

PERMIAN NON-MARINE BIVALVES FROM THE COLLIO AND GUNCINA FORMATIONS (SOUTHERN ALPS, ITALY): REVISED BIOSTRATIGRAPHY AND PALAEOBIOGEOGRAPHY

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Abstract. Non-marine bivalves are key fossils in Permian continental stratigraphy and palaeogeography. Although known since the end of 19th century, the occurrences from the continental basins of the Southern Alps have never been extensively studied. The non-marine bivalves from the Lower Permian Collio Formation (Brescian pre-Alps) are herein revised, and those from the Guncina Formation (Athesian District) are described for the first time. These two units yielded non-marine bivalves belonging to the genus *Palaeomutela sensu lato*, which is widespread in the Permian continental successions of eastern Euramerica. Three *Palaeomutela* morphotypes have been herein described: oval-subtriangular, subtrapezoidal and elongated. The latter includes several specimens herein assigned to *Palaeomutela (Palaeonodonta) berrutii* sp. nov. and dominates the Collio Formation association. The Guncina Formation yielded also the genus *Redikorella*, for the first time co-occurring on the same stratigraphic horizon of *Palaeomutela*, herein assigned to *Palaeomutela (Palaeonodonta) guncinaensis* sp. nov. To-date, it was generally accepted that the first members of the genera *Palaeomutela* and *Redikorella* occurred during the Ufimian (late Kungurian of the global scale) in the non-marine basins of the Cis-Ural Foredeep and of Angara, respectively. Such new finds in the early-middle Kungurian of southwestern Europe, well constrained by radioisotopic dating, suggest new global first appearance (First Appearance Datum) and a possible new center of origin of these genera. This fact raises new questions on biostratigraphy, palaeobiogeography and palaeoecology, which will require further research. If we assume that the genera *Palaeomutela* and *Redikorella* had only one center of origin, we need to hypothesise possible migration routes from SW Europe to the continental basins of Eastern Europe and Angara. Apparently, such migration could be better supported by a Pangaea B palaeogeographic configuration.

INTRODUCTION

The non-marine bivalve genus *Palaeomutela* Amalitzky, 1892 gives the name to the so called *Palaeomutela* (or East European) Fauna, which is wide-

spread in the Permian continental successions of eastern Euramerica formed in the northern semiarid belt. Since the works of Amalitzky (1892, 1895), the genus *Palaeomutela* is well-known for its bipolar distribution, evidenced by the similarity among Upper Permian non-marine bivalves of Eastern Europe, South America (Brazil), and South Africa (Silantiev 2018; Guerrini et al. 2020).

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There are two different hypotheses on the origin of this genus: 1) from the heterodont family Anthracosiidae Amalitzky 1892, and 2) from the palaeotaxodont family Ctenodontidae Wörhmann, 1893 (Gusev 1990). Nevertheless, the origin of the genus as well as its marine ancestors are still uncertain.

According to a recent review (Silantiev 2018), the genus *Palaeomutela* sensu lato (s.l.) (Silantiev & Carter 2015) appeared at the end of the Kungurian (late Cisuralian). The first occurrences of this genus are known from the lower part of the predominantly continental Solikamsk Formation (Ufimian Stage of the Russian General Stratigraphic Chart – RGSC) of the Cis-Ural Foredeep. No radiometric dating of the Solikamsk Formation is available.

Traditionally, it is assumed that the origin and First Appearance Datum (FAD) of *Palaeomutela* is in the Cis-Ural Foredeep (Silantiev 2018). In this contribution, we describe the bivalve collections from the Collio and Guncina Formations of North Italy (Kungurian, late Cisuralian). These new data allow us to reconsider the hypotheses on the origin and first occurrence of this genus and shed light on the timing of the invasion of the genus *Palaeomutela* into the continental realm and its location, within the strike-slip basins of the Western European sector of the Variscan Chain.

GEOLOGICAL SETTING

The Collio Formation consists of siliciclastic and subordinate volcanic rocks and represents the most known Lower Permian continental unit from Italy (Cassinis et al. 2012; Marchetti et al. 2015a and references therein). This formation was deposited in the transtensional Collio Basin, situated between the Brescia and Trento provinces (Fig. 1). The Collio Formation is a 700-800-m-thick succession, which overlays the volcanic Lower Quartz Porphyries and is overlain by the alluvial Dosso dei Galli Conglomerate, with a transitional contact characterised by a coarsening-upwards trend (Fig. 1). The Collio Formation is divided in two members: the lower Pian delle Baste member and the upper Val Dorizzo member (Cassinis 2007; IS-PRA 2016), separated by the lowest volcanoclastic bed named Dasdana I (e.g. Breitkreuz et al. 2001).

The Pian delle Baste member is characterised by a fining- and thinning-upward trend, from massive coarse sandstone to fine-grained tabular sandstone and laminated mudstone, so from alluvial fan to sand sheet and lacustrine palaeoenvironments (e.g. Ori et al. 1988). The overlying Val Dorizzo member, mostly consisting of sandstone, is characterized by the occurrence of several volcanoclastic layers in its lower part (Dasdana beds), in the Val Dorizzo area.

Fossils of the Collio Formation are mainly vertebrate and invertebrate traces (Curioni 1870; Berruti 1970; Haubold & Katzung 1975; Ceoloni et al. 1987; Conti et al. 1991, 1997; Santi 2007; Contardi & Santi 2009; Avanzini et al. 2011; Marchetti et al. 2013a, 2013b, 2014, 2015a, 2018; Santi et al. 2020) and less abundant plant remains (Geinitz 1869; Remy & Remy 1978; Visscher et al. 2001), freshwater jellyfishes, bivalves and rare conchostracans (Curioni 1870, 1877; Berruti 1967, 1970; Conti et al. 1991; Marchetti et al. 2015a). Some palynological research was carried out by Clement-Westerhoff et al. (1974), Doubinger (in Cassinis & Doubinger 1991, 1992) and Pittau (in Cassinis et al. 2000).

The study of a palynomorph association from the Collio Formation allowed Cassinis & Doubinger (1991, 1992) to suggest a late Artinskian, Kungurian or early Ufimian age (according to the Russian General Stratigraphic Chart). The tetrapod footprint association is considered as a reference for the *Erpetopus* footprint biochron of Voigt & Lucas (2018), and indicates a late Artinskian-Kungurian age as well (e.g. Schneider et al. 2020). The Collio Formation is constrained between the radiometric ages (U–Pb system; MAT262 thermal ionisation mass spectrometer, ETH Zurich) of 283.1 ± 0.6 Ma of the underlying Lower Quartz Porphyries and 279.8 ± 1.1 Ma of the overlying Auccia Volcanite (Schaltegger & Brack 2007). Hence, the age of this unit is currently constrained in the early Kungurian of the International Chronostratigraphic Chart (ICC 2021/10, see also Permophiles, vol. 69, p. 43).

The Guncina Formation is a siliciclastic unit up to 250-m-thick, deposited in the prevalently volcanic Athesian District, a caldera complex extending for about 70 x 70 km between the Trento and Alto Adige/Südtirol provinces of N Italy (Fig. 1). The episodic breaks in the volcanic output may

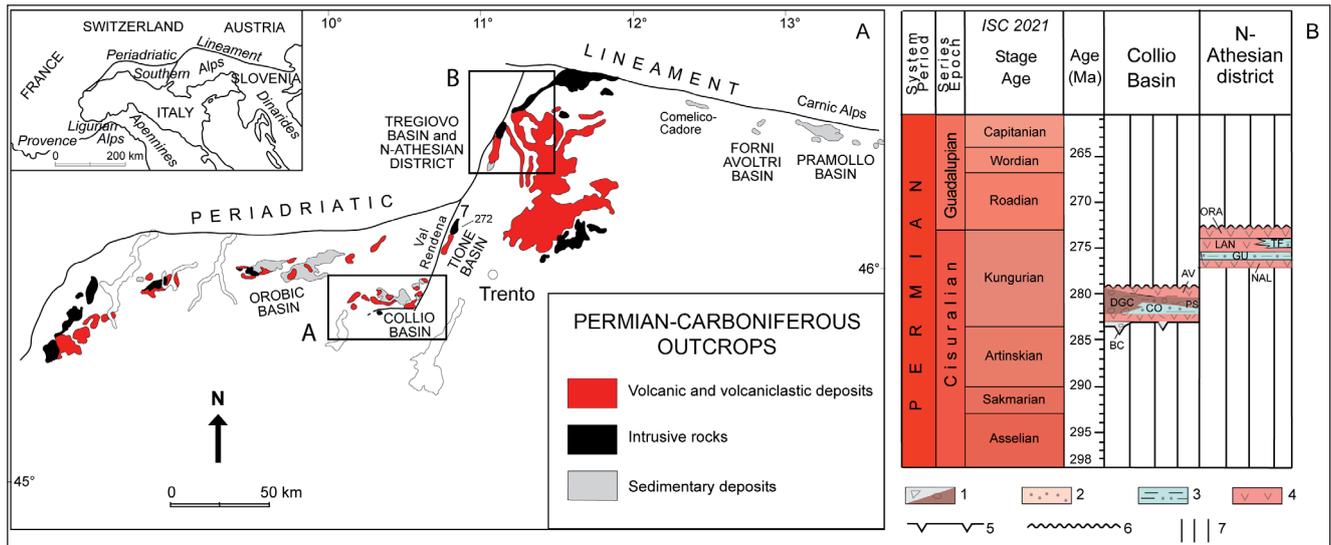


Fig. 1 - A) general and simplified distribution of the Late Carboniferous to Early Permian rocks in the Southern Alps, North Italy, and location of the basins subject of this work. A: Collio Basin; B: Tregiovo Basin and N-Athesian District). B) Selected and simplified Permian stratigraphic columns of the studied central-eastern Southern Alps basins. Lithostratigraphic units (from bottom): BC, Basal Conglomerate; CO, Collio Formation; DGC, Dosso dei Galli Conglomerate (PS, Pietra Simona Member); AV, Auccia Volcanics; TF, Tregiovo Formation; GU, Guncina Formation; LAN, Andriano Formation; NAL, Nalles Formation, ORA, Ora Formation. Legend: 1. Mostly conglomerates and breccias; 2. Mostly sandstones; 3. Mostly siltstones to mudstones; 4. Undifferentiated volcanic rocks. Other symbols: 5. Unconformity; 6. Erosional surface; 7. Stratigraphic gap.

have lasted few million years; the stasis is recorded by the formation of small sedimentary sub-basins with fluvial and lacustrine sediments that preserve plant remains, sporomorphs, conchostracans, bivalves, ostracods, trace fossils and tetrapod remains (e.g. Leonardi 1959; Remy & Remy 1978; Neri et al. 2000; Fritz & Krainer 2006; Avanzini et al. 2007, 2008, 2010; Marchetti et al. 2015b; Forte et al. 2017; 2018a, 2018b). The Guncina Formation crops out in the NW area of the Athesian District (Fig. 1), in the Val Adige between the village of Nalles and the town of Bolzano/Bozen. Matrix-supported conglomerates and breccias characterise both the base and the top of the unit. Medium- to coarse-grained sandstones are abundant. Anyway, medium- to fine-grained sandstones, siltstones and claystones occur locally and are occasionally interbedded with thin limestones and chert levels that preserve microspore and pollen grains (Krainer & Spötl 1998; Hartkopf-Fröder et al. 2001). According to Marocchi et al. (2008), the Guncina Formation is constrained between the U-Pb radiometric ages of 276.7 ± 1.1 Ma on the underlying Nalles Formation (rhyolitic ignimbrites) and of 274.2 ± 2.1 Ma on the overlying Andriano Formation (rhyolitic lavas). These radiometric ages correspond to the upper Kungurian of the ICC 2021/10.

FOSSIL LOCALITIES

The bivalves from the lacustrine deposits of the Collio Formation, collected by the priest Giovanni Bruni (1816-1880), were first mentioned by Curioni (1870) from the Pulpito locality of the Pian delle Baste member. In the sixties, bivalves were newly collected by Berruti (1967, 1970) from the Val Dorizzo member – informal member F of the Collio Formation of Cassinis (1966) – in the Laghetto Dasdana and Malga Dasdana Busa localities (identified with numbers 1, 2 and 3 of Berruti 1970), and studied by the same author with the contribution of Dr. Eva Paproth (Geologische Landesamt Nordrhein-Westphalen, Krefeld). Berruti (1970) hypothesised that these bivalves belong to the Permian genus *Palaeanodonta* Amalitzky, 1895; conversely, Dr. Eva Paproth assumed that these forms can be conditionally attributed to the Late Carboniferous-Early Permian genus *Anthraconia* Trueman & Weir, 1946. Both authors, in order to support their assumptions, used only the external features of the shells, so their conclusions can be considered as preliminary.

The mudstone deposits of the Guncina Formation include plant remains and bivalves, found in the Soprabolzano/Oberbozen locality and men-

tioned by Giannotti (1963). These plant remains have been later described by Remy & Remy (1978), while bivalves have never been described so far.

MATERIAL AND METHODS

Two collections of bivalves, both containing several dozens of specimens, have been studied.

The first collection, sampled by Berruti (1967, 1970), comes from the Val Dorizzo member of the Collio Formation (continental Collio Basin; Upper Trompia Valley, Laghetto Dasdana and Malga Dasdana Busa localities, Brescian pre-Alps, Lombardy); the second one was sampled by Giannotti (1963) and comes from the continental Guncina Formation (northwestern Athesian District, Soprabolzano/Oberbozen locality, Alto Adige/Südtirol province).

About 30 bivalve specimens have been photographed with high resolution and different magnification using a Wild M3B stereomicroscope, equipped with a Bresser MikroCamII 12MB digital camera. Later, the software Adobe Bridge and Adobe Photoshop were applied for both automatic focus stacking and lateral photo merging. Size information was obtained from additional photographs of all bivalves with scale bars attached. In some cases, the shell outline and main growth lines were reproduced with the software CorelDRAW Graphics Suite.

The bivalve taxonomy above the genus level follows Carter et al. (2011) and Silantiev & Carter (2011). The diagnosis, description, and discussion of Palaeomutelidae, genus *Palaeomutela*, and its subgenera are given according to Silantiev (2014) and Silantiev & Carter (2015). The diagnosis of *Redikorella* follows Silantiev (1994). The standard biometric parameters (H) height and (L) length were measured at different stages of shell growth: H1, L1, H2, L2, etc. (Fig. 2A). For different stages of shell growth, the height-to-length ratio (H/L) was calculated. The analysis of changes in the H/L ratio of the shell throughout their growth in length is an assessment of their isometric or allometric growth.

The description of subtriangular shells of the genus *Redikorella* includes the shell width (w) and the angle (α) between the dorsal margin and the main diagonal.

The description of additional external diagnostic features (initial shell and the intersection of the growth lines with the dorsal margin) is given according to Silantiev & Urazaeva (2017). The term “initial shell” designates the subumbonal part of the shell that is bounded by the first distinct line marking the start of the growth of the postlarval shell (dissoconch). The expression “the intersection of the growth lines with the dorsal margin” considers the morphology of all observed growth lines conjugated with the dorsal margin posterior to the umbo.

The bivalve collections are housed at the Museo Civico di Scienze Naturali of Brescia (Italy) (MCSNBS).

SYSTEMATIC PALAEOONTOLOGY

Order *Actinodontida* Douvillé, 1912

Superfamily Palaeomuteloidea Lahusen, 1897

(nom. transl. et correct. Silantiev & Carter, 2011:16
ex Palaeomutelidae Lahusen, 1897: 355)

The superfamily includes only the family Palaeomutelidae.

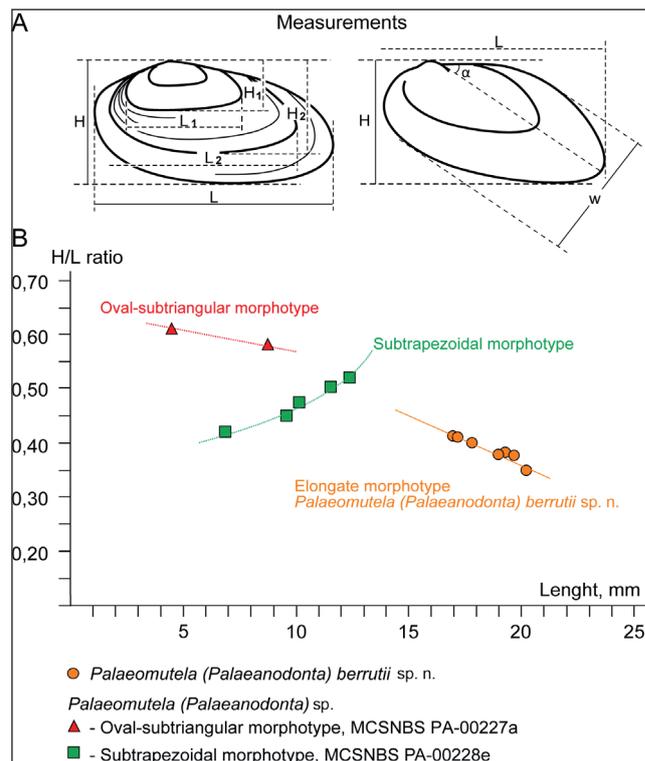


Fig. 2 - Height and H/L ratio plotted against length of shells of oval-subtriangular, trapezoidal and elongate *Palaeomutela* from Collio and Guncina formations. A) Standard biometric parameters of shells of non-marine bivalves: (L1, L2, L) shell length at different growth stages; (H1, H2, H) shell height at different growth stages; (w) shell width; (α) the angle between the dorsal margin and the main diagonal; B) dependence of the H/L ratio on the shell length.

Family Palaeomutelidae Lahusen, 1897 emend.

Silantiev, 2015 in Silantiev & Carter, 2015

Type genus: *Palaeomutela* Amalitzky, 1892a: 63 emend. Silantiev, 2014, Permian.

Diagnosis: Shell oval, *Unio*-like, lanceolate, varying in elongation, equivalve, inequilateral; ligament external, opisthodontic. The hinge plate is located in front of and behind the beaks; wide in thick-walled shells and narrow in thin-walled shells. Hinge pseudotaxodont, highly variable up to toothless. The teeth are lamellar and tuberculate; the number of teeth may be reduced to complete disappearance turning the hinged plate into a toothless one. The shells are composed mainly of aragonite. Varieties of cross-lamellar microstructure predominate. Ornamentation composed of thin dichotomizing growth lines and coarser growth folds.

Genera. *Palaeomutela* Amalitzky, 1892a emend. Silantiev, 2014, Permian, cosmopolitan; *Oligodontella* Gusev, 1963, Upper Permian, East Europe; *Neonuculites* Liang Zhong-fa, 1982, Upper Permian, north-eastern China and Inner Mongolia.

Genus *Palaeomutela* Amalitzky, 1892 emend. Silantiev, 2014

Type species: *Palaeomutela verneuili* Amalitzky, 1892; Middle–Upper Permian, Urzhumian and Severodvinian stages (Wordian–Carnian) of the East European Platform.

Diagnosis: Shells ranging from small to large-sized (from 5 mm to 10 cm long; on average 2 cm), oval, *Unio*-like, lanceolate, varying in elongation, equivalve, inequilateral; ligament external, opisthodontic; ligament groove distinct. Ornamentation composed of thin dichotomizing growth lines and coarser growth folds. Hinge pseudotaxodont. In thick-walled shells (1.5–3.0 mm thick), hinge plate differentiated into anterior and posterior branches (series) and umbonal region and having 20–50 curved lamellate and tuberculate teeth. Thin-walled shells (less than 1.5 mm thick) with less differentiated hinge area; number of teeth at most 20 and occasionally decreasing (subgenus *Palaeonodonta*) to complete disappearance.

Shells composed mostly of aragonite; calcite only fixed in thin upper part of external layer with simple prismatic structure. Variants of crossed lamellar microstructure prevailing, including branching commarginal (most of the external layer), radial (middle layer), crossed lamellar, and irregular complex crossed lamellar (internal layer).

Comparison. *Palaeomutela* is similar in external outline to the Carboniferous genera *Anthracosia* King, 1856 and *Carbonicola* McCoy in Sedgwick & McCoy, 1855, which have one or several cardinal teeth, differing from them in the pseudotaxodont hinge. It differs from the Carboniferous *Anthraconaia* Trueman & Weir, 1946, which have a duplivincular, slightly amphidetic ligament and lack hinge plate and teeth, in the external opisthodontic ligament and the hinge plate with (or reduced) pseudotaxodont teeth.

Remarks. *Palaeomutela* is very similar in external outline to elongate trapeziform (“atypical” anthracosiid-like morphotypes) specimens of *Anthraconaia*. For cases where the internal structure of the shells is not observed, Silantiev & Urazaeva (2017) suggested using several additional external features to differentiate *Palaeomutela* and *Anthraconaia*. Additional external features of *Anthraconaia* include: the initial shell is triangular in outline; growth lines are thin and smooth (non-dichotomous); the intersection of the growth lines with the dorsal margin is regular.

Additional external features of *Palaeomutela* distinguishing it from the *Anthraconaia* include an initial shell that is oval in outline, thin dichotomizing growth lines alternating with rougher growth folds; irregular intersection of the growth lines with the dorsal margin – one or more points of convergence of growth lines with the dorsal margin are usually observable.

Subgenera. *Palaeomutela* (*Palaeomutela*) Amalitzky, 1892 emend. Silantiev, 2015 in Silantiev & Carter, 2015; *Palaeomutela* (*Palaeonodonta*) Amalitzky, 1895 emend. nov. Silantiev, 2015 in Silantiev & Carter, 2015.

Subgenus *Palaeomutela* (*Palaeonodonta*) Amalitzky, 1895 emend. Silantiev, 2015 in Silantiev & Carter, 2015

Type species: *Unio castor* D’Eichwald, 1860; Middle Permian, Kazanian stage (Roadian) of the East European Platform.

Diagnosis: Thin-walled shells (less than 1.5 mm thick) with reduced pseudotaxodont hinge; hinge plate narrow, consisting of either two branches (anterior and posterior) or only one reduced posterior branch. Anterior branch with 1–5 tuberculate teeth. Posterior branch with 1–5 dental plates or tubercles. Distal part of posterior branch occasionally with relatively small subhorizontal plates resembling lateral teeth of heterodont hinges. Number of teeth in branches of hinge plate occasionally decreasing down to complete disappearance (toothless or edentulous hinge).

Species. About 50 species in the East European Platform and Cisuralian (Permian, upper Kungurian – Changhsingian), Western Europe (Lower Permian, Rotliegend), Salt Range of Pakistan, north-eastern China and Inner Mongolia, South Africa, Antarctica (for details see Silantiev & Carter, 2015).

Palaeomutela (*Palaeonodonta*) *berrutii* sp. nov.

Fig. 3; Tab. 1

Etymology: In honor of Giuseppe Berruti, expert of the geology of the Brescia Province and collector of the specimens housed at the Museo Civico di Scienze Naturali in Brescia (Italy).

Holotype: Internal mold of opened valves (butterfly shell) with partly preserved recrystallized shell layer (MCSNBS PA-00220d); Val Trompia, Dasdana; Collio Formation, Kungurian stage.

Material: Butterfly shell with recrystallized shell layers (MCSNBS PA-00220e); four internal molds of butterfly shells with partly preserved recrystallized shell material (MCSNBS PA-00220d – holotype; MCSNBS PA-00221a, the specimen is coated by glue; MCSNBS PA-00228a; MCSNBS PA-00235b); four internal molds of butterfly shells (MCSNBS PA-00220a; MCSNBS PA-00220b; MCSNBS PA-00221a; MCSNBS PA-00222d); internal mold of closed shell with partly preserved recrystallized shell layers in the hinge plate area (MCSNBS PA-00220c); composite molds of closed shells (MCSNBS PA-00228d); composite mold of butterfly shell (MCSNBS PA-00225a).

Type locality: Locality 1 (Dasdana) described by Berruti (1970); 45° 50' 57" N 10° 23' 02" E.

Occurrence: Upper part of the Collio Formation (Val Dorrizzo member); localities Laghetto Dasdana and Malga Dasdana Busa (Berruti 1967, 1970; Marchetti et al. 2015a).

Diagnosis: Small (length usually < 20 mm), elongate, transversely elliptical, with little or no obliquity of the antero-posterior axis. Umbones small, tapered, not rising above the long straight dorsal margin. Posterior margin tapered, obliquely asymmetrically rounded,

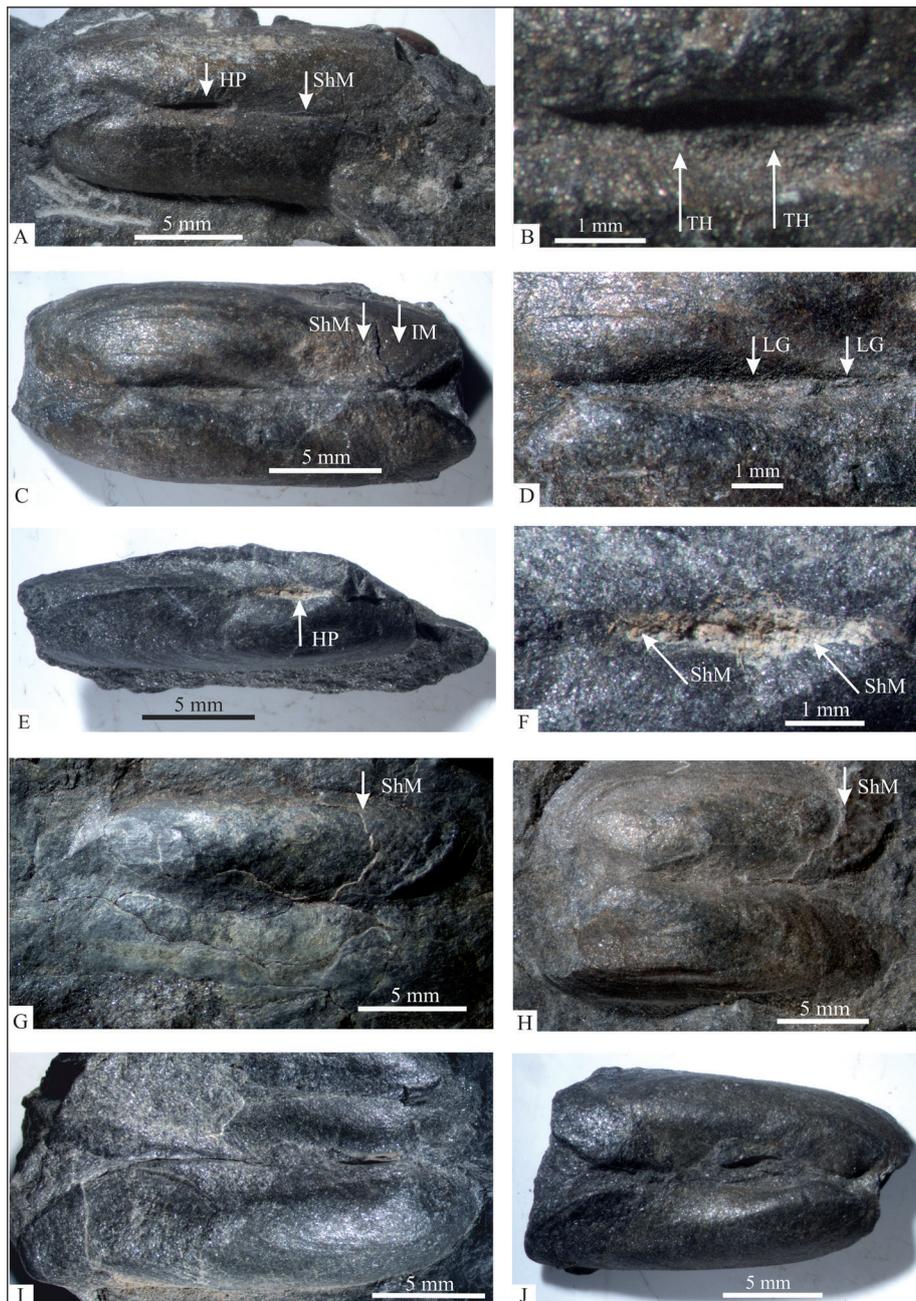


Fig. 3 - Non-marine bivalve *Palaeomutela (Palaeodontia) berrutii* sp. nov.; Collio Formation, Val Trompia, Dasedana locality.

A, B) Holotype, internal mold of butterflyed shell with partly preserved recrystallized shell layer (MCSNBS PA-00220d); (A) general view, imprint of the hinge plate (HP) and preserved recrystallized shell material (ShM); (B) enlarged hinge plate imprint with faint imprints of thin, plate-like (lamellar) pseudotaxodont teeth (TH). C, D) Butterflyed shell with recrystallized shell material (MCSNBS PA-00220e); (C) general view, the posterior end of the right valve is lacking shell material (ShM) and presents a fragment of the inner mold (IM); (D) enlarged portion of dorsal margin with the fragments of thin external, opisthodontic ligament (LG). E, F) Internal mold of closed shell with partly recrystallized shell material preserved in the hinge plate area (MCSNBS PA-00220c); (E) general view with the cavity of the hinge plate (HP); (F) enlarged portion of dorsal margin, cavity of the hinge plate possesses preserved shell material (ShM). G) Internal mold of butterflyed shell (MCSNBS PA-00235b); right valve with partly preserved recrystallized shell material (ShM). H) Internal mold of butterflyed shell (MCSNBS PA-00228a); right valve with partly preserved recrystallized shell material (ShM). I) Composite mold of butterflyed shell (MCSNBS PA-00225a); left valve is crushed. J) Internal mold of butterflyed shell (MCSNBS PA-00220a); dorsal margin is covered by rock material. Abbreviations: HP: hinge plate; HPc: cavity of the hinge plate; IM: inner mold; LG: ligament; ShM: shell material; TH: teeth.

MCSNBS	Length (L) mm	Height (H) mm	H/L
PA-00220a	17.9	7.2	0.40
PA-00220c	17.2	7.1	0.41
PA-00220d, holotype	17.0	7.0	0.41
PA-00220e	19.2	7.2	0.38
PA-00225a	20.1	7.1	0.35
PA-00228a	19.0	7.0	0.37
PA-00235b	19.7	7.1	0.36

Tab. 1 - Measurements of the non-marine bivalve *Palaeomutela (Palaeodontia) berrutii* sp. nov.

slightly truncated in upper posterior angle, passing without angulation into the long, uniformly convex curve of the ventral margin; the ventral curve passes without interruption but with shortening radius into the high, rounded anterior margin; the antero-dorsal margin slopes downward with a very shallow concavity to about a tenth of the height from the umbones. In both valves carina slopes obliquely from the umbo towards to the middle part of the posterior end; the length of the anterior end is about a fourth of the total length.

Anterior umbonal slope straight, inclined at 40°; H/L 0.35–0.41; convexity low.

Description. The holotype (MCSNBS PA-00220d) has two valves open and united at the hinge (butterflied) and is represented by internal mold

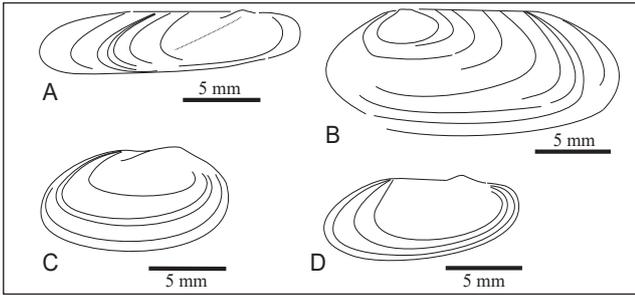


Fig. 4 - Irregular intersection of the growth lines with the dorsal margin of the non-marine bivalves from the Collio Formation, Val Trompia, Dasdana; at least one point of convergence of growth lines with the dorsal margin are observable. A) *Palaeomutela (Palaeanodonta) berrutii* sp. nov., right valve of the specimen MCSNBS PA-00220c illustrated in the Fig. 3 E; B) *Palaeomutela (Palaeanodonta) berrutii* sp. nov., left valve of the specimen MCSNBS PA-00228a; C) *Palaeomutela (Palaeanodonta)* sp., right valve of the specimen MCSNBS PA-00228e illustrated in the Fig. 5 D; D) *Palaeomutela (Palaeanodonta)* sp., right valve of the specimen MCSNBS PA-00228c illustrated in the Fig. 5.

with small fragment of preserved shell material (Fig. 3A). The left valve has an impression of the hinge plate which is located just behind the umbo and is about 3.0 mm in length and 0.5 mm in width. The surface of the hinge plate is covered with faint oblique grooves resembling the impressions of thin pseudotaxodont plate-like (lamellar) teeth (Fig. 3B).

The imprint of the hinge plate observed in specimen MCSNBS PA-00220c (Fig. 3E, F) is similar to that of the holotype in shape, position and size, but is infilled by altered shell material (Fig. 3 F).

The fragments of thin external, opisthodontic ligament are observable at the hinge of butterflyed specimen MCSNBS PA-00220e preserved in the mode of recrystallized shell (Fig. 3C, D).

The length of adult shells ranges from 15 to 20 mm, reaching the maximum length of 20.1 mm. The H/L ratio, ranging from 0.41 to 0.35, tends to decrease with the shell growth (Fig. 2B).

The initial shell is oval in outline generally resembles the adult shell. The ornamentation is represented by thin concentric dichotomizing growth lines. The intersection of the growth lines with the dorsal margin is irregular – at least one point of convergence of growth lines with the dorsal margin is observable (Fig. 4).

Comparison. The hinge plate which is located just behind the umbo and faint oblique grooves resembling the impressions of thin pseudotaxodont plate-like (lamellar) teeth distinguishes *P. (P.) berrutii* sp. nov. from the *Palaeanodonta* sp. described by Ea-

gar (2005, fig. 17, Pl. 2, fig. 42; collection of Dr. Eva Paproth, 1961) from the Lower Rotliegend of Northern Europe (Wahnwegen Shales).

Comparison of *P. (P.) berrutii* sp. nov. with other non-marine bivalves listed (e.g. Flügel, 1960) from the Lower Permian of western Europe requires a detailed re-examination of these collections (which have been described previously based on external features only) and may be carried out in future studies.

Remarks. In association with *Palaeomutela (Palaeanodonta) berrutii* sp. nov. there are several single specimens of bivalves whose features suggest that they belong to the same subgenus *Palaeomutela (Palaeanodonta)* but to other species. They are discussed below as morphotypes.

The oval-subtriangular morphotype is represented by specimen MCSNBS PA-00227a (Fig. 5A–C). The shell is 8.7 mm in length and 5.1 mm in height; the H/L ratio is 0.59. The external outline is oval-subtriangular, with a narrowly rounded posterior margin tends to decrease very slightly (up to 5 %) with the shell growth (Fig. 2B). Dorsal view of the partially fractured hinge margin shows the cavity of the relatively thick hinge plate (Fig. 5C). This morphotype differs from *P. (P.) berrutii* sp. nov. in having a shorter subtriangular shell and a higher H/L ratio.

The subtrapezoidal or *Unio*-like morphotype is represented by specimen MCSNBS PA-00228e. The shell is 12.2 mm in length and 6.3 mm in height; the H/L ratio is 0.51. The external outline is subtrapezoidal, moderately elongated, with a slightly oblique posterior margin. The H/L ratio of the specimen increases from 0.42 to 0.51 (up to 15 %) with the shell growth, demonstrating the growth trend opposite to that of *P. (P.) berrutii* sp. nov. (Fig. 2B). Preserved recrystallized shell material is covered by a concentric dichotomous sculpture. The intersection of the growth lines with the dorsal margin is irregular – one point of convergence of growth lines with the dorsal margin is observable (Fig. 4C).

The collection contains two more elongate specimens that confidently differ from *P. (P.) berrutii* sp. nov. in the character of the posterior end of the shell. In one case the shell expands backwards (MCSNBS PA-00228c; Fig. 4 E; Fig. 5 E), in the other case the shell narrows backwards (MCSNBS PA-00228d; Fig. 5 F). The significance of these fea-

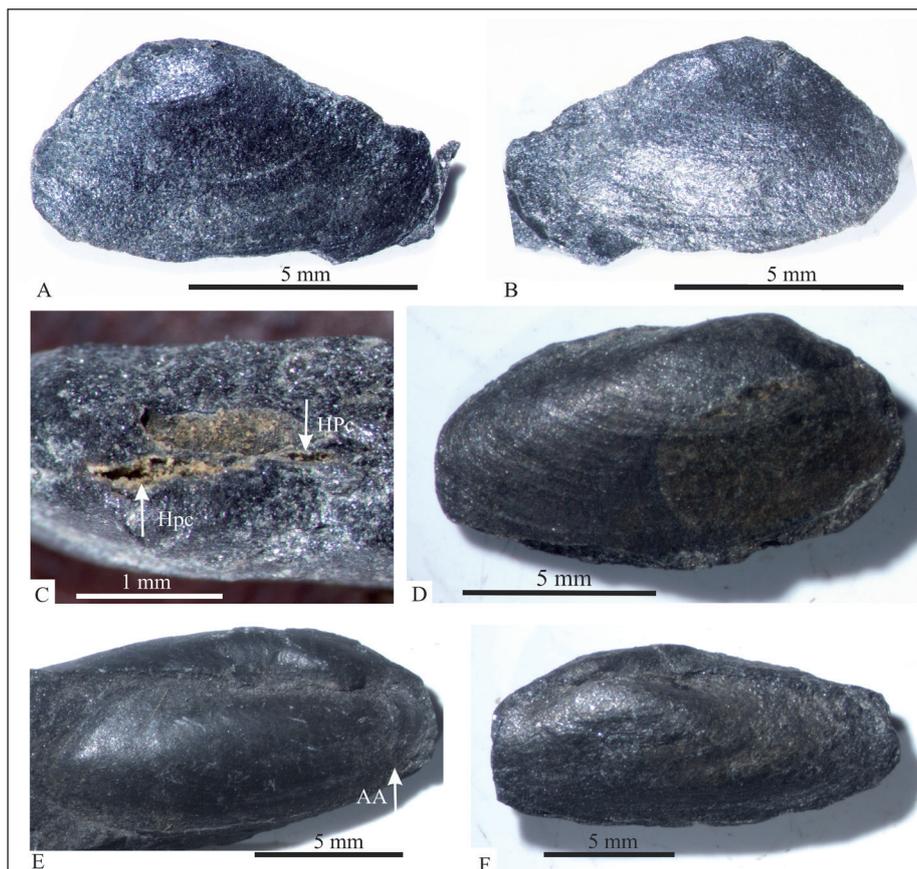


Fig. 5 - Non-marine bivalve *Palaeomutela (Palaeonodonta)* sp.; Collio Formation, Val Trompia, Dadsana. A-C) Oval-subtriangular morphotype, internal mold of closed shell (MCSNBS PA-00227a): (A) left valve; (B) right valve; (C) cavity of relatively thick hinge plate (HPc). D) Subtrapezoidal or *Unio*-like morphotype (MCSNBS PA-00228e); left valve with preserved recrystallized shell material; a concentric dichotomous sculpture is observed on the posterior part of the valve. E) Elongate morphotype with expanded posteriorly shell (MCSNBS PA-00228c); crescent-shape imprint of anterior adductor (AA). F) Elongate morphotype with narrowed posteriorly shell, composite mold (MCSNBS PA-00228d). Abbreviations: AA: anterior adductor; HPc: cavity of the hinge plate.

tures requires further investigation in more representative material.

The elongated morphotype from the Collio Formation established herein as *P. (P.) berrutii* sp. nov. is represented by the largest number of specimens. This is the morphotype described, illustrated and biometrically measured by Berruti (1970, p. 23–26, figs. 8–9). Berruti (1970) preliminarily referred this morphotype to the ‘edentulous’ genus *Palaeonodonta* Amalitzky, 1895. Conversely, Dr. Eva Paproth (personal comm. in Berruti 1970) provisionally assigned the Collio bivalves to the genus *Anthraconaia* Trueman and Weir, 1946. The genus *Palaeonodonta* Amalitzky, 1895 is currently regarded as a subgenus of *Palaeomutela* Amalitzky, 1892 emend. Silantiev, 2014. In the present study, the differentiation between *Anthraconaia* and *Palaeomutela* is discussed earlier in the description of the genus *Palaeomutela*.

***Palaeomutela (Palaeonodonta) guncinaensis* sp. nov.**

Fig. 6A, B; Tab. 2

Etymology: Named after the fossil-bearing unit, the Guncina Formation.

Holotype: Internal mold of right valve with partly preserved shell material (MCSNBS PA-00067a); locality Soprabolzano/Oberbozen (=Nop), 46° 31' 17.4" N, 11° 22' 50.1" E, Athesian District, Italian Southern Alps; Guncina Formation, Kungurian Stage.

Material: Holotype MCSNBS PA-00067a.

Type locality and occurrence: The same as the holotype.

Diagnosis: Small, moderately elongate, subtrapezoidal, with no obliquity of the antero-posterior axis. Umbones broadly based, not rising conspicuously above the straight dorsal margin. Posterior end blunt, with symmetrically rounded margin, not truncate. Ventral margin straight, passes with obtuse angulation into rounded anterior margin. Anterior end is about a fourth of the total length, with low, rounded lobe well defined by the concavity of the anterior umbonal slope inclined at 30°. Carina is absent. H/L 0.44; convexity very low.

Description. The holotype is an internal mold of right valve with partly preserved shell material (Fig. 6A, B; MCSNBS PA-00067a). The shell is 12.0 mm in length and 5.3 mm in height; the H/L ratio is 0.44. The anterior part of hinge plate is observed as impression just behind the umbo and is about 2.0 mm in length and 0.4 mm in width; the posterior

MCSNBS	Length (L), mm	Height (H), mm	H/L
PA-00067a	12.0	5.3	0.44

Tab. 2 - Measurements of the non-marine bivalve *Palaeomutela (Palaeonodonta) guncinaensis* sp. nov.

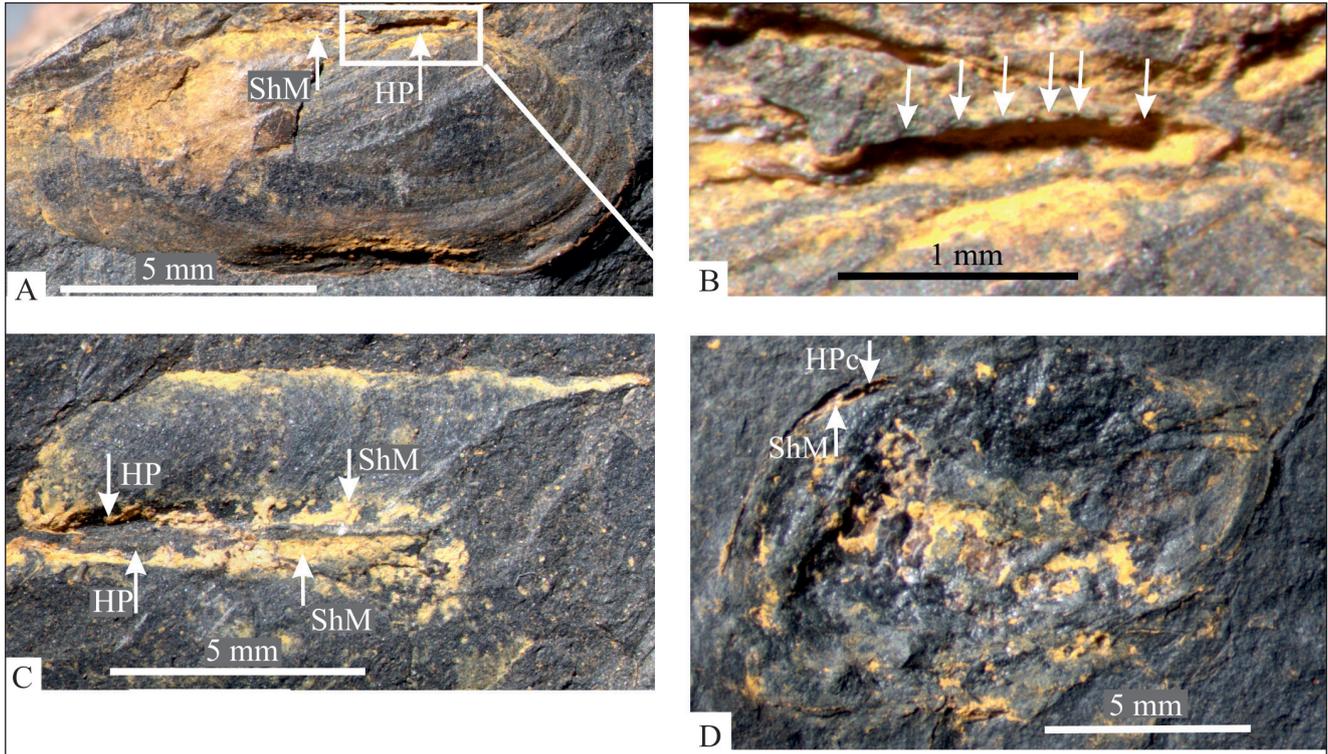


Fig. 6 - Non-marine bivalves from Guncina Formation. A, B) Non-marine bivalve *Palaeomutela (Palaeonodonta) guncinaensis* sp. nov.; holotype (MCSNBS PA-00067a), internal mold with partly preserved shell material (brownish yellow); (A) general view; (B) imprint of hinge plate (HP) with a row of small faint rounded impressions representing the imprints of node-like pseudotaxodont teeth (white arrows); the posterior part of the hinge plate is hidden beneath the brownish-yellow shell material (ShM). C) Non-marine bivalve *Palaeomutela (Palaeonodonta)* sp. (MCSNBS PA-00073e), fragmentary umbonal area of butterflyed shell; internal mold with shell material (ShM) preserved on the relatively broad and elongate hinge plate (HP). D) Non-marine bivalve *Redikorella* sp., internal mold (MCSNBS PA-00073a), right valve; cavity of the hinge plate (HPc) with preserved shell material (ShM). Abbreviations: HP: hinge plate; HPc: cavity of the hinge plate; ShM: shell material.

part of the hinge plate is hidden beneath the brownish-yellow shell material, the total length of the hinge plate is approximately 4 mm.

The surface of the hinge plate impression possesses a row of small faint rounded impressions representing the imprints of node-like pseudotaxodont teeth (Fig. 6B).

The H/L ratio of the holotype MCSNBS PA-00067a decreases from 0.46 to 0.44 (about 4.5 %) with the shell growth. The surface of internal mold preserves the ornament of concentric dichotomous growth lines.

Comparison. *P. (P.) guncinaensis* sp. nov. differs from *P. (P.) berrutii* sp. nov. by moderately elongate shell, broadly based umbones, blunt and symmetrically rounded posterior end, low anterior lobe and carina lacking.

Remarks. In association with *P. (P.) guncinaensis* sp. nov. there are several specimens of bivalves in fragmentary preservation (Fig. 6C, D). The relatively broad and elongate hinge plate (Fig. 6C), broadly based umbones and thin concentric dichotomizing

growth lines (Fig. 6D) suggest assigning these specimens to the subgenus *Palaeomutela (Palaeonodonta)*.

Order **Cardiida** Férussac, 1822 in 1821–1822
 Suborder **Anthracosiidina** Silantiev & Carter, 2011
 Superfamily Prilukielloidea Starobogatov, 1970
 Family Senderzoniellidae Betekhtina, Starobogatov,
 & Jatsuk, 1987
 Genus *Redikorella* Silantiev, 1994

Type species: *Redikorella kanevi* Silantiev, 1994; Lower Permian, Solikamskian regional stage, upper part; Kungurian stage; Cis-Ural Foredeep.

Diagnosis: Shell elongate sub-triangular (antraconautiform), sub-rectangular, sub-oval, equivalved, relatively thick, multi-layered. The closed opisthodontic ligament is located in a strong elongate ligament groove which is placed between the dorsal margin and the hinge plate. Hinge plate with many (10–30) small teeth which have a form of thin straight or slightly curved parallel plates; the angle between the teeth and the dorsal margin is 40°–80°. Sometimes, the teeth of the distal part of hinge plate have the shape of irregular curved nodes. Ornamentation of more or less regularly alternating coarse and fine concentric growth lines; internal molds sometimes with very thin radial striae.

Microstructure. Aragonite shell with a well-defined, relatively thick outer layer irregular simple prismatic (ISP); the structure of the middle and inner layers is laminar, matte or nacreous (the available SEM images do not allow exact determination). The absence of extended layers in the inner layer suggests a matte structure, but this could also be due to diagenesis.

Comparison. *Redikorella* differs from externally similar (subtriangular) genera of Naiaditidae, occurring in the Upper Palaeozoic of Eurasia, by the relatively thick multilayered shell, well defined ligament groove and hinge plate with pseudotaxodont teeth.

Species. Four species – *Redikorella kanevi* Silantiev, 1994; *R. alta* (Pogorevitsch), *R. explanata* (Kanev), *R. starobogatovi* (Kanev) in the Cis-Ural Foredeep, East-European Platform and Pechora Coal Basin; Permian (upper Kungurian) Solikamskian regional stage, upper part.

Redikorella sp.

Fig. 6E, F; Tab. 3

Material: Internal mold of closed shell with partly preserved shell material (MCSNBS PA-00073a); locality Soprabolzano/Oberbozen (= Nop), Athesian District, Italian Southern Alps; Guncina Formation, Kungurian stage.

Description. Shell sub-triangular (anthraconautiform), equivalved, relatively thick, slightly deformed (impressed). Initial shell angularly rounded. The angle between dorsal margin and main diagonal (α) is 45° ; the postero-dorsal angle is slightly rounded with a curvature of about 115° . A small cavity, observed on the posterior end of a dorsal margin (Fig. 6F), allow suggesting the presence of a hinge plate. Shell material is preserved on the distal (posterior) end of hinge plate where it turns to the posterior margin of the shell.

Ornamentation of fine concentric growth lines is preserved on the anterior part of the shell.

Remarks. There are no reliable data on the occurrence of subtriangular non-marine bivalves in the Permian deposits of Western Europe. Therefore, it seems important to describe and illustrate this form.

The cavity of suggested hinge plate differs this specimen from externally similar (subtriangular) Naiaditidae.

MCSNBS	Length (L) mm	Height (H) mm	Width (w) mm	H/L	w/L
PA-00073a	13.5	9.0	10.0	0.67	0.74

Tab. 3 - Measurements of the non-marine bivalve *Redikorella* sp.

SYSTEMATICS: ADDITIONAL REMARKS ON TAPHONOMY AND PRESERVATION

Collio Formation

As regards the collection from the Collio Formation, most of bivalves come from a thin layer of black mudstone, occurring in the upper part of the succession (Val Dorizzo member), in the localities Laghetto Dasdana and Malga Dasdana Busa (Berruti 1967, 1970; Marchetti et al. 2015a). Bivalves are represented by external, internal and/or composite molds of either closed or open (butterflied), at various degrees, shells.

Non-marine bivalves from the Collio Formation are partly preserved in “composite molds”. McAlester (1962) proposed this term to describe a preservation in which the original shell material is dissolved, and the imprints of the internal and external surfaces of the shell are compacted together and, therefore, visible on the same bedding plane. According to Bambach (1973, p. 410) “...composite molds occupy no volume and are only single impression surfaces, which reflect both external and internal features of the shell.” Composite mold fossils are formed in the early stages of sediment compaction. They become deformed along with the host rock during subsequent plastic deformation. A preservation as composite molds suggests that the original shells were dominantly or entirely composed of aragonite (McAlester 1962).

The bivalve assemblage of the Collio Formation contains three morphological types externally differentiated from each other by shell elongation, which is reflected by a different H/L ratio: 1) oval-subtriangular (H/L = 0.55 – 0.62), 2) subtrapezoidal or *Unio*-like (H/L = 0.42 – 0.52), and 3) elongated (H/L = 0.30 – 0.45). The elongation of the latter morphotype is not the result of post-burial deformation, because the elongation does not show preferential orientation compared to the bedding plane, whereas the tectonic deformation is necessarily orientated.

Berruti (1970, p. 26) provides the following description of the elongated morphotype (translated from Italian): “Shells equivalve, inequilateral,

elongated, expanded posteriorly, slightly inflated, the umbo is small, the carina is distinct and descends to the middle part of the posterior margin, which is slightly widened; the anterior margin is lowered and has the shape of a tongue; the ventral margin is curved. The ornament is represented by thin concentric growth lines”.

Berruti (1970) preliminarily referred these bivalves to the ‘toothless’ genus *Palaeonodonta* Amalitzky, 1895. Conversely, Dr. Eva Paproth (personal comm. in Berruti 1970) provisionally assigned the Collio bivalves to the genus *Anthraconaia* Trueman and Weir, 1946.

As it was recently stated by Silantiev & Carter (2015), several important internal and microstructural features of *Palaeonodonta* (i.e., external opisthodontic ligament, reduced pseudotaxodont hinge, crossed lamellar shell microstructure) allow to recognise it as a subgenus within the genus *Palaeomutela* Amalitzky, 1892.

A modern view on the relationships of *Palaeomutela* (*Palaeonodonta*) Amalitzky, 1895 and *Anthraconaia* Trueman & Weir, 1946 is discussed in detail by Silantiev & Carter (2015). We note that the presence of cavities resembling a relatively thick hinge plate exclude the assignment of the Collio forms to the genus *Anthraconaia*.

On the other hand, a thickening of the dorsal margin directly behind the umbones distinguishes these forms from the “*Palaeonodonta*” described by Eagar (2005, fig. 17, Pl. 2, fig. 42) from the Lower Rotliegend of Northern Europe (Wahnwegen Shales, coll. Dr. Eva Paproth 1961; Eagar 2005).

We highlight some features in the description of all of these three morphotypes, which indicate that they belong to the genus *Palaeomutela* Amalitzky, 1892 emend. Silantiev, 2015: 1) the cavity resembling a relatively thick hinge plate (MCSNBS Dasdana PA-00220c; PA-00220d; PA-00220e; PA-00225a; PA-00227a), with the poorly preserved imprints of plate-form teeth (Dasdana PA-00220c); 2) the poorly preserved imprint of the external ligament groove (PA-00220d; PA-00220e); and 3) the concentric dichotomous sculpture (PA-00228e).

We should stress that microstructures of the bivalve shell from the Collio Formation are not preserved. Complex crossed-lamellar microstructure is a very important feature of the genus *Palaeomutela*, although this is not necessary for an assignment to this genus.

Nevertheless, from all the above-described diagnostic features, we assigned these forms to the genus *Palaeomutela* Amalitzky, 1892 emend. Silantiev, 2015. Several specimens of the elongated morphotype are herein assigned to *Palaeomutela* (*Palaeonodonta*) *berrutii* sp. nov. In the Cis-Ural Foredeep, the earliest *Palaeomutela* s.l. appears in the geological record in the uppermost part of the Kungurian (Silantiev 2014) representing a well-formed assemblage with a wide range of morphotypes.

Guncina Formation

The bivalve collection of Giannotti (1963) from the Guncina Formation, Soprabolzano/Oberbozen (=Nop) locality, are studied for the first time and are represented by several specimens. The collection was sampled by Giannotti (1963). Bivalves are preserved as internal molds of open shells. This kind of preservation allows to determine the internal features of the shells. The shell material is partly preserved in the form of light yellow-grey mineral substance.

The shells are about 12 mm long. The external outline is subtrapezoidal or *Unio*-like, resembling the outline of the morphotype 2 of the Collio Formation. The shells are moderately elongated with a slightly oblique posterior margin. The H/L ratio, ranging from 0.39 to 0.46, tends to slightly decrease with the shell growth. The H/L ratio of the specimen MCSNBS PA-00067a decreases from 0.46 to 0.44 (about 4.5 %) with the shell growth and the H/L ratio of the specimen MCSNBS PA-00073d decreases from 0.42 to 0.39 (about 7.2 %). The surface of internal molds preserves the imprint of the external ligament groove and the ornament of concentric dichotomous growth lines. The imprints of a relatively thick hinge plate lie directly behind the umbo. The surface of the hinge plate shows small nodes or plates resembling pseudotaxodont teeth. A relatively thick hinge plate with imprints of node-like (or plate-like) pseudotaxodont teeth allow to confidently assign all these forms to *Palaeomutela* Amalitzky, 1892 sensu lato emend. Silantiev, 2015 (in Silantiev & Carter 2015). Additional features, like the concentric dichotomous sculpture and the external ligament groove, support this decision.

This material is herein assigned to *Palaeomutela* (*Palaeonodonta*) *guncinaensis* sp. nov.

The shell material requires additional mineralogical investigation. For the moment being, we

only note that the aragonite shells of *Palaeomutela* from the Permian coal-bearing successions of the Pechora and Kuznetsk Basins in some cases have a similar preservation with primary aragonite shells (Silantiev & Urazaeva 2013).

On the same bedding plane of the same specimen with *Palaeomutela* sp., a single internal (?) mold of a triangular bivalve shell is observed. The shell is slightly deformed (impressed) and has a length of 13 mm. A small cavity, observed on the posterior end of a dorsal margin, allow suggesting the presence of a hinge plate. This subtriangular form can be assigned to pseudotaxodont *Redikorella* Silantiev, 1994, which is widespread in the uppermost part of the Kungurian stage of the Cis-Ural Foredeep. It is interesting to note that in the Kungurian of the Cis-Ural Foredeep, *Redikorella* and *Palaeomutela* always occur in lacustrine facies associations but on different stratigraphic horizons, possibly reflecting diverse ecological niches, whereas they occur in lacustrine facies associations but on the same bedding plane in the material from the Guncina Formation of N Italy.

DISCUSSION

Palaeozoic invading faunas

The dominance of elongated specimens in the Collio Formation bivalve assemblage is noteworthy and is a characteristic feature of the so-called “invading fauna” of molluscs. Eagar (1973, 1974, 1977, 2005) proposed the concept of invading (and established) faunas of non-marine bivalves for the Carboniferous non-marine genus *Carbonicola* within the Pennine Basin delta (Scotland and English Midland, UK). Eagar (1977) also suggested that non-marine bivalves *Carbonicola* are descendants of the marine genus *Sanguinolites* Hind (1900). The external features and living habitats of invading fauna have been described (Eagar 1977, p. 537) as follows: “In invading faunas, shells tend to be elongate, having low height/length ... ratios, short anterior ends ... and low obesities. They characterize silty to sandy sediments commonly showing evidence of comparatively rapid deposition and of episodes of turbulence. The shells may be associated with burrows, referred to *Pelecypodichnus* Seilacher and with escape shafts...”

The elongated shell allows the mollusks to move quickly through both the sediment and es-

cape burials during unfavorable living conditions: mostly during the rapid deposition of terrigenous material. The dominance of elongated shells in the bivalve assemblage from the Collio Formation can be seen as possible evidence of the belonging (or proximity) of this bivalve assemblage to an invading fauna more or less recently adapted to a non-marine environment.

In the Cis-Urals, the first beds with *Palaeomutela* are known from the lower part of Solikamsk Formation, lying directly above the thick (100–300 m) salt-bearing strata of the Kungurian stage. Within the succession, the shaly marlstones with *Palaeomutela* are intercalated with anhydrite, halite and gypsum as well as with thin marl interlayers containing marine fossils (Silantiev 1994, 1998). This suggests that *Palaeomutela* originally colonized brackish-water environments of the Cis-Urals.

In the Cis-Urals and East European Platform, *Palaeomutela* penetrated freshwater fluvial environments only in the latest Kungurian or in the earliest Roadian (Sheshma Formation). Bivalves of *Palaeomutela* retained the ability to inhabit coastal-marine (brackish-water) environments up to the end of the Kazanian (= Roadian of the ICC). In particular, in the uppermost part of the Kazanian stratotype, beds with *Palaeomutela* are adjacent to the beds containing conodonts, brachiopods and other marine fossils (Chalimbadja & Silantiev 1998; Nurgaliev et al. 2015).

These facts indicate a high tolerance of *Palaeomutela* to variability of water salinity, which is characteristic of many invasive bivalve lineages at the first stage of their life history.

Current concept of bivalve invasions

The term “non-marine bivalves” was introduced by Davies & Trueman (1927) to indicate bivalves living in freshwater and estuarine (brackish) environments. It is generally accepted that non-marine bivalves existed in estuarine and continental environments that varied widely in salinity, but did not inhabit most marine ecosystems (Trueman & Weir 1946; Eagar 2005).

A number of physical and chemical parameters (e.g., alkalinity, salinity, total hardness, depth, nutrient levels, dissolved oxygen content, etc.) are used to characterise modern and ancient freshwater and brackish environments, of which salinity is the most relevant and most commonly applied (Mackie & Claudi 2010).

It should be recognised that the terms “marine”, “saline”, “brackish” and “freshwater” require to be clearly defined, as all the environments to which they refer are characterised by a wide range of salinity.

In the context of the environmental setting, the term “marine” refers to all oceanic environments (e.g. marshes, intertidal zones, lagoons, etc.); the term “freshwater” includes continental aquatic settings (e.g. streams, ponds, wetlands, open and closed basin lakes etc.); the term “estuaries” designates an intermediate environment between marine and continental realms. In the context of the salt content of water, the terms “freshwater”, “brackish” and “saline” are commonly used to describe the general salinity. The terms “saline” and “brackish” refer to salinity above freshwater but less than normal seawater, which is about 35 ppt. Many studies use a more detailed scheme that includes the following definitions of salinity: “freshwater” salt content is roughly 0–0.5 ppt, “oligohaline” – 0.5–5 ppt, “mesohaline” – 5–18 ppt, “polyhaline” – 18–30 ppt, “eugaline” – 30–40 ppt (including normal seawater), and “hyperhaline” – above 40 ppt (Bright et al. 2018).

The 5 ppt (oligohaline-mesohaline boundary) and 18 ppt (mesohaline-polyhaline boundary) salinity values are the most relevant salinity barriers for most estuarine and lacustrine (including inland seas) organisms (Bulger et al. 1993; Plotnikov & Aladin 2011). Most freshwater continental organisms inhabit salinities below 0.5 ppt. Some of the more salt-tolerant freshwater continental organisms can persist at salinities of 0.5–5 ppt (up to the upper oligohaline limit), but rarely at higher values. Most marine organisms prefer to live in normal salinities (35 ppt); some of them are tolerant of salinities as low as 18 ppt (the upper mesohaline limit) and only the most tolerant occur below 5 ppt (the lower mesohaline limit (Bulger et al. 1993; Attrill & Rundle 2002; Bright et al. 2018).

Apparently, the marine ancestors of the Palaeozoic non-marine bivalves Palaeomutelidae were able to overcome two most relevant salinity barriers at 18 and 5 ppt. This allowed their descendants *Palaeomutela* to develop a very broad salinity tolerance, which they possessed in their evolutionary history from the late Kungurian to the end of the Roadian. After the Roadian, *Palaeomutela* began to prefer predominantly freshwater environments (see above).

Water salinity is the most important, but not the exclusive adaptive challenge for invasive aquatic organisms.

Continental brackish (‘non-marine’) environments (lakes and inland seas) may have salinities similar to marine ecosystems, but otherwise their chemical composition is usually quite different. Most important is the difference in Ca to carbonate alkalinity ratio (Ca/ALK), which has a key influence on the habitability of organisms (e.g. diatoms, ostracods, gastropods and bivalves) in continental brackish-water environments (Bright et al. 2018).

Normal marine water has a small range of salinity fluctuation (33–37 ppt), stable homogeneous solute composition (Na and Cl comprise about 85%) and high Ca to carbonate alkalinity ratio (Ca/ALK) of about 9.

Continental brackish-water lakes undergo significant changes in water chemistry (ion proportions) as a result of saturation and precipitation of different mineral phases, due to the so-called “brine evolution” (Eugster and Hardie 1978). Brine evolution leads to a decrease in the Ca/ALK ratio and changes in other ionic ratios. As a result, the water of non-marine basins begins to differ significantly from marine settings. Consequently, invasive groups are forced either to adapt to a variety of ionic mix or to colonise habitats with an acceptable ionic mixture.

This fundamental difference between marine and continental (non-marine) brackish-water ecosystems requires additional adaptation from invasive organisms and is the cause of the ecological distinction between marine and continental biota (Gray 1988; Bennett 2008; Bright et al. 2018).

From a physiological point of view, the migration of organisms between marine and continental environments is limited primarily by differences in osmotic pressure gradients and ion concentrations (Remane & Schlieper 1971; Prosser 1973).

While marine water is similar in concentration and ionic composition to the fluid of living organisms, freshwater differs sharply from it by its low concentrations and different ionic ratios. The low concentration of solutes forces freshwater organisms to reduce membrane permeability and expend more energy to regulate osmotic pressure.

Generally, adaptation to freshwater habitats limits tolerance to higher salinity. In contrast, marine organisms generally lack adaptations to maintain water-salt balance at lower salinities (Pennak

1985, Deaton & Greenberg 1991). This may result in isolated brackish-water bivalve communities that are neither freshwater nor marine (Graf 2013).

Marine organisms that have invaded brackish or saline continental lakes have a wide tolerance to salinity (e.g., strong osmoregulators). At the same time, the environments into which they invade predictably have increased Na and Cl content and higher Ca/ALK values close to those of marine water (Anadón 1992; Plaziat 1993; Bright et al. 2018)

Based on the taxonomic composition of extant bivalve lineages only, Gray (1988), following the concept of Hutchinson (Hutchinson & Edmondson 1967), assumed twelve invasions of bivalves in freshwater environments. Modern phylogenetic work suggests the independent radiations into freshwater of at least three extant lineages: Unionoidea, Sphaeriidae, and Cyrenidae; meanwhile, the problem of identifying the marine ancestors of these lineages capable of adapting to freshwater (e.g. parental care and lack of planktonic veliger) is still not completely resolved (Graf 2013).

It can be assumed that certain lineages of marine ancestors of the Palaeozoic non-marine bivalves also invaded freshwater environments at different times. However, Palaeozoic non-marine bivalves are considered independent of modern freshwater bivalve lineages (Weir 1969; Graf 2013).

The ability to invade freshwater environments requires evolutionary innovations that have not been achieved by many large groups of marine organisms (e.g., Anthozoa, Echinodermata, Brachiopoda, etc.).

It is thought that once this innovation appears in a clade, many of its members begin to possess the adaptation to freshwater invasion, which can occur repeatedly within the clade (Gray 1988). Thus, the bivalve Infraclass Heteroconchia, which includes Unionida, Anthracosioidea, Palaeomuteloidea, and others extinct and extant non-marine taxa (Carter et al. 2011), contains a suspiciously large number of brackish and freshwater lineages. This supports the suggestion that the diversity of ecological niches inhabited by a taxonomic group may indicate its potential to invade freshwater environments and that all invaders would have to possess a phylogenetic bias (Lee & Bell 1999).

The life history strategy of invaders must include the adaptations necessary for living in freshwater environments. Freshwater environments

differ from marine ones in smaller size, greater fragmentation and ephemerality, in less consistent food supply, more variability of temperature and salinity. Life history strategies of invasive bivalves may include investment in osmoregulation, reproductive plasticity, development of parasitic larvae (glochidia and lasidium) (Gray 1988; Lee & Bell 1999; Montes et al. 2020; Skawina 2021).

Obviously, the upper Palaeozoic non-marine bivalves had to possess such evolutionary innovations as salinity tolerance (reduced membrane permeability) and reproductive plasticity; at the same time, the presence of parasitic larvae in these bivalves still remains unconfirmed.

The ancestors of freshwater invaders are thought to have lived in environments with a wide temporal and/or spatial variability of salinity, as it is under these conditions that they may have developed a robust tolerance to salinity fluctuations (Lee & Bell 1999).

Invasive organisms change their tolerance to salinity over time. Bivalves lineages that have invaded freshwater relatively recently (e.g., dreissenids) have less effective osmoregulation in freshwater than lineages (sphaeriids and unionids) that have invaded freshwater much earlier (Dietz et al. 1996; Walton 1996). On the other hand, there is evidence that some ancient lineages of invasive bivalves have lost their salinity tolerance (Deaton & Greenberg 1991). This indicates the variability of adaptive capacity in the evolutionary history of invasive groups and is consistent with the data on *Palaeomutela*. The fact that the ancestors of *Palaeomutela* began to colonize new uninhabited environments (new ecological niches), which suddenly (catastrophically fast) replaced the marine ecological niches, suggests the absence of competition from the indigenous fauna, which simply did not exist. The lack of competition enhances the ability for freshwater adaptation and allows further habitat expansion (Fitch & Ayala 1994; Lee & Bell 1999).

It is assumed that the ability to invade non-marine environments is maximised at low latitudes with minimal fluctuations in water temperature. High latitude environments with a wide range of temperature fluctuations are less favorable for this. In general, invasive organisms should be adapted to temperature variation, which is one of the specific features of non-marine environments (Hutchinson 1957).

Temperature affects metabolic rate, ion uptake rate and membrane permeability, but this effect varies in different species. At high temperatures, some species of modern invasive bivalves (e.g., dreissenids) have difficulty in osmoregulating (Spidle et al. 1994), whereas other species acquire a greater tolerance to salinity (Andreeva & Andreev 2003; Aladin et al. 2009).

Modern invasive bivalves use both opportunistic r-selected (e.g., dreissenids) and K-selected (e.g., unionids) strategies.

For example, Zebra mussels are free spawners with earlier maturation, faster growth and higher fecundity (Mackie & Claudi 2010). Some marine invasive species with a similar strategy have an almost continuous breeding season allowing them to saturate the water column with planktotrophic larvae for about 10 months of the year (Montes et al. 2020).

Adaptations of unionids to breeding have recently been examined in detail by Barnhart et al. (2008) and Haag (2012) and summarised by Skawina (2021). Female unionids brood larvae within the modified gills; the duration of brooding period is short (weeks), or long (months). Most recent unionids produce larvae that temporarily parasitize on fish-host until juveniles become capable to independent life on the bottom. Larvae of some species are parasitic on amphibians (Barnhart et al. 2008), or have direct development.

An unusual reproductive strategy resembling r-selection has recently been described in some unionids. It consists of breeding a huge number of small larvae (with low cost) that can cause a very high infestation of the host fish (Barnhart et al. 2008; Haag 2013; Patterson 2018).

The co-occurrence of early unionids with different fish groups is reported by many authors (e.g., Ortiz-Sepulveda et al. 2020; for a detailed review see Skawina 2021). Some of these fish groups are known from the Palaeozoic (hybodontid sharks, lungfish, Palaeonisciformes, etc.).

Modern studies based on molecular clocks, direct fossil evidence and mitogenomic phylogenetic reconstructions suggest that early unionids or even their marine/brackish-water ancestors already possessed traits that facilitated their acquisition of parasitic relationships with fishes after invasion of freshwater (e.g., Bogan & Hoeh 2000; Barnhart et al. 2008; Skawina 2021).

The geological record lacks direct evidence of a parasitic relationship between early unionids and fish. Similarly, we have no direct evidence that Palaeozoic non-marine bivalves used the same reproductive strategy. Nevertheless, the wide geographical distribution of Carboniferous and especially Permian non-marine bivalves suggest that they probably used a similar parasitic reproductive strategy.

Igger (2011) described the Upper Carboniferous insects Neoptera bearing tiny bivalve prodissoconchs and dissoconchs exclusively on the dorsal wing membrane. He assumed that bivalve larvae settled the wings after the insects died and drifted using this tool until fossilization. To date, this appears to be the only evidence in the geological record of the relationship between Palaeozoic non-marine bivalves and insects. Whether Palaeozoic non-marine bivalves used insects for spreading (at least by drifting) remains a matter of speculation.

In general, drifting is a common feature of the life history and ecology of many marine bivalves, regardless of their mode of development. Some marine brooding bivalves lacking a planktonic larval stage disperse as juveniles and small adults by drifting with water currents using mucous threads (Martel & Chia 1991). Obviously, this mechanism could have been used by the ancestors of Palaeozoic non-marine bivalves for long-distance dispersal.

Until 1957, the relicts of glacial invertebrates of the lakes of Northern Europe were suggested to have reached this area from Siberian coastal waters via the ocean. Then it was stated (Seegerstråle 1982) that a marine route was unacceptable, and that the relicts had invaded Northern Europe along a continental freshwater route represented by a system of proglacial lakes. The distance of the invasion was more than 4,000 km.

The rate of vertebrate (fish) invasions is quite high, due to the fact that adaptation after invasion of organisms to freshwater environments can occur within a few years (Klepaker 1993). Extant freshwater bivalve lineages closely related to host fish seem to have a similar rate of invasion.

For example, the invasion of Eurasian Coelaturini (Unionidae) took no more than three million years to colonise central East Africa and then gave rise to separate lineages that inhabited the Tanganyika and Victoria regions (Ortiz-Sepulveda et al. 2020). The distribution of bivalves (and their fish hosts)

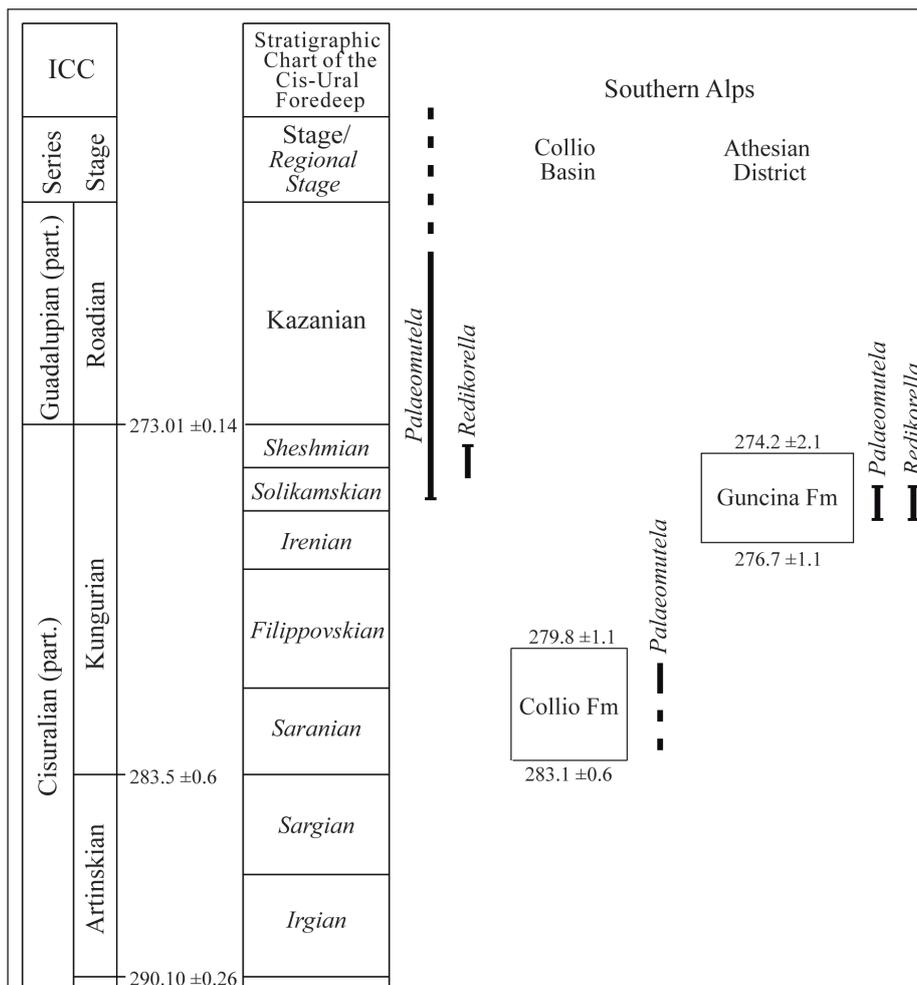


Fig. 7 - First occurrence data of *Palaeomutela* and *Redikorella* in the Cis-Ural Foredeep and Southern Alps.

occurred along lake and river systems throughout the East African Rift System; the approximate distance was 5000 km.

Origin and distribution of *Palaeomutela* through time

Establishing the genus *Palaeomutela*, Amalitzky (1892a, b) considered its hinge to be a modified dentition of the Carboniferous *Carbonicola*, and hence *Palaeomutela* is a direct descendant of that genus. This conclusion was based on the analogy of the transformation of the schizodont hinge of the Mesozoic-Cenozoic Unionidae Rafinesque, 1820 into the pseudotaxodont teeth (secondary taxodont dentition) of Mutelidae Gray, 1847 (= Iridinidae Swainson, 1840).

This analogy provided the basis for the name of the genus *Palaeomutela*. The presumed relationship between *Palaeomutela* and *Carbonicola* allowed Amalitzky (1892a, b) to assign *Palaeomutela* to Anthracosiidae Amalitzky, 1892. This assumption was supported by Cox (1932) and Weir (1969).

Wohrmann (1893) recognized similarities in *Palaeomutela* dentition with the taxodont hinge of *Palaeoneilo* Hall & Whitfield, 1869 and assigned *Palaeomutela* to Ctenodontidae Wohrmann, 1893. This view was supported by Tschernyshev (1943) and Gusev (1990).

Bailey (1983), based on the similarity of the hinge, suggested that *Palaeomutela* are phylogenetic descendants of marine *Nyassa* Hall & Whitfield, 1869.

Bailey (1983) and Pojeta et al. (1986) placed *Nyassa* and *Palaeomutela* in the same family Palaeomutelidae.

Currently, the superfamilies Nyassoidea S. A. Miller, 1877 and Palaeomuteloidea Lahusen, 1897 are placed either in Order Actinodontida Deschaseaux, 1952 (Carter et al. 2011) or in Order Unionida J. Gray, 1854 (Nevesskaja et al. 2013).

Thus, three points of view on the origin of *Palaeomutela* have emerged by now: 1) *Palaeomutela* are descendants of the Carboniferous non-marine *Carbonicola* (Amalitzky 1892a, b; Cox 1932; Weir

1969); 2) *Palaeomutela* are descendants of marine taxodonts (Wohrmann 1893; Tschernyshev 1943; Gusev 1990); 3) *Palaeomutela* are descendants of marine nyassids (Bailey 1983; Pojeta et al. 1986).

In general, we could agree with Weir (1969) that the origin of the *Palaeomutela* and Palaeomutellidae is cryptic.

To date, it was generally accepted that the genus *Palaeomutela* s.l. appeared at the beginning of the Ufimian Age (Solikamskian, corresponding to late Kungurian of the ICC) in the non-marine basins of the Cis-Ural Foredeep and in the eastern marginal area of the East European Platform (Silantiev 2018) (Fig. 7).

Between the latest Kungurian and the Roadian, *Palaeomutela* s.l. appeared for the first time in coal-bearing basins of Angara, including: the Pechora, Tunguska and Kuznetsk Basins (Betekhtina & Tokareva, 1988), the Tarim Basin (Chang 1988; Fong 1996; Chen & Shi 2003), the Junggar Basin (Yang et al. 1986; Sheng & Jin 1994), and both the Turpan Basin and the Bogda Shan Folded Belt (Brand et al. 1993).

Subsequently, starting from the Capitanian, *Palaeomutela* s.l. occurred for the first time in the Cathaysian and Gondwanan basins. Within the Cathaysian Realm, *Palaeomutela* s.l. is known from the Qiliangshan Folded Belt (fluvial-lacustrine Zhongshigong Formation, Lopingian) (Sheng & Jin 1994) and from the South China Region (Yunnan Province, Xuanwei Formation, Changhsingian) (Guo 1985). Within the Gondwanan Realm, *Palaeomutela* s.l. is known from the Capitanian of Parana Basin (Brazil) (Guerrini et al. 2020), Falkland Islands (Simoes et al. 2012) and Kilombero Rift Valley (Tanzania) (Cox 1932, 1936). During the Lopingian, it is widespread in the Ruhuhu Basin (Tanzania) (Cox 1932, 1936), the Zambezi Basin (Kenya) (Gregory 1921; Weir 1938), the Luangwa Basin (Malawi) (Jones 1890; Newton 1910), the mid-Zambezi Basin (Hind 1903; Bond 1946; Bond 1954), the Main Karoo Basin (Amalitzky 1895; Rilett 1975), and the Ohio Range of the Horlick Mountains (Antarctic Platform) (Bradshaw 1984).

During the late Kungurian, some non-marine bivalve genera, which first appeared in Angara basins, were also found in slightly younger units in basins of the Cis-Ural Foredeep and then in basins of the East European Platform. This includes *Redikorella* Silantiev, 1994 and other genera, which

are characteristic components of the Angara Fauna (Silantiev 2016).

However, on the basis of the data shown in this work, the occurrence of *Palaeomutela* in the early Kungurian of N Italy suggests a new FAD for this genus, which is in the Val Dorizzo member of the Collio Formation (Fig. 7), constrained between the radiometric ages of 283.1 ± 0.6 Ma and 279.8 ± 1.1 Ma (Schaltegger & Brack 2007). This genus occurs also in the late Kungurian Guncina Formation of N Italy, constrained between the radiometric ages of 276.7 ± 1.1 Ma and 274.2 ± 2.1 Ma (Marocchi et al. 2008).

Nevertheless, the occurrence of *Redikorella* in the Guncina Formation of N Italy raises questions on the actual first appearance of this genus (FAD), which may have been either in the Guncina Formation of N Italy or in the Angara basins.

Palaeobiogeographic considerations

On the basis of the data shown in this work, new finds of *Palaeomutela* and *Redikorella* in the Kungurian of the continental strike-slip basins of the western Tethyan sector of the Variscan collisional chain may suggest a new center of origin of both genera. This fact raises new palaeobiogeographical questions requiring further research.

The question on why *Palaeomutela* (and possibly also *Redikorella*) occurs first in the Southern Alps is currently not easy to answer. It can be only assumed that the marine *Palaeomutela* ancestors initially invaded the non-marine environments that were formed on the peri-Tethyan coasts. Undoubtedly, the erosion of the Variscan orogeny produced a large volume of continental volcanogenic-terrigenous sediments and so might have contributed to the invasion of marine bivalves into the non-marine realm, as Eagar (1977, p. 536) noted: "In these particular circumstances therefore the delta invaded the bivalves, rather than vice versa".

If this assumption is correct, we need to assume that the intracontinental basins of the Southern Alps were located close or potentially had also some connection with marine environments. Direct evidence of this connection has not yet been preserved in the geological record even though a questionable occurrence of poorly-preserved marine fossils (calcareous foraminifera) from the upper part of Pizzo del Diavolo Formation of the Orobian Basin has been reported (Sciunnach 2001). Nev-

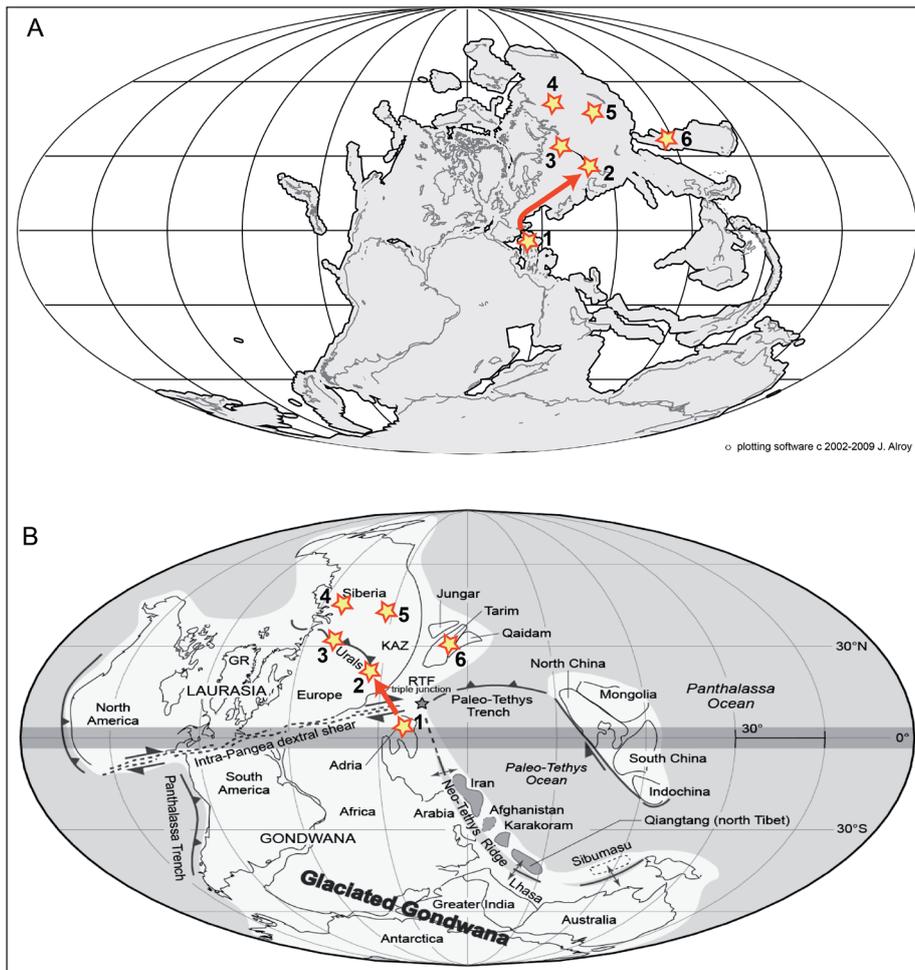


Fig. 8 - Lower Permian localities of non-marine bivalve *Palaeomutela* sensu lato. A) “Classic” Pangaea palaeogeography. Map from Alroy (2013), modified. B) “Pangaea B” palaeogeography (from Muttoni & Kent 2019, modified). (1) Southern Alps, Collio Formation (early Kungurian), Guncina Formation (late Kungurian); (2) East European Platform, Volga–Ural Basin and Cis-Ural Foredeep, Solikamsk Formation (late Kungurian); (3) Pechora Basin, Inta Formation (late Kungurian); (4) Kuznetsk Basin, Mitino Formation (late Kungurian); (5) Tunguska Basin, Lower Pelyatka Subformation (late Kungurian); (6) Tarim Basin, Kupukuziman Formation (late Kungurian) (localities 2–6 after Silantiev, 2018). Red arrows indicate the supposed direction of the first *Palaeomutela* migration.

ertheless, many authors have located the Southern Alps in southwestern Europe and surrounded by the Tethys Sea, even though in different palaeogeographic positions (e.g. Ziegler & Stampfli 2001; von Raumer et al. 2013; Cassinis et al. 2012).

If we assume that the genera *Palaeomutela* and *Redikorella* had a single center of origin, we need to argue possible migration routes from the Southern Alps area (Adria s.l.) to the continental basins of Eastern Europe and Angara (Fig. 8A). In this scenario, the cradle of the freshwater *Palaeomutela* evolution is located in the Italian Southern Alps basins (early Kungurian, Collio Formation), from which this genus migrated in a first step to the intramontane or perimontane basins of Cis-Ural Foredeep and the eastern marginal area of the East European Platform (late Kungurian) and, in a second step, into the coal-bearing basins of Angara. A third step was the migration into the Gondwanan basins (Wordinian). *Redikorella* may have had a different migration route, because it appeared in Angara before than in the Cis-Ural Foredeep and the East European platform. *Redikorella* may have appeared in the Southern

Alps and then migrated to Angaraland, from which it later invaded the Cis-Ural Foredeep and the East European Platform.

According to palaeomagnetic studies, mainly developed in the last twenty years, an intra-Pangaea dextral shear zone (Irving 2004) may have developed within the Greater Variscan orogeny and was active to transform Pangaea B to Pangaea A from ~275 to 260 Ma (see for a review Muttoni & Kent 2019 and Kent & Muttoni 2020). In this reconstruction, during the Early Permian, the African continent was considerably shifted to the east compared to the classic Pangaea reconstruction and thus Adria (comprising the Southern Alps), which was an African promontory, was directly beneath the southeastern Eurasia border and more or less in line with the Urals (Fig. 8B).

This palaeogeographic scenario, in which the Cisuralian units of N Italy and the Urals were much closer, would better explain why there are no records of *Palaeomutela*, excluding bias problems, in all the area between the Southern Alps and the East European Platform. Noteworthy, such palaeoge-

graphic reconstruction would shorten and make more feasible the migration routes of these bivalves across continental eastern Eurasia.

Another hypothesis may imply that the invasion of the marine ancestors of *Palaeomutela* (and *Redikorella*) into the continental realm took place in different places at about the same time. This would imply a parallel homeomorphic development of marine ancestors of non-marine genera in different continental basins. Nevertheless, there is no direct evidence for this assumption, and the independent coevolution of the same species from identical marine ancestor genera in different places can be phylogenetically excluded.

CONCLUSIONS AND FUTURE PERSPECTIVES

A comprehensive study of the collections of bivalves from the Cisuralian Collio Formation (Collio Basin) and Guncina Formation (Athesian District) of the Italian Southern Alps is the subject of this contribution.

Some new features are added to the description of these bivalves: a relatively thick hinge plate with imprints of node-like (or plate-like) pseudotaxodont teeth, an external ligament groove, and a concentric dichotomous sculpture. Based on these features, we can assume that the Collio and Guncina Formations bivalves belong to the genus *Palaeomutela* sensu lato. Three morphotypes have been recognised: oval-subtriangular, subtrapezoidal and elongated. Specimens of the later have been assigned to *Palaeomutela (Palaeonodonta) berrutii* sp. nov. The Collio Formation includes all three morphotypes. The Guncina Formation includes only the subtrapezoidal morphotype, herein assigned to *Palaeomutela (Palaeonodonta) guncinaensis* sp. nov. The elongated morphotype dominates the Collio Formation bivalve assemblage. This allows considering the Collio Formation bivalve assemblage as a fauna invading for the first time the non-marine environments of the peri-Tethyan coast. The upper Kungurian Guncina Formation also contains *Redikorella* Silantiev, 1994, found for the first time on the same stratigraphic surface of *Palaeomutela*.

The new FAD of *Palaeomutela* is in the Collio Formation, which is dated early Kungurian through radioisotopic ages. The non-marine bivalves from the upper Kungurian Guncina Formation, also

dated through radioisotopic ages, confirm the hypothesis about the *Palaeomutela* FAD from the lower Kungurian Collio Formation. The occurrence of *Redikorella* from the upper Kungurian Guncina Formation may also represent a FAD. The new finds of *Palaeomutela* and *Redikorella* from the Kungurian of the continental basins of the peri-Tethyan coast suggest a new possible center of origin of both genera. Possible migration routes from SW Europe to the continental basins of Eastern Europe and Angara are better supported by a Pangaea B configuration, because it would imply a much shorter migration distance, whereas no *Palaeomutela* occurrences are known from areas in between. This might be due of course to research and/or preservation bias. Nevertheless, the support to a Pangaea B configuration and in general, the possible analogies between the Kungurian biotas from N Italy and Russia is worth to be further investigated.

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