

New observations and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (= *M. inexpectata*), *Blackfordia virginica*, and *Moerisia* sp. in the San Francisco Estuary*

CLAUDIA E. MILLS¹ and JOHN T. REES^{2,3}

¹Friday Harbor Laboratories and Department of Zoology, University of Washington, 620 University Road, Friday Harbor, WA 98250 U.S.A. E-mail: cemills@u.washington.edu

²Bay/Delta Shore Institute, California State University, Hayward Building 7, 751 West Midway, Alameda Point, CA 94501

³Department of Biological Sciences, California State University, Hayward, CA 94542 U.S.A.

SUMMARY: New observations of *Maeotias*, *Blackfordia*, and *Moerisia* in low salinity waters of the San Francisco Bay estuary allow better understanding of the life cycles and natural history of these three genera of invading hydrozoans. *Maeotias inexpectata* Ostroumoff, 1896 is found to be a junior synonym of *Maeotias marginata* (Modeer, 1791). Moreover, *M. inexpectata* Ostroumoff, 1896b is an incorrect subsequent spelling of *M. inexpectata* Ostroumoff, 1896a. The clear presence of marginal statocysts in the medusa of this species places it back in the family Olindiidae of the Limnomedusae. Polyps previously attributed to *Maeotias* in San Francisco Bay are now known to belong to a *Moerisia* sp., whose medusa has also recently been found in the estuary system. Solitary *Moerisia* polyps have been found in the field amongst the general fouling fauna on floating docks in the Napa River. Small simple primary polyps of *M. marginata* were obtained in the laboratory. Polyps of *Blackfordia virginica* have been found in abundance in the field covering the valves of nonindigenous barnacles in the Napa River and laboratory-cultured colonies are pictured here along with their newly-released and juvenile medusae.

Key words: *Maeotias inexpectata*, *Maeotias marginata*, *Blackfordia virginica*, *Moerisia* sp., Olindiidae, Limnomedusae, Leptomedusae, San Francisco Bay, Cnidaria.

INTRODUCTION

Further observations in low salinity tributaries to San Francisco Bay of hydromedusae and their polyps in the genera *Maeotias*, *Blackfordia*, and *Moerisia* have revealed a number of

errors in the Mills and Sommer (1995) paper, which first described the presence of two of these invasive species in California. We take this opportunity to clarify a number of important details concerning the nomenclature and biology of *Maeotias marginata* (= *inexpectata*), *Blackfordia virginica* and *Moerisia* sp. and to add a few new observations.

*Received September 12, 1999. Accepted January 17, 2000.

RESULTS AND DISCUSSION

Maeotias marginata (Modeer, 1791)

We have recently determined, thanks to a question by Ron Ates of Zaandam in the Netherlands, that *Maeotias inexpectata* Ostroumoff, 1896 is actually a junior synonym of *Maeotias marginata* (Modeer, 1791). The intricate early history of the synonymies of this distinct, yet confusing species were enumerated by Hummelinck (1938b, 1941). Kramp (1961), missing its significance, synonymized the highly distinct *M. marginata* with *Craspedacusta sowerbii* Lankester, 1880. Examination of the figures of Baster (1765), republished by Hummelinck (1938b, 1941) with accompanying detailed description, as well as two specimens in poor condition (COEL. 2046) from the Zoological Museum, University of Amsterdam, collected in there in 1889, leaves little doubt that there is only one species of *Maeotias*, which should therefore henceforward be called *Maeotias marginata* (Modeer, 1791). The specimens of Baster, subsequently described by Modeer as *Medusa marginata*, were up to 40 mm in diameter in life (Hummelinck, 1941). Most of our Petaluma River specimens were less than 35 mm in diameter, but a few exceptional animals reaching 50 mm in diameter have been collected in nearby Suisun Slough (see below), another tributary to San Francisco Bay. In all aspects they agree with the description detailed by Hummelinck (1941) for *M. marginata*.

With regard to the correct spelling of the junior synonym *M. inexpectata*, it has been pointed out that Ostroumoff described this species twice in 1896, and although *inexpectata* (Ostroumoff, 1896b) is better Latin, this spelling of the name is predated by three months by a description using the spelling *inexpectata* (Ostroumoff, 1896a), which therefore takes precedence as the original and correct spelling of this species name.

Statocysts were not observed around the bell margin of *Maeotias marginata* (as *M. inexpectata*) by Mills and Sommer (1995). Further observation of living specimens in August 1995 and on subsequent occasions showed unquestionably that *Maeotias* does indeed have numerous marginal statocysts (see also Rees and Gershwin, 2000). Such statocysts are clearly described and illustrated by Ostroumoff (1896b), as well as by Borcea (1928), Hummelinck (1941) and Denayer (1973), so any questions about their existence can be laid to rest.

The presence of marginal statocysts undermines placement of *Maeotias* within the Anthomedusae by Mills and Sommer (1995). At this time, until molecular genetic phylogenies are able to clearly sort out some of these relationships, it seems best to restore *Maeotias* to the family Olindiidae in the Limnomedusae.

In addition to the locations summarized by Mills and Sommer (1995) for *Maeotias marginata* in the Black Sea, Sea of Azov, Loire River estuary, Chesapeake Bay, South Edisto River estuary in South Carolina, and the San Francisco Estuary system in California, *M. marginata* has also been collected at least twice in the Netherlands. It was collected during the summer of 1762 in freshwater environments of the estuarine Spaarne River near Haarlem [making that collection one of the earliest known marine introductions (J.T. Carlton, personal communication)] and during July 1889 in the brackish Plantage Muidergracht canal, Amsterdam (Hummelinck, 1938b, 1941). Both of these locations occasionally received salt water from the Zuiderzee at that time (but do not now). The occurrence of live *M. marginata* in freshwater (Baster, cited by Hummelinck 1938a, 1938b, 1941) is not out of agreement with laboratory observations (C.E.M., unpublished) that San Francisco Bay specimens can survive in pond water [0 psu (practical salinity units)] for five days in good condition, and died only on the eleventh day in entirely fresh water. *Maeotias marginata* has most recently been collected in August 1999 at several locations in the Moonsund (Väinameri) Sea area of the Baltic Sea in western Estonia in salinity near 6.5 psu (R. Vainola, personal communication; Vainola and Oulasvirta, 1999).

Within the San Francisco Estuary, *Maeotias marginata* medusae have recently been found in additional low-salinity locations in north San Francisco Bay, including the Napa River and Suisun Slough (Rees and Gershwin, 2000). Field notes from California Fish and Game and U.S. Fish and Wildlife Service collections in the upper San Francisco Estuary near the confluence of the San Joaquin and Sacramento Rivers (personal communication to J.T.R.) indicate that *M. marginata* has been present in very low salinity portions of the San Francisco Bay estuary at least since 1959, moving the date of first observation back by 33 years if true, although no preserved specimens are available for verification. *M. marginata* has not yet been found elsewhere on the Pacific coast of North America.

Additional field and laboratory work revealed another surprise about *Maeotias* in California. Although Mills and Sommer (1995) reported only male medusae in the Petaluma River, a few female *M. marginata* (among numerous males) were found in the Napa River in September 1998. Eggs produced by these females were fertilized in the laboratory and developed into tiny, simple, primary polyps without tentacles (see Rees and Gershwin, 2000), very different than those polyps figured as *Maeotias* by Mills and Sommer (1995) (see below under *Moerisia*), but not out of character with other known limnopolyps such as *Craspedacusta*. Growth of these primary polyps did not occur in laboratory culture and they subsequently disintegrated without further development.

***Blackfordia virginica* Mayer, 1910**

The first *Blackfordia virginica* specimens (medusae) were collected in the Napa River and the Petaluma River in the San Francisco Estuary, in 1970 and 1974 respectively, and were deposited in the California Academy of Science (Mills and Sommer, 1995). *B. virginica* polyps (Fig. 1a, b) were first discovered in the field in September 1997, densely covering living nonindigenous barnacles, *Balanus improvisus*, collected near the water line on floating docks in the Napa River at the public boat launch in John F. Kennedy Park (although a fragment of a *B. virginica* hydroid colony was tentatively identified and figured by Mills and Sommer (1995) from the gut of a *Maeotias marginata* medusa collected in 1993). Salinity in the Napa River was 19 psu and temperature about 16°C at the time of collection. The polyps were growing both on the outer valves and on opercular valves of the barnacles. Individual polyps and gonophores (each containing a single medusa) arise directly from creeping stolons. Both are very small, not exceeding 0.5 mm in height. The polyps have webbing between the tentacles. Positive identification of *B. virginica* was accomplished by raising medusae produced by these polyps to maturity in the laboratory. A newly-released medusa and older juvenile medusa are shown in Figure 1c and 1d.

Other than the San Francisco Bay estuary, the only other American west coast location known for *Blackfordia virginica* is Coos Bay, Oregon, where medusae were collected in both July 1998 (one specimen) and July 1999 (thousands seen) by James Carlton and identified by C.E.M. No polyps were located.

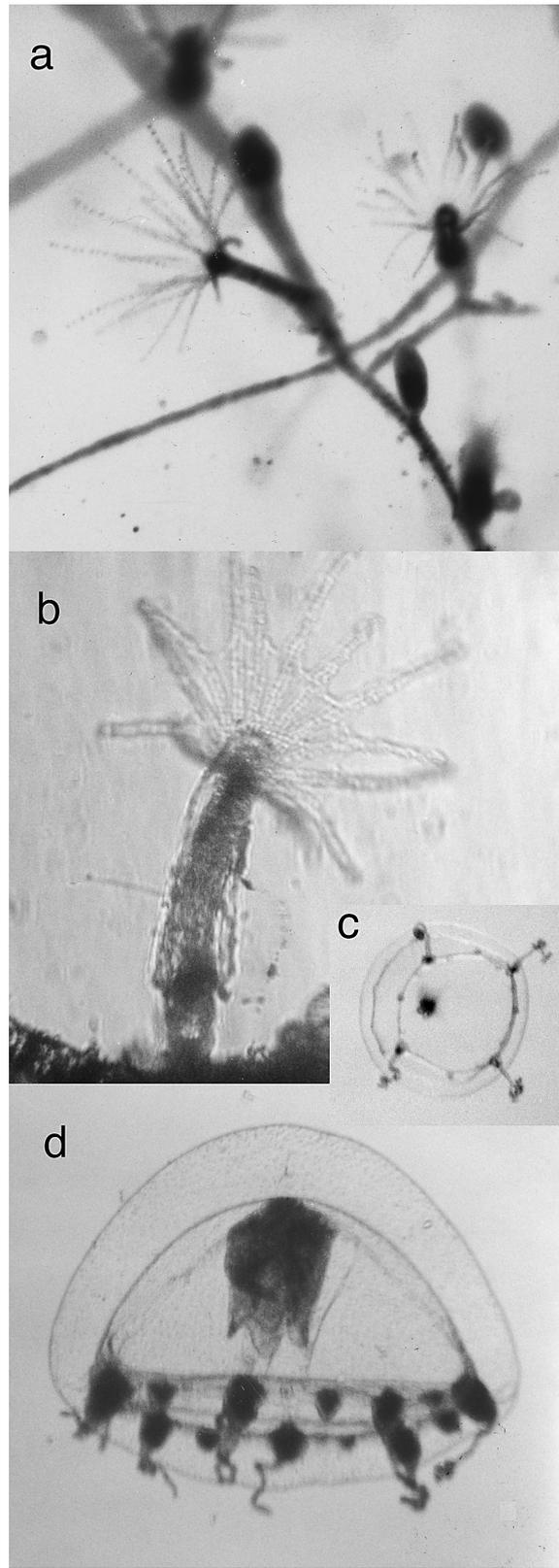


FIG. 1. – *Blackfordia virginica*. (a) polyp colony growing on glass slide, (b) single polyp showing webbing between tentacles, 0.5 mm tall measured from substrate to tip of tentacles, (c) newly-released medusa with four perradial marginal tentacles and four developing interradial tentacle bulbs, 0.8 mm bell height and diameter. (d) 16-tentacle juvenile medusa, bell 1.3 mm high and 1.6 mm diameter.

Moerisia sp.

Solitary polyps similar to those described as *Maeotias* by Mills and Sommer (1995) from the Petaluma River (collected in 1993, the first record of this hydroid in the San Francisco Estuary) have now also been found in the field in the San Francisco Estuary in the Napa River amongst the float-fouling community. These polyps have been identified through laboratory rearing as those of *Moerisia* [whose description they match, as noted by Mills and Sommer (1995)] rather than *Maeotias* (see Rees and Gershwin, 2000). Furthermore, the newly-released medusae of *Moerisia* have ocelli, which are not present in *Maeotias*, and only 4 tentacles rather than the 24 tentacles on newly-released *Maeotias marginata* (see Rees and Gershwin, 2000). Adult *Moerisia* sp. medusae have subsequently been collected in the same Suisun Slough site in the San Francisco Estuary where *M. marginata* was also present (Rees and Gershwin, 2000).

The San Francisco Bay system is now at least the third region in which all three genera of invasive hydromedusae, *Maeotias*, *Blackfordia* and *Moerisia* have become established. All are considered to be native to the Black Sea region (Calder and Burrell, 1969) and have also all been reported in the Chesapeake Bay (Calder and Burrell, 1969). The three genera are tolerant of very low salinities, but there may be other variables that cause them to move together. *Maeotias* and *Blackfordia* appeared together with the Atlantic American and European hydromedusa *Nemopsis bachei* in the Loire estuary (Denayer, 1973). [*Nemopsis bachei* has also been collected in the Zuiderzee (Kramp, 1961), not far from the region where *Maeotias* was found there, and is common in the Chesapeake Bay (Calder, 1971)]. A fourth "Sarmatic" hydroid (thought native to the Black and/or Caspian Seas), *Cordylophora caspia* (Pallas, 1771) which does not produce medusae, is also found in very-low salinity sites in the San Francisco estuary (Cohen and Carlton, 1995). *C. caspia* is apparently the most invasive of the group, and is known to be established in a large number of very-low salinity sites worldwide.

ACKNOWLEDGEMENTS

Several people contributed to the corrections and observations reported here. Most recently, Ron Ates

inquired whether Modeer's *Medusa marginata* might be the same as *Maeotias inexpectata*. The 1997 collections of the polyps of *Blackfordia virginica* and *Moerisia* sp. were made during the Fourth San Francisco Bay Expedition, a rapid assessment inventory for nonindigenous marine species organized by Andrew Cohen. The 1998 collection of the female *M. marginata* and subsequent development of primary polyps occurred during the Fourth Workshop of the Hydrozoan Society at the Bodega Marine Laboratory, University of California. Thanks to Jim Carlton for sharing his collections of *Blackfordia virginica* from Oregon and to Shin Kubota for help in collecting in the Napa River. Thanks to Lisa Gershwin, who followed up the tip for *Maeotias* in Suisun Slough and for noting the precedence of *inexpectata* over *inexpectata*. Thanks to Dale Calder, who was the first to see the likelihood that our large solitary polyps were *Moerisia* rather than *Maeotias*, and for providing helpful comments on this manuscript. Thanks to Rob van Soest for supplying Dutch material from 1889 for study, and to Risto Vainola, who apprised us of the discovery of *Maeotias* in the Baltic Sea in 1999. J.T.R. wishes to acknowledge aid from the Interagency Ecological Program and the California Department of Water Resources (DWR agreement #B-81818) to California State University, Hayward and the CSUH Bay/Delta Shore Institute. We are sorry to preside over the demise of yet another imaginative species name with this paper.

REFERENCES

- Baster, J. – 1765. *Natuurkundige Uitspanningen*, 2(2): 55-108, Tables V-IX and *Opuscula subseciva*, 2(2): 53-99, Tables V-IX.
- Borcea, I. – 1928. *Maeotias inexpectata*, dans le Liman de Razelm (Roumanie). *Ann. Sci. Univ. Jassy*, 15: 286-298.
- Calder, D.R. – 1971. Hydroids and hydromedusae of southern Chesapeake Bay. *Virginia Inst. Mar. Sci., Special Papers Mar. Sci.*, 1: 1-125.
- Calder D.R. and V.G. Burrell Jr. – 1969. Brackish water hydromedusa *Maeotias inexpectata* in North America. *Nature*, 222: 694-695.
- Cohen, A.N. and J.T. Carlton. – 1995. *Biological Study: Non-indigenous aquatic species in a United States estuary: A case study of the biological invasions of the San Francisco Bay and Delta*. U.S. Fish and Wildlife Service and the National Sea Grant College Program, Connecticut Sea Grant, 246 pp. and 5 unpaginated appendices.
- Denayer, J.-C. – 1973. Trois méduses nouvelles ou peu connues des côtes françaises: *Maeotias inexpectata* Ostroumov, 1896, *Blackfordia virginica* Mayer, 1910, *Nemopsis bachei* Agassiz, 1849. *Cah. Biol. Mar.*, 14: 285-294.
- Hummelinck, P.W. – 1938a. Een nederlandse vondst van de zoetwaterkwal *Craspedacusta* in 1762. *Hand. Hydrobiol. Club, Amsterdam*, 1(2): 1-3.
- Hummelinck, P.W. – 1938b. Ein niederländischer Fund von

- Craspedacusta marginata* (Modeer) im Jahre 1762. *Zool. Anz.*, 124 (11/12): 333-336.
- Hummelinck, P.W. – 1941. Medusenfunde von *Maeotias marginata* (Modeer) in den Niederlanden. *Zool. Anz.*, 136 (1/2): 9–17.
- Kramp, P.L. – 1961. Synopsis of the medusae of the world. *J. Mar. Biol. Assoc. U.K.*, 40: 1-469.
- Mills, C.E. and F. Sommer. – 1995. Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexpectata* and *Blackfordia virginica*, invade San Francisco Bay. *Mar. Biol.*, 122: 279-288.
- Ostroumoff, A. – 1896a. Zwei neue Relicten-Gattungen im Azow'schen Meere. *Zool. Anz.*, 19(493): 30.
- Ostroumoff, A. – 1896b. Résultats scientifiques de l'expédition "d'Atmanai". *Bull. Acad. Sci. St-Petersbourg*, Sér 5, 4-5: 389-408. (In Russian)
- Rees, J.T. and L.A. Gershwin. – 2000. Non-indigenous hydromedusae in California's upper San Francisco Estuary: life cycles, distribution, and potential environmental impacts. *Sci. Mar.*, this volume.
- Vainola, R. and P. Oulasvirta. – 1999. Hyttelomainen hydromedusa loytyi Viron Vainamerelta [An invading hydromedusa from Moonsund Sea area, Estonia]. *Helsingin Sanomat*, 25.9.1999: D3. (Also on the Internet at: <http://www.saunalahti.fi/~alleco/nettimedusa2.html>).