THE RELATIONSHIPS OF THE MEDITERRANEAN TROCHID GASTROPODS 'MONODONTA' MUTABILIS (PHILIPPI, 1846) AND 'GIBBULA' RICHARDI (PAYRAUDEAU, 1826)

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ABSTRACT

The Mediterranean trochid gastropods currently known as Monodonta mutabilis (Philippi, 1846) and Gibbula richardi (Payraudeau, 1826) are shown, on both morphological and electrophoretic grounds, to be sibling species, and therefore congeneric. The generic name Phorcus Risso, 1826 should be used for these species, which may be more closely related to the Mediterranean Trochocochlea species than to other species classified in Gibbula.

The oldest appropriate genus-group name for the Mediterranean species currently classified as Monodontata (M. articulata, M. turbinata) is Trochocochlea Möörch, 1852. The earliest type species designation for Osilinus Philippi, 1847 is that of Trochus constritus Lamarck, 1822 by Herrmannsen (1847), which would make Osilinus a valid senior synonym of the widely used name Austrocochlea Fischer, 1885 and not of Trochocochlea as commonly accepted. A ruling of the International Commission on Zoological Nomenclature will be sought for the case.

INTRODUCTION

The Mediterranean trochid gastropod species currently known as Monodonta mutabilis (Philippi, 1846) has long (Bucquoy, Dautzenberg & Dollfus, 1885; Pilsbry, 1889; Ghisotti & Melone, 1975) been recognized as having conchological traits intermediate between those of two other littoral species, Monodonta articulata (Lamarck, 1822) and Gibbula richardi (Payraudeau, 1826), with which it shares a very similar habitat in the mediolittoral of rocky shores.

Thus paper reassesses the relationships among these species using allozyme electrophoresis and external morphology of the head-foot. A working hypothesis to be tested was that Monodonta mutabilis morphs might be hybrids between M. articulata and G. richardi. Previous studies using allozymes (Cesari & Pranovi, 1990) compared Monodonta articulata, M. mutabilis and M. turbinata (Born, 1780) but did not include Gibbula richardi.

Bucquoy, Dautzenberg & Dollfus (1885), Ghisotti & Melone (1972, 1975) and Cesari & Pranovi (1989) provide good figures and synonymies of the species discussed here. We will thus only stress the morphological characters of interest for the discussion.

MATERIALS AND METHODS

This work is based on material collected specifically to address this particular problem (hereafter 'new material'), and examination of all holdings of relevant species in the Muséum National d'Histoire Naturelle, Paris (hereafter 'MNHN collection').

Monodonta articulata (Lamarck, 1822)


MNHN collection: Mediterranean France—Collioure, Cerbère, Cap Leucate (specimens figured in Bucquoy, Dautzenberg & Dollfus, 1885); Menton, Nice, Cannes, St Raphaël, St Tropez, Porquerolles, La Seyne, Toulon, Sanary, Marseille, Aigues Mortes, Sète (all Locard collection as Trochocochlea turbiiformis von Salis, 1793); Cannes, St Raphaël, Porquerolles, Toulon, Sanary, Sète, (Locard collection as Trochocochlea retusa Monterosato, 1888); Marseille, Palavas (Locard collection as Trochocochlea trivialis Monterosato, 1888); La Seyne (Locard collection as Trochocochlea depauwera Monterosato, 1888); Cannes, La Seyne, Marseille (Locard collection as Trochocochlea siintensis Recluz, 1843).

Corsica—Ajaccio, Bonifacio (Locard
collection as *T. turbiformis*); Ajaccio, Cap Corse, Barcaggio (Locard collection as *T. retusa*); Ajaccio (Locard collection as *T. sitiensis*). **Spain**—Barbate, Tarifa, Algeciras, all leg. E. Fischer-Piette. **Italy**—Palermo, Lampedusa (Locard collection as *T. turbiformis*); Messina, Lampedusa (Locard collection as *T. depaupera*). Liguria (Locard collection as *T. sitiensis*); Chioggia (Locard collection as *T. retusa*). Viareggio (Monersoto leg. et det., syntypes of *T. retusa*). **Morocco**—Tangier (Pallary collection, syntypes of *T. blainvillei* Pallary, 1902); Tangier (Locard collection, as *T. blainvillei*). Cap Malabata near Tangier (leg. E. Fischer-Piette); Tetouan (leg. Buchet). **Algeria**—Oran (Locard collection); Oran (H. Fischer collection). **Tunisia**—Stax (Pallary collection; with manuscript name *Trophocochlea evoluta*); Djerba (H. Fischer collection); Cherchell (leg. de la Seigliere); Bône (now Annaba; H. Fischer collection). **Libya**—Farwa lagoon, leg. Naas, 1986). **Lebanon**—Saida (Pallary collection); ‘Syrie’ (Locard collection).

**Gibbula richardi** (Payraudeau, 1826)


**MNHN collection:** Mediterranean **France**—Lectotype and paratype of *Phorcus margaritaceus* Risso, 1826; Roussillon (specimens figured in Bucquoy, Dautzenberg & Dollfus, 1885); Menton, Nice, St Raphael, St Tropez, Porquerolles, La Seyne, Toulon, Marseille, Martigues, Sète (all Locard collection). **Corsica**—Syntypes of *Monodonta richardi* Payraudeau, 1826; Ajaccio (Locard collection). **Italy**—San Remo; Varigotti, Savona province; Capri (Staadt collection); Naples (Locard collection). **Algeria**—Oran (Locard collection); Oran (H. Fischer collection); Cavallo, near Djidjelli (leg. Joly). **Lebanon**—Beyrouth, Tartous (Pallary collection).

**Monodonta mutabilis** (Philippi, 1846)


**MNHN collection:** Mediterranean **France**—Cerbère, Cap Leucate (specimens figured in Bucquoy, Dautzenberg & Dollfus, 1885); Toulon, Nice (Locard collection as *Trophocochlea sitiensis* Recluz, 1843); Agde (early XIX. cent. collection; with manuscript name *Monodonta mongini* Philibert; Cap Ferrat (leg. Bouchet, 3/1980); Sanary (Gofas leg. 1968). **Corsica**—Cap Corse (Locard collection, as *T. sitiensis*). **Croatia**—Lovran (H. Fischer collection). **Turkey**—‘Dardanelles’ (XVIIe cent. label).

The following populations were used for electrophoresis: *Monodonta articulata* from Endoume, *M. mutabilis* from Endoume and Les Embiez (lumped as one population) and from Piran, Bay of Trieste; *Gibbula richardi* from Endoume and from Rincón de la Victoria. The number of specimens processed for electrophoresis is detailed in Table 2.

The specimens to be used for electrophoresis were collected in the mediolittoral zone of rocky shores, and brought alive to the laboratory; then frozen at −80°C until processing, up to four months later. Some specimens collected in 1992 and stored at −30°C proved inactive enzymatically in 1995 and had to be discarded.

Whole specimens used for electrophoresis were individually removed from their shells, ground in a 0.25 M sucrose solution (5 μl solution per mg weight of soft parts) and centrifuged at 11,000 rpm for 40 minutes at 4°C, for large specimens, part of the foot and part of the digestive gland was used. The supernatant was then split into 20 μl doses and refrozen at −30°C until use. Specimens were given a serial number and their shell stored in the collection as a reference. Samples were migrated using vertical polyacrilamide gel electrophoresis in refrigerated Pharmacia GE 2/4 tanks. A pre-run (15′ at 25 volts, 15′ at 50 volts) was intended to settle the samples in the well; electrophoresis was then performed at 150 volts for 2 to 3 hours according to the enzymes examined.

Eleven enzyme systems (Table 1) were assayed for all the species. The running buffer was Tris/citric acid pH 8.5 for gel and tank (for all except PGM and SOD), or Tris/Hydrochloric acid pH 9 in gel and Tris/Glycine pH 9 in tank (for PGM and SOD).

The staining recipes were taken or modified from Richardson et al. (1986), Pasteur et al. (1987), Backeljau (1989a, 1989b) or Murphy et al. (1990); IDH was stained using MgCl₂ instead of the erroneous MnCl₂ commonly mentioned in the literature. The gels were photographed, using them as negatives in contact over a sheet of black-and-white photographic paper.

Three specimens from the Endoume population of *Monodonta articulata* were included in every run and used as a reference for the migration distance, measured as a percentage of the migration of the most common isozyme of *M. articulata* named A.

The electromorphs were designated by a letter from B to N in order of increasing mobility. The data were scored in a matrix of individual genotypes and analyzed using the BIOSYS 1.7 software package (Swofford, 1989; Swofford & Selandar, 1981) to calculate allele frequencies and Nei's (1972) genetic distance between populations. Conformity to Hardy-Weinberg expectations was tested with alternative groupings/spitting of populations according to morphology, with a χ² test applied with Yates' correction for continuity (Pasteur et al., 1987: 171).
RELATIONSHIPS OF 'MONODONTA' MUTABILIS

Table 1. Enzyme abbreviations and EC codes of enzyme systems investigated.

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<th>Abbreviation</th>
<th>EC Code</th>
<th>Polarity</th>
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<td>Aspartate Aminotransferase</td>
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<td>Phosphoglucomutase</td>
<td>2.7.5.1</td>
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RESULTS

External morphology

**Monodonta articulata**

The shell is solid, conical, up to 30 mm high and 25 mm broad. The columella has a distinct bulge anteriorly and is bordered by a narrow callus, sometimes (particularly in juveniles) leaving a tiny umbilical chink uncovered. The sculpture is of weak, unequal spiral cords which may be indistinct on worn specimens. The colour pattern consists of a subsutural row of crimson flames, and of narrow articulated stripes of crimson and white, alternating with slightly broader bands bearing delicate, crowded vertical lines.

The living animal has an oval-elongate foot. The sole is plain whitish, with a papillate edge; the sides are orange on their lower part, grading upwards to a dark greenish brown middle part and to a pale green epipodium. There are four pairs of relatively small epipodial tentacles, with scattered small black spots. The cephalic tentacles are slender, annulated with black and pale orange. The cephalic lappets, eye stalks and neck lobe are the same pale yellow as the epipodium, whereas the upper side of the snout has a vivid pattern with a black band along the front edge, a bright orange band next to it, and then an area with weaker transverse black stripes between this and the cephalic lappets.

**Gibbula richardi**

The shell is moderately solid, low conical, up to 18 mm high and 18 mm broad. The columella is narrow, slightly concave and without an anterior bulge; there is a broad, widely open and deep umbilicus. The surface of the shell is smooth, a rather unusual feature in Mediterranean trochids. The colour pattern of the shell is extremely variable, and usually consists of purple, reddish or yellow spots forming spiral rows and divaricate axial lines, on a greenish to brownish background. The living animal has an oval-elongate foot. The sole is plain whitish, with a papillate edge; the sides are brownish, more or less covered with dark spots, grading to a pale yellow epipodium. There are three pairs of relatively small, colourless epipodial tentacles. The cephalic tentacles are slender, with black rings. The cephalic lappets, eye stalks and neck lobes are the same pale yellow as the epipodium, whereas the upper side of the snout has a vivid pattern with a black band along the front edge, a bright orange band next to it, and then an area with weaker transverse black stripes between this and the cephalic lappets.

**Monodonta mutabilis**

The shell is moderately solid, low conical, up to 18 mm high and 18 mm broad. The columella has a well-defined bulge anteriorly and is bordered by a very narrow callus; there is a distinct, narrow and deep umbilicus. The sculpture is of weak, unequal spiral cords which may be indistinct on worn specimens. The colour pattern consists of small crimson-red spots, widely spaced along the cords and arranged to form axial flames with a slight offset from one cord to the next; the spots may be present along all cords, or only on every other cord. The living animal is essentially similar to *G. richardi*.

Electrophoresis

LAP (Leucine Amino-Peptidase), LDH
(Lactate Dehydrogenase), ODH (Octopine Dehydrogenase), PGM (Phosphoglucomutase) did not give readable gels, either due to lack of activity or lack of resolution, and were not further considered. The resolution with MPI and PGI was satisfactory, but these enzyme systems feature high intraspecific polymorphism with many shared or indistinguishable alleles, making them of little use for interspecific comparisons. Five other systems (AAT, IDH, MEN, MDH, SOD) with low or moderate intraspecific polymorphism, were taken into account (Table 2).

All populations show good agreement with expected allele frequencies assuming Hardy-Weinberg equilibrium. The values of P (probability for the deviation from expected allele frequencies to be due to sampling artefacts) are above 0.9 for most polymorphic enzyme systems of Monodonta articulata from Endoume (SOD), M. mutabilis from Endoume (AAT, MDH, IDH, SOD) and Trieste (MDH, IDH), and Gibbula richardi (AAT, IDH, SOD). The poorest fit is found for MDH in Gibbula richardi from Endoume ($\chi^2 = 2.6, P = 0.10$), for AAT and IDH in Monodonta articulata from Endoume ($\chi^2 = 0.4, P = 0.53$, and $\chi^2 = 1.2, P = 0.26$). Pasteur et al. (1987: 172) consider that P values well under 0.05 are needed to show that Hardy-Weinberg equilibrium is not achieved.

M. mutabilis and G. richardi share alleles at all investigated loci and the merging of the two taxa in the populations from Les Embiez/Endoume still yields low $\chi^2$ values in the test for Hardy-Weinberg equilibrium for AAT and IDH (polymorphic) and for MEN (fixed, shared).

### Table 2. Allele frequency in five populations of Monodonta articulata, M. mutabilis and Gibbula richardi from the Mediterranean. ART: M. articulata, Endoume; MU1: M. mutabilis, Les Embiez and Endoume; MU2: M. mutabilis, Trieste; RI1: Gibbula richardi, Endoume; RI2: G. richardi, Rincón.

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<th>ART</th>
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<th>Population</th>
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RELATIONSHIPS OF 'MONODONTA' MUTABILIS

The two species differ only in a nearly fixed alternative allele for SOD: *Monodonta mutabilis* shares the A allele with *M. articulata*, whereas the B allele dominates in *Gibbula richardi*. There is also a qualitative difference in the AAT gels, where a very weak activity (not detectable on photographs) is seen at ca. 1/5 of the migrated distance of the main band in *Gibbula richardi* and not in *Monodonta mutabilis*. This results in a genetic distance (Nei, 1972) of 0.21 to 0.24 between the two species.

**DISCUSSION**

The results of the electrophoresis demonstrate that *Monodonta mutabilis* is a distinct species. The genetic isolation between this species and *M. articulata* is overwhelmingly demonstrated by fixed (AAT, MEN) or nearly fixed (MDH, IDH) alternative alleles. The isolation of *Gibbula richardi* is only supported by the alternative fixed alleles for SOD, but this is held as definitive because it was observed in sympatric populations.

The number of shared alleles with similar frequencies in *M. mutabilis* and *G. richardi* indicates a very close relationship. The genetic distances observed between these two species are on the borderline between usual figures for interspecific and intraspecific distances (Thorpe, 1983). We may thus consider *Gibbula richardi* and *Monodonta mutabilis* as sibling species.

The shared morphological characters also support a very close relationship. Both have three pairs of epipodial tentacles (four in other *Monodonta* spp.). The peculiar black/orange anterior border of the snout is shared by *M. mutabilis* and *G. richardi*, and is not found in any of the other *Gibbula* for which data (Gofas, unpublished drawings) are available [e.g. *G. racketti* (Payraudeau, 1826), *G. rarilinata* (Michaud, 1829), *G. tingiiana* Pallary, 1901, *G. varia* (Linné, 1758), *G. guttadauri* (Philippi, 1836), *G. vimontiae* Monterosato, 1884]; it is therefore interpreted as a reliable synapomorphy.

On these grounds, it is not acceptable to place the two species *mutabilis* and *richardi* in different genera. One possibility is to restore both to the same genus as *M. articulata*. This is not satisfactory because of the importance given to the number of epipodial tentacles in trochid systematics. Moving *Monodonta mutabilis* to *Gibbula* (type species: *Trochus magus* Linné, 1758; SD Herrmannsen, 1847) is not satisfactory either because the characters shared with *M. articulata* (the black bar on the snout, and the SOD allele A) suggest that they both belong to a monophyletic group. From this and from the nomenclatural notes in the appendix, we suggest the use of the name *Phorcus* Risso, 1826 as a valid genus with *P. richardi* and *P. mutabilis* as included species. The other species currently classified

![Figure 1. Cluster analysis using unweighted pair group method (UPGMA). Coefficient used: Nei (1978) unbiased genetic distance between populations.](https://academic.oup.com/mollus/article-abstract/63/1/57/978308)
in *Gibbula* are also in need of reassessment, and a complete phylogenetic analysis of the group will certainly result into further splitting of *Gibbula*.

The present distributions of *Phorcus richardi* and *P. mutabilis* are broadly overlapping, but distinct. *Phorcus mutabilis* is well established in the Adriatic (Cesari & Pranovi, 1989), and has a rather limited distribution in the Western Mediterranean basin (not found on the Spanish coast South of Tarragona, nor on the North African coast); it often prefers disturbed habitats such as newly built piers or the rocky edges of artificial beaches. Conversely, *P. richardi* is found throughout the Mediterranean, reaches the Eastern entrance of the strait of Gibraltar, but seems to be missing in the Adriatic sea (not cited by Cossignani *et al.*, 1992). A possible scenario may be that *P. mutabilis* has been isolated from *P. richardi* in the Adriatic during the Pliocene and later spread out and came into contact with its sister species.

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**APPENDIX**

Nomenclatural notes on the genera *Monodonta*, *Osilinus*, *Trochocochlea*, *Phorcus* and *Mutilastra*

*Monodonta* Lamark, 1799 is based on the Indo-Pacific species *Monodonta labio* Linné, 1758 (type species by monotypy); it is characterized by a very strong columellar tooth, unusual among the tribe Gibbulini in which it is classified (Hickman & McLean, 1990). Related species with a weakly developed tooth or bulge on the columella have been separated at the subgeneric or generic rank, according to opinions.

*Osilinus* Philippi, 1847 (February) was introduced in a long sentence (pp. 19–20), which translated 'next to [the true *Monodonta*] we can find a construction, in a species-group starting from *M. constricta*, [M.] *taeniata*, and going into *M. fragaroides*, *Trochus crassus* . . . where instead of the clearly defined tooth of *T. labio*, there is only a small bulge (. . .) and I propose therefore the denomination *Osilinus*, from a species here belonging and named *Osilin* by Adanson (. . .)'. Herrmannsen (1847, vol. 2: 167) shortly afterwards designated the Australian species; *Trochus constrictus* 'Macleay' (=*Trochus constrictus*. Lamark, 1822) as the type species. This designation has been overlooked by later authors, so that most works followed Wenz (1938) and considered *Monodonta fragaroides* Lamark, 1822 (=*Trochus turbinatus* Born, 1778) as the type species (see discussion in Herbert, 1994).

This would make *Osilinus* an objective senior synonym of *Austrocochlea* Fischer, 1885, and the valid name for an Australian–New Zealand species group. The authors do not favour the view that a valid nomenclatural act should be suppressed simply because it has been overlooked. However, because the name *Austrocochlea* is widely accepted and the genus includes many abundant littoral species of the Southern Hemisphere, the authors intend to apply to the International Commission for Zoological Nomenclature for a type species designation which would maintain the current use of *Austrocochlea* for the Australian–New Zealand species and of *Osilinus* for European and West African ones.

*Trochocochlea* is a pre-Linnean name originating with Klein (1753), and first cited by Herrmannsen (1847: May) without any included species. The name was made available by Mörch (1852) who included *T. constricta* (Lamark) and *T. turbinata* (Born) among other species and cited *Osilinus* as a synonym. We could not trace any designation prior to Bucquoy, Dautzenberg & Dollfus (1885), who selected *Trochus turbinatus* as type species and thus made it the earliest name (following *Osilinus*) for the European and West African species-group discussed here. *Nepheusa* Leach, 1852 was published the same year as Mörch's work but has never been used subsequently; its type species (by monotypy) *Trochus crassus* Pulteney, 1799 is a common Western European Atlantic species, congeneric with *T. turbinatus*.

There are two other obsolete generic names for this group, both based on *Trochus crassus*. *Gibbium* Gray, 1842 is preoccupied by *Gibbium* Scopoli, 1777 (Coleoptera) and needs not be further considered. *Trochus* Leach in Gray, 1847 first appeared in the publication (Gray, 1847a) of Leach's manuscript of the classification of the British Mollusca, with *Trochus crassus* as sole included species, but may be considered one of the numerous misspellings (e.g. *Thicola*, *Aphorais*, *Simia*) literally transcribed from Leach. It was nevertheless mentioned by Gray (1847b: 143) as a synonym of *Labio* Oken,
1815, which does not make it available as, to our knowledge, it has never been subsequently adopted as a valid name. *Labio* is not available either, as Oken (1815) is on the Official Index of Rejected Works.

*Caragolus* Monterosato, 1884 was introduced to replace what Monterosato (1884b) considered a misuse of *Trochocochlea. Monodonta turbinata* 'Bonn.' (typographical error for Born in Monterosato, 1884b) was designated as type species of *Caragolus* by Crosse (1885), making it an objective synonym of *Trochocochlea.*

*Phorpus* Risso, 1826 was based on *Phorpus marginates* Risso, 1826 (type species by monotypy). We have examined the lectotype (designated by Arnaud, 1978) of *P. marginates* syntypes of *Monodonta richardi* Payraudeau, 1826 in MNHN, and syntypes of *P. margantaceus* Arnaud, 1978) of *Monodonta* we have examined the lectotype (designated by Crosse (1885), making it an objective synonym of *Trochocochlea. Monodonta* turbinata).

Nordsieck (1974) used *Osilinus* as a genus for the European species of 'Monodonta' and initiated current usage. He introduced as subgenera *Mutiastra* with *Trochus mutabilis* Philippi, 1846 as the type species, and *Pseudosilinus* with *Trochus edulis* Lowe, 1842 (a Madeiran species) as type species.

**REFERENCES**


