

The first record of *Maeotias marginata* (Cnidaria, Hydrozoa) from the Baltic Sea: a Pontocaspian invader

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An exotic hydromedusa, *Maeotias marginata* (Modeer, 1791) (= *M. inexpectata* Ostroumoff, 1896) (Limnomedusae, Olindiidae) was observed 1999 in the Väinameri area of the northern Baltic Sea, western Estonia. The genuine brackishwater species is considered native to the Sea of Azov – Black Sea estuaries. It has earlier been found introduced also in low-salinity habitats in the Netherlands, France, and both coasts of North America. The identity of the Baltic and North American *Maeotias* was confirmed using molecular characters (sequence of the mitochondrial COI gene).

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INTRODUCTION

Along with the global increase of transoceanic and other long-distance aquatic introductions (e.g. Carlton & Geller 1993), the influx of non-indigenous species to the Baltic basin has been accelerating in recent years (Gollasch & Leppäkoski 1999). A common source is the Pontocaspian fauna, which has long evolved to cope with the brackish-freshwater boundary, in isolation from estuarine faunas elsewhere in the world. Once provided an opportunity, Pontocaspian taxa have proved to be efficient colonizers of both brackish and freshwater environments in Europe and North America (Ricciardi & Rasmussen 1998; Lee & Bell 1999). During the past decade, two new Pontocaspian invaders were established in the northern Baltic Sea: *Hemimysis anomala* Sars, 1907 (Crustacea, Mysida) and *Cercopagis pengoi* (Ostroumov, 1892) (Crustacea, Cladocera). Previous colonizers involve the hydroid *Cordylophora caspia* (Pallas, 1771) and the zebra mussel *Dreissena polymorpha* (Pallas, 1771) (e.g. Panov & al. 1999).

We report on another Pontocaspian species, the hydromedusa *Maeotias marginata* (Modeer, 1791) (= *M. inexpectata* Ostroumoff, 1896) (Cnidaria, Hydrozoa, Limnomedusae, Olindiidae), which was first observed in the Baltic in 1999. No indigenous shallow-water hydromedusae are known from the northern Baltic,

whereas some species are found in the deeper waters of the central and southern Baltic (e.g. *Sarsia* spp.; Ackefors & Hernroth 1972).

RESULTS AND DISCUSSION

OBSERVATION OF *MAEOTIAS MARGINATA* IN THE NORTHERN BALTIC

Observations of *M. marginata* were first made by PO when scuba diving in the shallow-water Väinameri area (Moonsund), in connection with a bottom biotope survey, on 24 August 1999. Väinameri is bordered by the west coast of Estonia and the large Hiiumaa and Saaremaa islands (Fig. 1). Within a week, a dozen or so specimens were spotted also at three other sites in the sea area, within 30 km of each other. At several other localities no hydromedusae were seen. The depths at the *M. marginata* sites were 1-5 m. The bottom was sandy, covered by patches of *Zostera marina* meadow with associated *Zannichellia major* and *Potamogeton* spp. Water temperature was 17.6 °C; salinity in the area is generally 6-7 (Suursaar & al. 1998).

The exotic hydromedusa co-occurred with the abundant resident scyphomedusa *Aurelia aurita*. *M. marginata* was seen to perform a typical vertical hydromedusan feeding migration behaviour, travelling be-

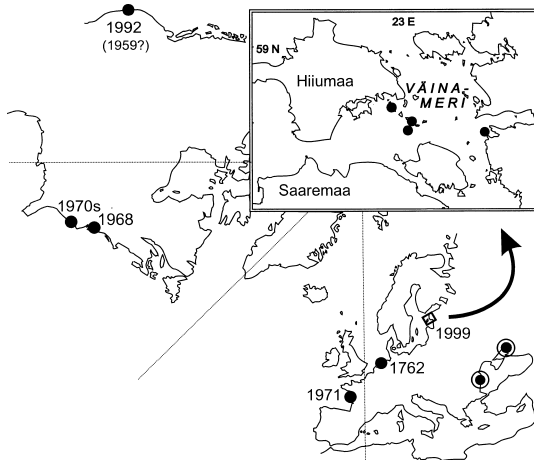


Fig. 1. The recorded spread of *Maeotias marginata* from the native Pontocaspian area (see Mills & Sommer 1995, Mills & Rees 2000 for references), and location map of the Baltic observations in western Estonia in 1999.

tween the bottom and surface (cf. Dumont 1994). With rhythmic pulsations the animal ascended towards the surface, then spread its umbrella wide flat, marginal tentacles extended, and slowly drifted down, to finally stay on the bottom for a while in the same wheel-like conformation. The zooplankton diet of *M. marginata* has been studied, from stomach contents, by Mills & Sommer (1995).

TAXONOMY AND ZOOGEOGRAPHY

While *M. marginata* is considered to be of Pontocaspian origin, it has earlier been found introduced in a number of low-salinity localities also elsewhere (Fig. 1). The Pontocaspian populations were initially described as *M. inexpectata* from the estuaries of the Don and Kuban rivers in the Sea of Azov (Ostroumov 1896a, 1896b), and then from the Danube estuary (Borcea 1928). The species has thereafter been recorded from western France (Loire estuary; Denayer 1973) and from temperate North American estuaries on both the Atlantic and Pacific coasts (Calder & Burrell 1969; Mills & Sommer 1995). Hummelinck (1941) and Mills & Rees (2000) however noted that the first finds of *Maeotias* were actually from the Netherlands, in 1762 and 1889, and should be referred to *Maeotias marginata* (Modeer, 1791) (for the complex record of nomenclature see Hummelinck 1938). While Hummelinck (1941) hesitated synonymizing the Dutch and Pontocaspian forms, Mills & Rees (2000) considered them conspecific: *M. marginata* takes priority as the name for the taxon, and the genus remains monotypic. The Pontocaspian origin has not been questioned.

M. marginata is a true brackishwater species, reported

previously from salinities 4-15, and possibly lower. Both field and laboratory observations indicate that salinities higher than 15 are lethal for the medusa stage (Mills & Rees 2000). Elsewhere the introductions of *M. marginata* have been associated with two further Pontocaspian hydromedusae, *Blackfordia virginica* Mayer, 1910 and *Moerisia* sp. (see Mills & Rees 2000); their appearance also in the Baltic is worth monitoring.

ON MORPHOLOGY

The umbrella of *M. marginata* is roughly hemispherical, up to 50 mm wide. Gonads hang from the distal 2/3 of four distinctive radial canals; the live animal appears opaquely white (in contrast to *Aurelia*), and has a reddish shadow around the bell margin. The margin is bordered by a dense fringe of several hundred tentacles, all of identical structure and up to 0.5 mm thick (Fig. 2). Characteristic of *Maeotias* are also the c. 50 centripetal canals, branching up from the marginal ring canal (for more vivid photographs of *M. marginata*, see Mills & Sommer 1995, Rees & Gershwin 2000, and Wrobel 2000).

One individual of the Väinameri *M. marginata* was taken alive to the laboratory and deposited at the Zoological Museum, University of Helsinki. The identification of the specimen from the original illustrations (Ostroumov 1896b; Borcea 1928; Kramp 1961) could be confusing, and departures from the more recent accounts were also evident. The tentacles were relatively contracted (less than 2/3 bell diameter). The top of the subumbrella has previously been depicted as conical or peaked (Ostroumov 1896b; Denayer 1973; Rees & Gershwin 2000), whereas that of the Baltic specimen was flat. Also, the velum was notably broad ($> 0.5 \times$ bell radius) (Fig. 2, cf. Mills & Sommer 1995). Plausibly these deviations could be due to the physiological condition of the specimen when imported to the laboratory. Yet to confirm the specific identity we used DNA characters, independent of any environmental or physiological influences.

MITOCHONDRIAL COI GENE SEQUENCE

DNA was extracted from a tentacle of the Baltic specimen with a CTAB procedure (Doyle & Dickson 1987). For reference, a DNA preparation from a *M. marginata* individual collected 1997 from the San Francisco Bay estuary was received from Dr. A.G. Collins (University of California, Berkeley). A segment of the mitochondrial COI gene (cytochrome C oxidase subunit I) was PCR amplified using the universal metazoan primers of Folmer & al. (1994), and sequenced using the same primers, on an ABI PRISM 377 automated sequencer. Sequences were deposited in the GenBank database under accession numbers AF383926, AF383927.



The COI sequences of the Baltic and San Francisco Bay specimens showed 99.7 % identity. Only two nucleotide differences were observed in the 648-bp segment compared; both were synonymous substitutions of the 3rd codon position. In a comparative framework of mtDNA divergence (e.g. Williams 2000), the observed similarity corroborates the specific identity of the Baltic and San Francisco Bay invaders. At the same time, the difference observed rules out a common clonal origin of the introductions.

Our data seem to be the first published COI gene sequences from the Hydrozoa, whereas other mtDNA genes have been studied in the genus *Hydra* (Pont-Kingdon & al. 2000). In contrast to the ordinary circular mtDNA structure, hydrozoans possess a linear mitochondrial molecule; *Hydra* even has two linear ones (Bridge & al. 1992). The cnidarian mitochondrial genetic code also deviates from those in other metazoans (Pont-Kingdon & al. 2000); the *M. marginata* COI sequence fits this code, where TGA encodes tryptophan. The sequence shows a marked codon bias against codons ending in G and C, though not as strong as that in *Hydra*. The overall nucleotide composition A:T:C:G (%) in our data was 25:40:16:19.

PROPAGATION

Most plausibly the introduction of *M. marginata* has been by ship ballast exchange, probably through the benthic polyp stage. The simple polyp of *M. marginata* was first observed by Rees & Gershwin (2000). Hydrozoan polyps also propagate asexually and produce resting stages, pedal cysts (e.g. Mills & Sommer 1995). The importance and efficiency of the asexual mode for colonizing hydrozoans, and the inefficacy of sexual medusae for established stocks, is evident from the fact that introduced medusa populations are often unisexual, i.e., probably derived from and propagated through one or a few colonizing genets of single sex (Dumont 1994). In the invasion of *M. marginata* to the San Francisco Bay, only male medusae were found during the first years (Mills & Rees 2000). Also the Estonian population may have been spreading asexually for some time before the observation of medusae in 1999. Assuming this non-planktonic mode of reproduction, the population could well have remained relatively localized at the initial area of introduction for some time, and therefore unobserved.

The wide occurrence of medusae in the shallow-water Väinameri area in 1999 may be related to the unusually warm summer, whereas normally the species would remain unnoticed although budding, cysting and even release of medusae would be taking place. No further records of *M. marginata* were made in 2000, despite the current alertness for invasive fauna (E. Leppäkoski, S. Olenin, personal communication). Summer temperatures

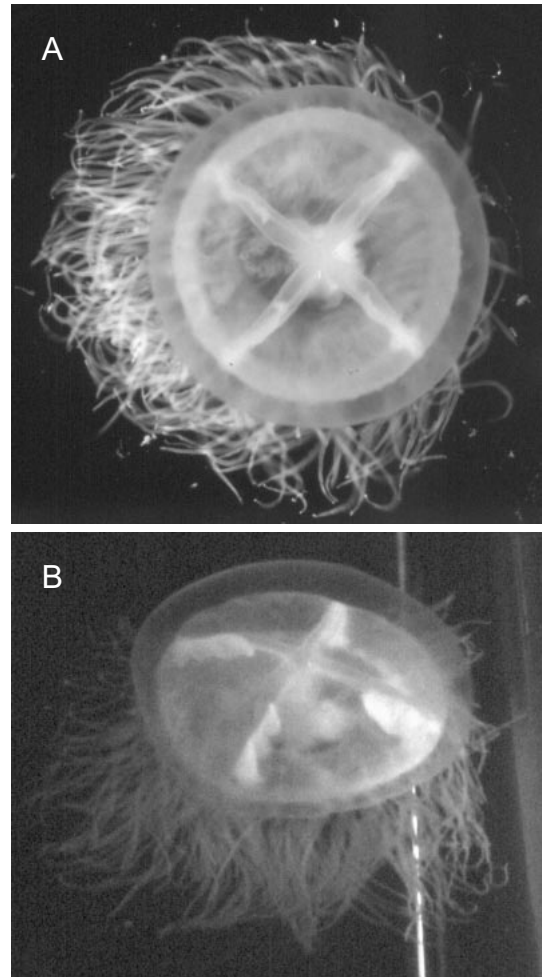


Fig. 2. *Maeotias marginata* in the laboratory (A) from above, (B) obliquely from above. The diameter of the animal is 32 mm. Photo: Ritva Talman, FMNH.

are likely to prove decisive for the eventual success of *Maeotias* in the Baltic. In terms of salinity, the Baltic should provide an ideal environment. While this seems to be an extreme penetration of *M. marginata* into boreal waters, winter conditions should not be so restrictive: even the Sea of Azov, the area of origin, regularly gets ice cover.

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