



New Paleontological Evidence for *Theodoxus micans* (Gaudry & P. Fischer, 1867) from the Megara Basin (Greece) and Its Relationship to the Extant Species *Theodoxus meridionalis* (R. A. Philippi, 1836) [†]

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Abstract

The Megara Basin in Greece contains Neogene–Quaternary deposits rich in lacustrine and marine mollusc assemblages. The shell morphology of *T. micans* resembles that of both fossil and extant species, notably *Theodoxus meridionalis*, while intraspecific variability complicates taxonomic discrimination. The operculum appears to provide more stable diagnostic features. Material from the historical collection of the Museum of Geology and Paleontology (NKUA), including specimens from Alepochori and the Mavratza Ravine, yielded opercula identified as belonging to *T. micans*. These results support the interpretation that *Theodoxus micans* represents a junior synonym of the extant species *Theodoxus meridionalis*.

Keywords: *Theodoxus micans*; *Theodoxus meridionalis*; operculum; taxonomy; Megara Basin; Pliocene; Pleistocene; Greece

1. Introduction

The Balkan Peninsula, hosts one of the world’s freshwater biodiversity hotspots [1,2]. Freshwater gastropods constitute an important component of this biodiversity [2], and fossil evidence suggests that the present-day freshwater gastropod fauna of Europe largely reflects post-Pleistocene faunal restructuring following repeated glacial–interglacial cycles [3].

Within this context, the family Neritidae Rafinesque, 1815, is well represented in freshwater habitats, notably by the genus *Theodoxus* Montfort, 1810, which is distributed throughout Europe, western Asia, and northern Africa [4–6]. Species of *Theodoxus* represent common and characteristic elements of the freshwater to mesohaline aquatic malacofauna across the Western Palearctic [4–6].

Molecular evidence further indicates that the present diversity of the genus originated through Miocene vicariance events associated with the fragmentation of the Tethys Sea [5]. The genus also possesses a rich fossil record in Europe, ranging from the Miocene to the Pleistocene; its oldest known representative, however, has been reported from the Paleocene of Belgium [7].

Species of *Theodoxus* possess a calcareous operculum [8], which functions as a protective structure sealing the shell aperture. While early species descriptions relied almost exclusively on shell morphology, later studies have shown that shell characters alone are



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often unreliable due to intraspecific variation [4–6]. In contrast, the operculum has been proposed to bear diagnostic characters [4–6], although its diagnostic reliability has been questioned by other studies [9].

The study of fossil freshwater gastropods in Greece dates back to the 19th century, including studies from Rhodes [10], followed by more recent studies such as [11] from Chios, [12] from Kos, from the Atalanti Basin [13], from Achaea [14,15], and from Lesvos [16].

For the Megara region, the most significant early works are those of Gaudry [17], who first described *Theodoxus micans*, and Fuchs [18], who documented a diverse assemblage of gastropods and bivalves from the Isthmus of Corinth, including localities at Kalamaki and Megara, and provided a more detailed description of the species. A more comprehensive stratigraphic and palaeontological analysis of the Megara Basin palaeofauna was later presented by Papp & Steininger [19].

In the present study, we re-evaluate fossil material of *T. micans* from the Megara Basin (Figure 1b), Greece (housed at NKUA), to clarify its stratigraphic occurrence and compile published records documenting the species' presence in the Greek territory during the Pliocene and Pleistocene (Figure 1a). For the first time, a description of the operculum is provided, and its potential taxonomic utility is assessed. Comparative examination with extant material allows evaluation of morphological continuity between fossil and recent populations, offering new insights into the species' evolutionary history and palaeobiogeography. Photographic documentation of the syntypes of *T. micans* (Gaudry & Fischer, 1867, [17]) from MNHN, France, was consulted for taxonomic comparison.

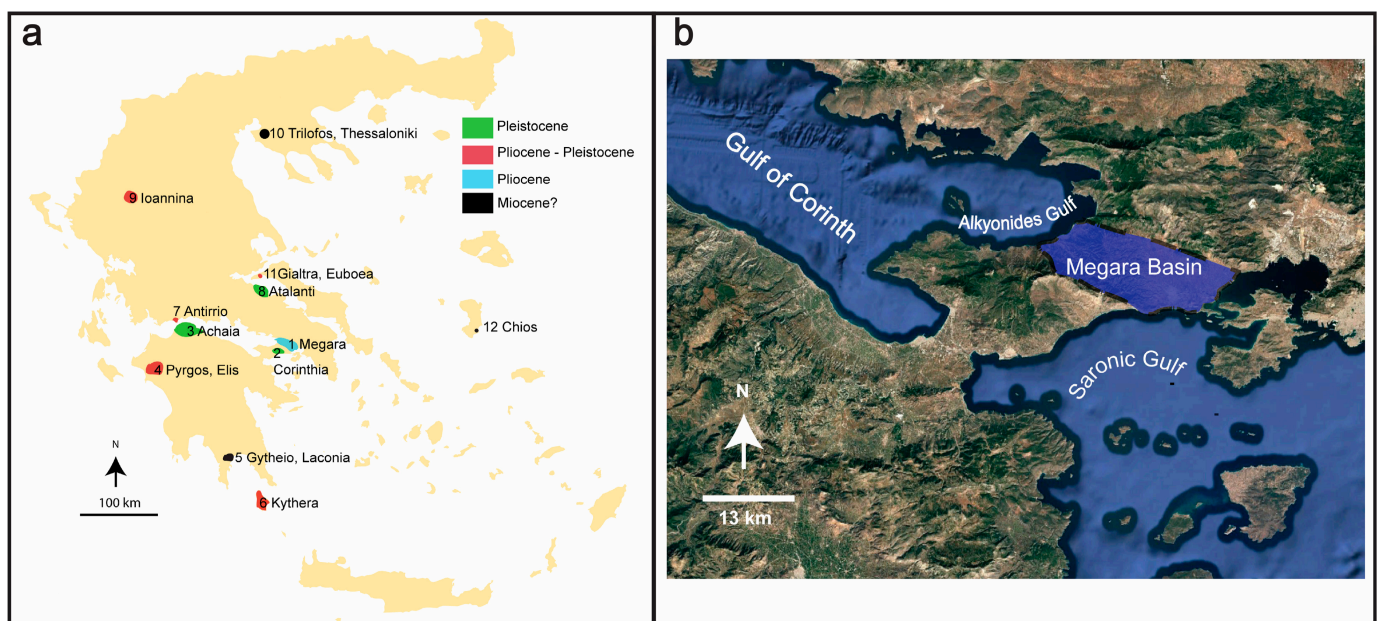


Figure 1. (a) Map of Greece showing the known occurrences of *Theodoxus micans* (numbers correspond to points on the map). (1) *T. micans*, Megara [17–19], Pliocene (this study); (2) *Theodoxus* sp., Corinthia, Sousaki, Early Pleistocene [20]; (3) *T. micans*, Achaea, late Early–Middle Pleistocene [14,15]; (4) *T. micans*, Pyrgos, Elis, Upper Pliocene–Pleistocene [21]; (5) *T. micans*, Gytheio, Laconia, late Miocene [22]; (6) *T. micans*, Kythera, Pliocene [23]; (7) *T. (Neritaea) varius callosus*, Antirrio, Aetolia-Acarnania, Early Pleistocene? [24]; (8) *T. micans*, Atalanti, Phthiotis, late Early Pleistocene [13,15]; (9) *T. micans*, Pamvotida, Ioannina, Pliocene–Pleistocene [25]; (10) *T. micans*, Trilofos, Thessaloniki, Miocene [26]; (11) *T. micans*, Gialtra, Euboea, Pliocene–Pleistocene [27]; (12) *T. micans*, Chios, Miocene [11]. Question marks indicate uncertain taxonomic assignment or age. (b) Satellite image of the study area, with the Megara Basin highlighted in blue shading. Map data ©2026 Google [28].

2. Geological Setting—Megara Basin

The Megara Basin, located east of the Corinthian Gulf and bounded by the Alkyonides Gulf to the north and the Saronic Gulf to the south (Figure 1b), is a Neogene–Quaternary extensional basin with deposits exceeding 1 km in thickness [29]. The basin comprises several lithostratigraphic units (Figure 2a,b), predominantly coarse alluvial deposits, conglomerates, sandstones, and marls of fluvial and lacustrine origin, with minor intercalations of marine–brackish sediments [29]. The basin basement consists of Mesozoic limestones and peridotites [29]. The tectono-sedimentary evolution of the basin was controlled by rift-margin fault migration and normal faulting, generating accommodation space for sediment accumulation and influencing basin morphology [30]. A volcanic ash layer within the upper stratigraphic succession (the Pagae Ash; Figure 2a,b) has been radiometrically dated to the late Pliocene, providing a chronological framework for the deposits [30]. The basin is rich in fossil mollusks, both marine and lacustrine [17–19]. Further details on the stratigraphic and tectonic context of the Megara Basin are provided in [29,30].

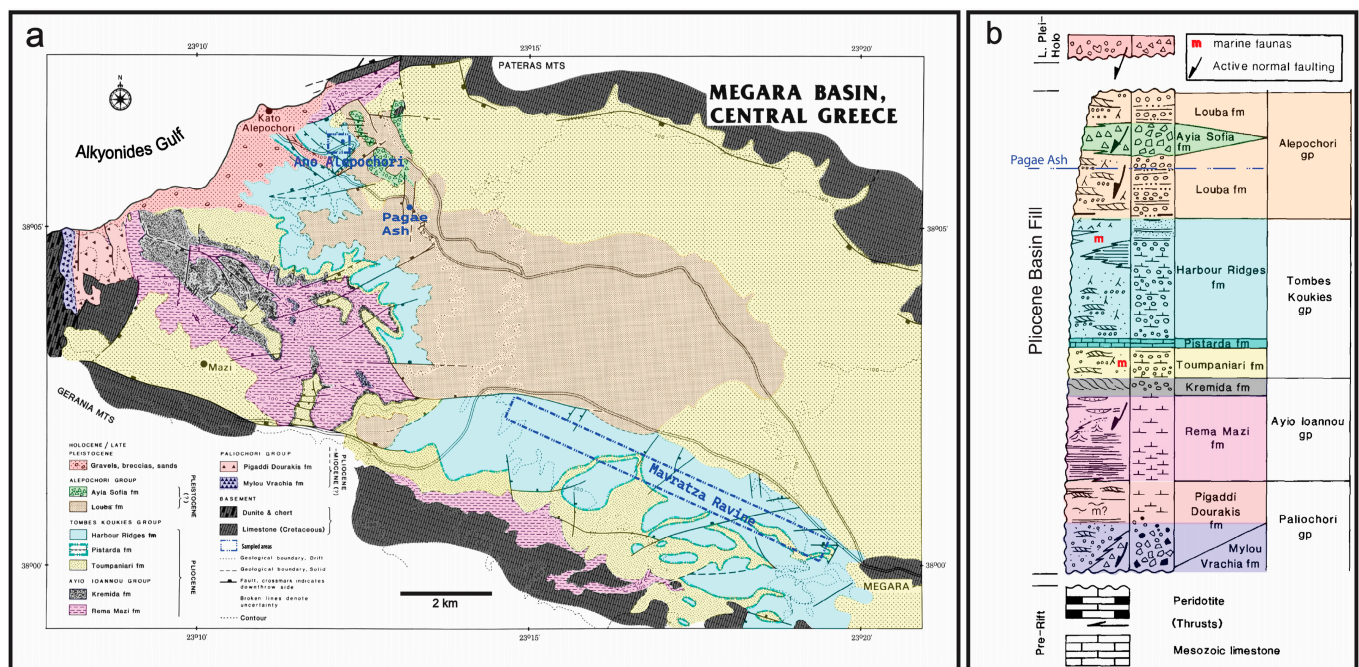


Figure 2. (a) Geological map of the Megara Basin modified after [29]; (b) Lithostratigraphic column of the Megara Basin, modified after [29]; the legend corresponds to that shown in panel (a). The blue dashed line indicates the position of the Pagae Ash layer, the age of which was determined by Leeder et al. [30].

3. Materials and Methods

The material examined consists of both bulk fossiliferous sediments and previously sorted fossil specimens from 20th-century sampling and research, housed at the National and Kapodistrian University of Athens (NKUA), Museum of Geology and Paleontology, Invertebrate Collection (catalog numbers MGPA-000090366–000093952). This catalog series includes material from the Megara Basin, among which are 940 shells and four opercula identified as *Theodoxus micans*. Fossil specimens were hand-picked where necessary under a Leica M165 C stereomicroscope (Leica Microsystems, Heerbrugg, Switzerland), which is housed at the National and Kapodistrian University of Athens (NKUA).

In addition, comparative material collected by the author from the Sousaki Basin (Corinthia) and additional material from the Synania Formation (Achaia, Greece) were examined for comparison.

Photographs of the syntypes of *T. micans* from the Muséum national d'Histoire naturelle (MNHN, France), were consulted for taxonomic comparison. Images of NKUA material were captured using a Leica M165 C stereomicroscope equipped with a Leica IC90 E camera (Leica Microsystems, Heerbrugg, Switzerland). Figures were prepared using Adobe Illustrator CS6 and Photoshop CS6.

Systematics, shell measurements, and operculum terminology follow [4,5], with systematic updates based on [31] and other relevant literature. Shell height (sh) and shell width (sw) were measured for all examined specimens using calibrated digital images in ImageJ (version 1.54g, Windows, bundled with 64-bit Java 8) [32]. To eliminate the effect of absolute size, a shape index (height-to-width ratio, sh/sw) was calculated for each specimen following established morphometric procedures in gastropod systematics, e.g., [5]. Descriptive statistics (mean, standard deviation, minimum, and maximum) were obtained for each population. Morphological variation and overlap among populations were visualized using scatterplots generated using Microsoft Excel. The analyzed material includes fossil specimens of *T. micans* Megara, Corinthia (study area of [20]), and Achaea (study area of [14,15]). The specimens from Corinthia and Achaea are deposited in the Invertebrate Collection of the Museum of Geology and Paleontology, National and Kapodistrian University of Athens (NKUA), catalog numbers (MGPA-000095007–000095022). One syntype specimen of *T. micans* was included in the statistical analysis. The specimen is documented with a photograph by Gaëlle Doitteau, available at GBIF [33]. Comparative material of *T. meridionalis* was obtained from illustrated specimens of [4] (Figures 6I, S, O; 7E and 8A, E, M) and [9] (Figures 14, 19, 32, 39 and 43). Comparative material of *T. fluviatilis* was measured from figures in [4] (Figures 9A,E,I,M,T and 10A,E,I) and [9] (Figures 47, 49, 53 and 59). The dataset used for the statistical analysis is provided in the Supplementary Materials (Table S1).

4. Systematic Paleontology

Class Gastropoda Cuvier, 1795 [34]

Subclass Neritimorpha Koken, 1896 [35]

Order Cycloneritida Frýda, 1998 [36]

Superfamily Neritoidea Rafinesque, 1815 [37]

Family Neritidae Rafinesque, 1815 [37]

Subfamily Neritinae Poey, 1852 [38]

Genus *Theodoxus* Montfort, 1810 [39]

Type species: *Theodoxus lutetianus* Montfort, 1810 [39] (synonym of *Theodoxus fluviatilis* (Linnaeus, 1758) [40]); by original designation.

Theodoxus meridionalis (R. A. Philippi, 1836) [41]

Figures 3–7 (includes specimens previously referred to *T. micans*)

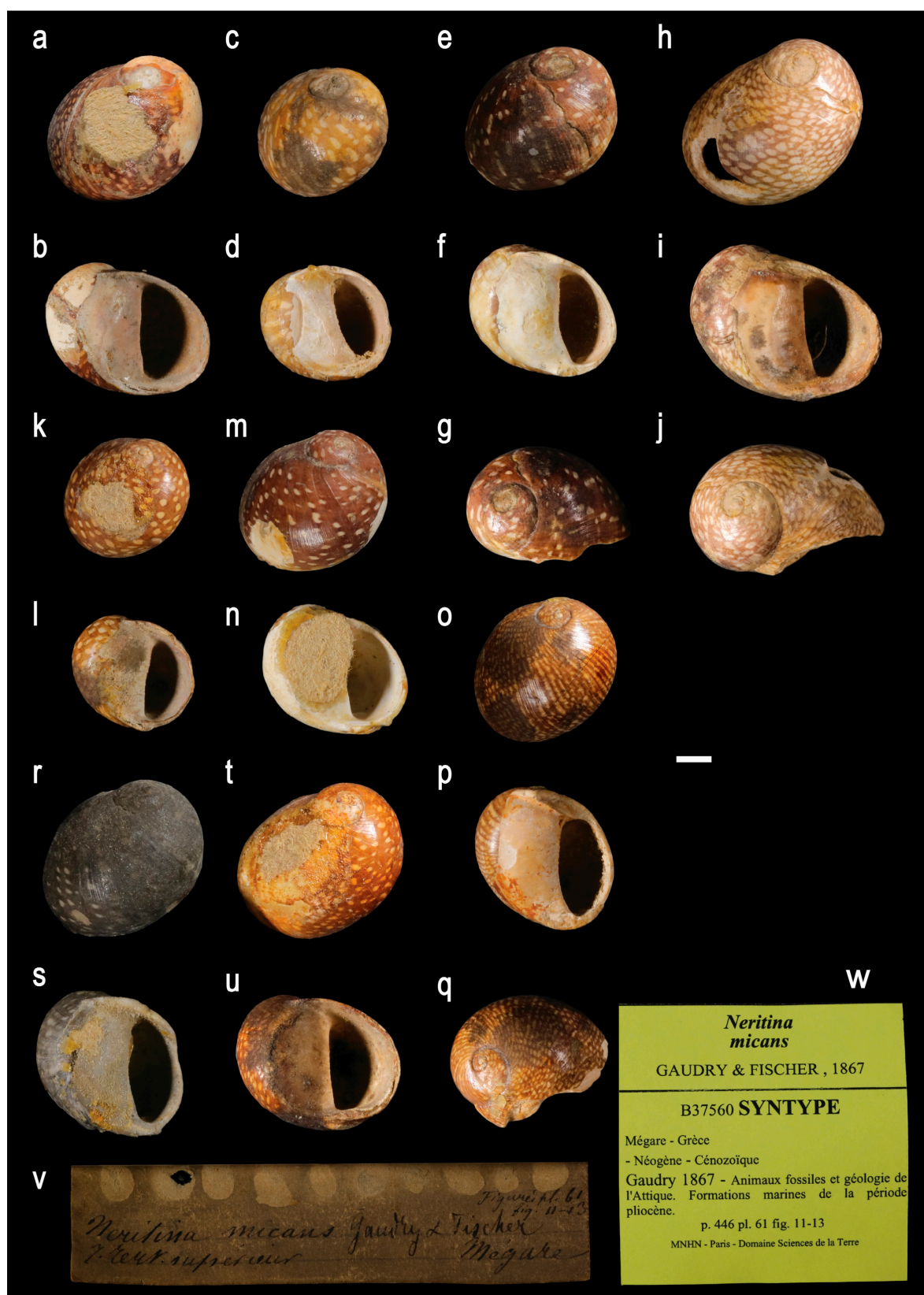


Figure 3. Syntypes of *Theodoxus micans* (Gaudry & P. Fischer, 1867, [17]) from the Megara Basin, Greece, deposited in National Museum of Natural History, France (MNHN.F.B 37560). Dorsal view: (a,c,e,h,k,m,o,r,t); apertural view: (b,d,f,i,l,n,p,s,u); apical view: (g,j,q); Historical Label: (v); Museum Label: (w). Scale bar = 2 mm. Photographs courtesy of Q. Wackenheim (MNHN, Paris), used with permission.

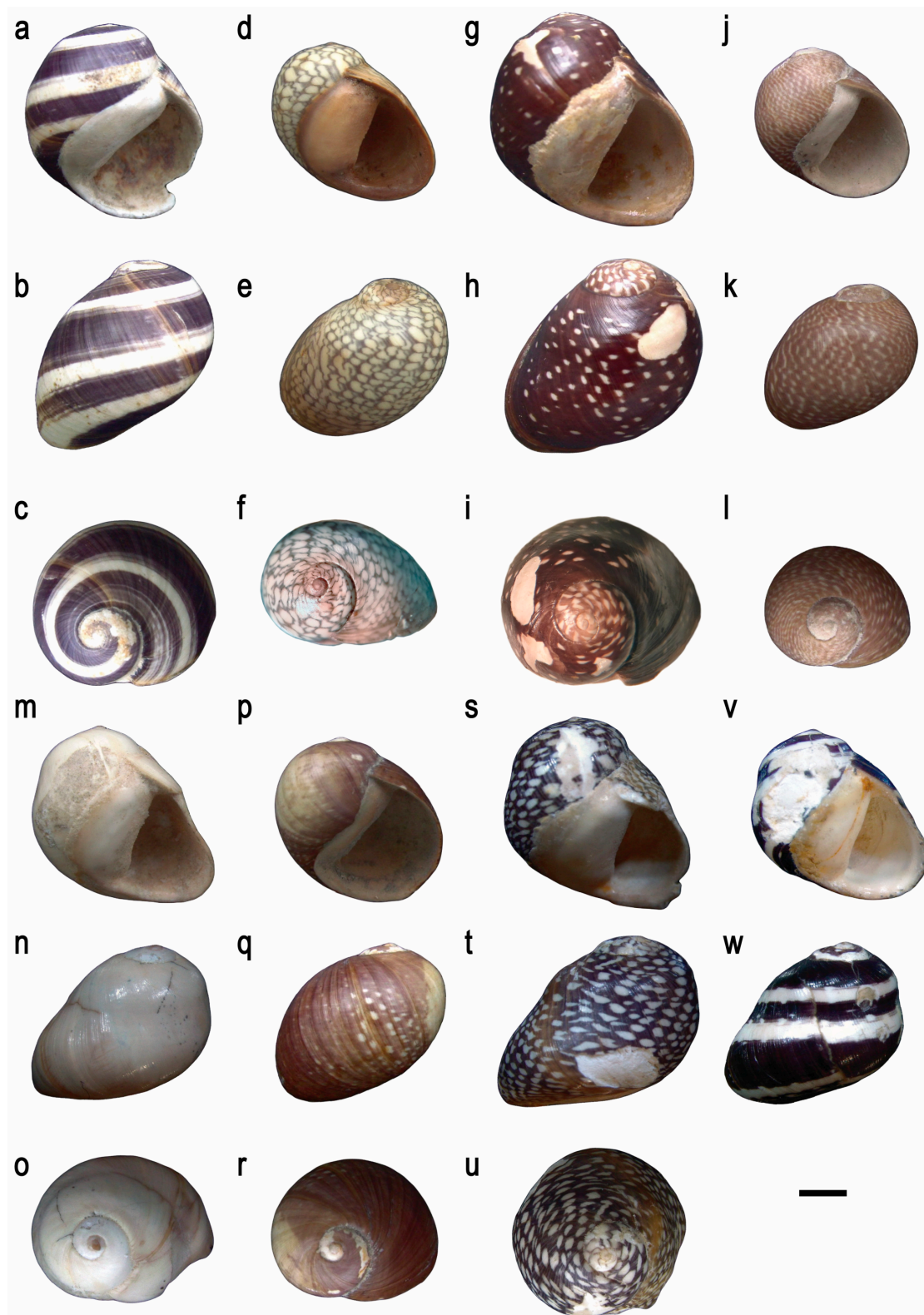


Figure 4. *Theodoxus micans* (Gaudry & P. Fischer, 1867, [17]) from the Megara Basin, Greece, deposited in the Museum of Geology and Paleontology, National and Kapodistrian University of Athens (MGPA, NKUA). Specimens a–f originate from Ano Alepochori, and specimens (g–w) from the Mavratza Ravine. (a–c) (MGPA-000093823), (d–f) (MGPA-000093874), and (g–w) (MGPA-000093563–MGPA-000093568). Apertural view: (a,d,g,j,m,p,s,v); dorsal view: (b,e,h,k,n,q,t,w); apical view: (c,f,i,l,o,r,u). All specimens (a–u) were used in the statistical analysis. Scale bar = 2 mm.

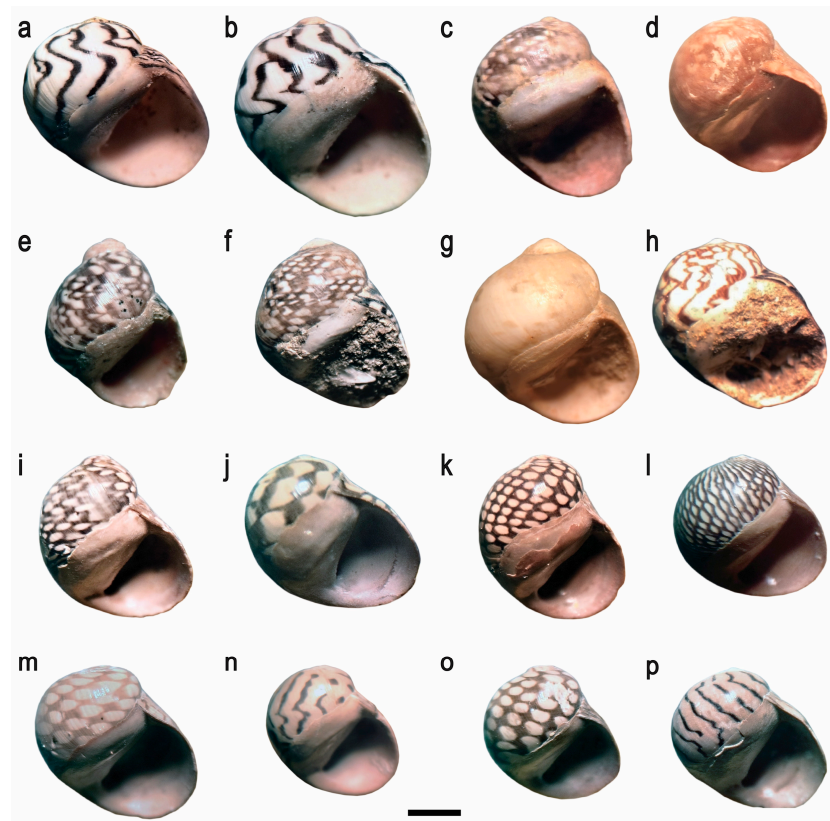


Figure 5. *Theodoxus micans* (Gaudry & P. Fischer, 1867, [17]) from Achaëa (a–h) and Corinthia (i–p), Greece. All specimens are deposited in the Museum of Geology and Paleontology, National and Kapodistrian University of Athens (NKUA). Catalog numbers MGPA-000095007–MGPA-000095022 correspond to the illustrated specimens in increasing order. All specimens (a–p) are shown in apertural view and were used in the statistical analysis. Scale bar = 2 mm.

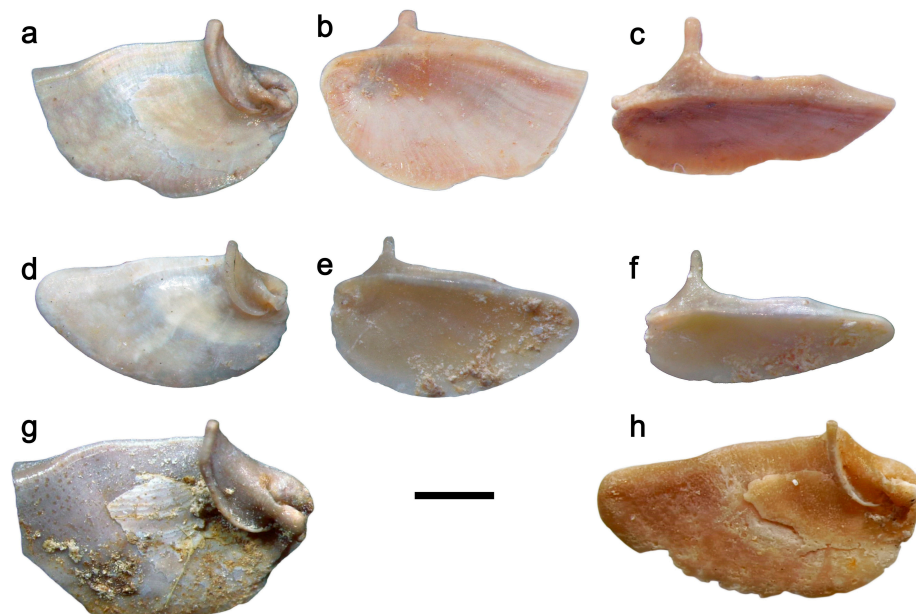


Figure 6. Opercula of *Theodoxus micans* (Gaudry & P. Fischer, 1867, [17]) from the Megara Basin, Greece, deposited in the Museum of Geology and Paleontology, National and Kapodistrian University of Athens (MGPA, NKUA). Specimens (a–c) and (d–f) originate from Ano Alepochori, and (g,h) from the 'Mavratza Ravine. (a–c) (MGPA-000093824), (d–f) (MGPA-000093875), (g) (MGPA-000093569) (h) (MGPA-000093570). Inner view: (a,d,g,h); outer view: (b,e); lateral view: (c,f). Scale bar = 1 mm.

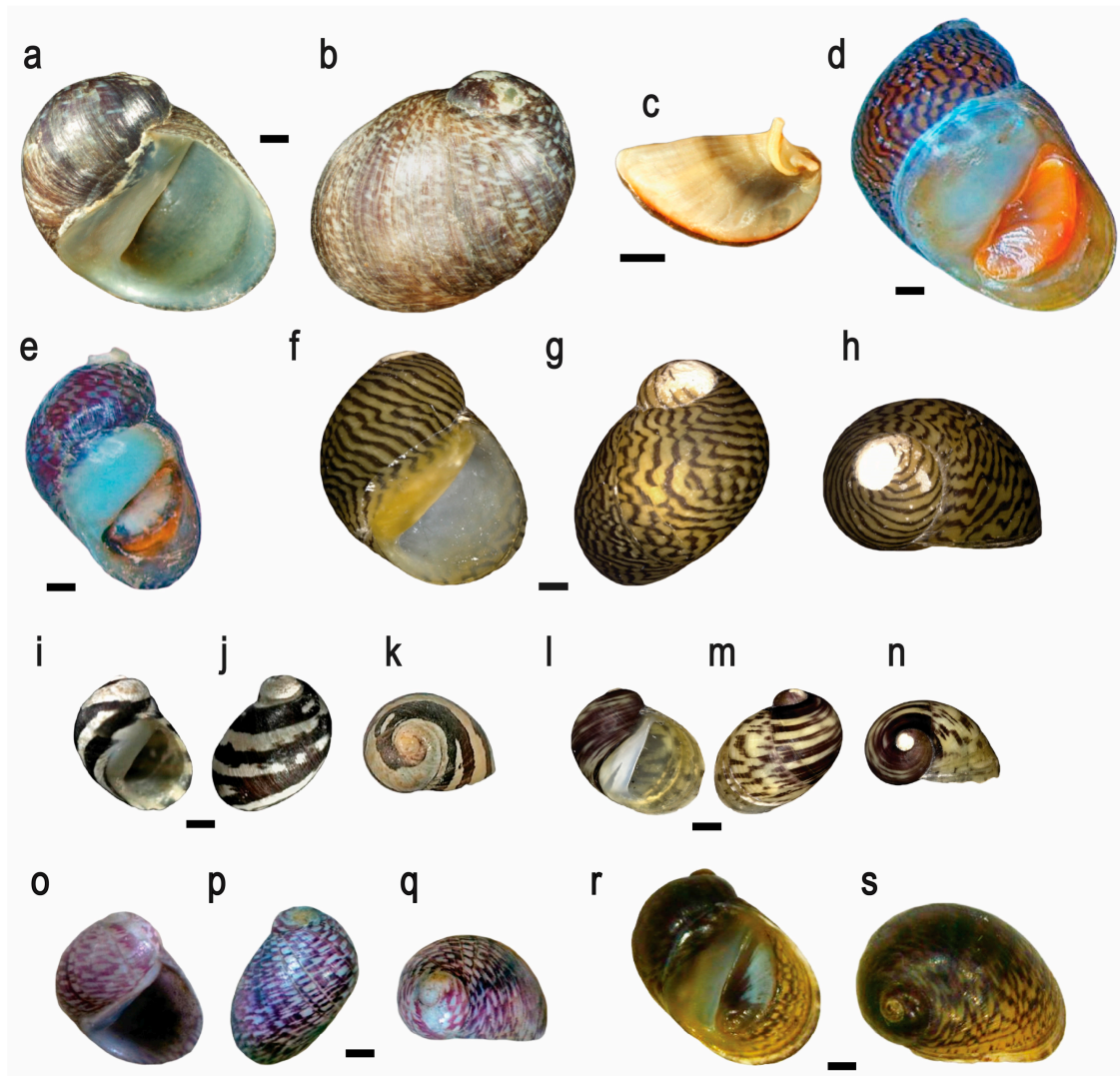


Figure 7. *Theodoxus meridionalis* (R. A. Philippi, 1836, [41]). (a,b,d–s) Shells from different geographic areas; (c) operculum of *T. meridionalis*. Figures (a–c,f–n) are adapted from Ref. [4], and figures (d,e,i–k,o–s) are adapted from Ref. [9]. Both references also include additional species (e.g., *T. fluviatilis*) used here for comparative purposes. All specimens (a,b,d–s) were included in the statistical analysis. Scale bar = 1 mm.

Neritina baetica Lamarck, 1822 [42]: 188.

Neritina varia: Menke, 1828 [43]: 27 (nomen nudum).

Neritina callosa Deshayes in Geoffroy Saint-Hilaire et al., 1835 [44]: 156, pl. 19, Figures 16–18.

Nerita meridionalis R. A. Philippi, 1836 [41]: 159–160, pl. 9, Figure 13.

Neritina micans Gaudry & Fischer in Gaudry 1867 [17]: 446, pl. 61, Figures 11–13 (syn. nov).

Neritina micans: Fuchs 1877 [18]: 14, pl. 3, Figures 5–16.

Neritina micans: Oppenheim 1891 [45]: 462.

Theodoxus (Calvertia) micans micans: Papp 1947 [23]: 117, pl. 9 (1), Figure 11A,B.

Theodoxus micans: Gillet & Geissert 1971 [26]: 128, pl. 6 (1), Figure 7; pl. 8 (3), Figure 2.

Theodoxus (Neritea) micans: Schütt & Besenecker 1973 [11]: 7, pl. 1, Figure 3.

Theodoxus micans micans: Gillet et al., 1979 [27]: 566, pl. 30 (3), Figure 7.

Theodoxus (Neritea) micans: Papp & Steininger 1979 [19]: 9, pl. 1, Figures 25 and 26.

Theodoxus (Neritaea) varius callosus: Schütt in Symeonidis et al., 1986 [24]: 339, pl. 4, Figures 1 and 2.

Theodoxus micans micans: Schütt 1988 [22]: 146, pl. 1, Figure 1.

Theodoxus micans: Frogley & Preece 2004 [25]: 247.

Theodoxus micans: Koskeridou & Ioakim, 2009 [13]: 97.

Theodoxus micans: Esu & Girotti 2015 [14]: 67.

Theodoxus sp.: Papadopoulou et al., 2019 [20]: 52, Figure 7A–C.

Theodoxus baeticus: Sands et al., 2020 [4]: 31, Figures 6–8 (cum syn.).

Theodoxus micans: Esu & Girotti 2020 [15]: 61, Figure 2A–E.

Type material: A set of nine syntypes of *T. micans* from the Megara Basin is housed in MNHN (collection number MNHN.F.B.37560) (Figure 3). All shells represent a single morphotype. No opercula are available.

Description: The study specimens from Megara, Achaea and Corinthia, consist of three rapidly expanding whorls (Figures 4 and 5). Height up to 9.1 mm, width up to 8.7 mm. Outline globose to subglobose; subglobose forms shaped by slight elongation and lateral compression of the body whorl. Spire is usually slightly protruding but varies between individuals within the same population. Shells with a relatively flattened to slightly protruding spire are present. Body whorl comprising about 90% of the total shell height. A shallow depression may develop along the peripheral zone. **Protoconch** consisting of 0.5–0.6 whorls, with smooth microsculpture. The protoconch–teleoconch boundary is generally indistinct, marked only by subtle growth lines on the early teleoconch. Teleoconch surface smooth, with fine growth lines. **Periostracum** is highly variable in color pattern, including zigzag lines, irregular blotches, spiral bands, or combinations thereof. **Body whorl** generally globose; the peripheral depression, when present, may extend toward the palatal side but remains shallow and variable in expression. **Aperture** D-shaped; straight columellar margin with smooth or bearing weak, often imperceptible denticles. Columellar plate is variably developed and calcareous.

Operculum: A distinct apophysis is present on the inner side (Figure 6). A well-defined pseudoapophysis extends obliquely from the midsection of the apophysis toward the basal portion, forming an angle of approximately 30°. The rib shield is weakly developed and low. A moderate callus is present. Overall morphology is consistent with that observed in extant *Theodoxus meridionalis* (Figure 7c).

Stratigraphic record: The fossil record of *T. micans* currently extends from Pliocene deposits of the Megara Basin (Tombes–Koukies Group) according to the stratigraphic data from [29,30], to the late Early–Middle Pleistocene deposits of the Koumares Member (upper Synania Formation) in Achaea, dated between 0.781 and 0.4 Ma [14,15]. Overlying marine deposits are correlated with Marine Isotope Stage (MIS 11), providing a maximum age constraint for *T. micans*. Published records further suggest that the species had a wider distribution across the Greek territory (see Figure 1a). At present, to our knowledge, no younger records of the species have been reported.

Remarks: Although the systematic placement of *Theodoxus meridionalis* is now well established (see [4,9]), *T. micans*, originally described by Gaudry [17] as a distinct species closely related to *Neritina baetica* Lamarck, 1822 [= *T. meridionalis* (R. A. Philippi, 1836), [41]], was based solely on limited shell morphological characters. The original description emphasized similarities in color patterns, while distinguishing *T. micans* by its larger size and more globular shell shape, leading to its recognition as a separate taxon. Fuchs [18] subsequently emphasized the extensive intraspecific variability of *T. micans*, noting that the description and illustrations provided by Gaudry and Fischer correspond to only a relatively rare morphotype, despite the species being very abundant in the freshwater deposits of the Megara Basin. According to Fuchs [18], most specimens display considerable variation, including lateral flattening, shell constriction, and a pronounced downward deflection of the last whorl near the aperture. The same species was also reported as very common in Rhodes, where these features appear even more pronounced (Fuchs [18]). Since

its original description, *T. micans* has been reported from multiple localities across Greece (see Figure 1a and synonymy list). Among these, only Schütt [24] referred to *Theodoxus (Neritaea) varius callosus* (Deshayes, 1835, [44]), now considered a synonym of *T. meridionalis*, as a fossil taxon comparable to extant representatives from Greece.

In their discussion of *T. micans*, Esu & Girotti [15] described morphotypes from Achaea (late Early–Middle Pleistocene deposits) with a pyramidal shell shape and a gibbous last whorl, which they considered similar to specimens reported from Kos and Rhodes. They also noted that these morphotypes were originally described by Fuchs [18] and were later assigned by Bukowski [10] to *T. hellenicus*. However, Esu & Girotti [15] did not consider these forms to belong to *T. micans*. The populations examined here from the Megara Basin and Achaea fall within the morphological plasticity of *T. micans*. The absence of opercula, however, precludes reliable assessment of morphological similarity or potential association between *T. micans* and *T. hellenicus*. Nevertheless, the taxa reported from Kos and Rhodes require further investigation.

T. micans co-occurs with *Theodoxus patrae* Esu & Girotti, 2015, in the Pleistocene deposits of Achaea but can be distinguished by the presence of five to six raised spiral carinate shells [14]. The fossil species *Theodoxus macedonicus* Wenz, 1943, from the Ptolemais Basin, differs primarily in having a prominent parietal callus of considerable thickness and a more stable color pattern, consisting of a light-colored shell with dark zig-zag lines [46]. However, no data are available for the operculum, and re-evaluation of this species in comparison with extant taxa, such as *Theodoxus danubialis* (C. Pfeiffer, 1828, [47]), would be valuable. *Theodoxus carinatus* (T. Fuchs, 1877), also differs by possessing a distinct peripheral carina on the shell [18]. *Theodoxus subdoricus* Schütt, 1976, possibly of Miocene age from Attica [48], exhibits an operculum with a pseudoapophysis and a globose shell and likewise warrants further investigation.

Among extant species occurring in Greece that show shell similarity to *T. micans*, one *Theodoxus callosus* (Deshayes, 1835, [44]) is currently regarded as a synonym of *T. meridionalis* [4], and has been reported in Greece [4], including Lakes Trichonida and Lysimachia (Aetolia-Acarnania, western Greece) [49,50].

Additionally, *T. fluviatilis*, which also occurs in Greece (e.g., Andros Island) [51], resembles *T. micans* in shell characteristics, particularly in the color pattern, such as the presence of white blotches (e.g., Figure 10A in work of [4]). However, despite these similarities in shell morphology, the two extant species can be distinguished based on opercular characters: *T. fluviatilis* lacks a pseudo-apophysis, in contrast to *T. meridionalis*, in which this structure is present [4,6]. Furthermore, within its broader morphological spectrum, the shell of *T. meridionalis* (Figure 7) may display a more pyramidal aspect compared to *T. fluviatilis*, which typically exhibits a lower spire and a more expanded body whorl, as documented in the literature (e.g., Figures of [4,9]). This pattern is also reflected in the morphometric data (Table 1) and the scatter plot (Figure 8), which support our visual observations. The synonymization of *T. micans* with *T. meridionalis*, rather than with *T. fluviatilis*, is supported by the fact that the type material falls entirely within the morphological range of *T. meridionalis*. This interpretation is reinforced by the presence of opercula associated with shell specimens showing continuous variation from more spherical to more pyramidal forms, without any consistent or non-overlapping characters that would support the recognition of a distinct species.

Both shell and operculum morphology correspond to the range observed across multiple populations of extant *T. meridionalis* (Figure 7), while remaining distinguishable from other known fossil species from Greece. No consistent diagnostic features were identified in the examined material that would clearly separate *T. micans* from *T. meridionalis*. These observations support the synonymy of *T. micans* with *T. meridionalis*.

Table 1. Descriptive statistics of shell height-to-width ratios (sh/sw) for the studied *T. micans* populations (Megara, Corinthia, and Achaea) and comparative *T. meridionalis* and *T. fluviatilis* populations. N = sample size; Mean = mean sh/sw ratio; SD = standard deviation; Min = minimum value; Max = maximum value.

Population/Taxon	N	Mean sh/sw	SD	Min	Max
Megara (<i>T. micans</i>)	9	1.00	0.05	0.93	1.08
Corinthia (<i>T. micans</i>)	8	1.01	0.09	0.91	1.14
Achaea (<i>T. micans</i>)	8	1.05	0.09	0.92	1.20
<i>T. meridionalis</i>	12	1.05	0.13	0.95	1.37
<i>T. fluviatilis</i>	12	0.91	0.08	0.78	1.12

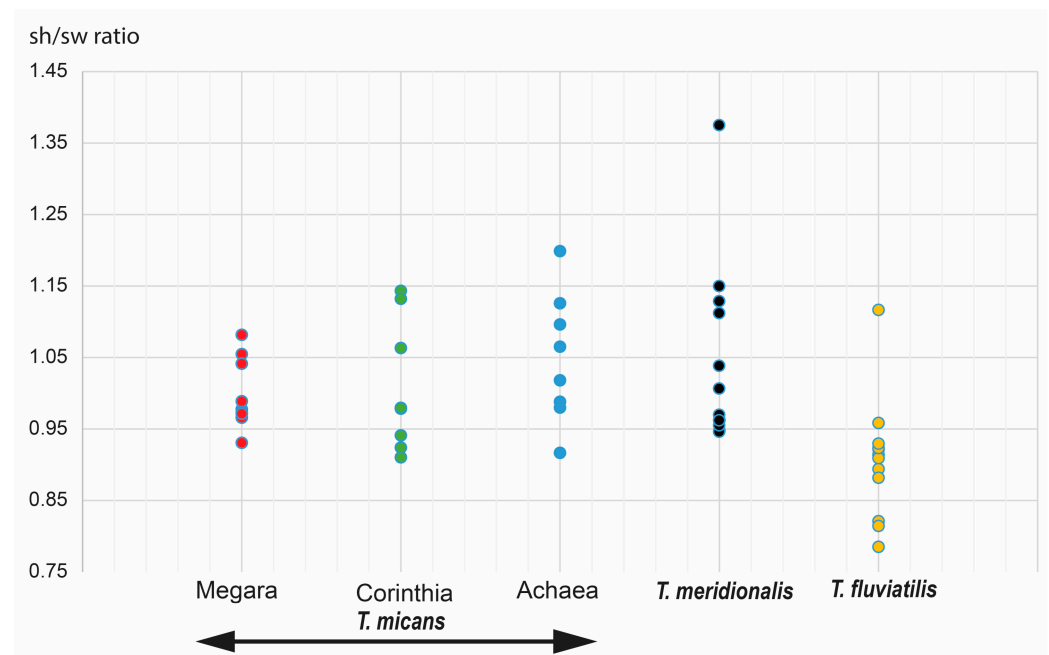


Figure 8. Scatterplot of shell height-to-width ratios (sh/sw) for individual specimens. Populations are indicated as follows *Theodoxus* specimens: *T. micans* from Megara (red); Corinthia (green); Achaea (blue); *T. meridionalis* (black); and *T. fluviatilis* (yellow). Overlap between *T. micans* populations and *T. meridionalis* is evident, average *T. fluviatilis* values lie at lower sh/sw ranges, reflecting broader shells.

5. Discussion

Both Fuchs and Gaudry appear to have studied sections from the Mavratza Ravine, which is also mentioned by Papp & Steininger [19]. Part of the examined NKUA material bears original labels indicating provenance from the Mavratza Ravine. Moreover, the fossil fauna included several of the species described by both authors in their works. Gaudry [17] further noted that the fossil material from the Megara Basin was collected from lacustrine deposits occurring both above and below marine horizons. According to [29], two main appearances of marine intervals are recognized in the Tombes–Koukies Group (Toumpaniari fm and Harbour Ridges fm).

Based on Gaudry's descriptions and the revised stratigraphic framework of [29], the fossil material studied here most likely derives from units belonging to the Tombes–Koukies Group (Figure 2b), comprising the Toumpaniari, Pistarda, and Harbour Ridges formations. The travertine horizons referred to by Gaudry as the 15th and 9th beds, possibly related to fault-controlled deposition, can be correlated with travertine levels within the Pistarda Formation. Additionally, the lignite layer described as the 6th bed corresponds to lignite-bearing horizons within the Harbour Ridges Formation.

The stratigraphic succession described by Gaudry [17] closely resembles that of the Tombes–Koukies Group as defined in subsequent geological studies. Moreover, the geographic extent indicated by Gaudry [17]—from the settlement of Megara towards the Geraneia Mountains—largely coincides with areas currently assigned to the Tombes–Koukies Group. The stratigraphic range of *T. micans* therefore appears to be largely restricted to the Tombes–Koukies Group and has not been documented from older deposits of the basin.

Our re-examination of the syntypes housed in MNHN, together with NKUA material from the Megara Basin, indicates that the characters previously used to distinguish *T. micans* fall within the morphological variability observed in extant *T. meridionalis*. Operculum morphology—unknown in the original description by Gaudry [17]—appears to offer comparatively more stable diagnostic characters. Given the well-documented plasticity of shell morphology in *Theodoxus* [4,9], shell characters alone, in many cases do not justify species-level separation.

While extensive population-level morphometric analyses and integrative approaches could further refine species boundaries within *Theodoxus*, such data are currently unavailable for both fossil and modern comparative material from the region. Based on the available morphological evidence, including the re-examination of type material and opercular characters, no stable diagnostic features justify the maintenance of *T. micans* as a distinct species. The available evidence consistently supports the interpretation of *T. micans* as conspecific with *T. meridionalis*.

The present revision highlights that species-level assessment in *Theodoxus* should rely on a combined evaluation of shell morphology, opercular characters, and population-level variability rather than on single diagnostic traits. Consideration of intraspecific plasticity is essential to avoid taxonomic over-splitting.

Limitations of the Study

The aim of this study was to investigate the systematic validity of *Theodoxus micans* in Greece through comparison with the most morphologically similar extant and extinct species using taxonomically confirmed material. Efforts were made to include only well-preserved shells that display a representative range of variability. Nonetheless, several limitations should be acknowledged. Sample sizes are relatively small for certain populations, and fossil preservation may have affected shell measurements. While sh/sw ratios were used to remove the effect of absolute size, other morphological features (e.g., aperture shape) were not quantified. Moreover, due to the scarcity of fossilized opercula, no morphometric measurements could be performed on opercula, limiting the assessment of opercular variation across populations. Comparative data for *T. meridionalis* and *T. fluviatilis* were obtained from the literature and may include methodological differences. In addition, stratigraphic correlations for many fossil populations are limited, highlighting the need for further research to clarify temporal and palaeoenvironmental contexts.

6. Conclusions

The stratigraphic range of the fossil record of this taxon currently extends from the Pliocene deposits of the Megara Basin (Tombes–Koukies Group) to the late Early and Middle Pleistocene deposits of the Koumares Member, located in the upper part of the Synania Formation, dated between 0.781 and 0.4 Ma. Published records indicate that this taxon had a relatively widespread distribution across several regions of Greece. Extant populations of *Theodoxus meridionalis* are also recorded in Greece based on published literature, including historically documented localities such as Lake Trichonida.

Descriptive statistics of shell height-to-width ratios (sh/sw) are presented in Table 1. The sh/sw ratios of the *T. micans* populations from Megara, Corinthia, and Achaia show

considerable similarity (Mean 1.00–1.05; SD 0.05–0.09), indicating broadly similar shell morphology among the three localities. These fossil populations derive from three different geographic areas, which likely contribute to the observed intraspecific variability while still maintaining a high degree of morphological consistency.

T. meridionalis exhibits mean values comparable to those of *T. micans* (Mean 1.05; SD 0.13), indicating close morphometric affinity between the fossil and extant populations. In contrast, *T. fluviatilis* shows generally lower sh/sw ratios (Mean 0.91; SD 0.08), corresponding to relatively broader shells; overlap with *T. micans* and *T. meridionalis* occurs mainly at the extreme values of the distributions rather than across the central tendency of the dataset.

Re-examination of *Theodoxus micans* syntypes housed in (MNHN, France), together with comparative material from NKUA, demonstrates that the characters previously considered diagnostic fall within the morphological variability of *T. meridionalis*. Shell shapes range from rounded to slightly compressed. No stable or non-overlapping characters supporting species-level distinction were identified in the examined material, and *T. micans* is therefore interpreted as a junior synonym of *T. meridionalis*.

In addition, the presence of opercula bearing a pseudo-apophysis consistent with that of *T. meridionalis*, the overlapping mean values between the fossil populations and those of *T. meridionalis*, the continuous stratigraphic occurrence of *T. micans* across several regions of Greece from the Pliocene to the late Early Pleistocene, and the present-day distribution of *T. meridionalis* in Greece collectively support the interpretation that *T. micans* as a junior synonym of *T. meridionalis*.

Future Studies

The next stage of the proposed research is to focus on the re-evaluation of other fossil *Theodoxus* species in Greece, which should include a larger number of specimens, the recovery of additional opercula, and a broader assessment of intraspecific morphological variability, in order to be able to further utilize the verified fossil archives for further studies, phylogeny, palaeobiogeography, etc.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/blsf2026060003/s1>, Table S1: Dataset of shell measurements used for the statistical analysis (Excel file).

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