

**Origins of the Dinaric troglobiotic mussel and its correct taxonomical classification. *Congeria* or *Mytilopsis* (Bivalvia: Dreissenidae)?**

Izvor dinarske troglobiotske školjke in njena pravilna taksonomska uvrstitev.  
*Congeria* ali *Mytilopsis* (Bivalvia: Dreissenidae)?

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**Abstract:** After an analysis of the literature, it is proposed to taxonomically reorder the troglobiotic mussel *Congeria kusceri* Bole 1962 as *Mytilopsis kusceri* (Bole 1962). The species had been described and attributed to *Congeria* when the extant and fossil *Mytilopsis* spp. were all regarded members of that genus. The position of the cave species within the genus *Mytilopsis* and Dreisseninae is discussed and its inclusion into *Mytilopsis* is substantiated. In this way we will avoid further missapprehension in biogeographical and phylogenetic discussions. The cave mussel may further be regarded a relict of the diverse fauna in the Miocene Dinaric Lakes System.

**Keywords:** Mollusca, Bivalvia, cave fauna, *Congeria kusceri*, taxonomy

**Izveček:** Po analizi literature je podan predlog, da se troglobiotsko školjko *Congeria kusceri* Bole 1962 taksonomsko prerazporedi kot *Mytilopsis kusceri* (Bole 1962). Vrsta je bila opisana in dodeljena rodu *Congeria*, ko so tako recentne, kot fosilne vrste rodu *Mytilopsis* obravnavali kot pripadnice rodu *Congeria*. Obravnavan je položaj vrste znotraj rodu *Mytilopsis* in poddružine Dreisseninae, podana je utemeljitev prerazporeditve. S tem se bomo lahko izognili nadaljnim nesporazumom pri filogenetskih in biogeografskih razpravah. Jamsko školjko lahko še vedno imamo za relikv pestre favne v miocenskem Dinarskem pozezerju.

**Ključne besede:** Mollusca, Bivalvia, jamska favna, *Congeria kusceri*, taksonomija

## Introduction

The shells of a tentatively troglobiotic mussel were found by the Slovene malacologist Ljudevit Kuščer in 1930s in the spring Stinjevac near Vrgorac in Croatian Dalmacija. They were recognized as *Congeria* sp. and published in a list of the Dinaric cave fauna by Stanko Karaman (1935). J. Štirn, in 1956 (pers. com.) found live '*Dreissena*' in the cave Žira jama in Turkovići, Popovo polje, S Hercegovina. It could be im-

mediately supposed that this animal can only be conspecific or related to the Kuščer's *Congeria*, since no *Dreissena* was known to occur within the inner parts of the Dinaric karst (own data). The closest localities of *Dreissena* are in lower reaches of the subpannonian river Sava (Matoničkin and Pavletić 1972) and in the Drim drainage at the SE extreme of Dinarides and in the Northern Hellenides (Albrecht et al. 2007; Wilke et al. 2010), namely in the lakes of Skadar, Ohrid, and Prespa (Skadarsko jezero/Liqueni i Shkodrës, Ohridsko



Figure 1: Aggregations of mussels *Mytilopsis kusceri* (Bole 1962) (syn. *Congeria kusceri*) in the cave Žira jama, Popovo polje in 1950s.

Slika 1: Agregacija školjke *Mytilopsis kusceri* (Bole 1962) (syn. *Congeria kusceri*) v jami Žira, Popovo polje v 1950ih letih.



Figure 2: A shell of *Mytilopsis kusceri* (Bole 1962) (syn. *Congeria kusceri*) from its type locality, Žira jama, Popovo polje, Bosnia and Herzegovina.

Slika 2: Lupina *Mytilopsis kusceri* (Bole 1962) (syn. *Congeria kusceri*) iz tipskega nahajališča, jame Žira jama, Popovo polje, Bosna in Hercegovina.

ezero/L. i Ohrit, Prespansko ezero/Limni Megáli Préspe/L. i Prespes). Triggered by the Štirn's finding and after our joint visiting the Žira jama (Fig. 1), Bole described the mussel taxonomically as *Congeria kusceri* (Bole 1962) (Fig. 2).

In the meantime and after that, representatives of the same or a related taxon could be recognized also in the '*Dreissensia polymorpha fluviatilis* var. *elata* or var. *occidentalis*' found and published by the karstologist Katzer already in 1921 from karst springs in Lušci polje, Bosnia and Herzegovina. The same with '*Dreissensia polymorpha*' found in some caves of Hercegovina by Remy (1953). These literature data were 'discovered' only after the Bole's description. We also found the mussels in some additional localities in Hercegovina, Bosanska Krajina (W Bosna), Croatian Dalmacija and Lika, and the most north-western in Bela Krajina (SE Slovenia) (Sket 1970, 1992; Bole and Velkovrh 1986; Bole 1992; Jalžić 1998, 2001; Schütt 2000). So, *Congeria kusceri* joined the other most prominent Dinaric troglobionts as a truncated 'holodinaric' biogeographic element (Sket

1994; ammended in Sket and Zagmajster 2006), with scattered localities along all the Dinarides from their NW, up to the SE Hercegovina and Dalmacija. Some other holodinaric elements are *Proteus anguinus* Laurenti (Amphibia; Sket 1997), *Marifugia cavatica* Absolon et Hrabě (Polychaeta: Serpulidae; Sket 1983; Kupriyanova et al. 2009), *Troglodiptomus sketi* Petkovski (Copepoda: Diaptomidae; Brancelj 1991), genus *Titanethes* s. str. (Oniscidea: Trichoniscidae; Strouhal 1939) etc. However, they all are reaching as far to the NW to include a bit of the Italian territory, which is not the case with the mussel. Some anatomical data and biological considerations have been published by Morton et al. (1998).

Stepien et al (2001) analyzed the DNA and compared *C. kusceri* with the related *Mytilopsis leucophaeata* and *Dreissena polymorpha*. The attribution of this species to the genus *Congeria* they took for granted. Finally, Bilandžija et al. (2010) are trying to molecularly establish relations between extant populations of *C. kusceri*. Their study is in progress.

Dinaric karst developed on the Adriatic microplate dividing the western branch of Tethys into a smaller Paratethys sea and the paleo-Mediterranean. During middle Miocene this land was intermittently an island or attached as a peninsula to the European plate (Rögl and Steininger 1984; Popov et al. 2004). A series of freshwater lakes forming the Dinaric Lake System developed in the Dinaric depressions and the bivalvian genus *Mytilopsis* radiated in it exceedingly (Kochansky-Devide et Slišković 1978; Harzhauser and Mandić 2004, 2008; Prelogović 1975). Karstification started to form underground water conduits here in Pliocene at the latest (Melik 1958), but according to new findings already in the Early Miocene (Bosák 2010). This enabled surface animals to extend their populations into subterranean habitats.

## Discussion

### *Position of Congeria kusceri within Dreissenidae*

With its relatives, *Congeria* constitutes the subfamily Dreissenidae: Dreisseninae (Nuttall

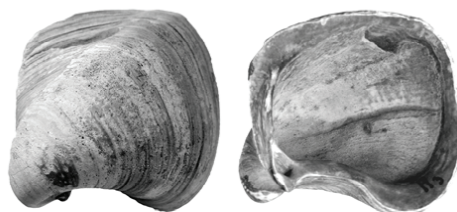


Figure 3: A fossil shell of *Congeria subglobosa* Partsch 1836 from Pannonian (Late Miocene) strata in Vösendorf, S of Wien, Austria. Photo NHM Wien.

Slika 3: Fosilna lupina vrste *Congeria subglobosa* Partsch 1836 iz panonskih (pozni miocen) plasti v Vösendorf, južno od Dunaja, Avstrija. Foto NHM Wien.

1990; Harzhauser and Mandić 2004). The genus *Congeria* Partsch, 1836 was erected for an extinct thick-shelled species *Congeria subglobosa* Partsch, 1836 (Fig. 3). All other fossil species of the genus, as it is conceived today, are similar, they are supposed to have been inhabitants of the dysoxic muddy lake bottom, probably living in symbiosis with chemosynthetic bacteria; such a group of species was endemic to the Paratethyan basins, exhibiting a particular radiation in the long-lived lake Pannon during the Pannonian (Tortonian) (Harzhauser and Mandić 2004, 2010). The stratigraphic range of the genus ranges between 11.5 and 5.5 Ma. The probably last representatives were several Pontian (Messinian) species of the Eastern Paratethys getting extinct with the end of the Miocene (Stevanović et al. 1989; Krijgsman et al. 2010).

However, morphologically closer to *Congeria kusceri* are species of the related genus *Mytilopsis* Conrad 1958, erected for the extant species *Mytilus leucophaeatus* Conrad, 1831, i.e. for the actual *Mytilopsis leucophaeata* (Conrad, 1831), synonym *M. cochleata* (Kickx, 1835). The generally accepted eight extant species of *Mytilopsis* are all mytiliform, byssate, inhabiting brackish waters at the sea edges, mainly in tropics. This is presented as the most ancient genus of Dreisseninae, originating probably from the Eocene brackish Corbiculidae (Nuttall 1990). The initial important morphological diversification of *Mytilopsis* started only in the Early Miocene (Kochansky-Devide and Slišković 1978, 1981; Harzhauser and Mandić 2004). Their diversity

was particularly rich in the Dinaric Lake System on the Dinaric land. That radiation occurred distinctly prior to the late Miocene branching of *Congeria*. The late Miocene history of the Dinaric Lake System is still obscure (De Leeuw et al. 2010; Mandic et al., 2011) but also if partly synchronous with Lake Pannon, *Congeria* never managed to invade that fresh water environment (Harzhauser and Mandic 2010). *Mytilopsis* was treated as vanished in Europe towards the end of Pliocene and appeared again in historic times due to anthropogenic introduction (Verween et al. 2010). The relation between *Congeria* and *Mytilopsis* is supported by the shared character of attachment of the anterior byssal retractor muscle to a special lobe of the anterior shell septum called the *apophysis* (Morton 1993).

The third of the extant dreissenine genera, *Dreissena*, also developed from within *Mytilopsis*; it was characterized by a reduction of the apophysis. Virtually the only character by which fossil shells of *Mytilopsis* may be distinguished from *Dreissena* is the presence of the *apophysis*. However, at the occasion of description of a large series of Miocene *Mytilopsis* species from Dinaric area (as *Congeria*), Kochanski-Devide and Slišković (1978: 34) say (translated from Serbo-Croatian): 'In the rich ... material the apophysis ... could rarely be seen ... (Most) species could only be attributed to *Congeria* by their phylogenetic bounds or by external similarity ... Probably a *Dreissena* is among them ...'. This means that the reduction of the apophysis evidently took place a number of times convergently. Therefore, it is questionable when did just the phyletic line (clade) containing the type species *Dreissena polymorpha* split off the main *Mytilopsis* lineage. In the scheme by Nuttall (1990: Fig. 1) the split between *Mytilopsis* and *Dreissena* is approximately 7 Mya, ("million years ago") while according to Verween et al. (1910: Fig. 2) as much as 30 Mya; although all authors refer to Steininger et al. 1985. According to Harzhauser and Mandic (2004, 2010) the first certain *Dreissena* representatives inhabited the late Miocene Lake Pannon. Particular diversity peaks lasted up to the Pleistocene extinction, since then being only slightly diversified but highly invasive. It spread beyond Europe first in recent times (Thienemann 1950; Steininger et al. 1985; Harzhauser and Mandic 2004).

Thus, the **actual concept of Dreisseninae** is as follows: *Mytilopsis* sensu the recent authors (Nuttall 1990; Harzhauser and Mandic 2004, 2010) is the earliest and most plesiomorphic genus, originating in the Eocene and still existing in brackish waters circumtropically. *Dreissena* originated from within *Mytilopsis*, retaining generally its shape and developing higher resistance towards fresh water. The aberrant, apomorphic genus *Congeria*, branched from *Mytilopsis* developing complex morphologic and physiological adaptations. In contrast to the troglobiotic freshwater '*Congeria*' *kusceri*, the genuine *Congeria* was limited to the brackish water Paratethys basins and finished its existence at approximately 5.5 Ma.

This scheme might be formally questionable, but it is evolutionarily most logical and therefore reasonable, appealing. Under a strict analysis it might appear to be in discord with the priority law of ICZN (1999; which is valid for extant as well as for extinct species). It violates also the cladists' principle interdicting paraphyletic taxa (Mayr and Ashlock 1991: 223). And finally, it is seemingly in contradiction with the existence of the extant mytiloid mussel *Congeria kusceri* in European fresh waters.

I will try to entangle here only the last problem, which is of only a formal character. I am suggesting to transfer the cave mussel into the other genus and recombine its name as *Mytilopsis kusceri* (Bole 1962) comb. n. This proposal can be supported at least by four facts. First, *C. kusceri* is conchologically and anatomically similar to *Mytilopsis* being mytiloid in shape, developing byssal threads and possessing the characteristic apophysis. Second, the genetic distances between *C. kusceri* and *M. leucophaeata* is only of the same size category as between two species of the related *Dreissena*, *D. polymorpha* (Pallas 1771) and *D. bugensis* (Andrusov 1897) (Stepien et al. 2001). Third, *M. leucophaeata* used to be in some periods mainly mentioned as *Congeria cochleata* (e.g. Wolff 1969; Thienemann 1950) and most fossil species from the Dinaric area were described as *Congeria* spp. (e.g. Kochanski-Devide and Slišković 1981). As such, '*Congeria*' was also known to Bole (1962; pers comm.); in fact, Bole explicitly considered his *C. kusceri* to be closely related to *Congeria cochleata* (= *Mytilopsis leucophaeata*) rather than to fossil Pannonian *Congeria* spp. In other words,



the Bole's classification of his new species was meant as for *Congeria* which included the branch *Mytilopsis*. Most probably, the same was true with the cave mussel's first discoverer L. Kuščer. And fourth, *Congeria* s. str. has never been found in the area of Dinaric lakes, while *C. kusceri* inhabits just the Dinaric karst. This new combination will be valid as long as *Congeria* and *Mytilopsis* persist to be regarded separate genera.

*Position of C. kusceri within Mytilopsis; a relict?*

Stepien et al. (2001), according to genetic markers suppose the split between *M. leucophaeata* and *C. kusceri* approximately 5–15 Mya (while it was calculated to 10–13 Mya for *Dreissena bugensis* and *D. polymorpha*). The species may well have been separated soon after the decline of the Miocene Dinaric Lake System (ca 15 Mya according to Harzhauser and Mandic 2008) in which the genus *Mytilopsis* radiated. The Miocene species were morphologically (conchologically) very diverse, but mytiloid shape was not uncommon. The mytiloid shape of shells is very common in byssate mussels in general, one may suppose that it developed (or even re-stored) in many unrelated lineages also within the genus in question. Similar fossil species are e.g. *M. hercegovinensis* (Kochansky-Devide et Slišković 1978) or *M. acuta* (Kochansky-Devide et Slišković 1981). Although *M. hercegovinensis* is explicitly defined as 'sharply carinate' and with a 'curved and sharp top', the figures (Kochansky-Devide et Slišković 1978: Sl. 4, 1-4; Tab. II, 1-18) show a wide intraspecies variation including also rounded shells. All extant *Mytilopsis* spp. and *C. kusceri* may fall within this spectrum of polymorphism. *M. hercegovinensis* was found widely across NW Hercegovina, N and W Bosna and Middle Dalmacija. According to authors, the sediments with *M. hercegovinensis* were of the lower part of the middle Miocene which would mean their origin at the down of the Dinaric Lake System. The similar but more local *M. acuta* was even younger.

The direct ancestor-descendant relationship between *M. hercegovinensis* and *C. kusceri* is not impossible, but the dreissenid shells are too poor in diagnostic characters and at the same time too variable to allow any serious hypothesis. It is in

any case probable that either *M. hercegovinensis* or a related species, with the progressing karstification of the territory found possibility to invade subterranean waters. This could have happened polytop, in different locations, as it happened or is even happening now in some crustaceans: *Asellus aquaticus* (Sket 1965; Prevorčnik et al. 2002; Verovnik et al. 2001), the genus *Monolistra* (Sket 1986), *Proteus* (Sket 1997). After the strong reduction of surface lake- and river-systems which caused extinction of surface populations, cave mussel populations got isolated and developed further independently. Molecular analyses clearly show that most holodinaric subterranean elements diversified into endemic local races or even species. This was shown for e.g. the shrimp *Troglocaris* s. str. (Sket and Zakšek 2009), the serpulid tube worm *Marifugia* (Zakšek et al. in prep.). Recent investigations in *C. kusceri* (Bilandžija et al. 2010) show that we may expect similar results in this mussel.

## Conclusion

*Congeria kusceri* is only distantly related to the extinct Pannonian *Congeria* spp. It is purely **freshwater, troglotibiotic**, and biogeographically a truncated **holodinaric** (Fig. 4) animal. As long as *Mytilopsis* and *Congeria* are taxonomically regarded separate genera, *C. kusceri* has to be attributed to the former. Such a way we will avoid some misapprehension in biogeographical and speleobiological discussions.

Its relatives naturally closest in time, ecology (mainly freshwater) and space (Europe) are: *M. rhodanica* (Fontannes 1882) in West European Messinian (Late Miocene, ca 6 Ma; Nuttall, 1990), ca. 6 latest, probably late Miocene species from the residual Dinaric freshwater lakes (ca. 10 Mya, Kochansky-Devide and Slišković 1981), ca. 30 Late Pannonian species of Lake Pannon and Lake Kosovo (Late Miocene, ca. 6 Mya; Harzhauser and Mandic 2008, 2010; Geary et al. 2010) and about 20 Dacian/Kimmerian Eastern Paratethys species (Pliocene, ca. 5 Mya; Harzhauser and Mandic 2010).

Locally, it shows some morphological and distributional similarity with *M. hercegovinensis* from the middle Miocene deposits of the Dinaric Lake System. So, the Dinaric mussel *Mytilopsis*

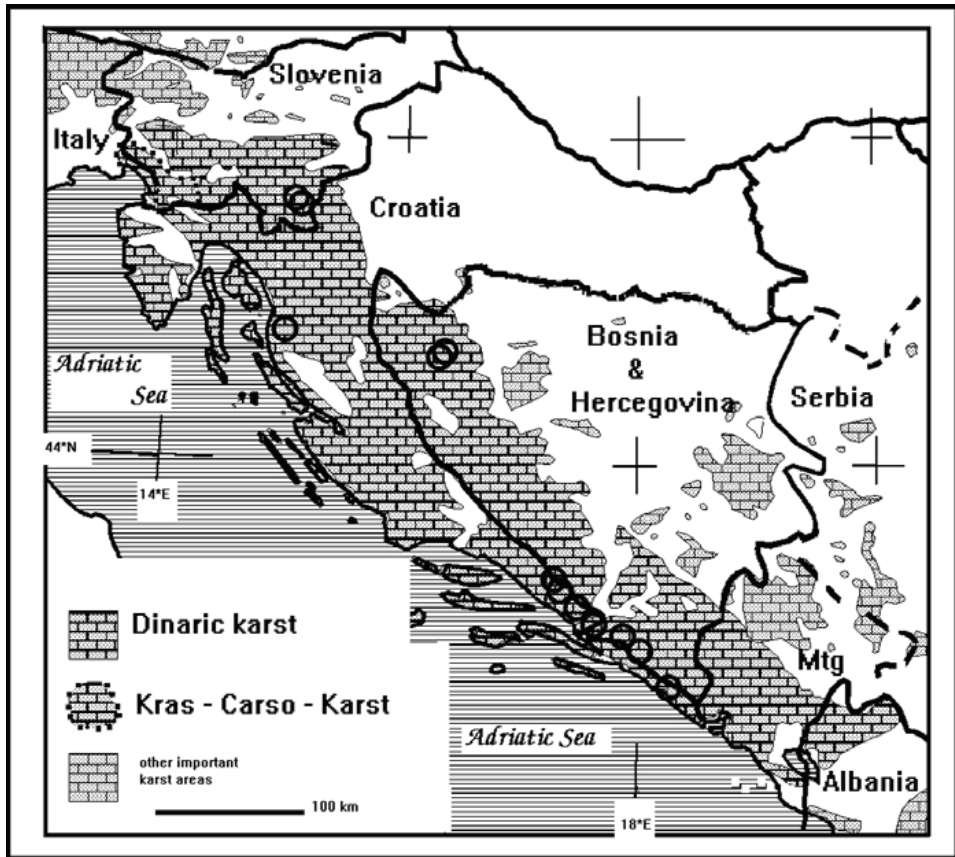


Figure 4: Known distribution of *Mytilopsis kusceri* (Bole 1962), syn. *Congeria kusceri*; open circles – localities. Slika 4: Znana razširjenost školjke *Mytilopsis kusceri* (Bole 1962), syn. *Congeria kusceri*; krogi – lokalitete.

*kusceri* (Bole 1962) (synonyma: *Congeria* sp. Kuščer, in Karaman 1935; *Congeria kusceri* Bole 1962) seems to be a **relict** of the Miocene lake fauna of the same region where it is still living.

## Povzetek

Lupine domnevno troglobiotiske školjke je našel slovenski malakolog Ljudevit Kuščer v 1930h letih v izviru Stinjevac v Dalmaciji. Pod imenom *Congeria* sp. je najdbo objavil Karaman (1935). Že pred tem in pozneje so najdbe školjk, ki so jih pripisali rodu *Dreissena* našli tudi drugi, a trikotničarke v resnici ni v dinarskem krasu. J. Štirn je našel žive školjke v jami Žira ob Popo-

vem polju, na kar je J. Bole (1962) vrsto opisal kot *Congeria kusceri*.

Pozneje smo to vrsto našli po obsežnem območju dinarskega krasa; nahajališča so raztresena po Hercegovini in Dalmaciji, v Bosanski Krajini, Liki in Beli Krajini. Tako se je jamska školjka izkazala za holodinarski biogeografski element, le da ne sega do skrajnih meja območja na severozahodu. Popolnejšo holodinarsko razširjenost izkazujejo najimenitnejši dinarski troglobionti: močeril *Proteus anguinus* Laurenti (Amphibia), jamski cevkar *Marifugia cavatica* Absolon et Hrabě (Polychaeta: Serpulidae), ceponožec *Troglo diaptomus sketi* Petkovski (Copepoda: Diaptomidae), rod mokric *Titanethes* s. str. (Oniscidea: Trichoniscidae) in še nekateri.

Dinarski kras se je razvil na Jadranski mikroplošči, ki je nekaj časa kot otok ali k Evropski plošči prislonjen polotok delila rokav Tetide na manjšo Paratetis in večji paleo Mediteran. V miocenu je bilo na tem območju obsežno Dinarsko pojezerje (Dinarski jezerski sistem), najpozneje v pliocenu pa je začelo zakrasevanje. S tem so se nekatere živali lahko razširile tudi v podzemlje.

Rod *Congeria* Partsch 1836 je bil postavljen za fosilno, debelolupinasto vrsto *Congeria subglobosa* Partsch 1836, sorodne vrste iz Vzhodne Paratetide in iz jezera Panon so ji podobne. Morfološko pa je *Congeria kusceri* bolj podobna vrstam sorodnega rodu *Mytilopsis* Conrad 1958; ta je bil postavljen za živečo vrsto *Mytilus leucophaeatus* Conrad 1831, s tem prerazporejeno kot *Mytilopsis leucophaeata* (Conrad 1831), sinonim še *M. cochleata* (Kickx 1835). Rod naj bi nastal v eocenu in se posebej razbohotil v sladkovodnem miocenskem Dinarskem pojezerju.

Danes imajo *Mytilopsis* za izvorno vejo podružine Dreissenidae: Dreisseninae, od nje pa naj bi se odcepila rodova *Congeria* in *Dreissena*. *Congeria* je bila omejena na Vzhodno Paratetido in jezero Panon in je z zatonom slednjega tudi izumrla. *Dreissena* je bila po naravi omejena na Ponto-kaspijski sistem, a se je *D. polymorpha* s posredovanjem človeka v preteklem stoletju razširila po Evropi, invazivni vrsti *D. polymorpha* in *D. bugensis* sta celo hud ekološki problem v ZDA. Osem splošno priznanih vrst rodu *Mytilopsis*

danes poseljuje somornico, večinoma v tropih, semkaj pa štejejo tudi obilico fosilnih vrst.

Ugotovili so, da se *C. kusceri* od vrste *M. leucophaeata* molekulsko razlikuje le približno toliko, kot sta različni vrsti sorodnega rodu *Dreissena*, *D. polymorpha* in *D. bugensis*. Omeniti tudi velja, da je Bole poimenoval vrsto *C. kusceri* v času, ko so ime *Mytilopsis* večinoma imeli za sinonim rodu *Congeria*; in Bole celo izrecno omenja, da je *C. kusceri* podobna vrsti *M. cochleata*.

Lahko torej domnevamo, da je vrsta *C. kusceri* dejansko nastala iz ene od dinarskih vrst rodu *Mytilopsis*, ki se je ob zatonu Dinarskega pojezerja in zakrasevanju dinarskega območja uspela razširiti v podzemlje in tam tudi ohraniti. Torej dejansko je relikvitar tamkajšnje terciarne favne.

Navidez obrobna taksonomska sprememba, ki jo predlagam, sploh ni nepomembna. S prerazporeditvijo in preimenovanjem jamske školjke v *Mytilopsis kusceri* (Bole 1962) se bomo izognili marsikateremu nesporazumu v filogenetskih in speleobioloških razpravah.

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