).

Conservation status. Least Concern (Van Damme 2014).

Mytilopsis leucophaeata (Conrad, 1831)

*1831 *Mytilus leucophaeatus* Conrad: 263–264, pl. 11, fig. 13.
2013 *Mytilopsis leucophaeata* (Conrad, 1831). – Kijashko in Bogutskaya et al.: 320, fig. 107.

Status. Invasive Pontocaspian species.

Type locality. Southern coast of eastern United States.

Distribution. Black Sea Basin, Caspian Sea, coasts of western Europe, Caribbean, and northern South America.

Remarks. The species, native to the southern coast of North America, was first introduced in Europe in 1835 (Heiler et al. 2010). In the Pontocaspian region, it first appeared in the northern Black Sea Basin in 2002 and was first collected in the Caspian Sea in 2009 (Heiler et al. 2010). It is easily distinguished from Pontocaspian dreissenids by the presence of an aphophysis near the hinge.

Conservation status. Least Concern (Cummings 2011).

Gastropoda

Family Neritidae Rafinesque, 1815

Theodoxus danubialis (Pfeiffer, 1828)

*1828 *Nerita danubialis* Pfeiffer: 48, pl. 8, figs 17, 18.
2009 *Theodoxus danubialis* (C. Pfeiffer, 1828). – Fehér et al.: figs 2a–k, 4a–c, 5a–c.
2012 *Theodoxus danubialis* (Pfeiffer, 1828). – Welter-Schultes: 27, unnumbered text figures.
2016 *Theodoxus* (*Theodoxus*) *danubialis* (Pfeiffer, 1828). – Vinarski and Kantor: 156 [and synonyms therein].

Status. Accepted native species.

Type locality. Danube River, Vienna, Austria.

Distribution. Danube River catchment, central to south-eastern Europe, as well as northern Italy (Fehér et al. 2009).

Taxonomic notes. The latest phylogenetic data supports a sister relationship between *Theodoxus danubialis* and the clade containing *T. fluviatilis* and *T. velox* (AFS, unpublished data). Some authors believe *T. danubialis* and *T. prevostianus* may represent different species given some level of genetic, ecological, and morphological differentiation (Fehér et al. 2009, Welter-Schultes 2012; but see also Bandel 2001). More recent unpublished results may suggest that the genetic level of differentiation between these species is more indicative of intraspecific diversity within a single species (AFS, unpublished data).

Conservation status. Least Concern (Tomovic et al. 2010).

Theodoxus fluviatilis (Linnaeus, 1758)

*1758 *Nerita fluviatilis* Linnaeus: 777.
1865 *Theodoxus fluviatilis* var. *subthermalis* Issel: 22–23.
1886 *Neritina euxina* Clessin: 55.
1908 *Neritina danubialis* var. *danasteri* Lindholm: 214–215.
?1972 *Theodoxus dniestroviensis* Put': 80–82, text fig. 5.
?1999 *Th. dniestroviensis* Put', 1972. – Anistratenko et al.: 19, figs 4, 8.
1999 *Th. fluviatilis* (Linnaeus, 1758). – Anistratenko et al.: 13–15, figs 3, 4.
2005 *Theodoxus fluviatilis* (Linnaeus, 1758). – Anistratenko: 7–8, text figs 3, 4.
2012 *Theodoxus euxinus* (Clessin, 1886). – Welter-Schultes: 27, unnumbered text figures.
2012 *Theodoxus fluviatilis* (Linnaeus, 1758). – Welter-Schultes: 28, unnumbered text figures.

2015 *Theodoxus fluviatilis* (Linnaeus, 1758). – Glöer and Pešić: 88–91, figs 1, 3–5, 9, 13–34.
2016 *Theodoxus* (*Theodoxus*) *fluviatilis* (Linnaeus, 1758). – Vinarski and Kantor: 154–155 [pars, excluding synonyms *sarmatica* and *velox*].
2016 *Theodoxus* (*Theodoxus*) *euxinus* (Clessin, 1886). – Vinarski and Kantor: 155.
2016 *Theodoxus* (*Theodoxus*) *subthermalis* (Bourguignat in Issel, 1865). – Vinarski and-Kantor: 157–158.

Status. Accepted native species.

Type locality. Near Uppsala, Sweden. The lectotype was designated by Anistratenko (2005).

Distribution. Widely distributed all over Europe, Anatolia, and north-western Africa. Within the Pontocaspian region, it is a common component of the lower reaches of Black and Azov Sea drainages (specifically in Bulgaria, Romania, and Ukraine). Towards the east, the species extends at least as far as the Don River system in Russia and the coastal rivers of Georgia, but it is absent from the Caspian system. Records of this species from Iran and western Asia are likely misidentifications (AFS, unpublished data).

Taxonomic notes. *Theodoxus fluviatilis* exhibits considerable variation in shell colouration and shape (Glöer and Pešić 2015). Unpublished molecular data confirm the synonymy of a number of taxa such as *Theodoxus euxinus* syn. n., *T. danasteri*, and *T. subthermalis* syn. n., and further suggest the inclusion of *T. saulcyi* and *T. heldreichi* (AFS, unpublished data). A final decision concerning the status of *T. dniestroviensis* Put', 1972 described from the Dniester River (Rukhotyn village, Khotyn district, Chernivtsi region, Ukraine) is not possible at the moment. Despite appropriate efforts, we were unable to trace the type specimens of this species. Based on the original description and illustration (Put' 1972) it was considered as a junior synonym of *T. fluviatilis* by Anistratenko et al. (1999) having an unusual colour pattern. *Theodoxus milachevichi* was described as a subfossil from the Crimean coast. It closely resembles morphotypes of both *T. fluviatilis* and *T. velox* V. Anistratenko in O. Anistratenko et al., 1999 and might be synonym of either species (compare type material illustrated in Kantor and Sysoev 2006). However, the morphological variability of the taxa involved, as well as the lacking possibility of acquiring genetic data for *T. milachevichi*, complicates a decision on the independence or synonymy of this species.

Conservation status. Least Concern (Kebapçı and Van Damme 2012).

Theodoxus pallasi Lindholm, 1924

°1838 *Neritina liturata* Eichwald: 156–157 [**non** *Neritina liturata* Schultze, 1826].
*1924 *Theodoxus pallasi* Lindholm: 33, 34 [**nom. nov.** pro *Neritina liturata* Eichwald, 1838, **non** Schultze, 1826].
1947 *Theodoxus* (*Theodoxus*) *pallasi* var. *nalivkini* Kolesnikov: 106, 110.
1976 *Theodoxus pallasi* Lindholm, 1924. – Akramovskiy: 88, text fig. 23, pl. 1, figs 1, 2.
1994 *Theodoxus astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova and Pirogov: 8–9, fig. 1(1, 2).
1994 *Theodoxus astrachanicus* Starobogatov et al.: 8–9, fig. 1(1, 2).

2009 *Theodoxus pallasi* Lindholm, 1924. – Filippov and Riedel: 70, 72, 74, 76, fig. 4g–i.
2011 *Theodoxus astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova & Pirogov, 1994. – Anistratenko et al.: 54–55, fig. 1(6).
2012 *Theodoxus pallasi* Lindholm, 1924. – Welter-Schultes: 29, unnumbered text figures.
2016 *Theodoxus* (*Theodoxus*) *astrachanicus* Starobogatov in Starobogatov, Filchakov, Antonova & Pirogov, 1994. – Vinarski and Kantor: 155–156.
2016 *Theodoxus* (*Theodoxus*) *pallasi* (Lindholm, 1924). – Vinarski and Kantor: 156–157 [and synonyms therein].
2017 *Theodoxus pallasi* Lindholm, 1924. – Anistratenko et al.: 221, figs 4, 7, 10, 11.
2018 *Theodoxus pallasi* Lindholm, 1924. – Neubauer et al.: 48–51, fig. 4A–F.

Status. Accepted Pontocaspian species, name uncertain.

Type locality. "Inter Fucos littoris Derbendensis viva" (living among algae on the shores of Derbent), Dagestan, Russia.

Distribution. Present along the Caspian Sea shores, in the Volga River, and the Sea of Azov. Lived until the late 1980s in the Aral Sea but is possibly extinct there now (Andreev et al. 1992, Aladin et al. 1998, Micklin et al. 2014).

Taxonomic notes. Eichwald (1838) introduced the species *Neritina liturata* based on material from the shores of Derbent (Dagestan, Russia, northwestern Caspian Sea). That name is invalid as it is a junior primary homonym of *N. liturata* Schultze, 1826; it was replaced by Lindholm (1924) with *Theodoxus pallasi* (see also Anistratenko et al. 2017). *Theodoxus pallasi* is a widely used name, but a major nomenclatural change might be due. Unpublished molecular data suggest that all *Theodoxus* from the Caspian Sea, Azov Sea, and Armenian lakes Sevan and Yerevan, as well as several mineral springs and streams in the Khorasan provinces of Iran, belong to a single species (AFS, unpublished results). The oldest name available for that group is *Theodoxus major* Issel, 1865, described from Lake Sevan in Armenia (originally as variety of the unavailable name *T. schirazensis*). Akramovskiy (1976) noted the similarity of *T. pallasi* and *T. major* and considered the latter as a morphotype of the former. Although he did not explicitly state it, he thereby suggested the two taxa to be synonymous. This view was adopted by Vinarski and Kantor (2016), who listed *major* in synonymy of *pallasi*, although Issel's (1865) name has priority. The potential synonymy also involves *T. schultzii*. Despite the characteristic appearance of the syntypes, the presence of intermediate morphologies in samples taken on shores of Azerbaijan and Kazakhstan in 2016 and 2017 (pers. obs. OA, VA, FW) indicates a close relationship with *T. pallasi*. The radulae of these two species differ in the relative width of the central and marginal teeth (see Zettler 2007 and compare Anistratenko et al. 2017).

Unfortunately, the types of *T. major*, supposed to be in the Museo Regionale di Scienze Naturali, Torino, are inaccessible at the moment due to museum renovation (E Gavetti, pers. comm., Oct 2018). We refrain from a final conclusion on the synonymy of the species involved until information on the types of all taxa as well as published molecular data are available. For details on the taxonomic relationship between *T. pallasi* and *T. astrachanicus*, see discussion in Anistratenko et al. (2017).

Conservation status. Data Deficient (Van Damme and Kebapçı 2014).

Theodoxus schultzii (Grimm, 1877)

*1877 *Neritina Schultzii* Grimm: 77–78, pl. 7, fig. 5, pl. 8, fig. 16.
1909 *Neritina* (*Ninnia*) *Schultzei* [sic] Grimm. – Andrusov: 106–107, pl. 6, fig. 38.
?1947 *Theodoxus* (*Ninnia*) *schultzi* [sic] var. *jukovi* Kolesnikov: 106, 110.
1950 *Theodoxus* (*Ninnia*) *schultzei* [sic] (Grimm). – Kolesnikov: 215–216, pl. 26, figs 12, 13.
1969 *Theodoxus schultzi* [sic] (Grimm, 1877). – Logvinenko and Starobogatov: 344, fig. 357.
?1974 *Theodoxus zhukovi* [sic] Kolesnikov, 1947. – Starobogatov: 255, text fig. 223.
2007 *Theodoxus* (*Theodoxus*) *schultzii* (Grimm, 1877). – Zettler: 249, figs 2–5.
2016 *Theodoxus* (*Theodoxus*) *schultzii* (Grimm, 1877). – Vinarski and Kantor: 157.

Status. Pontocaspian species, status uncertain.

Type locality. Caspian Sea, in two localities, given by Grimm (1877) as 43°17'N, 01°03'E, 40 fathoms, and 42°48'N, 01°22'E, 48 fathoms. Since the longitude was calculated relative to the geographic position of Baku, situated approximately at 50E, the correct longitude should be about 51°00'E (Vinarski and Kantor 2016).

Distribution. Middle and southern Caspian Sea basins, between 15 and 100 m (Logvinenko and Starobogatov 1969).

Taxonomic notes. See discussion of *T. pallasi* for notes on the potential synonymy with *T. major* Issel, 1865. The status of *T. jukovi* still requires confirmation (Vinarski and Kantor 2016).

Conservation status. Not assessed.

Theodoxus velox V. Anistratenko in O. Anistratenko et al., 1999

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

Status. Pontocaspian species, name uncertain.

Type locality. Dnieper Delta, Zbur'ivka liman, Ukraine.

Distribution. This species was believed to be restricted to drainage systems of the northern Black Sea coast (even though the Oskol River lies far from the Black Sea coast), but unpublished molecular data suggest it may be distributed as far north as the eastern part of the Baltic Sea and as far south as Anatolia (AFS, unpublished data).

Taxonomic notes. The species was listed as junior synonym of *T. fluviatilis* by Vinarski & Kantor (2016). *Theodoxus velox* is indeed challenging to differentiate from some regional morphotypes of that species given the overlap in shell patterns. Unpublished molecular data indicate however that *T. velox* belongs to a different molecular clade (AFS, unpublished data). The distribution range of that clade overlaps with the range of *T. sarmaticus* (Lindholm, 1901), which is widely accepted as a junior synonym of *T. fluviatilis* in the literature (e.g., Vinarski and Kantor 2016). A revision of the taxa involved and study of the type material is required to solve the synonymy issues.

Conservation status. Not assessed.

Family Cochliopidae Tryon, 1866

Eupaludestrina stagnorum (Gmelin, 1791)

*1791 *Helix stagnorum* Gmelin: 3653.
1975 *Falsihydrobia streletzkiensis* Chukhchin: 121.
2012 *Heleobia stagnorum* (Gmelin, 1791). – Welter-Schultes: 39, unnumbered text figures.
2012 *Semisalsa stagnorum* (Gemlin, 1791). – Kroll et al.: 1520.

Status. Accepted, native Pontocaspian or immigrant species.

Type locality. Kaasjeswater, Zierikzee, the Netherlands.

Distribution. Coastal areas of Europe and the Mediterranean region, extending to North Africa and east to Iran (Glöer 2002). Occurrence in Black Sea according to, e.g., Chukhchin (1975) and in the Caspian Sea (TW, unpublished data).

Taxonomic notes. We find the attribution of this species to the genus *Eupaludestrina* unsatisfactory, yet a further revision is required to establish and stabilise the generic attribution as there is considerable confusion. It is commonly classified in the South American genus *Heleobia* (e.g., Prié 2011), whereas Kroll et al. (2012) suggested that this species belongs to the genus *Semisalsa*, a group of European Cochliopidae distinct from *Heleobia*. However, *Semisalsa* is currently listed as junior synonym of *Eupaludestrina* Mabille, 1877 (type species: *Hydrobia macei* Paladilhe, 1867, by subsequent designation by Kadolsky 2008). Following Kadolsky (2008), *Eupaludestrina* is currently ranked as subgenus of *Heleobia* in MolluscaBase (2018), but both the phylogenetic and geographic distinction of the European and American species suggest separation on the genus level.

Remarks. It is unclear whether the species is native to the Pontocaspian area or a recent immigrant.

Conservation status. Least Concern (Prié 2011).

Family Hydrobiidae Stimpson, 1865

Remarks. The Hydrobiidae form the most species-rich mollusc group in the Pontocaspian region. However, in general, useful shell characters are few and highly variable (Wilke and Delicado in press). Descriptions in the past have often been very general, and illustrations of types are notably poor for several of the endemic taxa. A strong tendency of naming large numbers of species has developed throughout the 20th century (e.g., Logvinenko and Starobogatov 1969), but for some groups where morphological and genetic analyses could be performed (e.g., *Caspiohydrobia* spp.) it has been demonstrated that actual species numbers were much lower than the number of species described (Haase et al. 2010). For many of the endemic species, especially in the genus *Turricaspia*, the apparent loss of types, combined with the lack of living material makes it impossible to assess their taxonomic status. Currently, a number of taxonomic works is in progress on the endemic Pontocaspian hydrobiid groups, and some different insights on the genus-level classifications exist. Here, we adopt a conservative approach, mostly based on Neubauer et al. (2018).

Subfamily Caspiinae Dybowski, 1913

Remarks. The distinction of the genera *Caspia*, *Ulskia*, and *Clathrocaspia* follows Neubauer et al. (2018). The three taxa are differentiated based on details of the protoconch and the expression of teleoconch sculpture. *Caspia* s. s. is characterised by a single distinct but fine spiral keel below the suture. It is usually smooth, yet within the type species some reticulate ornament can be found. Species of *Clathrocaspia* expose a distinctive, reticulate pattern on the teleoconch and a malleate protoconch with faint spiral threads. The aperture of *Clathrocaspia* often develops a distinct flat base. The discinction of the two genera is subject of current research. *Ulskia* also has a malleate protoconch but with more distinct spiral threads; teleoconch sculpture is occasionally present as minute elongate nodules.

Caspia baerii Clessin & Dybowski in Dybowski, 1887

*1887 *Caspia Baerii* Clessin & Dybowski in Dybowski: 36–37.
1888 [*Caspia*] *Baerii* n. sp. – Dybowski: 79, pl. 3, fig. 4a, b.
1969 *Pyrgula* (*Caspia*) *baerii* (Cless. & Dyb.). – Logvinenko and Starobogatov: 377, fig. 367(3).
2016 *Caspia baerii* Clessin & W. Dybowski in W. Dybowski, 1888. – Vinarski and Kantor: 224.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea and possibly Danube Delta (Romania). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia baerii*).

Taxonomic notes. The type material is stored in the von Baer collection of Caspian Sea molluscs in the Zoological Museum of Lviv University (Ukraine) and comprises more than a hundred syntypes (Anistratenko et al. 2018). The slender shell, the presence of a fine spiral keel below the suture, and the occasionally weakly reticulated surface distinguish this species from congeners.

Conservation status. Not assessed.

Caspia valkanovi (Golikov & Starobogatov, 1966)

*1966 *P.*[*yrgula*] (*Caspia*) *baeri* [sic] *valkanovi* Golikov & Starobogatov: 354–355, fig. 1(9).
2006 *Caspia valkanovi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 88, pl. 41, fig. N.

Status. Pontocaspian species, identity uncertain.

Type locality. Off Crimea, station 18, sample 173.

Distribution. Endemic to the Black Sea Basin.

Taxonomic notes. The identity and status of this subfossil taxon, described from phaseoline silt, are somewhat uncertain. The holotype illustrated in Kantor and Sysoev (2006) is poorly preserved and does not allow a proper assessment of its validity. The general shape and size are indicative of the genus *Caspia* and it looks like a variety that might even be a synonym of *C. baerii*. Furthermore, we are not entirely certain as to the stratigraphic age of the stratigraphic origin of this species. The phaseoline silt is a marine Holocene unit, yet it contains reworked Late Pleistocene Neoeuxinian (Pontocaspian) species (FW, pers. obs.).

Conservation status. Not assessed.

Clathrocaspia brotzkajae (Starobogatov in Anistratenko & Prisjazhnjuk, 1992)

*1992 *Caspia* (*Clathrocaspia*) *brotzkajae* Starobogatov in Anistratenko & Prisjazhnjuk: 18–19, fig. 2a.
2016 *Caspia brotzkajae* Starobogatov in Anistratenko & Prisjazhnjuk, 1992. – Vinarski and Kantor: 224.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea shores of Dagestan, Russia, at ca. 60 m.

Distribution. Presently endemic to the Caspian Sea. The species was also recorded from the Holocene of Danube Delta, Ukraine (Anistratenko and Prisjazhnjuk 1992).

Taxonomic notes. The species differs from its congeners in the bulbous shape, with a ratio of body whorl height/shell height of approx. 3/4, as well as regarding the expanded aperture.

Conservation status. Not assessed.

Clathrocaspia gmelinii (Clessin & Dybowski in Dybowski, 1887)

*1887 *Caspia Gmelinii* Clessin & Dybowski in Dybowski: 37–38.
1888 [*Caspia*] *Gmelini* [sic] n. sp. – Dybowski: 79, pl. 3, fig. 7a, b.
1969 *Pyrgula* (*Caspia*) *gmelinii* (Cless. & W. Dyb.). – Logvinenko and Starobogatov: 378, fig. 367(7).
?1969 *Pyrgula* (*Caspia*) *sowinskyi* Logvinenko and Starobogatov: 378, fig. 367(4).
?1977 *Pyrgula* (*Caspia*) *gaillardi* Tadjalli-Pour: 107, pl. 2, fig. 8.
2015 *Caspia gmelinii* Clessin & W. Dybowski, 1887. – Boeters et al.: 178, figs 1–6.
2016 *Caspia gmelinii* Clessin & W. Dybowski in W. Dybowski, 1888. – Vinarski and-Kantor: 224.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea, recorded from the middle and southern parts. This species was mentioned from depths between 200 and 300 m in the

South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia gmelinii*).

Taxonomic notes. The broad shell and the heavily reticulated surface distinguish this species from congeners. *Pyrgula sowinskyi*, from the middle and southern Caspian Sea, and *P. gaillardi*, from the Caspian Sea shore between Astara and Hashtpar (= Talesh), Iran, closely resemble *C. gmelinii* in terms of shell shape, the shape of the aperture, and the distinct reticulate teleoconch sculpture. Very likely, the two species are synonyms of *C. gmelini*. Since the type material of Logvinenko and Starobogatov (1969) has not been found, and the whereabouts of the material of Tadjalli-Pour (1977) is unknown, a re-examination of these species has to be postponed. Here, we suggest to treat them as nomina dubia until more information becomes available.

Conservation status. Data Deficient (same for *P. sowinskyi*; Son 2011a, Vinarski 2011o).

Clathrocaspia isseli (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Caspia*) *isseli* Logvinenko & Starobogatov: 378, fig. 367(6).
2016 *Pyrgula isseli* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 239.

Status. Pontocaspian species, identity uncertain.

Type locality. Southern Caspian Sea (no details), between 40–75 m water depth.

Distribution. Endemic to the Caspian Sea.

Taxonomic notes. This species hardly differs from *C. pallasii* and might be a junior synonym. Observations on Holocene material from the southern and northern Caspian Sea shores (VA, TN, FW) suggest that the minor differences range within intraspecific variability but further studies (preferentially involving DNA) are required to solve the identity of this taxon. The classification in *Clathrocaspia* is based on the reticulate sculpture typical of that genus.

Conservation status. Data Deficient (Vinarski 2011j).

Clathrocaspia knipowitschii (Makarov, 1938)

*1938 *Caspia gmelini* [sic] var. *Knipowitschii* Makarov: 1058.
?1966 *P.*[*yrgula*] (*Caspia*) *gmelini* [sic] *aluschtensis* Golikov and Starobogatov: 354, fig. 1(8).
1966 *P.*[*yrgula*] (*Caspia*) *makarovi* Golikov and Starobogatov: 353–354, fig. 1(5).
?1987 *Caspia gmelinii stanislavi* Alexenko and Starobogatov: 33, fig. 1.
1992 *Caspia* (*Clathrocaspia*) *knipowitchi* Makarov, 1938. – Anistratenko and Prisjazhnjuk: 19, fig. 2b.
2006 *Caspia knipowitchi* [sic] Makarov, 1938. – Kantor and Sysoev: 87–88, pl. 41, fig. J.
2006 *Caspia makarovi* (Golikov et Starobogatov, 1966). – Kantor and Sysoev: 88, pl. 41, fig. L.
2013 *Caspia knipowitchii* [sic] Makarov, 1938. – Anistratenko: 53–55, figs 1A–I, 3A–D, 5A–D.

2013 *Caspia makarovi* (Golikov & Starobogatov, 1966). – Anistratenko: 56–59, figs 2A–E, 3E.
2016 *Caspia knipowitchi* [sic] Makarov, 1938. – Vinarski and Kantor: 224.
2016 *Caspia makarovi* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 225.
?2016 *Caspia stanislavi* Alexenko & Starobogatov, 1987. – Vinarski and Kantor: 225.

Status. Accepted Pontocaspian species.

Type locality. Ukraine, in the Dniester River (exact locality not specified).

Distribution. Azov Sea and northern Black Sea Basin. Known from the Holocene of Danube Delta, Ukraine (Anistratenko and Prisjazhnjuk 1992).

Taxonomic notes. *Clathrocaspia knipowitschii*, *C. makarovi*, *C. gmelini aluschtensis*, and *C. stanislavi* were all described from the northern margin of the Black Sea. After detailed morphological comparison of *C. knipowitschii* and *C. makarovi* syn. n. and preliminary genetic analyses (TW, unpublished data), we conclude that both taxa should be considered synonyms. Very likely, also *C. gmelini aluschtensis* and *C. stanislavi* are synonyms of *C. knipowitschii*, but a final decision on that matter requires investigation of the type material.

Conservation status. Least Concern (same for *C. makarovi*; Son 2011b, c).

Clathrocaspia logvinenkoi (Golikov & Starobogatov, 1966)

*1966 *P.*[*yrgula*] (*Caspia*) *logvinenkoi* Golikov & Starobogatov: 354, fig. 1(7).
2006 *Caspia logvinenkoi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 88, pl. 41, fig. I.
2007a *Caspia* (*Clathrocaspia*) *logvinenkoi* (Golikov & Starobogatov, 1966). – Anistratenko: 25–26, fig. 2.
2016 *Caspia logvinenkoi* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 224–225.

Status. Accepted Pontocaspian species.

Type locality. Don Delta, Russia.

Distribution. Known only from the type locality.

Taxonomic notes. The species has distinctive shell characters: broad conical shape with a weak subsutural bulge and apically thickened peristome.

Remarks. The type material was collected by Mordukhay-Boltovskoy in 1937 and comprises two specimens, the holotype and the paratype. Three additional specimens were collected from the same region in 2006 (Anistratenko 2007a). The salinity at the type locality fluctuates between freshwater and ca. 1‰.

Conservation status. Not assessed. In the fifty years since the description of this species five specimens have been collected; this is likely evidence of its rarity. Known only from two close localities, *C. logvinenkoi* appears to have an extremely narrow distributional range in the Azov–Black Sea Basin, being endemic to the Taganrog province (e.g., Anistratenko 2007a).

Clathrocaspia milae (Boeters, Glöer & Georgiev, 2015)

*2015 *Caspia milae* Boeters, Glöer & Georgiev in Boeters et al.: 180–183, figs 9–21.

Status. Pontocaspian species, identity uncertain.

Type locality. Bulgaria, Danube Island Vardim (43°37'N, 25°28'E).

Distribution. Only known from type locality.

Taxonomic notes. This species closely resembles *C. knipowitschii* concerning shape, size, and sculpture. According to Boeters et al. (2015), the two species differ in the degree of cover of the umbilicus, the shape of the peristome and the size and number of whorls of the protoconch. Molecular and/or more in-depth morphological and anatomical studies are required to confirm that these apparently minor differences are sufficient to separate the species.

Remarks. If the species would be confirmed, it concerns a Pontocaspian species whose distribution currently is outside prime Pontocaspian habitat, yet Boeters et al. (2015) implied they would expect that several of the *Caspia* records from the lower Danube and Razim Lake complex might be attributed to *C. milae* as well. The Razim Lake complex is Pontocaspian habitat.

Conservation status. Not assessed.

Clathrocaspia pallasii (Clessin & Dybowski in Dybowski, 1887)

*1887 *Caspia Pallasii* Clessin & Dybowski in Dybowski: 37.
1888 *Caspia Pallasii* n. sp. – Dybowski: 79, pl. 3, fig. 3a, b.
1969 *Pyrgula* (*Caspia*) *pallasii* (Cless. & W. Dyb.). – Logvinenko and Starobogatov: 378, fig. 367(5).
2016 *Pyrgula pallasii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 241.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea.

Taxonomic notes. This species differs from the other Caspian species *C. gmelinii* in its very slender shape.

Conservation status. Not assessed.

Ulskia behningi (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Ulskia*) *behningi* Logvinenko & Starobogatov: 380, fig. 367(13).
2016 *Pyrgula behningi* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 236.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the southern Caspian Sea, in the vicinity of the Kura River mouth, 39°05'N, 49°48'E, 120 m.

Distribution. Type locality only.

Taxonomic notes. The drawings provided by Logvinenko and Starobogatov (1969) sketch a broad and conical shell. As such, it differs from the more elongate and ovoid *Ulskia ulskii* (Neubauer et al. 2018). A revision is required to clarify its taxonomic status.

Conservation status. Data Deficient (Vinarski 2011f).

?*Ulskia derzhavini* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Ulskia*) *derzhavini* Logvinenko & Starobogatov: 379, fig. 367(9).
2016 *Pyrgula derzhavini* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 237.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle and southern Caspian Sea, 45–81 m.

Distribution. Type locality only.

Taxonomic notes. The species differs from *U. ulskii* and *U. behningi* in the very slender elongate shape and the presence of a subsutural band; this suggests *P. derzhavini* might be likely a member of *Caspia* s.s. A revision is required to clarify its taxonomic status and generic placement.

Conservation status. Not assessed.

Ulskia ulskii (Clessin & Dybowski in Dybowski, 1887)

*1887 *Caspia Ulskii* Clessin & Dybowski in Dybowski: 38–39.
1888 [*Caspia*] *Ulskii* n. sp. – Dybowski: 79, pl. 3, fig. 8a, b.
1969 *Pyrgula* (*Ulskia*) *nana* Logvinenko and Starobogatov: 379–380, fig. 367(12).
1969 *Pyrgula* (*Ulskia*) *schorygini* Logvinenko and Starobogatov: 379, fig. 367(11).
2016 *Pyrgula ulskii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 244.
2018 *Ulskia ulskii* (Clessin & W. Dybowski in W. Dybowski, 1887). – Neubauer et al.: 52–54, fig. 5A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Western part of the Caspian Sea. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia ulskii*, *T. schorgyni,* and *T. nana*).

Taxonomic notes. This species was recently studied by Neubauer et al. (2018), who considered *P. nana* and *P. schorygini* as its junior synonyms.

Conservation status. Not assessed.

Subfamily Hydrobiinae Stimpson, 1865

Remarks. In addition to the taxa discussed below, the following species of Hydrobiinae have been mentioned from the Black Sea basin (updated statuses after MolluscaBase 2018a): *Hydrobia aciculina* (Bourguignat, 1876), *H. acuta* (Draparnaud, 1805), *H. euryomphala* (Bourguignat, 1876), *H. mabilli* (Bourguignat, 1876) [currently accepted as *Peringia mabilli*], *H. macei* Paladilhe, 1867 [currently accepted as *Heleobia macei*], *H. procerula* (Paladilhe, 1869) [currently considered a synonym of *H. acuta*] (Anistratenko et al. 2011). These species were described from the Western Mediterranean and their occurrence in the Black Sea region requires re-investigation; partly the records might be misidentifications of the species of *Ecrobia* listed below or *Eupaludestrina* (Cochliopidae) listed above.

Ecrobia grimmi (Clessin in Dybowski, 1887)

*1887 *Hydrobia grimmi* Clessin in Dybowski: 55–56.
1888 [*Hydrobia*] *grimmi* Clessin. – Dybowski: 79, pl. 3, fig. 2.
2009 *Caspiohydrobia grimmi* (Clessin & Dybowski, 1888). – Filippov and Riedel: 70–72, 74–76, fig. 4a–d.

Status. Accepted native Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea; Aral Sea; salt lakes near Chelyabinsk, Russia (Shishkoedova 2010); Lake Sawa, Iraq (Haase et al. 2010); Arabian (Persian) Gulf (Glöer and Pešić 2012); possibly also northern and central Kazakhstan and Tajikistan (Vinarski and Kantor 2016), however, no molecular data are known to confirm the identity of the Central Asian snails. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Caspiohydrobia curta* and *C. gemma*).

Taxonomic notes. Most of the species that have been assigned to the genus *Caspiohydrobia* Starobogatov, 1970, including its type species, *Pyrgohydrobia eichwaldiana* Golikov & Starobogatov, 1966, range within the morphological variability of *E. grimmi*. Previous examination of some *Caspiohydrobia* juvenile shells (Filippov and Riedel 2009, Anistratenko 2013, fig. 4A–C) as well as reproductive systems and radula did not find any criteria to support differentiation. Probably, all of the thirty *Caspiohydrobia* species listed by Kantor and Sysoev (2006) and Vinarski and Kantor (2016) for the Caspian Sea are morphotypes of a single species. Prelimary genetic analyses of *Caspiohydrobia* spp. from salt lakes near Chelyabinsk, Russia (TW, unpublished data) support this assumption.

Conservation status. Data Deficient (Vinarski 2011b).

Ecrobia maritima (Milaschewitch, 1916)

*1916 *Hydrobia maritima* Milaschewitch: 60–61, pl. 2, fig. 34.
1973 *Hydrobia pontieuxini* Radoman: 15–16.

1977 *Ventrosia pontieuxini* (Radoman, 1973). – Radoman: 210, pl. 21, figs 19, 20.
1992 *Pseudopaludinella cygnea* Anistratenko in Anistratenko and Prisjazhnjuk: 17, fig. 1a.
1992 *Pseudopaludinella inflata* Anistratenko in Anistratenko and Prisjazhnjuk: 17–18, fig. 1b.
1992 *Pseudopaludinella ismailensis* Anistratenko in Anistratenko and Prisjazhnjuk: 18, fig. 1c.
2011 *Pseudopaludinella pontieuxini* (Radoman, 1973). – Anistratenko et al.: 78, pl. 3, fig. 4.
2015 *Graecoanatolica yildirimi* Glöer and Pešić: 49–50, figs 10–14.

Status. Accepted, Pontocaspian species.

Type locality. Black Sea, at Feodosiya and Adler (Crimea, Ukraine).

Distribution. Black Sea Basin; northern Aegean Sea; Lake Sarikum, Turkey; northern Adriatic Sea.

Taxonomic notes. *Hydrobia pontieuxini*, described from the Black Sea coast in Mangalia, Romania, has been considered a synonym of *E. maritima* based on molecular data (Kevrekidis et al. 2005). Herein, we also consider the *Pseudopaludinella* species introduced by Anistratenko and Prisjazhnjuk (1992) as junior synonyms of *E. maritima* based on morphological similarities. A proper revision is still pending.

Conservation status. Not assessed.

Ecrobia ventrosa (Montagu, 1803)

*1803 *Turbo ventrosus* Montagu: 317, pl. 12, fig. 13.
2012 *Ecrobia ventrosa* (Montagu, 1803). – Kadolsky: 69–70.
2012 *Hydrobia ventrosa* (Montagu, 1803). – Welter-Schultes: 40, unnumbered text figures.

Status. Accepted, immigrant species.

Type locality. On the Kent coast (United Kingdom), at Folkstone and Sandwich.

Distribution. Widespread along the coastal zones of northern and western Europe, the Mediterranean Sea, the Russia White Sea; introduced into the western Black Sea.

Taxonomic notes. Unpublished genetic data (TW) suggest that most previous records of *E. ventrosa* in the Black Sea are likely misidentifications of *E. grimmi*. A notable exception is a recent, genetically confirmed record from Constanța, Romania (Osikowski et al. 2016). Probably, the French species *Paludestrina arenarum* Bourguignat, 1876, *P. leneumicra* Bourguignat, 1876, *P. paludinelliformis* Bourguignat, 1876, and *Ventrosia cissana* Radoman, 1977, which have been listed for the Black Sea Basin (Anistratenko 1991, Anistratenko and Prisjazhnjuk 1992, Anistratenko et al. 2011), are junior synonyms or misidentifications of this species.

Conservation status. Least Concern (Van Damme 2011a).

Subfamily Pyrgulinae Brusina, 1882

Remarks. The genus concepts of Pontocaspian Pyrgulinae follow the revision of Neubauer et al. (2018). Further change is expected in several of the keeled species here listed under ?*Turricaspia* (?*T. aenigma*, ?*T. basalis*, ?*T. dimidiata*, ?*T. pseudobacuana*, and ?*T. pseudodimiata*) that may be grouped in their own genus for which the name *Trachycaspia* Dybowski & Grochmalicki, 1917 (type species: *Rissoa dimidiata* Eichwald, 1838) is available. However, such a decision will require further documentation.

Clessiniola variabilis (Eichwald, 1838)

*1838 *Paludina variabilis* Eichwald: 151–152.
1838 *Paludina Triton* Eichwald: 152.
1874 *Bithynia*? *Eichwaldi* Martens: 81.
?1887 *Caspia Grimmi* Clessin and Dybowski in Dybowski: 39
?1888 [*Caspia*] *Grimmi* n. sp. – Dybowski: 79, pl. 3, fig. 5a, b.
1887 *Clessinia Martensii* Clessin and Dybowski in Dybowski: 43.
1888 *Clessinia Martensii* n. sp. – Dybowski: 79, pl. 2, fig. 5.
1902a *Clessinia ahngeri* Westerlund: 45–46.
1966 *P.*[*yrgula*] (*Clessiniola*) *pseudotriton* Golikov and Starobogatov: 356–357, fig. 2(3
?1969 *Pyrgula* (*Caspiella*) *derbentina* Logvinenko and Starobogatov: 374, fig. 366(8).
1969 *Pyrgula* (*Caspiella*) *ovum* Logvinenko and Starobogatov: 374, fig. 366(9).
1969 *Pyrgula* (*Caspiella*) *trivialis* Logvinenko and Starobogatov: 374–375, fig. 366(10).
1987 *Turricaspia* (*Clessiniola*) *variabilis* (Eichwald, 1838). – Alexenko and Starobogatov: 34, text fig. 5.
1987 *Turricaspia* (*Clessiniola*) *triton* (Eichwald, 1838). – Alexenko and Starobogatov: 34, text fig. 3.
1987 *Turricaspia* (*Clessiniola*) *martensii* (Clessin & Dybowski in Dybowski, 1888). – Alexenko and Starobogatov: 34, text fig. 4.
1987 *Turricaspia* (*Clessiniola*) *bogensis* (Küster, 1852). – Alexenko and Starobogatov: 34.
2006 *Turricaspia variabilis* (Eichwald, 1838). – Kantor and Sysoev: 111, pl. 49, fig. J.
2011 *Turricaspia martensii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Anistratenko et al.: 86, fig. 3(17).
2011 *Turricaspia triton* (Eichwald, 1838). – Anistratenko et al.: 85–86, fig. 3(16).
2011 *Turricaspia variabilis* (Eichwald, 1838). – Anistratenko et al.: 85, fig. 3(15).
2014 *Turricaspia variabilis*. – Taviani et al.: 4, fig. 3b.
?2016 *Turricaspia derbentina* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 247.
2016 *Turricaspia martensii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 248.
2016 *Turricaspia ovum* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 248–249.
2016 *Turricaspia pseudotriton* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 249.
2016 *Turricaspia triton* (Eichwald, 1838). – Vinarski and Kantor: 250.
2016 *Turricaspia trivialis* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 250–251.
2016 *Turricaspia variabilis* (Eichwald, 1838).– Vinarski and Kantor: 251.
2018 *Clessiniola variabilis* (Eichwald, 1838). – Neubauer et al.: 60–63, fig. 7A–I.

Status. Accepted Pontocaspian species.

Type locality. At the Volga River mouth near Astrakhan, and towards the Caspian Sea; also in recently lithified fossil limestone at the shores of Dagestan, Russia.

Distribution. Caspian Sea, Azov Sea, and northern Black Sea region. This species was mentioned in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia variabilis, T. derbentica,* and *T. trivialis*).

Taxonomic notes. Neubauer et al. (2018) recently demonstrated the high variability of this species. Comparison of available illustrations and descriptions of the species listed in the synonymy list indicates that all of them range within this species' variability. Consequently, we consider all of them as junior synonyms of *C. variabilis*. A more in-depth review of the type material of the species involved is required to confirm this approach.

The status of *Paludina bogensis* Dubois in Küster, 1852, which was listed as a valid species of *Turricaspia* by Anistratenko and Stadnichenko (1995), is still unclear. That species was described from the Zapadnyi Bug River in Poland and closely resembles *C. variabilis*. It is, however, unlikely that a Pontocaspian species typical of oligohaline conditions occurs so far away in a pure freshwater environment. "*Paludina eichwaldi* Krynicki, 1837" found in the literature is a nomen nudum. Martens (1874) provided measurements and made the name available, but he listed *Paludina variabilis* Eichwald, 1838 in synonymy, which has priority. Dybowski (1887) obviously overlooked this and considered *Nematurella eichwaldi* Krynicki a valid species. We follow Vinarski and Kantor (2016) and consider the species as a junior synonym of *Clessiniola variabilis*.

Conservation status. Least Concern (Cioboiu et al. 2011).

Laevicaspia abichi (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Caspiella*) *abichi* Logvinenko & Starobogatov: 372, fig. 366(3).
2016 *Pyrgula abichi* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 235.

Status. Accepted Pontocaspian species.

Type locality. Southern and western parts of the Middle Caspian Sea, 36–120 m.

Distribution. Middle and South Caspian Basin. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia abichi*).

Taxonomic notes. The species differs from the *L. cincta* in its much larger size, the conical shape, the narrower subsutural band, and the larger aperture (compare Neubauer et al. 2018).

Conservation status. Data Deficient (Vinarski 2011e).

Laevicaspia caspia (Eichwald, 1838)

*1838 *Rissoa caspia* Eichwald: 154–155.
non 1888 *Micr*.[*omelania*] *caspia* Eichw. sp. – Dybowski: 78, pl. 1, fig. 1.

?1896 *B.*[*uliminus*] (*Napaeus*?) *goebeli* Westerlund: 188.
1915 *Micromelania* (?) *curta* Nalivkin: 21–22, 31, pl. 6, figs 1, 2 [pars, non figs 3, 4, 7, 9–14].
1915 [*Micromelania* (?) *curta*] var. *plano-convexa* Nalivkin: 22, 31, pl. 6, figs 15–18.
non 1915 *Micromelania caspia* Eichw. – Nalivkin: 22, 31, pl. 6, figs 5, 6 [pars, non fig. 8].
non 1917 *Micromelania* (*Turricaspia, Laevicaspia*) *caspia* Eichw. – Dybowski and Grochmalicki: 5–8, 36–38, pl. 1, figs 1–3.
non 1969 *Pyrgula caspia* (Eichw.). – Logvinenko and Starobogatov: 369–370, fig. 364(1).
2006 *Turricaspia caspia* (Eichwald, 1838). – Kantor and Sysoev: 106, pl. 49, fig. M.
2016 *Turricaspia caspia* (Eichwald, 1838). – Vinarski and Kantor: 246.
2018 *Laevicaspia caspia* (Eichwald, 1838). – Neubauer et al.: 63–66, fig. 8A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. In fossil limestone of Dagestan, Russia.

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia caspia* and *T. curta*).

Taxonomic notes. For a detailed discussion about the identity of this species, its synonyms and former misidentifications, see Neubauer et al. (2018).

Conservation status. IUCN indicates “Least Concern” (Vinarski 2012), but the true status of this species is highly uncertain.

Laevicaspia cincta (Abich, 1859)

*1859 *Rissoa cincta* Abich: 57, pl. 2, fig. 6.
?1887 *Caspia Orthii* Clessin & Dybowski in Dybowski: 40.
?1888 [*Caspia*] *Orthii* n. sp. – Dybowski: 79, pl. 3, fig. 6.
1969 *Pyrgula* (*Caspiella*) *cincta* (Abich). – Logvinenko and Starobogatov: 372, fig. 366(4).
2006 *Pyrgula cincta* (Abich, 1859). – Kantor and Sysoev: 98, pl. 47, fig. L.
2016 *Pyrgula cincta* (Abich, 1859). – Vinarski and Kantor: 236–237.
2018 *Laevicaspia cincta* (Abich, 1859). – Neubauer et al.: 66–68, fig. 9A–H.

Status. Accepted Pontocaspian species.

Type locality. Gulf of Baku, Azerbaijan.

Distribution. Southern Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. For a detailed discussion about the identity of this species and its synonym, see Neubauer et al. (2018).

Conservation status. Data Deficient (Vinarski 2011g).

Laevicaspia conus (Eichwald, 1838)

*1838 *Rissoa Conus* Eichwald: 155.

non 1876 *Eulima conus*, Eichw?. – Grimm: 154–156, pl. 6, fig. 14.
non 2006 *Turricaspia conus conus* (Eichwald, 1838). – Kantor and Sysoev: 106, pl. 48, fig. J.
2016 *Turricaspia conus conus* (Eichwald, 1838). – Vinarski and Kantor: 246–247.
2018 *Laevicaspia conus* (Eichwald, 1838). – Neubauer et al.: 69–71, fig. 9I–P [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. In fossil limestone of Dagestan, Russia.

Distribution. Endemic to the Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia conus*).

Taxonomic notes. For a detailed discussion about the identity of this polymorphic species and previous misidentifications, see Neubauer et al. (2018).

Conservation status. Data Deficient (Vinarski 2011p).

?*Laevicaspia ebersini* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxypyrgula*) *ebersini* Logvinenko & Starobogatov: 368, fig. 363(7).
2016 *Pyrgula ebersini* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 238.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the middle Caspian Sea, 0–50 m water depth.

Distribution. Type locality only.

Taxonomic notes. We cannot verify the status of this species given the inadequate descriptions and illustrations and its general resemblance to other species that were described earlier.

Conservation status. Data Deficient (Vinarski 2011h).

?*Laevicaspia ismailensis* (Golikov & Starobogatov, 1966)

*1966 *P.*[*yrgula*] *ismailensis* Golikov & Starobogatov: 358, fig. 2(11).
2006 *Turricaspia ismailensis* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 108, pl. 50, fig. A.
2016 *Turricaspia ismailensis* (Golikov & Starobogatov, 1966). – Vinarski and Kantor: 248.

Status. Accepted Pontocaspian species.

Type locality. Ukraine, Danube Delta, lakes Yalpug and Kugurlui.

Distribution. North-western Black Sea Basin (Anistratenko and Stadnichenko 1995).

Taxonomic notes. Based on the illustration of the holotype in Kantor and Sysoev (2006), we tentatively place the species in the genus *Laevicaspia*. A more detailed study is necessary to clarify its systematic position.

Conservation status. Vulnerable (Son and Cioboiu 2011).

Laevicaspia kolesnikoviana (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966)

*1966 *P.*[*yrgula*] (*Caspiella*) *kolesnikoviana* Golikov & Starobogatov: 357–358, fig. 2(8–9).
1969 *Pyrgula* [(*Caspiella*)] *kolesnikoviana* Logv. & Star. – Logvinenko and Starobogatov: 372, fig. 366(1).
2006 *Pyrgula kolesnikoviana* Logvinenko & Starobogatov in Golikov & Starobogatov, 1966. – Kantor and Sysoev: 100, pl. 47, fig. N.
2016 *Pyrgula kolesnikoviana* Logvinenko & Starobogatov in Golikov & Starobogatov, 1966. – Vinarski and Kantor: 239.
2018 *Laevicaspia kolesnikoviana* (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966). – Neubauer et al.: 71–73, fig. 10A–E, K, N.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea, northward of Apsheron Peninsula, north-westward from Kamni Dva Brata Island, 40°47'N, 49°42'E, 30 m water depth.

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia kolesnikoviana*).

Taxonomic notes. For a detailed discussion about the identity of this species, see Neubauer et al. (2018).

Conservation status. Data Deficient (Vinarski 2011k).

Laevicaspia kowalewskii (Clessin & Dybowski in Dybowski, 1887)

*1887 *Caspia Kowalewskii* Clessin & Dybowski in Dybowski: 40–41.
1888 [*Caspia*] *Kowalewskii* n. sp. – Dybowski: 79, pl. 3, fig. 9a–c.
2006 *Pyrgula kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 100, pl. 47, fig. M.
2016 *Pyrgula kowalewskii* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 239–240.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea, recorded from southern basin (Logvinenko and Starobogatov 1969) and middle basin (personal observation based on material from Dagestan region, TAN, FW). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia kowalewskii*).

Taxonomic notes. This species differs from *L. kolesnikoviana* in its bigger size, broader shape, and thinner peristome. *Laevicaspia cincta* can be distinguished based on the stouter shape and the presence of a narrow subsutural band.

Conservation status. Not assessed.

Laevicaspia lencoranica (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Eurycaspia*) *lencoranica* Logvinenko & Starobogatov: 357, fig. 358(14).
2016 *Pyrgula lencoranica* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 240.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. Based on the illustrations provided in Kantor and Sysoev (2006), this species differs from *L. cincta* and *L. kowalewskii* in the conical shape and large body whorl. A revision is required to assure its status as distinct species.

Conservation status. Not assessed.

Laevicaspia lincta (Milaschewitch, 1908)

*1908 *Micromelania lincta* Milaschewitch: 991.
?1966 *P.*[*yrgula*] (*Caspiella*) *azovica* Golikov and Starobogatov: 357, fig. 2(7).
?1966 *P.*[*yrgula*] (*Caspiella*) *boltovskoji* Golikov and Starobogatov: 357, fig. 2(4).
?1966 *P.*[*yrgula*] (*Caspiella*) *crimeana* Golikov and Starobogatov: 358, fig. 2(10).
?1966 *P.*[*yrgula*] (*Caspiella*) *limanica* Golikov and Starobogatov: 357, fig. 2(6).
?1966 *P.*[*yrgula*] (*Caspiella*) *lindholmiana* Golikov and Starobogatov: 357, fig. 2(5).
?1966 *P.*[*yrgula*] (*Laevicaspia*) *iljinae* Golikov and Starobogatov: 358–359, fig. 2(14).
?1966 *P.*[*yrgula*] (*Laevicaspia*) *milachevitchi* Golikov and Starobogatov: 359, fig. 2(15).
?1966 *P.*[*yrgula*] (*Laevicaspia*) *ostroumovi* Golikov and Starobogatov: 358, fig. 2(13).
?1966 *P.*[*yrgula*] (*Turricaspia*) *borceana* Golikov and Starobogatov: 359, fig. 2(16).
?1966 *P.*[*yrgula*] (*Turricaspia*) *nevesskae* Golikov and Starobogatov: 359, fig. 2(17).
?1987 *Turricaspia abichi phaseolinica* Alexenko and Starobogatov: 33.
?1987 *Turricaspia* (*Caspiella*) *derbentina borysthenica* Alexenko adn Starobogatov: 34–35, fig. 6.
?1987 *Turricaspia* (*Laevicaspia*) *grigorievi* Alexenko and Starobogatov: 35, fig. 7.
?1987 *Turricaspia* (*Laevicaspia*) *meneghiniana ukrainica* Alexenko and Starobogatov: 35, fig. 9.
?2006 *Euxinipyrgula azovica* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 95, pl. 44, fig. K.
?2006 *Euxinipyrgula borysthenica* (Alexenko & Starobogatov, 1987). – Kantor and Sysoev: 95, pl. 44, fig. J.
?2006 *Euxinipyrgula grigorievi* (Alexenko & Starobogatov, 1987). – Kantor and Sysoev: 95, pl. 44, fig. I.
?2006 *Euxinipyrgula limanica* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 95, pl. 44, fig. H.
2006 *Euxinipyrgula lincta* (Milaschewitsch, 1908). – Kantor and Sysoev: 95–96, pl. 45, fig. D.
?2006 *Euxinipyrgula milachevitchi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 96, pl. 45, fig. C.
?2006 *Euxinipyrgula ostroumovi* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 96, pl. 45, fig. B.

?2006 *Euxinipyrgula ukrainica* (Alexenko & Starobogatov, 1987). – Kantor and Sysoev: 95, pl. 45, fig. A.
?2006 *Turricaspia boltovskoji* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 105–106, pl. 48, fig. K.
?2006 *Turricaspia borceana* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 106, pl. 49, fig. B.
?2006 *Turricaspia conus lindholmiana* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 107, pl. 48, fig. L.
?2006 *Turricaspia crimeana* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 107, pl. 48, fig. C.
?2006 *Turricaspia iljinae* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 108, pl. 49, fig. D.
?2006 *Turricaspia nevesskae* (Golikov & Starobogatov, 1966). – Kantor and Sysoev: 109, pl. 49, fig. L.

Status. Accepted Pontocaspian species.

Type locality. Kotlabukh Lake, Odessa Region, Ukraine (approximately 45°25'35"N, 28°59'41"E).

Distribution. Limans and lower reaches of rivers Don, Dnieper, Dniester, and Southern Bug entering the northern Black Sea Basin and the Azov Sea (Taganrog Bay), as well as in coastal lakes Kotlabukh and Yalpug (Vinarski and Kantor 2016). The record of an undescribed subspecies of *T. boltovskoji* from the Caspian Sea mentioned by Anistratenko and Stadnichenko (1995) is probably based on a misidentification.

Taxonomic notes. Golikov and Starobogatov (1966) and Alexenko and Starobogatov (1987) introduced a plethora of names for morphologically similar species from the northern Black Sea Basin, partly deriving from subfossil horizons. They differ from *Laevicaspia lincta* slightly in the number of whorls and outline shape, but overall range within its morphological variability. Here, we consider them tentatively all junior synonyms of *L. lincta*. Since Starobogatov's type material is unknown, support for this approach requires collection of new material from the type localities of these taxa. Molecular data confirmed the conspecifity of *L. lincta* and *L. milachevitchi* (Wilke et al. 2007).

Conservation status. Least Concern (Son 2011e).

?*Laevicaspia marginata* (Westerlund, 1902)

*1902a *Nematurella marginata* Westerlund: 45.
2013 *Pyrgula marginata* (Westerlund, 1902). – Vinarski et al.: 85, fig. 2F.
2016 *Pyrgula marginata* (Westerlund, 1902). – Vinarski and Kantor: 240.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea, "near Krasnojarsk" (Westerlund 1902a). This statement is clearly erroneous since Krasnojarsk is situated in Siberia. Most probably, Westerlund meant Krasnovodsk (nowadays Turkmenbashi) in Turkmenistan (Vinarski et al. 2013).

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia marginata*).

Taxonomic notes. The status of this species is uncertain. The illustrations of the type material by Vinarski et al. (2013) suggest a tentative placement in the genus *Laevicaspia*. It shows close similarities with *L. sieversii* (Clessin in Dybowski, 1887). A careful revision of the species is required to clarify its taxonomic status and systematic placement.

Conservation status. Not assessed.

Laevicaspia sieversii (Clessin in Dybowski, 1887)

*1887 *Nematurella Sieversii* Clessin in Dybowski: 45–46.
1888 *Nematurella Sieversi* [sic] n. sp. – Dybowski: 78, pl. 2, fig. 1.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea.

Taxonomic notes. This species has not been found since its first description, its identity is unclear (Vinarski and Kantor 2016). Judging from the description and drawing in Dybowski (1887), we suggest a systematic placement in *Laevicaspia*. It might be related to *L. conus* (Eichwald, 1838).

Conservation status. Not assessed.

?*Turricaspia aenigma* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Celekenia*) *aenigma* Logvinenko & Starobogatov: 375, fig. 366(12).
2016 *Pyrgula aenigma* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 235.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea, northward of Apsheron Peninsula, 75 m.

Distribution. Type locality only.

Taxonomic notes. The identity of this species is unclear. The illustrations of the holotype in Kantor and Sysoev (2006) show a small shell with four whorls, of which the latter two bear a distinct keel. The small size and the relatively large protoconch suggest that the type specimen is a juvenile shell. More specimens (including adult material) are required to shed light on this species' identity.

Conservation status. Not assessed.

Turricaspia andrussowi (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania* (*Turricaspia*) *andrussowi* Dybowski & Grochmalicki: 125–126, pl. 3, fig. 31a, b.
?1969 *Pyrgula* (*Oxypyrgula*) *dubia* Logvinenko and Starobogatov: 368, fig. 363(5).

?1969 *Pyrgula* (*Oxypyrgula*) *turkmenica* Logvinenko and Starobogatov: 368, fig. 363(6).
2006 *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 104–105, pl. 48, fig. A [pars, excluding synonymy].
2016 *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 245 [pars, excluding synonymy].
2018 *Turricaspia andrussowi* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 74–76, fig. 11A, BB.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea. The two tentative synonyms were recorded from the western part of the middle Caspian Sea and the eastern part of the southern Caspian Sea, respectively. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *T. turkmenica*, *T. dubia*, and *T. andrussowi*).

Taxonomic notes. The species was recently investigated by Neubauer et al. (2018). *Pyrgula dubia* and *P. turkmenica* are tentatively considered juveniles and thus junior synonyms of this species.

Conservation status. Not assessed.

?*Turricaspia basalis* (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania dimidiata* var. *basalis* Dybowski & Grochmalicki: 131, pl. 3, fig. 36a, b.
1969 *Pyrgula* (*Trachycaspia*) *laticarinata* Logvinenko and Starobogatov: 359, fig. 359(3).
2006 *Pyrgula basalis basalis* (B. Dybowski & J. Grochmalicki, 1915). – Kantor and Sysoev: 97, pl. 46, fig. A.
2006 *Pyrgula basalis laticarinata* Logvinenko & Starobogatov, 1968. – Kantor and Sysoev: 97, pl. 46, fig. B.
2016 *Pyrgula basalis basalis* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 236.
2016 *Pyrgula basalis laticarinata* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 236.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *T. laticarinata*).

Taxonomic notes. The species is characterised by a massive keel near the lower suture. ?*Turricaspia dimidiata* is distinguished based on its more centrally placed keel. This distinction is tentative and only based on comparison of available illustrations; we are aware of the possibility that these differences might not be diagnostic. Moreover, the keel seems to become stronger with increasing water depth (Starobogatov 1968).

Pyrgula laticarinata Logvinenko & Starobogatov, 1969, which differs from *T. basalis* only in the strength of the keels, was considered a junior synonym by Neubauer et al. (2018).

Conservation status. Not assessed.

?*Turricaspia bogatscheviana* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxypyrgula*) *bogatscheviana* Logvinenko & Starobogatov: 367, fig. 363(2).
2016 *Turricaspia bogatscheviana* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 245.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. The description and drawing of this species provided by Logvinenko and Starobogatov (1969) do not allow an evaluation whether it is a distinct species or synonym of a previously species.

Conservation status. Not assessed.

Turricaspia chersonica Alexenko & Starobogatov, 1987

*1987 *Turricaspia* (*Oxypyrgula*) *chersonica* Alexenko & Starobogatov: 35–36, fig. 10.
2016 *Turricaspia chersonica* Alexenko & Starobogatov, 1987. – Vinarski and Kantor: 246.

Status. Pontocaspian species, identity uncertain.

Type locality. Ukraine, in the Dnieper Delta.

Distribution. Type locality only.

Taxonomic notes. The status of this species is highly uncertain. The slender conical shell illustrated by Alexenko and Starobogatov (1987) suggest classification in the genus *Turricaspia*, which is otherwise only known from the Caspian Sea.

Conservation status. Data Deficient (Son 2011d).

Turricaspia columna (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxypyrgula*) *columna* Logvinenko & Starobogatov: 368, fig. 363(8).
2016 *Pyrgula columna* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 237.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the southern Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. The species has not been found since its first description, and the whereabouts of the type material is unknown. Logvinenko and Starobogatov (1969) illustrate a small slender shell with convex whorls. It might well be a juvenile of another species.

Conservation status. Not assessed.

Turricaspia concinna (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *concinna* Logvinenko & Starobogatov: 365, fig. 362(3).
2016 *Pyrgula concinna* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 237.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle Caspian Sea, 25–80 m.

Distribution. Type locality only.

Taxonomic notes. The illustrations provided by Logvinenko and Starobogatov (1969) indicate a large conical shell with nine convex whorls and a large, slightly inflated last whorl. These features are reminiscent of *T. meneghiniana* (Issel, 1865). However, *T. concinna* has not been found since its first description. The type material has been very recently detected in the collections of ZIN and awaits further study.

Conservation status. Not assessed.

Turricaspia dagestanica (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *dagestanica* Logvinenko & Starobogatov: 361, fig. 360(3).
2016 *Turricaspia dagestanica* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 247.

Status. Pontocaspian species, identity uncertain.

Type locality. Western shore of the middle Caspian Sea.

Distribution. Middle and south Basin of Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The status of this species is highly uncertain. The illustrations of Logvinenko and Starobogatov (1969) show a slightly distorted shell with weakly convex whorls and a thin line below the suture. We are uncertain whether it might concern a growth aberration of a more common species.

Conservation status. Data Deficient (Vinarski 2011r).

Turricaspia dimidiata (Eichwald, 1838)

*1838 *Rissoa dimidiata* Eichwald: 156.
?1947 *Turricaspia bakuana* Kolesnikov: 108, 112.
2006 *Pyrgula dimidiata* (Eichwald, 1838). – Kantor and Sysoev: 99, pl. 46, fig. K.
?2006 *Pyrgula bakuana* (Kolesnikov, 1947). – Kantor and Sysoev: 97, pl. 47, fig. C.
2016 *Pyrgula dimidiata* (Eichwald, 1838). – Vinarski and Kantor: 238.
2016 *Pyrgula bakuana* (Kolesnikov, 1947). – Vinarski and Kantor: 236–237.

Status. Accepted Pontocaspian species.

Type locality. In fossil limestone of Dagestan, Russia.

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. Although there is little doubt about the validity of this species, its true identity and possible synonyms are unclear. Eichwald's (1838) description clearly indicates a slender shell with median keel. His type material is unfortunately unknown. The high number of keeled species complicates an evaluation what is the "true" *T. dimidiata* and what are synonyms. We tentatively consider *Turricaspia bakuana* Kolesnikov, 1947 a junior synonym of this species, based on its slender shell with median keel matching Eichwald's description as well as the prevailing concept of *T. dimidiata* (compare Kantor and Sysoev 2006). More data are required to support this view.

Conservation status. Not assessed.

Turricaspia eburnea (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Laevicaspia*) *eburnea* Logvinenko & Starobogatov: 370, fig. 365(1).
2016 *Turricaspia eburnea* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 247.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the southern Caspian Sea.

Distribution. South Caspian Basin. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The identity of this species is unclear. Its shell resembles *T. lyrata* (Dybowski & Grochmalicki, 1915) in terms of general shape and the large, flat protoconch; it differs from that species in the large size. The type material has been very recently found in the collection of ZIN and awaits further study. Until then, we refrain from a final decision on the species' status, but we have severe doubt that *Pyrgula eburnea* is a distinct species.

Conservation status. Not assessed.

Turricaspia elegantula (Clessin & Dybowski in Dybowski, 1887)

*1887 *Micromelania elegantula* Clessin & Dybowski in Dybowski: 33.
1888 [*Micromelania*] *elegantula* n. sp. – Dybowski: 78, pl. 1, fig. 7a–c.
2016 *Turricaspia elegantula* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 247–248.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. There is considerable confusion about the identity of this species. Dybowski (1887) described and illustrated a very slender shell with a distinct whorl profile showing a straight-sided upper half and a convex lower half. In contrast, the illustrations in Logvinenko and Starobogatov (1969) suggest a similarly slender yet distorted shell with near almost sided whorls and expanded aperture. A restudy of the type material of *T. elegantula* show close similarities to *T. spica*. It differs from that species in the more slender outline and flattened whorls.

Conservation status. Not assessed.

Turricaspia eulimellula (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania* (*Turricaspia*) *eulimellula* Dybowski & Grochmalicki: 123–125, pl. 3, fig. 27a, b.
2006 *Pyrgula eulimellula* (B. Dybowski & J. Grochmalicki, 1915). – Kantor and Sysoev: 99–100, pl. 46, fig. L.
2016 *Pyrgula eulimellula* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 238–239.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle Caspian Sea Basin (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The nearly straight-sided, strongly attached whorls easily distinguish this species from most other *Turricaspia* species. Only *Turricaspia grimmi* (Clessin & Dybowski in Dybowski, 1887) has a similar whorl arrangement, but its shell is slightly wider and the whorls are weakly stepped and bear a thin subsutural band.

Conservation status. Not assessed.

Turricaspia fedorovi (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *fedorovi* Logvinenko & Starobogatov: 362, fig. 360(2).
2016 *Pyrgula fedorovi* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 239.

Status. Pontocaspian species, identity uncertain.

Type locality. Western part of the middle Caspian Sea, 80 m.

Distribution. Middle and South Caspian Basin. This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The slender elongate shell with whorls slowly increasing in height distinguishes this species from its congeners. However, a proper assessment of the species' status requires investigation. The whereabouts of the type material is unknown and no other records of this species are known, so we are not able to verify the status of this species.

Conservation status. Not assessed.

Turricaspia grimmi (Clessin & Dybowski in Dybowski, 1887)

*1887 *Micromelania Grimmi* Clessin & Dybowski in Dybowski: 27–29.
1888 [*Micromelania*] *Grimmi* n. sp. – Dybowski: 78, pl. 1, fig. 2a–c.
2006 *Pyrgula grimmi* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 100, pl. 46, fig. L.
2016 *Pyrgula grimmi* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 239.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Southern Caspian Sea Basin (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The peculiar morphology with straight-sided, weakly stepped whorls with a thin subsutural band is unique among Caspian Pyrgulinae. See above for a comparison with *T. eulimellula*.

Conservation status. Data Deficient (Vinarski 2011i).

Turricaspia lyrata (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania* (*Turricaspia*) *spica* var. *lyrata* Dybowski & Grochmalicki: 117, pl. 2, fig. 18.
2006 *Pyrgula lirata* [sic] (B. Dybowski & J. Grochmalicki, 1915). – Kantor and Sysoev: 101, pl. 46, fig. E.
2016 *Pyrgula lirata* [sic] (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 240.
2018 *Turricaspia lyrata* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 77–79, fig. 12A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea (after Logvinenko and Starobogatov 1969); it occurs in the western part of the middle and southern Caspian Sea basins, but these authors used a slightly different concept of the species. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Turricaspia lirata*).

Taxonomic notes. See Neubauer et al. (2018) for a detailed discussion of the species and its synonyms.

Conservation status. Not assessed.

Turricaspia marisnigri Starobogatov in Alexenko & Starobogatov, 1987

*1987 *Turricaspia lirata marisnigri* Starobogatov in Alexenko & Starobogatov: 33.

Status. Pontocaspian species, identity uncertain.

Type locality. "Meotida" station 24, sample 229, near the coast of Crimea, in phaseoline silt (Holocene).

Distribution. Type locality only.

Taxonomic notes. The species can be distinguished based on its extremely slender shell with whorls slowly increasing in size. Still, clarification of its identity as well as its generic classification requires investigation of additional material.

Conservation status. So far only known from Holocene deposits of the type locality; species might be extinct. Within Holocene deposits in the Black Sea small amounts of reworked Late Pleistocene "Neoeuxinian" faunas are found (FW, pers. obs.), and therefore the stratigraphic origin of such Pontocaspian species is uncertain.

Turricaspia meneghiniana (Issel, 1865)

*1865 *Bythinia Meneghiniana* Issel: 21, pl. 1, figs 12, 13.
1902a *Micromelania subulata* Westerlund: 47.
?1969 *Pyrgula caspia* (Eichw). – Logvinenko and Starobogatov: 369–370, fig. 364(1) [**non** *Rissoa caspia* Eichwald, 1838].
non 1987 *T.*[*urricaspia*] *meneghiniana meneghiniana* (Iss.). – Alexenko and Starobogatov: 35, fig. 8.
2006 *Turricaspia meneghiniana* (Issel, 1865). – Kantor and Sysoev: 109, pl. 49, fig. E.
2016 *Turricaspia meneghiniana* (Issel, 1865). – Vinarski and Kantor: 248.
2018 *Turricaspia meneghiniana* (Issel, 1865). – Neubauer et al.: 79–81, fig. 13A–K [and synonyms therein].

Status. Accepted Pontocaspian species.

Type locality. Baku, Azerbaijan; (sub?)fossil.

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. The species was recently discussed in detail by Neubauer et al. (2018), who also discussed previous misidentifications.

Conservation status. Not assessed.

Turricaspia nossovi Kolesnikov, 1947

*1947 *Turricaspia nossovi* Kolesnikov: 108, 111.
2006 *Pyrgula nossovi* (Kolesnikov, 1947). – Kantor and Sysoev: 101, pl. 45, fig. G.
2016 *Pyrgula nossovi* (Kolesnikov, 1947). – Vinarski and Kantor: 241.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The very slender shape and the characteristic, highly convex whorls that slowly and regularly increase in height distinguish the species from most congeners. *Pyrgula vinogradovi* Logvinenko & Starobogatov, 1969 and *P. astrachanica* Pirogov, 1971, which show very similar traits, might be junior synonyms. A more in-depth study is required to solve their statuses.

Conservation status. Data Deficient (Vinarski 2011l).

?*Turricaspia obventicia* (Anistratenko in Anistratenko & Prisjazhnjuk, 1992)

*1992 *Caspia* (*Clathrocaspia*) *obventicia* Anistratenko in Anistratenko & Prisjazhnjuk: 19–20, fig. 2b.

Status. Uncertain Pontocaspian species.

Type locality. Well 37 near Kiliya, Izmail district, Odessa region, Ukraine (from Holocene sediments).

Distribution. Type locality only.

Taxonomic notes. This species was originally attributed to the genus *Caspia* due to its small shell. A study of the holotype of this species, specifically its protoconch characteristics, suggest placement in the genus *Turricaspia*. Further studies are required to assure its validity.

Remarks. The species is known only from the holotype. The occurrence of *Turricaspia* in the Black Sea Basin is unusual, as almost all other pyrguline Black Sea species are assigned to the genus *Laevicaspia* (but see remark at *T. spica* for another unusual occurrence).

Conservation status. So far only known from Holocene deposits of the type locality; species might be extinct.

?*Turricaspia pseudobacuana* (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Eurycaspia*) *pseudobacuana* Logvinenko & Starobogatov: 358, fig. 358(16).
2016 *Pyrgula pseudobacuana* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 241.

Status. Pontocaspian species, probably junior synonym.

Type locality. Southern Caspian Sea, 50–80 m.

Distribution. South Caspian Basin. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The slender shell with a keel near the lower suture is reminiscent of *T. basalis* (Dybowski & Grochmalicki, 1915). The short description and poor drawing precluded the verification of its status. The type material has been very recently detected in the collection of ZIN and awaits further study.

Conservation status. Not assessed.

?*Turricaspia pseudodimidiata* **(Dybowski & Grochmalicki, 1915)**

*1915 *Micromelania* (*Turricaspia*) *pseudodimidiata* Dybowski & Grochmalicki: 126–128, pl. 3, fig. 32a, b.
?1969 *Pyrgula* (*Eurycaspia*) *pseudodimidiata* (Dyb. et Gr.). – Logvinenko and Starobogatov: 357, fig. 358(15).
?2006 *Pyrgula pseudodimidiata* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 102, pl. 47, fig. G.
2016 *Pyrgula pseudodimidiata* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 241.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea (no details).

Distribution. Southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The identity of this species is uncertain. Dybowski and Grochmalicki (1915) describe and illustrate a shell with eight convex whorls bearing a weak, hardly protruding, irregular shaped keel near the lower suture. According to these authors, the keel varies considerably between a thin thread, a blunt bulge, or a weak thickening at the suture. In contrast, the drawings provided by Logvinenko and Starobogatov (1969) and reproduced by Kantor and Sysoev (2006) suggest a shell with straight-sided whorls and a distinct keel. Inspection of the type material is required to clarify the status of this species.

Conservation status. Not assessed.

Turricaspia pseudospica **(Logvinenko & Starobogatov, 1969)**

*1969 *Pyrgula* (*Oxypyrgula*) *pseudospica* Logvinenko & Starobogatov: 366, fig. 363(1).
2016 *Pyrgula pseudospica* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 241–242.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle and southern Caspian Sea, 15–75 m.

Distribution. Type locality only.

Taxonomic notes. The identity of this species is unclear. Judging from the drawing by Logvinenko and Starobogatov (1969), showing a small slender shell with ca. 6.5 convex whorls, the species might be based on a juvenile specimen. Moreover, it could be a junior synonym of the similarly shaped *T. spica* (Eichwald, 1855).

Conservation status. Not assessed.

Turricaspia pulla (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania* (*Turricaspia*) *caspia* var. *pulla* Dybowski & Grochmalicki: 111, pl. 1, fig. 6a.
1969 *Pyrgula* [(*Turricaspia*)] *pulla* (Dyb. et Gr.). – Logvinenko and Starobogatov: 361–362, fig. 360(8).
2006 *Pyrgula pulla* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 102, pl. 46, fig. C.
2016 *Pyrgula pulla* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 242.
2018 *Turricaspia pulla* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 81–82, fig. 14A–J.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea, reported from the middle and southern Caspian Sea basins (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The species can be easily distinguished from other *Turricaspia* species based on its relatively broad shell, the low-convex whorls, and its small size (Neubauer et al. 2018).

Conservation status. Data Deficient (Vinarski 2011m).

Turricaspia pullula (Dybowski & Grochmalicki, 1915)

*1915 *Micromelania* (*Turricaspia*) *caspia* var. *pullula* Dybowski & Grochmalicki: 111–112, pl. 1, fig. 7.
1969 *Pyrgula* [(*Turricaspia*)] *pullula* (Dyb. et Gr.). – Logvinenko and Starobogatov: 366–367, fig. 363(3).
2006 *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915). – Kantor and Sysoev: 109, pl. 50, fig. B.
2016 *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915). – Vinarski and Kantor: 249.
2018 *Turricaspia pullula* (B. Dybowski & Grochmalicki, 1915). – Neubauer et al.: 82–84, fig. 14K–L.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Endemic to the Caspian Sea, reported from the western part of the middle Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. The very characteristic tripartite whorl profile allows an easy identification and discrimination from other Pontocaspian Pyrgulinae (Neubauer et al. 2018).

Conservation status. Data Deficient (Vinarski 2011s).

Turricaspia rudis (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *rudis* Logvinenko & Starobogatov: 362, fig. 360(5).
2016 *Pyrgula rudis* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 242.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle and southern Caspian Sea, 50–100 m.

Distribution. Type locality only.

Taxonomic notes. The status of this species is unclear. The drawing provided by Logvinenko and Starobogatov (1969) shows strong similarities to *T. grimmi* in terms of the nearly straight-sided whorls and the large aperture. Since the whereabouts of the type material is unknown, we refrain from a final conclusion on the potential synonymy.

Conservation status. Data Deficient (Vinarski 2011n).

Turricaspia sajenkovae (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *sajenkovae* Logvinenko & Starobogatov: 361, fig. 360(4).
2016 *Turricaspia sajenkovae* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 249–250.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. The available drawing of this species suggests a very slender shell with highly convex whorls bearing a subsutural band. The type material has not been found, and the identity of this species remains unclear.

Conservation status. Data Deficient (Vinarski 2011t).

Turricaspia similis (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Caspiella*) *similis* Logvinenko & Starobogatov: 375, fig. 366(11).
2016 *Pyrgula similis* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 243.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the middle Caspian Sea, 20–50 m.

Distribution. Middle and southern Caspian Basin. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. Judging from the drawing in Logvinenko and Starobogatov (1969), presenting a small slender shell with ca. 5.5 highly convex whorls, the species might be based on a juvenile specimen. It might be a junior synonym of the similarly shaped *T. meneghiniana* (Issel, 1865). Without investigating the type material, which has not been found in the ZIN collection, the identity of this species remains unclear.

Conservation status. Not assessed.

Turricaspia simplex (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxypyrgula*) *simplex* Logvinenko & Starobogatov: 367–368, fig. 363(4).
2016 *Pyrgula simplex* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 243.

Status. Pontocaspian species, identity uncertain.

Type locality. Middle Caspian Sea, 40–120 m.

Distribution. Middle and southern Caspian Sea. This species was mentioned from depths between 200 and 900 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. As for the previous species, it is highly uncertain whether this taxon is a distinct species. It might also be based on a juvenile and could be a synonym of an earlier described species, perhaps *T. pulla* or *T. lyrata*.

Conservation status. Not assessed.

Turricaspia spasskii (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *spasskii* Logvinenko & Starobogatov: 361, fig. 360(7).
2016 *Turricaspia spasskii* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 250.

Status. Accepted Pontocaspian species.

Type locality. Western part of the middle Caspian Sea.

Distribution. Middle and southern Caspian Sea. This species was mentioned from depths between 200 and 300 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The fast growing whorls terminating in a large body whorl with expanded aperture are characteristic for this species and facilitate discrimination from other *Turricaspia* species.

Conservation status. Data Deficient (Vinarski 2011u).

Turricaspia spica (Eichwald, 1855)

*1855 *Paludina spica* Eichwald: 303–304, pl. 10, figs 8, 9.
?1992 *Turricaspia spica* (Eichw.). – Anistratenko and Prisjazhnjuk: 18, fig. 2d.
2006 *Turricaspia spica* (Eichwald, 1855). – Kantor and Sysoev: 110, pl. 49, fig. F.
2009 *Turricaspia* cf. *spica* (Eichwald, 1855). – Filippov and Riedel: 70, 72, 74, 76, fig. 4e, f.
2016 *Turricaspia spica* (Eichwald, 1855). – Vinarski and Kantor: 250.

Status. Accepted Pontocaspian species.

Type locality. Ostrov Chechen’ (island in NW Caspian Sea), Dagestan, Russia.

Distribution. Endemic to the Caspian Sea. Occurred also in the Aral Sea during the Holocene (Filippov and Riedel 2009) but now extinct there. It has been reported from the Holocene of Danube Delta (Anistratenko and Prisjazhnjuk 1992) (see below).

Taxonomic notes. As the oldest described species presently attributed to *Turricaspia*, the validity of this species is without doubt. Its identity, however, is poorly known, given the limited information and poor drawing provided by Eichwald (1855), as well as the largely diverging concepts applied by later authors (see Neubauer et al. 2018 for a detailed discussion of the matter). We have a geographic record (Anistratenko and Prisjazhnjuk 1992) that is outside the Caspian–Aral distribution range of this genus. Comparison of the Danube material with Caspian specimens suggests the identification might be correct, yet further detail study is required to assess whether the Danube record might actucally not be an unusual form of *Laevicaspia lincta*.

Conservation status. Not assessed.

Turricaspia turricula (Clessin & Dybowski in Dybowski, 1887)

*1887 *Micromelania turricula* Clessin & Dybowski in Dybowski: 34.
1888 [*Micromelania*] *turricula* n. sp. – Dybowski: 78, pl. 1, fig. 3a–c.
2006 *Turricaspia turricula* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 111, pl. 49, fig. I.
2016 *Turricaspia turricula* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 244.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea. This species was mentioned from depths between 200 and 500 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017).

Taxonomic notes. The species is characterised by a slender conical shell with weakly convex whorls with weak subsutural swelling and a slightly inflated body whorl with large aperture.

Conservation status. Not assessed.

Turricaspia uralensis (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Turricaspia*) *uralensis* Logvinenko & Starobogatov: 359, fig. 360(1).
2016 *Pyrgula uralensis* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 244.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the northern Caspian Sea.

Distribution. Type locality only.

Taxonomic notes. Logvinenko and Starobogatov (1969) illustrated a comparably small shell with eight highly convex whorls, large body whorl, and large aperture. Reliable assessment of the species' status requires investigation of the type material, which has only been discovered in ZIN in June 2018 and awaits further study.

Conservation status. Not assessed.

Turricaspia vinogradovi (Logvinenko & Starobogatov, 1969)

*1969 *Pyrgula* (*Oxypyrgula*) *vinogradovi* Logvinenko & Starobogatov: 368, fig. 363(9).
?1971 *Pyrgula astrachanica* Pirogov: 249–251, fig. 1.
?2006 *Turricaspia astrachanica* (Pirogov, 1971). – Kantor and Sysoev: 105, pl. 48, fig. B.
2006 *Turricaspia vinogradovi* (Logvinenko & Starobogatov, 1968). – Kantor and Sysoev: 111, pl. 50, fig. C.
2016 *Turricaspia vinogradovi* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 251.

Status. Pontocaspian species, identity uncertain.

Type locality. Northern Caspian Sea.

Distribution. Northern Caspian Sea and Volga Delta (Logvinenko and Starobogatov 1969).

Taxonomic notes. The species as illustrated by Logvinenko and Starobogatov (1969) is based on a slender shell with highly convex whorls. The same traits are also typical for *Pyrgula astrachanica*; in fact, the type of *T. vinogradovi* could be a juvenile of that species. Moreover, both of them might be synonyms of *Turricaspia nossovi* Kolesnikov, 1947. Since a part of the type material of the species involved is lacking and some of the taxa are based on incomplete or presumably juvenile specimens, the identities of *Pyrgula astrachanica* and *Turricaspia vinogradovi* remain unresolved.

Conservation status. *Turricaspia vinogradovi* has not been assessed by the IUCN, *T. astrachanica* is marked as "Data Deficient" (Vinarski 2011q).

Hydrobiidae incertae sedis

Abeskunus brusinianus (Clessin & Dybowski in Dybowski, 1887)

*1887 *Zagrabica Brusiniana* Clessin & Dybowski in Dybowski: 52–53.
1888 *Zagrabica Brusiniana* n. sp. – Dybowski: 79, pl. 2, fig. 7.
2006 *Pseudamnicola brusiniana* (Clessin & W. Dybowski in W. Dybowski, 1888). – Kantor and Sysoev: 114, pl. 51, fig. J.
2016 *Pseudamnicola brusiniana* (Clessin & W. Dybowski in W. Dybowski, 1888). – Vinarski and Kantor: 222.
2018 *Abeskunus brusinianus* (Clessin & W. Dybowski in W. Dybowski, 1887). – Neubauer et al.: 87–88, fig. 16A–I.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969, Parr et al. 2007). Mirzoev and Alekperov (2017) mention *Pseudamnicola brusinianus* from depths between 200 and 400 m in the South Caspian Basin of

Azerbaijan but we are not entirely certain whether these records might include other *Abeskunus* species as well.

Taxonomic notes. For a detailed description and discussion, see Neubauer et al. (2018).

Conservation status. Least Concern (Vinarski 2011c).

Abeskunus depressispira (Logvinenko & Starobogatov, 1969)

*1969 *Pseudamnicola* (*Abeskunus*) *depressispira* Logvinenko & Starobogatov: 381, fig. 367(14).
2016 *Pseudamnicola depressispira* Logvinenko & Starobogatov, 1968. – Vinarski and Kantor: 222–223.

Status. Accepted Pontocaspian species.

Type locality. Western part of the southern Caspian Sea, northward of Kuraginsky Kamen' [= Kür Daşı] Island (approximately 39°01'05"N, 49°20'02"E), 81 m water depth.

Distribution. In addition to the type locality, specimens have been found in Holocene material retrieved near the Kura Delta, a few kilometres north of the type locality.

Taxonomic notes. Current investigations on recently collected Holocene material from the south-western Caspian Sea confirm that this species belongs to the genus *Abeskunus*. The finely ribbed, low trochiform shell facilitates distinction from its congeners. The species epithet is based on the Latin noun *spira*, spire, and is to be considered a noun in apposition (ICZN 1999, Art. 31.2.1.).

Conservation status. Data Deficient (Vinarski 2011d).

Abeskunus exiguus (Eichwald, 1838)

°1837 *Lithoclypus* [sic] *Caspius* m. – Krynicki: 58 (nomen nudum).
*1838 *Paludina exigua* Eichwald: 152–153.
1863 *Bithinia sphaerion* Mousson: 409–410.
1874 *Lithoglyphus*? *Caspius* Krynicki. – Martens: 80.
1877 *Lithoglyphus caspius* Grimm: 82–84, pl. 9, fig. 8.
1977 *Pseudamnicola* (*Abeskunus*) *brusiniana michelae* Tadjalli-Pour: 108, pl. 2, fig. 9.
2016 *Pseudamnicola exigua* (Eichwald, 1838). – Vinarski and Kantor: 223.
2016 *Pseudamnicola sphaerion* (Mousson, 1863). – Vinarski and Kantor: 223.

Status. Accepted Pontocaspian species.

Type locality. In fossil (likely Pleistocene) limestone of Dagestan, Russia.

Distribution. Western Caspian Sea, known from northern and southern parts. Records from the eastern Caspian Sea by Logvinenko and Starobogatov (1969) could not be confirmed.

Taxonomic notes. An in-depth study of the literature suggests that the names *Paludina exigua*, *Bithinia sphaerion* syn. n., and *Lithoglyphus caspius* all refer to the same species. The name *Lithoglyphus caspius* was made available by Martens (1874) by referring to the description and illustration of Eichwald's species, rendering *L. caspius* a junior objective synonym of *Abeskunus exiguus*. All three taxa share the globular shape, short spire, and inflated last whorl. The subspecies *Pseudamnicola brusiniana michelae* syn. n. from Iranian coasts of the Caspian Sea closely resembles *A. exiguus* and is herein considered a synonym as well. *Abeskunus exiguus* differs from *A. brusinianus* in the highly globular shell with small spire. A revision of the species is currently being prepared.

Conservation status. Not assessed.

Andrusovia andrusovi Starobogatov, 2000

*2000 *Andrusovia andrusovi* Starobogatov: 39–41, fig. 1B.
2016 *Andrusovia andrusovi* Starobogatov, 2000. – Vinarski and Kantor: 214.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the South Caspian Sea (39°05'N, 52°35'E).

Distribution. Middle and southern Caspian Sea (Starobogatov 2000).

Taxonomic notes. The species is very similar to the type species of *Andrusovia*, *A. dybowskii*, regarding the low spire. Investigation of the type material is required to clarify whether both taxa are distinct.

Remarks. Only recently, paratypes of this species were detected at the Zoological Museum of Moscow University. A study of the taxonomy of *Andrusovia* is currently under way.

Conservation status. Not assessed.

Andrusovia brusinai Starobogatov, 2000

*2000 *Andrusovia brusinai* Starobogatov: 41, fig. 1C.
2016 *Andrusovia brusinai* Starobogatov, 2000. – Vinarski and Kantor: 214.
2018 *Andrusovia brusinai* Starobogatov, 2000. – Neubauer et al.: 54–56, fig. 6F–K, M–N.

Status. Pontocaspian species, identity uncertain.

Type locality. Eastern part of the middle Caspian Sea (42°42.5'N, 51°32.5'E), at 80 m water depth.

Distribution. Northern, middle, and southern Caspian Sea (Starobogatov 2000, Neubauer et al. 2018).

Taxonomic notes. The species was recently described in detail by Neubauer et al. (2018). The species was distinguished from *A. dybowskii* and *A. andrusovi* by the higher spire, but this is a variable character. Currently, the taxonomy of *Andrusovia* species is the subject of further study.

Remarks. Starobogatov (2000) mentioned that the type material is housed in the ZIN collection, but we were unable to find the holotype and it is presumed lost. Only recently, paratypes of this species were detected at the Zoological Museum of Moscow University and are currently being studied.

Conservation status. Not assessed.

Andrusovia dybowskii Brusina in Westerlund, 1902b

*1902b *Andrusovia Dybowskii* Westerlund: 133.
? 2000 *Andrusovia dybowskii* Brusina in Westerlund, 1903. – Starobogatov: 39, fig. 1A.
2016 *Andrusovia dybowskii* Brusina in Westerlund, 1903. – Vinarski and Kantor: 214.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Starobogatov 2000).

Taxonomic notes. Apparently, Brusina considered both the more conical and flatter shells ("conoidea vel discoidea") to belong to a single species. Starobogatov (2000) in turn referred only the flat type to as *Andrusovia dybowskii* and considered the conical ones to belong to separate species (*A. brusinai* and *A. marina*). The recently rediscovered type material represents the conico-globular type and is currently subject of study by V. Anistratenko and collaegues.

Conservation status. Not assessed.

Andrusovia marina (Logvinenko & Starobogatov, 1969)

*1969 *Horatia* (*Caspiohoratia*) *marina* Logvinenko & Starobogatov: 382, fig. 367(18).
2000 *Andrusovia marina* (Logvinenko & Starobogatov, 1969). – Starobogatov: 41–42, fig. 1D.
2016 *Andrusovia marina* (Logvinenko & Starobogatov, 1968). – Vinarski and Kantor: 214–215.

Status. Pontocaspian species, identity uncertain.

Type locality. Northern slope of the middle Caspian Sea Basin, 43°32.5'N, 49°17.5'E, 60 m water depth.

Distribution. Middle and southern Caspian Sea (Starobogatov 2000). This species was mentioned from depths between 200 and 400 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Horatia marina*).

Taxonomic notes. According to Neubauer et al. (2018), this species might be a senior synonym of *A. brusinai* Starobogatov, 2000. Inspection of recently discovered type material appears to support that view, but more in-depth studies are required to evaluate the status of this species.

Remarks. The holotype is not traced and presumed lost. Only recently, paratypes of this species were detected at the Zoological Museum of Moscow University and are currently being studied.

Conservation status. Not assessed.

Family Lithoglyphidae Tryon, 1866

Lithoglyphus naticoides (Pfeiffer, 1828)

*1828 *Paludina naticoides* Pfeiffer: 45–46, pl. 8, figs 1, 2, 4.
2012 *Lithoglyphus naticoides* (Pfeiffer, 1828). – Welter-Schultes: 41, unnumbered text figures.
2016 *Lithoglyphus naticoides* (C. Pfeiffer, 1828). – Vinarski and Kantor: 253.

Status. Accepted native species.

Type locality. In the Danube at Vienna, Austria, and at Pesth (today part of Budapest), Hungary.

Distribution. Originally only in rivers entering the Black Sea, in the Danube up to Regensburg (Germany). After 1800, also introduced to Elbe and Rhine regions by artificial canals; after 1900 in France (Welter-Schultes 2012). Very common in the Volga Delta (Vinarski et al. 2018).

Conservation status. Least Concern (Van Damme 2011b).

Family Tateidae Thiele, 1925

Potamopyrgus antipodarum (Gray, 1843)

*1843 *Amnicola antipodarum* Gray: 241.
1951 *Potamopyrgus jenkinsi* E. A. Smith 1889. – Grossu: 693–695, fig. 1a–d.
1966 *P.*[*yrgula*] (*Trachycaspia*?) *grossui* Golikov and Starobogatov: 359.
1991 *Potamopyrgus polistchuki* Anistratenko: 75, fig. 1(2).
1995 *Potamopyrgus alexenkoae* Anistratenko in Anistratenko and Stadnichenko: 92–93, fig. 69.
2012 *Potamopyrgus antipodarum* (Gray, 1843). – Welter-Schultes: 40, unnumbered text figures.

Status. Accepted species, invasive.

Type locality. New Zealand (no details).

Distribution. Originally from New Zealand, probably introduced in 1859 to England, in 1872 to Tasmania, in 1895 to mainland Australia, in ca. 1900 to European mainland (Ponder 1988), and in 1987 to North America (Zaranko et al. 1997).

Taxonomic notes. The two Black Sea species *P. polistchuki* syn. n. and *P. alexenkoae* syn. n. are here considered as junior synonyms of *P. antipodarum*, differing only very weakly in outline. Vinarski and Kantor (2016) listed *Pyrgula* (*Trachycaspia*?) *grossui* syn. n. Golikov & Starobogatov in the synonymy of *T. dimidiata* (Eichwald, 1838). Golikov and Starobogatov (1966) introduced this species as new name for the supposedly misidentified *Potamopyrgus jenkinsi* sensu Grossu (1951) from Razim Lake in Romania. The shell they later illustrated (Golikov and Starobogatov 1972) indeed shows similarities with *T. dimidiata*. The shell illustrated in Grossu (1951), however, is completely different and shows a keeled form of *P. antipodarum*.

Conservation status. Least Concern (Van Damme 2013).

Family Planorbidae Rafinesque, 1815

Gyraulus eichwaldi (Clessin & Dybowski in Dybowski, 1887)

°1876 *Pl.*[*anorbis*] *Eichwaldi*. – Grimm: 157 (nomen nudum).
*1887 *Planorbis Eichwaldi* Clessin & Dybowski in Dybowski: 49–52.
1888 *Planorbis Eichwaldi* Grimm. – Dybowski: 79, pl. 2, fig. 11a–c, pl. 3, fig. 10a–c.
?1966b *Anisus* (*Andrusowia*) [sic] *eichwaldi infundibularis* Logvinenko and Starobogatov: 1472, fig. 4.
?1977 *Anisus djalali* Tadjalli-Pour: 109, pl. 2, fig. 10.
2016 *Gyraulus* (*Gyraulus*) *eichwaldi* (Grimm in W. Dybowski, 1888). – Vinarski and Kantor, 2016: 378.

Status. Accepted Pontocaspian species.

Type locality. Caspian Sea (no details).

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentionedfrom depths between 200 and 900 m in the South Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Anisus eichwaldi*).

Taxonomic notes. The species is characterised by a relatively large, asymmetrical shell. *Anisus eichwaldi infundibularis* is probably a morphotype of *G. eichwaldi*. We are uncertain about the status of *Anisus djalali* Tadjalli-Pour, 1977 as the description is very brief and the photographs are not very clear. It may be within the range of the morphological variability of *G. eichwaldi*.

Conservation status. Not assessed.

Gyraulus dybowskii (Kolesnikov, 1947)

*1947 *Planorbis eichwaldi* var. *dybowskii* Kolesnikov: 109, 112, fig. in tab. 1.
1966b *Anisus* (*Andrusowia*) [sic] *kolesnikovi* Logvinenko and Starobogatov: 1473, fig. 5.
1966b *Anisus* (*Andrusowia*) [sic] *kolesnikovi sublittoralis* Logvinenko and Starobogatov: 1472–1473, fig. 6.
2016 *Gyraulus* (*Gyraulus*) *kolesnikovi* (Logvinenko & Starobogatov, 1966). – Vinarski and Kantor, 2016: 379.

Status. Pontocaspian species, identity uncertain.

Type locality. Caspian Sea, 40°37'N, 50°52'E, 115 m.

Distribution. Middle and southern Caspian Sea (Logvinenko and Starobogatov 1969). This species was mentioned from depths between 200 and 300 m in the South

Caspian Basin of Azerbaijan (Mirzoev and Alekperov 2017, who reported the species as *Anisus colesnikovi* [sic]).

Taxonomic notes. Logvinenko and Starobogatov (1966b) considered this species and *Andrusovia dybowskii* Brusina in Westerlund, 1902b to belong in the same genus, *Anisus* (*Andrusovia*), rendering *P. dybowskii* Kolesnikov, 1947 a junior homonym. Therefore, they introduced *A. kolesnikovi* as replacement name. Since both taxa do clearly not belong to the same genus or even the same family, the replacement name is to be discarded.

The species resembles *G. eichwaldi* regarding the general habitus; it differs in the more pronounced angle at the transition between whorl flank and apical plane. A revision is required to investigate if the Caspian *Gyraulus* species are distinct species or morphotypes of *G. eichwaldi*. The generic placement follows Vinarski and Kantor (2016). Note that those authors listed the earlier described *P. eichwaldi dybowskii* Kolesnikov, 1947 as a synonym of *G. kolesnikovi*.

Conservation status. Least Concern (for *Anisus kolesnikovi*; Vinarski 2011a).

Gyraulus sulcatus (Logvinenko & Starobogatov, 1966, non Hilgendorf, 1867)

*1966b *Anisus* (*Andrusowia*) [sic] *sulcatus* Logvinenko & Starobogatov: 1474, fig. 7.

2016 *Gyraulus* (*Gyraulus*) *sulcatus* (Logvinenko & Starobogatov, 1966). – Vinarski and Kantor, 2016: 382.

Status. Pontocaspian species, identity uncertain, name invalid.

Type locality. Caspian Sea, 42°45'N, 48°29'E, 79 m.

Distribution. Middle Caspian Sea (Logvinenko and Starobogatov 1969).

Taxonomic notes. The species in its present combination as *Gyraulus sulcatus* (following Vinarski and Kantor 2016) is invalid as it is a secondary homonym of the Miocene *Gyraulus sulcatus* (Hilgendorf, 1867). We refrain here from introducing a replacement name as the species' status is uncertain. It resembles *G. eichwaldi* and *G. kolesnikovi* in outline shape and differs only in the more pronounced angle between whorl flank and apical plane and the shallow furrow on the apical side. An in-depth revision is required to clarify if *Gyraulus sulcatus* is a distinct species or a mere morphotype of *G. eichwaldi* (Clessin & Dybowski in Dybowski, 1887).

Conservation status. Not assessed.

Discussion and conclusions

The annotated check-list presented here is a first attempt to assess the species diversity of the Pontocaspian molluscs by experts working in different countries and fields (neontology, palaeontology, biogeography, phylogenetics). Hitherto, progress has been limited by a number of factors: (1) fresh material for genetic studies is available only for few nominal species, and (2) the type series of many species are lost or at least have not yet been found. This concerns not only the species described by Eichwald or Grimm in the

19th century; the type specimens of many species established by Starobogatov and his co-workers in the 1960–2000s could not be traced in ZIN (Kantor and Sysoev 2006, Vinarski and Kantor 2016). Furthermore, progress has been limited by (3) a lack of representative shell samples to undertake quantitative statistical analyses of conchological variation, and (4) insufficient ecological and distribution data for many of the species.

Three species that have been reported from the Pontocaspian region are not included in this list. The bithyniid gastropod *Alocinma caspica* (Westerlund, 1902) has been described from the east side of the Caspian Sea (Beriozkina et al. 1995 indicated this record is probably from the vicinity of Krasnovodsk, Turkmenistan). However, Starobogatov et al. (2004) argued the species lives in waterbodies of Bol'shoy Balkhan (Turkmenistan) and probably not in the Caspian Sea itself (Vinarski et al. 2013, Vinarski and Kantor 2016). Furthermore, two *Pseudamnicola* species have been described from Lake Razim in Romania (*P. leontina* Grossu, 1986 and *P. razelmiana* Grossu, 1986) that is prime Pontocaspian habitat. Like bithyniids, *Pseudamnicola* has not been reported as a Pontocaspian group elsewhere, and probably they are freshwater species that live in the surrounding streams or in springs. For now, we have excluded these species from the Pontocaspian species list.

This list contains 55 accepted and a further 44 uncertain endemic Pontocaspian mollusc species (Table 2), here defined as species that are considered to be endemic for at least one of the Pontocaspian basins. There are 14 native and three immigrant species (at least in one of the Pontocaspian basins), even though some species may be native or endemic in one of the basins and have become invasive in another of the Pontocaspian Basins. All species that have an uncertain status belong to the Pontocaspian category. The Caspian Sea Basin has the highest number of accepted endemic Pontocaspian species (48) but also poses the greatest taxonomic challenges, with a further 37 species whose status are unclear.

The species richness estimate reflects the current shift of molluscan systematics from morphology-based to integrated studies, with increasing contributions of molecular and statistical species delineation approaches (Vinarski 2018). It has recently been shown that many nominal taxa of fresh- and brackish-water snails and mussels described on the basis of their shell characters (the Pontocaspian molluscs rarely were described on the base of anatomical studies) lack a genetic support (with few exceptions such as e.g., Popa et al. 2012, Stepien et al. 2013) and thus do not represent evolutionary meaningful units. On the other hand, cryptic speciation is known within many taxa of molluscs in long-lived lakes (Albrecht et al. 2006), and the Pontocaspian biota may include some previously unrecognised species. Thus, we consider our check-list rather as a starting point for further integrated research, not a definitive and fixed inventorisation of the Pontocaspian molluscs.

Anyone who reads this list or works such as Logvinenko and Starobogatov (1969) or Vinarski and Kantor (2016) may think that the Caspian Sea still maintains its unique and species-rich mollusc fauna. However, the actual state of affairs is problematic as many species thought to be endemic to this large saline lake have not been found since their description, and recent attempts to obtain fresh material for genetic studies mostly failed. Clearly, the conservation status of Pontocaspian species is insufficiently known. With our working list we aim to assist in the necessary follow-up conservation assessments.

Table 2. Pontocaspian mollusc species list. Abbreviations: Status: A – accepted, U – uncertain. Basins: AS – Aral Sea, BSB – Black Sea Basin, CSB – Caspian Sea Basin. Species are E – endemic, EX – extinct, IM – immigrant, IN – invasive, N – native (definitions in Table 1); *species encountered alive during the PRIDE program expeditions by participants; †very fresh material of species encountered, but not living specimens.

Species	Status	BSB	CSB	AS
Mytilaster minimus (Poli, 1795)*	A	N	IN	IM/EX
Adacna laeviuscula (Eichwald, 1829)	A	?	E	
Adacna fragilis Milaschewitsch, 1908	U	E		
Adacna minima Ostroumov, 1907	A		E	E/EX?
Adacna minima ostroumovi (Logvinenko & Starobogatov, 1967)	U		E	
Adacna vitrea (Eichwald, 1829)	A	E	E	E/EX?
Adacna vitrea glabra Ostroumov, 1905	U	E	E	
Adacna vitrea bergi (Starobogatov, 1974)	U			E/EX?
Cerastoderma glaucum (Bruguière, 1789) s.l.*	A	N	IN	IN?
Cerastoderma sp. A [non *C. rhomboides* (Lamarck, 1819)]*	A	N	IN	IN?
Didacna baeri (Grimm, 1877)	A		E	
Didacna barbotdemarnii (Grimm, 1877)*	A		E	
Didacna eichwaldi (Krynicki, 1837)	A		E	
Didacna longipes (Grimm, 1877)*	A		E	
Didacna parallela Bogachev, 1932	A		E	
Didacna praetrigonoides Nalivkin & Anisimov, 1914	A		E/EX	
Didacna profundicola Logvinenko & Starobogatov, 1966†	A		E	
Didacna protracta (Eichwald, 1841)	A		E	
Didacna pyramidata (Grimm, 1877)	A		E	
Didacna trigonoides (Pallas, 1771)*	A		E	
Hypanis plicata (Eichwald, 1829)	A	E	E	
Monodacna acuticosta (Logvinenko & Starobogatov, 1967)	A		E	
Monodacna albida (Logvinenko & Starobogatov, 1967)	A		E	
Monodacna caspia (Eichwald, 1829)	A		E	?
Monodacna colorata (Eichwald, 1829)*	A	E	IM	
Monodacna filatovae (Logvinenko & Starobogatov, 1967)	U		E	
Monodacna knipowitschi (Logvinenko & Starobogatov, 1966)	U		E	
Monodacna polymorpha (Logvinenko & Starobogatov, 1967)	U		E	
Monodacna semipellucida (Logvinenko & Starobogatov, 1967)	A		E	
Abra segmentum (Récluz, 1843)*	A	N	IN	IN
Corbicula fluminalis (Müller, 1774)	A		N/IN	
Dreissena bugensis Andrussov, 1897†	A	E/IN	IN	
Dreissena caspia Eichwald, 1855	A		E/EX	E/EX
Dreissena elata Andrusov, 1897	U		E/EX	
Dreissena grimmi (Andrusov, 1890)*	A		E	
Dreissena polymorpha (Pallas, 1771) s.l.*	A	N	N	N
Mytilopsis leucophaeata (Conrad, 1831)*	A	IN	IN	
Theodoxus danubialis (Pfeiffer, 1828)*	A	N		
Theodoxus fluviatilis (Linnaeus, 1758)	A	N		
Theodoxus pallasi Lindholm, 1924*	A	N	N	N/EX?
Theodoxus schultzii (Grimm, 1877)*	U		E	
Theodoxus velox V. Anistratenko in O. Anistratenko et al., 1999	A	N		
Eupaludestrina stagnorum (Gmelin, 1791)	A	N/IM	N/IM	
Caspia baerii Clessin & Dybowski in Dybowski, 1887	A	E?	E	
?*Caspia valkanovi* (Golikov & Starobogatov, 1966)	U	E		
Clathrocaspia brotzkajae (Starobogatov in Anistratenko & Prisjazhnjuk, 1992)	A	?E	E	
Clathrocaspia gmelinii (Clessin & Dybowski in Dybowski, 1887)	A		E	
Clathrocaspia isseli (Logvinenko & Starobogatov, 1969)	U		E	

Species	Status	BSB	CSB	AS
Clathrocaspia knipowitschii (Makarov, 1938)	A	E		
Clathrocaspia logvinenkoi (Golikov & Starobogatov, 1966)	A	E		
Clathrocaspia milae Boeters, Glöer & Georgiev, 2015	U	E		
Clathrocaspia pallasii (Clessin & Dybowski in Dybowski, 1887)	A		E	
Ulskia behningi (Logvinenko & Starobogatov, 1969)	U		E	
?Ulskia derzhavini (Logvinenko & Starobogatov, 1969)	U		E	
Ulskia ulskii (Clessin & Dybowski in Dybowski, 1887)	A		E	
Ecrobia grimmi (Clessin in Dybowski, 1887)*	A		N	N
Ecrobia maritima (Milaschewitsch, 1916)*	A	N		
Ecrobia ventrosa (Montagu, 1803)	A	IM		
Clessiniola variabilis (Eichwald, 1838)	A	E	E	
Laevicaspia abichi (Logvinenko & Starobogatov, 1969)	A		E	
Laevicaspia caspia (Eichwald, 1838)	A		E	
Laevicaspia cincta (Abich, 1859)	A		E	
Laevicaspia conus (Eichwald, 1838)	A		E	
?*Laevicaspia ebersini* (Logvinenko & Starobogatov, 1969)	U		E	
?*Laevicaspia ismailensis* (Golikov & Starobogatov, 1966)	A	E		
Laevicaspia kolesnikoviana (Logvinenko & Starobogatov in Golikov & Starobogatov, 1966)	A		E	
Laevicaspia kowalewskii (Clessin & Dybowski in Dybowski, 1887)	A		E	
Laevicaspia lencoranica (Logvinenko & Starobogatov, 1969)	U		E	
Laevicaspia lincta (Milaschewitsch, 1908)	A	E		
?*Laevicaspia marginata* (Westerlund, 1902)	U		E	
Laevicaspia sieversii (Clessin in Dybowski, 1887)	U		E	
?*Turricaspia aenigma* (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia andrussowi (Dybowski & Grochmalicki, 1915)	A		E	
?*Turricaspia basalis* (Dybowski & Grochmalicki, 1915)	U		E	
?*Turricaspia bogatscheviana* (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia chersonica Alexenko & Starobogatov, 1987	U	E		
Turricaspia columna (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia concinna (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia dagestanica (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia dimidiata (Eichwald, 1838)	A		E	
Turricaspia eburnea (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia elegantula (Clessin & Dybowski in Dybowski, 1887)	U		E	
Turricaspia eulimellula (Dybowski & Grochmalicki, 1915)	A		E	
Turricaspia fedorovi (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia grimmi (Clessin & Dybowski in Dybowski, 1887)	A		E	
Turricaspia lyrata (Dybowski & Grochmalicki, 1915)	A		E	
Turricaspia marisnigri Starobogatov in Alexenko & Starobogatov, 1987	U	E/EX?		
Turricaspia meneghiniana (Issel, 1865)	A		E	
Turricaspia nossovi Kolesnikov, 1947	A		E	
?*Turricaspia obventicia* (Anistratenko in Anistratenko & Prisjazhnjuk, 1992)	U	E		
?*Turricaspia pseudobacuana* (Logvinenko & Starobogatov, 1969)	U		E	
?*Turricaspia pseudodimidiata* (Dybowski & Grochmalicki, 1915)	U		E	
Turricaspia pseudospica (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia pulla (Dybowski & Grochmalicki, 1915)	A		E	
Turricaspia pullula (Dybowski & Grochmalicki, 1915)	A		E	
Turricaspia rudis (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia sajenkovae (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia similis (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia simplex (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia spasskii (Logvinenko & Starobogatov, 1969)	A		E	
Turricaspia spica (Eichwald, 1855)	A	?E	E	?E
Turricaspia turricula (Clessin & Dybowski in Dybowski, 1887)	A		E	

Species	Status	BSB	CSB	AS
Turricaspia uralensis (Logvinenko & Starobogatov, 1969)	U		E	
Turricaspia vinogradovi (Logvinenko & Starobogatov, 1969)	U		E	
Abeskunus brusinianus (Clessin & Dybowski in Dybowski, 1887)	A		E	
Abeskunus depressispira (Logvinenko & Starobogatov, 1969)	A		E	
Abeskunus exiguus (Eichwald, 1838)	A		E	
Andrusovia andrusovi Starobogatov, 2000	U		E	
Andrusovia brusinai Starobogatov, 2000	U		E	
Andrusovia dybowskii Brusina in Westerlund, 1902	A		E	
Andrusovia marina (Logvinenko & Starobogatov, 1969)	U		E	
Lithoglyphus naticoides (Pfeiffer, 1828)*	A	N	IM?	
Potamopyrgus antipodarum (Gray, 1843)*	A	IM		
Gyraulus eichwaldi (Clessin & Dybowski in Dybowski, 1887)†	A		E	
Gyraulus dybowskii (Kolesnikov, 1947)	U		E	
Gyraulus sulcatus (Logvinenko & Starobogatov, 1966)	U		E	

Most taxonomic difficulties were encountered for the bivalve genera *Monodacna* and *Dreissena* and the Pyrgulinae gastropods (especially genera *Turricaspia* and *Laevicaspia*). Furthermore, there is an urgent need to assess whether representatives of species complexes in the three main Pontocaspian basins (Aral Sea, Caspian Sea, Black Sea) concern separate species as several of these regional populations are in immediate danger of extinction or already extinct (for example with the disappearance of the Aral Sea). Combined methodological efforts will enable us to estimate the extent and characterise the nature of Pontocaspian faunal turnover, and this species list is a first attempt in the required uniform taxonomic base.

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RESEARCH ARTICLE

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Two new species of *Beraba* Martins, 1997 and new geographical records of Eburiini (Coleoptera, Cerambycidae)

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Abstract

Two new species of *Beraba* from Colombia (Bolívar) are described: *Beraba anae* **sp. n.** and *Beraba angeli* **sp. n.** The most recent key to species of the genus was modified to incorporate the new species. The male of *Beraba limpida* Martins, 1997 is described and illustrated for the first time. Moreover, the geographical distribution of 12 species of Eburiini is expanded.

Keywords

Atlántico, Bolívar, Caribbean, *Eburodacrys*, taxonomy, longhorn beetle, tropical dry forest

Introduction

The tribe Eburiini is currently composed of 24 genera and 268 species, all of them with a geographical distribution restricted to North, Central (including the Caribbean) and South America (Botero and Monné 2018).

The genus *Beraba* Martins, 1997 was described to gather together the species described initially in *Eburia* Lacordaire, 1830 having a bright aspect, antennomere III longer than IV, and femora with spines restricted to the inner margin. Later, Galileo and Martins (2000) transferred *Eburodacrys cheilaria* Martins, 1967 to the genus. Currently, the genus includes 18 species distributed from Panama to South America. Three of these species – *B. inermis* Martins & Galileo, 2002, *B. marica* Galileo & Martins, 2000 and *B. piriana* Martins, 1997 – are known to occur in Colombia (Botero 2015; Tavakilian and Chevillotte 2018).

In this work two new species of *Beraba* are described, *B. anae* sp. n. and *B. angeli* sp. n.; the male of *B. limpida* Martins, 1997 is redescribed and the geographical distribution is expanded for 12 species. The key proposed by Botero (2015) for *Beraba* is modified to include the new species.

Material and methods

The material examined was obtained in Colombia, from the tropical dry forest in the Reserva La Flecha (RLF), Bolívar and the Reserva Campesina la Montaña (RCM), Atlántico. These locations were sampled from February to May 2018 by using a UV light trap, white light trap, manual capture, and the sampling was supplemented by visits to entomological collections.

The material currently resides in the following institutions, which are subsequently referred to by their acronyms:

ANDES-E	Colección Entomológica, Museo de Historia Natural, Universidad de Los Andes, Bogotá, Colombia (Yiselle Patricia Cano);
IAVH	Instituto de Investigaciones de Recursos Biológicos "Alexander von Humboldt", Villa de Leyva, Colombia (Jhon Cesar Neita);
MPUJ	Pontificia Universidad Javeriana, Bogotá, Colombia (Igor Dimitri Forero, Giovanny Fagua);
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (Sônia Casari, Antonio Santos-Silva);
UARC	Universidad del Atlántico, Puerto Colombia, Colombia (Neis José Martínez).

Photographs were taken with a Canon EOS Rebel T3i DSLR camera, Canon MP-E 65mm f/2.8 1–5× macro lens, controlled by Zerene Stacker focus stacking software. Measurements were taken in "mm" using a measuring ocular Hensoldt/Wetzlar - Mess 10 in the Leica MZ6 stereomicroscope, also used in the study of the specimens. References and geographical distributions were ascertained in Martínez (2000), Monné (2018) and Tavakilian and Chevillotte (2018) catalogs.

Results

Cerambycidae Latreille, 1802
Cerambycinae Latreille, 1802
Eburiini Blanchard, 1845

***Beraba anae* sp. n.**
http://zoobank.org/8E564587-C14F-4F52-8D96-14D8AB7CDA29
Figs 1–5

Type material. Holotype female from Colombia, Bolívar: San Jacinto (Reserva La Flecha, 324 m, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 15.IV.2018, García, K coll., UV light trap, MPUJ_ENT 0064073 (MPUJ). Paratype, male from Colombia, Bolívar: San Jacinto (Reserva La Flecha, 324 m, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 15.IV.2018, García, K coll., white light trap (UARC).

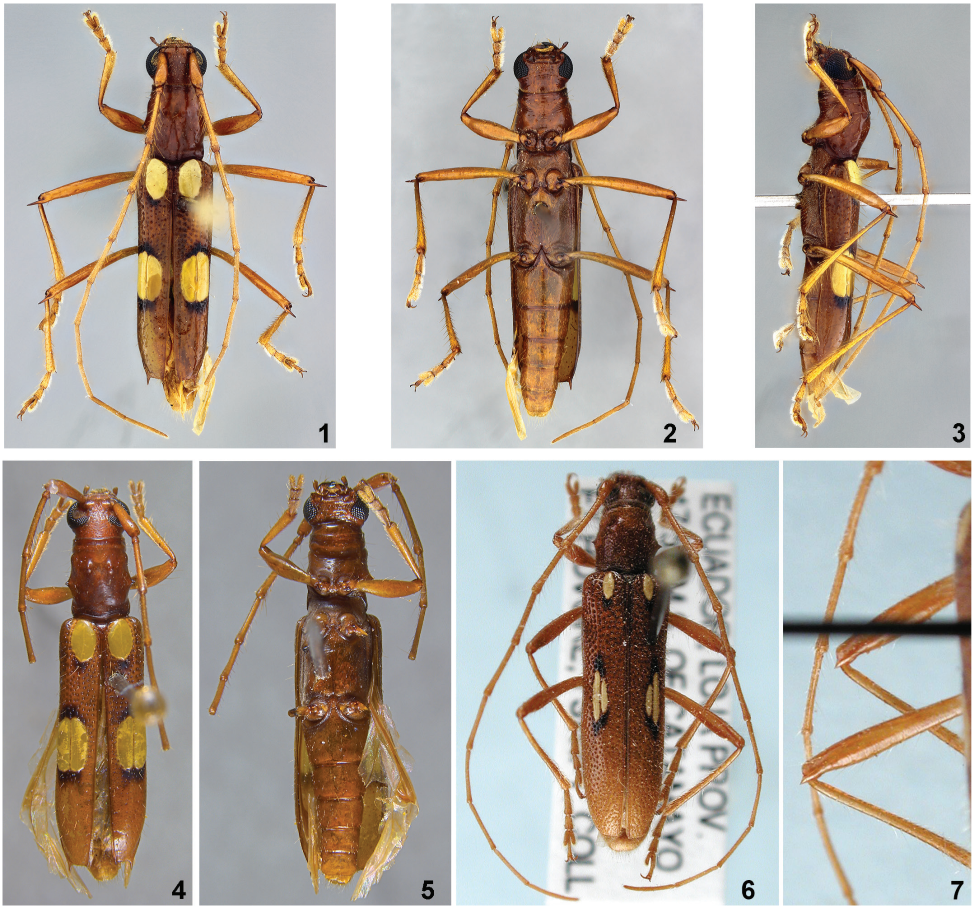
Diagnosis. Surface of pronotum smooth with pronotal tubercles of same color as remainder; eburneous callosities subrounded, posterior ones placed at same level and subequal in size; elytral costae absent; meso- and metafemora with a long spine; elytral apex truncate, with spine at outer margin.

Description. ***Female.*** Integument brownish orange. Apex of lateral tubercles of prothorax darker. Antennae, femora and tibiae slightly lighter. Scutellum brown. Posterior region of anterior eburneous callosity and, anterior and posterior region of posterior eburneous callosities black.

Body covered with long, erect sparse setae, denser at inner face of protibiae, protarsomeres and basal antennomeres.

Head. Upper ocular lobes well separated, distance between them about 4 times width of upper lobe. Antennae exceeding elytral apices at antennomere VIII. Antennal formula (ratio) based on length of antennomere III: scape = 0.73; pedicel = 0.15; IV = 0.84; V = 0.82; VI = 0.82; VII = 0.82; VIII = 0.80; IX = 0.75; X = 0.64; XI = 0.76.

Thorax. Prothorax (including lateral tubercles) slightly longer than wide. Sides of prothorax with tubercles distinct, acute at apex; antemedian gibbosity slightly elevated. Surface of pronotum smooth, with sparse shallow punctures, and a few sparse long setae arising from each puncture. Pronotum with two anterior tubercles weakly elevated, rounded at apex, and a centro-longitudinal slightly elevated gibbosity. Prosternum smooth with a few sparse long erect setae. Prosternal process expanded at apex, width at narrowest point equal to one fifth of procoxal cavity width. Prosternal process, meso and metaventrite covered with dense goldish pubescence, denser and longer at lateral regions. Elytra about three times longer than prothorax; surface with moderately dense, coarse punctures on anterior half, finer and shallow toward apex. Each elytron with 3 eburneous callosities: one anterior, elliptical; two posterior slightly elongated, subequal, about one fifth of elytral length, not distinctly separated, external starting



Figures 1–7. 1–5 *Beraba anae* sp. nov.: **1** dorsal view, holotype female **2** ventral view, holotype female **3** lateral view, holotype female **4** dorsal view, paratype male **5** ventral view, paratype male **6–7** *Beraba iuba* Martins, 1997.

slightly ahead of inner one; elytral costae absent. Apex of elytra truncate, with external spine, and a very small sutural spicule.

Abdomen. Ventrites finely, sparsely punctate, sparser on median region; with a few long, sparse whitish setae. Apex of ventrite V slightly emarginate.

Variability. In the paratype (male), the posterior eburneous callosities start at the same point. The ventrite V is shorter and square-shaped in males, with apex truncate.

Measurements. Holotype female: Total length, 10.6; prothorax length, 2.4; prothorax width at its widest point, 2.1; elytral length, 7.0; humeral width, 2.4. Paratype male: Total length, 11.3; prothorax length, 2.3; prothorax width at its widest point, 2.0; elytral length, 7.0; humeral width, 2.2.

Etymology. The species epithet is in honor of Ana López Guerrero, mother of the first author, in appreciation of her love and support through all my life, the reason for all of my achievements.

Discussion. *Beraba anae* sp. n. is similar to *B. iuba* Martins, 1997 (Figs 6–7) and *B. moema* Martins, 1997 in having only one elliptical eburneous callosity at the anterior region of each elytron, tubercles of the pronotum concolor with remaining surface and posterior eburneous callosities starting at the same level. *Beraba anae* sp. n. differs from *B. iuba* in having the posterior eburneous callosities elliptical in shape and subequal in size (in *B. iuba,* the posterior callosities are more elongated and the inner one is shorter than the external one), spined elytral apex (unarmed in *B. iuba*), and in the long meso- and metafemoral spines, longer than the scape (shorter than the scape in *B. iuba*). *Beraba anae* sp. n. differs from *B. moema* in the surface of the pronotum smooth, eburneous callosities narrowed and subrounded, posterior callosities with similar size, elytral costae absent, and elytral apex truncate. In *B. moema*, the surface of pronotum is coarsely punctuate, eburneous callosities are narrowed with the posteroexternal at least twice length of the internal, the elytral costae are visible, and the elytral apex is obliquely truncate.

Beraba angeli sp. n.

http://zoobank.org/596B3878-6A51-4F68-B659-1CAB4D72B47E

Figs 8–11

Type material. Holotype male from Colombia, Bolívar: San Jacinto (Reserva La Flecha, 324 m, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 16.IV.2018, García, K. coll., white light trap, MPUJ_ENT 0064074 (MPUJ). Paratype, male from Colombia, Bolívar: San Jacinto (Reserva La Flecha, 324 m, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 15.IV.2018, García, K. coll., UV light trap (UARC).

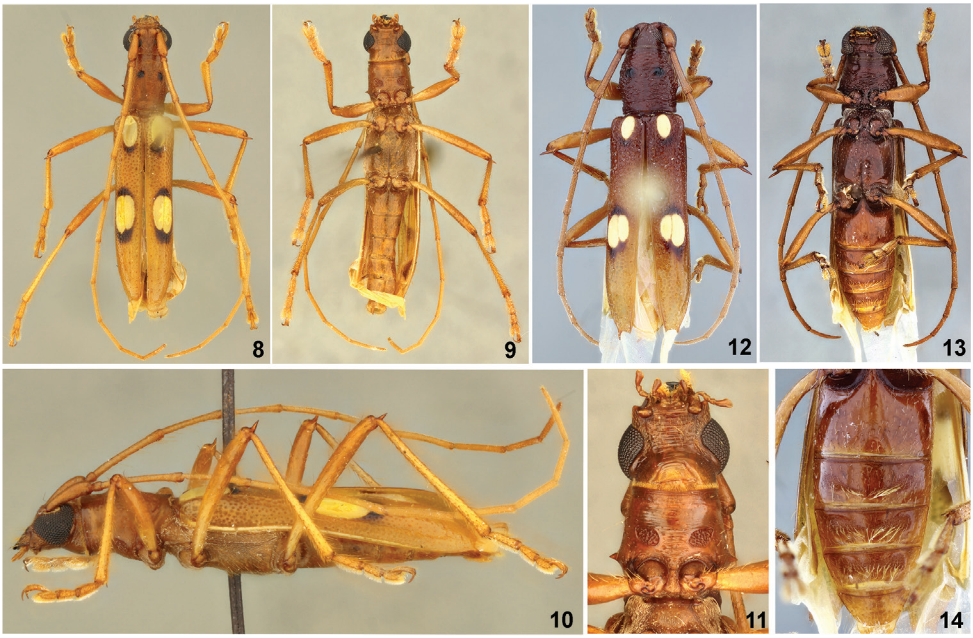
Diagnosis. Surface of pronotum with wrinkles; pronotal tubercles black and well-elevated; males with sexual punctation on prosternum; femoral spines of same color as remainder; eburneous callosities with similar size; elytral apex with external spine.

Description. ***Male.*** Integument brownish orange, legs slightly lighter. Pronotal tubercles, posterior region of anterior eburneous callosity, and anterior and posterior region of posterior eburneous callosities black.

Body covered with long, erect and sparse yellowish setae.

Head. Upper ocular lobes well separated, distance between them about 3 times width of upper lobe. Antennae exceeding elytral apices at antennomere VIII. Antennal formula (ratio) based on length of antennomere III: scape = 0.57; pedicel = 0.11; IV = 0.83; V = 0.83; VI = 0.83; VII = 0.80; VIII = 0.74; IX = 0.69; X = 0.63; XI = 0.80.

Thorax. Prothorax (including lateral tubercles) longer than wide. Sides of prothorax with tubercles distinct and acute at apex. Surface of pronotum coarsely punctate with transverse wrinkles, more distinct on posterior half, with a few long sparse whitish setae. Pronotum with two anterior tubercles well elevated, rounded at apex, and a centro-longitudinal slightly elevated gibbosity. Prosternum with transverse sulcus, glabrous, with long yellowish setae, finely transversely striate, coarsely punctate on posterior half, with two well-defined areas of sexual punctation. Prosternal process expanded at apex, width at narrowest point equal to one fourth of procoxal cavity width. Pros-



Figures 8–14. 8–11 *Beraba angeli* sp. nov., holotype, male: **8** dorsal view **9** ventral view **10** lateral view **11** detail of prosternum. **12–14** *Beraba marica* Martins & Galileo, 1999: **12** dorsal view **13** ventral view **14** detail of ventrites.

ternal process, meso- and metaventrite covered with dense golden pubescence, denser and longer laterally. Elytra about three times longer than prothorax; surface with moderately dense, coarse punctures on anterior half, finer and shallower toward apex. Each elytron with 3 subrounded eburneous callosities: one anterior; two posterior subfused, subequal, starting at same level, external slightly curved. Elytral costae absent. Apex of elytra truncate, with external spine and dentiform projection at sutural angle.

Abdomen. Ventrites finely sparsely punctate, sparser on median region; with a few moderately long, sparse yellowish setae. Apex of ventrite V truncate.

Measurements. Holotype male: total length, 9.5; prothorax length, 1.9; prothorax width at its widest point, 1.7; elytral length, 6.3; humeral width, 2.0. Paratype male: total length, 11.9; prothorax length, 2.5; prothorax width at its widest point, 2.5; elytral length, 8.1; humeral width: 2.7.

Etymology. The species epithet is in honor of Angel García Hernandez, father of the first author, as a thank you for all the support, love and happiness he has given to me.

Discussion. *Beraba angeli* sp. n. is similar to *B. marica* Galileo & Martins, 1999 (Figs 12–14) and *B. inermis* Martins & Galileo, 2002 in having only one elliptical eburneous callosity on the anterior region of each elytron, tubercles of the pronotum black, and surface of the pronotum only with wrinkles or with wrinkles and some interspersed punctures. *Beraba angeli* sp. n. differs of *B. marica* in having the pronotal tubercles distinctly elevated, prosternum with areas of sexual punctation (Fig. 11), and the male ventrites not modified (in *B. marica* the tubercles are slightly elevated, prosternum does not show sexual punctation, and ventrites II–IV show depressed areas with long yellowish setae on the posterior margin in males, as in Fig. 14). *Beraba angeli* sp. n. differs of *B. inermis* in the posterior eburneous callosities of similar size, and apex of the elytra with an external spine (in *B. inermis,* the posteroexternal eburneous callosities is, at least, twice the length of internal, and the external apex of the elytra is unarmed).

According to the most recent key to species of *Beraba* (Botero, 2015), the two new species can be inserted as follows:

7(4) Tubercles of pronotum of same color as remainder of pronotum **8**
– Tubercles of pronotum black (contrasting in color from remainder of pronotum) **11**
8(7) Posteroexternal eburneous callosity of elytra placed at beginning of apical third and distant internal callosity. Brazil (Rio de Janeiro) .... ***B. angusticollis* (Zajciw, 1961)**
– Posterior eburneous callosities of elytra placed at same level **9**
9(8) Meso- and metafemora with short inner spine, shorter than length of scape; elytral apex unarmed (Figs 6–7). Colombia (Bolívar), Ecuador (Pichincha) .... ***B. iuba* Martins, 1997**
– Meso- and metafemora with long inner spine, longer than length of scape; elytral apex with spines **10**
10(9) Surface of pronotum coarsely punctate; eburneous callosities narrowed, posteroexternal eburneous callosity at least twice length of internal; elytral costae visible; elytral apex obliquely truncate. Ecuador (El Oro, Guayas, Manabi) .... ***B. moema* Martins, 1997**
– Surface of pronotum smooth; eburneous callosities wider, subrounded; posterior eburneous callosities with similar size; elytral costae absent; elytral apex truncate (Figs 1–5). Colombia (Bolívar) .... ***B. anae* sp. n.**
11(7) Apex and spines of femora of same color as remainder **12**
– Apex and spines of femora black, contrasting with adjacent color **16**
12(11) Surface of pronotum only with wrinkles or with wrinkles and some interspersed punctures **13**
– Surface of pronotum only with punctures, without wrinkles **15**
13(12) Posteroexternal eburneous callosities at least twice length of internal; external apex of elytra unarmed. Colombia (Amazonas, Bolívar, Cundinamarca, Valle del Cauca) .... ***B. inermis* Martins & Galileo, 2002**
– Posterior eburneous callosities with similar size; apex of elytra with external spine **14**
14(13) Pronotal tubercles slightly elevated; prosternum without sexual punctation; ventrites II-IV of males with depressed areas and with long yellowish setae on posterior margin of those areas (Figs 12–14). Colombia (Atlántico, Bolívar, Magdalena, Santander) .... ***B. marica* Galileo & Martins, 1999**
– Pronotal tubercles distinctly elevated; prosternum with areas of sexual punctation (Fig. 11); ventrites of males not modified (Figs 8–11). Colombia (Bolívar) .... ***B. angeli* sp. n.**

15(12) Basal eburneous callosities narrowed and elongated; elytral costae visible behind posterior callosities. Bolivia (Santa Cruz) .... ***B. tate* Galileo & Martins, 2010**

– Basal eburneous callosities short and subrounded; without elytral costae visible behind posterior callosities (Figs 15–19). Colombia (Bolívar), Venezuela........ ***B. limpida* Martins, 1997**

16(11) Pronotum rugosely punctate **17**

– Pronotum smooth or only with microsculpture **19**

17(16) Scape black or darker than flagellomeres; prothorax subparallel-sided; eburneous callosities elongate and thin. Brazil (Goiás, Maranhão, Mato Grosso, Piauí) .... ***B. decora* (Zajciw, 1961)**

– Scape with same color as flagellomeres; prothorax curved at sides or narrowed toward anterior margin; eburneous callosities elliptical **18**

18(17) Lateral tubercle of prothorax small; posterior eburneous callosities starting anteriorly at same level; apex of elytra with black area. French Guiana .... ***B. odettae* Martins & Galileo, 2008**

– Lateral tubercle of prothorax long and acute; posteroexternal eburneous callosity starting behind internal one; apex of elytra without black area. Peru.... ***B. spinosa* (Zajciw, 1967)**

19(16) Prothorax longer than wide, anterior region of epipleura without projection, metafemora exceeding elytral apex. Brazil (Amazonas), French Guiana .... ***B. cauera* Galileo & Martins, 1999**

– Prothorax as long as wide; anterior region of epipleura with projection, metafemora not exceeding elytral apex. Brazil (Mato Grosso do Sul), Bolivia (Cochabamba, Santa Cruz), Paraguay .... ***B. cheilaria* (Martins, 1967)**

Beraba limpida Martins, 1997

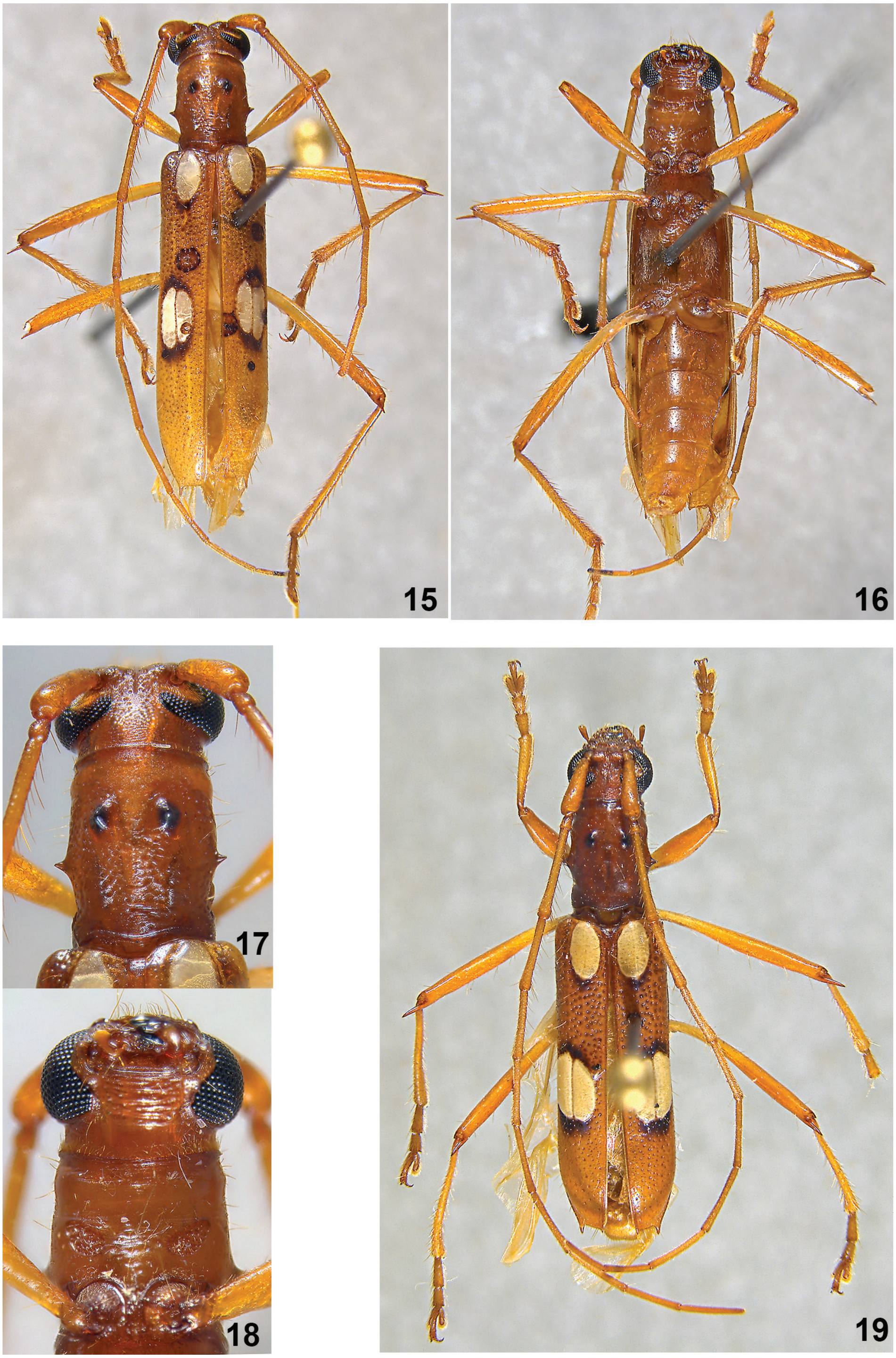
Figs 15–19

Material examined. Colombia, Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 27.IV.2017, I. Mendoza coll., light trap (UARC). Venezuela, Aragua: El Limón, 1 male, 23.V.1997, F. Fernandez coll., mercury light (MZSP).

Redescription. Male. Integument dorsally orange, brownish orange ventrally. Posterior region of head, pronotum, lateral tubercles of prothorax and legs brownish orange. Elytra and scutellum yellowish orange. Pronotal tubercles, posterior region of anterior eburneous callosities and, region around posterior eburneous callosities black.

Body covered with long, erect, sparse setae, denser on inner surface of tibiae, tarsomeres and basal antennomeres.

Head. Posterior region of head, scape and basal antennomeres with dense punctuation. Distance between upper lobes about three times width of upper lobe. Antennae exceeding elytral apices at apex of antennomere VIII. Prothorax (including lateral tubercles) 1.14 times longer than wide; lateral tubercles distinctly visible, acute at apex.



Figures 15–19. *Beraba limpida* Martins, 1997. **15–18** male: **15** dorsal view **16** ventral view **17** detail of pronotum **18** detail of prosternum **19** female, dorsal view.

Thorax. Surface of pronotum with coarse dense punctuation; with two anterior elevated tubercles rounded at apex. Prosternum smooth on central region, with long, erect setae and a few punctures, with evident sexual punctation at lateral sides concentrated on subrounded areas (Figs 16, 18). Coxae and mesoventral process covered with dense whitish pubescence. Meso- and metaventrite with long erect setae and covered with dense whitish pubescence laterally. Femora and tibiae fine and long; apex of meso- and meta-femora with long inner spine.

Elytra about 3.5 times longer than prothorax; surface with dense, coarse punctures basally, finer and shallow toward apex. Each elytron with three eburneous callosities: one basal, elliptical; two posterior, slightly elongated, inner one slightly smaller than external one, not distinctly separated from each other. Posteroexternal callosity about one fifth of elytral length, starting ahead of internal one. Elytral costae absent. Apex of elytra with external long spine, about 0.8 times as long as the pedicel and with acute sutural projection.

Measurements. Male. Total length, 10.3; prothorax length, 2.1; prothorax width at its widest point, 1.9; elytral length, 7.3; humeral width, 2.0.

Discussion. *Beraba limpida* was described by Martins (1997) based on a single female specimen, and until now the male remained unknown. Among the known males of *Beraba*, just one species has sexual punctation, *B. piriana* Martins, 1997. The sexual punctation in this species covers the entire prosternum and extends to the lateral region of the pronotum. Herein, we report sexual punctation for the first time in other two species of *Beraba*: *B. limpida* and *B. angeli* sp. n. In those species, the sexual punctation covers the entire surface of the pronotum, and is concentrated in subrounded areas on sides of the prosternum (Figs 9, 11, 16, 18).

One specimen of *Beraba tate* Galileo & Martins, 2010 was illustrated by Galileo et al. (2008) as being *B. limpida*. Later, Galileo and Martins (2010) recognized that this specimen belongs to a new species, and described it as *B. tate*. However, Galileo et al. (2008) remains wrongly listed in the references on *B. limpida* (see Monné 2018; Tavakilian and Chevillotte 2018). In order to correct this error, we point out that this reference should appear on *B. tate*.

New geographical records

Beraba inermis Martins & Galileo, 2002

Geographical distribution. Colombia (Cundinamarca, Valle del Cauca). New department records are added: Amazonas and Bolívar (Colombia).

Specimens examined. Colombia, Amazonas: Leticia, 1 female, 1.V.2001, Sarmiento Paula coll., Andes-E1162 (ANDES-E); Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 27.IV.2017, I. Mendoza coll., light trap (UARC).

Beraba iuba Martins, 1997

Geographical distribution. Ecuador. A new country record from Colombia (Bolívar) is added.

Specimen examined. Colombia, Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 27.IV.2017, I. Mendoza coll., light trap (UARC).

Beraba limpida Martins, 1997

Geographical distribution. Venezuela. A new country record from Colombia (Bolívar) is added.

Specimens examined. Colombia, Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 1 female, 27.IV.2017, I. Mendoza coll., light trap (UARC).

Beraba marica Galileo & Martins, 2000

Geographical distribution. Colombia (Bolívar). New department records are added: Atlántico, Magdalena and Santander (Colombia).

Specimen examined. Colombia, Atlántico: Usiacurí; (Reserva Campesina La Montaña, 10°46'2.6"N, 75°0.2'34"W, tropical dry forest), 1 male, 14.V.2018, K. García coll., UV light trap (UARC); Magdalena: (Road Minka-Cerro Kennedy, 11°07'31"N, 74°06'07"W, 1000 m), 1 female, 7–8.VI.2018, V. Sinyaev coll. (MZSP); Santander: Carmen de Churucí (Vereda La Belleza, Finca Santiago, Campamento, 06°34'49.5"N, 73°34'15.1"W, 801 m, Bosque húmedo tropical), 18–25.II.2018, Neita, J. C. coll., “captura manual”, CAS–00039 (IAVH).

Beraba piriana Martins, 1997

Geographical distribution. Panama, Colombia (Magdalena). New department records are added: Atlántico and Bolívar (Colombia).

Specimens examined. Colombia, Atlántico: Baranoa (10°47'56.04"N, 74°55'19.56"W), 2 males, 4.IV.2017, I. Mendoza coll., manual capture (UARC); Usiacurí; (Reserva Campesina La Montaña, 10°46'2.6"N, 75°0.2'34"W, tropical dry forest), 1 male, 1 female, 12.V.2018, K. García coll., white light trap (UARC); 1 female, 12.V.2018, K. García coll., UV light trap (MZSP); 1 female, 12.V.2018, K. García coll., manual capture (UARC); Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 2 males, 1 female, 16.IV.2018, K. García col., UV light trap (UARC); Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 27.IV.2017, I. Mendoza coll., light trap (UARC); Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 female, 6.VI.2016, J. Barraza coll., van someren-rydon (UARC).

Eburodacrys asperula Bates, 1880

Geographical distribution. Honduras, Mexico (Veracruz), Guatemala, Costa Rica, Panama, Venezuela. A new country record from Colombia (Magdalena) is added.

Specimens examined. Colombia, Magdalena (Road Minka-Cerro Kennedy, 11°07'31"N, 74°06'07"W, 1000 m), 1 male, 1 female, 7–8.VI.2018, V. Sinyaev coll. (MZSP).

Eburodacrys callixantha Bates, 1872

Geographical distribution. Honduras, Mexico (Jalisco, Oaxaca), Nicaragua, Panama, Venezuela. A new country record from Colombia (Magdalena) is added.

Specimen examined. Colombia, Magdalena: San Pablo; (La Clarita, 10°52'37.3"N, 74°08'03.9"W), 3 males, 28.V.2017, I. Mendoza and L. Martinez coll., light trap (UARC).

Eburodacrys coalescens Bates, 1884

Geographical distribution. Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama. A new country record from Colombia (Atlántico) is added.

Specimens examined. Colombia, Atlántico: Usiacurí; (Reserva Campesina La Montaña, 10°46'2.6"N, 75°0.2'34"W, tropical dry forest), 2 females, 12.V.2018, K. García coll., white light trap (MZSP, UARC).

Eburodacrys havanensis Chevrolat, 1862

Geographical distribution. Cuba, Mexico, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Cundinamarca, Huila, Meta, Putumayo, Quindío, Santander, Tolima), Venezuela, Bolivia (Beni, Santa Cruz), Brazil (Mato Grosso, Mato Grosso do Sul, Goiás, Distrito Federal, Maranhão, Piauí, Pernambuco, Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul), Paraguay. A new department record from Bolívar (Colombia) is added.

Specimens examined. Colombia, Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 13.IV.2018, K. García coll., white light trap (UARC); 1 male, 27.IV.2017, I. Mendoza coll., light trap (UARC).

Eburodacrys moruna Martins, 1997

Geographical distribution. Colombia (Magdalena). New department records are added: Atlántico and Bolívar (Colombia).

Specimens examined. Colombia, Atlántico: Usiacurí (Reserva Campesina la Montaña, 10°46'2.6"N, 75°0.2'34"W, tropical dry forest), 1 female, 14.VI.2018, J. Sarmiento coll., pitfall (UARC). Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 female, 27.IV.2017, I. Mendoza coll., light trap (UARC).

Eburodacrys santossilvai Botero, 2017

Geographical distribution. Venezuela. A new country record from Colombia (Atlántico, Bolívar) is added.

Specimens examined. Colombia, Atlántico: Usiacurí; (Reserva Campesina La Montaña, 10°46'2.6"N, 75°0.2'34"O, tropical dry forest), 1 female, 14.V.2018, K. García coll., UV light trap (UARC); Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 female, 16.III.2018, K. García coll., UV light trap (UARC); 2 males, 27.IV.2017, I. Mendoza coll., light trap (UARC).

Eburodacrys triocellata (Stal, 1857)

Geographical distribution. Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Colombia (Antioquia, Arauca, Boyacá, Caldas, Cesar, Cundinamarca, Magdalena, Meta, Tolima, Valle del Cauca), Venezuela. New department records are added: Amazonas, Atlántico and Bolívar (Colombia).

Specimen examined. Colombia, Amazonas: Leticia, female, 1.V.2001, Daniel Matute coll., Andes-E384 (ANDES-E); Atlántico: Usiacurí; (Reserva Campesina La Montaña, 10°46'2.6"N, 75°0.2'34"W, tropical dry forest), 1 female, 15.II.2018, K. García coll., white light trap (UARC); 1 female, 12.V.2018, K. García coll., manual capture (UARC); 2 females, 12.V.2018, K. García coll., white light trap (UARC); Bolívar: San Jacinto (Reserva La Flecha, 09°51'12.4"N, 75°10'41.4"W, tropical dry forest), 1 male, 1 female, 16.IV.2018, K. García coll., UV light trap (UARC); 2 male, 5 females, 27.IV.2017, I. Mendoza coll., light trap (UARC).

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RESEARCH ARTICLE

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New dustywings (Neuroptera, Coniopterygidae) from mid-Cretaceous amber of Myanmar reveal spectacular diversity

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Abstract

Two new genera and species of Coniopterygidae (Neuroptera) are described and illustrated from mid Cretaceous (Cenomanian) amber of Myanmar. *Mulleroconis hyalina* **gen. n. et sp. n.**, attributed to the Coniopteryginae, bears a unique combination of venation characters and an abdomen without plicatures. The second new genus, attributed to the Aleuropteryginae, i.e. *Palaeoconis azari* **gen. n. et sp. n.**, displays a unique pattern of crossveins 1m-cua and 2mp2-cua, with the latter crossing the pigmented spot. A check-list of all fossil genera and species of Coniopterygidae is provided.

Keywords

Upper Cretaceous, Cenomanian, Burmite, Insecta, Neuropterida, wing venation

Introduction

Neuroptera is one of few insect orders with a remarkably rich fossil history and spectacular diversity of morphotypes during the Mesozoic. The two early Permian families Permithonidae and Permoberothidae are currently considered as the stem groups of the clade Eidoneuroptera (Neuroptera + Megaloptera) (Prokop et al. 2015; Engel et al. 2018). Current views of phylogeny based on molecular and morphology datasets support the family Coniopterygidae as a sister group to Euneuroptera comprising all remaining recent families of Neuroptera (Winterton et al. 2010; Wang et al. 2017; Winterton et al. 2017, 2018; Randolf et al. 2017; Engel et al. 2018).

Coniopterygidae (dustywings) are an unusual family of Neuroptera with minute body-size, strongly reduced venation and, especially, wings covered by a waxy secretion. Dustywings are predators with larvae and adults feeding on mites, aphids, and sternorrhynchans. Currently, the family comprises 571 species assigned to 23 genera (Engel et al. 2018). They are divided into the three Recent subfamilies: Aleuropteryginae, Coniopteryginae, and Brucheiserinae, along with a single fossil one, Cretaconiopteryginae (Liu and Lu 2017). This current subdivision into four subfamilies needs to be tested by a global phylogenetic analysis of the fossil and extant taxa of this family, but it is out of the scope of the present paper. Meinander (1975) described the oldest *Juraconiopteryx zherichini* assigned to Coniopterygidae from the Upper Jurassic of Karatau in Kazakhstan, while the family is supposed to have diverged from the other Neuroptera during the Late Permian (Winterton et al. 2018). However, the record of dustywings is mainly known from amber inclusions of the following localities (see Table 1): Lower Cretaceous (Lebanon – Hammana (Neocomian), Spain – Cantabria (Albian), France – Charente – Maritime (Albian); Upper Cretaceous (Myanmar – Hukawng Valley (Cenomanian), U.S.A. – New Jersey, (Turonian), Russia – Taimyr Peninsula, (Cenomanian to Santonian), Canada – Alberta (Campanian); Eocene – India – Gujarat (Ypresian), France – Oise, Le Quesnoys (Ypresian), Baltic (Late Eocene), Ukraine – Rovno (Late Eocene); and Miocene – Dominican Republic (Burdigalian). For a long time, the Late Cretaceous amber from New Jersey was known for its high richness of neuropteran diversity (Grimaldi 2000). However, due to extensive sampling of Burmese amber during last decades it was revealed that it contains a surprisingly diverse and abundant neuropteran fauna currently attributed to 21 families, including Coniopterygidae (Grimaldi et al. 2002; Makarkin 2016; Ross 2018). Despite the fact, that the inclusions of dustywings in Burmese amber are considerably rare, six species assigned to five genera have been described so far (Ross 2018). The majority of assigned genera belong to the subfamily Aleuropteryginae. The subfamily Coniopteryginae has only two recorded genera and Brucheiserinae is still without any fossil evidence (Perrichot et al. 2014; Engel 2004, 2016; Makarkin 2016; Liu and Lu 2017, see Table 1).

Herein we report two new genera and species of Aleuropteryginae and Coniopteryginae from the Cenomanian amber of Myanmar. These new taxa are based on morphological characters with special attention to the wing venation and structure of the antennae.

Table 1. List of extinct genera and species of Coniopterygidae.

MESOZOIC	
JURASSIC	
Subfamily Aleuropteryginae	
Juraconiopteryx Meinander, 1975	Callovian/Oxfordian; Kazakhstan
†*J. zherichini* Meinander, 1975	
CRETACEOUS	
Subfamily Aleuropteryginae	
Achlyoconis Engel, 2016	Cenomanian; Myanmar
†*A. heptatrichia* Engel, 2016	
Alboconis Nel et al., 2005	Albian; France
†*A. cretacica* Nel et al., 2005	
Apoglaesoconis Grimaldi, 2000	Turonian; U.S.A.
†*A. ackermani* Grimaldi, 2000	
†*A. cherylae* Engel, 2002	Turonian; U.S.A.
†*A. luzzii* Grimaldi, 2000	Turonian; U.S.A.
†*A. swolenskyi* Grimaldi, 2000	Turonian; U.S.A.
Garnaconis Perrichot & Nel in Perrichot et al., 2014	Turonian; France
†*G. dupeorum* Perrichot & Nel, 2014	
Glaesoconis Meinander, 1975	Cenomanian; Myanmar
†*G. baliopteryx* Engel, 2004	
†*G. cretica* Meinander, 1975	Santonian; Russia
†*G. nearctica* Grimaldi, 2000	Turonian; U.S.A
†*G. popovi* Makarkin & Perkovsky, 2017	Santonian; Russia
Libanoconis Engel, 2002	Barremian; Lebanon
†*L. fadiacra* Whalley, 1980	
†*L. siberica* Makarkin & Perkovsky, 2019	Cenomanian; Russia
Palaeoconis Ružičková, Nel & Prokop, n. gen.	Cenomanian, Myanmar
†*P. azari* Ružičková, Nel & Prokop, n. sp.	
Subfamily Coniopteryginae	
Jurasiatypus Kaddumi, 2005	Albian; Jordan
†*J. cretatus* Kaddumi, 2005	
Libanosemidalis Azar et al., 2000	Barremian; Lebanon
†*L. hammanaensis* Azar et al., 2000	
Mulleroconis Ružičková, Nel & Prokop, n. gen.	Cenomanian, Myanmar
†*M. hyalina* Ružičková, Nel & Prokop, n. sp.	
Paranimboa Engel, 2016	Cenomanian; Myanmar
†*P. litotes* Engel, 2016	
†*P. groehni* Sziráki, 2016	Cenomanian; Myanmar
Phtanoconis Engel, 2004	Cenomanian; Myanmar
†*P. burmitica* Engel, 2004	
Subfamily Cretaconiopteryginae	
Cretaconiopteryx Liu & Lu, 2017	Cenomanian; Myanmar
†*C. grandis* Liu & Lu, 2017	
CENOZOIC	
Subfamily Aleuropteryginae	
Archiconiocompsa Enderlein, 1910	Priabonian; Russia
†*A. prisca* Enderlein, 1910	

Archiconis Enderlein, 1930	Priabonian; Russia
†*A.electrica* Enderlein, 1930	
Geroconiocompsa Engel, 2010	Priabonian; Russia
†*G. ostara* Engel, 2010	
Hemisemidalis Meinander, 1972	Priabonian; Poland
†*H. kulickae* Dobosz & Krzemiński, 2000	
Neoconis Enderlein, 1930	Burdigalian/Langhian; Dominican Republic
†*N. paleocaribis* Grimaldi & Engel, 2013	
Pararchiconis Nel, 1991	Rupelian; France
†*P. quievreuxi* Nel, 1991	
Spiloconis Enderlein, 1907	Burdigalian/Langhian; Dominican Republic
†*S. glaesaria* Meinander, 1998	
†*S. oediloma* Engel & Grimaldi, 2007	Burdigalian/Langhian; Dominican Republic
†*S. eominuta* Grimaldi & Engel, 2013	Ypresian; India
Subfamily Coniopteryginae	
Coniopteryx Curtis, 1834	Burdigalian/Langhian; Dominican Republic
†*C. antiquua* Engel & Grimaldi, 2007	
†*C. timidus* Hagen, 1856	Priabonian; Poland
Neosemidalis Enderlein, 1930	Holocene, Benin
†*N. enderleini* Meunier, 1910	
Parasemidalis Enderlein, 1905	Ypresian; France
†*P. eocenica* Nel et al., 2005	
†*P. sharovi* Meinander, 1975	Priabonian; Russia
Semidalis Enderlein, 1905	Priabonian; Russia
†*S. fritschi* Enderlein, 1930	

Material and methods

All herein examined specimens are preserved in Burmese amber recovered from the deposits in northern Myanmar (Hukawng Valley, Kachin) (Cruickshank and Ko 2003; Grimaldi and Ross 2017). The age of these fossiliferous layers was previously considered as Late Albian or Early Cenomanian on the basis of palynomorphs (Cruickshank and Ko 2003), and recently confirmed as the lowermost Cenomanian (98.79 ± 0.62 Ma) by radiometric analysis of zircons (Shi et al. 2012). The record from this locality has recently been reviewed by Grimaldi and Ross (2017). Contemporary investigations on various insect lineages has emphasized the tremendous diversity and disparity of the entomofauna (e.g., Grimaldi and Ross 2017), as well as its impact on an understanding of changes in Late Cretaceous biotas along with the Late Cretaceous-Paleogene faunal turnover, such as replacement by specialized angiosperm pollinators and evidence of remarkable parasitoid strategies (e.g., Grimaldi et al. 2002; Batelka et al. 2016, 2018, in press; Huang et al. 2016; Makarkin 2016).

The material was studied with Leica MZ12.5 stereomicroscope and Olympus BX40 microscope, and photographed using a Canon D550 digital camera mounted on a tripod and coupled with a MP-E 65 mm macro-lens, or attached to an Olympus BX40. The original photographs were processed using Adobe Photoshop CS4, while some images we prepared a series of focal layers which were them combined using the focus-stacking software packages Helicon Focus Pro or Zerene Stacker. The specimens reported herein are originally from the private collection of Patrick Müller, Käshofen, Germany (accession numbers abbreviated as BUB – Burmese Bernstein). All type specimens are deposited in the Museum für Naturkunde, Berlin.

Terminology of wing venation nomenclature and interpretation of veins follow Breitkreuz et al. (2017) who studied the wing venation and tracheation across the neuropteran families. Abbreviations of longitudinal veins: C – costa, ScP – subcosta posterior, R – radius, RA/ RP – radius anterior/ posterior, M – media, MA/ MP – media anterior/ posterior, Cu – cubitus, CuA/CuP – cubitus anterior/ posterior, A – anal vein.

Systematics

Order Neuroptera Linnaeus, 1758
Family Coniopterygidae Burmeister, 1839
Subfamily Coniopteryginae Burmeister, 1839

***Mulleroconis* gen. n.**

http://zoobank.org/CC3D1487-6C5F-4998-BDF4-F52D6E8731BE

Type species. *Mulleroconis hyalina* gen. et. sp. n.

Diagnosis. Forewing hyaline; one straight crossvein in proximal part of costal area; ScP2 diverges obliquely from ScP1; crossvein ra-rp absent; crossvein rp-ma undulated; M without macrosetae reaching posterior wing margin with two branches; crossvein cua-cup straight and aligned with 2cup-a1.

Etymology. The generic name is a combination collector's surname (Müller) and the Greek 'conis' meaning dust. The generic name is feminine in gender.

***Mulleroconis hyalina* gen. et. sp. n.**

http://zoobank.org/F8CCB036-E564-4C4A-94E2-3C50CD92C8E6
Figures 1, 2

Holotype. BUB 2907; lowermost Cenomanian amber (Shi et al. 2012); Myanmar, Kachin, Hukawng Valley; preserved in a polished, transparent yellow piece of amber (5.68 × 5.00 × 1.09 mm), deposited in the Museum für Naturkunde, Berlin (ex. coll. Patrick Müller). The holotype is in amber syninclusion with one representative of the Auchenorrhyncha.

Etymology. The specific epithet is after the hyaline forewing membrane.

Diagnosis. As for the genus (*vide supra*).

Description. Male. Body length ca. 1.17 mm (measured from tip of head to tip of genitalia). Head poorly preserved, only the last three segments of one maxillary palp

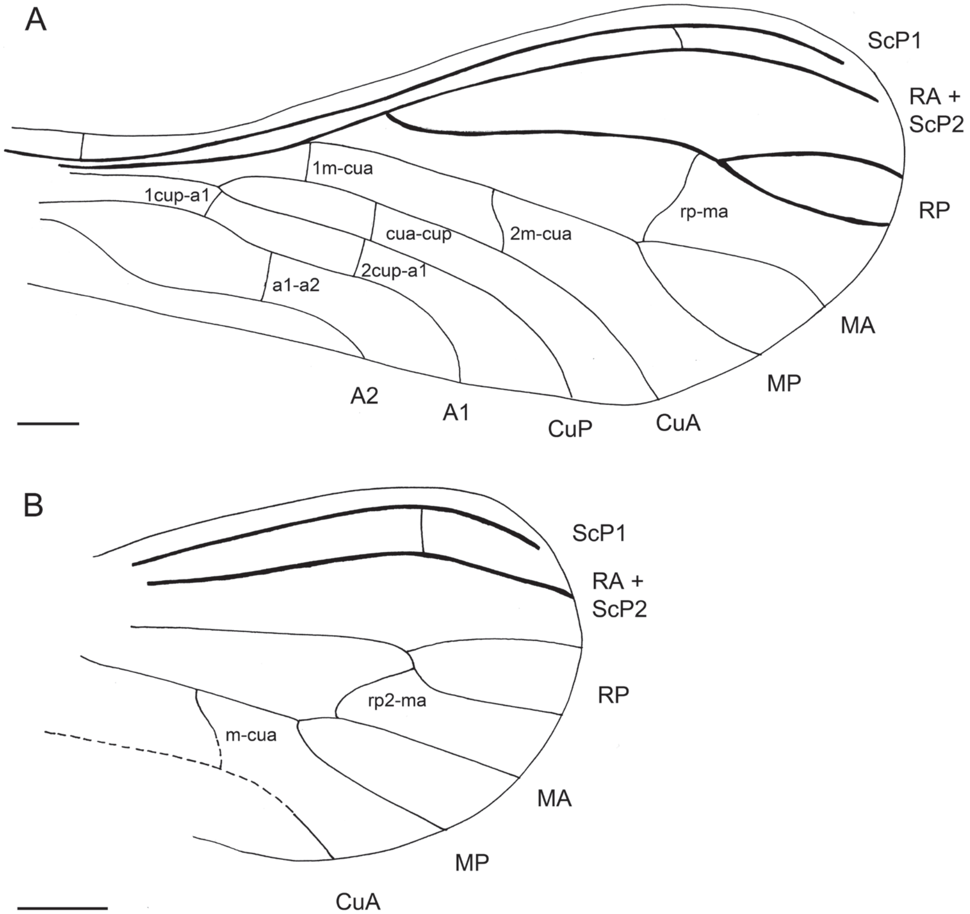

Figure 1. *Mulleroconis hyalina* gen. et. sp. n., holotype BUB 2907. **A** Drawing of left fore wing **B** drawing of left hindwing. Scale bar: 100 μm.

are visible and the terminal segment is distinctly broader and longer than two remaining. Length of terminal palpomere ca. 0.09 mm. Thorax length ca. 0.28 mm.

Forewing ca. 1.46 mm long, ca. 0.65 mm wide; ScP1 long and parallel to costal margin; Scp2 present; division of R into RA and RP at about one-third wing length; RA simple distally connected to ScP2, parallel to ScP1; RP forked; rp-ma markedly sinuate, near the fork RP1 and RP2, connected to MA; stem of M running close to stem of R, briefly connecting each other, M distally branched into MA and MP, without stiff setae; crossveins 1m–cua and 2m-cua present, 1m–cua near the base of wing, between M and CuA, 2m-cua slightly sinuate, between M and CuA, situated slightly behind midwing; CuP separated from CuA near the base of wing; cua-cup present, located at level of division veins RA and RP; crossveins 1cup-a1 and 2cup-a1 present, 1cup-a1 connected to CuP near to fork of CuA and CuP, 2cup-a1 almost aligned with cua-cup; A1 and A2 clearly connected near the base of wing, a1-a2 present. Hindwing

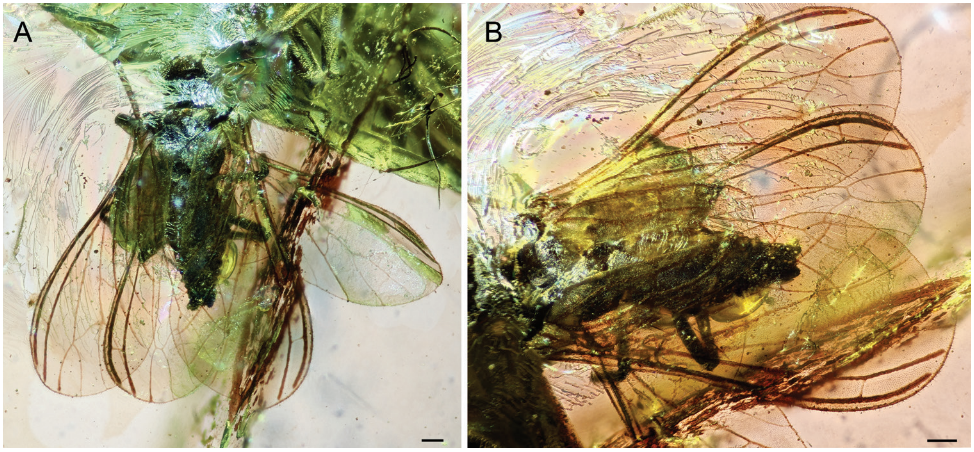

Figure 2. *Mulleroconis hyalina* gen. et. sp. n. holotype BUB 2907. **A** Habitus dorsally **B** wing venation – detail. Scale bar: 100 µm.

ca. 1.25 mm long, ca. 0.55 mm wide with venation very similar to forewing, differing in position of sinuate crossvein rp2-ma; crossvein m-cua partially preserved and basal part of wing with hardly recognizable venation pattern. Legs slender; fore femora (only left femur is visible) a bit shorter and wider than femora of second and third pair of legs; tibias covered with setae; tarsi five-segmented; first tarsomere distinctly longer than remaining tarsomeres; fifth tarsomere elongated with two apical claws. Abdomen large, length 0.64 mm, width 0.22 mm, including genitalia, with widest part approximately in middle of its length, greatly tapering to narrow apical segments; abdominal plicatures absent. Genital structures hardly discernible, presumably below projection of gonarcus, ultimate apices of parameres visible from dorsal view.

Discussion. *Mulleroconis* gen. n. can be attributed to the Coniopteryginae based on the following combination of forewing characters: M is bifurcate (a trait occurring in almost all members of this subfamily) (Makarkin and Perkovsky 2019), the absence of two macrosetae on the media, the presence of only one crossvein between RP and M (in our species between RP and MA), and the absence of the abdominal plicatures. The Mesozoic record of Coniopteryginae currently comprises four genera, i.e. *Jurasiatypus* Kaddumi, 2005; *Libanosemidalis* Azar et al., 2000; *Paranimboa* Engel, 2016 and *Phthanoconis* Engel, 2004 (see list below). All four genera share the presence of two basal crossveins in the costal space, unlike *Mulleroconis* gen. n. In addition, *Libanosemidalis*, *Paranimboa* and *Jurasiatypus* differ from *Mulleroconis* gen. n. in the presence of one crossvein between RA (ScP2) and RP. *Libanosemidalis,* described from the Lower Cretaceous amber of Lebanon, differs from *Mulleroconis* gen. n. in the presence of rp2-ma while in *Mulleroconis* gen. n. the crossvein rp-ma is shifted proximally, followed by a single crossvein between M and CuA and the presence of crossvein a2 connecting A2 and the hind margin of the wing (Azar et al. 2000). *Paranimboa* and *Phthanoconis* are both known from the Cenomanian amber of Myanmar (Engel 2016; Sziráki 2016, 2017). *Paranimboa* has a simple RP unlike in *Mulleroconis* gen. n. where the RP has two terminal branches. Furthermore, it differs in the position of the crossvein between RP and M and in the position of crossvein 1cup-a1 which is branching off from point where Cu is divided into CuA and CuP and in the presence of crossvein a2 (Engel 2016; Sziráki 2016, 2017).

Phthanoconis and *Jurasiatypus* both differ from *Mulleroconis* gen. n. in the presence of a single crossvein between M and CuA and in the complete absence of crossveins between CuA and CuP, CuP and A1, as well as between A1 and A2. Moreover, *Phthanoconis* differs from *Mulleroconis* gen. n. in the absence of a crossvein between RP and M (Engel 2004). *Jurasiatypus* was based on single found specimen (holotype) from the Lower Cretaceous amber of the Kurnub in Jordan (Kaddumi 2005). It differs from *Mulleroconis* gen. n. in the position of the crossvein between RP2 and MA (Kaddumi 2005).

Subfamily Aleuropteryginae Enderlein, 1905

Palaeoconis gen. n.

http://zoobank.org/D2E45555-5EB3-4C36-A9D9-D448DD3D6675

Type species. *Palaeoconis azari* gen. et. sp. n.

Diagnosis. Antennae with 19 flagellomeres. Forewing with three pigmented spots; two crossveins present in apical part of costal area. Crossvein rp2-ma approximately as long as basal abscissa of RP2. Media with one macroseta, ending with three terminal branches. Crossveins 1m-cua, 2mp2-cua and a1 present. Abdomen with discernible plicatures on sternites II-IV.

Etymology. The generic name is a combination of Palaeo and the suffix conis meaning dust.

Palaeoconis azari gen. et. sp. n.

http://zoobank.org/D2FC29B5-FFBE-42C7-AD0B-FD637B5011E7
Figures 3, 4

Holotype. BUB 2914; lowermost Cenomanian amber (Shi et al. 2012); Myanmar, Kachin, Hukawng Valley; preserved in a polished, transparent yellow piece of amber (9.18 × 6.77 × 2.18 mm), deposited in the Museum für Naturkunde, Berlin (ex. coll. Patrick Müller). The amber piece contains also one syninclusion of an imago of Diptera.

Etymology. The specific epithet honors Prof. Dany Azar (Lebanese University, Fanar, Lebanon), friend and colleague of AN and JP and worldwide known palaeoentomologist.

Diagnosis. As for the genus (*vide supra*).

Description. Male. Body length ca. 1.93 mm (measured from tip of head to tip of genitalia). Head hypognathous, ca. 0.34 mm. Compound eyes well developed, 0.22 mm x 0.14 mm (from lateral view). Antennae 21-segmented (with 19 flagellomeres),

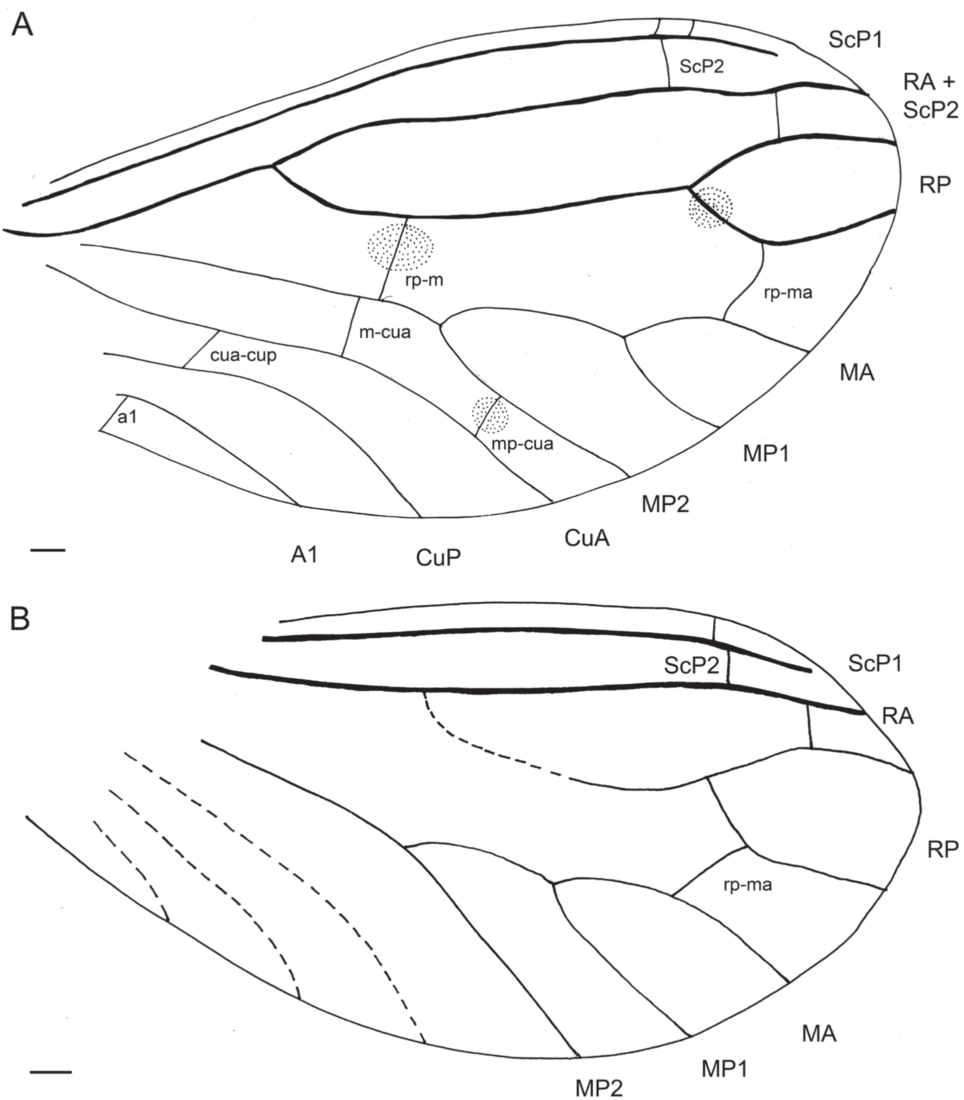

Figure 3. *Palaeoconis azari* gen. et sp. n., holotype BUB 2914. **A** Drawing of right fore wing **B** drawing of left hindwing. Scale bars: 100 μm.

scape and pedicel stouter, longer and broader than flagellomeres, first flagellomere longer and wider than remaining flagellomeres, flagellomeres subquadrate, nearly as long as wide, terminal flagellomere conical. Maxillary palps five-segmented, fifth segment distinctly larger than other palpomeres, length of fifth segment ca. 0.12 mm. Labial palps three-segmented, third segment larger than remaining. Thorax well developed. Prothorax narrower and overall smaller than meso- and metathorax.

Forewing ca. 2.19 mm long, ca. 0.93 mm wide; two distinct apical crossveins in costal area; division of ScP1 and ScP2 0.31 mm from wing apex; R branching into RA and RP 0.48 mm from wing base; RA simple, distally ending connecting with branch of ScP2; RP branched into RP1 and RP2; ra-rp1 present; first spot on basal abscissa of RP2 near RP1 (near place where is RP forked); crossvein rp-m oblique crossing dark spot about mid-length; M with three branches (MA, MP1 and MP2), M with one stiff seta near crossvein rp-m (Figs 3A, 4C); crossvein rp2-ma relatively long, approximately as long as basal abscissa of RP2; crossvein 1m–cua near rp-m, but not aligned; crossvein 2mp2-cua near to wing apex, with third spot over it; crossveins cua-cup and a1 present. Hindwing ca. 2.12 mm long, ca. 0.92 mm wide; venation pattern very similar to forewing with exception of only single crossvein between C and ScP, wing membrane in hindwing hyaline without any pigmented spots; crossveins ra-rp1 and rp2-ma present; basal part of hindwing without clearly recognizable venation.

Legs long and slender; femora covered with fine and sparse setae; tibiae covered with stiff and dense setae; tarsi five-segmented, first tarsomere distinctly longer than remaining tarsomeres, terminal tarsomere elongated ending with two claws, tarsi covered with fine dense setae. Abdomen large and broad, tapered to the end (visible from lateral view only); plicatures present on sternites II-IV; length of abdomen including genitalia 1.22 mm, width 0.54 mm. Structures of external genitalia hardly discernible with exception of domed and well-sclerotized ectoproct in lateral view and the caudal projection of gonarcus below.

Discussion. *Palaeoconis* gen. n. can be attributed to the Aleuropteryginae based on the presence of two crossveins between RP and M and also the presence of plicatures on abdominal sternites II-IV. Nevertheless, Zimmermann et al. (2009) considered this last character as a symplesiomorphy of the Coniopterygidae. However, *Palaeoconis* does not possess in the forewings two long stiff setae on M, which is the diagnostic character for Aleuropteryginae. In contrast to this, the absence of these setae on the media and the presence of three-branched media are considered as plesiomorphic characters typical for Mesozoic Coniopterygidae (Engel 2002). In addition, *Palaeoconis* possesses in forewing crossvein a1 connecting A1 to posterior wing margin. According to Engel (2016) the subfamily Aleuropteryginae contains 14 genera (Mesozoic and Cenozoic), i.e., *Achlyoconis* Engel, 2016; *Alboconis* Nel et al., 2005; *Apoglaesoconis* Grimaldi, 2000; *Archiconiocompsa* Enderlein, 1910; *Archiconis* Enderlein, 1930; *Garnaconis* Perrichot and Nel in Perrichot et al. 2014; *Geroconiocompsa* Engel, 2010; *Glaesoconis* Meinander, 1975; *Hemisemidalis* Meinander, 1972; *Juraconiopteryx* Meinander, 1975; *Libanoconis* Engel, 2002; *Neoconis* Enderlein, 1930; *Pararchiconis* Nel, 1991, and *Spiloconis* Enderlein, 1907.

Achlyoconis, *Alboconis*, *Apoglaesoconis*, *Glaesoconis*, and *Libanoconis* share the presence of two distinct basal crossveins in the costal area, and in addition *Achlyoconis, Alboconis* and *Libanoconis* share the presence of crossvein a1–a2, vein A2 and crossvein a2. These traits separate these genera from *Palaeoconis* gen. n. In addition, *Glaesoconis* described from the Lower Cretaceous Myanmar amber differs from *Palaeoconis* gen. n. by a distinctly shorter crossvein rp2-ma , single crossvein m–cua, presence of A2 and four pigmented spots on wing membrane instead of three in *Palaeoconis* (Engel 2004). *Libanoconis*, known from the Lower Cretaceous amber of Lebanon, differs from *Palaeoconis* gen. n. in the positions of crossveins between M and CuA (1m–cua is near to wing base; 2m–cua approximately at mid-length of wing), and lack pigmented spots

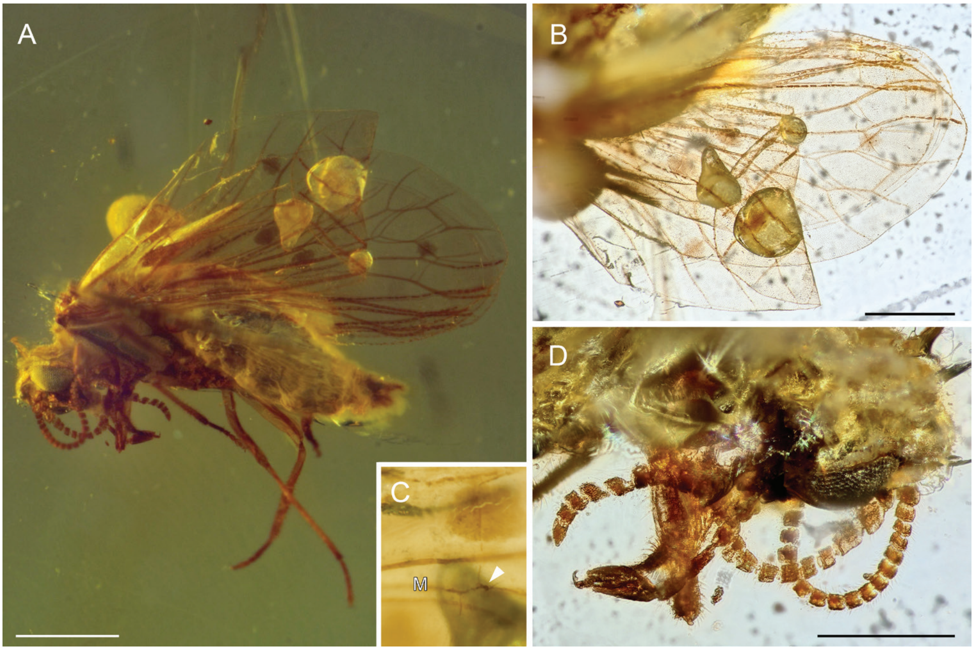

Figure 4. *Palaeoconis azari* gen. et sp. n., holotype BUB 2914. **A** Habitus lateral view **B** wing venation and spots **C** detail of forewing venation with stiff seta on vein M **D** head from dorso-lateral view showing antennae, terminal segment of maxillary palp and eye. Scale bars: 500µm (**A, B**); not in scale: (**C**); 50 µm (**D**).

on membrane (Engel 2002; Nel et al. 2004). *Achlyoconis* described from the Upper Cretaceous amber of northern Myanmar differs from *Palaeoconis* gen. n. in the presence of seven thickenings with specialized setae on M, positions of crossveins 1m-cua and 2m-cua, presence of a single crossvein between CuP and A1, and four pigmented spots (Engel 2016). *Alboconis*, described from the Lower Cretaceous French amber, differs from *Palaeoconis* gen. n. by a two branched media bearing two long setae, crossvein between CuA and R+M, and two crossveins between CuP and A1 (Nel et al. 2004). *Apoglaesoconis* and *Garnaconis* share the following features such as M with two long setae, presence of crossveins cup–a1; a1–a2, vein A2 and absence of pigmented spots on wing membrane. *Apoglaesoconis*, from the Late Cretaceous amber of New Jersey, differs from *Palaeoconis* gen. n. by one crossvein between RP and M, branches RP2 and MA forming a cross, and by a single crossvein between M and CuA (Engel 2002). *Garnaconis*, from the Late Cretaceous amber of Vendée in northwestern France, differs from *Palaeoconis* gen. n. in the remote positions of separated transverse ScP2 and crossvein between RA+ScP2 and RP1 (see Fig. 3), unlike both being aligned in *Garnaconis*. *Palaeoconis* gen. n. bears two crossveins beween RP and M, a two-branched media with setae instead of only one crossvein between RP2 and MA and a three-branched media without setae in *Garnaconis* (Perrichot et al. 2014). *Juraconiopteryx*, Upper Jurassic of Kazakhstan, represents the oldest record of Coniopterygidae. Wing venation of *Juraconiopteryx* is very poorly preserved (Meinander 1975), therefore we are unable to make a reliable comparison with *Palaeoconis.*

Conclusion

In this contribution we extended our knowledge on past diversity of Coniopterygidae. Two new genera and species assigned to the two subfamilies Aleuropteryginae and Coniopteryginae are herein described and illustrated from the Early Cenomanian amber of Myanmar. These new taxa are established mainly on the basis of wing venation patterns, number of antennal flagellomeres along with other body structures like abdominal plicatures. Our research uncovers spectacular diversity of Coniopterygidae in mid-Cretaceous ecosystems and in the same time supports the antiquity of this group that seems to have had a remarkable evolutionary stasis since the mid-Cretaceous.

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