

An elusive ancestry of Neogastropoda:  
a potential of Maturifusidae, Pseudotritoniidae,  
and Purpurinidae as the stem groups

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# An elusive ancestry of Neogastropoda: a potential of Maturifusidae, Pseudotritoniidae, and Purpurinidae as the stem groups

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## ABSTRACT

Notwithstanding considerable efforts and new data on gastropod evolution collected in the recent decades, the origin of Neogastropoda remains still elusive. In this contribution we compare and discuss members of three extinct families previously proposed as possible neogastropod stem groups, i.e., Maturifusidae Gründel, 2001, Pseudotritoniidae Golikov & Starobogatov, 1987, and Purpurinidae Zittel, 1895. Their morphological characteristics, especially the differences in protoconch morphology, strongly suggest that they should all be considered as separate clades. The taxonomic status and the composition of each family is here reviewed and accordingly revised. *Angularia kittli* n. sp. is introduced from the Carnian (Late Triassic) of the St. Cassian Formation (Italy).

**KEY WORDS**

Neogastropoda,  
Tonnoidea,  
Mesozoic,  
taxonomy,  
evolution,  
morphology,  
protoconch,  
larval shell,  
phylogeny,  
new combination,  
new species.

It differs from its congeners in having a more pronounced axial ornamentation, which makes it similar to *Fossacerithium* Gerasimov, 1992 from the Jurassic. However, the protoconch of the new species is unknown and therefore its taxonomic position is tentative. An evolutionary lineage from the oldest known purpurinid species of genera *Khetella* Beisel, 1977 and *Cretadmete* Blagovetshenskiy & Shumilkin, 2006 to the recent tonnoids is proposed. We conclude that in the Jurassic, purpurinids were divided into two groups. One of them, represented by *Khetella*, could be considered as the ancestor of Tonnoidea, while the other, represented by *Fossacerithium*, can be interpreted as the ancestor of Neogastropoda. Maturifusidae most likely went extinct without direct descendants. The relation of Pseudotrioniidae to the neogastropod lineage remains uncertain.

**RÉSUMÉ**

*L'origine introuvable des Néogastéropodes : le potentiel des Maturifusidae, Pseudotrioniidae et Purpurinidae comme groupes-souches.*

Malgré des efforts considérables et de nouvelles données sur l'évolution des gastéropodes obtenues dans les dernières décennies, l'origine des Néogastéropodes reste difficile à cerner. Dans cette contribution nous comparons et discutons les membres des trois familles éteintes proposées auparavant comme groupes-souches des Néogastéropodes : Maturifusidae Gründel, 2001, Pseudotrioniidae Golikov & Starobogatov, 1987 et Purpurinidae Zittel, 1895. Leurs caractères morphologiques, en particulier les morphologies différentes des protoconques, suggèrent fortement qu'ils doivent être considérés comme clades séparés. Nous passons en revue la composition de chaque famille, et nous présentons une révision taxonomique. Nous décrivons *Angularia kittli* n. sp., une nouvelle espèce du Carnien (Trias supérieur) de la formation de San Cassian; elle diffère des autres représentants du même genre par une ornementation axiale plus prononcée, ce en quoi elle ressemble aux *Fossacerithium* Gerasimov, 1992 jurassiques. Toutefois, nous ne connaissons pas la protoconque de cette nouvelle espèce, c'est pourquoi ses relations phylogénétiques restent hypothétiques. Nous proposons la lignée évolutive conduisant des plus anciens purpurinidés, appartenant aux *Khetella* Beisel, 1977 et *Cretadmete* Blagovetshenskiy & Shumilkin, 2006, aux tonnoïdes contemporains. Nous concluons que, dans le Jurassique, il a existé deux groupes des purpurinidés : l'un, représenté par *Khetella*, pourrait être considéré comme l'ancêtre des Tonnoidea; l'autre, représenté par *Fossacerithium*, pourrait être interprété comme l'ancêtre des Néogastéropodes. Les Maturifusidés se sont éteints, le plus probablement sans descendance. La relation des Pseudotrioniidés à la lignée des Néogastéropodes n'est pas certaine.

**MOTS CLÉS**

Néogastéropodes,  
Tonnoidea,  
Mésozoïque,  
taxonomie,  
évolution,  
morphologie,  
protoconque,  
coquille larvaire,  
phylogénie,  
combinaison nouvelle,  
espèce nouvelle.

**INTRODUCTION**

Gastropods are the most successful and diverse class of molluscs occurring in the majority of environments reflecting their great evolutionary success (e.g. Ponder *et al.* 2020). They also display a rich fossil record throughout the Phanerozoic. The early evolutionary history of many gastropod groups, however, is difficult to decipher since the shells of gastropods are commonly poorly preserved due to their prevailing aragonite mineralogy and numerous convergences in morphology. One of these groups is Neogastropoda – the most successful and highly diversified modern group of gastropods consisting of 17 105 living species (according to Encyclopedia of life <https://eol.org/pages/2447>) – nearly one-fourth of all gastropods. Their rapid evolution is a classical example of an adaptive radiation based on the adoption of a carnivorous life style that has occurred mainly since the mid-Cretaceous and persists until today (e.g. Wenz 1939, 1940; Taylor *et al.* 1980; Ponder & Lindberg 1997; Modica & Holford 2010). Neogastropods are active predators (also scavengers and some ectoparasites) and their hunting innovations are considered a crucial factor in their rapid radiation in the mid-Cretaceous

(Taylor *et al.* 1980; Modica & Holford 2010). The monophyly of the group based on the phylogenetic analysis of morphological characters (e.g. Ponder & Linberg 1997; Ponder *et al.* 2008) was confirmed also by molecular data (Cunha *et al.* 2009; Ossa *et al.* 2015; Lemarcis *et al.* 2022), according to which neogastropods are nested in Hypsogastropoda (*sensu* Ponder & Linberg 1997; see also Bouchet *et al.* 2017) and belong to “siphonate” caenogastropods, which also contain Tonnoidea Suter, 1913 (1825), Stromboidea Rafinesque, 1815 and Cypraeoidea Rafinesque, 1815 as more distant relatives. Tonnoidea is also proposed as the closest living sister group to Neogastropoda (see Cunha *et al.* 2009 for details).

According to the classification of Bouchet *et al.* (2017), the order Neogastropoda includes 58 families in eight superfamilies and 11 families unassigned to superfamily. This classification differs significantly from the previous nomenclator by Bouchet & Rocroi (2005), where Neogastropoda comprise of 31 families grouped in six superfamilies and six families unassigned to superfamily. These changes highlight the dynamics in the research on the phylogeny and taxonomy of Neogastropoda, especially regarding their fossil representatives. The increase of the number of families not assigned

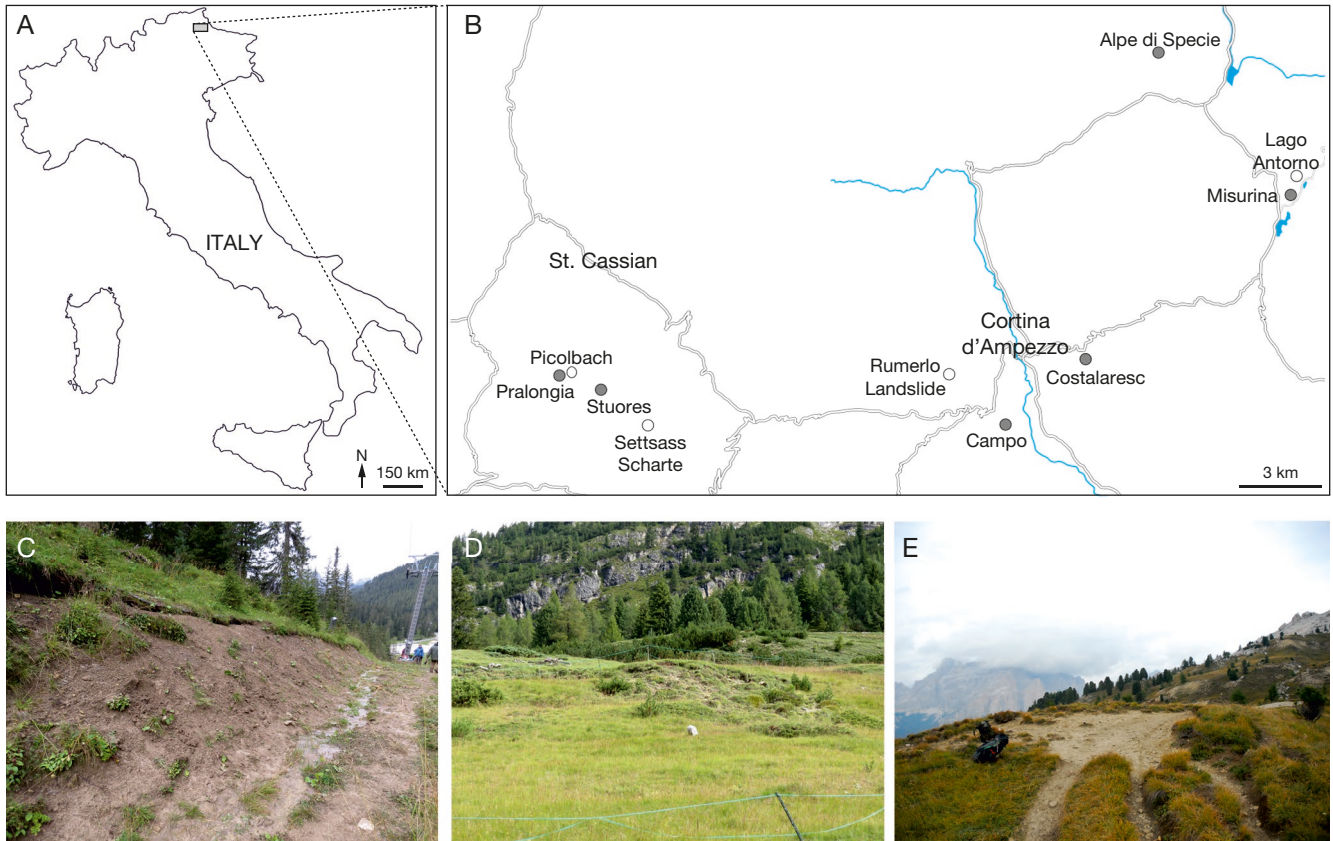


FIG. 1. — **A, B**, Location of the sampling localities in South Tyrol, North-eastern Italy (**B**) and their position on the map of Italy (**A**); localities, where specimens (see Table 1) were found, are marked in **grey**; **C-E**, examples of sample locations: **C**, Misurina Skilift; **D**, Alpe di Specie; **E**, Stuoeres.

to superfamilies in the newest classification (Bouchet *et al.* 2017) resulted largely from the inclusion of some families into the order Neogastropoda, which were previously assigned to other higher gastropod taxa or had unclear systematic position.

The identification of the neogastropod stem group in the fossil record is challenging since it is based solely on comparative shell morphology of extinct taxa. Three families – Purpurinidae Zittel, 1895, Pseudotrioniidae Golikov & Starobogatov, 1987 and Maturifusidae Gründel, 2001 – were proposed so far as possible neogastropod stem groups (Taylor *et al.* 1980; Szabó 1983; Bandel 1993; Riedel 2000; Kaim 2004). Ponder (1973) also discussed Palaeozoic Subulitidae (Soleniscidae) as possible ancestors. The shells of most living neogastropods are fusiform with a pronounced anterior siphonal canal and also posterior canal or notches. Reticulate teleoconch ornaments are very common. One could expect that potential ancestors also display this type of shell morphology. The larval shells of living neogastropods are rather large and the size of the hatchings is also large when compared to those of “lower caenogastropods” such as cerithiids or littorinids (Bandel 1975; see Nützel 2014: 486, fig. 8). The mutual relationships of Purpurinidae, Pseudotrioniidae and Maturifusidae including possible synonymy of the Triassic Pseudotrioniidae and Jurassic Maturifusidae was a matter of debate in the last decade, but remained largely unresolved due to differences in the aperture morphology and teleoconch

ornamentation as well as a lack of information on protoconchs of the type species of respective type genera (Nützel 2010; Szabó 2011; Nützel & Gründel 2015; see also the Historical Background and Discussion chapters for details). In the early accounts, Purpurinidae were proposed to be ancestors of Neogastropoda (Taylor *et al.* 1980) or Tonnoidea (Bandel 1993), while some other authors considered Maturifusidae as better candidates (Riedel 2000; Kaim 2004). In the first version of the gastropod nomenclator (Bouchet & Rocroi 2005) Pseudotrioniidae were synonymized with Purpurinidae and located in the superfamily Littorinoidea, while in the second edition (Bouchet *et al.* 2017) both families are placed in Neogastropoda (not assigned to any superfamily) as separate entities and the Maturifusidae are synonymized with Pseudotrioniidae – Maturifusidae were not assigned to any superfamily among Hypsogastropoda by Bouchet & Rocroi (2005).

This paper aims at summarizing previous studies on alleged ancestral groups of Neogastropoda in an attempt to shed some new light on problematic aspects in each of the families discussed herein. We also present new materials from the Upper Triassic (Carnian) of the St. Cassian Formation (Dolomites, Italy) and Upper Cretaceous (Campanian) of Coon Creek (Tennessee, United States), which provide additional insights for the systematics and mutual relations of the discussed groups.

TABLE 1. — Type specimens (**asterisked**) and new material from the St. Cassian Formation (Dolomites, Italy) discussed in this paper.

Locality	Species	Number of specimens
Alpe di Specie	<i>Purpurina macrostoma</i> (Kittl, 1894)	14
Campo	<i>Purpurina macrostoma</i>	1
Costalaresc	<i>Angularia pleurotomaria</i> (Münster, 1841)	6
Misurina	<i>Angularia subpleurotomaria</i> (Münster, 1841)	3
Misurina Skilift	<i>Angularia pleurotomaria</i>	1
Pralongia	<i>Angularia subpleurotomaria</i>	1
Stuores	<i>Angularia pleurotomaria</i>	1
Stuores	* <i>Pseudoscalites elegantissimus</i> von Klipstein, 1892 ( <i>in</i> Kittl 1892)	1
St. Cassian formation, probably Stuores	* <i>Angularia subpleurotomaria</i>	3
St. Cassian formation, probably Stuores	* <i>Angularia pleurotomaria</i>	1
St. Cassian	* <i>Pseudotrionium venustum</i> (Münster, 1841)	1
St. Cassian	* <i>Pseudotrionium laubei</i> (Kittl, 1894)	1

## MATERIAL AND METHODS

The new Triassic material under this study was collected during two fieldtrips to the Dolomites (Italy) in 2018 and 2020 respectively. The samples were collected from the following localities: Lago Antorno, Misurina Skilift, Alpe di Specie, Settsass Scharte, Stuores Meadows, Picolbach, Pralongia, Costalaresc, and Rumerlo (Fig. 1). Additional material came from collection efforts of AN and AK in 2010. The samples were hand-picked from the surface outcrops in the field as well as bulk samples were collected and then washed on the sieves (0.375 mm mesh size) in the laboratory of the Institute of Paleobiology PAS. All fossil remains were picked out from the resulting residues and gastropod specimens were separated. Then specimens belonging to the families in question (Maturifusidae, Pseudotrioniidae, Purpurinidae) were selected and studied. 13 shells of interest were found in the material collected in 2018-2020 and 14 shells came from previous field campaigns (Table 1). The specimens collected in 2018-2020 were documented on SEM at the Institute of Paleobiology PAS. Additional unpublished material was used for line drawings of *Maturifusus* Szabó, 1983 (Callovian, Middle Jurassic of Łuków, Poland) and of *Paladmete* Gardner, 1916 (Campanian, Upper Cretaceous of Coon Creek, Tennessee, United States). A new specimen of *Astandes densatus* Wade, 1917, the type species of *Astandes* Wade, 1917 has been recovered from a bulk sample collected in the type locality of Coon Creek Formation during the fieldwork in 2022.

To identify relationships between the taxa in question and analyze their affinities we performed an extensive survey of the available literature.

### INSTITUTIONAL ABBREVIATIONS

GBA	Geologische Bundesanstalt, Vienna;
MNHN	French National Museum of Natural History, Paris;
MPRZ	Rinaldo Zardini Paleontological Museum in Cortina d'Ampezzo;
NHMW	Natural History Museum, Vienna;
PZO	Naturmuseum Südtirol, Bozen;
SNSB-BSPG	Bavarian State Collection for Palaeontology and Geology, Munich;
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

## HISTORICAL BACKGROUND

### MATURIFUSIDAE

Szabó (1983: 44) placed the new genus *Maturifusus* in the family Buccinidae based on a comparison to similar Pleistocene to Recent species of *Plicifusus* Dall, 1902. Apart from the type species, *M. densicostatus* Szabó, 1983, Szabó (1983: 44) also included *Fusus piettei* Hébert & Deslongchamps, 1860 in the genus and noted that the generic assignment of other Mesozoic fusiform species is pending further investigations. The first description of the protoconch morphology – including embryonic whorl sculpture with distinct tubercles – was provided by Gründel (2001: 74), who also erected the monogeneric family Maturifusidae and noted that the genus *Maturifusus* is quite isolated from other, well investigated Jurassic gastropods, and its connections to younger genera are unclear. Subsequent studies showed that the distinct tubercles on the embryonic whorl are easily altered post-mortem (Guzhov 2004; Kaim 2004) since initial shells are usually recrystallized and/or corroded, therefore such micro-ornaments are usually not preserved in fossil gastropod specimens (Nützel 2014).

Gründel (2001) established the new monogeneric family Maturifusidae based on the genus *Maturifusus* without enlisting the species belonging to the genus (apart from the type species). However, several species were already described by Schröder (1995), Gründel (1998, 1999, 2001), Nützel & Erwin (2004) (Table 2) and two revisions have been published by Kaim (2004) and Guzhov (2004). Kaim (2004) synonymized *Maturifusus* with Late Cretaceous *Astandes* and attributed *Astandes* to the family Maturifusidae. Furthermore, Kaim (2004) argued that the protoconchs of *Maturifusus* (his *Astandes*) somewhat resemble those of some Buccinidae and suggested it could be an ancestral group for neogastropods. He reviewed previously described species and placed *M. montagi* Gründel, 1998 in the synonymy with *A. conspicuus* (Eichwald, 1868). Also, he expressed doubts about the allocation of *M. ticurelatus* (Gründel, 2001) and *M. keyserlingianus* (Rouillier, 1846) into separate species as *M. conspicuus* has a wide range of intraspecific variability (Kaim 2004: 104).

Guzhov (2004) included thirteen species in *Maturifusus* and described one new species (see Table 2). While discussing the composition of Maturifusidae he included also two

TABLE 2. — Species attributed to *Maturifusus* Szabó, 1983 or *Astandes* Wade, 1917 and their revised taxonomic position.

Reference	Species name as in original reference	According to publication		Taxonomic position herein
		Age	Distribution Locality	
<b><i>Maturifusus</i> Szabó, 1983</b>				
Szabó 1983: 44	<i>Maturifusus densicostatus</i> Szabó, 1983 <i>Fusus piettei</i> Hébert & Deslongchamps, 1860	Middle Jurassic Jurassic (Oxfordian)	Bakony Mts, Hungary Montreuil-Bellay, France	<i>Maturifusus</i> <i>?Maturifusus</i>
Gerasimov 1955: 195	<i>Brachytrema keyserlingiana</i> (Rouillier, 1846) <i>Brachytrema incerta</i> (d'Orbigny, 1845) <i>Brachytrema kostromense</i> Gerasimov, 1955	Jurassic (Oxfordian) Jurassic (Kimmeridgian-Tithonian) Jurassic (Callovian)	Moscow region, Russia Moscow region, Russia Kostroma region, Russia	<i>Maturifusus</i> <i>?Khetella</i> <i>Maturifusus</i>
Gründel 1977: 190	<i>Maturifusus</i> sp. 1	Jurassic (Bathonian)	Kłęby, Poland	<i>Maturifusus</i>
Yamnichenko 1987: 125	<i>Fusus caseus</i> Yamnichenko, 1987 <i>Fusus crassus</i> Yamnichenko, 1987	Jurassic (upper Bajocian)	Kharkiv and Dniepr regions, Ukraine	<i>Maturifusus</i>
Schröder 1995: 40	<i>Maturifusus szaboi</i> Schröder, 1995 <i>Fusus piettei</i> <i>Fusus bernouillensis</i> (Loriol) ( <i>Fusus</i> sp. ined. aff. <i>Bernouillensis</i> Lor. sp. in Andreae 1887) <i>Alaria alternans</i> Terquem & Jourdy, 1869	Jurassic (Aalenian) Jurassic (Oxfordian) Jurassic (Hettangian, Sinemurian) Jurassic (Bathonian)	Hambühren, Germany Montreuil-Bellay, France Bernouil, France Clapes, France	<i>Maturifusus</i> <i>?Maturifusus</i> <i>?Aporrhaidae</i> <i>?Aporrhaidae</i>
Gründel 1998: 17	<i>Maturifusus montagi</i> Gründel, 1998	Jurassic (Oxfordian)	Rogätz, Germany	<i>Maturifusus</i>
Gründel 1999: 644	<i>Maturifusus grimmensis</i> Gründel, 1999	Jurassic (Pliensbachian-Toarcian)	Western Pomerania, Germany	<i>Maturifusus</i>
Gründel 2001: 75	<i>Maturifusus ticurelatus</i> Gründel, 2001	Jurassic (Bathonian)	Kłęby, Poland	<i>Maturifusus</i>
Kiel 2001: 89	<i>Maturifusus?</i> sp.	Cretaceous (Campanian)	Torallola, Spain	<i>?Aporrhaidae</i>
Nützel & Erwin 2004: 391	<i>Maturifusus?</i> <i>siphonatus</i> Nützel & Erwin, 2004	Triassic (upper Norian)	Wallowa Terrane, Idaho, United States	<i>?Triphoroidea</i>
Guzhov 2004: 391	<i>Maturifusus caseus</i> (Yamnichenko, 1987) <i>Maturifusus conspicuus</i> (Eichwald, 1868) <i>Maturifusus densicostatus</i> Szabó, 1983 <i>Maturifusus grimmensis</i> Gründel, 1999 <i>Maturifusus keyserlingianus</i> (Rouillier, 1846) <i>Maturifusus kostromensis</i> (Gerasimov, 1955) <i>Maturifusus mosquensis</i> Guzhov, 2004 <i>Maturifusus piettei</i> (Hebert & Deslongchamps, 1860) <i>Maturifusus piquus</i> (Beisel, 1983) <i>Maturifusus purpuriniformis</i> (Conti, 1982) <i>Maturifusus szaboi</i> Schröder, 1993 <i>?Maturifusus nassoides</i> (Eudes-Deslongchamps, 1842) <i>?Maturifusus zeisei</i> (Wollemann, 1903)	Jurassic (upper Bajocian) Jurassic (Oxfordian, ?lower Kimmeridgian) Middle Jurassic Jurassic (upper Pliensbachian) Jurassic (Oxfordian-lower Kimmeridgian) Jurassic (lower Callovian-middle Oxfordian) Jurassic (upper Tithonian) Jurassic (Callovian) Jurassic (upper Kimmeridgian) Jurassic (lower Bajocian) Jurassic (upper Aalenian) Jurassic (Bajocian) Cretaceous (Aptian-Albian)	Kharkiv and Dniepr regions, Ukraine European Russia, Germany Bakony Mts, Hungary Germany European Russia European Russia European Russia France northern Siberia, Russia Italy Germany France Germany	<i>Maturifusus</i> <i>Maturifusus</i> <i>Maturifusus</i> <i>Maturifusus</i> <i>Maturifusus</i> <i>Maturifusus</i> <i>Maturifusus</i> <i>Purpurina</i> <i>?Maturifusus</i> <i>Cretadmete</i> <i>Purpurina</i> <i>Maturifusus</i> <i>?Maturifusus</i> <i>?Maturifusus</i>
Gründel 2005: 79	<i>Maturifusus conspicuus</i> (Eichwald, 1868)	Jurassic (upper Callovian)	Saratov region, Russia	<i>Maturifusus</i>
Blagovetschenskiy & Shumilkin 2006: 147	<i>Cretadmete neglecta</i> Blagovetschenskiy & Shumilkin, 2006 <i>Cretadmete gracillima</i> (Wollemann, 1903) <i>Cretadmete kostromensis</i> (Gerasimov, 1955) <i>Cretadmete piccua</i> (Beisel, 1983)	Cretaceous (upper Hauterivian) Cretaceous (Aptian-Albian) Jurassic (middle Callovian, Upper Oxfordian-lower Kimmeridgian) Jurassic-Cretaceous (Kimmeridgian-Valanginian)	Ulyanovsk Region, Russia Northern Germany Volga River Region, northern Siberia, Russia northern Siberia, Russia	<i>Cretadmete</i> <i>Cretadmete</i> <i>Maturifusus</i> <i>Cretadmete</i>

TABLE 2. — Continuation.

Reference	Species name as in original reference	According to publication		Taxonomic position herein
		Age	Distribution Locality	
	<i>Cretadmete? conspicua</i> (Eichwald, 1868)	Jurassic (middle-upper Oxfordian)	central regions of Russia	<i>Maturifusus</i>
	<i>Cretadmete? keyserlingiana</i> (Rouillier, 1846)	Jurassic (Oxfordian-lower Kimmeridgian)	Russian Platform, Russia	<i>Maturifusus</i>
Gründel 2007: 86	<i>Maturifusus grimmensis</i> Gründel, 1999	Jurassic (Pliensbachian)	Usedom Depression, Germany	<i>Maturifusus</i>
Nützel & Gründel 2015: 75	<i>Maturifusus grimmensis</i>	Jurassic (upper Pliensbachian)	Franconia, Germany	<i>Maturifusus</i>
<b>Astandes Wade, 1917</b>				
Wade 1917: 298	<i>Astandes densatus</i> Wade, 1917	Cretaceous (Campanian)	Tennessee, United States	<i>Astandes</i>
Wade 1926: 157	<i>Astandes densatus</i>	Cretaceous (Campanian)	Tennessee, United States	<i>Astandes</i>
Sohl 1960: 298	<i>Astandes densatus</i>	Cretaceous (Campanian)	Tennessee, United States	<i>Astandes</i>
Sohl 1967: 24	<i>Astandes densatus</i>	Cretaceous (Campanian)	Wyoming, Montana, Colorado, Tennessee, United States	<i>Astandes</i>
Beisel 1983: 76	<i>Astandes kostromensis</i> (Gerasimov, 1955)	Jurassic (Upper Oxfordian-lower Kimmeridgian)	Siberia, Russia	<i>Cretadmete</i> (only the material of Beisel 1983)
	<i>Astandes piccuus</i>	Jurassic-Cretaceous (Kimmeridgian-Valanginian)	Siberia, Russia	<i>Cretadmete</i>
Gerasimov 1992: 95	<i>Astandes conspicuus</i> (Eichwald, 1868)	Jurassic (Oxfordian)	Russian Platform, Russia	<i>Maturifusus</i>
	<i>Astandes keyserlingianus</i> (Rouillier, 1846)	Jurassic (Oxfordian, Kimmeridgian)	Russian Platform, Russia	<i>Maturifusus</i>
	<i>Astandes kostromensis</i> (Gerasimov, 1955)	Jurassic (Callovian, Oxfordian, Kimmeridgian)	Russian Platform, Siberia, Russia	<i>Maturifusus</i>
Dockery 1993: 71	<i>Cerithioderma nodosa</i> Dockery, 1993	Cretaceous (Campanian)	Mississippi, United States	<i>Astandes</i>
Kaim 2004: 102	<i>Astandes conspicuus</i> (Eichwald, 1868)	Jurassic (Callovian-Oxfordian)	Russia and Poland	<i>Maturifusus</i>
	<i>Astandes kostromensis</i> (Gerasimov, 1955)	Jurassic (Callovian)	Siberia, Russia, and Poland	<i>Maturifusus</i>
	<i>Astandes ticurelatus</i> (Gründel, 2001)	Jurassic (Bathonian)	Poland and Germany	<i>Maturifusus</i>
Kaim 2008: 168	<i>Astandes conspicuus</i> (Eichwald, 1868)	Jurassic (Callovian)	Łuków, Poland	<i>Maturifusus</i>
	<i>Astandes kostromensis</i> (Gerasimov, 1955)	Jurassic (Callovian)	Łuków, Poland	<i>Maturifusus</i>
Kaim 2012: 373	<i>Astandes ticurelatus</i> (Gründel, 2001)	Jurassic (Bathonian)	Gnaszyn, Poland	<i>Maturifusus</i>
Bandel & Dockery 2012: 98	<i>Astandes nodosus</i> (Dockery, 1993)	Cretaceous (Campanian)	Mississippi, United States	<i>Astandes</i>

other genera into the family: *Rhynchocerithium* Cossmann, 1906 and *Khetella* Beisel, 1977 (Guzhov 2004: 483). In the discussion of the genus *Rhynchocerithium* he noted that the number of species and the taxonomic position of the genus are only tentatively accepted, because its teleoconch morphology is typical for members of Cryptaulacidae Gründel, 1976 (Cerithiimorpha), while protoconch and aperture resemble those of the family Maturifusidae (Guzhov 2004: 531). Conversely, Kaim (2004) placed *Rhynchocerithium* into Cerithiidae Fleming, 1822 citing the cerithiid-like protoconch and early teleoconch of the type species illustrated by Gründel (1997). The genus *Khetella* was primarily attributed to Columbelleriidae Zittel, 1895 (junior synonym of Colombellinidae Fischer, 1884) by Beisel (1977) and then questionably to Buccinidae

by Blagovetshenskiy & Shumilkin (2006). The protoconch of the Siberian *Khetella bojarkae* Beisel, 1977, illustrated for the first time by Kaim & Beisel (2005: 44), is similar to that of purpurinids, and therefore these authors suggested that the genus belongs to Purpurinidae. The attribution of *Maturifusus* to Purpurinidae was also proposed by Bandel (1993, 2006) based on an alleged similarity in protoconch morphology.

Another genus commonly attributed to the family Maturifusidae is *Astandes* (Fig. 2), which is known exclusively from the Late Cretaceous (Campanian-Maastrichtian) of the United States (Colorado, Mississippi, Montana, Tennessee, Wyoming) (Wade 1917, 1926; Sohl 1960, 1967) and consists of only two described species: the type species, *A. densatus* Wade, 1917, and *A. nodosus* (Dockery, 1993) (Dockery 1993; Bandel &



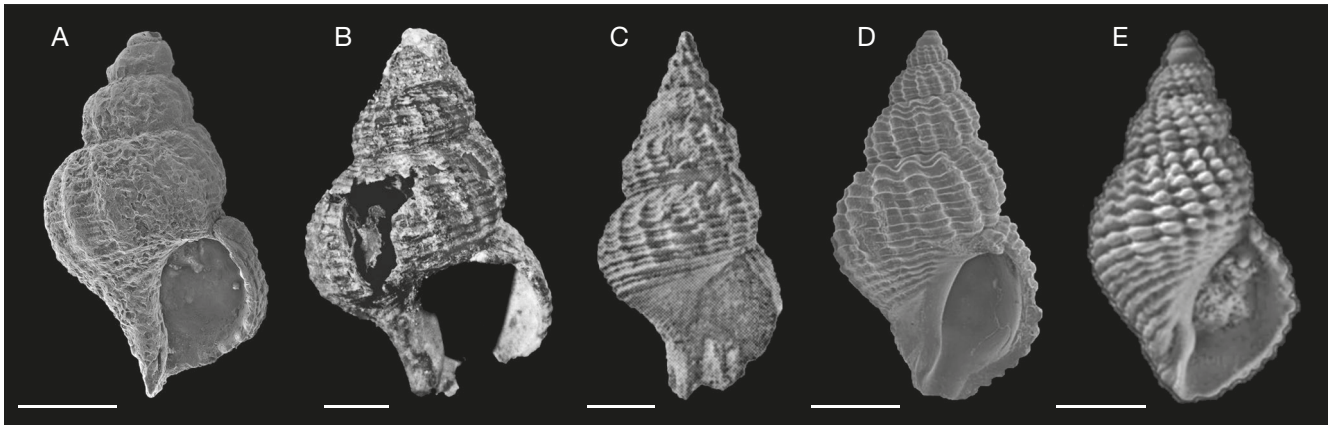


FIG. 2. — Selected species of *Astandes* Wade, 1917 and *Maturifusus* Szabó, 1983: **A**, *Astandes densatus* Wade, 1917 from Coon Creek, Tennessee, United States, upper Campanian (Upper Cretaceous); ZPAL Ga. 21/1; **B**, *Astandes densatus* from the Ripley Formation, Tennessee, United States, upper Campanian (Upper Cretaceous). Holotype USNM 32944. Current state of the holotype; **C**, *Maturifusus densicostatus* Szabó, 1983 from Bakony Mts., Somhegy: condensed Subfurcatum and Garantiana zones, Middle Jurassic. This specimen was figured by Szabó (1983: pl. 3, fig. 14); holotype J 10141; **D**, *Maturifusus conspicuus* (Eichwald, 1868) from Łuków (block in glacial drift), Podlasie, Poland, Callovian (Middle Jurassic). This specimen was figured by Kaim (2004: fig. 83C<sub>1</sub>); MZ VIII Mg 4227/7; **E**, *Maturifusus keyserlingianus* (Rouillier, 1846) from the town of Shchurovo (Zarech'e District), Russia, middle Oxfordian (Upper Jurassic). This specimen was figured by Guzhov (2004: pl. 7, fig. 5A); GMM, no. 12/38. Credits: B, photo courtesy of Anders Warén. Scale bars: 2 mm.

Dockery 2012). While describing the new genus, Wade (1917) proposed to include two other species known from the Upper Cretaceous of Europe: *Triton cretaceum* Müller, 1851 (Müller 1851: 47, pl. 5, fig. 2; Holzapfel 1887-1888: 113, pl. 10, figs 5-7) and the closely related form *Tritonium* cf. *cretaceum* Müller, 1851 (Kaunhowen 1897: 77, pl. 9, 13, fig. 4, 12). However, none of these species were later revised in the context of their attribution to the genus *Astandes* apart from the straightforward inclusion of *T. cretaceum* to *Astandes* (without any comment) by Pietzonka *et al.* (2023).

Bandel (2006) suggested that *Astandes* might be related to Pyrifusidae based on protoconch morphology, but later he placed it in Trichotropidae Gray, 1850 (junior synonym of Capulidae Fleming, 1822) (Bandel & Dockery 2012) arguing that *Astandes* and *Maturifusus* differ in the protoconch morphology despite their similarity in teleoconch morphology. Bandel & Dockery (2012) also noted that the protoconch of *Astandes* is similar in shape and size to that of the genus *Undoriptera* Guzhov, 2014 (family Aporrhaidae Gray, 1850), but its ornamentation is different (Bandel 2016).

#### PSEUDOTRITONIIDAE

The family was erected by Golikov & Starobogatov (1987) as a subfamily of the family Cerithiidae and it is monogeneric to date. In the original diagnosis, the family is characterized by “axial ornamentation strongly predominating over the spiral one” (Golikov & Starobogatov 1987). Type species of *Pseudotritonium* Wenz, 1940 has been described from the Carnian (Upper Triassic) of the St. Cassian Formation in Italy as *Scalardia venusta* Münster, 1841 (Münster 1841: 103, pl. 10, fig. 28). Münster's specimen was later illustrated by Kittl (1894: pl. 11, fig. 3), and then selected by Nützel (2010: 17, fig. 4) as the lectotype (Fig. 3B). Laube (1868) remarked the rarity of specimens of *Scalardia venusta* and differences from other members of *Scalardia* Lamarck, 1801 (today *Epitonium* Röding, 1798), which would have allowed

diagnosing a separate genus, but the poor preservation of the material deterred him from doing so. He also described two new species, *Fasciolaria avena* Laube, 1868 and *Fasciolaria karreri* Laube, 1868, which Kittl (1894) later attributed to the new genus *Palaeotriton* Kittl, 1894 (Kittl 1894: 236) in addition to two other new species, *P. laubei* Kittl, 1894 and *Palaeotriton macrostoma* Kittl, 1894. Kittl (1894) also assumed that *Palaeotriton* might be a descendant of the Pseudomelaniidae R. Hoernes, 1884 as well as some other siphonostome gastropods (not listed) suggesting that his *Paleotriton* (now *Pseudotritonium*) belongs to Neogastropoda and placed the entire group into the family Fusidae (historically a catch all for buccinoid gastropods). Moreover, Kittl (1894) synonymized also *Cerithium*(?) *ventricosum* Klipstein, 1845 (Klipstein 1845: 182, pl. 11, fig. 34) and *Fasciolaria karreri* Laube, 1868 with *P. venustum*. Additionally, he highlighted the conspicuous similarity between *P. venustum*, *P. laubei*, and *P. macrostoma*, noting that their main distinction lies solely in the number of axial ribs. However, to ascertain whether these taxa can be synonymized or if they are distinct species, “new, well-preserved material is required” (Kittl 1894: 236). The new material collected in the Dolomites indicates that these similarities noted by Kittl (1894) might be only superficial – at least in the case of *P. macrostoma* and *P. venustum* (see below).

Cossmann (1906: 205) placed *Palaeotriton* in Purpurinidae with some doubts, noting its similarity to nassariid *Nassa* Lamarck, 1799 on the one hand and to the capulid *Cerithioderma* Conrad, 1860 on the other. He also discussed Kittl's (1894: pl. 11, figs 6-9) picture of *P. macrostoma*, which indicates the thickening of a peristome and, probably, a holostomous aperture. Later Wenz (1940) replaced *Palaeotriton* – a junior homonym of *Palaeotriton* Fitzinger, 1837 (Amphibia) – with the new name *Pseudotritonium* (Wenz 1940: 732) and assigned it, with hesitation, to the subfamily Paracerithiinae Cossmann, 1906 of the family Procerithiidae Cossmann, 1906.

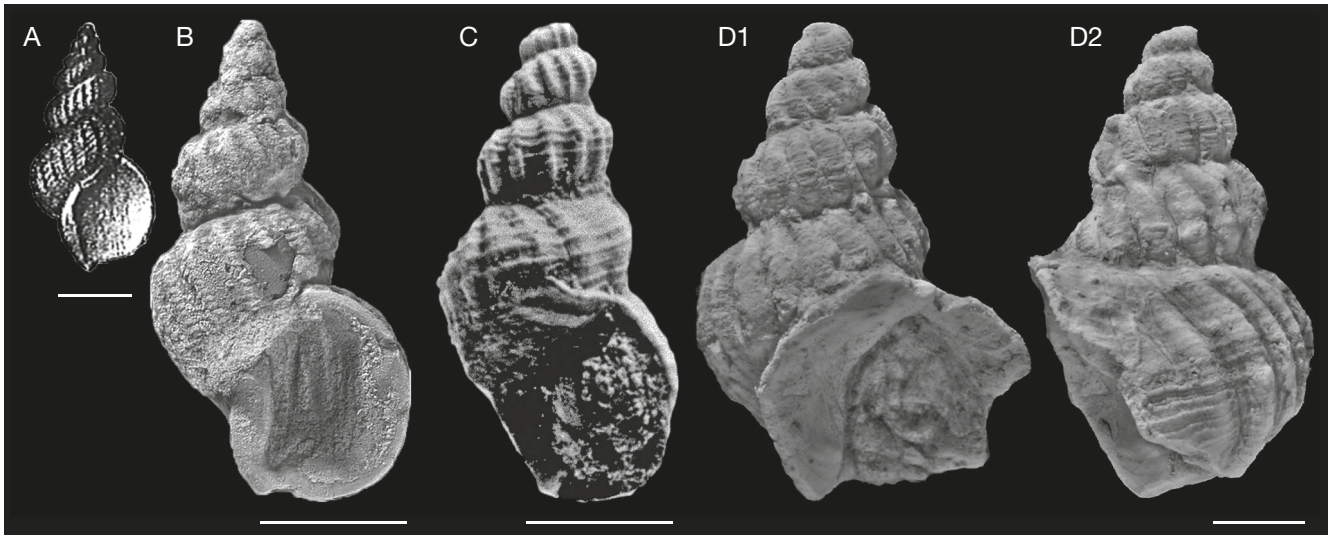


FIG. 3. — *Pseudotrionium* Wenz, 1940 species from the St. Cassian Formation (Triassic), South Tyrol, Italy: **A**, *Pseudotrionium venustum* (Münster, 1841) figured by Münster (1841: pl. 10, fig. 28); **B**, *Pseudotrionium venustum*, lectotype, SNSB-BSPG AS VII 1871, selected from Münster's collection by Nützel (2010: fig. 4); **C**, *Pseudotrionium laubei* (Kittl, 1894) from Alpe di Specie figured by Zardini (1978: pl. 38, fig. 10), MPRZ No 3909 S-L; **D**, *Pseudotrionium laubei*, holotype, NHMW: Kittl 1894: 238, 9(20)/10: **D1**, aperture view; **D2**, lateral view. Scale bars: 2 mm.

Haas (1953) doubtfully assigned to *Pseudotrionium* several specimens from the Late Triassic of Peru (not reviewed by Ferrari 2015 in her partial revision of Haas' (1953) material) noting their dissimilarity to other members of Procerithiidae investigated in his paper. Comparing them with other species of *Pseudotrionium*, he concluded that they are most similar to *P. macrostoma* from the St. Cassian Formation (Kittl 1894), which in our opinion is closer to Purpurinidae than to Pseudotrioniidae judging from its shell outline and ornamentation.

Zardini (1978: 54) introduced the new species, *Pseudotrionium milierensis* Zardini, 1978, based on a well-preserved shell and noted its similarity to *P. avena*. He also described *P. macrostoma*, *P. laubei* and *P. venustum* without attributing the genus to any particular family.

Pironi *et al.* (2021) discussed the similarity of *Pseudotrionium* to *Ederazyga* Pironi, Monari & Todd, 2021 of the family Zygopleuridae Wenz, 1938. The differences in teleoconch sculpture are particularly diagnostic: *Pseudotrionium* has prosocline axial ribs, whereas *Ederazyga* is characterized by opisthocline ribs.

#### PURPURINIDAE

Partial revision of the family has been provided by Guzhov (2004) and more comprehensive revision is pending. Here, we address in detail only those genera that do not fit to the concept of Guzhov (2004).

#### *Purpurina d'Orbigny*, 1850

The genus include numerous species that never been revised since their initial description. As a result, the systematic composition of this genus is pending a thorough revision in a separate paper.

#### *Angularia* Koken, 1892

The genus was established by Koken (1892) who placed it in Loxonematidae Koken, 1889 and simultaneously proposed that it is a probable predecessor of *Purpurina*. Wöhrmann &

Koken (1892) included three species into *Angularia*: *Turbo subpleurotomarius* Münster, 1841, *Turbo pleurotomarius* Münster, 1841, and *A. marginata* Wöhrmann & Koken, 1892 (Wöhrmann & Koken 1892: 198, pl. 14, fig. 3). Laube (1868) assigned *T. subpleurotomarius*, from the St. Cassian Formation, to *Loxonema* Phillips, 1841 (Laube 1868: 66, pl. 24, fig. 23) and introduced *Loxonema latescalata* Laube, 1868. Kittl (1892) placed the latter species into synonymy of *Purpurina pleurotomaria* (Münster, 1841) along with the type species of *Angularia*, i.e., *Purpurina subpleurotomaria* (Münster, 1841) (Kittl 1892: 63-65), and discussed the differences between these two species. However, the specimen attributed by Kittl (1892) to *Purpurina pleurotomaria* differs from the original description by Münster (1841: pl. 12, fig. 23) and represents a new species of *Angularia* described below (see below for remarks to clarifying the differences between these two species). He also introduced *Purpurina vaceki* Kittl, 1892, which in our opinion may indeed belong to *Purpurina*. Later, Kittl (1894) attributed one more new species to the genus, i.e., *Purpurina loxonemoides* (Kittl, 1894) (Kittl 1894: 251, pl. 8, fig. 4), which, however, differs significantly from all other members of the Purpurinidae due to its narrow elongated shell and very small size and most likely represents zygopleuroids or even cimids.

The oldest so far known records of *A. pleurotomaria* (Münster, 1841) and *A. subpleurotomaria* (Münster, 1841) have been reported by Broili (1907) from the Ladinian (Middle Triassic) of the Pachycardientuffe in South Tyrol (Italy). Cossmann (1909: 3) designated *Turbo subpleurotomarius* Münster, 1841 as the type species of *Angularia* and placed the genus into the family Purpurinidae. Wenz (1939) followed this interpretation. Kutassy (1927, 1937) described two new species of the genus: *A. multinodosa* Kutassy, 1937 and *A. plicata* (Kutassy, 1927) and one variety *A. plicata* var. *varicostata* Kutassy, 1937, from the Triassic near Budapest, Hungary. Zardini (1978) assigned

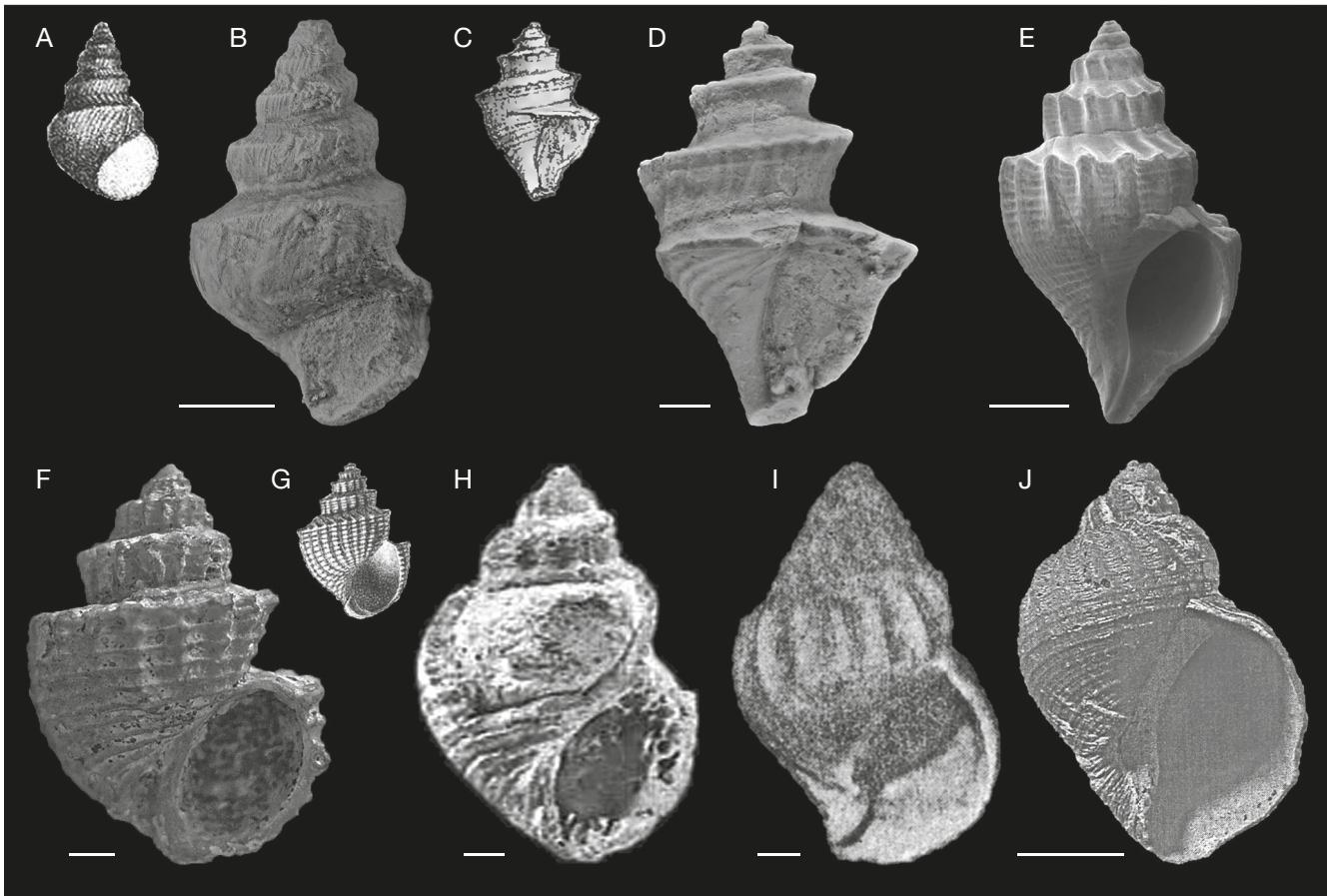


Fig. 4. — Type species of purpurinid genera: **A**, *Angularia subpleurotomaria* (Münster, 1841) from South Tyrol (Italy), St. Cassian Formation, Carnian (Upper Triassic). This specimen was figured by Münster (1841: pl. 12, fig. 24); **B**, *Angularia subpleurotomaria* from Costalaresc, South Tyrol (Italy), St. Cassian Formation, Carnian (Upper Triassic). Lectotype, SNSB-BSPG AS VII 1800, height 8.6 mm, width 5.3 mm; **C**, *Pseudoscalites elegantissimus* von Klipstein, 1892 (*in* Kittl 1892) from Stuores (Italy), St. Cassian Formation as was figured by Kittl (1892: pl. 6, fig. 12); **D**, *Pseudoscalites elegantissimus* from Stuores, St. Cassian Formation (Triassic). Lectotype, GBA 1894/005/0007, height 16.3 mm; **E**, *Fossacerithium formosum* (Eichwald, 1868) from Łuków (block in glacial drift) (Podlasie, Poland), Callovian (Middle Jurassic). This specimen was figured by Kaim (2004: 108, fig. 87A1); MZ VIII Mg 4230/3; **F**, *Purpurina bellona* d'Orbigny, 1850 from St. Vigor (Calvados, France, Bajocian). The photograph was made by Andrzej Kaim in 2004 in the De Vibraye collection of Typothèque in the Muséum national d'Histoire naturelle; Syntypes, MNHN R.53; **G**, *Purpurina bellona* from France, Jurassic as was figured by d'Orbigny (1850: pl. 331, fig. 2); **H**, *Purpurina bellona* from Calvados, France, Bajocian (Jurassic). This specimen was figured by Fischer & Weber (1997: pl. 23, fig. 26a, b); neotype, no. IPM-R.9158; **I**, *Khetella bojarkae* Beisel, 1977 from the bank of the Left Boyarka River, Russia (north of Central Siberia), lower Kimmeridgian (Jurassic). This specimen was figured by Beisel (1977: fig. 1a); holotype, N 553/260; **J**, *Cretadmete neglecta* Blagovetshenskiy & Shumilkin, 2006 from the town of Slantsevyi Rudnik, Ulyanovsk Region, Russia, upper Hauterivian, Decheni Zone (Lower Cretaceous). This specimen was figured by Blagovetshenskiy & Shumilkin (2006: pl. 6, fig. 1a); holotype, UKM, no. 155/1. Scale bars: B, D-F, H-J, 2 mm; A, C, G, size not given.

*A. pleurotomaria* and *A. subpleurotomaria* to *Purpurina* and described an additional new species, *P. costata* Zardini, 1978, from the St. Cassian Formation.

Bandel (1993, pl. 14, fig. 4) was the first to illustrate the protoconch of the Triassic purpurinid in detail (identified as *Angularia subpleurotomaria* but actually *A. pleurotomaria*). He noted that these protoconchs display a sinusigera at its terminus, so they can be compared to protoconchs of neogastropods, even though the small dimensions resemble those of Littorinoidea Children, 1834, Rissooidea Gray, 1847 and Stromboidea Rafinesque, 1815 (Bandel 1993: 26).

Nützel & Senowbari-Daryan (1999) identified a Norian-Rhaetian specimen from central Iran as *Angularia* sp. However, due to the poor preservation of this specimen, a more precise identification was not possible (Nützel & Senowbari-Daryan 1999: 107, pl. 3, fig. 10). Subsequently, the stratigraphic range of the genus has been expanded by the introduction of a new species, *A. rectecostata* Nützel &

Erwin, 2004 from the Late Triassic of United States (Wallowa Terrane, Idaho) (Nützel & Erwin 2004). Later, Gründel (2010) assigned *Natica subangulata* d'Orbigny, 1850 to *Angularia*, which differs significantly from the type species of *Angularia* in several aspects and in our opinion it is closer to *Purpuroidea* Lycett, 1848 of Littorinimorpha than to Purpurinidae.

The controversy regarding the validity of the genus name (homonymy with a bryozoan taxon) was resolved by Nützel *et al.* (2022) and the name *Angularia* for the genus was confirmed. Also, a new species, *A. corallina* from the latest Triassic of Austria, was added to the genus (Nützel *et al.* 2022).

#### *Cretadmete Blagovetshenskiy & Shumilkin, 2006*

The genus has been classified by Blagovetshenskiy & Shumilkin (2006) in the family Admetidae and later placed in Purpurinidae by Kaim *et al.* (2017). Except for the type species, *C. neglecta* (Fig. 4), Blagovetshenskiy & Shumilkin (2006) included five more species into the genus: *C. gracillima* (Wollemann, 1903),

*C. kostromensis* (Gerasimov, 1955), *C. piccua* (Beisel, 1983), *C.? conspicua* (Eichwald, 1868), and *C.? keyserlingiana* (Rouillier, 1846). Kaim *et al.* (2017) described additional species of *Cretadmete* from the upper Tithonian (Upper Jurassic) of Svalbard, however, because of the fragmentary preservation they left it in open nomenclature.

*Fossacerithium* Gerasimov, 1992

This taxon was initially established by Gerasimov (1992) as a subgenus. For additional remarks, refer to the genus description below.

*Khetella* Beisel, 1977

The genus was erected by Beisel (1977) with *Khetella bojarkae* Beisel, 1977 as type species. However, Beisel (1977) indicated that the most common and widely distributed species of *Khetella* is *Buccinum incertum* d'Orbigny, 1845 (d'Orbigny in Murchison *et al.* 1845) from the Upper Jurassic-Lower Cretaceous of Eastern Europe (Fig. 5). Beisel (1977) placed the genus into the family Columbelleriidae (junior synonym of Colombellinidae) based on its characteristic shell shape with complicated morphology of the aperture including anterior and posterior canals. He noted that species of Columbelleriidae from the northern regions have a simplified aperture morphology which lacks a posterior canal, and that the Siberian species, *K. bojarkae* (Beisel 1977), has an even more simplified morphology: a considerably weakened spiral ornament, which is indeed very characteristic to members of the Columbelleriidae. He also noted that *Khetella* differs from *Colombellina* in having a simplified morphology of the aperture that lacks a posterior canal. Other than the type species *K. bojarkae*, Beisel (1977) included four other species into this genus: *K. brunsvicensis* (Wollemann, 1900), *K. incerta* (d'Orbigny, 1845), *K. septentrionalis* (Tullberg, 1881), *K. ?gaultica* (d'Orbigny, 1842). In a later publication he added a fifth species, *K. ventrosa* Beisel, 1983.

Guzhov (2004: 526) placed *Khetella* in family Maturifusidae and mentioned twelve species, including four newly described species: *K. formosifomis*, *K. glasunovi*, *K. gradata*, and *K. makaryevensis*. Except for the species already listed by Beisel (1977, 1983), he included also *Fusus formosus* Eichwald, 1868, *Purpurina hypermeceus* Cossmann, 1913 and *Fusus? liasicus* Dumortier, 1874.

An emended diagnosis of the genus *Khetella* was published by Kaim & Beisel (2005: 43) who also illustrated for the first time the protoconch of the Siberian *Khetella bojarkae* Beisel, 1977 (Kaim & Beisel 2005: 44, fig. 2). Based on characters of the protoconchs, these authors assigned the genus to the Purpurinidae, and furthermore suggested that the group might be a stem group of Neogastropoda (Kaim & Beisel 2005: 61).

When Blagovetshenskiy & Shumilkin (2006) emended the diagnosis of *Khetella* – apparently unaware of the contribution of Kaim & Beisel (2005) – they placed it provisionally in the family Buccinidae and extended the genus composition given by Beisel (1977, 1983) to fourteen species. They left the interpretation of the species included by Guzhov (2004) into *Khetella* without any remarks or discussions.

*Pseudoscalites* Kittl, 1892

The genus was established by Kittl (1892) with the type species *P. elegantissimus* von Klipstein, 1892 (in Kittl 1892) (Fig. 4D herein). An additional species, *P. cochlea* (Münster, 1841) from the St. Cassian Formation), has been identified by Karapınar & Nützel (2021). Dominici *et al.* (2024) described the species *P. karapınari* from the Middle Triassic of the South Alps (Northern Italy).

SYSTEMATIC PALEONTOLOGY

Order NEOGASTROPODA Wenz, 1938

Family Maturifusidae Gründel, 2001

TYPE GENUS. — *Maturifusus* Szabó, 1983.

DIAGNOSIS. — As for genus (monogeneric family).

RANGE. — Jurassic (Pliensbachian-Kimmeridgian).

Genus *Maturifusus* Szabó, 1983

TYPE SPECIES. — *Maturifusus densicostatus* Szabó, 1983; by original designation. Jurassic (upper Bajocian), Hungary.

EMENDED DIAGNOSIS. — Shell fusiform; protoconch large (approx. 1.5 mm high), high conical with about 4.5 whorls; embryonic shell of about one whorl and sculptured with distinct tubercles; larval shell with two strong spiral ribs and terminates with a sinusigera; teleoconch whorls convex with strong prosocline axial ribs and spiral cords; in the intersections of axial and spiral ornaments tubercles may occur; aperture oval with a distinct anterior canal.

SPECIES INCLUDED. — *Maturifusus densicostatus* Szabó, 1983, *M. conspicuus* (Eichwald, 1868) (senior synonym of *M. montagi* Gründel, 1998 according to Kaim, 2004), *M. caseus* (Yamnichenko, 1987) (senior synonym of *Fusus crassus* (Yamnichenko, 1987) according to Guzhov, 2004), *M. grimmensis* Gründel, 1999, *M. keyserlingianus* (Rouillier, 1846), *M. kostromensis* (Gerasimov, 1955), *M. szabo* Schröder, 1995, *M. ticurelatus* Gründel, 2001 (formal name for *Maturifusus* sp. 1 of Gründel, 1977).

Species *M.? nassoides* (Eudes-Deslongchamps, 1842), *M.? piettei* (Hebert & Deslongchamps, 1860) and *M.? zeisei* (Wollemann, 1903) can be attributed to *Maturifusus* pending a revision of the original material. Also, specimens illustrated by Guzhov (2004: pl. 8, figs 11, 12) as *Khetella formosa* (Eichwald, 1868) should in our opinion be assigned to a new species of *Maturifusus*. This, however, needs specimen-based revision that is not feasible at this time.

RANGE. — Jurassic (Pliensbachian-Kimmeridgian).

REMARKS

A shell fragment from the Campanian of Spain (Torallola) with preserved apical part and only one teleoconch whorl was identified by Kiel (2001) as *Maturifusus?* sp. (Kiel 2001: 90, pl. 25, fig. 1) due to possessing the protoconch sculptured with two spiral ribs, characteristic for this genus. Their position – lose to adapical and abapical suture of protoconch whorls – differs from those in *Maturifusus sensu stricto*. Actually, the abapical spiral may be an element of subsutural shelf and may

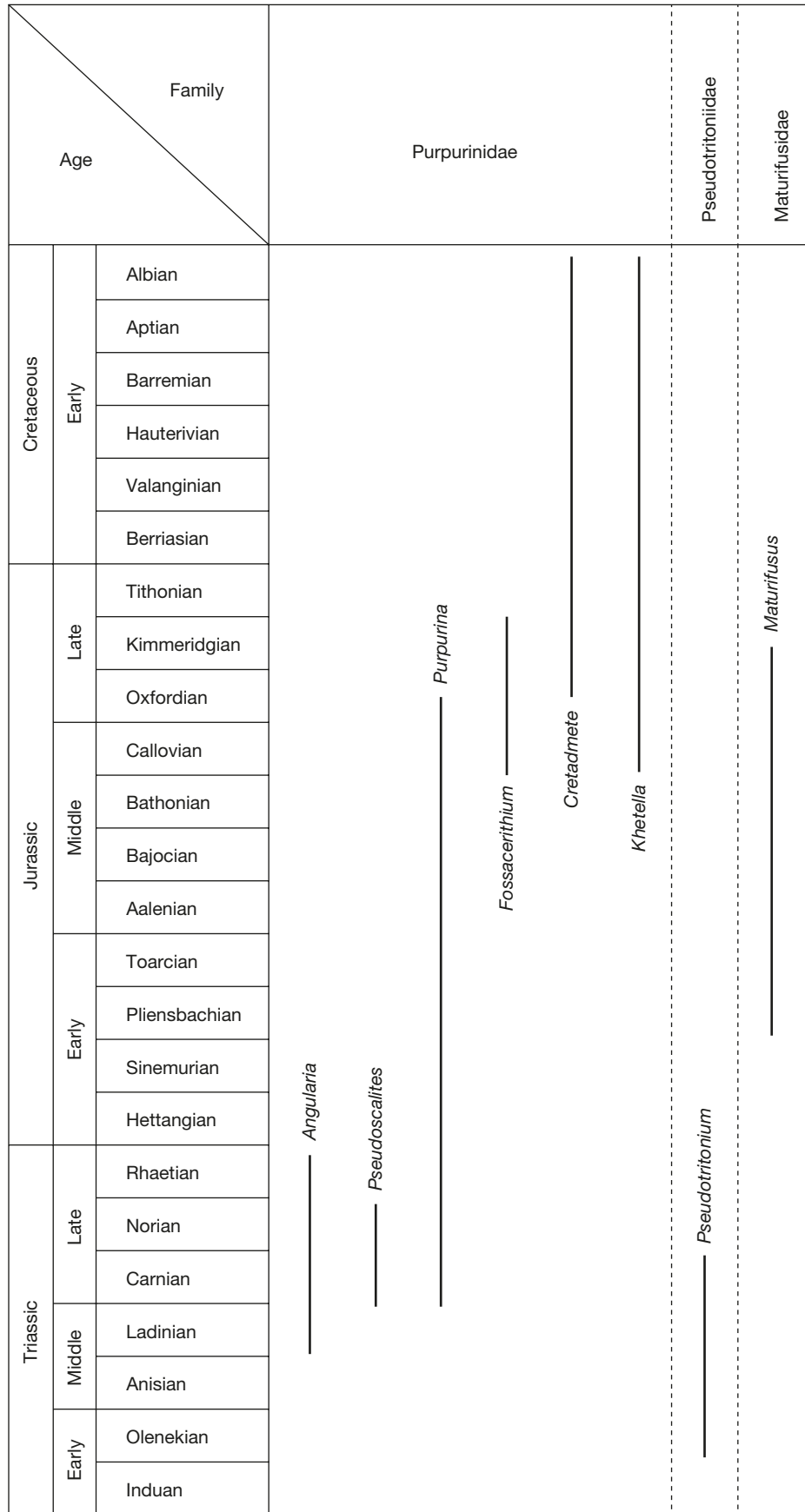


FIG. 5. — Stratigraphical distribution of the families Purpurinidae Zittel, 1895, Pseudotrioniidae Golikov & Starobogatov, 1987 and Maturifusidae Gründel, 2001.

have resulted from the diagenetic shell deformation. Morphological characteristics of the shell fragment suggest that it may belong to the Aporrhaidae rather than to Maturifusidae.

*Maturifusus? siphonatus* Nützel & Erwin 2004 from the Triassic (early late Norian) of United States (the Wallowa Terrane, Idaho) is characterized by very distinct siphonal canal and due to that feature it has been attributed to *Maturifusus* by Nützel & Erwin (2004: 391), with some doubts though. It differs, however, significantly from other members of Maturifusidae in general shell outline (more turreted than fusiform), height of the last whorl, which is separated from the base by a rib, and a narrow aperture. Taking the characters above into consideration we conclude that *Maturifusus? siphonatus* may belong to cerithioideans or triphoroideans (e.g. reminiscent of Jurassic species of *Cosmocerithium*) rather than to Maturifusidae. Nützel & Erwin (2004) compared it also to *Pseudotrironium*, which seems to be questionable as the type species of *Pseudotrironium* has a siphonal notch (and not a canal) and the other morphological characteristics also differ significantly.

The protoconch of the type species of *Astandes* was described as small, smooth and trochoid (Wade 1917: 298, pl. 17, figs 7, 8; Wade 1926: 157, pl. 54, figs 19, 20). However, the current state of holotype preservation deteriorated considerably since its original illustration does not allow for a more precise investigation of the protoconch (Fig. 2B). Subsequent efforts to collect this species have been unsuccessful (Sohl 1960, 1967) and the species appears to be extremely rare even at its type locality. Our extensive sampling in 2022 in the type locality resulted in a single specimen with corroded protoconch, but partially preserved aperture (Fig. 2A). The protoconch of another species of this genus – *A. nodosus* – has been described in detail by Dockery (1993), Bandel (2006), and Bandel & Dockery (2012) and remains the only source of information on the protoconch morphology in *Astandes*. Based on this protoconch, Bandel (2006) and Bandel & Dockery (2012, 2016) included *Astandes* into Trichotropidae, a family now synonymized with the Capulidae (Bouchet *et al.* 2017). The specimen of *Astandes densatus* (Fig. 2A) we collected in the Coon Creek type locality is very similar to maturifusids in all aspects except for the dentate outer lip of the aperture, a feature never observed in Maturifusidae, but present in the Colombellinidae and several other tonnoideans and neogastropods. Its protoconch morphology and ornamentation remains unknown.

Beisel (1983) and Gerasimov (1992) included some Late Jurassic and Early Cretaceous species from Siberia (Russia) into *Astandes* and placed the genus in the Trichotropidae (junior synonym of Capulidae). *Astandes kostromensis* (Gerasimov, 1955) and *A. picuus* Beisel, 1983 recognised by Beisel (1983) were later included in *Cretadmete* by Blagovetshenskiy & Shumilkin (2006: 147). According to Beisel's description (Beisel 1983: 76, pl. 4, fig. 2), it can be assumed that two of his specimens identified as *A. kostromensis* actually belong to an unidentified species of *Cretadmete* (Table 2) due to protoconch morphology (without two spiral ribs) and fine spiral ornamentation, while *A. kostromensis* of Gerasimov

(1955) belongs to *Maturifusus*. Also, all species identified by Gerasimov (1992) as species of *Astandes*: *A. conspicuus* (Eichwald, 1868), *A. keyerlingianus* (Rouillier, 1846), and *A. kostromensis* (Gerasimov, 1955) (Gerasimov 1992: 96) should be included into *Maturifusus*.

The type species of *Maturifusus*, *M. densicostatus*, is ornamented by spiral cords and spiral threads running in-between, which occur in the adapical part of the older whorls (Fig. 2C). This character, however, has never been observed in any other species of *Maturifusus* – the strong spiral cords occur without any secondary sculpture elements (Beisel 1983; Gerasimov 1992; Guzhov 2004; ; Kaim 2004) (Fig. 2D, E). This character and lack of the protoconch put a serious doubt at the identity and composition of the genus. Protoconchs of species included in *Maturifusus* depicted in Gründel (1977, 1998, 1999, 2001, 2007), Yamnichenko (1987), Schröder (1995), Kaim (2004, 2012), Guzhov (2004), and Nützel & Gründel (2015) differ strongly from those known from *Astandes nodosus* (Dockery 1993; Bandel & Dockery 2012) in shape and ornamentation though the protoconch of *A. densatus*, the type species of *Astandes*, is yet unknown.

Family PSEUDOTRITONIIDAE  
Golikov & Starobogatov, 1987

TYPE GENUS. — *Pseudotrironium* Wenz, 1940.

DIAGNOSIS. — As for genus (monogeneric family).

RANGE. — Triassic (Olenekian-Carnian).

Genus *Pseudotrironium* Wenz, 1940

TYPE SPECIES. — *Scalaria venusta* Münster, 1841; by typification of replaced name. Triassic (Carnian), Italy.

EMENDED DIAGNOSIS. — Shell fusiform; protoconch highly conical multispiral with abrupt transition to teleoconch; larval whorls convex and ornamented with faint oblique threads; teleoconch whorls convex with opisthocline axial ribs which are crossed by numerous finer spiral lirae; aperture wide, D-shaped; it seems to be siphonostomous.

SPECIES INCLUDED. — *Pseudotrironium venustum* (Münster, 1841), *P. laubei* (Kittl, 1894), *P. milierensis* Zardini, 1978, *P. sciaphosterum* (Batten & Stokes, 1986) and possibly *P. avena* (Laube, 1868).

RANGE. — Triassic (Olenekian-Carnian).

REMARKS

Only a few species of *Pseudotrironium* are known so far. They are rare and almost all of them occur exclusively in the deposits of the Upper Triassic of the St. Cassian Formation (Dolomites, Italy). The only species described outside this formation is *P. sciaphosterum* (Batten & Stokes, 1986), which was described from the Lower Triassic Moenkopi Formation (San Rafael Swell, Utah, United States) (Batten & Stokes 1986; Nützel 2010) and has preserved protoconchs.

In the following, species of *Pseudotrionium* are discussed:

*Pseudotrionium venustum* (Münster, 1841)

Kittl (1894) mentioned three specimens in total, including the original specimen from Münster's collection (Münster 1841). He also included in *P. venustum* one more shell described as *P. karreri* by Laube (1868). The species description by Zardini (1978) was based on eight specimens; however, their identification appears to be questionable since he apparently misidentified his specimens (see remarks to *P. laubei*). Our recent collection efforts in the St. Cassian Formation have failed to yield new specimens of this species.

*Pseudotrionium?* *avena* (Laube, 1868)

Kittl (1894: 238, pl. 11, fig. 11) discovered a single specimen in Laube's collection. Upon comparison with the specimen figured by Laube (1868: 4, pl. 21, fig. 2), Kittl noted that the characteristics are accurate, except for the presence of columellar folds, which were not mentioned in Laube's description. Kittl (1894) included *P?* *avena* into the genus with doubts due to eroded shell and the limited number of specimens.

*Pseudotrionium karreri* (Laube, 1868)

Synonymized with *P. venustum* by Kittl (1894).

*Pseudotrionium laubei* (Kittl, 1894)

Laube (1868) identified one specimen as *P. venustum*, which later Kittl interpreted as a new species *Pseudotrionium laubei* (Kittl, 1894: 238, pl. 11, fig. 11; Fig. 3D herein). After comparing this specimen (Fig. 3D) to the lectotype of *P. venustum* (Fig. 3B) and to the specimen illustrated and identified by Zardini as *P. venustum* (Zardini 1978: 54, pl. 38, fig. 10; Fig. 3C herein), we conclude that they belong to two distinct species. They differ in ornamentation, where *P. laubei* has spiral cords of two orders and *P. venustum* displays spiral cords of only one order. Moreover, the inner lip of *P. laubei* is wide, while in *P. venustum* it is rather narrow. Zardini's specimen appears to have a damaged inner lip, what could have inclined him to identify it as *P. venustum*. Otherwise, the shell shape of these two species is very similar and they are very difficult to tell apart when the preservation is imperfect.

*Pseudotrionium macrostoma* (Kittl, 1894)

This species is the most abundant among the species previously included in *Pseudotrionium*. Kittl (1894) listed nine specimens and Zardini (1978) mentioned 42 specimens. We identified 14 specimens of *P. macrostoma* in our collection (Table 1). Based on morphological characters we re-assigned this species to *Purpurina* (see below).

*Pseudotrionium milierensis* Zardini, 1978

Only one well preserved specimen is known. While comparing it with *P. avena*, Zardini (1978) noted their similarity in shell outlines. In our opinion *P. milierensis* differs from *P. avena* in having more numerous and thinner axial ribs.

*Pseudotrionium sciaphosterum* (Batten & Stokes, 1986)

Twenty-five specimens were studied by Batten & Stokes (1986). Nützel (2010) identified one additional topotypical juvenile specimen with well-preserved protoconch.

Family PURPURINIDAE Zittel, 1895

TYPE GENUS. — *Purpurina* d'Orbigny, 1850.

EMENDED DIAGNOSIS. — Shell robust, inflated, commonly with an adapical angulation of the whorl face; protoconch obtusely conical with smooth convex whorls and clearly visible demarcation between protoconch and teleoconch and a thickened apertural margin; shell sculptured with axial ribs and spiral cords; body whorl large; aperture large oval holostomous or siphonostomous.

GENERA INCLUDED. — *Purpurina* d'Orbigny, 1850, *Angularia* Koken, 1892, *Cretadmete* Blagovetshenskiy & Shumilkin, 2006, *Fossacerithium* Gerasimov, 1992, *Khetella* Beisel, 1977, *Pseudoscalites* Kittl, 1892.

RANGE. — Middle Triassic (Ladinian) to Early Cretaceous (Albian).

REMARKS

Purpurinidae is the most diverse family among possible neogastropod ancestors. Almost thirty genera were assigned to the family when they were first described (Table 3). Most of them differ significantly from *Purpurina* in shell shape and other morphological characteristics and were subsequently relocated to other higher gastropod taxa. Partial revision of the family composition has been provided by Guzhov (2004), but in our opinion, it requires further work since not all genera he attributed to the family actually belong to Purpurinidae.

Genus *Purpurina* d'Orbigny, 1850

TYPE SPECIES. — *Purpurina elegantula* d'Orbigny, 1850; by subsequent designation by Bouchet *et al.* 2017. Jurassic, France.

DIAGNOSIS. — Shell moderately large to medium sized; spire short; whorls more or less broad, angulated with adapical ramp; below angulation, whorl weakly convex and ornamented with numerous axial and spiral ribs; body whorl very large; base rounded with predominant spiral sculpture; aperture large, ovate; outer lip almost even up to angulation; thin inner lip covers umbilical chink (from Kaim 2004 emended from Wenz 1939).

RANGE. — Late Triassic (Carnian) to Late Jurassic (Oxfordian).

REMARKS

The genus *Purpurina* was established by d'Orbigny (1850) without the designation of its type species. Subsequently Bouchet *et al.* (2017) designated *Purpurina elegantula* d'Orbigny, 1850 as the type species. The genus is rich in species and many of them have never been revised (Kaim 2004: 107). Guzhov (2004) introduced *Globipurpurina* as subgenus of *Purpurina* (Guzhov 2004: 514, a subdivision not followed here) and assigned 23 species to the genus. In that composition, the genus as well as its systematic position is pending careful revision. Here, we address only the Triassic species of *Purpurina*: *P. macrostoma* n. comb.

TABLE 3. — List of genera which were classified as Purpurinidae Zittel, 1895 when first described. Genera included in the family by Guzhov (2004) are **asterisked**. Genera that are retained in the family in this work are marked by **bold face**.

Genus	Revised family position	Type species		
		Name	Age	Locality
<i>Andangularia</i> Haas, 1953	Zygopleuridae	<i>Pseudoscalites subarmatus</i> Jaworski, 1923	Triassic	Peru
<b><i>Angularia</i></b> * Koken, 1892	<b>Purpurinidae</b>	<i>Turbo subpleurotomarius</i> Münster, 1841	Triassic (Carnian)	South Tyrol, Italy
<i>Aristerozostrophia</i> Broili, 1907	Zygopleuridae	<i>Angularia gracilis</i> Broili, 1907	Triassic (Ladinian)	South Tyrol, Italy
<i>Cimoliocentrum</i> Cossmann, 1908	Cryptaulacidae	<i>Centrogonia cureti</i> Cossmann, 1900	Cretaceous (Barremian)	France
<i>Coronatica</i> Blanckenhorn, 1927	Ampullariidae	<i>Neritopsis ornata</i> Fraas, 1878	Cretaceous	Syria
<b><i>Cretadmete</i></b> Blagovetshenskiy & Shumilkin, 2006	<b>Purpurinidae</b>	<i>Cretadmete neglecta</i> Blagovetshenskiy & Shumilkin, 2006	Cretaceous (upper Hauterivian)	Russia
<i>Cyclobathmus</i> Knight, 1940	Microdomatidae	<i>Trepostira haworthi</i> Beede, 1907	Permian	United States
<i>Eucycloidea</i> * Hudleston, 1887	Eucyclidae	<i>Turbo bianor</i> d'Orbigny, 1850	Jurassic	France
<i>Globipurpurina</i> * subgen. Guzhov, 2004	Purpurinidae	<i>Purpurina sowerbyi</i> Waagen, 1866	Jurassic (lower Bajocian)	Germany
<i>Gonioconcha</i> Bonarelli, 1921	Eucyclidae	<i>Gonioconcha spinata</i> Bonarelli, 1921	Triassic	Argentina
<i>Hesperidina</i> Dubar, 1948	Vetigastropoda	<i>Hesperidina striolata</i> Dubar, 1948	Jurassic (Pliensbachian)	Morocco
<b><i>Khetella</i></b> Beisel, 1977	<b>Purpurinidae</b>	<i>Khetella bojarkae</i> Beisel, 1977	Jurassic (Kimmeridgian-Berriasian)	Siberia, Russia
<i>Kittlia</i> Cossmann, 1909	Prostyliferidae	<i>Natica pleurotomoides</i> Wissmann, 1841	Triassic	South Tyrol, Italy
<i>Leviathania</i> Pchelintsev, 1927	Leviathaniidae	<i>Natica leviathan</i> Pictet & Campiche, 1863	Cretaceous	Switzerland
<i>Moerkeia</i> * J.Bohm, 1895	Strombidae	<i>Angularia praefecta</i> Kittl, 1894	Triassic	Italy
<i>Nortonia</i> Wilson, 1889	Eucyclidae	<i>Turbo patroclus</i> d'Orbigny, 1850	Jurassic	France
<i>Ochetochilus</i> Cossmann, 1899	Vetigastropoda?	<i>Ochetochilus subvaricosus</i> Cossmann, 1899	Jurassic (Bathonian-Callovian)	France
<i>Parangularia</i> Kutassy, 1934	Turbinidae	<i>Purpuroidea hungarica</i> Kutassy, 1932	Triassic	Hungary
<i>Propemurchisonia</i> de Gregorio, 1930	? Ptenoglossa	<i>Propemurchisonia giulianensis</i> de Gregorio, 1930	Jurassic	Italy
<i>Pseudalaria</i> Hudleston, 1888	Mathildidae	<i>Turritella unicarinata</i> Deslongchamps, 1842	Jurassic	British Isles
<b><i>Pseudoscalites</i></b> * Kittl, 1892	<b>Purpurinidae</b>	<i>Pseudoscalites elegantissimus</i> Kittl, 1892	Triassic (lower Carnian)	South Tyrol, Italy
<i>Ptychostoma</i> * Laube, 1868	Prostyliferidae	<i>Natica pleurotomoides</i> Wissmann, 1841	Triassic	South Tyrol, Italy
<b><i>Purpurina</i></b> * d'Orbigny, 1850	<b>Purpurinidae</b>	<i>Purpurina elegantula</i> d'Orbigny, 1850	Jurassic	France
<i>Purpuroidea</i> Lycett, 1848	Littorinoidea	<i>Purpura moreausia</i> Buvignier, 1843	Jurassic	British Isles
<i>Silberlingiella</i> Frýda & Blodgett, 2003	Eustomatidae	<i>Silberlingiella ornata</i> Frýda & Blodgett, 2003	Triassic	Nevada, United States
<i>Trepostira</i> * Koken, 1892	Littorinidae	<i>Melania multistriata</i> Wöhrmann, 1889	Triassic	South Tyrol, Italy
<i>Tuberleviathania</i> Golvinova & Korotkov, 1986	Leviathaniidae	<i>Leviathania gerassimovi</i> Pchelintsev, 1926	Cretaceous	Caucasus
<i>Werfenella</i> Nützel, 2005	Paraturbinidae	<i>Turbo rectecostatus</i> Hauer, 1851	Triassic (Olenekian)	South Tyrol, Italy

*Purpurina macrostoma* (Kittl, 1894) n. comb.  
(Fig. 6)

*Palaeotriton macrostoma* Kittl, 1894: 237, pl. 11, figs 6-9.

*Scalaria venusta* – Laube 1868: 47, pl. 23, fig. 3, not Münster 1841 that is *Pseudotritonium venustum* (Münster, 1841).

MATERIAL EXAMINED. — Italy • 14 shells; South Tyrol, Alpe di Specie; PZO 16378, 16379, 16380, 16381, 16382, 16383, 16384, 16385, 16386, 16387, MPRZ 2021 1-061, 2021 1-062, 2021 1-063, 2021 1-064 • 1 shell; South Tyrol, Campo; MPRZ 2021 1-060.

RANGE. — Late Triassic of Tyrol (Italy).

DESCRIPTION

Shell cone-shaped, fusiform, last whorl higher than spire; protoconch heliciform, small, mammilated, consists of 2.5 preserved whorls with corroded surface of the apex as well as demarcation between the protoconch and teleoconch; teleoconch consists of more than three convex whorls separated by incised suture; large last whorl with height about two thirds of the shell height; strong, broad, rounded prosocline axial ribs, *c.* 11-14 per whorls, crossed by spiral

cords of two orders; the number of axial ribs increases during shell growth; ribs approximately as wide as interspaces; spiral cords cross axial ribs without nodular thickening at intersections; whole shell surface covered by strengthened growth lines; spiral cords slightly nodular when intersecting strengthened growth lines; aperture broken; columella slightly curved; base weakly convex with evenly rounded transition to whorl face.

REMARKS

Kittl (1894) attributed this species to *Palaeotriton* (replaced later by *Pseudotritonium*) and discussed its similarity to *P. venustum* (Münster, 1841), from which *P. macrostoma* n. comb. differs in shell outline and spiral ornamentation of two orders of strength. Zardini (1978: 54, pl. 38, figs 1, 2) identified some of his specimens as *Pseudotritonium macrostoma*, which differ from Kittl's (1894) type material in shell outline. Some specimens identified by Zardini (1978) as *P. laubei* better agree with the characteristics of *Purpurina macrostoma* n. comb. The protoconch morphology shown herein for the first time allows us to attribute this species to Purpurinidae.



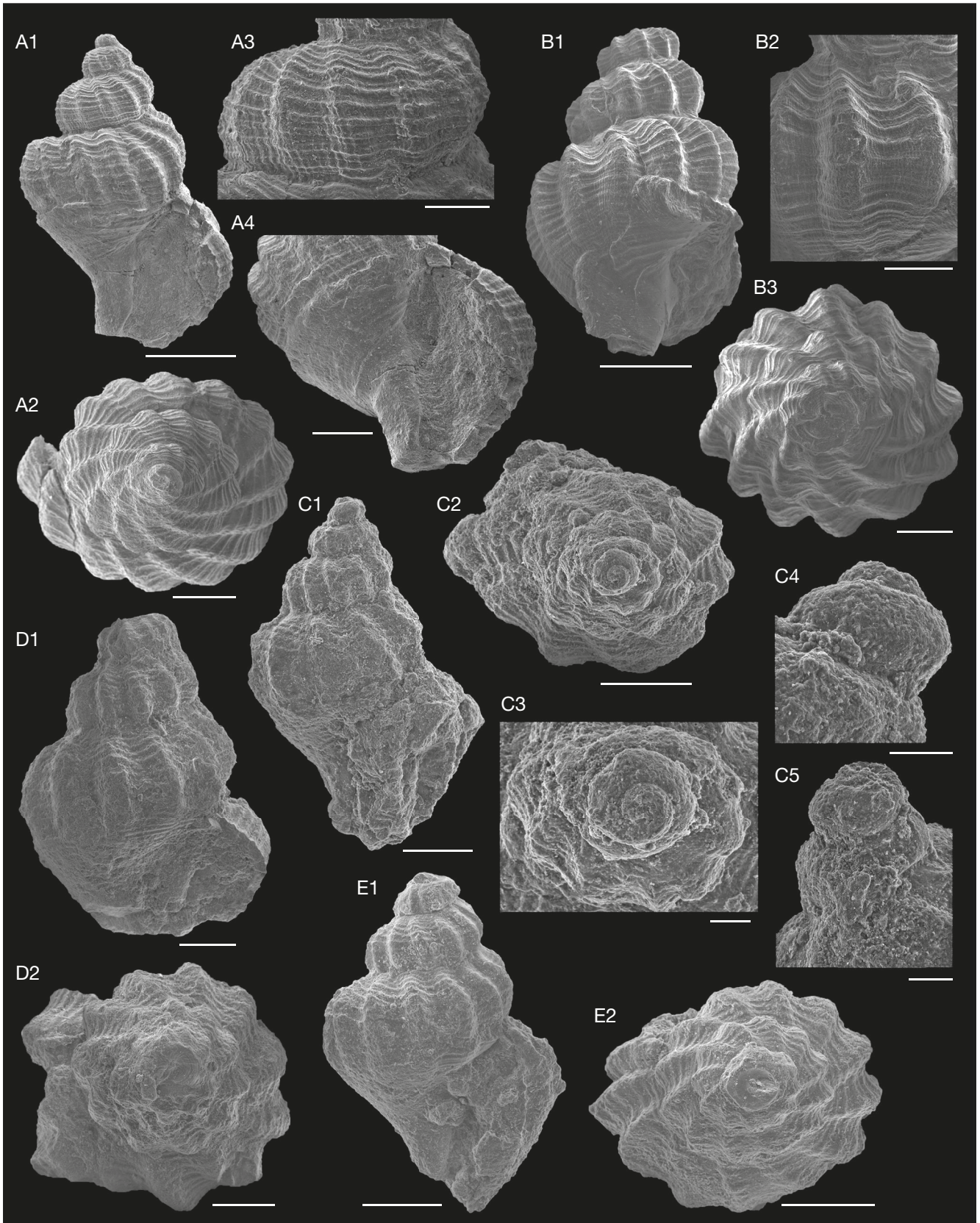


FIG. 6. — *Purpurina macrostoma* (Kittl, 1894) n. comb. from the Carnian of Alpe di Specie (South Tyrol, Italy): **A**, PZO 16381: **A1**, apertural view; **A2**, apical view; **A3**, lateral view, detail of ornamentation; **A4**, oblique basal view; **B**, PZO 16383: **B1**, lateral view; **B2**, lateral view, detail of ornamentation; **B3**, apical view; **C**, PZO 16382: **C1**, apertural view; **C2**, apical view; **C3**, apical view, detail of early whorls; **C4**, **C5**, lateral view, detail of early whorls; **D**, PZO 16386: **D1**, apertural view; **D2**, apical view; **E**, PZO 16387: **E1**, apertural view; **E2**, apical view. Scale bars: A1, B1, 2 mm; A2, A3, C1, C2, D1-E2, 0.5 mm; A4, B2, B3, 1 mm; C3-C5, 0.1 mm.

Genus *Angularia* Koken, 1892

TYPE SPECIES. — *Turbo subpleurotomarius* Münster, 1841, by subsequent designation by Cossmann, 1909. Carnian (Triassic), South Tyrol (Italy).

EMENDED DIAGNOSIS. — Shell with high, narrow spire and angulated whorls; the protoconch obtusely conical and comprises approximately three smooth whorls; the demarcation between the protoconch and the teleoconch is clearly visible with thickened apertural margin; shell surface ornamented with fine and strengthened curved growth lines of different thickness and density and fine spiral lirae; last whorl large; aperture broad; peristome thickened.

SPECIES INCLUDED. — *Angularia subpleurotomaria* (Münster, 1841), *A. pleurotomaria* (Münster, 1841), *A. marginata* Wöhrmann & Koken, 1892, *A. multinodosa* Kutassy, 1937, *A. plicata* (Kutassy, 1927), *A. costata* (Zardini, 1978), *A. rectecostata* Nützel & Erwin, 2004, *A. corallina* Nützel, Nose, Hautmann & Hochleitner, 2022 and described herein *Angularia kittli* n. sp.

RANGE. — Triassic (Ladinian-Rhaetian).

REMARKS

The larval shell of *Angularia* is shown here in detail based on well-preserved specimens from Costalaresc. It confirms the observations made by Bandel (1993, 1994) who pointed out that the protoconch of *Angularia* resembles those of Neogastropoda in morphology but it is much smaller. The small size of the first whorl reported herein, and the number of the protoconch whorls (Nützel 2014) clearly suggest that the species of *Angularia* from the St. Cassian Formation had planktotrophic larval development.

*Angularia subpleurotomaria* (Münster, 1841)  
(Figs 4A, B; 7B; 9A)

*Turbo subpleurotomarius* Münster, 1841: 115, pl. 12, fig. 24.

*Melania late-scalata* – Klipstein 1845: 190, pl. 12, fig. 29.

*Loxonema subpleurotomaria* – Laube 1868: 66, pl. 24, fig. 23.

*Purpurina subpleurotomaria* – Kittl 1892: 64, pl. 6, figs 6-9. — Zardini 1978: 31, pl. 14, fig. 3.

*Angularia (Purpurina) subpleurotomaria* – Broili 1907: 106, pl. 6, figs 31, 32.

*Angularia subpleurotomaria* – Cossmann 1909: 3, text-fig. 1.

Non *Angularia subpleurotomaria* – Bandel 1993: pl. 5, figs 3, 4, pl. 14, figs 2, 4; 1994: 139, pl. 5, fig. 17.

?*Angularia subpleurotomaria* – Bandel 2016: 159.

MATERIAL EXAMINED. — Italy • 7 specimens; South Tyrol; Casian beds, probably Stuoeres; lectotype SNSB-BSPG AS VII 1800 (designated herein); 2 paralectotypes; SNSB-BSPG AS VII 1801a, 1801b (designated herein) • 3 shells; South Tyrol; Misurina; PZO 16388, 16389, 16390 • 1 shell; South Tyrol; Pralongia; PZO 16391.

RANGE. — Ladinian-Carnian (Middle-Late Triassic) of Italy (Dolomites).

DESCRIPTION

Shell cone-shaped, moderately high-spined with gradate spire; protoconch obtusely conical and consists of about three smooth whorls, the demarcation between the protoconch and the teleoconch is clearly visible with thickened apertural margin; teleoconch consists of seven angulated whorls separated by incised suture; angulation in the upper third of the whorls; shell surface concave above angulation (ramp) and slightly convex below; a spiral cord situated on the ramp close to the adapical suture; shell surface ornamented with fine and strengthened growth lines of different thickness and density; lectotype with numerous densely spaced axial ribs that become weaker during ontogeny and eventually appear as strengthened growth lines; aperture oval with thickened outer and inner lips and broad, rounded anterior outlet; pseudumbilicus partly covered by columellar lip; base distinctly convex with evenly rounded transition to whorl face.

REMARKS

Shell ornamentation varies from delicate, represented by fine growth lines, to pronounced with strengthened growth lines that may be caused by the differences in the age of individuals, their preservation as well as intraspecific variability. *Angularia subpleurotomaria* differs from *A. pleurotomaria* in having a more slender shell and finer ornamentation.

The species was described as closely related to *A. pleurotomaria* which differ only in ornamentation (Münster 1841: 114, 115, pl. 12, figs 23, 24). Wöhrmann & Koken (1892: 198) noted that although both species are present in the collection from Schlern, they are difficult to separate, and transitional forms are present too. Nevertheless the material at our disposal displays a clear distinction between these two species.

*Angularia pleurotomaria* (Münster, 1841)  
(Figs 7A, C; 8A, B; 9B; Table 4)

*Turbo pleurotomarius* Münster, 1841: 114, pl. 12, fig. 23.

*Purpurina pleurotomaria* – Kittl 1892: 63, non pl. 6, figs 3-5. — Zardini 1978: 31, pl. 14, fig. 2.

*Angularia subpleurotomaria* – Bandel 1993: pl. 5, figs 3, 4, pl. 14, figs 2, 4. — Bandel 1994: 139, pl. 5, fig. 17.

MATERIAL EXAMINED. — Italy • 1 specimen; South Tyrol; Casian beds, probably Stuoeres; lectotype SNSB-BSPG AS VII 1799 • 6 shells; South Tyrol; Costalaresc; PZO 16372, 16373, 16374, 16375, 16376, 16377 • 1 shell; South Tyrol; Stuoeres; PZO 16393 • 1 shell; South Tyrol; Misurina Skilift; PZO 16392.

RANGE. — Ladinian-Carnian (Middle-Late Triassic) of Italy (Dolomites).

DESCRIPTION

Shell cone-shaped, moderately high-spined; protoconch obtusely conical, consisting of 2.7-3.0 whorls, 0.33-0.34 mm wide, 0.31-0.37 mm high (excluding base, measured from abapical suture); diameter of first whorl 0.11-0.12 mm; protoconch whorls smooth, convex; demarcation between protoconch

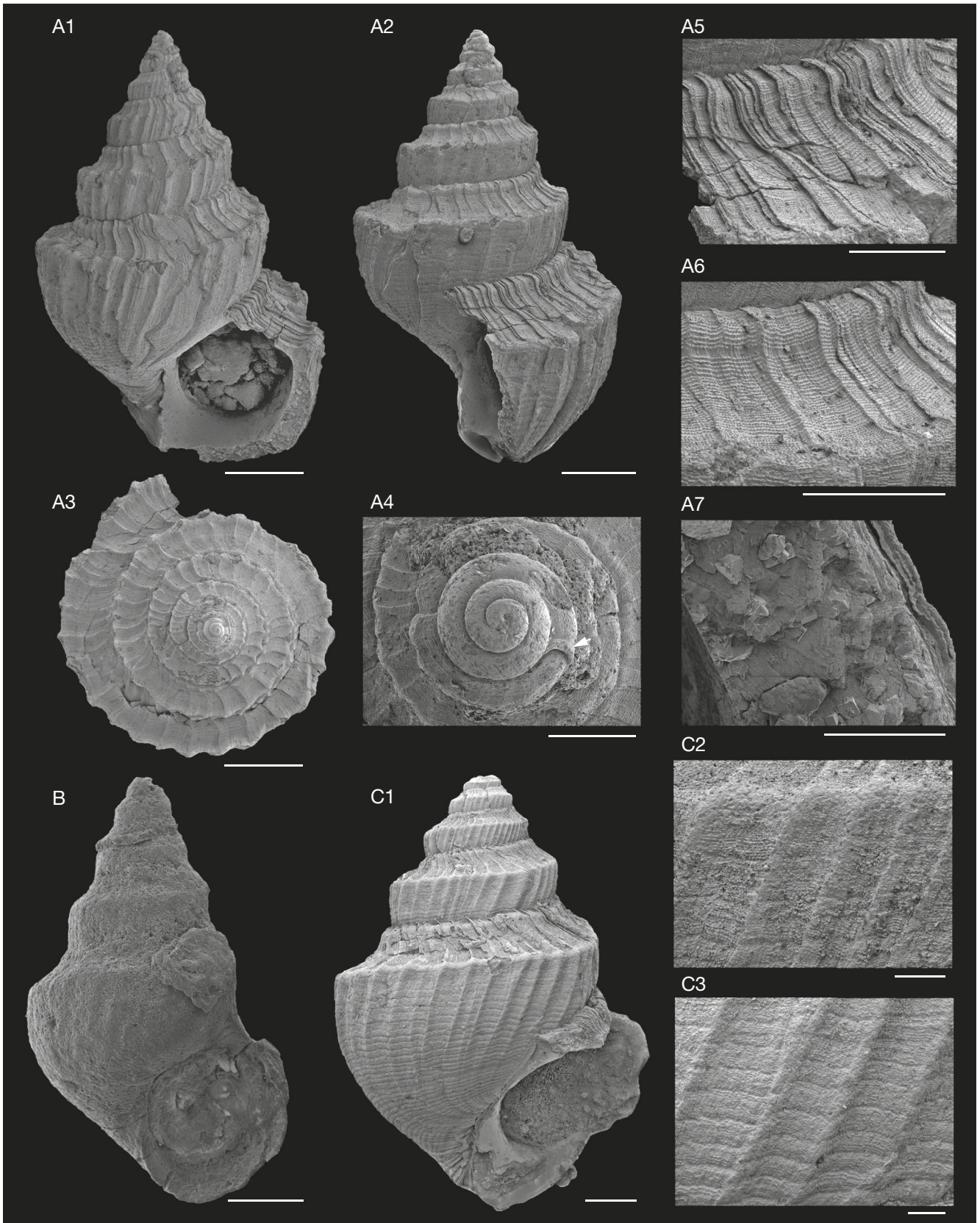


FIG. 7. — Two closely related species of *Angularia* Koken, 1892 from the St. Cassian Formation, Carnian (Late Triassic): **A, C**, *Angularia pleurotomaria* (Münster, 1841) from Costalaresc, South Tyrol (Italy): **A**, PZO 16374: **A1**, apertural view; **A2**, lateral view; **A3**, apical view; **A4**, detail apical view of early whorls, **arrow** indicates protoconch margin; **A5, A6**, detail of ornamentation; **A7**, crossed lamellar shell structure; **C**, PZO 16375: **C1**, apertural view; **C2, C3**, detail of ornamentation; **B**, *Angularia subpleurotomaria* (Münster, 1841) from Misurina, South Tyrol (Italy), PZO 16392. Scale bars: A1-A3, B, C1, 1 mm; A4, A7, C2, C3, 0.2 mm; A5, A6, 0.5 mm.

TABLE 4. — Protoconch measurements of *Angularia pleurotomaria* (Münster, 1841) (mm). Abbreviations: **DFW**, diameter of the first whorl; **DPC**, diameter of protoconch; **HPC**, height of protoconch; **WPC**, number of protoconch whorls.

SEM number	WPC	HPC	DPC	DFW
PZO 16372	2.7	0.33	0.33	0.12
PZO 16373	2.9	0.31	0.33	0.11
PZO 16377 (Fig. 8B)	2.9	0.32	0.34	0.11
PZO 16376 (Fig. 8A)	3.0	0.37	0.34	0.11

and teleoconch abrupt at sinusigera, clearly visible due to thickened opisthocyrt apertural margin; teleoconch consists of 5-7 angulated whorls separated by incised suture; angulation situated in the upper third of the whorls; shell surface concave above angulation and slightly convex below; on the ramp close to the adapical suture a spiral cord situated; shell surface ornamented with somewhat irregular axial ribs and numerous fine granulated spiral lirae forming a micro-ornament; abapical portion of the whorls ornamented with spiral grooves; aperture broken; pseudumbilicus partly covered by columellar lip; base weakly convex with grooves and evenly rounded transition to whorl face.

REMARKS

Kittl (1892) indicated an average of 20-24 axial ribs per whorl for this species. However, in his figure only about 14 ribs are present on the last whorl (Kittl 1892: pl. 6, figs 3-5). Therefore, the description refers to *Angularia pleurotomaria*, whereas the figure shows the new species *A. kittli* n. sp. For differences with the latter see below.

*Angularia kittli* n. sp.  
(Fig. 9C, D)

[urn:lsid:zoobank.org:act:D5E98955-903F-43F1-99B1-A68A9D4CA625](https://doi.org/10.21203/rs.3.rs-3111111/v1)

?*Loxonema latescalata* – Laube 1868: 65, pl. 24, fig. 21.

*Purpurina pleurotomaria* – Kittl 1892: pl. 6, figs 3-5.

?*Angularia (Purpurina) pleurotomaria* – Broili 1907: 106, pl. 9, fig. 33.

*Purpurina pleurotomaria* – Zardini 1978: 31, pl. 14, fig. 1; non fig. 2 that is true *Angularia pleurotomaria* (Münster).

MATERIAL EXAMINED. — **Holotype**. Italy • South Tyrol; Rumerlo; Carnian; Late Triassic; MPRZ No 1271 R-Z, illustrated in Zardini (1978: pl. 14, fig. 1).

DIAGNOSIS. — Shell cone-shaped, moderately high-spined, with gradate spire; teleoconch consists of at least five angulated whorls separated by incised suture; angulation situated in the upper third of the whorls; spiral cord situated close to the adapical suture; shell surface ornamented with strong, regularly spaced axial ribs crossed by spiral cords; aperture oval; pseudumbilicus partly covered by columellar lip; base weakly convex with evenly rounded transition to whorl face.

TYPE LOCALITY. — Italy, South Tyrol, Rumerlo.

DERIVATION OF THE NAME. — In honour of Ernst Kittl (1854-1913).

RANGE. — Carnian (Late Triassic) of Italy (Dolomites).

DESCRIPTION

Shell cone-shaped, moderately high-spined, with gradate spire; protoconch not preserved; teleoconch consists of five angulated whorls separated by incised suture; angulation situated in the upper third of the whorls; shell surface concave above angulation (ramp) and slightly convex below; on the ramp close to the adapical suture a spiral cord situated; shell surface ornamented with strong, regularly spaced axial ribs crossed by spiral cords; the number of axial ribs increases during the shell growth; aperture oval; pseudumbilicus partly covered by columellar lip; base weakly convex with evenly rounded transition to whorl face.

REMARKS

*Angularia kittli* n. sp. differs from *A. pleurotomaria* in displaying fewer axial ribs per whorl and in having spiral cords instead of grooves, while it differs from *A. subpleurotomaria* in having stronger axial ribs and distinct spiral ornamentation. *Angularia kittli* n. sp. differs from *Fossacerithium formosum* (Eichwald, 1868) in having thinner axial ribs and also their opisthocline direction (instead of prosocline in *F. formosum*). *A. kittli* n. sp. possesses also more spiral cords below the ramp, and a holostomatous aperture.

This species has been previously identified by Zardini (1978) as *Purpurina pleurotomaria* and according to him, it is quite common in the St. Cassian Formation – he lists more than 350 specimens.

Genus *Cretadmete*

Blagovetshenskiy & Shumilkin, 2006

TYPE SPECIES. — *Cretadmete neglecta* Blagovetshenskiy & Shumilkin, 2006, by orignal designation. Decheni Zone, Upper Hauterivian (Cretaceous), Slantsevyi Rudnik (Russia, Ulyanovsk Region).

DIAGNOSIS. — Shell small, fusiform; protoconch smooth, consisting of 2.5-3.0 convex whorls, separated from teleoconch by prominent commissure followed by convex whorls with distinct ornamentation; spiral ornamentation consists of numerous, narrow, somewhat flattened costulae; axial ornamentation consists of low, fairly wide, rounded costae, which vary in number from 14 to 25 on last whorl; axial costae bend more sharply in upper part of last whorl and flatten below; aperture semilunar; siphonal canal not separated from apertural margin (after Blagovetshenskiy & Shumilkin 2006).

SPECIES INCLUDED. — *Cretadmete piccua* (Beisel, 1983) and *C. gracillima* (Wollemann, 1903).

RANGE. — Late Jurassic (Late Oxfordian) to Early Cretaceous (Albian).

REMARKS

*C. ? conspicua*, *C. ? keyserlingiana* and *C. kostromensis* included into *Cretadmete* by Blagovetshenskiy & Shumilkin (2006) should be rather placed in *Maturifusus*. These species have more elongated apertures and their ornamentation is more similar to that of *Maturifusus*. Two specimens described as *Astandes kostromensis* by Beisel (1983: 76) have a “large protoconch with 2.5 smooth convex whorls” and besides, they differ significantly from the holotype as reported by Gerasimov

(1955: 196). We consider these two specimens to belong to a new species of *Cretadmete*, which simultaneously constitutes the oldest record of the genus (upper Oxfordian).

#### Genus *Fossacerithium* Gerasimov, 1992

TYPE SPECIES. — *Fusus formosus* Eichwald, 1868, by original designation. Oxfordian (Jurassic), Russia.

EMENDED DIAGNOSIS. — Shell fusiform; whorls angulated with adapical ramp; protoconch smooth, obtusely conical; the demarcation between the protoconch and the teleoconch is clearly visible, with a thickened apertural margin; shell surface ornamented with strong, wide axial ribs and weaker spiral cords; last whorl large; aperture oval with well pronounced anterior channel; columellar lip with callus covering umbilical area.

SPECIES INCLUDED. — *Fossacerithium formosum* (Eichwald, 1868) and *F. hypermeces* (Cossmann, 1913).

RANGE. — Jurassic (Callovian-Kimmeridgian).

#### REMARKS

Gerasimov (1992) erected the subgenus *Fossacerithium* for the Early Jurassic members of the genus *Paracerithium* (within the family Procerithiidae) with *Fusus formosus* Eichwald, 1868 as its type species, that he previously included in *Purpurina* (Gerasimov 1955: 179, pl. 39, fig. 12). Gerasimov (1992) provided only a brief characterisation of the new subgenus, which is, however, diagnostic enough to establish a new taxon. Since the type species of *Fossacerithium* differs significantly from the type species of *Paracerithium*, we accord full genus status to *Fossacerithium* and provide a more detailed emended diagnosis. The main character distinguishing *Fossacerithium* from *Paracerithium* is a very long siphonal canal, while species of *Paracerithium* have drop-shaped apertures reminiscent of Middle Jurassic rissoids, e.g. *Buignieria* Cossmann, 1921 (compare Kaim 2004 for *Buignieria* and Hikuroa & Kaim 2007 for *Paracerithium*). In addition to the type species, Gerasimov (1992) also included *Paracerithium* (*Fossacerithium*) *procerum* (Gerasimov 1992: 88). The latter is most likely a cerithiid, while *Paracerithium* (*Fossacerithium*) *formosum* belongs to purpurinids according to shell characteristics, including a large smooth, obtuse conical protoconch that is typical of this family (Kaim 2004: fig. 87). *Fossacerithium* differs from *Purpurina* in having an ellipsoidal peristome with well pronounced anterior channel and wide columellar lip with a callus covering its umbilical area. It differs from *Khetella* in shell outline, namely in having an angulation in the adapical portion of the whorls, a stronger spiral ornamentation and in the shape of the aperture.

#### *Fossacerithium formosum* (Eichwald, 1868) (Fig. 4E)

*Fusus formosus* Eichwald, 1868: 946, pl. 31, fig. 7.

*Fusus minutus* – Rouillier & Fahrenkohl 1849: 377, pl. 50, fig. 94 (non *Fusus minutus* Roemer 1836: 140).

*Purpurina formosa* – Gerasimov 1955: 179, pl. 39, fig. 12. — Kaim 2004: 108, fig. 87. — Kaim 2008: fig. 3h.

*Paracerithium* (*Fossacerithium*) *formosum* – Gerasimov 1992: 87, pl. 24, figs 1-5, 10.

?*Khetella formosiformis* Guzhov 2004: 526, pl. 8, figs 5-8.

?*Khetella formosa* – Guzhov 2004: 526, pl. 8, fig. 9.

*Khetella formosa* – Guzhov 2004: 526, pl. 9, fig. 1.

DESCRIPTION AND EMENDED DIAGNOSIS. — See Kaim (2004).

RANGE. — Middle to Late Jurassic of Russia and Poland.

#### REMARKS

Guzhov (2004: 524, pl. 8, fig. 8a) illustrated only one specimen of this species in apertural view with its aperture is eroded, so we attribute his material to the species with some doubt because the morphology of the aperture (oval with well pronounced anterior channel) is the main diagnostic character. On the other hand, the elongated body whorl, shell outline and inclined ramp strongly suggest that the specimen illustrated by Guzhov (2004) belongs to *Fossacerithium*.

Kaim (2004: 108) transferred the species to *Purpurina* stating that it differs significantly from the type species of *Paracerithium*, *P. acanthocolpum* Cossmann, 1902; the latter having much more slender shell, an angulation of the whorl instead of a subsutural ramp and a D-shaped peristome (compare Cossmann 1906; Gründel 1997; Hikuroa & Kaim 2007). He also abandoned the subgeneric name of *Fossacerithium* Gerasimov 1992, which we reinstate here as a full genus within the Purpurinidae.

#### Genus *Khetella* Beisel, 1977

TYPE SPECIES. — *Khetella bojarkae* Beisel, 1977, by original designation. Late Kimmeridgian (Jurassic), Levaja Bojarka River, northern part of Central Siberian Plateau, Russia.

EMENDED DIAGNOSIS. — Shell conical with weakly convex whorls; protoconch smooth and low-spined; demarcation between protoconch and teleoconch clearly visible; ornamentation consists predominantly of axial ribs; axial ribs sharply angulated in upper part of whorls forming distinct ramp and resulting in gradation of whorls; aperture D-shaped with anterior siphonal notch (compiled from Kaim & Beisel 2005 and Blagovetshenskiy & Shumilkin 2006).

SPECIES INCLUDED. — *Khetella bojarkae* Beisel, 1977, *K. incerta* (d'Orbigny, 1845), *K. makaryevensis* (Guzhov, 2004), *K. septentrionalis* (Tullberg, 1881), *K. ventrosa* Beisel, 1983, and *Khetella* sp. of Kaim & Beisel (2005) – the latter may represent a fully grown individual of *K. ventrosa* or a new undescribed species.

RANGE. — Late Jurassic (Callovian) to Early Cretaceous (Albian).

#### REMARKS

*Buccinum incertum* (d'Orbigny, 1845) depicted by Glazunova (1973: figs 1-5, 7) differs from the type species, *K. bojarkae*, in the smaller size and in having less pronounced spiral ribs (Beisel 1977). These differences could reflect intraspecific variability or preservation – the size difference of individuals

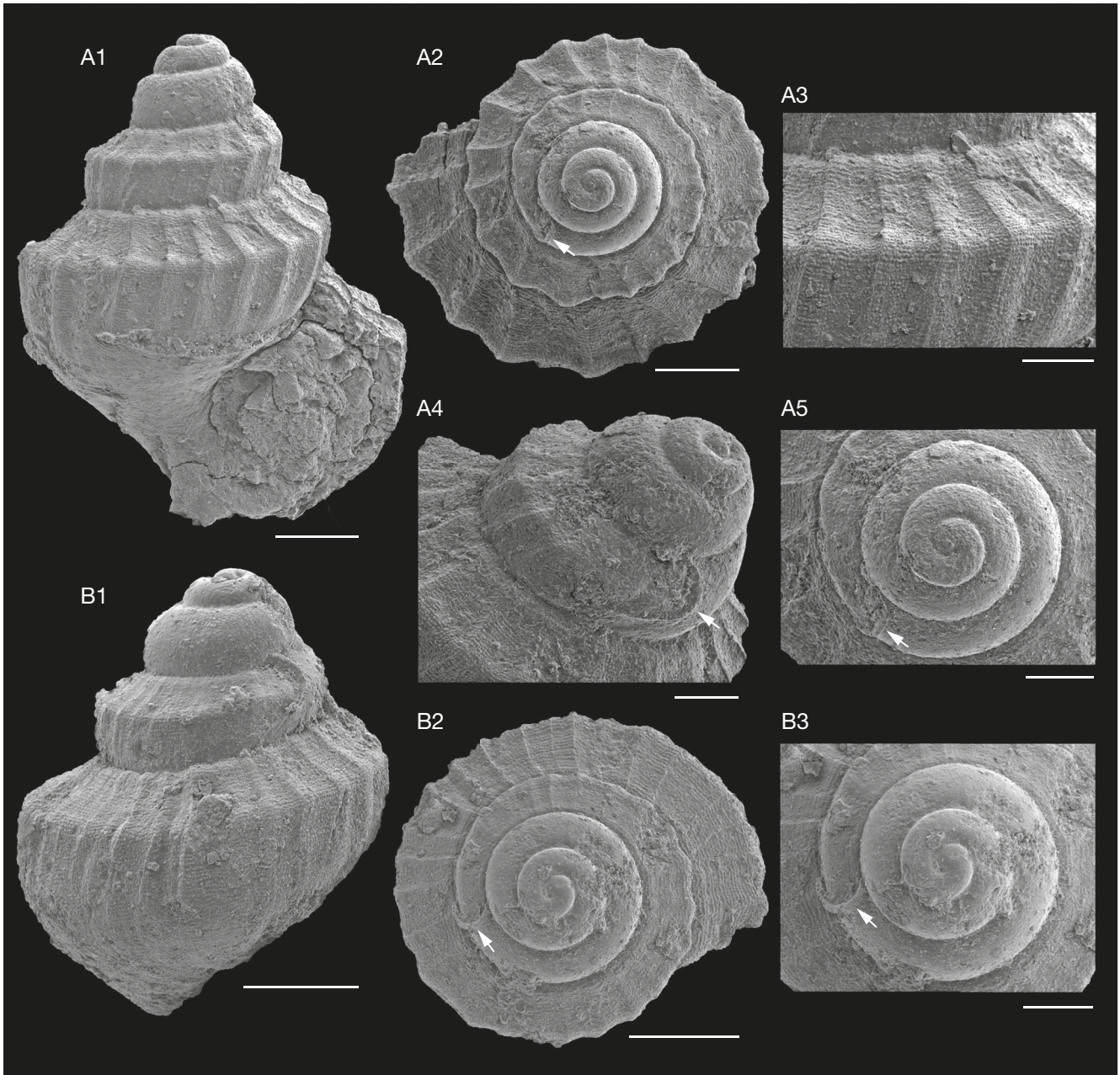


FIG. 8. — Juvenile shells of *Angularia pleurotomaria* (Münster, 1841) from the St. Cassian Formation, Carnian (Late Triassic), Costalaresc, South Tyrol (Italy): **A**, PZO 16376; **A1**, apertural view; **A2**, apical view; **A3**, detail of ornamentation; **A4**, detail view of early whorls; **A5**, detail apical view; **B**, PZO 16377, **B1** lateral view; **B2**, apical view; **B3**, detail apical view of early whorls. **Arrows** indicate protoconch margin. Scale bars: A1, A2, B1, B2, 0.2 mm; A3-A5, B3, 0.1 mm.

could also be ecophenotypical. According to Beisel's definition (1983: 75, pl.3, figs 16-17, 20), *K. ventrosa* is very similar to *K. incerta* in Glazunova's (1973) description and differs only in having a fine spiral ornamentation. This difference may be a result of imperfect preservation of the shell surface in Glazunova's (1973) materials of *K. incerta*. The new species variation of *K. incerta* var. *plana* described by Glazunova (1973: 81, pl. 43, fig. 6) cannot be attributed to the same genus as *K. incerta* according to its set of characters (most of all the elongated shell shape) and is reminiscent of some Cretaceous epitoniids (e.g. *Confusiscala* de Boury, 1909). The name itself is not available according to ICZN Code Art. 45.6.3.

Another species that can be included in *Khetella* is *Buccinum septentrionale* Tullberg, 1881 from the Late Jurassic (Oxfordian-Kimmeridgian) of Novaya Zemlya, Russia. Although its aperture is unknown, the ornamentation and gross shell morphology is typical of *Khetella* as already indicated by Guzhov (2004).

*Khetella brunsvicensis* (Wollemann, 1900: 174, pl. 8, figs 11, 12), included in *Khetella* by Beisel (1977), should be assigned to the genus *Purpurina* due to the distinct spiral ornamentation and its aperture morphology without distinct anterior channel. *K. ?gaultica* (d'Orbigny, 1842) that Beisel (1977, 1983) assigned to *Khetella* is based on a shell fragment of the last whorl (d'Orbigny 1842-1843: pl. 233, figs 1, 2), which

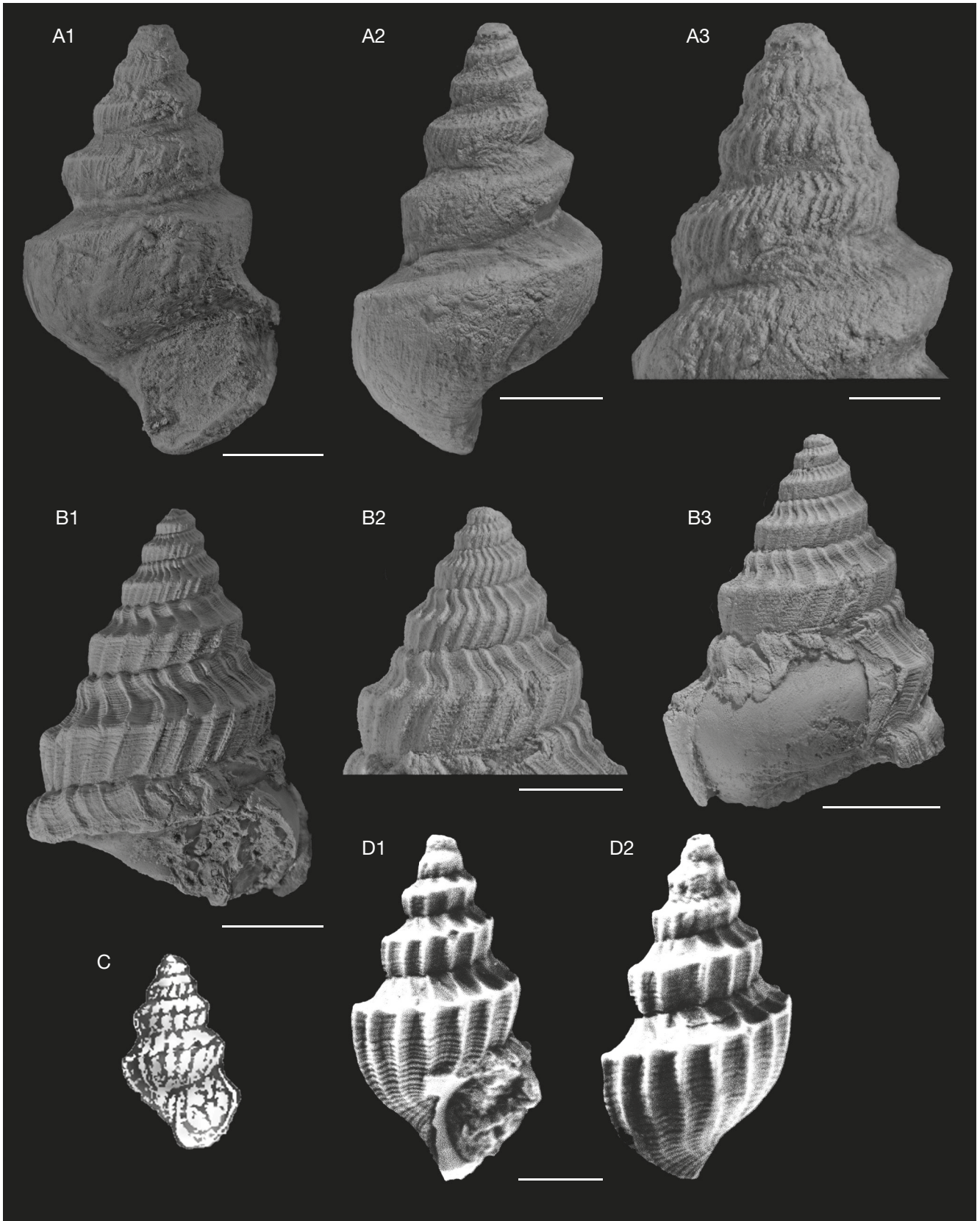


FIG. 9. — *Angularia* Koken, 1892 species from the St. Cassian Formation, Carnian (Late Triassic): **A**, *Angularia subpleurotomaria* (Münster, 1841) from Cassian beds, probably Stuoeres. Lectotype, SNSB-BSPG AS VII 1800: **A1**, apertural view; **A2**, lateral view; **A3**, detail view of early whorls; **B**, *Angularia pleurotomaria* (Münster, 1841) from Cassian beds, probably Stuoeres. Lectotype, SNSB-BSPG AS VII 1799: **B1**, apertural view; **B2**, detail view of early whorls; **B3**, lateral view; **C**, *Angularia kittli* n. sp. after original figure by Kittl (1892: pl. 6, fig. 3); **D**, specimen figured by Zardini (1978: pl. 14, fig. 1), holotype, MPRZ No 1271 R-Z: **D1**, apertural view; **D2**, lateral view. Scale bars: A1, A2, B1-B3, D, 2 mm; A3, 1 mm; C, size not given.

Kollmann (2005) identified as *Cosnia gaultina* (d'Orbigny, 1842) (Kollmann 2005: 152, pl. 11, fig. 6) and placed into the family Buccinidae. This specimen, however, is so fragmentary and poorly preserved that we refrain from discussing its generic or even familial position; it should be treated as a nomen dubium.

We assign the specimens illustrated by Guzhov (2004: pl. 8, figs 11, 12) and identified as *Khetella formosa*, to the family Maturifusidae because of their protoconch morphology (with two spiral ribs); they most likely belong to an undescribed new species. We think, that *Purpurina hypermece*s should be attributed to *Fossacerithium*, whereas *K. formosiformis* (Guzhov 2004: pl. 8, figs 5-9) should be placed in synonymy with *Fossacerithium formosum* based on protoconch morphology, ramp characters, shell shape and ornamentation. The separation of the new species *K. glasunovi* (Guzhov 2004: 530, pl. 8, figs 5-9) that was based on Glazunova's material attributed by her to *Buccinum incertum* (Glazunova 1973: 80, pl. 43, figs 1-7) is rather doubtful. *K. gradata* (Guzhov 2004: pl. 9, fig. 10a) should be assigned to the genus *Maturifusus* because of its gross shell morphology and possessing two spirals on the protoconch. *Fusus liasicus*, judging from the figure of Dumortier (1874: 163, pl. 37, fig. 11), possibly also belongs to *Maturifusus*.

The majority of species added by Blagovetshenskiy & Shumilkin (2006), based on illustrations from old monographs, most likely do not belong to the *Khetella* and require a detailed re-study. Blagovetshenskiy & Shumilkin (2006: 145, pl. 5, figs 1-4) also described a new species of *K. trautscholdi* and included to its synonymy the same taxa that were included by Guzhov (2004: 530) in the description of his new species of *K. glasunovi*. It seems therefore that *K. trautscholdi* should fall into the synonymy of *K. glasunovi*. This synonymization, however, should await a comprehensive review of entire material described by Glazunova (1973), Guzhov (2004), and Blagovetshenskiy & Shumilkin (2006) and its comparison to the type species of Beisel (1977).

#### Genus *Pseudoscalites* Kittl, 1892

TYPE SPECIES. — *Pseudoscalites elegantissimus* Klipstein, 1892 (in Kittl 1892), by original designation. Carnian (Triassic), South Tyrol (Italy).

EMENDED DIAGNOSIS. — Shell fusiform with elevated, gradate spire; whorls concave with pronounced angulation and carina; spiral ornamentation predominates over the axial; aperture broad with anterior and posterior canals.

SPECIES INCLUDED. — *Pseudoscalites elegantissimus* Klipstein, 1892 (in Kittl 1892), *P. cochlea* (Münster, 1841), *P. karapunari* Dominici, Danise & Tintori, 2024.

RANGE. — Triassic (Ladinian-Norian).

#### REMARKS

Haas (1953) attributed two specimens from the Late Triassic Pucara Group (Central Peru) to the genus, but they are more reminiscent of Eucyclidae. Nützel & Erwin (2004) described *Pseudoscalites* cf. *elegantissimus* from Wallowa Ter-

rane (Idaho, United States) and noted that their specimens are almost identical to the specimen illustrated by Bandel (1994: pl. 5, fig. 10). It is worth mentioning, that the specimen from Tyrol is three times smaller than material from Idaho and it remains uncertain whether it is of evolutionary or ecophenotypical importance.

#### DISCUSSION

In the first edition of the gastropod nomenclator by Bouchet & Rocroi (2005) Pseudotrioniidae were synonymized with Purpurinidae and placed in Littorinoidea, while Maturifusidae were placed in the Hypsgastropoda without allocation to any superfamily. In the second edition by Bouchet *et al.* (2017) Maturifusidae are synonymized with Pseudotrioniidae, while Purpurinidae are kept separately; both unassigned to any superfamily among Neogastropoda. It shows that the relationships between all these families have been in a state of flux in the last decades. One of the major obstacles for a clarification of the early evolution of Neogastropoda is the lack of data on the protoconch morphology of type species of type genera because this knowledge is crucial for the analysis of the higher level gastropod phylogeny (e.g. Thiriot-Quévieux 1972; Rodriguez Babio & Thiriot-Quévieux 1974). The mentioned families are extinct, so the identification of their relationships is based solely on comparative shell morphology. Various scenarios for the origin of Neogastropoda have been proposed, including a rather unlikely direct descent from Vetigastropoda or from Paleozoic siphonostomatous subulitids (Ponder 1973).

Certain members, such as the genus *Soleniscus* Meek & Worthen, 1861 or *Strobeus* de Koninck, 1881, of the heterogeneous essentially Paleozoic caenogastropod group Subulitoidea (Nützel *et al.* 2000) resemble the neogastropod ground pattern in having a siphonal canal and a fusiform shell shape. *Soleniscus* is wide spread in the Late Paleozoic and has a relatively large (> 1 mm), smooth conical larval shell (Nützel & Pan 2005). However *Soleniscus* has a smooth shell and lacks an angulation of the teleoconch whorls. Soleniscidae survived the end-Permian mass extinction but probably became extinct within the Early Triassic (Nützel 2005; Kaim *et al.* 2013) and it is unclear whether this family has later Mesozoic descendants.

In the last two decades, knowledge on the protoconch morphology of the members of the Mesozoic families Maturifusidae, Pseudotrioniidae, and Purpurinidae has increased significantly (Guzhov 2004; Kaim 2004; Nützel 2010), nevertheless, as outlined, the protoconchs of type species of potential ancestral neogastropod genera still remain unknown. However, differences between the known purpurinid and maturifusid types of protoconch are quite well constrained (see Figs 10; 11). All species of the monogeneric family Maturifusidae have highly conical multispiral protoconchs with convex whorls and two spiral ribs, one of which is situated near the abapical suture and the other above the middle part of the whorls. They display also an abrupt transition to the teleoconch (Figs 10D; 11). These characteristics may connect maturifusids to neogastropods,



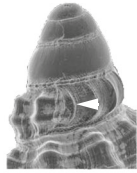


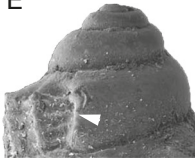



Age \ Taxa	Pseudotrioniidae	Purpurinidae	Maturifusidae	Neogastropoda
Recent	—			A 
Late Cretaceous				B 
Early Cretaceous				C 
Jurassic		E 	D 	
Triassic	G 	F 		

FIG. 10. — Comparison of protoconchs and their sizes of some neogastropod taxa and members of other families, which were proposed as neogastropod ancestors: **A**, the fascioliid *Latirus rugosissimus* (Locard, 1897), North Atlantic, Recent (Kaim 2004: fig. 82B); **B**, the pholidotomid *Paleopsephaea* sp., G2820-2, Tamil Nadu, India, middle Cenomanian (Late Cretaceous); **C**, Muricoidea gen. et sp. indet., Poland, Valanginian (Early Cretaceous) (Kaim 2004: fig. 82A); **D**, maturifusid *Maturifusus conspicuus* (Eichwald, 1868), ZPAL Ga. 9/325, Poland, Callovian (Middle Jurassic); **E**, *Fossacerithium formosus* (Eichwald, 1868), Poland, Callovian (Middle Jurassic) (Kaim 2004: fig. 87B<sub>3</sub>); **F**, *Angularia pleurotomaria* (Münster, 1841), PZO 16376, South Tyrol (Italy), Carnian (Late Triassic); **G**, *Pseudotrionium sciaphosterum* (Batten & Stokes, 1986), Utah (United States), Early Triassic (Nützel 2010: fig. 5.2b). **Arrows** indicate protoconch margin. All figures are given at the same scale. Scale bar: 0.5 mm.

most of which have an abrupt transition to the teleoconch and highly conical multispiral protoconchs (Figs 10A–C; 11). Also, the large size of the larval shell (1 mm height in the Early Jurassic *M. grimmensis*, see e.g. Nützel & Gründel 2015) suggests a relation to neogastropods since the larval shells of extant Neogastropoda are large. An affinity of maturifusids to modern buccinids (Neogastropoda) has been discussed by Szabó (1983) and Riedel (2000) identified *Maturifusus* as

derived caenogastropods. However, members of Maturifusidae differ by their gradate protoconchs ornamented with two strong spiral ribs, while neogastropod protoconchs usually have rounded whorls and a smooth or weakly ornamented shell surface. At the same time, maturifusid protoconchs are notably larger than the protoconchs of other Triassic and Jurassic caenogastropods, including cerithiids, which have similarly strong spirals on protoconchs.

The members of Purpurinidae have obtusely conical protoconchs with smooth convex whorls and clearly visible demarcation between protoconch and teleoconch expressed by thickened apertural margin. These characteristics connect the Triassic genus *Angularia* with Jurassic *Purpurina* (Figs 7; 8; 10E, F), whose protoconchs have been documented to date (Bandel 1993; Guzhov 2004; Kaim 2004).

Purpurinid protoconchs increased significantly in size (approximately four times) between the Triassic and Jurassic (see Fig. 10E, F). Extremely large sizes of Mesozoic (Jurassic) purpurinid protoconchs (Fig. 10E) may indicate that they are related to Cenozoic tonnoids (compare Craig *et al.* 2020; Fig. 11 herein). Molecular data have revealed a close relationship between Tonnoidea and Neogastropoda or even postulated inclusion of tonnoids to neogastropods (Osca *et al.* 2015; Harasewych *et al.* 2024) in a comparatively basal position, either alone or as a sister group of Volutidae or Cancellariidae (Cunha *et al.* 2009). This molecular evidence may support the earlier suggestions regarding their common origin (e.g. Haszprunar 1988). Thus, if ancestors of tonnoids are purpurinids, then maturifusids – should they be accepted as neogastropod ancestors – also have to be related to purpurinids with the common ancestor in the Triassic. Such an ancestor has not yet been reported so far.

Another possibility is that maturifusids are a group not closely related to Purpurinidae, and went extinct without direct descendants. In such a scenario both, tonnoids and neogastropods, could have evolved from purpurinids, with tonnoids separated from them in the Jurassic, perhaps in the Callovian. The comparison of *Khetella* (the oldest record known from the Early Callovian) and *Cretadmete* (Oxfordian-Albian) with alleged cancellariid *Paladmete* (described from the Upper Cretaceous by Sohl (1964) and Bandel & Dockery (2016)) and tonnoids (described from the Upper Cretaceous by Dockery (1993 and Eocene by Craig *et al.* (2020) and Recent (Bouchet & Warén 1993)) may support this assumption.

According to the current state of knowledge, the closest fossil relative to the hypothetical ancestor of neogastropods is *Fossacerithium* because it possesses a large protoconch and a well-developed anterior channel. The Jurassic *Fossacerithium formosum* is superficially similar in gross shell morphology to the Triassic *Angularia kittli* n. sp., but the latter lacks the derived character of the aperture (distinct anterior channel), which may have developed later in Jurassic forms. Regrettably, the protoconch of *Angularia kittli* n. sp. is unknown to date, therefore further collection effort is needed to substantiate its relations to the Jurassic *Fossacerithium*. Nevertheless, it can be assumed that purpurinids were divided into two groups in the Jurassic at the latest. One of these groups could be considered as the stem-group for Tonnoidea (*Khetella* and *Cretadmete*), while the other (*Fossacerithium*) could be seen as an ancestral form of Neogastropoda.

The protoconch of the type species of *Pseudotrironium*, the type genus of Pseudotrironiidae, is unknown. However, the protoconch of the Early Triassic species *Pseudotrironium sciaphosterum*

from the Moenkopi Formation of Utah (United States) is known (Nützel 2010; Fig. 11 herein). This species resembles *P. venustum* in gross shell morphology and cancellate teleoconch ornament. Nevertheless, the protoconch of *P. sciaphosterum* appears to be more similar to that of some recent Triphoroidea (for instance as in the cerithiopsid *Zachys* as depicted by Nützel 1998: pl. 2, fig. C) than to possible fossil ancestors of neogastropods or to their recent members. The protoconch of *P. sciaphosterum* is small (according to Nützel 1998 ca. three whorls 0.44 mm high and 0.27 mm wide). So, if both species of *Pseudotrironium* indeed belong to the same genus and/or family (that can be verified only if the protoconch of the type species will be found), evidence for a close relationship to the neogastropod lineage would be meager. It may also be speculated that heterobathy is observed here, where the larval stage exhibits plesiomorphic characteristics of an ancestral group, and the post-metamorphosis stage is apomorphic. Thus, the finding of the protoconch of *P. sciaphosterum* has added more controversy, because its morphology differs from those of members of the other families discussed earlier as well as from protoconchs of neogastropods.

In addition to their protoconch morphology (Fig. 11), the families in question differ from each other also in teleoconch characteristics. For instance, in the case of Maturifusidae the aperture is axially elongated with a rather long anterior canal (Fig. 2D, E), while Pseudotrironiidae have a wider aperture with a siphonal notch (Fig. 3). Members of Purpurinidae have a large, ovate holostomatous aperture in *Purpurina*. In *Khetella* and *Cretadmete*, the aperture is siphonostomatous with a short anterior channel and in *Fossacerithium* the anterior channel is well pronounced (Fig. 4).

Members of the families in question display also very uneven stratigraphic and geographic distribution. The majority of the Triassic records of Pseudotrironiidae and Purpurinidae come from the St. Cassian Formation which is result of the exceptional preservation of molluscs in these deposits, especially of small gastropods (see Roden *et al.* 2020). An exception is the oldest record of Pseudotrironiidae from the Early Triassic (Olenekian) of Utah (United States) (Batten & Stokes 1986; Nützel 2010). The oldest members of Purpurinidae were found in the Ladinian (Middle Triassic) and the last occurrence is known from the Albian (Early Cretaceous). Maturifusids appeared in the Early Jurassic (Late Pliensbachian) (Gründel 1999; Nützel & Gründel 2015; Schulbert & Nützel 2013) and became extinct by the end of the Late Jurassic, since the youngest record is known from the Early Kimmeridgian (Guzhov 2004). In addition to their uneven distribution, the number of their findings, even from rich tropical faunas like the one from the St. Cassian Formation, is extremely small. This could suggest, that they could have been top predators, what could explain their infrequent occurrence.

Therefore, based on the differences in shell morphology, especially on the aforementioned differences in protoconch morphology (Fig. 11), we consider all three families – Maturifusidae, Pseudotrironiidae, and Purpurinidae – as separate clades.

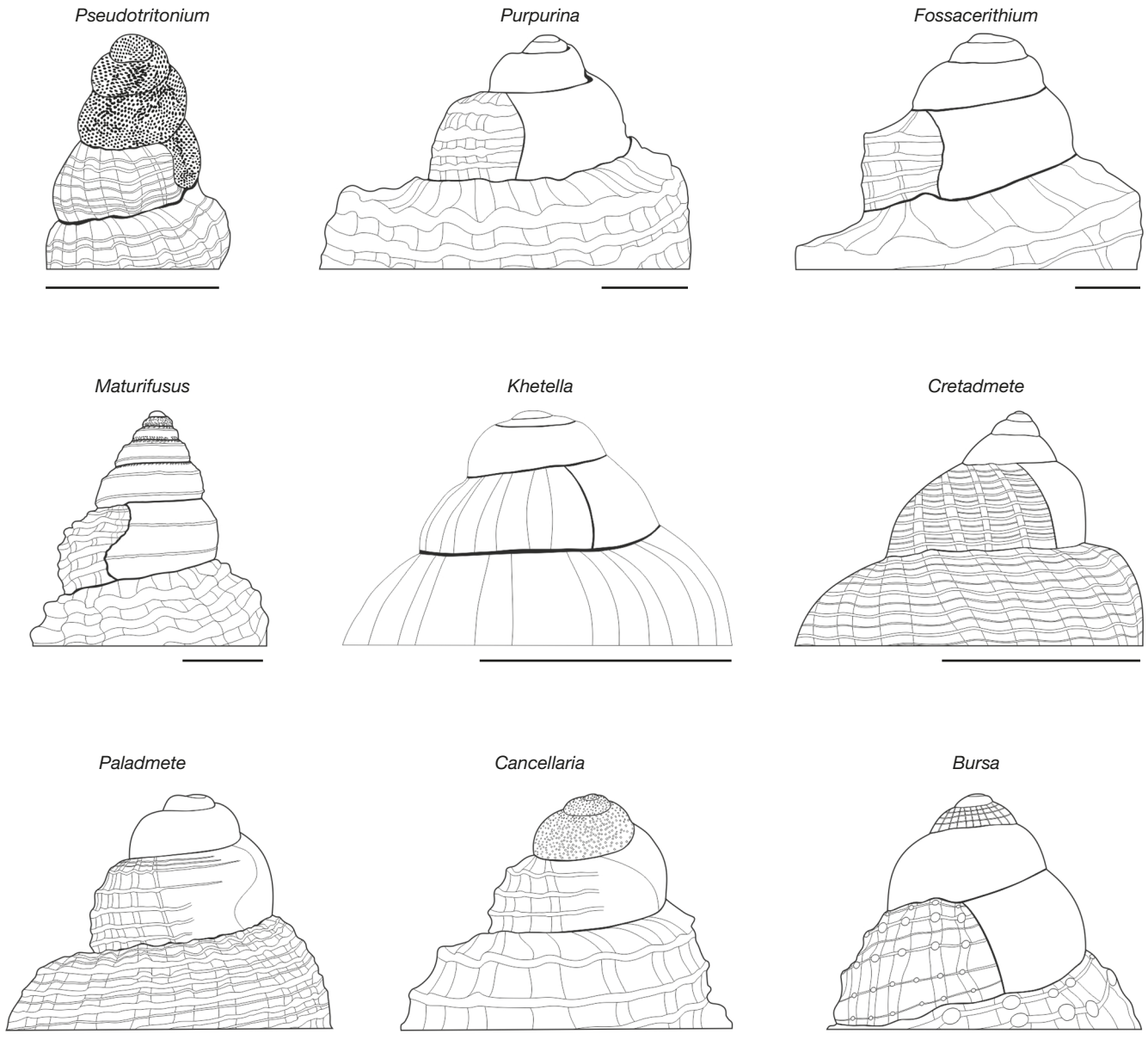


FIG. 11. — Main features of protoconch and early teleoconch in Pseudotritoniidae Golikov & Starobogatov, 1987, Maturifusidae Gründel, 2001, Purpurinidae Zittel, 1895, and crown Neogastropoda (Cancelariidae Forbes & Hanley, 1851) and Tonnoidea Suter, 1913 (1825) (Bursidae Thiele, 1925). *Pseudotritonium* Wenz, 1940 represented by *P. sciaphosterum* (Batten & Stokes, 1986) based on Nützel (2010) and unpublished photos. *Purpurina* d'Orbigny, 1850 based on *P. coronata* Hébert & Eudes-Deslongchamps, 1860 from Kaim (2004). *Fossacerithium* Gerasimov, 1992 based on *F. formosum* (Eichwald, 1868) from Kaim (2004). *Maturifusus* Szabó, 1983 based on unpublished photos of *M. ticurelatus* Gründel, 2001 from the Callovian of Łuków, Poland. *Khetella* Beisel, 1977 based on *K. bojarkae* Beisel, 1977 from Kaim & Beisel (2005). *Cretadmete* Blagovetshenskiy & Shumilkin, 2006 based on *C. neglecta* Blagovetshenskiy & Shumilkin, 2006 from Blagovetshenskiy & Shumilkin (2006). *Paladmete* Gardner, 1916 based on unpublished photos of *P. laevis* Sohl, 1964 from the Campanian of Coon Creek, United States. *Cancellaria* Lamarck, 1799 based on *C. corrosa* Reeve, 1856 from Petit & Harasewych (2013). *Bursa* Röding, 1798 based on *B. granularis* (Röding, 1798) from Sanders *et al.* (2017). Scale bars: 0.5 mm.

## CONCLUSIONS

Three extinct families considered herein – Maturifusidae, Pseudotritoniidae, and Purpurinidae – differ in taxonomic richness, stratigraphic distribution and morphological characteristics, especially in the protoconch morphology, which is crucial for the identification of high level taxa. We conclude, that all three should be kept as separate clades.

The generic composition of each family has been reviewed. The monogeneric family Maturifusidae ranges from Early to Late Jurassic (Pliensbachian-Kimmeridgian) and is represented by the following species: *Maturifusus densicostatus*, *M. conspicuus*, *M. caseus*, *M. grimmensis*, *M. keyserlingianus*, *M. kostromensis*, *M. szaboi*, *M. ticurelatus*, *M.?* *nassoides*, *M.?* *piettei* and *M.?* *zeisei*. The monogeneric family Pseudotritoniidae ranges from Early to Late Triassic (Olenekian-Carnian) and includes species: *Pseudotritonium venustum*, *P. laubei*, *P. milierensis*,

*P. sciaphosterum* and *P. avena*. The family Purpurinidae ranges from Middle Triassic (Ladinian) to Early Cretaceous (Albian) and includes the following genera: *Angularia*, *Cretadmete*, *Fossacerithium*, *Khetella*, *Pseudoscalites*, and *Purpurina*. The genus *Angularia* includes the following Middle to Late Triassic (Ladinian–Rhaetian) species: *A. subpleurotomaria*, *A. pleurotomaria*, *A. marginata*, *A. multinodosa*, *A. plicata*, *A. costata*, *A. rectecostata*, *A. corallina*, and *A. kittli* n. sp. The genus *Cretadmete* is represented by three Late Jurassic (Oxfordian) to Early Cretaceous (Albian) species: *C. neglecta*, *C. gracillima*, and *C. piccua*. Two species, namely *F. formosum* and *F. hypermece*, should be attributed to the genus *Fossacerithium*, which ranges from Middle to Late Jurassic (Callovian–Kimmeridgian). Genus *Khetella* ranges from Middle Jurassic (Callovian) to Early Cretaceous (Albian) and includes *K. bojarkae*, *K. incerta*, *K. makaryevensis*, *K. septentrionalis* and *K. ventrosa*. The genus *Pseudoscalites* is represented by three Middle to Late Triassic (Ladinian–Norian) species: *P. elegantissimus*, *P. cochlea*, and *P. karapunari*. The species composition of *Purpurina* is not revised here as it requires further detailed study of this species-rich genus and will be published elsewhere.

*Angularia kittli* n. sp. is described from the St. Cassian Formation and compared to other congeners found in the same formation, i.e., *A. subpleurotomaria* and *A. pleurotomaria*. The new species differs from the others in having a more pronounced axial ornamentation, which makes it similar to *Fossacerithium* from the Jurassic. However, the protoconch of *Angularia kittli* n. sp. is unknown, so that conclusions about its affinity requires confirmation by new specimens.

*Fossacerithium*, which originally was included into Procerithiidae by Gerasimov (1992), is confirmed to represent Purpurinidae.

*Paleotriton macrostoma* Kittl, 1894 from the Carnian (Late Triassic) of St. Cassian Formation classified so far as a species of *Pseudotritonium*, is reinterpreted here according to protoconch morphology and shell outline as the oldest record of *Purpurina* sensu stricto.

The morphological similarity between Jurassic purpurinids and recent tonnoids is suggestive of an evolutionary connection from the oldest species of *Khetella* and *Cretadmete* to the recent tonnoids, with the intermediate species of *Paladmete* from the Upper Cretaceous (Sohl 1964; Bandel & Dockery 2016) on the one hand and a number of tonnooid species from the Upper Cretaceous (Dockery 1993) and Eocene (Craig *et al.* 2020) on the other hand.

We also conclude that in the Jurassic, purpurinids were already divided into two groups. One of them, represented by *Khetella*, lead to Tonnoidea, while the other branch represented by *Fossacerithium*, could lead to Neogastropoda – a hypothesis, to be tested by future studies.

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