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The *Theodoxus* Montfort, 1810 species of North Africa (Gastropoda: Neritidae) with the description of a new species

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ABSTRACT: The species richness of the freshwater gastropods in Morocco is one of the highest in North Africa. *Theodoxus sandsi* sp.n. is a new gastropod from Morocco, which can be distinguished from its congeners by shell morphology and operculum criteria. The new species was found in the Middle Atlas massif, a cornerstone of the freshwater biodiversity in Morocco and North Africa in general. In addition, we discuss the taxonomic status of the problematic *Theodoxus* spp of Northern Africa.
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KEY WORDS: Neritidae, freshwater biodiversity, Middle Atlas, Morocco; endemism.

Виды рода *Theodoxus* Montfort, 1810 Северной Африки (Gastropoda: Neritidae), с описанием нового вида

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РЕЗЮМЕ: Показатели видового богатства пресноводных брюхоногих моллюсков Марокко — одни из наиболее высоких в Северной Африке. Новый вид *Theodoxus sandsi* sp.n. из Марокко отличается от других представителей рода морфологией раковины и особенностями оперкулума. Новый вид обнаружен в массиве Среднего Атласа, ключевого региона по биоразнообразию пресноводной биоты Марокко и всей Северной Африки. Дополнительно обсуждается таксономический статус проблемных видов *Theodoxus* Северной Африки.

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КЛЮЧЕВЫЕ СЛОВА: Neritidae, разнообразие пресноводной биоты, Средний Атлас, Марокко, эндемизм.

Introduction

Freshwater gastropods play an important role in freshwater ecosystems, mainly through their control of water quality and nutrient balance by grazing on algae and, to a lesser extent, as a food source for predators including a number of vertebrate species (Tachet *et al*., 2020). Gastropods of the family Neritidae Rafinesque, 1815, commonly known as Nerites, occur in freshwater, brackish and marine systems. These herbivorous snails are usually found in the mid to upper littoral zone and are known to be gregarious. The family consists of both species with restricted distribution and species with wider distribution (Abdul, 2016).

The calcareous operculum is one of the characteristics of the Neritidae family, it is a protective organ developed on the foot that allows the shell to be closed when the animal withdraws into it. It is a semicircular disc with a deposit of calcareous material on a horny layer. This calcareous layer has a large apophysis and the outer surface is often sculptured (Dekker, 2020). The operculum protects the snails from predator attacks and helps prevent desiccation avoiding severe dehydration of soft tissues even at high temperatures (Kaim, Sztajner, 2005).

The genus *Theodoxus* Montfort, 1810 is a genus of the family Neritidae that is a common component of freshwater ecosystems in the western Palearctic (Glöer, 2019; Sands *et al*., 2020). The taxonomy of *Theodoxus* species in North Africa is rather confused. Some early authors proposed names (under the genus *Neritina* Rafinesque, 1815):

Récluz (1841: 342) described *Neritina numidica* from Oran in the Atlas, from Tisi valley, as new and Reeve added in 1856 (p. 206) a new description of *N. africanus* but did not mention a type locality. Consindering the original drawings of *N. africanus* Reeve provided (1856, figs 138a, b) this species is more globular and somewhat smaller than 6 mm.

Bourguignat (1864: 269) listed *N. fluviatilis* from the region of Oran and some other localities in Algeria. However, according to Westerlund (1886), *N. fluviatilis* is distributed in northern and central Europe, not in Africa. Bourguignat also listed *N. numidica* from Algeria: Tlemcen, thermal spring Ain-Fekan, region of Constantine and Calle, and he described *N. maresi* from the thermal spring Ain-Khadra near Zerguin as new. Bourguignat was the first who described the operculum of *Theodoxus maresi* which has an apophyse and a pseudoapophysis ("deux petits sillons").

Paladilhe (1875: 95) described *Neritina maroccana* from Meknès, Morocco as new. Westerlund (1886: 154–155) listed from N-Africa only *Nerita numidica* from Algeria, and *Neritina maroccana* from Morocco (Meknès). Pallary (1904: 56) described *N. tingitana* from Tetouan as new and added in 1920, *N. marteli* (p. 154) and *N. djedida* (p. 155) from Oued Fes, Fès-Meknès region. Kristensen (1985) was the first to provide drawings of the opercula and described *Theodoxus numidicus* without a pseudoapophysis, *Th. meridionalis* with a pseudoapophysis and *Th. maresi* with a pseudoapophysis and one without. Finally, in 2020, Galindo described *Th. poppei* from Douar Ellil, NW Berkane, Oriental Region of Morocco as new.

In recent centuries, *Theodoxus* spp. have predominantly been described and identified by shell shape and pattern only. Both are not suitable for species identification alone and should be supported by features of the operculum. New research conducted recently in the Middle Atlas Massif of Morocco has revealed a new species of the genus *Theodoxus*. In this paper, we provide an overview of the nominal species of *Theodoxus* in North Africa, in addition to the description of *Th. sandsi* sp.n. discovered in Morocco.

Material and Methods

Fieldwork was carried out between 2014 and 2023, sampling several sites in northern Morocco, including the Atlas Mountains, Sebou and Mou-

louya River basins. Most of these sampling sites were visited several times. Our aim was to document the maximum macroinvertebrate biodiversity in the different microhabitats prospected at each sampling site. Samples were fixed in 75% ethanol. Dissection and measurements of opercula and shells were carried out using a stereomicroscope (Leica M205C) with a digital camera (Leica DMC5400). The type material is partly kept in the Zoologisches Museum Hamburg (ZMH) and partly in the authors' collection.

Results

Phylum Mollusca Cuvier, 1795
Class Gastropoda Cuvier, 1795
Order Cycloneritimorpha Frəda, 1998
Family Neritidae Rafinesque, 1815
Genus *Theodoxus* Montfort, 1810

Theodoxus africanus (Reeve, 1856)

COMMENTS. The type locality of this species is unknown (only mentioned as "Africa" in the original description). Reeve described predominately the shell pattern: with characteristic faintly pencilled blackish flexuous lines, more or less interrupted. Although Eichorst (2016) accepts *Theodoxus africanus* as a full species, the depicted specimen in his comprehensive monograph on the Recent Neritidae, has nothing in common with *Th. africanus* described, because the zig-zag-lines in Eichorst's species are diffuse and not pencilled. Considering the operculum of *Th. africanus sensu* Eichorst, 2016 has only a apophysis and a rib-shield, no pseudoapophysis. Consequently, it is possible that Eichorst depicted *Th. fluvatilis*. Altogether we can say that *Th. africanus* is a *nomen dubium*.

Theodoxus djedida Pallary, 1920

COMMENTS. The type locality of the species is at Oued Fes, Fez-Meknes Region, N. Morocco (around 34°03′25.6″N 5°00′03.9″W). Considering the original description and the photos of the types (Pallary, 1920, pl. II, figs 3–5) the shells are more globular than *Theodoxus sandsi* sp.n. This species has not been recorded since its description. The species *Th. djedida* and *Th. maroccana* occur in the same region, both shells are globular and of the same size according to the original descriptions, and the figures of the types look similar. We therefore suggest that *Th. djedida* is a junior synonym of *Th. maroccana*.

Theodoxus fluviatilis (Linnaeus, 1758)

COMMENTS. The type locality of this species is at Uppsala, Sweden (Linnaeus, 1767). *Th. fluviatilis* is the most widespread *Theodoxus* species in the Palearctic (Glöer, 2019). Considering North Africa, it was mentioned by Bourguignat (1864) around Oran, Algier, Oued-Smar, Harrach, bassin de Mustapha, and around Boudounou. The range of this species is the largest of *Theodoxus* genus in Morocco (Taybi *et al*., 2017; Mabrouki *et al*., 2023a).

Theodoxus maresi (Bourguignat, 1864)

COMMENTS. The type locality of this taxon is at Ain-Khadra (thermal spring) near Zerguin. (Algeria). Van Damme (1994: 5) synonymised this species with *T. numidicus*, on the other hand the shell of *T. maresi* is a globular and *T. numidicus* is broader than high. It is therefore possible that the two species are distinct.

Theodoxus maroccanus (Paladilhe, 1875)

COMMENTS. The type locality of this taxon is at Meknes, Morocco, it was assigned to *Theodoxus fluviatilis* (Ramdani *et al*., 1987). This species has never been mentioned in the literature. Van Damme *et al*. (2010) synonymised *Th. maroccana* with *Th. numidicus*, but considering the original description, both species differ in their proportions, *Th. maroccana* being globular (same height and width) and *Th. numidicus* being broader than tall. We therefore believe that both species are distinct.

Theodoxus marteli (Pallary, 1920)

COMMENTS. The type locality of this species is at Oued Fes, Fez-Meknes Region, North Morocco (around 34°03′25.6″N 5°00′03.9″W). *Theodoxus marteli* was collected and recorded recently from the Oriental Region of Morocco (Mabrouki *et al*., 2023a).

Theodoxus numidicus (Rŭcluz, 1841)

COMMENTS. The type locality of this species is a thermal spring found in Oran (Tisi Valley) Algeria. *Theodoxus numidicus* was recorded recently from the Oriental Region of Morocco (Mabrouki *et al*., 2023a).

Theodoxus vondeli (Pallary, 1936)

COMMENTS. The type locality of this species is in Beni Mellal area (Beni Mellal-Khenifra region), North Morocco (around 32°19′41.3″N 6°20′

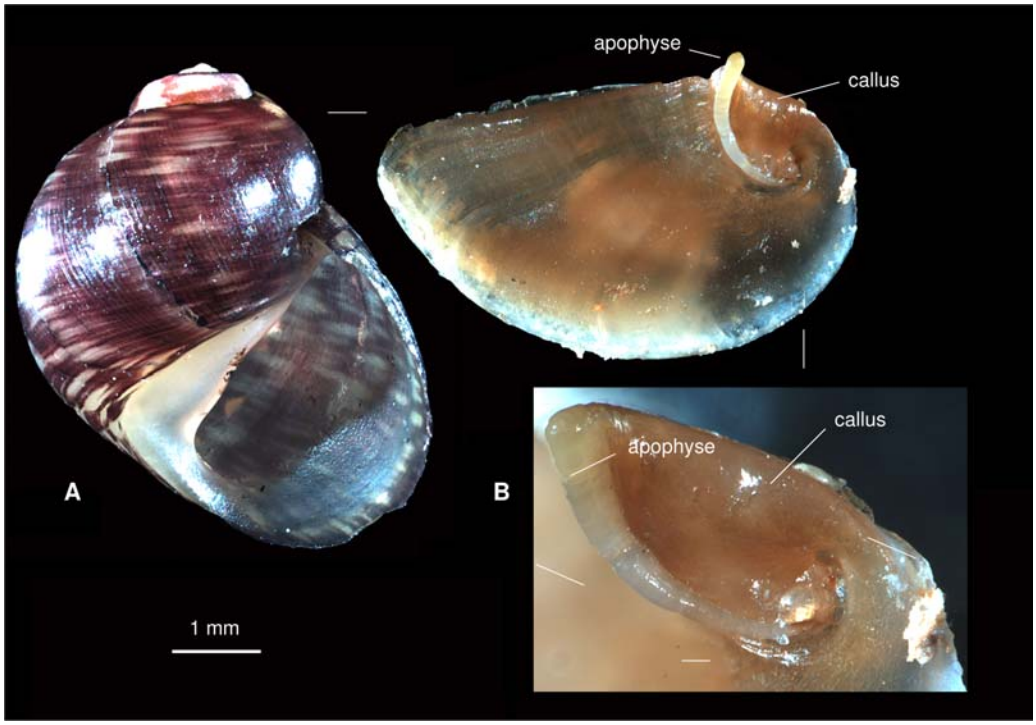

Fig. 1. Holotype of *Theodoxus sandsi* sp.n. A — shell, B — operculum.
Рис. 1. Голотип *Theodoxus sandsi* sp.n. A — раковина, B — оперкулум (крышечка).

06.4″W). Girod *et al*. (1980) assigned this species to a form of *Theodoxus fluviatilis*.

Theodoxus poppei Galindo, 2020

COMMENTS. The type locality of this recently described species is at Douar Ellil, NW Berkane, Ortiental Region of Morocco. Although the shell shape look different, considering the depicted operculum it could be a junior synonym of *Th. fluviatilis*. The latter is widespread and very abundant in the Oriental Region of Morocco (Taybi *et al*., 2017; Mabrouki *et al*., 2023a). *Theodoxus fluviatilis* is widely-distributed in the West Palearactic, known for its morphological plasticity and it comprises many different variations in shell shape and colour pattern, several previous nominal species have been attributed to it (Zettler, 2008; Glöer, Pešić, 2015; Anistratenko *et al*., 2022).

Theodoxus tingitana (Pallary, 1899)

COMMENTS. The type locality of the species is at Tangier cap Cantin Morocco, abundant in the waterways around Tetouan. Never been mentioned after the original description. According to MolluscaBase (www.molluscabase.org) this species is questionable. The species has been assigned to *Theodoxus fluviatilis* (Ramdani *et al*., 1987).

Theodoxus sandsi Mabrouki, Glöer etTaybi **sp.n.**
Figs. 1–2, 4C.

TYPE MATERIAL. **Holotype:** Adult specimen; shell 5.71 mm high and 4.89 mm broad; from the type locality: Ain Regrag spring (33°46′39.8″N 4°43′54.5″W), Sefrou Province, Fez-Meknes region, Middle Atlas, Morocco. Collected on 09/04/2022, (ZMH 141518). **Paratypes:** 2 paratypes in ethanol from the type locality (ZMH 141519) 2 in coll. Glöer, 4 in ethanol from: El Menzel, Ain Timedrine (33°44′48.3″N 4°33′03.4″W), Sefrou Province, Fez-Meknes region, Middle Atlas, Morocco, collected on 24/05/2022, (ZMH 141520), 2 in coll. Glöer. 5 paratypes from Ain Sidi Bouali spring at Lakliaa (33°46′24.3″N 4°42′22.9″W) (ZMH 141522), 5 coll. Glöer, Sefrou Province, Fez-Meknes region, Middle Atlas, Morocco, collected on 09/04/2022. 4 paratypes from Ain Chkef spring, Fez prefecture, Fez-Meknes region, Morocco (33°57′51.0″N 5°01′13.1″W), collected on 13/02/2021 (ZMH 141521), 2 coll. Glöer.

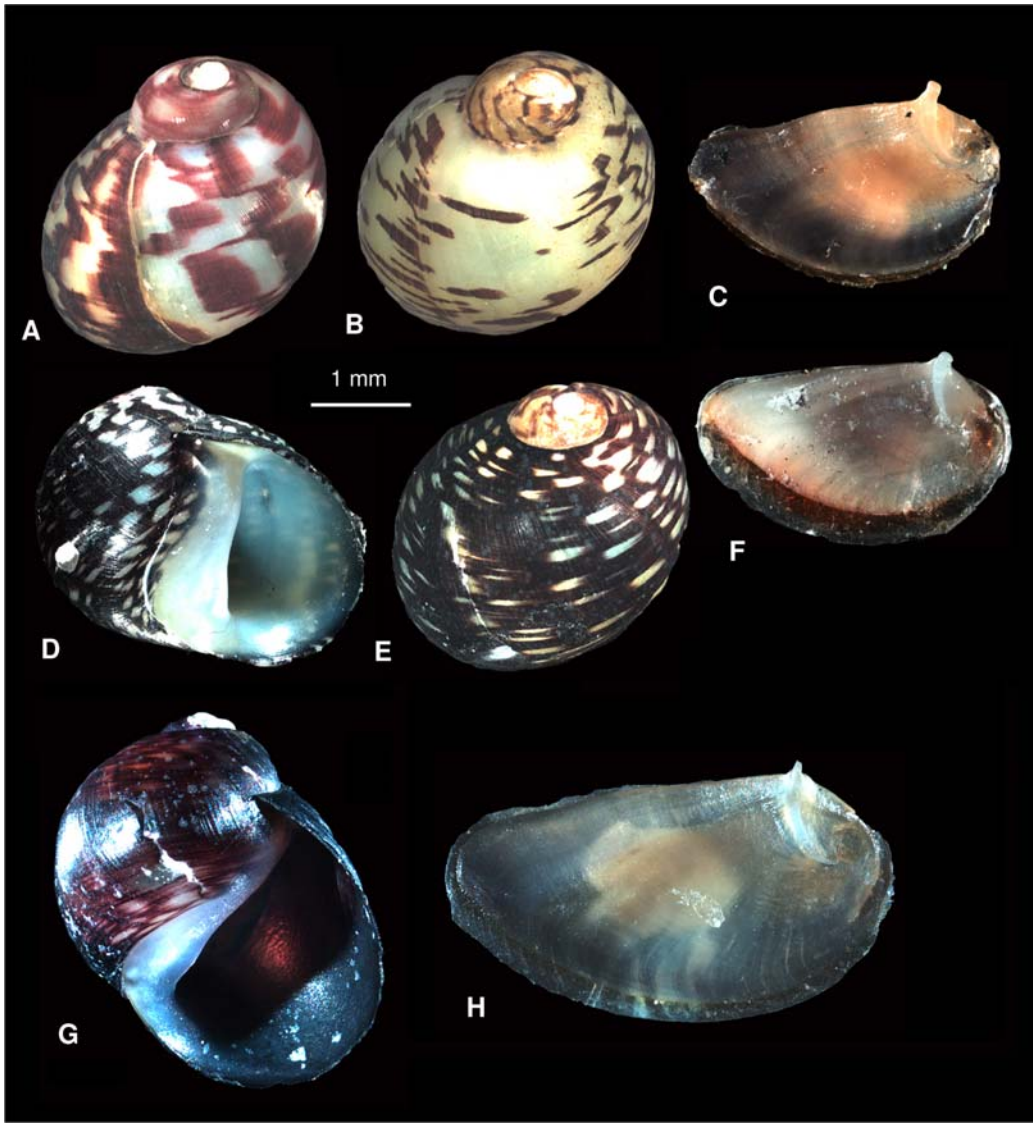

Fig. 2. Paratypes of *Theodoxus sandsi* sp.n.: A–F — from Ain Chkef, G–H — from Ain Timedrine.
Рис. 2. Паратипы *Theodoxus sandsi* sp.n.: A–F — из Ain Chkef, G–H — из Ain Timedrine.

TYPE LOCALITY. Ain Regrag spring 33°46′3 9.8″N 4°43′54.5″W, Sefrou Province, Middle Atlas, Morocco. Collected on 09/04/2022.

DESCRIPTION.

Shell: The shell is thick and elongated, globose (Figs. 1A, 2A, B, D, E, G). It is dark violet with irregular transversal spots. The columellar plate is trapeziform with a nearly straight border. The shell is 4.7–5.7 mm high and 4.8–6.6 mm broad. Colour and patterns of the shell are very variable (Fig. 2).

Operculum: The apophyse is simple and forms with the thick callus a groove for the muscle adductor. A pseudoapophyse and a rib shield are missing. Thus the upper border, right of the apophyse, is visible and not covered by the shield.

Differential diagnosis: *Theodoxus numidicus* and *Th. maresi* have a pseudoapophysis which is missing in *Th. sandsi* sp.n. *Th. fluviatilis* has an apophysis (rib) with a rib-shield which build a rib-pouch for the muscle adductor, both are missing in *T. sandsi* sp.n. (Figs 1B, 2C, F, H) Considering the original drawings of *Neritina africanus* Reeve (1856: figs 138a,b) provided this species is more globular and somewhat smaller than 6 mm. *Theodoxus poppei*

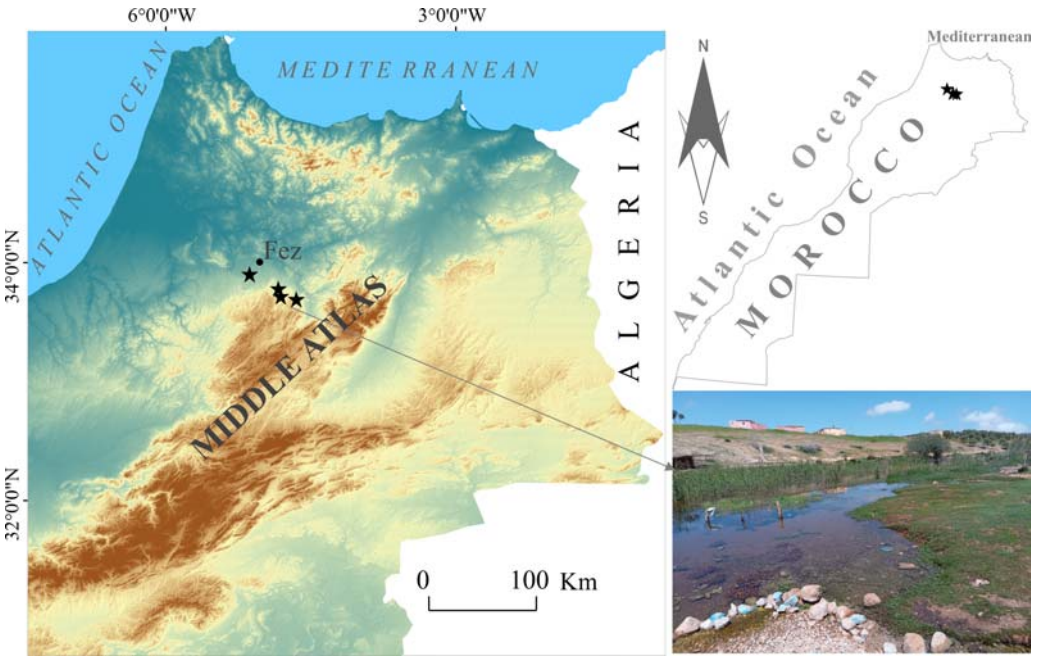

Fig. 3. Distribution range (black stars) and type habitat of *Theodoxus sandsi* sp.n. in the Middle Atlas.
Рис. 3. Распространение (черные звездочки) и типовой биотоп *Theodoxus sandsi* sp.n. в Среднем Атласе.

Galindo, 2020 has a rib-shield and no pseudoapophysis and is by this different from *Th. sandsi* sp.n. The shell of *Th. maroccana* is more globular (Paladilhe, 1875: 95, pl. 9, figs 26–28). *Th. tingitana* (Pallary, 1899: 148, pl. IX, fig. 9) has a low spire and a shell shape like *Th. fluviatiis*. *Th. vondeli* is much larger than *Th. sandsi* sp.n. and the columellar plate is broader and more rectangular. The operculum of *Th. poppei* Galindo, 2020, has a rib-shield (Galindo, 2020: 42, fig. 2) which is missing in *Th. sandsi* sp.n.

Form outside of North Africa, *Th. sandsi* sp.n. is somewhat similar to *Th. valentinus* (Graells, 1846) occurring in Spain, which is currently considered as extinct species, known only from a single spring in the Venta del Conde area, Valencia (Martínez-Ortí, Osca, 2023). However, *Th. valentinus* has that characteristic sinuosity in the lip, which gives it that trochiform shape, *Th. sandsi* sp n. does not have this characteristic in addition of having longer apophysis. The new species is also similar to *Theodoxus* spp of the *velascoi*/*meridionalis*/*baeticus* complex group, nowadays synonymized under *Th. baeticus* (Lamarck, 1822), this species presents an operculum with a pseudoapophysis of variable extension towards the edge of the operculum (Glöer, 2018, 2023; Sands *et al*., 2020), while in the operculum of *Th. sandsi* sp.n. the rib shield is missing and has no pseudapophysis.

ETYMOLOGY. Named after Arthur Francis Sands for his comprehensive work on *Theodoxus* genus.

HABITAT. *Theodoxus sandsi* sp.n. was found in different rheocrenous natural springs located in the Middle Atlas. All the localities belong to Sebou River basin. The sediment of the springs is made up of blocks, stones, pebbles and sand (Fig. 3). *Theodoxus sandsi* sp.n. shares its habitat with other freshwater molluscs, including the micro-endemic and recently described Hydrobiidae species i.e. *Pikasia smenensis* Taybi, Glöer et Mabrouki, 2021 at Ain Chkef spring; *Ainiella zahredini* Taybi, Glöer et Mabrouki, 2022 at Ain Regrag and Ain Sidi Bouali springs and *Menzella timedrinensis* Mabrouki, Glöer et Taybi, 2023 at Ain Timedrine spring. Through its distribution range in the Middle Atlas, the new *Theodoxus* species seems to require running waters and good environmental conditions (see Taybi *et al*., 2021, 2022a and Mabrouki *et al*., 2023b for more details on ecology and water parameters).

Identification key for *Theodoxus* spp. of North Africa

1. Shell height greater than shell diameter 2
– Shell globular, or shell diameter greater than shell height 3

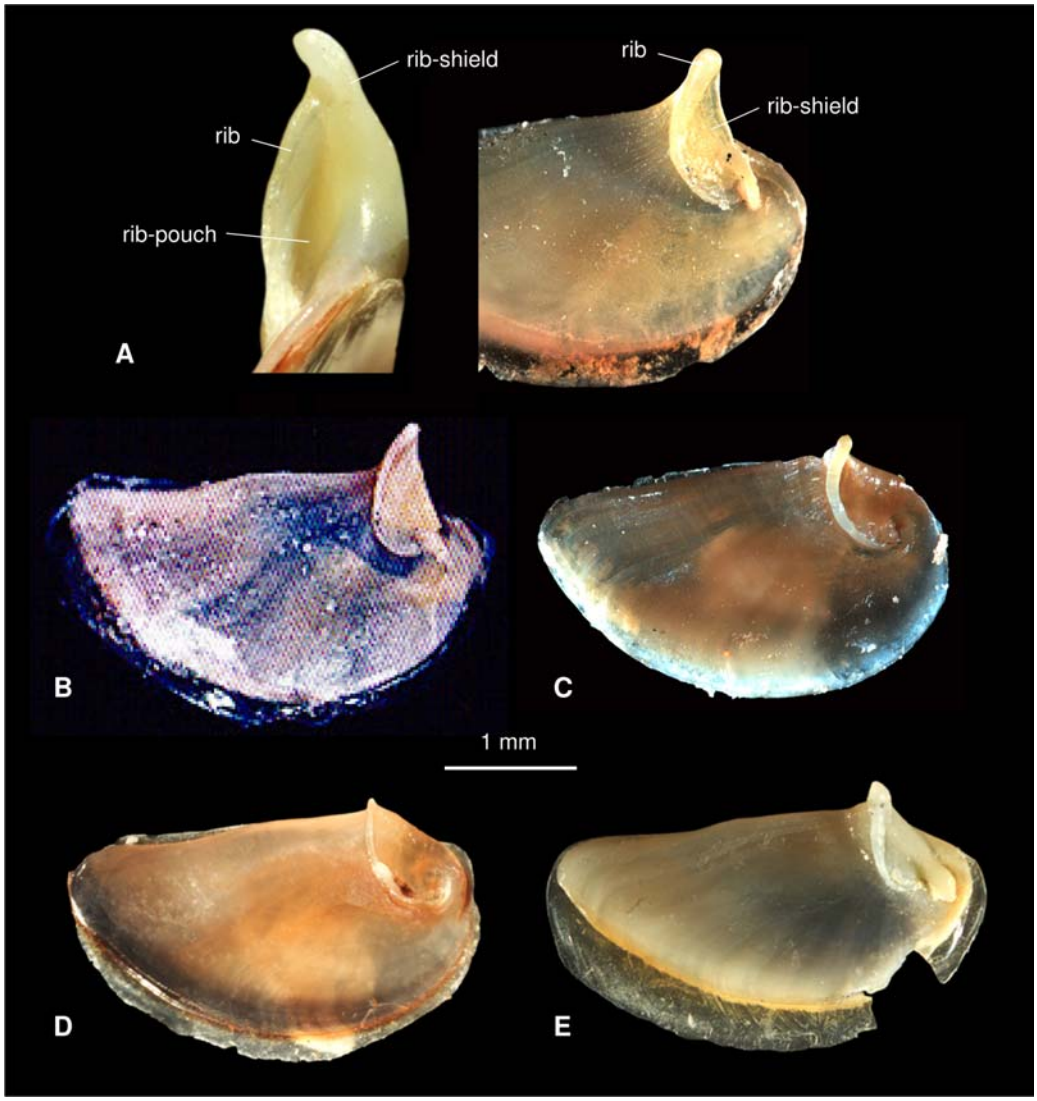

Fig. 4. The opercula of the *Theodoxus* spp. of Morocco. A — *Th. fluviatilis*, B — *Th. poppei* (after Galindo, 2020), C — *Th. sandsi* sp.n., D — *Th. numidicus*, E — *Th. marteli*.
Рис. 4. Оперкулумы (крышечки) видов *Theodoxus* из Марокко.

2. Rib shield exists, pseudoapophysis missing .... *Theodoxus poppei*
– Rib shield missing, no pseudapophysis..... ..... *Theodoxus sandsi* sp.n.
3. Shell broader than high 4
– Shell globular 5
4. Pseudoapophysis absent .... *Theodoxus fluviatilis*
– Pseudoapophysis present ....*Theodoxus numidicus*
5. Pseudoapophysis strong and curved in the plane ..... *Theodoxus marteli*, *T. maroccana**

NOMENCLATURAL ACTS. This work and the nomenclatural acts it contains have been registered in ZooBank. The ZooBank Life Science Identifiers (LSID) for this publication are: http://zoobank.org/

* Due to lack of information, no differences between *T. marteli* and *T. maroccana* are known, both species could be conspecific.

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Discussion

Theodoxus sandsi sp.n. can be distinguished from its congeners by the shell and operculum characters. The new species is endemic to the rheocrenous springs of the Middle Atlas massif. This mountain range is among the best watered mountain chains in the country and is of great hydrogeological interest in North Africa, revealing great diversity of wetland habitats, ranging from natural and artificial lakes, to cold rivers and springs (Taybi *et al*., 2020; Mabrouki *et al*., 2023b, c). Therefore, it occupies a privileged place among the Moroccan regions of major interest for the conservation of wetland biodiversity.

Based on shell morphology and operculum criteria, our findings raise the known biodiversity of the *Theodoxus* genus in North Africa to four confirmed species i.e. *Theodoxus fluviatilis*, *Th. marteli*, *Th. numidicus* and *Th. sandsi* sp.n. While *Th. poppei* could be a junior synonym of *Th. fluviatilis,* the taxonomic status of *Th. africanus*, *Th. djedida*, *Th. maresi*, *Th. tingitana*, *Th. maroccana* and *Th. vondeli* must by questioned. Identity confirmation of these species has to be cross-checked by study of the type species, samples of the nominal taxa from their type localities is required for a re-investigation combining genetic, anatomical, shell and operculum morphological characters.

According to the ecoregional delimitation given by the freshwater ecoregions of the world-conservation science program (FEOW) (https://www.feow.org), *Theodoxus merteli* and *Th. numidicus* belong to the Mediterranean Northwest African ecoregion, *Th. sandsi* sp.n. belong to the Atlantic Northwest African ecoregion, and finally, *Th. fluviatlis* to both ecoregions (Mabrouki *et al*., 2023a).

Although the knowledge of the freshwater gastropods of Morocco has advanced significantly in recent years, the inventory list of the freshwater mollusc fauna of Morocco is certainly still incomplete. Many new species and genera new to science were described recently, including (Glöer *et al*., 2020a, b, Mabrouki *et al*., 2022a, b, c; Taybi *et al*., 2022a, b, c), showing high degree of regional endemism. About 80% of freshwater mollusc species are endemic to the North African region (Van Damme *et al*., 2010). Unfortunately, these organisms are one of the most threatened freshwater taxa (Kay, 1995). Especially taxa that have certain requirements in terms of environmental quality. The genus *Theodoxus* requires good environmental conditions of aquatic habitat such as high water quality and current velocity (Pérez-Quintero, 2007). These requirements put the *Theodoxus* species of North Africa in a delicate situation, given the many issues caused by human activity.

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Compliance with ethical standards

CONFLICTS OF INTEREST: The authors declare that they have no conflicts of interest.

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