



Moitessier's pea clam *Pisidium moitessierianum* (Bivalvia, Sphaeriidae): a cryptogenic mollusc in the Great Lakes

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Received 19 November 1999; in revised form 24 May 2000; accepted 20 June 2000

Key words: bivalve mussel, *Pisidium*, Sphaeriidae, Great Lakes, cryptogenic species, biological invasion

Abstract

Pisidium moitessierianum Paladilhe, 1866, a small pea clam native to Europe, was identified for the first time from the lower Great Lakes basin based on an examination of historical collections of *Pisidium* performed by V. Sterki in 1894 and 1903 and new material collected during 1997 and 1998. During recent surveys, *P. moitessierianum* individuals were found in the St. Clair River delta, Lake St. Clair and western Lake Erie, but were not detected in the Detroit River or western Lake Ontario. *Pisidium moitessierianum* was collected on sand, silty sand and mud substrata from water depths ranging between 0.6 and 5.4 m. Populations occurred at an average density of 51 ind. m⁻² and included juveniles and adults. All individuals were less than 2.0 mm in length. We examined the structure of the umbos and hinge, surface sculpture and shape of the shell, and the anatomy of gills, mantle and nephridia in populations from the lower Great Lakes and Ukrainian inland basins (Dnieper River and Lake Beloye). The results indicated that the Great Lakes' pea clams match European specimens of *P. moitessierianum* in these conchological and anatomical characteristics. As with other nonindigenous sphaeriids in the Great Lakes, *P. moitessierianum* was likely introduced through shipping activities into the Great Lakes, possibly as early as the 1890s.

Introduction

Human activities have greatly increased the rate and spatial scale of dispersal of nonindigenous aquatic species around the world. The Laurentian Great Lakes provide perhaps the best documented case studies of biological invasion of nonindigenous species, and molluscs are probably the best studied group of introduced invertebrates in this region (Hall & Mills, 2000). Taxonomic work on molluscan fauna of the Great Lakes basin and adjacent waters by the late 1800s permitted subsequent workers to detect at least nine species of gastropods and eight species of bivalves that had been transferred to this region and that established reproducing populations (Table 1). Mills et al. (1993) and Zaranko et al. (1997) reported that molluscs account for roughly 10% of all recognized introductions in the Great Lakes-St. Lawrence River system. However, this fraction of introduced mol-

luscs appears underestimated because some molluscan taxa recognized as introductions in this region (e.g. *Pisidium henslowanum* and *P. supinum*; Clarke, 1981) were not taken into account in Mills et al. (1993) and Zaranko et al. (1997).

Two of the most notorious invaders in the Great Lakes are the Ponto-Caspian bivalves *Dreissena polymorpha* and *D. bugensis*, both of which were found in the late 1980s. Since its discovery in 1988, *D. polymorpha* has dispersed throughout the Great Lakes basin and invaded several major neighbouring drainages including the St. Lawrence, Hudson and Mississippi rivers (Hebert et al., 1989; Ludyanskiy et al., 1993). *Dreissena bugensis* is also spreading, albeit more slowly, and now ranges from the Detroit River to the St. Lawrence River (Mills et al., 1996a; I.A. Grigorovich, unpubl. data). Rapid dispersal and colonization of dreissenids were attributed

Table 1. Introduced molluscs established in the Great Lakes-St. Lawrence system since the 1860s. Year of discovery of *Pisidium amnicum* that was misidentified as North American native *Pisidium bakeri* at time of first sighting is marked with*

Class	Family	Species	Common name	Year of Discovery	Native region	Reference	
Bivalvia	Sphaeriidae	<i>Pisidium amnicum</i> (Müller, 1774)	greater European pea clam	1897*	Eurasia-Africa	Mills et al. (1993)	
		<i>Pisidium henslowanum</i> (Sheppard, 1825)	Henslow's pea clam	<1916	Eurasia	Herrington (1962)	
		<i>Sphaerium corneum</i> (Linnaeus, 1758)	European fingernail clam	1952	Eurasia	Herrington (1962)	
		<i>Pisidium supinum</i> Schmidt, 1850	humpback pea clam	1959	Europe	Clarke (1981)	
	Corbiculidae	<i>Corbicula fluminea</i> (Müller, 1774)	Asiatic clam	1980	Asia	Mills et al. (1993)	
	Dreissenidae	<i>Dreissena polymorpha</i> (Pallas, 1771)	zebra mussel	1988	Ponto-Caspian	Hebert et al. (1989)	
		<i>Dreissena bugensis</i> Andrusov, 1897	quagga mussel	1989	Ponto-Caspian	Mills et al. (1996a)	
	Unionidae	<i>Lasmigona subviridis</i> (Conrad, 1835)	lasmigona	<1959	Atlantic	Mills et al. (1993)	
	Gastropoda	Valvatidae	<i>Valvata piscinalis</i> (Müller, 1774)	European valve snail	1897	Eurasia	Mills et al. (1993)
		Viviparidae	<i>Viviparus georgianus</i> (Lea, 1834)	banded mystery snail	<1906	Mississippi	Mills et al. (1993)
<i>Cipangopaludina chinensis malleata</i> (Reeve, 1863)			Chinese mystery snail	1931	Asia	Mills et al. (1993)	
<i>Cipangopaludina japonica</i> (Von Martens, 1860)			Japanese mystery snail	1940s	Asia	Mills et al. (1993)	
Bithyniidae		<i>Bithynia tentaculata</i> (Linnaeus, 1767)	faucet snail	1871	Eurasia	Mills et al. (1993)	
Hydrobiidae		<i>Gillia altilis</i> (Lea, 1841)	buffalo pebble snail	1918	Atlantic	Mills et al. (1993)	
		<i>Potamopyrgus antipodarum</i> (Gray, 1843)	New Zealand mud snail	1991	New Zealand	Zaranko et al. (1997)	
Pleuroceridae		<i>Elimia virginica</i> (Say, 1817)	horn snail	1860	Atlantic	Mills et al. (1993)	
Lymnaeidae		<i>Radix auricularia</i> (Linnaeus, 1758)	European ear snail	1901	Eurasia	Mills et al. (1993)	

to their high fecundity, production of adhesive byssal threads, possession of pelagic larval stages and wide range of physiological tolerances (Mackie, 1991; Morton, 1997). Another invasive bivalve, *Corbicula fluminea*, was discovered on Vancouver Island, British Columbia in 1924 and now occurs across much of the United States and southern Ontario, including the St. Clair River-western Lake Erie corridor (McMahon, 1982, 2000; Mills et al., 1993; I.A. Grigorovich, unpubl. data).

Sphaeriid clams lacking planktonic larvae are also capable of rapid dispersal and colonization of new geographical areas because they possess passive means of dispersal, ability to tolerate adverse environmental conditions, and hermaphroditic and ovoviparous nature which allows establishment of a new population from a single individual (Mackie, 1979; Burky, 1983; Stadnichenko, 1984). Among 29 species of sphaeriids known from the Great Lakes, four are recognized as introductions from Europe (Mackie et al., 1980; Clarke, 1981). Three of these species – *Sphaerium corneum*, *Pisidium amnicum* and *P. henslowanum* – subsequently extended their ranges to the lower Great Lakes, St. Lawrence River and several adjacent basins (Herrington, 1962; Mackie et al., 1980; Mills et al., 1996b; this study). Conversely, the

fourth species, *P. supinum*, has been recorded only from Lake Ontario (Mackie et al., 1980).

Because new sphaeriid taxa were described well into the early 1900s (e.g. Sterki, 1895, 1905), some exotic species could have been erroneously reported as North American or Holarctic in distribution. For example, Mills et al. (1993) described a noteworthy example of how the introduced pea clam, *P. amnicum*, was misidentified and treated as a North American species, *P. bakeri*, for >18 years after its discovery in the Great Lakes in 1897. Furthermore, small populations of exotic species may remain undetected for an extended time and become discovered only after populations have grown large. Two exotic sphaeriid species, *S. corneum* and *P. supinum*, were detected in the Great Lakes in the 1950s; however, it is unclear whether they were recent invaders at that time (Herrington, 1962; Clarke, 1981). We cannot be certain how these sphaeriids invaded North America, but their introductions may have resulted from the transfer of sand, mud or gravel ballast carried by transoceanic ships prior to 1900. In practice, introduced species of the Sphaeriidae could not be easily identified at the time of their arrival in North America because the North American and European species-level classifications in this group employed different criteria for

recognizing species (Herrington, 1962; Kuiper, 1962; Ellis, 1978; Piechocki, 1989).

All these arguments suggest that the actual number of introduced sphaeriid species in the Great Lakes may be underestimated. We tested this possibility by sampling a series of habitats in the lower Great Lakes in search of introduced sphaeriid species. We selected the Lake Erie-St. Clair River region for our survey where unusual concentrations of introduced clams and other nonindigenous taxa have been observed probably as a result of ballast discharge from commercial and recreational boats (Mills et al., 1993).

Here we confirm the presence of reproducing populations of the Moitessier's pea clam, *P. moitessierianum*, in 4 of 53 sites in the Lake Erie-St. Clair River corridor. Subsequent examination of type material of *P. punctatum* s.l. revealed that *P. punctatum* s.str. and *P. punctatum* var. *armatum* Sterki, 1905 correspond to the description of Eurasian native *P. moitessierianum* Paladilhe, 1866. Although we discuss some taxonomic aspects of these intraspecific forms of *P. punctatum* s.l. Sterki, 1895, we did not attempt to review the present state of knowledge about relationships between the former species and *P. moitessierianum*, which is the topic of a separate paper (Korniushin et al., in review). In this study, we describe morphological and reproductive characteristics of specimens collected from the lower Great Lakes and contrast them with characteristics of individuals from Ukrainian basins. We also review aspects of *P. moitessierianum*'s biology, ecology and distribution in Eurasia. Following Chapman & Carlton (1991), we analyze the ecological and geographical aspects of *P. moitessierianum* occurrence in the Laurentian Great Lakes to deduce its origin in North America.

Materials and methods

Between August 1997 and October 1998, 154 benthic samples were collected from 53 sites on the Detroit and St. Clair rivers, on Lake St. Clair, and on the western basin of Lake Erie (Figure 1). These habitats are situated within the Lake Erie-St. Clair River zoogeographical region, defined by Clarke (1981) based on the occurrence of freshwater molluscs. The surveyed sites represent a combination of riverine and lacustrine habitats. Of 53 sites, 22 were situated in shallow water and nearshore zones (<1.5 m). One of these sites, located in the Detroit River near Amherstburg, Ontario, was surveyed routinely on a monthly sched-

ule from March 1998 to July 1999. On 27 August 1998, additional collections were made at five sites on the western basin of Lake Ontario in a coastal zone (≤ 27 m). Bottom substrates at the sites ranged from silt and sand to gravel and bedrock. Sites <1.5 m depth were sampled mainly from a boat using a sled dredge (inlet 0.38 m, mesh 250 μm) or by sweeping a dip net (mesh opening 250 μm) through submerged vegetation and across rocks and bottom substrates. At deeper sites (i.e. between 1.5 and 27 m), samples were collected using a ponar grab (area 225 cm^{-2}) or bottom sled dredge. The sled dredge was lowered to the bottom and dragged between 10 and 100 m depending on the type and amount of bottom sediments.

Ukrainian collections of *P. moitessierianum* were gathered from the Dnieper River, upstream from the Kanev reservoir, near Kiev, during July 1987 and from Lake Beloye, Volyn Region, during September 1998. Ukrainian samples were collected using a drag dredge.

All samples were initially preserved in 5% sugar-formalin. In the laboratory, samples were washed through a series of sieves (with mesh opening of 2000–125 μm) and transferred to 70% ethanol within a few days. This technique permitted preservation and subsequent microscopic analysis of *P. moitessierianum* soft tissues.

Specimens of *P. moitessierianum* were separated from other material and dissected under a stereomicroscope. We employed both light (12–100 \times) and scanning electron microscopy (S.E.M.; 70–600 \times ; JEOL JSM-6300 Stereoscan) to examine morphological characters of *P. moitessierianum*. In total, we examined 50 specimens of *P. moitessierianum* from the lower Great Lakes and >50 individuals from Ukrainian basins.

Voucher specimens of *P. moitessierianum* collected from the lower Great Lakes were deposited in the molluscan collections of the American Museum of Natural History, New York, and the Field Museum of Natural History, Chicago.

In addition, one of us (AVK) examined historical collections of *Pisidium punctatum* s.l. – two syntypes of *P. punctatum* Sterki, 1895, Museum of Comparative Zoology, Cambridge, Massachusetts (MCZ) 112563, Tuscarawas River, Bear Run, tributary of Mahoning River, Portage Co., Ohio, Coll. V. Sterki, 1894; five syntypes of *P. punctatum* var. *armatum* Sterki, 1905, Carnegie Museum of Natural History, Pittsburg (CMNH) 4642, Tuscarawas River, Navarre, Stark Co., Ohio, Coll. V. Sterki, 28 October 1903.

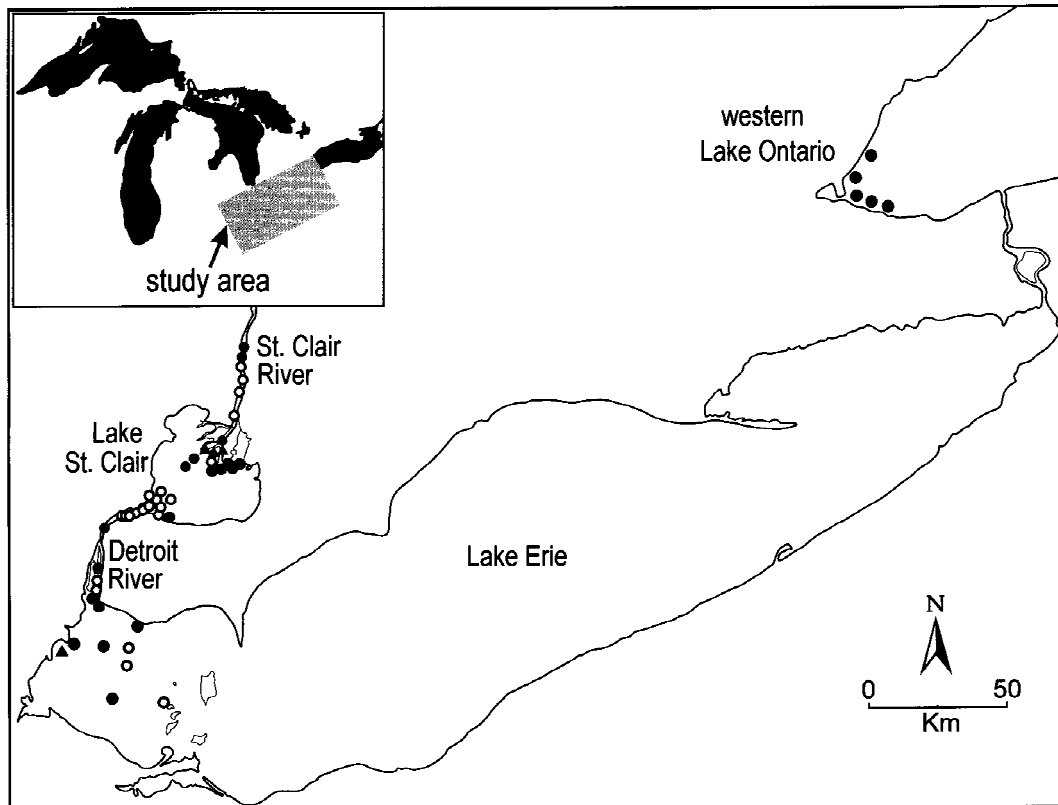


Figure 1. Map showing localities of *Pisidium moitessierianum* (triangles) and other *Pisidium* taxa (solid circles) in the lower Great Lakes during July–October 1997 and March–October 1998. Open circles denote the absence of *Pisidium* spp.

The structure of nephridia and gills (i.e. ctenidia) has proved successful for diagnosing the genus *Pisidium* (Korniushin, 1997, 1998). We used both soft tissues and shell characteristics for identification of *P. moitessierianum*. Anatomical structures were studied in dissected specimens *in situ*. Gills and mantle were stained respectively with Grenacher's carmine and water eosine, and then mounted in Canada balsam to provide permanent slides for detailed observations.

As illustrated in Figure 2, we measured 1. shell length as the distance between the most remote points of the anterior and posterior margins; 2. shell height as the distance from the tip of the umbo to the inferior, most remote point of ventral margin; 3. shell width as the distance between the most remote points in the contour of frontal sections through valves enclosed; and 4. hinge height as the distance between dorsal and ventral margins of the hinge plate at the cardinal teeth. Shell dimensions were measured with an ocular micrometer to the nearest 0.01 mm. We also measured brood size. The three structural indices, including the

ratio of shell height – shell length, ratio of shell width – shell height, and ratio of hinge height – shell height, were used to characterize the shell structure.

Differences in shell dimensions between the Great Lakes and Ukrainian populations were assessed using *t*-tests. We limited analysis of geographic size variation to modern North American and Ukrainian collections of *P. moitessierianum*, which were produced by using fairly similar collecting and processing techniques. To identify the primary differences in shell shape among North American and European populations, we also conducted a Multivariate Analysis of Variance (MANOVA) on the three structural shell indices, using the geographical source of the populations (North America/Europe) as an independent, categorical variable.

Abbreviations

A1 – anterior inner lateral tooth; A2 – anterior lateral tooth; A3 – anterior outer lateral tooth; aa – anterior

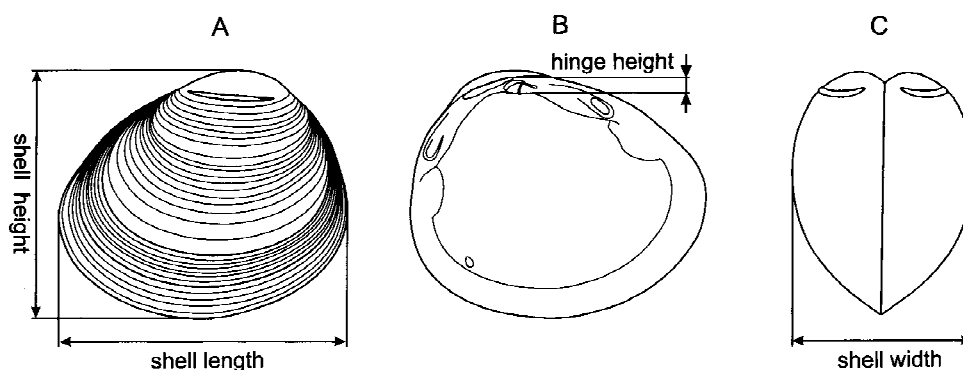


Figure 2. External (A) and internal (B) lateral view of left valve and frontal view (C) of valves enclosed of *Pisidium moitessierianum* showing measurements of shell length, shell height, shell width and hinge height parameters.

adductor; bp – brood pouch; C2 – inner cardinal tooth; C3 – cardinal tooth; C4 – outer cardinal tooth; dg – digestive gland; dl – dorsal lobe; es – exhalant siphon; esr – exhalant siphon retractor; isr – inhalant siphon retractor; irm – inner radial mantle muscles; ll – lateral loop; lp – labial palp; orm – outer radial mantle muscles; P1 – posterior inner lateral tooth; P2 – posterior lateral tooth; P3 – posterior outer lateral tooth; pa – posterior adductor; pt – pericardial tube.

Results and discussion

Morphometrics

Because some morphological features of adults may differ in young *Pisidium*, we limit descriptions of the shell characteristics and soft tissues largely to adult *P. moitessierianum* with a shell length ≥ 1.3 mm.

Overall structural indices of *P. moitessierianum* shell did not differ significantly between the continents (MANOVA, Wilks' lambda=0.77, $F=2.6$, $df=3, 26$, $P=0.072$) (Table 2). However, univariate tests indicated that North American and European specimens differed significantly in the shell height to shell length ratio ($F=5.0$, $df=1, 28$, $P=0.033$), but not with respect to the shell width to shell height ratio ($F=0.001$, $df=1, 28$, $P=0.977$) or the hinge height to shell height ratio ($F=0.6$, $df=1, 28$, $P=0.449$). Mean adult shell length for North American individuals was slightly but insignificantly (t -test, $P=0.16$) larger than that observed for their European counterparts (see Table 2). The differences in shell height (t -test, $P=0.34$), shell width (t -test, $P=0.59$) and hinge height (t -test, $P=0.36$) were also statistically insignificant between the continents.

Specimens of *P. moitessierianum* examined in this study ($n>100$) were characterized by valve size not exceeding 1.9 mm. Maximum adult shell length of *P. moitessierianum* in the Great Lakes is closely matched by that (1.8 mm) observed in Lake Pääjärvi, southern Finland (Holopainen & Hanski, 1986). In contrast, Stadnichenko (1984) reported that *P. moitessierianum* reaches a length of 2.8 mm in the rivers Psel and Zherev, Dnieper River drainage, Ukraine. Nevertheless, our field observations on the North American and European populations do not support this size pattern. The largest *P. moitessierianum* we have observed in European basins had valves 2.3 mm long (see Kornushin, 1996). Thus, *P. moitessierianum* is distinctive by its very small size. The maximum adult shell length of *P. moitessierianum* overlaps only values recorded for three other *Pisidium* taxa from the Great Lakes basin, namely, *Pisidium cruciatum* Sterki, 1895 (2.0 mm), *Pisidium insigne* Gabb, 1868 (2.0 mm), and *P. punctatum* s.l. (1.7 mm) (Clarke, 1981).

Shell and viscera morphology

Great Lakes individuals of *P. moitessierianum* possess punctal canals (i.e. pores) extending from the internal surface of the shell to the outer periostracum (Figure 3A–C). These canals are thought to facilitate gas exchange and waste removal when the valves are closed (Burky, 1983). S.E.M. examination shows that these canals do not penetrate the outer shell layer (Figure 4). European *P. moitessierianum* specimens differ from their North American counterparts by the absence of punctal canals (Figure 3D). We observed considerable variation among individuals from the Great Lakes in the density of punctal canals and therefore question their diagnostic utility. Similar intra- and interpop-

Table 2. Morphometric characteristics of *Pisidium moitessierianum* shells in the lower Great Lakes and Ukrainian waterbodies. All dimensions are in mm. Numbers represent mean and standard deviation (in parentheses). Mean values that are significantly different between localities are marked with*

Locality	Dimensions					Indices		
	Number of clams	Shell length	Shell height	Shell width	Hinge height	Shell height – Shell length ratio	Shell width – Shell height ratio	Hinge height – Shell height ratio
Great Lakes	15	1.51 (0.20)	1.34 (0.18)	0.76 (0.35)	0.09 (0.01)	0.88* (0.01)	0.55 (0.20)	0.064 (0.005)
Ukrainian basins	15	1.42 (0.14)	1.28 (0.13)	0.70 (0.26)	0.08 (0.02)	0.90* (0.01)	0.55 (0.20)	0.062 (0.009)

ulation variability in the density of punctal canals established for the Eurasian population of *Pisidium casertanum* (Poli, 1795) was attributed to exposure to different environmental situations (Araujo & Korniusshin, 1998). The greater number of punctal canals can ensure more intensive oxygen uptake in habitats with low oxygen tension. This fits well with our observations of *P. moitessierianum* from the lower Great Lakes. Animals collected from mud had a greater density of punctal canals than comparable individuals sampled from sand substrates (Figure 3A–B).

Individuals of *P. moitessierianum* from the Great Lakes resemble those from Ukrainian basins in gross shell morphology and correspond to published descriptions (Kuiper, 1962; Ellis, 1978; Stadnichenko, 1984). First, shell outline varies from rounded to triangular-trapezoid in shape (Figure 4A, B). The shell is typically rather high in appearance (mean shell height – shell length ratio 0.88–0.90) and moderately inflated (mean shell width to shell height ratio 0.55). The most prominent points of the anterior and posterior margins of the shell are located at a point substantially lower than 1/2 shell height (see Figures 2 and 4A, B). The umbos barely project over the dorsal shell margin and exhibit some flattening (Figure 4A, B). On the dorsal shell side near the umbos, exists a fold (or ridge) disposed parallel to the growth lines (and separating the embryonic and definitive sections of the valve). The Moitessier's pea clam is quite thick-shelled. Its external surface is sculptured with coarse, concentric, uniformly-spaced striae (Figure 4C, D). The hinge is typically long and arched; the hinge plate is narrowed at the cardinal teeth and becomes thicker toward the lateral teeth (Figure 5A, B). In the right valve, the cardinal tooth (C3) is slightly curved and narrowed at its center and thickened towards the ends. Its posterior arm is more than twice the thickness of the anterior arm and is bifurcated. In the left valve, the

inner cardinal tooth (C2) has an appearance of a peg-like triangular structure and the outer cardinal tooth (C4) appears as a thin, slightly curved plate. The lateral teeth are swollen and massive. The ligament pit is enclosed (not visible from the dorsal side), short and relatively wide.

The anatomical characteristics of soft tissues could not be examined in Sterki's type material because the museum specimens were dry. We limit descriptions of the soft tissues to recently collected individuals from the lower Great Lakes and Ukrainian inland basins (Dnieper River and Lake Belye). *Pisidium moitessierianum* individuals from North America and Europe were similar with respect to the anatomy of gills, mantle and nephridia. The gill (i.e. ctenidium) is comprised of a single inner demibranch (Figure 6A–C). *Pisidium moitessierianum* lacks a normally developed outer demibranch (Korniusshin, 1997, 1998). A brood pouch composed of 9–10 filaments is positioned on the dorsal side of each of the two gills (Figure 6B, C). There is only an exhalant mantle cavity siphon having one pair of retractors (Figure 6D, E). The inhalant siphon is lacking. Instead, the mantle edges form a branchial-pedal slit with motile edges. However, retractors of the reduced inhalant siphon are present (Figure 6E). Inner radial muscles of the branchial-pedal slit are grouped in five poorly developed bundles, which are hardly visible without staining (Figure 6E). The outer radial mantle muscles are relatively long. The dorsal lobe of nephridium is clearly reduced, broad, and only slightly cleft (Figure 6F, G). The lateral loop adjoins the dorsal lobe, producing the S-shaped structure.

Identity of *Pisidium moitessierianum*

P. moitessierianum can be discriminated from other species of *Pisidium* native to North America by the following combination of features (Odhner, 1923; El-

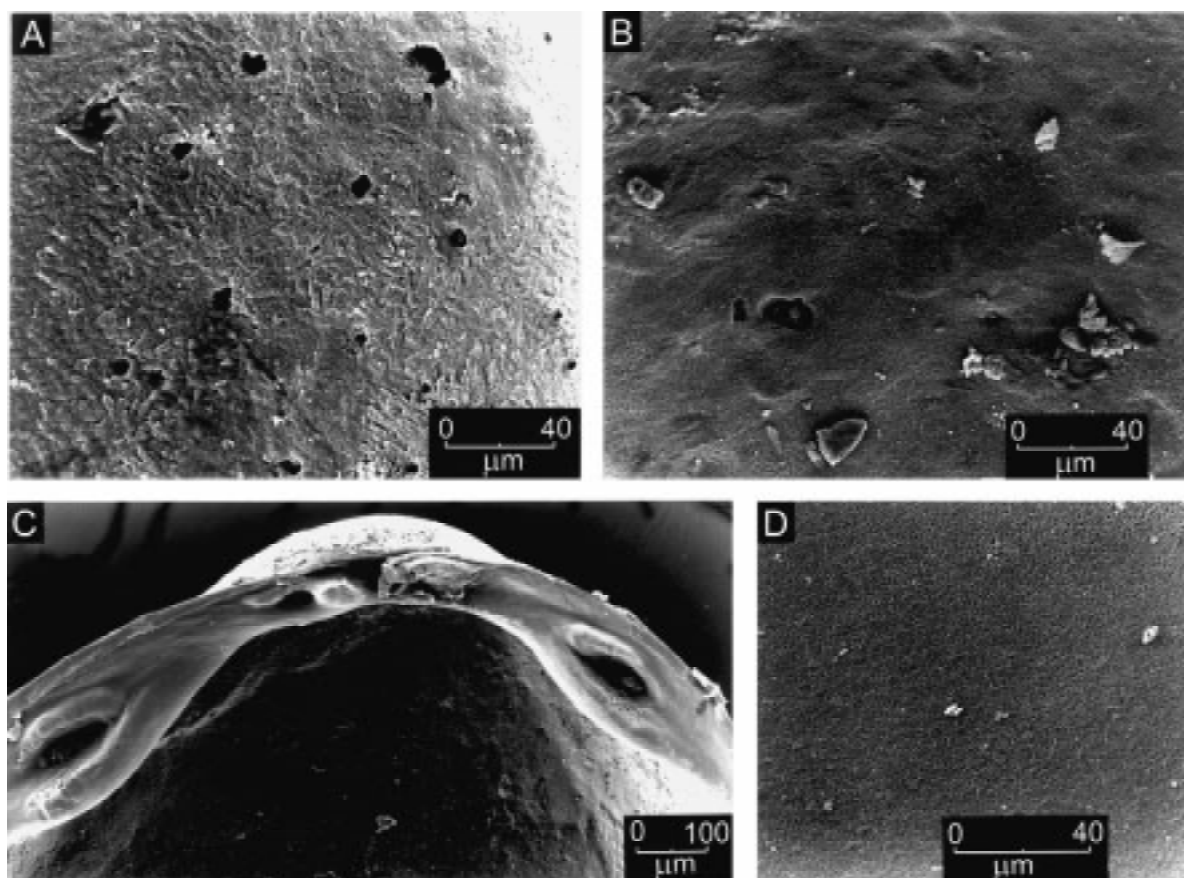


Figure 3. Features of inner face of *Pisidium moitessierianum* shell under S.E.M.: Great Lakes' specimens from mud habitat showing high density of punctal canals (A) and from sand habitat showing low density of punctal canals (B); lower magnification of region adjacent to hinge plate (C); Dnieper River individual lacking punctal canals on inner surface of shell (D).

lis, 1978; Piechocki, 1989; Korniusshin, 1996, 1998): umbos flattened, bordered by crescent-shaped folds; shell thick, sculptured with ribs; cardinal teeth C3 and C4 curved; lateral teeth swollen and heavy; dorsal lobe of nephridium slightly cleft, profoundly reduced; and inner radial muscles of pedal slit grouped in five poorly developed bundles. Another important character distinguishing *P. moitessierianum* from most North American native *Pisidium* taxa (excluding aforementioned *P. cruciatum*, *P. insigne* and *P. punctatum* s.l.) is the small adult shell length, typically less than 2.0 mm; North American congeners usually have a shell length ≥ 3.0 mm long (for details see Clarke, 1981).

Examination of type specimens of *P. punctatum* s.l. designated as *P. punctatum* s.str. (MCZ 112563) and *P. punctatum* var. *armatum* Sterki, 1905 (CMNH 4642) revealed that these specimens are not distinguishable from *P. moitessierianum* Paladilhe, 1866 in the shape and condition of the folds around the umbos

and the hinge morphology. A provisional synonymy of *P. punctatum* s.str. and *P. punctatum* var. *armatum* Sterki, 1905, under *P. moitessierianum* is, therefore, proposed here, until the taxonomic status of *Pisidium punctatum* s.l. Sterki, 1895 can be revised.

The shell and hinge outline of *P. moitessierianum* resembles that of another North American species, *P. cruciatum*, though they can be distinguished by differing orientation of the umbonal folds. Unlike *P. moitessierianum*, the latter possesses the U-shaped umbonal folds whose ends are perpendicularly directed to the ribs covering the outer periostracum. *P. moitessierianum* is superficially similar to young *P. compressum* Prime, 1852 and *P. lilljeborgi* var. *crisatum* Sterki, 1928 (synonym: *Pisidium lilljeborgi* Clessin, 1886) which have the folds of similar structure and orientation on the umbos. However, the former species is identifiable by its strong and heavy hinge and moderately inflated shell.

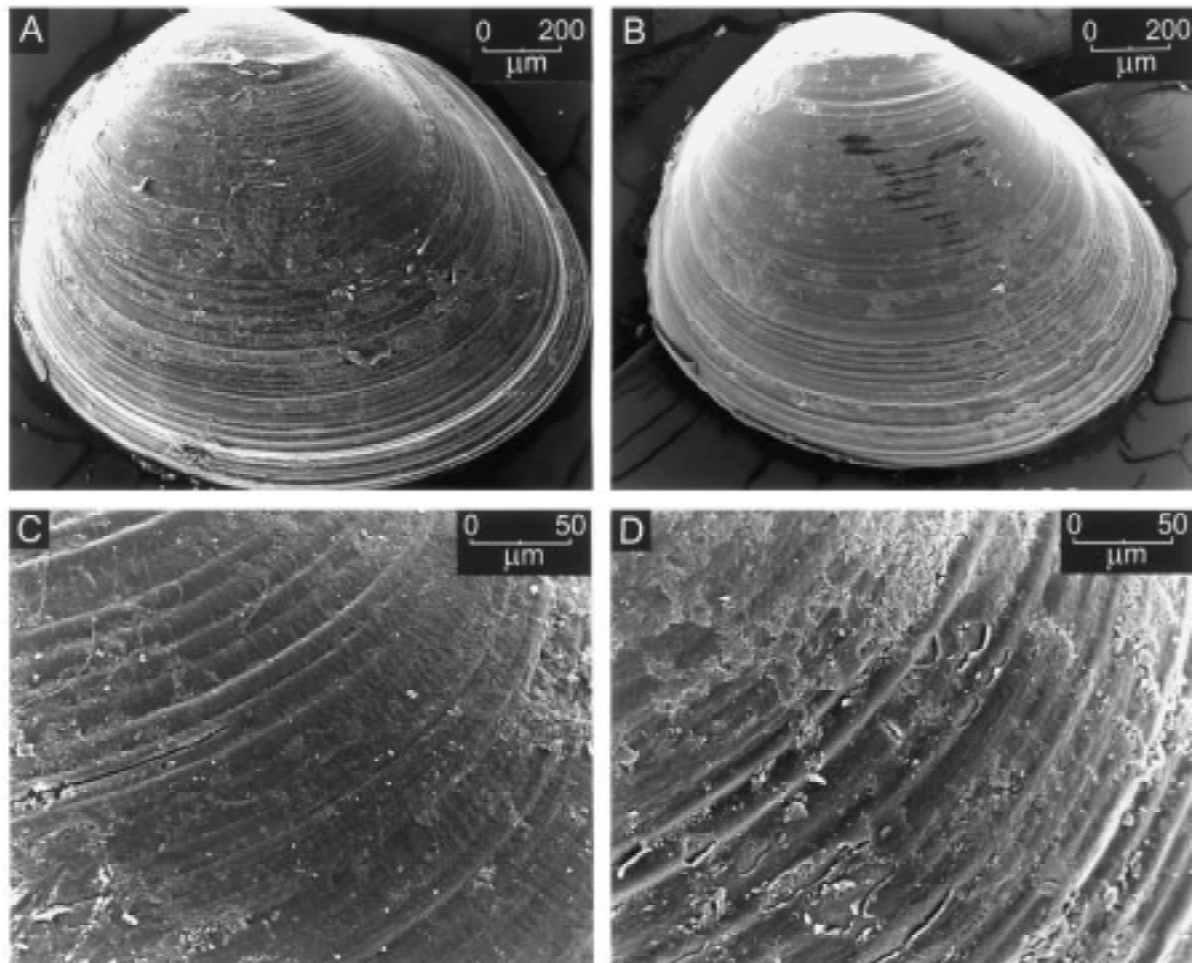


Figure 4. External features of *Pisidium moitessierianum* shell under S.E.M.: lateral view of right valve of individuals from the Great Lakes (A) and from Dnieper River (B); outer surface of right valve at high magnification showing sculptural ribs in specimens from the lower Great Lakes (C) and from Dnieper River (D).

Biology and ecology

Small, localized populations of *P. moitessierianum* ranging from solitary clams to 178 ind. per m² were found in the lower Great Lakes between July 1997 and October 1998. Abundance of this sphaeriid was on average 51 ind. m⁻² (SD=86) in western Lake Erie, Lake St. Clair and St. Clair River delta. Even this density may, however, overestimate abundance as few specimens were found in quantitative samples due to the small sampling area of the ponar grab. By comparison, the species typically achieves densities of 40–50 ind. m⁻² in the Volga River delta, Russia (Pirogov & Starobogatov, 1974). Frequency of occurrence of *P. moitessierianum* in the samples from the lower Great Lakes was only 4.5%, indicating a patchy distribution.

Unlike *P. moitessierianum*, other *Pisidium* spp. were encountered in >20% of samples.

In western Lake Erie, individuals of *P. moitessierianum* with a shell length of 1.1–1.2 mm strongly dominated the population, accounting for 40.0% of the population ($n=35$) in May 1998 (Figure 7). Small clams (≤ 0.8 mm) made up ca. 11.4% of the population of *P. moitessierianum* and were more abundant than larger individuals (1.7 mm; 2.9%). Size classes greater than 1.8 mm were not detected in May, but appeared in samples collected during August 1998. Observed differences in population size structure between May and August of 1998 may indicate the growth of individuals in the population during that period; however, detailed life history studies are needed to verify this.

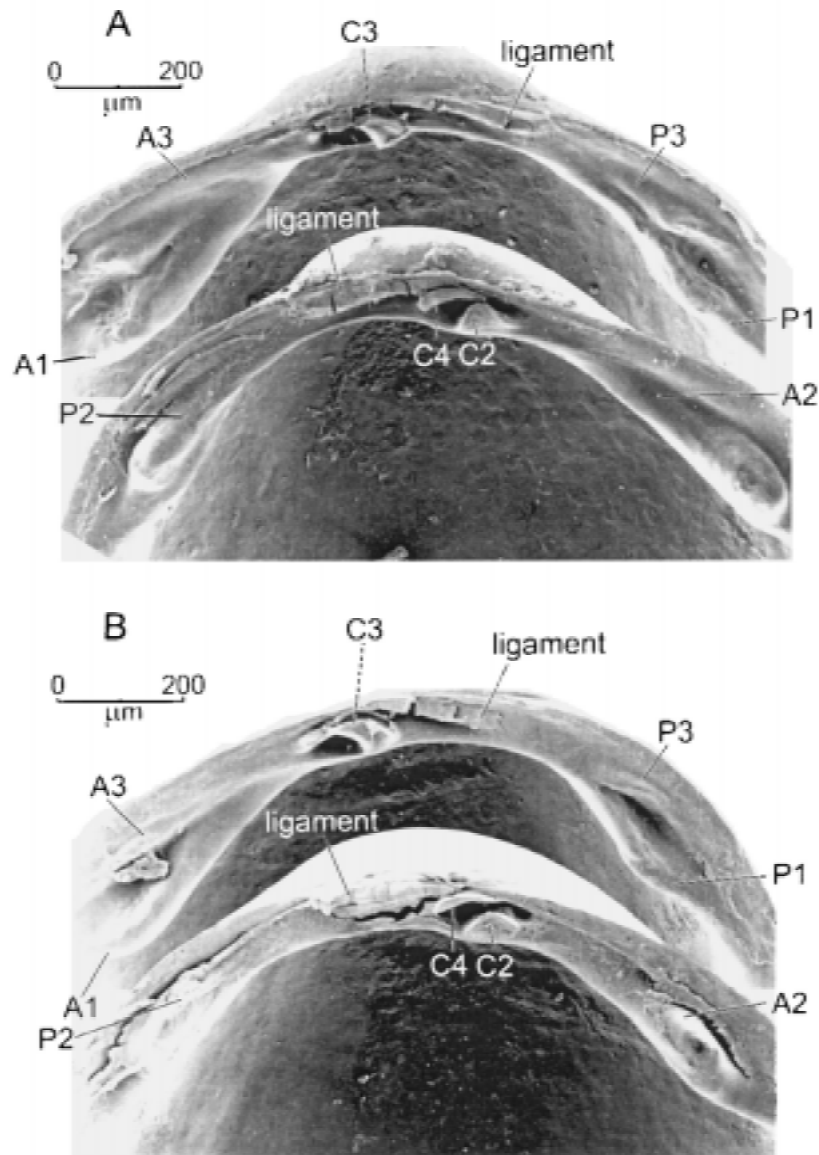


Figure 5. General hinge features in *Pisidium moitessierianum* from the lower Great Lakes (A) and from Dnieper River (B).

As with other *Pisidium* spp., *P. moitessierianum* reproduces by self-fertilization, with embryos developing in brood pouches. The minimal size of embryo-carrying *P. moitessierianum* observed in the Great Lakes was 1.1 mm. By comparison mature (gravid?) individuals of *P. moitessierianum* with valves 1.0 mm long were observed in Lake Pääjärvi, southern Finland (Holopainen & Hanski, 1986). Small-bodied, ovoviparous sphaeriid clams are thought to be limited in the brood size they can produce, since the young may achieve a shell length as great as one-third that

of the parent (see review, Mackie, 1984). Nonetheless we did not detect differences in fecundity among surveyed populations, even though North American specimens attained larger sizes than their European counterparts. In each population ($n \geq 5$ observations) gravid clams typically carried between five and ten embryos per individual. By comparison, brood size of 1–5 embryos per parent was observed in oligotrophic and mesogumic Lake Pääjärvi (Holopainen & Hanski, 1986). Thus, reproductive characteristics

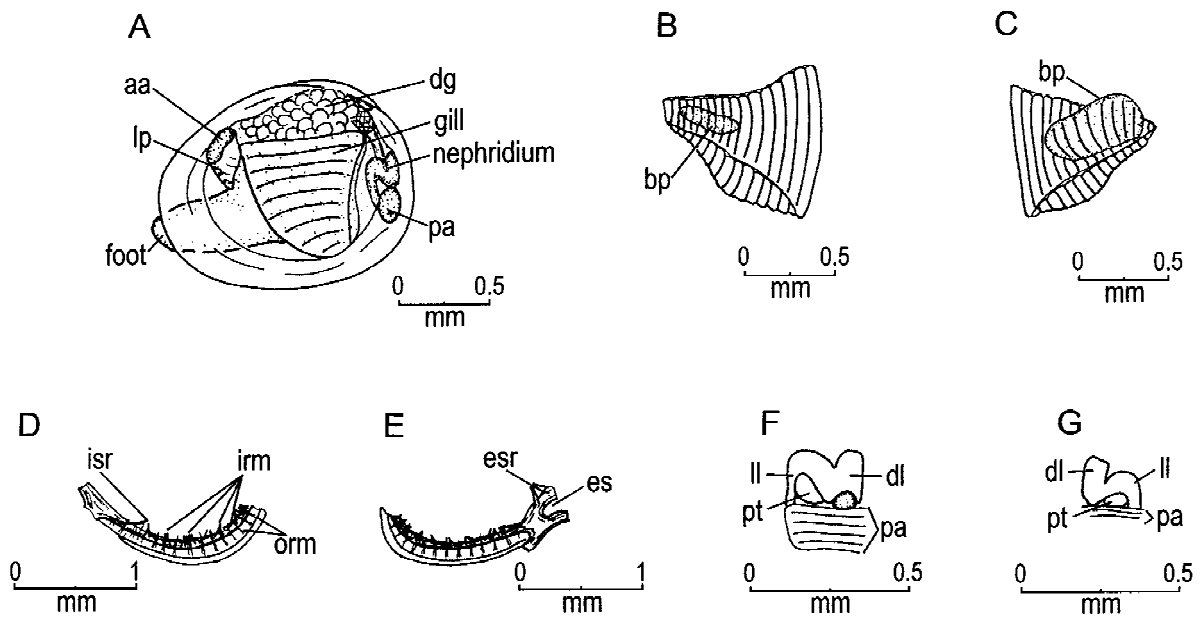


Figure 6. Anatomy of the soft tissues in *Pisidium moitessierianum* from the lower Great Lakes: general external anatomy under light dissecting microscope (A); gills bearing brood pouch at early (B) and late (C) stages of development; details of structure of mantle edge (D–E) and nephridium (F–G).

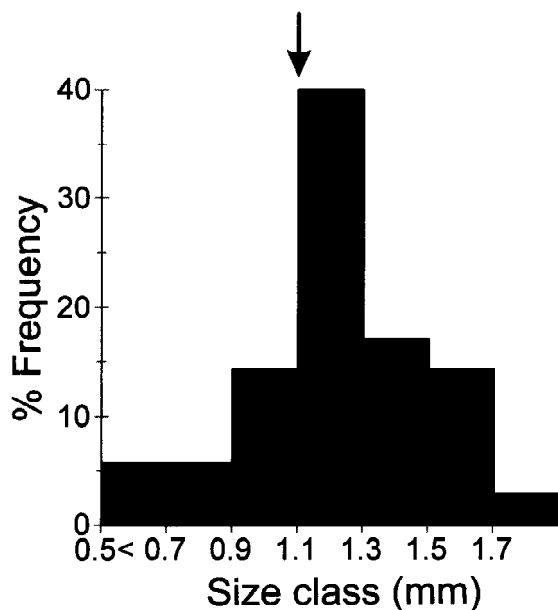


Figure 7. Length-frequency distribution of *Pisidium moitessierianum* from western Lake Erie in May, 1998 ($n=35$). Arrow indicates the minimal size of animals carrying embryos.

in *P. moitessierianum* may vary substantially among populations.

Studies on the Lake Pääjärvi population (Holopainen & Hanski, 1986) have shown that *P. moitessierianum* life span is 2 years. Gravid clams release embryos during July. Offspring attain a length of 0.6 mm at birth. Clams became fecund during August–September of the subsequent year at the age of 12–13 months, carrying on average 2.5 embryos per parent. Individuals of *P. moitessierianum* begin to reproduce when they reach a shell length of 1.0–1.8 mm. Gravid individuals comprise 40–70% of the population. The parturition occurs in July of the following year at the age of 24 months. Observations on North American populations of *P. punctatum* s.l. revealed that adults produce two broods per year, one in the spring and another in the fall (Clarke, 1981).

P. moitessierianum inhabits both lotic and lentic waters. In the Great Lakes, the pea clam occurred at depths ranging from 0.6 to 5.4 m. In European waters, it is encountered at 0.5–20 m (reviewed in Stadnichenko, 1984). In the Great Lakes, *P. moitessierianum* individuals were collected on sand, silty sand and mud substrata. Similar habitat types were reported for European populations, although they also utilize silty gravel and beds of aquatic macrophytes (Stadnichenko, 1984).

P. moitessierianum occurs most frequently in oligotrophic waters, where oxygen saturation is usually

above 50% (Stadnichenko, 1984). Tolerance of *P. moitessierianum* to reduced oxygen conditions has not been determined, though synoptic surveys indicate that it can tolerate some exposure to anoxia after ice cover formation in winter (Stadnichenko, 1984).

P. moitessierianum accounted for 0.003% (Lake St. Clair) – 0.205% (western Lake Erie) of total abundance of the macro- and meiozoobenthos (≥ 0.5 mm long) in the Great Lakes. It represented between 3 and 12% of the total sphaeriid density. In the Great Lakes, *P. moitessierianum* commonly co-occurred with *P. compressum*, the young of which can be misidentified with the former. Other prominent taxa coexisting with *P. moitessierianum* included tubificid and nauid oligochaetes, gastropods, larval chironomids and ephemeropterans.

Little is known of the ecological role of *P. moitessierianum* in its native region. Considering its scattered distribution and relatively low density in the Great Lakes, this sphaeriid likely has little ecological impact.

Occurrence and geographical distribution

P. moitessierianum was found at two of 10 sites surveyed in the St. Clair River, at one of 22 sites in Lake St. Clair and at one of 7 sites in western Lake Erie, but was not detected at 14 sites in the River Detroit nor at 5 sites in western Lake Ontario (see Figure 1). To date, the presence of this species has not been confirmed at other localities in North America. By comparison, *P. punctatum* s. lat. is broadly distributed in North America, from the Atlantic to the Pacific coast (Burch, 1975; Clarke, 1981). However, the distribution of its intraspecific forms, *punctatum* s. str. and *armatum*, conchologically identical to *P. moitessierianum*, remains unknown because they have been lumped together with the form *simplex* which is almost certainly a valid full species.

P. moitessierianum is wide-spread in Eurasia (see review by Stadnichenko, 1984, and Korniushev, 1996). Its native European distribution encompasses England, France, Germany, Switzerland (Lake Geneva), Poland, Hungary, Romania, Scandinavian countries, Estonia (Lake Võrtsjärv), Latvia, northwestern (Karelian Republic; regions Kaliningrad, Novgorod (Lake Ilmen) and Kalinin (the upper-Volga reservoirs)), central (River Oka) and southwestern (River Volga delta) Russia, and northern Ukraine. Its Asian range includes the River Irtysh basin in southwestern Siberia and northeastern Kazakhstan.

In Ukraine, the Moitessier's pea clam occurs in disjunct lake and river localities associated with the Dnieper River watershed, i.e. lakes Svityaz, Belye and Nobel (Ukrainian woodland zone), Dnieper River upstream the Kanev reservoir, lower Dnieper River, Dnieper-Bug tidal estuary, and tributaries Zheryv, Desna and Psiel (A.V. Korniushev, unpubl. data.). Further detail biogeographic survey is needed to deduce whether *P. moitessierianum* has a restricted or continuous distribution in other geographical regions of its Eurasian range.

Attributes of an invader?

The origin of *P. moitessierianum* in North America has yet to be resolved, but many European records indicate a Palaearctic origin. By contrast, its known North American occurrence is confined to the lower Great Lakes, suggesting its nonindigenous origin in the New World. The restricted range of *P. moitessierianum* in North America also contrasts with the broad geographical distribution of native North American sphaeriids, often extending from the Atlantic to the Pacific coast (Burch, 1975; Clarke, 1981). However, considering the problem in identifying *P. moitessierianum* in North America, it is possible that the species' range extends beyond the Laurentian Great Lakes. Occurrence and arrival sequence of introduced sphaeriid species are poorly understood in the Great Lakes due to insufficient taxonomic study; however, at least two Sphaeriidae, *P. amnicum* and *P. henslowanum*, were recognized as introductions from Europe prior to the early 1900s (see Herrington, 1962). It is possible that *P. moitessierianum* may have been misidentified as *P. punctatum* in the lower Great Lakes basin-St. Lawrence River in 1894 (Sterki, 1895). This suggests that it was overlooked or confused with *P. punctatum* or with other similar looking North American species for >100 years. The taxonomic and endemic status of *P. punctatum* has been a subject of controversy, as evidenced from its synonymy. For example, Herrington (1954) argued for recognition of *P. punctatum* as a senior synonym of *P. tenuilineatum* Stelfox, 1918, but later (Herrington, 1962) placed both taxa in synonymy with *P. punctiferum* (Guppy, 1867). Conversely, Kuiper (1962) recognized *P. punctatum*, *P. punctiferum* and *P. tenuilineatum* as separate species. Ellis (1978) and Piechocki (1989) treated *P. punctatum* as a junior synonym of *P. moitessierianum*.

P. moitessierianum co-exists with the introduced sphaeriids *P. amnicum*, *P. henslowanum* and *S.*

corneum in areas of intense vessel traffic in the lower Great Lakes (Clarke, 1981; this study). This further suggests that shipping activities were the probable entry vector for this species. Shipping activities have been implicated in transoceanic and intercontinental transfer of other molluscs introduced to the Great Lakes, including *Dreissena polymorpha*, *D. bugensis* and *P. amnicum* (Mills et al., 1993). Since the 1840s, oceanic-going vessels (including those from Europe) entered the Great Lakes through a network of canals (Mills et al., 1993, 1994). Prior to the early 1900s, most ships sailing in Lake Erie and the St. Lawrence seaway system used solid ballast (sand, mud, gravel or shoreline debris) for stabilization (see Mills et al., 1994). Accidental transport and release of sphaeriid clams with ballast materials may have facilitated their dispersal, since only one of these hermaphroditic and ovoviviparous clams can potentially found a viable population (Mackie, 1979, 1984). The survival of *P. moitessierianum* in ballast of a ship is possible considering its ability to tolerate the inhospitable conditions.

Other dispersal vectors that could potentially transfer *P. moitessierianum* within the Great Lakes basin include birds and insects (Mackie, 1979). Mackie (1979) experimentally demonstrated that six species of sphaeriids could withstand aerial exposure for 30–60 min as extra-marsupial larvae brooded by parent clams or as adults. Therefore, *P. moitessierianum* could potentially disperse overland by clamping its valves onto limbs of aquatic insects or feathers of waterfowl, as observed for other sphaeriid species (Mackie, 1979; Burky, 1983; Stadnichenko, 1984). Currents could also transfer small-bodied individuals of *P. moitessierianum* downstream. Although the actual mode by which this sphaeriid may have been transferred into the Great Lakes from Eurasia is not known, its disjunct global distribution is more simply explained from human-mediated dispersal, rather than from any of the natural mechanisms of dispersal.

If *P. moitessierianum* was introduced to North America >100 years ago, then the species has not greatly extended its range on this continent. The historical collections and recent surveys suggest that *P. moitessierianum* distribution in North America is restricted to habitats within the lower Great Lakes–St. Lawrence drainage – the sites where Sterki (1895) first discovered this pea clam in 1894.

In conclusion, this study established the identity of the Great Lakes' pea clam as *P. moitessierianum* based on analyses of shell and viscera morphology and review of the systematic literature. It is likely that

this species has been misidentified in the Great Lakes by previous investigations. The limited geographical distribution of *P. moitessierianum* in North America supports the view that the species was introduced to the Great Lakes. However, further studies of archived samples, museum materials and new field collections of *P. punctatum* s.l. are needed to resolve the origin and distribution of *P. moitessierianum* in North America. Genetic characterization of *Pisidium* from Laurentian Great Lakes and from European basins may also help elucidate taxonomic and biogeographic relationships between members of the genus.

Acknowledgements

We gratefully acknowledge Dr Gerry Mackie (Canada) for verifying our identification and providing specimens of *Pisidium* spp. from the Laurentian Great Lakes basin. We appreciate Dr A. Baldinger and Mr C. Sturm (U.S.A.) for allowing us to study *Pisidium* collections from their institutions. Dr Aleksandr Krakhmalnyi (Ukraine) and Mrs E. Wäsch (Germany) assisted with scanning electron microscopy. Dr Jan Ciborowski (Canada) provided statistical advice. Comments by Dr Gerry Mackie, Dr John Chapman, Ms Julianna Borbely, Mr Dave Banninga and an anonymous reviewer improved the manuscript. This study was supported by NATO and GLIER postdoctoral fellowships to IAG, by an Alexander von Humboldt fellowship to AVK and by an NSERC research grant to HJM.

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