

Polytypic *Mytilus edulis*, with a name for the Baltic subspecies (Bivalvia: Mytilidae)

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ABSTRACT

The four taxa of *Mytilus* represented in European waters are characterized morphologically, with references to distribution, nomenclature, and molecular data. The so-called Baltic *M. trossulus* is described as *M. edulis balthicus* subsp. nov. Only two *Mytilus* species are accepted in the area, viz. *M. edulis*, with *M. e. edulis*, *M. e. galloprovincialis*, and *M. e. balthicus* subsp. nov., and *M. trossulus*. To stabilize the use of *M. edulis*, the type locality of that taxon is restricted to the North Sea off the Dutch coast.

Key words: systematics, *Mytilus*, nomenclature, distribution, new subspecies.

INTRODUCTION

The binary system of nomenclature started with Linnaeus (1758). In that publication the genus *Mytilus* Linnaeus, 1758 and the common mussel *Mytilus edulis* Linnaeus, 1758 were described. The following c. 250 years brought an impressively large number of publications about various aspects of *Mytilus* populations and species. Despite all of this, the taxonomy and nomenclature of the genus remained problematic. Molecular methods, applied without reference to taxonomy and morphology have added considerably to the confusion. Here we intend to contribute to a better understanding of *Mytilus* taxonomy by stabilizing the nomenclature of the polytypic type species, *M. edulis*, while naming a subspecies that has been recognized as a separate taxon for a long time. We do not aim at an exhaustive literature study, an extensive phylogeography, or distribution maps for the various *Mytilus* species. That would require an

analysis of fossil *Mytilus* from both the northern and the southern hemispheres and an extensive search for records in many shell collections, which is beyond our capacities.

In a monograph on *Mytilus*, Gosling (1992) accepted that the Mediterranean *Mytilus* populations differ slightly from the North Sea populations in shell shape and that the two populations have a large hybrid zone in between. The taxonomy of this textbook example of a polytypic species with subspecies has not been interpreted uniformly. The North Sea *Mytilus edulis* and Mediterranean *M. galloprovincialis* are generally considered separate nominal taxa, but most authors have neglected the concept of subspecies or have not used the accompanying nomenclature (Skibinski et al. 1978, 1983; McDonald & Koehn, 1988; Väinölä & Hvilsum, 1991; Bierne et al., 2003; Riginos & Cunningham, 2005; Coghlan & Gosling, 2007; Breusing, 2012; Steinert et al., 2012; Saarman & Pogson, 2015; Coolen et al., 2020). As a false solution to this, Väinölä & Hvilsum (1991) proposed to consider *M. edulis* a superspecies with three semispecies.

There is consensus in the literature that the *Mytilus* populations of the Baltic Sea differ considerably from the populations of *M. edulis* in the North Sea, with a hybrid zone in between (Väinölä & Hvilsum, 1991; Riginos & Cunningham, 2005; Stuckas et al., 2009; Stuckas et al., 2017). On the basis of mainly molecular data, the Baltic mussels are usually referred to as *M. trossulus*, despite striking genetic differences and a hybrid zone connecting them to *M. e. edulis*. The Baltic *Mytilus* was described in great detail by Kautsky et al. (1990), with the results of transplantation experiments that made clear that their unique character states in DNA, allozymes and morphology cannot be entirely explained by ecophenotypic variation triggered by salinity. Obviously, the Baltic mussels represent a separate taxon that is now named below. Since Linnaeus (1758: 705) explicitly included the Baltic Sea for the range of *M. edulis*, we here designate a locus typicus restrictus in the North Sea for that taxon to conserve the use of this name in its current sense.

MATERIALS AND METHODS

A sample of live *Mytilus* recently collected at a locality in the Baltic Sea was used to characterize *M. e. balthicus* subsp. nov. morphologically. Additionally, some samples of *Mytilus* in the collection of Naturalis Biodiversity Center, Leiden, The Netherlands, were studied.

For 18 specimens of the type series the nDNA marker Me15/16 was determined. DNA was isolated using a special 3-day CTAB protocol for molluscs (van Haaren et al., 2021). To obtain the Me15/16 fragment we used the primers and the PCR program as described in Inoue (1995), followed by a HRM analysis ramping from 70 to 90 °C, with every 2 s a step of 0.1 °C, and a hold of 90 s of pre-melt conditioning on the first step. The PCR was done in a Qiagen Rotor-Gene Q apparatus, with a reaction mix consisting of 1 µL DNA, 6 µL Qiagen RM mix, 4 µL PCR-water (Qiagen), 0.5 µL forward and 0.5 µL reverse primer. Based on HRM analyses of the PCR products the preliminary identification of alleles could be done. The PCR products of the mussels that turned out to be homozygous for Me 15/16, were sequenced at MacroGen Europe in both directions. For the final identification of the alleles concerned, comparisons were made with *Mytilus* spp. Me15/16 sequences as deposited in Genbank (<https://www.ncbi.nlm.nih.gov>) by Inoue (1995).

Unpublished results of an investigation of 77 populations of *Mytilus* from The Netherlands, with over 4000 measured individuals, most of which checked for the Me15/16 molecular marker, were also used (Gittenberger et al., in prep.). Furthermore, we rely on data in the extensive literature.

Abbreviations. L = length; max. = maximal; Me15/16 ‘*edu*’ = nDNA marker Me15/16 allegedly diagnostic for *M. edulis* and ‘*tro*’ for *M. trossulus* (e.g. Inoue et al., 1995; Larraín et al., 2019); RMNH = National Biodiversity Center Naturalis, Leiden, the Netherlands.

TAXONOMIC PART

Mytilus edulis edulis Linnaeus, 1758

Figures 2–4, 6, 8, 16

Mytilus edulis Linnaeus, 1758: 705 (“Europaeo, Indico & M. Balthico”) [part.] — Bucquoy, Dautzenberg & Dollfus, 1890: 136, pl. 26 figs 1–4.

Mytilus edulis — Kautsky et al., 1990: 205, fig. 2 two left shells. Groenenberg et al., 2011: 96, fig. 1A–B.

Diagnosis. — Shell quite variable in shape, often with a distinct blunt ridge, relatively strong, more or less broad, often with sharply delineated colour rays reaching the edge, umbo rather obtuse; inside without an extension of the blackish border under the ligament. Length up to nearly 23 cm according to Tebble (1966: 40), but usually much smaller.

Notes. — There is confusion about the type locality of

M. edulis among authors who might not have been aware of some of the basic principles of taxonomy. Bierne et al. (2003: 458), incorrectly referring to “Bucquoy et al. 1898” and a “Linnaeus’ *M. edulis* type collection” regarded the mussels from the Baie de l’Aiguillon as “typical *M. edulis*”. However, Bucquoy, Dautzenberg & Dollfus (1890: 136) solely selected from that area “un type” for *M. edulis*, i.e. what they considered “la forme banale”, without any reference to a Linnean type series per se. McDonald & Koehn (1988: 115) incorrectly stated that “The type locality for *M. edulis* Linnaeus, 1758 is the North Atlantic.” Their reference to “the type specimen” is also incorrect since there are syntypes only (see below). Buyanovsky (2000: 43) also referred to the North Atlantic as the “type locality of the Linnean holotype”. According to Linnaeus (1758: 705), however, the wide range of *M. edulis* includes both the North Sea and the Balthic Sea. Since the population groups in these two seas are generally accepted now as separate taxa (McDonald & Koehn, 1988; Väinölä & Hvilson, 1991; Buyanovsky, 2000; Riginos & Cunningham, 2005; Stuckas et al., 2009), the location of the type locality of *M. edulis*, inside or outside the Baltic Sea, is relevant. This threat to the well-known name of the edible mussel was mentioned but not eliminated by McDonald & Koehn (1988: 115) and Väinölä & Hvilson (1991: 146).

There are only syntypes of *M. edulis* without locality data in the Linnean collections in the Linnean Society strong-room, London (#225) and at the University Zoological Museum, Uppsala (#500, #1026) (K. Way, personal communication 2017). The selection of a lectotype from those collections would be problematic anyway because of unrecorded additions to the original Linnean collection (Dance, 1967). Apart from that, restricting the type area is sufficient to ensure the use of *M. edulis* in its current sense. Therefore, to further the nomenclatorial stability of the nominal taxon *Mytilus edulis*, we here formally designate as its **locus typicus restrictus**: Europe (“Europaeo”), North Sea coast off the Dutch Delta Area in the south-western Netherlands.

Mytilus edulis balthicus subsp. nov.

Figures 9–13

Mytilus edulis — Kautsky et al., 1990: 205, fig. 2 two right shells. Not Linnaeus, 1758.

“Baltic mussels” Buyanovsky, 2000: 46.

“Baltic Sea *Mytilus trossulus*” Riginos & Cunningham, 2005: 385. Not Gould, 1850.

“Baltic *M. trossulus*” Stuckas et al., 2009: 147. Zbawicka et al., 2010: 45. Not Gould, 1850.

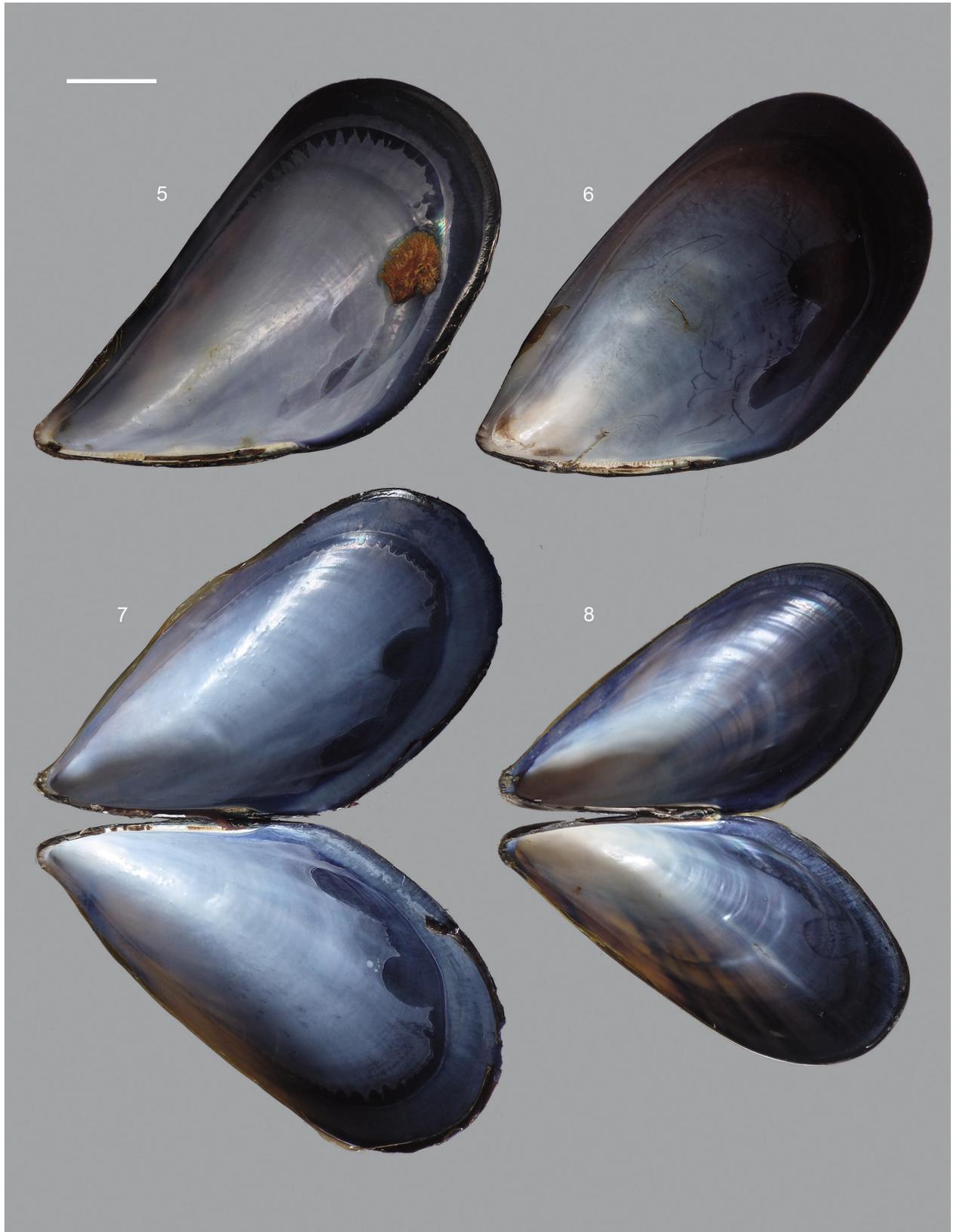
“Baltic Sea *M. trossulus*” Steinert et al., 2012: 388. Not Gould, 1850.

“Baltic *Mytilus*” Stuckas et al., 2017: 2765. Not Gould, 1850.

Mytilus trossulus — Piwoni-Piórewicz et al., 2017: 1. Not Gould, 1850.



Figures 1–4. *Mytilus* spec. **1.** *M. edulis galloprovincialis* Lamarck, 1819; Malta, Marsaxlokk, fish market, E. Gittenberger leg. vii.2021 (RMNH.MOL.511418), L 84.2 mm. **2–4.** *M. e. edulis* Linnaeus, 1758. **2.** The Netherlands, province of Zeeland, Grevelingen, Bommene de harhour, A. Gittenberger leg. 6.ix.2013 (RMNH.MOL.511419), homozygous for Me15/16 ‘edu’, L 65.0 mm. **3–4.** The Netherlands, province of Zeeland, Veerse Meer, off Veere, A. & E. Gittenberger leg. vii.2021 (RMNH.MOL.511420), L 54.7 mm [3], L 65.7 mm [4]. Scale bar = 1 cm.



Figures 5–8. *Mytilus* spec. **5, 7.** *M. edulis galloprovincialis* Lamarck, 1819. **5.** Greece, Ionian Islands, Lefkada harbour, E. Gittenberger leg. 3.vii.2011 (RMNH.MOL.511422), L 75.3 mm. **7.** Malta, Marsaxlokk, fish market, E. Gittenberger leg. vii.2021 (RMNH.MOL.511418), L 71.5 mm. **6, 8.** *M. e. edulis* Linnaeus, 1758. **6.** The Netherlands, province of Zeeland, Grevelingen, Bommenede harbour, A. Gittenberger leg. 6.ix.2013 (RMNH.MOL.511419), homozygous for Me15/16 ‘edu’, L 65.0 mm. **8.** The Netherlands, province of Zeeland, Veersche Meer, off Veere, E. Gittenberger leg. vii.2021 (RMNH.MOL.511420), L 54.7 mm. Scale bar = 1 cm.

Type series. — Holotype (RMNH.MOL.511426), L 29.4 mm, homozygous for the nDNA marker Me15/16 ‘edu’ (GenBank accession number OL321746), and paratypes (RMNH.MOL.511427/19) (4 Me15/16 ‘tro’, OL321742–321745, 5 Me15/16 ‘edu’, OL321747–321751, and 10 heterozygous specimens), Poland, Zachodniopomorskie province, 60 km N of Szczecin, Międzyzdroje, 53°56′18.8″N 14°27′32.6″E; J. Lacor & G. Keplin leg. 1.v.2021.

Diagnosis. — Shell fragile, relatively flat, with an indistinct ridge, umbo obtuse. Outside black or blackish brown apart from the grey umbones, without colour rays; inside with a light apical part, gradually darker brownish or blackish towards the margin. Length up to 32.5 mm.

Differentiation. — In both *M. e. edulis* and *M. e. galloprovincialis* the shells reach much larger dimensions than in *M. e. balthicus* in its natural environment (Kautsky et al., 1990) and may have radial rays on the outside, or discernible by transmitted light. According to Buyanovsky (2000: 46) and Wesselingh (2003: 40), there is no extension of the blackish border under the ligament in mussels of the Baltic Sea, but we observed it clearly in a shell from Sweden, Stockholms Skärgård (Fig. 11). In the transparent shells of the type series a whitish main part and a contrasting blackish border zone are lacking.

Variability. — *Mytilus e. balthicus* is characterized here on fresh specimens, collected alive at the type locality. The limited, old museum material, available to us from elsewhere in the Baltic Sea, does not enable a comprehensive summarizing description of the variability of this subspecies. Shells in these samples are not considered paratypes. Morphologically they agree well with the specimens in the type series, reaching only slightly larger dimensions (L max. c. 4 cm).

Along the German–Polish coast of the Baltic Sea, 200 km west of the type locality and 6 km north-west of Wismar, small *Mytilus* were found with L max. of 43.4 mm ($n = 8$). Further east, shells from the northern part of the island of Rügen (RMNH.MOL.321895) ($n \geq 25$) are equally small (L max. 27.7 mm), and they are only more solid than shells of the type series which were collected 100 km to the south-east. Piwoni-Piórewicz et al. (2017: 5) studied shells, with L max. of 44 mm ($n = 136$), from the Gulf of Gdańsk, Pomerania province, Poland, c. 330 km east of the type locality. We have seen similar samples from more northern localities in Sweden: Södermanland County, Saltsjöbaden, G. Gerrits leg. 28.vii.1955 (ZMA.MOLL.412361), L max. 30 mm ($n = 5$); Skärgård, S. Ekman leg. (RMNH.MOL.511428), L max. 31.2 mm ($n = 1$); Scania County, Landön, E. Flach leg. v.2003 (RMNH.MOL.511429), L max. 21.5 mm ($n \geq 25$). Probable additional records of this subspecies from Sweden are Malmöhus County, Ystad (Riginos & Cunningham, 2005: 383) and Södermanland County, Askö (Kautsky, Johannesson & Tedengren, 1990: 204), and from Finland, Uusimaa region, Tvärminne 20 km south-west of Ekenas (McDonald et al. 1991: 325).

Distribution. — The hybrid zone between *M. e. edulis* and *M. e. balthicus* borders the range of the latter subspecies in the south-west Baltic Sea (Väinölä & Hvilson, 1991; Riginos & Cunningham, 2005; Stuckas et al., 2009, 2017). As a consequence, a sharp distributional borderline cannot be indicated. The markers that have been used in the literature do not vary simultaneously, and there are no accompanying morphological data. A series of samples in RMNH (F.P. Wesselingh leg.) from along the Øresund and the south-west Baltic Sea from Hornbaek in the north to Køge in the south (on the eastern coast of Sjælland, Denmark) are morphologically most similar to *M. e. edulis*. These samples will be described in more detail elsewhere. A sample from the south-west Baltic Sea in near Boltenhagen, Mecklenburg-Vorpommern, Germany (RMNH.MOL.511425) also differs from the type series by having more solid and larger shells, with L max. of 61.4 mm ($n = 12$). These samples are also considered intermediate between *M. e. edulis* and *M. e. balthicus*.

Phylogeography. — *Mytilus trossulus* dispersed from the Pacific into the Atlantic during the early Holocene (c. 7,500 years ago) when it reached the entrance to the Baltic Sea which had been completely frozen until then (Väinölä & Hvilson, 1991; Beaumont et al., 2008). Ancestral *M. e. balthicus* invaded the Baltic area initially as a peripheral isolate of *M. trossulus*. Later, *M. edulis* dispersed into the present North Sea and the range of *M. trossulus* became more northern, resulting in the disjunction between *M. trossulus* and *M. e. balthicus* and the present, secondary hybrid zone between *M. e. edulis* and *M. e. balthicus* (Riginos & Cunningham, 2005).

Notes. — Apparently, the conspicuous “dwarf size” of the Baltic mussels (Varvio et al., 1988: 57), which has been reported repeatedly (Kautsky et al., 1990; Riginos & Cunningham, 2005; Breusing, 2012; Piwoni-Piórewicz, 2017), has not triggered any nomenclatorial act, despite the fact that it has been known for decades and now that these mussels cannot simply be regarded as an ecophenotypic form of either *M. edulis* or *M. trossulus* (Theisen, 1978; Varvio, Koehn & Väinölä, 1988; Väinölä & Hvilson, 1991).

The 18 specimens of the type series for which the nDNA marker Me15/16 was analysed (see Inoue et al., 1995; Larrain et al., 2019) made clear that this marker cannot be used to identify *M. e. balthicus*: six mussels, which includes the holotype, were homozygous for the so-called *edulis* allele, four mussels were homozygous for the so-called *trossulus* allele, and eight were heterozygous.

Apart from its relatively low salinity, the Baltic Sea differs from the North Sea by its small tidal range, by having much of the surface water frozen in winter, and by the absence of *Asterias rubens* Linnaeus, 1758 as the main predator (Kautsky et al., 1990; Piwoni-Piórewicz et al., 2017). Kautsky et al. (1990) extensively studied both naturally occurring *M. e. balthicus* in the brackish Baltic Sea and transplanted mussels in the North Sea. The transplanted *M. e. balthicus* reached the same length as *M. e. edulis* but they were thinner

shelled and with relatively small adductor muscles. Kautsky et al. concluded that variation in growth rates of these mussels in the two seas might largely be explained by the physiological differences related to salinity, whereas rates of survival and morphological differences might be determined mainly genetically. In an article on the mineralogy and chemistry of shells of *M. e. balthicus*, Piwoni-Piórewicz et al. (2017) presented detailed ecological data for the southern Baltic Sea.

There are substantial differences in both nuclear and mitochondrial DNA between so-called Baltic *Mytilus trossulus*, *M. trossulus* from elsewhere, and *M. edulis*. The Baltic Sea mussels are “the most extreme example” of genetic individuality because of “complete asymmetric introgression of *M. edulis* female mtDNA into Baltic Sea populations” (Riginos & Cunningham, 2005: 383); as a consequence, “there are no pure *M. trossulus* mussels, just remnants of their original genome in Baltic Sea populations” (Riginos & Cunningham, 2005: 395). Differences between the genomes of *M. trossulus* in America and Scotland versus *M. e. balthicus* in the Baltic Sea are also reported by Stuckas et al. (2009), Zbawicka et al. (2010), and Fraïsse et al. (2016).

Derivatio nominis. — The epithet *balthicus* is a male adjective referring to the range of this subspecies.

***Mytilus edulis galloprovincialis* Lamarck, 1819**

Figures 1, 6–7

Mytilus galloprovincialis Lamarck, 1819:126 (“la Méditerranée, près de Martigues, en Provence”).

Diagnosis. — Shell moderately strong, relatively broad and flat; umbo narrowed, slightly curved, mostly without colour rays; inside without an extension of the blackish border under the ligament. Length up to 85 mm.

Distribution. — Between North Sea *M. e. edulis* and Mediterranean *M. e. galloprovincialis* there is a broad, heterogeneous hybrid zone accompanied by differential introgression. This is indicated by molecular analyses (Skibinski et al., 1983; Gosling, 1992; Bierne et al., 2003). According to Coghlan & Gosling (2007: 841), this zone encompasses over 1,400 km of coastline, from western France to northern Scotland. Overlooking the possibility that the molecular marker Me15/16 may occur in several *Mytilus* taxa at different percentages (see below), Coolen et al. (2020) extended the so-called hybrid zone between *M. e. edulis* and *M. e. galloprovincialis* into even the entire North Sea. The data regarding shell morphology in this area are insufficient, however. The morphologically determined borderline area might be much narrower (Verduin, 1979). As a consequence, taxonomically, the distribution of *M. e. galloprovincialis* cannot be indicated in more detail.

In the absence of detailed distributional data for the recent past, speculations about invasive or imported *M. e. galloprovincialis* (Kijewski et al., 2009; Steinert et al., 2012;

Saarman & Pogsoni, 2015) are poorly founded. Our ancient DNA analyses showed that the percentages of so-called *edulis* and *galloprovincialis* alleles has not changed in the Dutch province of Zeeland for over 70 years (Gittenberger et al., in prep.).

Notes. — Even in areas where hybridization is unlikely, shell morphology does not always allow a differentiation between *M. e. edulis* and *M. e. galloprovincialis*. However, relatively broad and flat shells of *M. e. edulis* in quiet waters have a more obtuse umbones than shells of *M. e. galloprovincialis*. Seed (1974) and especially Verduin (1979) have shown this by morphometric methods, which were also applied by Groenenberg et al. (2011) who demonstrated that the broad-shelled mussels from the Dutch delta region have to be considered *M. e. edulis* both genetically and morphologically. For a detailed comparison of both subspecies in shell shape, thickness, transparency, hinge plate teeth, and colour in normal versus transmitted light, see Seed (1974) and Verduin (1979).

The allegedly diagnostic molecular marker Me15/16 cannot be used to differentiate between *M. e. edulis* and *M. e. galloprovincialis* (Groenenberg et al., 2011). It is an adhesive protein gene, linked to the byssus thread glue and the fastening of the mussels to the substrate.

Its presence relates to the turbulence in the habitat of the mussels. Individual mussels with relatively broad, flat shells are more often found in quiet waters, where the allegedly diagnostic marker for *M. e. galloprovincialis* is also most common. However, by investigating individual specimens both genetically and morphologically, it turned out that shell width is independent of Me15/16 (Gittenberger et al., in prep.).

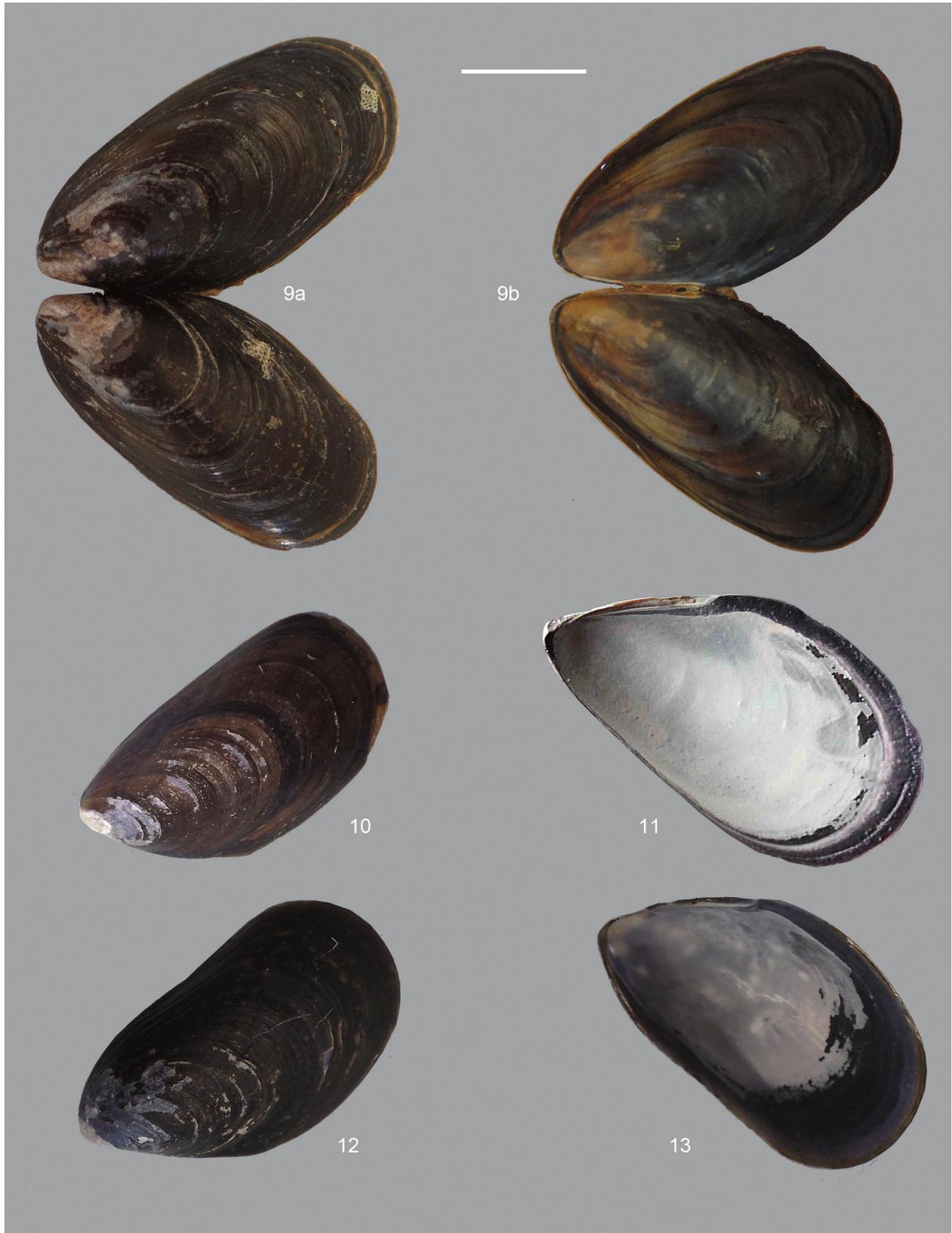
***Mytilus trossulus* Gould, 1850**

Figures 14–15

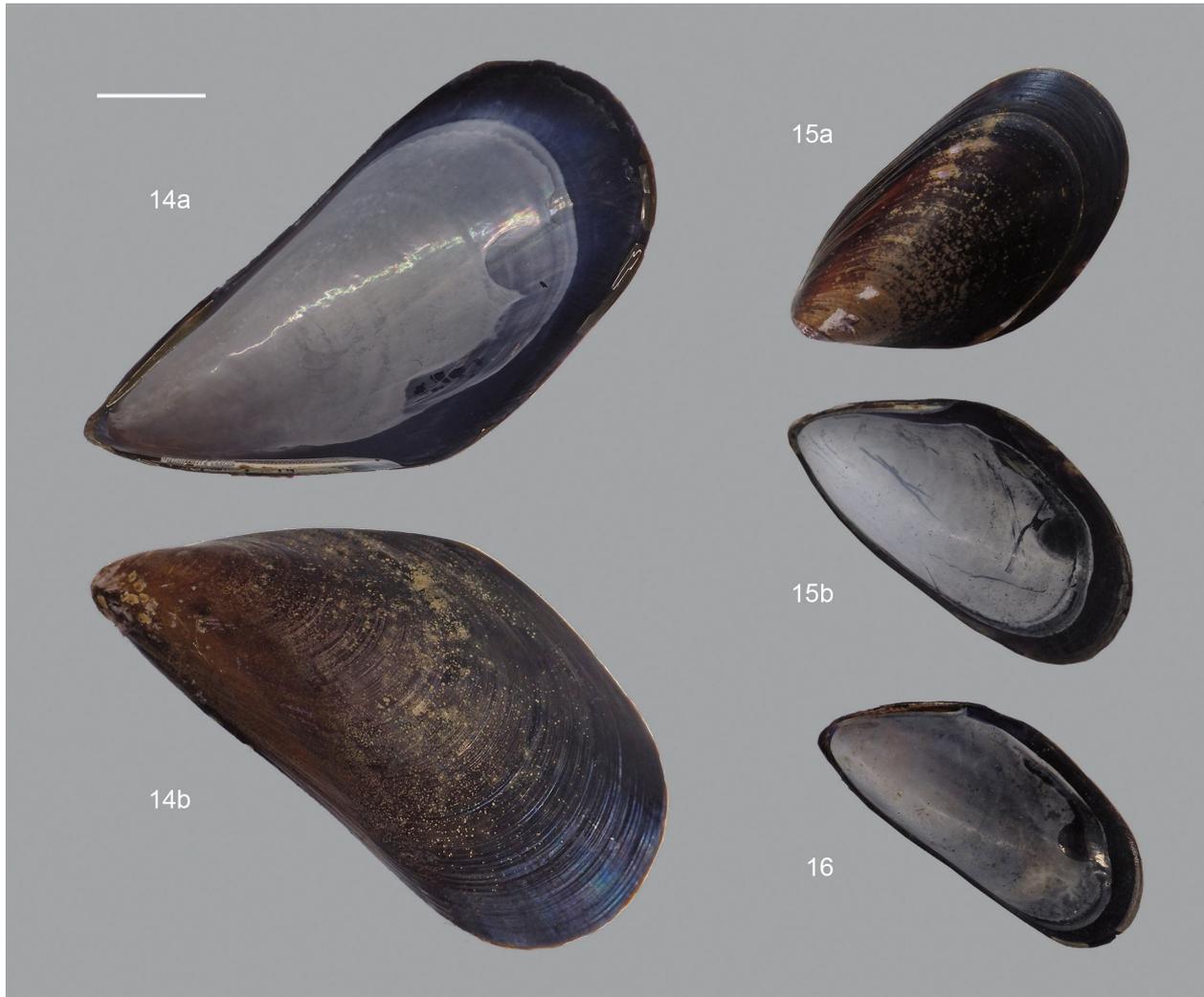
Mytilus trossulus Gould, 1850: 344 (“Killimook, Puget Sound, Oregon”). Buyanovsky, 2000: 45, figs 1B, 2D, F. Wesselingh, 2003: 40, unnumbered figs.

Diagnosis. — Shell strong, without colour rays, with an extension of the blackish border under the ligament; its maximum size comparable to that of *M. edulis edulis*. Length up to 10 cm (Piwoni-Piórewicz, 2017: 5).

Distribution. — In the northern hemisphere *M. trossulus* is circumarctic (Buyanovsky, 2000; Wesselingh, 2003: 40). This species is distributed in the northern Pacific Ocean, viz. western North America and eastern Asia, and in the northern Atlantic and scattered localities in Scandinavia (shells in RMNH, Fig. 15) and Scotland (Zbawicka et al., 2010). A false record from the Netherlands (Oosterschelde) (Śmietanka et al., 2004) is based on the presence of an allegedly diagnostic allele. Some typical shells of the “circumarctic form of *M. trossulus* [translated]” washed ashore in the Netherlands (Wesselingh, 2003: 40, unnumbered fig.) are insufficient proof of the occurrence of this species off the Dutch coast.



Figures 9–13. *Mytilus edulis balthicus* subsp. nov. **9.** Poland, Zachodniopomorskie province, 60 km N of Szczecin, Międzyzdroje, 53°56' 18.8"N 14°27'32.6"E, J. Lacor & G. Keplin leg. 1.v.2021 (holotype, RMNH.MOL.511426), homozygous for Me15/16 'edu', L 29.4 mm. **10, 12-13.** Germany, Mecklenburg-Vorpommern, Rügen, Wittow near Putgarten, Cap Arkona beach, 3.viii.2009 (RMNH.MOL.32189), L 25.2 mm [10], 27.7 mm [13], 26.6 mm [12]. Scale bar = 1 cm. **11.** Sweden, Södermanland County, Stockholm, Skärgård, S. Ekman leg. (RMNH.MOL.511428), L 31.2 mm.



Figures 14–16. *Mytilus* spec. **14–15.** *M. trossulus* Gould, 1850. 14. USA, Oregon, Newport, 44°39'N 124°04'W, G. Lambert leg. 18.x.2010 (RMNH.MOL.33333), L 56.8 mm. **15.** Norway, Romsdal, Romsdalsfjord, Åndalsnes, C.A. van der Willigen leg. (RMNH.MOL.511424), L 35.0 mm. **16.** *M. e. edulis* Linnaeus, 1758. Norway, Romsdal, Romsdalsfjord, Åndalsnes, C.A. van der Willigen leg. (RMNH.MOL.511421), L 33.0 mm. Scale bar = 1 cm.

Since hybridization between *M. trossulus* and *M. edulis* is incidental (Riginos et al., 2004; Fraïsse et al., 2016; Stuckas et al., 2017), we consider these taxa to be separate species.

DISCUSSION

Molecular methods have been a blessing for taxonomy in most cases, whereby DNA analyses have been fundamental for the identification of molluscan species (Gittenberger & Gittenberger, 2011). To some extent the genus *Mytilus* exemplifies the opposite. While taxonomy is supposed to be about taxa, such as biological species or subspecies with their exclusive, specific place in the ecosystem, much of the literature on these mussels stops at the level of alleles. The alleles are then blindly given species status. The presence

of a species is accepted when an individual is homozygous for an allegedly diagnostic allele and a mussel is considered a hybrid individual when it is heterozygous for that allele. As a consequence, hybrids are sometimes reported from areas where the hybridizing (sub)species do not occur, or introgression or an invasion is postulated but overlooking natural heterozygosity as an alternative explanation. The dogmatic use of particular alleles as molecular markers for identification, without any reference to morphology, has hindered the understanding of *Mytilus* species as natural entities (Śmietanka et al., 2004; Breton et al., 2006; Coghlan & Gosling, 2007; Kijewski et al., 2009; Steinert et al., 2012; Coolen et al., 2020).

Most authors neglect morphology, assuming that morphological character states are useless anyway. This may explain the fact that the diagnostic inside colour pattern of

shells of *M. trossulus* is taken into account by only a minority of authors (Buyanovsky, 2000; Wesselingh, 2003).

Mytilus edulis, *M. galloprovincialis*, and *M. trossulus* were recognized and described as long as 260, 200, and 170 years ago, respectively. Later on, it became increasingly clear that not every single *Mytilus* shell can be identified easily by morphometric methods (Verduin, 1979). For example, Vervoenen et al. (2000), in a study on Pliocene North Sea mussels, started from an earlier morphometric study by McDonald et al. (1991) but eventually returned to a qualitative discrimination of the Recent mussel taxa.

All this does not explain the fact that disjunct *M. trossulus* and *M. e. balthicus* have hitherto been considered the same in nomenclature, despite striking differences in morphology, ecology, and genetic characters, and a hybrid zone between *M. e. edulis* and *M. e. balthicus*.

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