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NEOPYCNODONTE STENZEL, 1971 (BIVALVIA: OSTREIDA: PYCNODONTEINAE) – AN INTERESTING GRYPHEID FOSSIL OYSTER FROM THE CROATIAN NATURAL HISTORY MUSEUM COLLECTIONS

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Bivalves of the genus *Neopycnodonte* Stenzel, 1971 (Ostreida: Gryphaeidae) are known as common bioconstructors from the mesophotic marine environments of the Cenozoic era. Along with mussels, they are among the first taxa to colonize natural and artificial hard substrates, but they live somewhat deeper, being most common between 50 and 150 m.

More than eighty specimens of fossil *Neopycnodonte* from the Neogene deposits of Mt. Medvednica, the Samoborsko gorje Hills, the Glinsko Pokuplje area and Siena (Italy) are housed in the Croatian Natural History Museum (CNHM) under the names: *Ostrea cochlear* Poli, 1795, *Picnodonta cochlear* (Poli, 1795) and *Picnodonta* (*Ostrea*) *cochlear* (Poli, 1795) var. *navicularis* (Brocchi, 1814). The presence of the Pycnodonteinae subfamily was also recorded from several areas in Croatia during the preparation of the Basic Geological Maps. Like many other oysters, pycnodonteins are highly variable in shape and there have been some doubts concerning their taxonomy. The authors support one of the previously suggested taxonomical schemes (Freneix, 1975), assigning the fossil specimens from CNHM to the species *Neopycnodonte navicularis* (Brocchi, 1814), which is considered a direct ancestor of the recent *N. cochlear* (Poli, 1795).

Key words: Pycnodonteinae, Gryphaeidae, Croatian Natural History Museum, taxonomy, palaeobiogeography, palaeoenvironment

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Školjkaši roda *Neopycnodonte* Stenzel, 1971 (Ostreida: Gryphaeidae) značajni su graditelji biokonstrukcija u mezofotičnim morskim okolišima tijekom cijele kenozojske ere. Slično kao i dagnje, brzo koloniziraju prirodne i umjetne čvrste podloge, no, za razliku od njih, žive nešto dublje, najčešće na dubinama između 50 i 150 m.

Više od osamdeset primjeraka fosilnih *Neopycnodonte* iz neogenskih naslaga Medvednice, Samoborskog gorja i Glinskoga Pokuplja, kao i iz Siene u Italiji, čuva se u zbirkama Hrvatskoga priro-

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doslovnog muzeja (HPM), gdje su izvorno inventirane kao: *Ostrea cochlear* Poli, 1795, *Picnodonta cochlear* (Poli, 1795) i *Picnodonta* (*Ostrea*) *cochlear* (Poli, 1795) var. *navicularis* (Brocchi, 1814). Osim toga, školjkaši iz podporodice Pycnodonteinae pronađeni su u Hrvatskoj na više lokaliteta tijekom izradbe Osnovne geološke karte. Poput drugih kamenica, piknodonteine su jako varijabilnoga oblika i postoje sumnje vezane za njihovu taksonomsku odredbu. Autori se ovdje priklanjaju jednom od ranije objavljenih mišljenja (Freneix, 1975) i primjerke neopiknodonti iz HPM-a pribrajaju jedinstvenoj vrsti *Neopycnodonte navicularis* (Brocchi, 1814), koja se smatra neposrednim pretkom recentne vrste *N. cochlear* (Poli, 1795).

Ključne riječi: Pycnodonteinae, Gryphaeidae, Hrvatski prirodoslovni muzej, taksonomija, paleobiogeografija, paleookoliš

INTRODUCTION

Oysters are thick-shelled sessile gregarious bivalves well known from the fossil record throughout the Mesozoic and Cenozoic eras. They are able to create spacious bioconstructions, thus diversifying marine habitats and increasing biodiversity (e.g., Angeletti & Taviani, 2020; Cardone *et al*., 2020; Castellan *et al*., 2022). While the representatives of the family Ostreidae (e.g., genera *Ostrea*, *Crassostrea*) in most cases occur in the intertidal and very shallow subtidal environments, members of the family Gryphaeidae (particularly the genus *Neopycnodonte*, subfamily Pycnodonteinae) are inhabitants of water depths usually below 25 m, first occurring in the Palaeogene and producing bioconstructions at least since the Miocene Epoch (e.g., Angeletti & Taviani, 2020 and references therein). They are also known as encrusters of artificial substrates (e.g., Bakran-Petricioli *et al*., 2015a, 2015b, 2017).

MATERIALS AND METHODS

While re-examining the Cenozoic fossil oysters stored in the Croatian Natural History Museum (CNHM) for the preparation of the virtual exhibition "Oysters from the ancient seas" (Bošnjak *et al*., 2023), the authors were struck by the importance of some species of *Neopycnodonte* as possible indicators of the mesophotic (deeper subtidal) habitats in the Middle Miocene of the Central Paratethys, similar to some newly published data from the Mediterranean region (Angeletti & Taviani, 2020; Cardone *et al*., 2020).

The grypheid oysters presented here are housed in four CNHM collections: Miocene fauna of Zaprešić-Breg near Samobor; Pliocene and Miocene Fauna of Glinsko Pokuplje and the Zrinjsko-Dvorska valley; the Marine Miocene II collection; and the Vanda Kochansky-Devidé collections. Specimens were collected in various Miocene localities of Northern Croatia (Tab. 1). Additionally, specimens of *Neopycnodonte* are part of one of the CNHM comparative collections from Italy, but these were not included in the study due to insufficient stratigraphic data on their collection site.

Samples from the CNHM collections were photographed with a Canon EOS 6D camera, using a Canon zoom lens, EF 24–105mm 1:3.5-5.6 IS STM.

The authors further considered other *Neopycnodonte* findings in Croatia from published papers and the Basic Geological Maps (e.g., Šikić *et al*., 1979; Šimunić *et al*., 1981; Basch, 1983; Jovanović & Magaš, 1986; Jamičić *et al*., 1987, 1989; Pikija, 1987; Šparica *et al*., 1987).

Tab. 1. Neogene *Neopycnodonte* housed in the Croatian Natural History Museum collections. Legend: * = temporary inventory number; ** = not included in this paper.

Croatian Natural History Museum collection	Original name	Revised name	Locality	Age	Inventory number	Number of specimens
Miocene fauna of Zaprešić-Breg near Samobor	*Ostrea cochlear* Poli, 1795	*Neopycnodonte navicularis* (Brocchi, 1814)	the Samoborsko gorje Hills	Middle Miocene (Langhian and early Serravallian / Badenian)	6.231./1379.	2
Pliocene and Miocene fauna of Glinsko Pokuplje and the Zrinjsko-Dvorska valley	*Pycnodonta cochlear* Poli, 1795	*Neopycnodonte navicularis* (Brocchi, 1814)	Glinsko Pokuplje	Middle Miocene (Langhian and early Serravallian / Badenian)	5.977./1126., 5.978./1127.	5
Marine Miocene II collection	*Ostrea cochlear* Poli, 1795	*Neopycnodonte navicularis* (Brocchi, 1814)	Mt. Medvednica	Middle Miocene (Langhian and early Serravallian / Badenian)	6.467./1615., 6.468./1616., 6.469./1617., 6.470./1618., 6.471./1619.	13
Vanda Kochansky-Devidé collections	*Pycnodonta cochlear* (Poli, 1795)	*Neopycnodonte navicularis* (Brocchi, 1814)	Mt. Medvednica	Middle Miocene (Langhian and early Serravallian / Badenian)	565./401.- 411.; 691./664.-666.*	59
Tertiary fauna of Italy (Miocene)**	*Picnodonta* (*Ostrea*) *cochlear* (Poli, 1795) var. *navicularis* Brocchi, 1814		Siena, Italy	Neogene	8.241./723.	6

* temporary inventory number
** not included in this paper

SYSTEMATICS

Family: Gryphaeidae Vyalov, 1936

Subfamily: Pycnodonteinae Stenzel, 1971

Genus: *Neopycnodonte* Stenzel, 1971

Type species: *Neopycnodonte cochlear* (Poli, 1795)

Neopycnodonte navicularis (Brocchi, 1814) (Fig. 1)

* 1814 *Ostrea navicularis*, p. nob. – Brocchi, p. 565.

1873 *Ostrea cochlear* Poli – Pilar, p. 91.

1897 *Pycnodonta cochlear* (Poli) var. *navicularis* (Brocchi) – Sacco, p. 22, pl. 8, figs. 2–6.

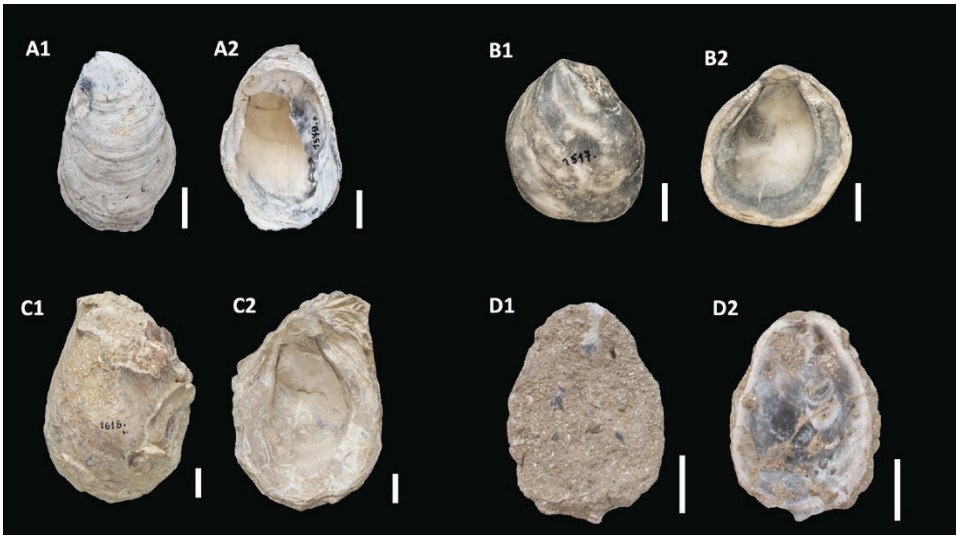

Fig. 1. Part of the specimens of the species *Neopycnodonte navicularis* (Brocchi, 1814) housed in the CNHM collections. Data on specimens available in Tab. 1. Legend: A: Inv. No. 1379., Zaprešić Brijeg, Samoborsko gorje Hills, A1 – exterior side, A2 – interior side; B: Inv. No. 1617., Markuševec, Mt. Medvednica, B1 – exterior side, B2 – interior side; C: Inv. No. 1616, Čučerje, Mt. Medvednica, C1 – exterior side, C2 – interior side; D: Inv. No. 691./665, Podsused, Mt. Medvednica, D1 – exterior side, D2 – interior side. Scale bar: 10 mm.

1910 *Pycnodonta cochlear* Poli var. *navicularis* Brocchi – Schaffer, p. 21, pl. 11, fig. 6.

1929 *Ostrea cochlear* Poli – Šuklje, p. 6.

1944 *Pycnodonta cochlear* Poli – Kochansky, p. 247

1957 *Pycnodonta cochlear* (Poli) – Kochansky-Devidé, p. 41

1960 *Pycnodonta cochlear* var. *navicularis* (Brocchi, 1814) – Kojumdgieva & Strachimirov, p. 77, pl. 27, figs. 2–3.

1975 *Neopycnodonte navicularis* (Brocchi) – Freneix, p. 443–448, text-figs. 14, 15.

1986 *Neopycnodonte navicularis* (Brocchi, 1814) – Studencka, p. 47, pl. 7, figs. 5, 6a–b.

1994 *Neopycnodonta navicularis* (Brocchi, 1814) – Ben Mousa, p. 115, pl. 7, figs. 4–5.

1998 *Neopycnodonte navicularis* (Brocchi, 1814) – Studencka *et al*., p. 133.

2020 *Neopycnodonte navicularis* (Brocchi, 1814) – Mandic *et al*., p. 60, figs. 4U–V, 5A–B.

2021 *Neopycnodonte navicularis* (Brocchi, 1814) – Filek *et al*., p. 11, 14, fig. 7B.

Material: 85 specimens of the Middle Miocene (Langhian and early Serravallian / Badenian) grypheid oysters housed in the CNHM collections listed in Tab. 1, some shown in Fig. 1.

Description: Valves of various sizes, ovoidal-elongated shape, inequivalve (left valve concave, right valve slightly concave or flat). Exterior surface decorated with concentric lamellae or smooth, in a few specimens covered by sediment and / or encrusters. Some specimens do not have the interior side of the shell visible because of sediment infill. In specimens with a visible interior, it is smooth. Adductor muscle scar sub-circular in outline. Ligament area triangular, with chomata in a few samples.

Remarks: Most of the housed specimens were published and described in Pilar (1873), Šuklje (1929), Kochansky (1944) and Kochansky-Devidé (1957). Gorjanović-Kramberger (1894) mentioned findings of the species *Ostrea cochlear* Poli from the "Mediterranean" (= Langhian-lower Serravallian / Badenian) marls on Samoborsko gorje Hills. Šuklje (1929) listed findings of the same species from the Zaprešić Brijeg locality on the Samoborsko gorje Hills and described a few specimens as very well preserved, and some of them as damaged, but still determinable. Specimens from the Glinsko Pokuplje area were described by Pilar (1873) as *Ostrea cochlear* Poli from the Miocene marine deposits. Kochansky (1944) described the findings of *Picnodonta cochlear* Poli from Mt. Medvednica and stated that most of the specimens collected during her research on Mt. Medvednica actually belong to *N. navicularis* (originally *P. cochlear* var. *navicularis*). Specimens of *Neopycnodonte* were found in the "Tortonian" (= Langhian and lower Serravallian / Badenian) marls and "litavac" limestone, and as well in the "Burdigalian" (= Langhian and lower Serravallian / Badenian) sandstones. Later, Kochansky-Devidé (1957) mentioned new findings of the same species from the Badenian marls of the southwestern slopes of Mt. Medvednica.

Specimens originally referred to as a pycnodontein species "*cochlear*" housed in the CNHM collections (Fig. 2) correspond to the species *Neopycnodonte navicularis* (Brocchi, 1814) according to e.g., Freneix (1975), Studencka (1986), Studencka *et al*. (1998), Ben Mousa (1994), Mandic *et al*. (2020), Filek *et al*. (2021), Talmat *et al*. (2022 and references therein). As a morphologically highly variable species, *N. navicularis* has long been considered a synonym for, or variety or subspecies of *N. cochlear*. Its species level taxonomic status was finally fixed by Freneix (1975), who pointed out the morphological differen-

Fig. 2. Museum labels from the CNHM collections showing the original determination of the studied specimens.

tiation toward *Neopycnodonte cochlear* and confirming their diverging stratigraphic ranges – *N. navicularis* from Miocene to Pliocene, and *N. cochlear* from Pliocene to Recent.

Distribution and stratigraphic range: Specimens from the CNHM collections are collected from various localities in Northern Croatia (the Samoborsko gorje Hills, the Glinsko Pokuplje area, Mt. Medvednica) as seen in Tab. 1. In terms of age the deposits were originally assigned to the "Helvetien", "Tortonian" and "Burdigalian" (e.g., Kochansky, 1944), all referring today to the Middle Miocene – Langhian-early Serravallian / Badenian age (e.g., Ćorić *et al*., 2009). The species *Neopycnodonte navicularis* is distributed in the Central Paratethys (Egerian to Badenian), Eastern Paratethys (Tarkhanian to Chokrakian), and in the Mediterranean and NE Atlantic (Early Miocene to Pliocene) (Mandic *et al*., 2020, and references therein; Filek *et al*., 2021).

RESULTS AND DISCUSSION

Taxonomy of Gryphaeidae Vyalov, 1936

Gryphaeidae is a family of subtidal bivalves belonging to the superfamily Ostreoidea Rafinesque, 1815, with three subfamilies recorded in the WoRMS Base, including the subfamily Pycnodonteinae Stenzel, 1959 (MolluscaBase, 2023).

The genus *Neopycnodonte*, one of the genera within this family, was established in 1971 by Stenzel (Stenzel in Moore, 1971). It includes the two extant species, *Neopycnodonte cochlear* (Poli, 1795) and *Neopycnodonte zibrowii* Gofas, C. Salas & Taviani, 2009 (MolluscaBase, 2023).

In palaeontological papers, a fossil species *N. navicularis* (Brocchi, 1814) is additionally adduced, with a stratigraphic range from the upper Oligocene to the Pliocene (e.g., Freneix, 1975; Studencka, 1986; Mandic *et al*., 2020; Filek *et al*., 2021; Talmat *et al*., 2022 and references therein; Paleobiology Database). Species name *navicularis* was previously used at the level of variety (e.g., Hörnes, 1870; Sacco, 1897; Kojumdgieva & Strachimirov, 1960), and subspecies, e.g., *Pycnodonte* (*Pycnodonte*) *cochlear navicularis* (Brocchi, 1814) (e.g., de Bortoli & Hladilová, 2015 and references therein). In the literature referring to the CNHM collections, specimens of *N. navicularis* were determined as *Ostrea cochlear* (Pilar, 1873; Šuklje, 1929) and *Pycnodonte cochlear* (Kochansky, 1944; Kochansky-Devidé, 1957).

The species *Neopycnodonte cochlear* and *N. navicularis* are closely related. However, their distinct species level classification was validated by Freneix (1975).

Stratigraphic range and palaeoenvironment

Numerous papers (e.g., Freneix, 1975; Studencka, 1986; Ben Mousa, 1994; Mandic *et al*., 2020 and references therein; Talmat *et al*., 2022) place the first occurrence of *N. navicularis* in the Early Miocene of the Mediterranean basin and the Paratethys. Yet, most currently, the oldest occurrence of the species has been detected from the late Oligocene of North Alpine Foreland Basin in Upper Austria (Filek *et al*., 2021). Its migration to the Boreal domain (Belgium, Netherlands) took place during the Middle Miocene (Freneix *et al*., 1988, Ben Mousa, 1994; Talmat *et al*., 2022). Findings of *N. navicularis* are common in the Middle Miocene of the Paratethys (e.g., Studencka, 1986; Studencka *et al*., 1998; Mandic *et al*., 2020). During the Pliocene, *N. navicularis* was still widespread in the Mediterranean Sea, replaced then by its direct descendant, the extant species *N. cochlear* (e.g., Freneix, 1975; Talmat *et al*., 2022). Fossil findings are shown in Fig. 3.

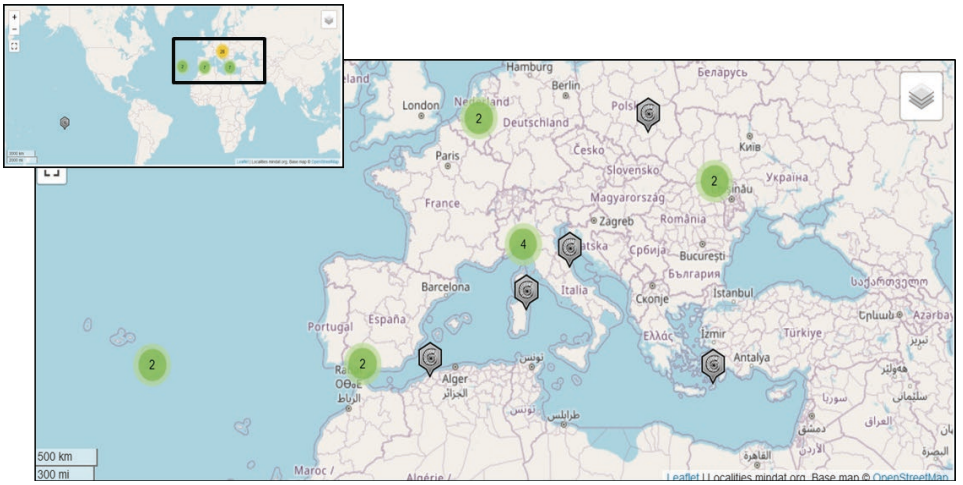

Fig. 3. Fossil findings of the genus *Neopycnodonte* (Mindat.org, https://www.mindat.org/taxon-2286103.html, October 2023)

Considering the palaeoenvironment, *N. navicularis* was a temperate-water oyster, living on various substrates in low-turbidity waters at estimated depths of between 50 and 300 m (Malatesta, 1974, from Talmat *et al*., 2022). According to Ben Mousa (1994), *N. navicularis* had palaeoecological requirements similar to those of the recent *N. cochlear*.

N. cochlear is today widespread in the Mediterranean Sea, Atlantic Ocean, Pacific Ocean, Indian Ocean, and the Red Sea (Fig. 4). It lives cemented on hard substrates in mesophotic waters along the continental margins and slopes. It is especially abundant at depths of between 25 and 150 m (Global Biodiversity Information Facility, 2022, from Talmat *et al*., 2022). Massive bioconstructions ("reefs") composed of *N. cochlear* in the Mediterranean Sea were recently described by Angeletti & Taviani (2020) and Cardone *et al*. (2020). They were discovered at depths of between 40 and 130 m, sometimes up to 600 m distant from the coastline. These reefs consist of irregularly arranged live and dead *N. cochlear* shells cemented one over the other forming a framework of a high structural complexity. Together with other secondary structuring taxa, such as sclera-

ctinians, serpulids and bryozoans as well as with binding and bioeroding poriferan taxa, these bioconstructions are biodiversity hotspots (Cardone *et al*., 2020).

Significant efforts have been recently made to review the available information on mesophotic habitats in the Mediterranean Sea, natural and anthropogenic threats that endanger them, and to evaluate the efficiency of the current legislative framework in providing instruments for their protection (Castellan *et al*., 2022 and references therein). The ability of Pycnodonteinae to inhabit rather deep subtidal habitats possibly enables them to survive under the conditions of global warming (AquaMaps, 2019). However, a combination of threats, such as a rise in seawater temperature, more intense and frequent heat waves, progressive ocean acidification, fishing activities, and littering could harm their mesophotic reefs.

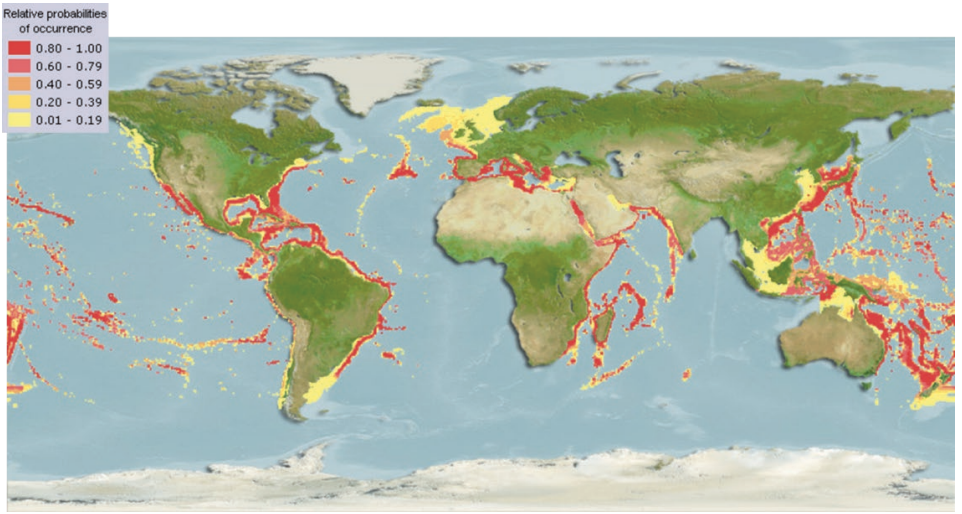

Fig. 4. Computer generated distribution maps for *Neopycnodonte cochlear.* AquaMaps (2019, October).

Findings of fossil Pycnodonteinae in Croatia

Together with the documented finding places of specimens housed in the CNHM, V. Kochansky-Devidé mentioned the findings *of Neopycnodonte* oysters at a number of other Miocene localities on Mt. Medvednica (Kochansky, 1944; Fig. 5).

Neogene *Neopycnodonte* (in most cases under the name *Pycnodonta cochlear*) from the territory of Croatia are mentioned in Explanatory notes for sheets of the Basic Geological Map of Yugoslavia (in alphabetical order): Daruvar L33–95 (Jamičić *et al*., 1989), Ivanić-Grad L33–81 (Basch, 1983), Kostajnica L33–106 (Jovanović & Magaš, 1986), Orahovica L33–96 (Jamičić *et al*., 1987), Sisak L33–93 (Pikija, 1987), Slavonski Brod L34–97 (Šparica *et al*., 1987), Varaždin L33–69 (Šimunić *et al*., 1981) and Zagreb L33–80 (Šikić *et al*., 1979) (Fig. 6). There are several mentions of grypheid oysters in Palaeogene (middle Eocene) deposits: sheets Crikvenica L33–102 (*Pycnodonte brongniarti* (Bronn, 1831), Šušnjar *et al*., 1973), Labin L33–101 (*Pycnodonte archiaci* (Bellardi), Šikić & Polšak, 1973) and Rovinj L33–100 (*Pycnodonte archiaci* (Bellardi), Polšak & Šikić, 1973) (Fig. 6).

Pycnodontein oysters are also noticed at JU Kamenjak (Javna Ustanova Kamenjak) area in Istria ("Kamenjak" Public Institution).

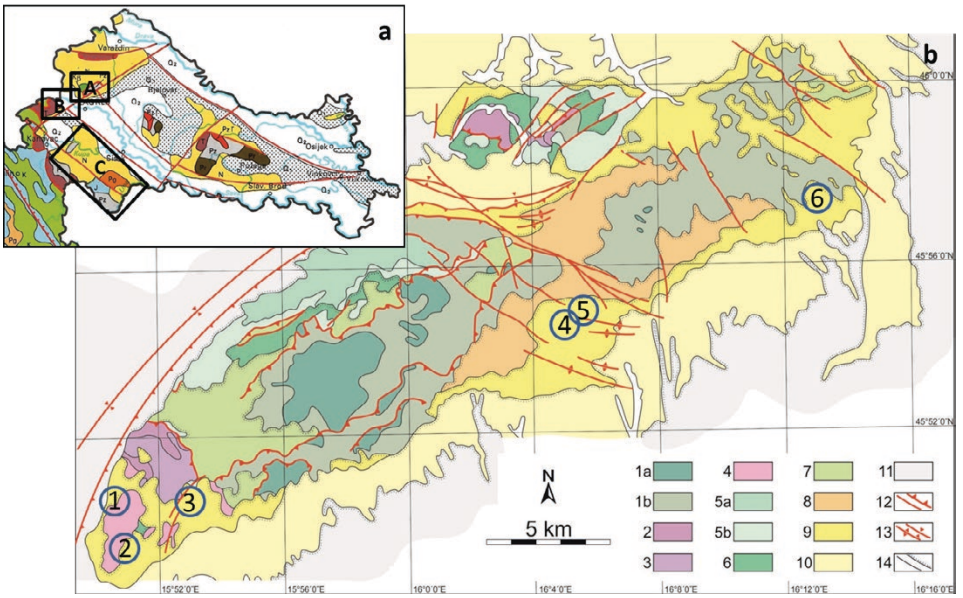

Fig. 5. Findings of *Neopycnodonte* oysters in north-western and central Croatia: **a)** Locations of *N. cochlear* samples housed in the CNHM collections: A. Mt. Medvednica; B. Zaprešić Brijeg; C. Glinsko Pokuplje. Geological map partly after Velić, I. & Velić, J. (1995). **b)** Field findings of *Neopycnodonte* on the Mt. Medvednica mentioned by Kochansky (1944). Localities (numbers in circles 1–6): 1–Jarek, 2–Podsusedsko dolje, 3–Bizek, 4–Sv. Barbara, 5–Goranec, 6–Zelina (Zagrad). Geological map after Tomljenović (2002). Legend: 1a,b. Silurian to Middle Triassic metamorphics; 2–4. Triassic sedimentary rocks; 5 a,b. Mesozoic ophiolites; 6. Aptian to Cenomanian marine sedimentary rocks; 7. Uppermost Cretaceous to Palaeocene rocks; 8. Lower to Middle Miocene freshwater deposits; **9. Middle Miocene dominantly marine deposits**; 10. Upper Miocene brackish deposits; 11. Pliocene freshwater deposits; 12. Tectonic faults; 13. Fold axes; 14. Normal and transgressive boundaries.
Gryphaeid oysters were found in the Middle Miocene deposits (9.), bolded in the Figure caption and marked by the yellow color on the map.

Findings of recent Pycnodonteinae in Croatia

Neopycnodonte cochlear is a very common bivalve on hard substrate in the eastern part of the Adriatic Sea at depths below 20 m (Bakran-Petricioli *et al*., 2015a, 2015b, 2017). However, up to now massive bioconstructions of *N. cochlear* as described by Angeletti & Taviani (2020) and Cardone *et al*. (2020) have not been noted in Croatian waters. Aggregations of *N. cochlear* were noted at a depth of 100 m on a seamount to the south of Biševo Island (central Adriatic) as shown in Figure 7a (from Bakran-Petricioli, 2011, page 150). *N. cochlear* is also very abundant at greater depths on man-made structures in the Adriatic Sea like gas platforms (Bakran-Petricioli *et al*., 2015b; Bakran-Petricioli *et al*., 2017; Figs 7b and 7c), sewage outlets (Fig. 7d) and shipwrecks (Petricioli & Bakran-Petricioli, 1989).

While the finding of *N. cochlear* at a depth of 100 m on a seamount to the south of Biševo Island (central Adriatic, Fig. 7a) was obtained during actual biological benthic survey of natural communities, all the other findings were coincidental. On all seven gas platforms in the north Adriatic that we surveyed, this species is the most common in the fouling on deeper parts of constructions (mostly below 20 m depth, Figs 7b and

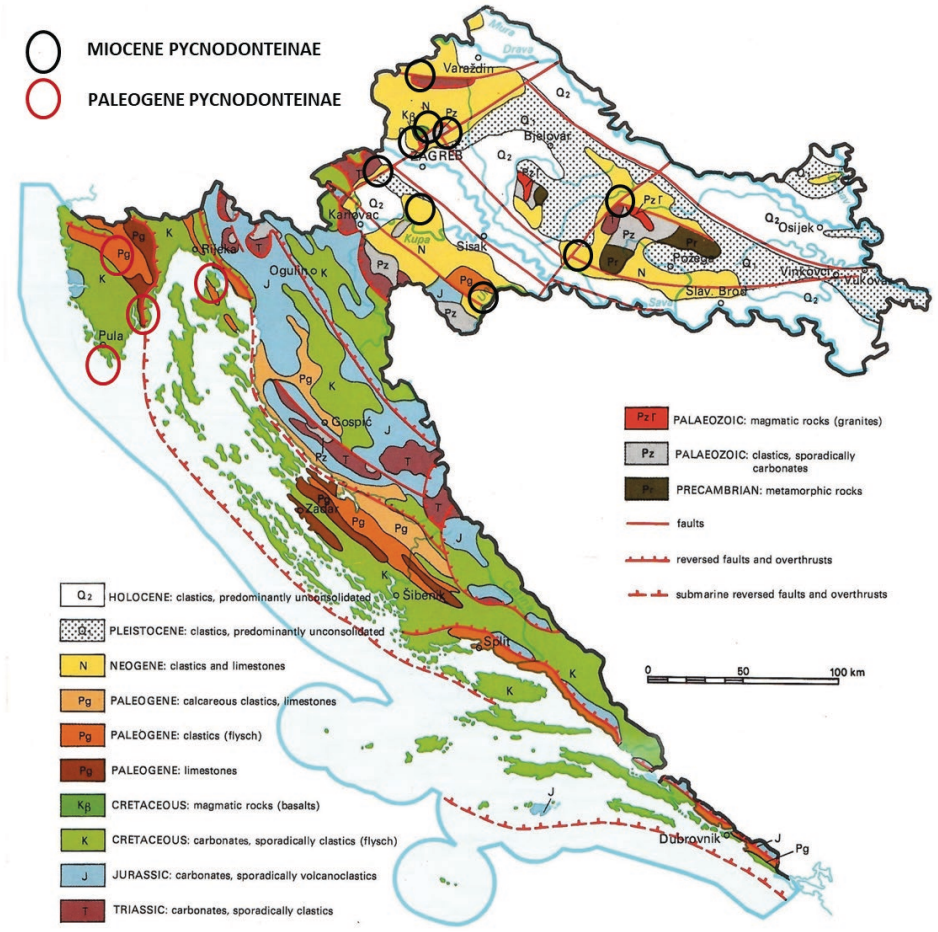

Fig. 6. Fossil record of Palaeogene and Neogene Pycnodonteinae in Croatia based on the CNHM collections and data from the published papers. Geological map after Velić, I. & Velić, J. (1995).

7c). In 2015 survey on IKA A platform (which had spent 10 years in the sea at that time), we estimated that at a depth of 38 m the wet mass of fouling was 30 to 50 kg/m^2 and consisted 85–100 % of *N. cochlear* (Bakran-Petricioli *et al*., 2015b). All the platforms are in the open sea, 40 to 60 km from the coast, on the sediment bottom which is 35–60 m deep.

Aggregations of *N. cochlear* were also noted on pipes of sewage outlets: Kolovare outlet in Zadar (central Adriatic) on 30 m deep and 500 m from the coast; and on the Cavtat outlet (south Adriatic, Fig. 7d), on 65 m deep and 200 m from the coast. Also, aggregations of *N. cochlear* were noted on the sparse remains of parts of the pontoon bridge in Masleničko Ždrilo near Zadar (central Adriatic), on shaded lower and overhanging portions of metal construction below 10 m depth, 30 m from the coast. The pontoon bridge was built in 1993 during the war in Croatia and later, after the war, removed.

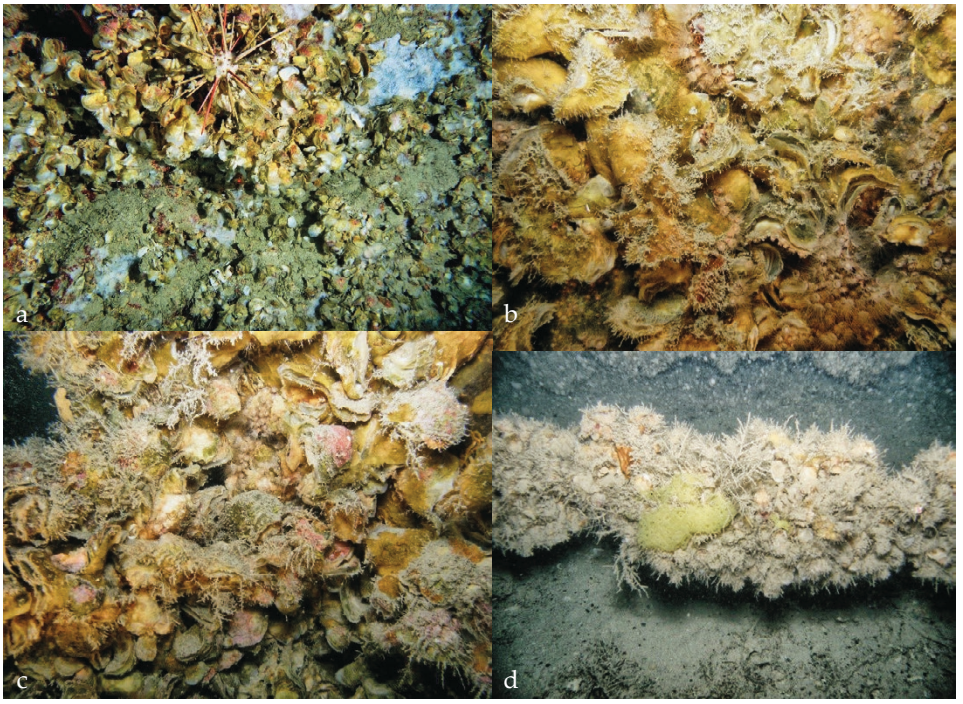

Fig. 7. Recent findings of aggregations of *Neopycnodonte cochlear* in the eastern part of Adriatic: **a)** on a seamount to the south of Biševo Island (central Adriatic), 100 m depth, photo taken with the camera of a remotely operated vehicle (photo by Simonepietro Canese) during 2010 common expedition of Institute of Oceanography and Fisheries, Split (Croatia) and Istituto Superiore per la Protezione e la Ricerca Ambientale, Rome (Italy), from Bakran-Petricioli, 2011, page 150; **b)** on Marica gas platform (north Adriatic), depth 24 m; **c)** on IKA A gas platform (north Adriatic), depth 38 m; **d)** on the sewage outlet Cavtat (south Adriatic), depth 65 m; (Figures b, c and d: photo by Donat Petricioli).

The most interesting finding of *N. cochlear* was on the shipwreck of m/t *Brigitta Montanari* (Petricioli & Bakran-Petricioli, 1989). The ship with a cargo of vinyl chloride monomer sank in November 1984 to a depth of 82 m between the islets of Tetovišnjak and Mrtovnjak near Žirje Island (central Adriatic). The wreck was raised in June 1988 because of the environmentally dangerous cargo. On parts of vertical and overhanging surfaces of the wreck the most abundant fouling organism was *N. cochlear*. During the 3.5 years in which the wreck was on the 80 m deep bottom in the central Adriatic the estimated density of this bivalve reached 1000 ind./m^2 (size of shells was 6–73 mm) and the estimated wet mass 8 kg/m^2 (Petricioli & Bakran-Petricioli, 1989).

CONCLUSIONS

- Pycnodonteinae oysters of the Middle Miocene age are housed in the Croatian Natural History Museum collections (Miocene fauna of Zaprešić-Breg near Samobor; Pliocene and Miocene Fauna of Glinsko Pokuplje and the Zrinjsko-Dvorska valley; Marine Miocene II collection; Vanda Kochansky-Devidé collections).
- They are catalogized under the original names: *Ostrea cochlear* Poli, 1795, *Picnodonta cochlear* (Poli, 1795) and *Picnodonta* (*Ostrea*) *cochlear* (Poli, 1795) var. *navicu-*

laris Brocchi, 1814. However, according to recent knowledge, all the specimens stored in the CNHM collections should be classified as *Neopycnodonte navicularis* (Brocchi, 1814).

- The occurrence of fossil Pycnodonteinae, known from a number of localities in Croatia, points to the mesophotic environment of shelf subtidal and slope habitats, between 25 and 300, in most cases between 50 and 150 m.
- The recent pycnodontein species, *Neopycnodonte cochlear*, is quite common and widely distributed in the eastern Adriatic, from south to north, from thirty metres to tens of kilometres from the shore, in the mesophotic zone from 10 to more than 100 m deep. It can be considered a pioneer species as it colonizes suitable hard substrata as well as man-made structures in the sea rapidly and in abundance.

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