

LOWER PERMIAN CONCHOSTRACANS (CLAM SHRIMPS) FROM SEDIMENTARY UNITS OF THE ATHESIAN VOLCANIC GROUP (SOUTHERN ALPS, N-ITALY)

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Abstract. The present study describes two occurrences of clam shrimps (“Conchostraca”). Following a form-based classification of Schneider et al. (2005, 2022) and Schneider & Scholze (2018), the conchostracans have been classified as *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine. They come from the Guncina and Tregiovo formations, respectively. These units are part of the northern Athesian Volcanic Group, North Italy. All of this material were obtained from grey coloured, fine-grained siliciclastic, lacustrine deposits of Kungurian (late Cisuralian, late Early Permian) age. Their carapace valves in lateral view are marked by concentric ribs. Often, growth lines can be observed to decrease in their preservation towards the umbonal area of the valve. An open nomenclature is applied to the taxonomy at the species level herein, because of either limited number of individuals or a plastic deformation due to tectonics. So far, the records reported herein are restricted geographically and stratigraphically to respective single occurrences. Further studies are recommended to establish their full biostratigraphic ranges.

INTRODUCTION

Continental sedimentary deposits of the Athesian Volcanic Group of the Southern Alps area (Fig. 1), including both the Guncina and Tregiovo formations, are well-known for remarkable plant

macrofossils and sporomorphs of Early Permian age (e.g., Remy & Remy 1978; Neri et al. 1999; Vischer et al. 2001; Fritz & Krainer 2006; Marchetti et al. 2015, 2022; Wachtler 2016; Forte et al. 2018a, 2018b, 2023; Forte & Kustatscher 2023; Vallé et al. 2023). In contrast, the faunal content in these sequences has experienced much less attention by previous workers, with only vertebrate and invertebrate traces (e.g., Avanzini et al. 2008, 2011; Mar-

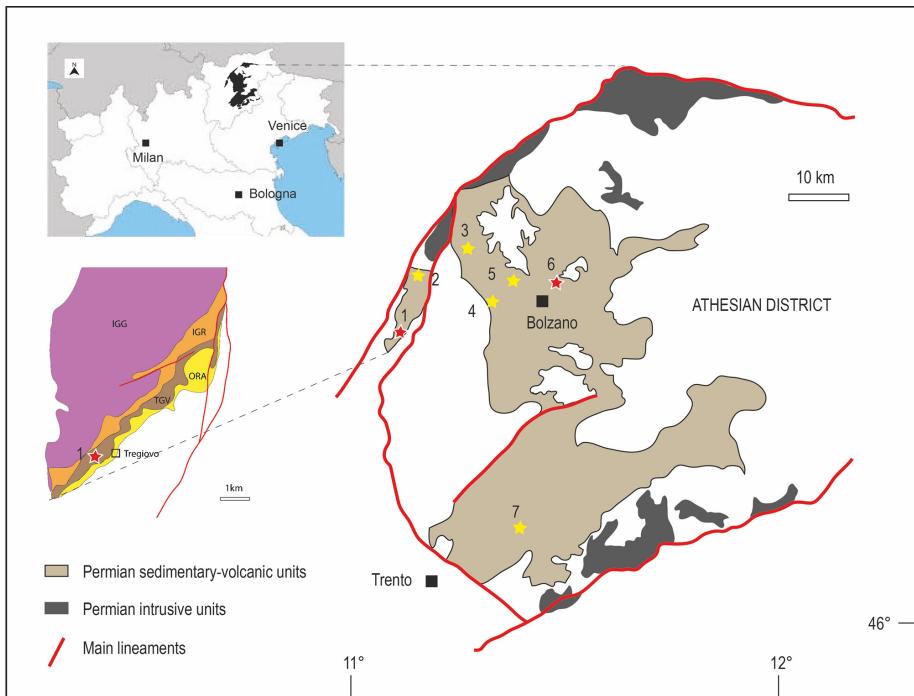


Fig. 1 - Geological setting and fossiliferous localities of the Athesian Volcanic Group of the Southern Alps, northern Italy. Stars represent the main fossiliferous localities: 1 Tregiovo, 2 Kleiner Laugen/Luco Piccolo, 3 Sinich/Sinigo, 4 Grissian/Grissiano, 5 Gidl, 6 Oberbozen/Soprabolzano, 7 Val di Pinè. Conchostracans were found in localities 1 and 6. IGG = Gargazzone Formation, IGR = Gries Formation, TGV = Tregiovo Formation, ORA = Ora Formation, Predonico Member.

chetti et al. 2015, 2022; Santi et al. 2020), a tetrapod (Leonardi 1959) and some bivalves (Silantiev et al. 2022) being described from there. Additionally, literature data on volcanic Zircon U/Pb-isotope ages (Schaltegger & Brack 2007; Marocchi et al. 2008; Cassinis et al. 2012) as well as first findings of fossil conchostracans (Marchetti et al. 2015) stimulated the present study. Conchostracans (“Conchostraca”, i.e., a paraphyletic order of fossil branchiopod Crustacea) are small-sized crustaceans that can be preserved in the fossil record as both valves of the crustacean carapace and, more rarely, remnants of the chitinous crustacean “soft” body (e.g., Orr et al. 2008). Their most comparable extant descendants are clam shrimps (=Branchiopoda: Phyllopoda: Diplostraca). The taxonomic classification of fossil conchostracans is often based on the carapace valve in lateral view (e.g., Scholze & Schneider 2015); alternatively, few other methods such as characteristic valve microstructures (i.e., ornamentation; e.g., Sabirova et al. 2019; Li 2020), landmarks on lateral carapace valves (e.g., Stoyan et al. 1994), and computer-based geometric morphometrics (i.e., Eigen-/Fourier-shape analyses; e.g., Monferran et al. 2013; Hethke et al. 2018; Prosuzhikh et al. 2019; Miao et al. 2021) have been applied for their classification as well.

In the present study, the carapace valve morphologies of conchostracans from the Guncina and Tregiovo formations of the Athesian Volcanic

Group are described for the first time. It is hoped that this will serve as motivation for more comprehensive studies of both conchostracan taxonomy and biostratigraphy in the Early Permian on a regional (i.e., southern Alps; the present study) to inter-regional (e.g., Schneider & Scholze 2018; Schneider et al. 2020) scale.

GEOLOGICAL SETTING

In the Southern Alps region, multiple formations of small-sized sedimentary basins are intercalated within volcanic rocks of the Athesian Volcanic Group (or Athesian District). The conchostracan materials of the present study were obtained from fine-grained, lacustrine siliciclastics of the Guncina and Tregiovo formations, the latter being part of the Tregiovo Basin. It is a small basin that extends N–S about 9 km and W–E for about 3 km (e.g., Marchetti et al. 2015) within the northwestern part of the Athesian Volcanic Complex. The Guncina Formation instead outcrops in the northern part of the Athesian Volcanic Complex in the Adige Valley (e.g., Avanzini et al. 2007).

The up to 250 m thick Guncina Formation (Fig. 2) is composed of a mixed volcanic-siliciclastic succession with local fluvial and lacustrine deposits that bear a wide spectrum of coarse- and fine-grained siliciclastics and, more rarely, thin limestone

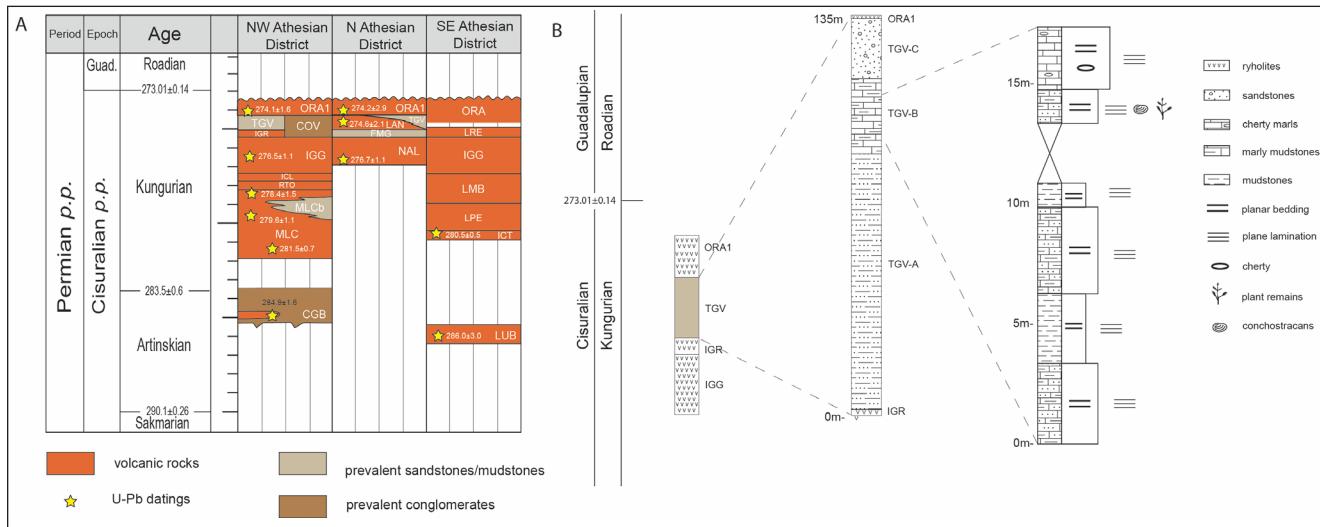


Fig. 2. A) Cisuralian stratigraphy of the Athesian District of the Southern Alps (Italy). Acronyms: CGB = Basal Conglomerate, MCL = Monte Luco Formation, MCLb = siliciclastic units of MCL, RTO = Sarentino Formation, ICL = Castel Leone Formation, IGG = Gargazzone Formation, IGR = Gries Formation, TGV = Tregiovo Formation, COV = Verano Formation, ORA1 = Ora Formation, Predonic Member, NAL = Nalles Formation, FMG = Guncina Formation, LAN = Andriano Formation, LUB = Buss Formation, ICT = Castelliere Formation, LPE = Pin`e Formation, LMB = Cembra Formation, LRE = Regnana Formation, ORA = Ora Formation. Star represents radiometric dates (see references in the text). B) Lithologic profiles of Le Fraine section.

and chert beds (e.g., Krainer & Spötl 1998; Avanzini et al. 2007; Silantiev et al. 2022). The Guncina Formation overlies volcanic rocks of the Nalles Formation, and underlies volcanics of the Andriano Formation (e.g., Avanzini et al. 2007). U/Pb isotope ages of 276.7 ± 1.1 Ma for the Nalles Formation as well as isotope ages from the Andriano Formation of 274.6 ± 2.1 Ma indicate a correlation of the Guncina Formation with the late Kungurian Stage (uppermost stage of the Cisuralian; e.g., Avanzini et al. 2007; Marocchi et al. 2008). The conchostracans from the Guncina Formation occur in greyish coloured, laminated clay- to siltstone beds that had been collected previously in the Oberbozen locality. The exact fossil-bearing horizon has not been relocated, but similar facies have been observed in the same area (Fig. 3A). From this locality, both plants and bivalves have been described by previous workers (e.g., Giannotti 1963; Remy & Remy 1978; Silantiev et al. 2021, 2022); the conchostracans studied herein co-occur on the bivalve-bearing slabs. Other fossils from the Guncina Formation include only sporomorphs (Hartkopf-Fröder et al. 2001; Hartkopf-Fröder 2019; Vallé et al. 2023) and tetrapod footprints (Marchetti et al. 2022).

The Tregiovo Formation (Fig. 2) forms a sedimentary succession up to 200 m thick. Marchetti et al. (2015) described in detail numerous sedimentary lithofacies of the Tregiovo Formation that

include laminated clay- to siltstone deposits, marly limestone beds, and chert layers, which indicate a floodplain to lacustrine palaeoenvironment; however, coarse-grained alluvial fan deposits can occur at the base and the top of the unit. Volcanic rocks of the Athesian Volcanic Group both underly (i.e., ignimbrites of the Gargazzone Formation) and overly (rhyolitic tuffs of the Perdonig Member of the Ora Formation) the Tregiovo Formation which have been isotopically (U/Pb) dated to 276.5 ± 1.1 Ma and 274.1 ± 1.6 Ma, respectively (Avanzini et al. 2007; Marocchi et al. 2008). Thus, the age of the Tregiovo Formation is constrained to the upper Kungurian Stage (uppermost stage of the Cisuralian; e.g., Marchetti et al. 2015). This formation includes abundant and well-preserved plant remains (e.g., Remy & Remy 1978; Visscher et al. 2001; Marchetti et al. 2015; Forte et al. 2017, 2018a, 2018b; Forte & Kustatscher 2023), abundant but generally poorly-preserved sporomorphs (Klau 1965; Cassinis & Doubinger 1991, 1992; Barth & Mohr 1994; Neri et al. 1999; Forte et al. 2018a) and tetrapod footprints (Marchetti et al. 2015, 2022). Also, invertebrate traces have been described (Marchetti et al. 2015). The occurrence of conchostracans has only been mentioned so far (Marchetti et al. 2015). The conchostracans studied herein were collected from the upper part of the lacustrine facies of the Tregiovo Formation, in the Le Fraine locality (Fig. 2B,

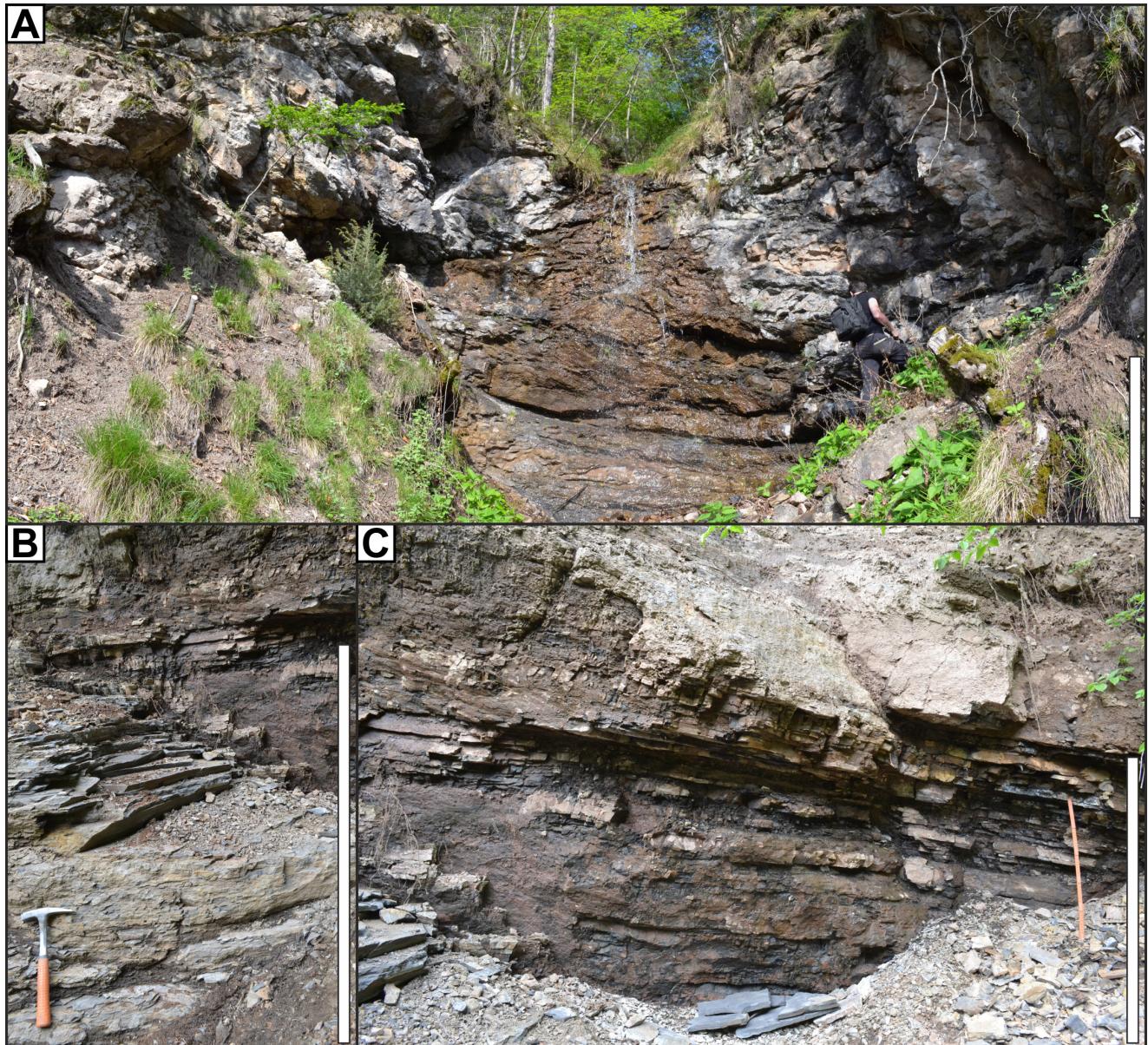


Fig. 3 - Representative field photographs of continental deposits in the Guncina and Tregiovo formations (Kungurian, Early Permian), from which the conchostracan specimens of the present study have been obtained. A) Guncina Formation in the Oberbozen (also called Soprabolzano) outcrop section. B, C) Tregiovo Formation in the Le Fraine section. White scale bars are 1 m in height.

3B, 3C). A stratigraphic section about 135 m thick was described previously by Marchetti et al. (2015: see therein fig. 2) and Forte et al. (2018b: fig. 4). In its lower part, this section is composed mainly of dark greyish, laminated, fine-grained siliciclastics of a lacustrine facies, whereas the upper part of the section is composed predominantly of alluvial sandstones and conglomerates (e.g., Forte et al. 2018a, 2018b). The new stratigraphic section, measured along the western side of the bridge at Le Fraine, is about 17 m thick (Fig. 2B) and includes the conchostracan horizon, which corresponds also to the plant site B of Forte et al. (2018a). It belongs

to the carbonate-chert unit B of Marchetti et al. (2015), and its top can be approximately correlated with the base of the intraclastic breccias described in the same work.

MATERIAL AND METHODS

Two sets of conchostracan samples were studied herein. One set had been collected by Giannotti (1963) from the Guncina Formation in the Soprabolzano/Oberbozen locality (geographic coordinates $46^{\circ}31'17.4''\text{N}$, $11^{\circ}22'50.1''\text{E}$), although the exact fossiliferous level has not been specified. It is stored in the fossil collection of the Museo Civico di Scienze Naturali di Brescia (specimen acronym MCSNBS) in the city of Brescia, Italy. A second set of conchostra-

cans samples was collected from the Le Fraine locality ($46^{\circ}26'11.4''N$, $011^{\circ}02'50.6''E$) during recent fieldworks by the authors. A new 17 m thick stratigraphic section (Fig. 2B) has been measured and correlated with the stratigraphic section of Marchetti et al. (2015). This material is stored in the MUSE - Museo delle Scienze (specimen acronym MUSE-*pn*, for 'provisory number') in the city of Trento, Italy.

The valve morphology of the carapace has been studied using stereomicroscopes (Wild M3B for the sample set from the Oberbozen locality; Leica MZ12 for samples from the Le Fraine locality) equipped with a digital camera (Bresser MikroCamII). The computer software Adobe Photoshop 2021 was used for vertical focus stacking of digital photographs that figure the carapace valves. For the sample set from the Oberbozen locality, a mirror tube was used additionally to make microscopic line drawings of conchostracan carapace valves directly under the stereomicroscope. The graphic software suite CorelDRAW 2021 was used for digitizing and including both photographs and line drawings into figures for the present study. Images of larger rock slabs showing plant fragments or conchostracan mass-occurrences were photographed using a digital reflex camera (Nikon D3100) with a macro lens (AF-S Micro-Nikkor 60 mm). Finally, for both descriptions of the carapace valve and metric measurements of valve parameters, the methodology and terminology proposed by Scholze & Schneider (2015) was applied herein.

RESULTS

Oberbozen locality

The Guncina Formation in the Oberbozen locality is rich in plant remains, but faunal components such as bivalves and conchostracans are rarer. As a result, 10 conchostracan individuals from the Oberbozen section were recorded in the museum collection only. They are co-occurrences on bivalve-bearing slabs composed of greyish coloured siltstones with a small proportion of fine-grained sand (Fig. 4). Due to this low number of available carapace valves, they can be only determined preliminarily taxonomically as *Pseudestheria* form Oberbozen. Most of the valves are preserved as combination of internal casts (i.e., moulds/steinkerns) and remnants of shell substance. The shell substance or its derivate (i.e., pseudomorphs by replacing minerals) looks very thin, slightly glossy, and grey in colour. A tectonic (post-sedimentary; i.e. diagenetic) deformation of carapace valves can be observed that is indicated individually either by lateral elongation or lateral compression of respective carapace valves. Vertically, the carapace valves show less intensive, only moderate compaction, which also accounts for the internal casts of the bivalves. The latter were taxonomically determined as *Palaeomutela* (*Palaeoanodonta*) *guncinaensis* Silantiev et al., 2022 and *Redikorella* sp. Silantiev et al., 2022. In contrast to the conchostracans, most of these bivalves show yellowish coloured remnants of their shell substance (Fig. 4A, B).

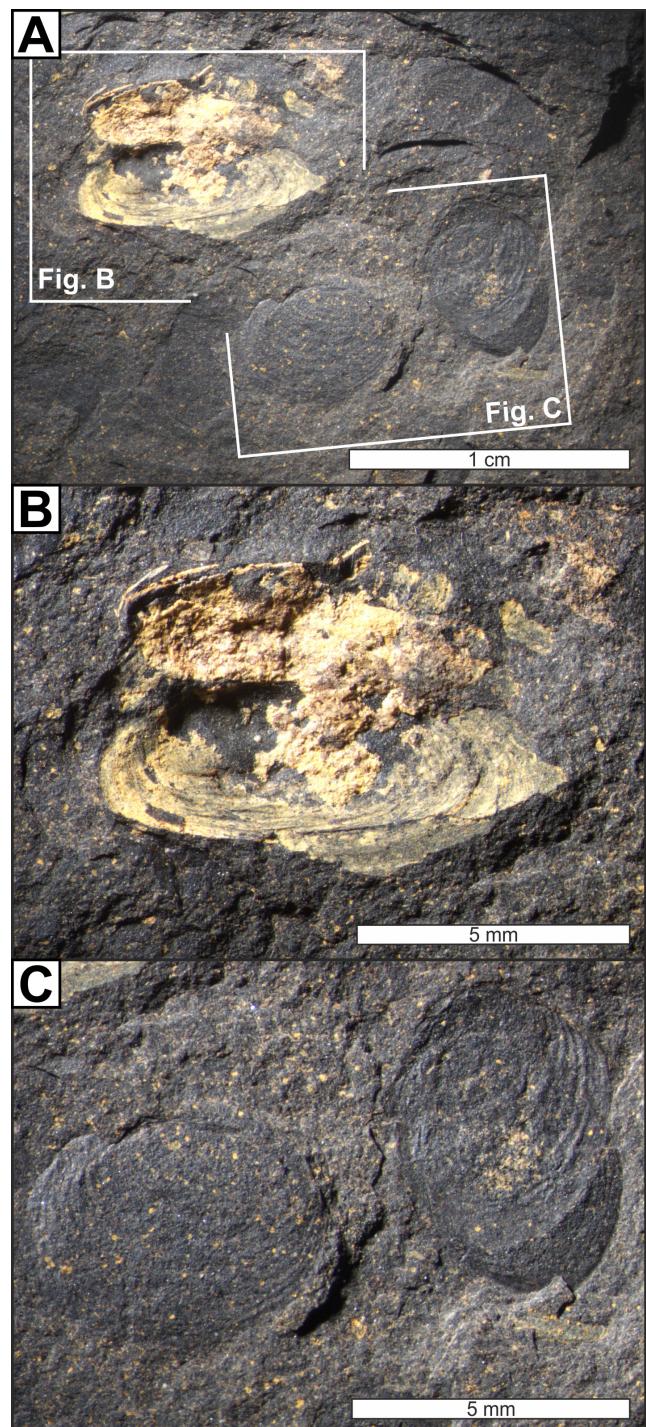


Fig. 4 - A fossil assemblage from the Oberbozen section (Guncina Formation; Kungurian, Early Permian); collection no. MCSNBS PA-00073. A) Co-occurrence of bivalves and conchostracans in a grey coloured, slightly fine-sandy siltstone. B) Bivalves identified as *Palaeomutela* (*Palaeoanodonta*) sp., following Silantiev et al. (2022). C) Conchostracans of the present study, determined preliminarily as *Pseudestheria* form Oberbozen; carapace valves in lateral view; left and right valves of the right individual were slightly shifted against each other before final deposition and, therefore, are partially not overlapping each other.

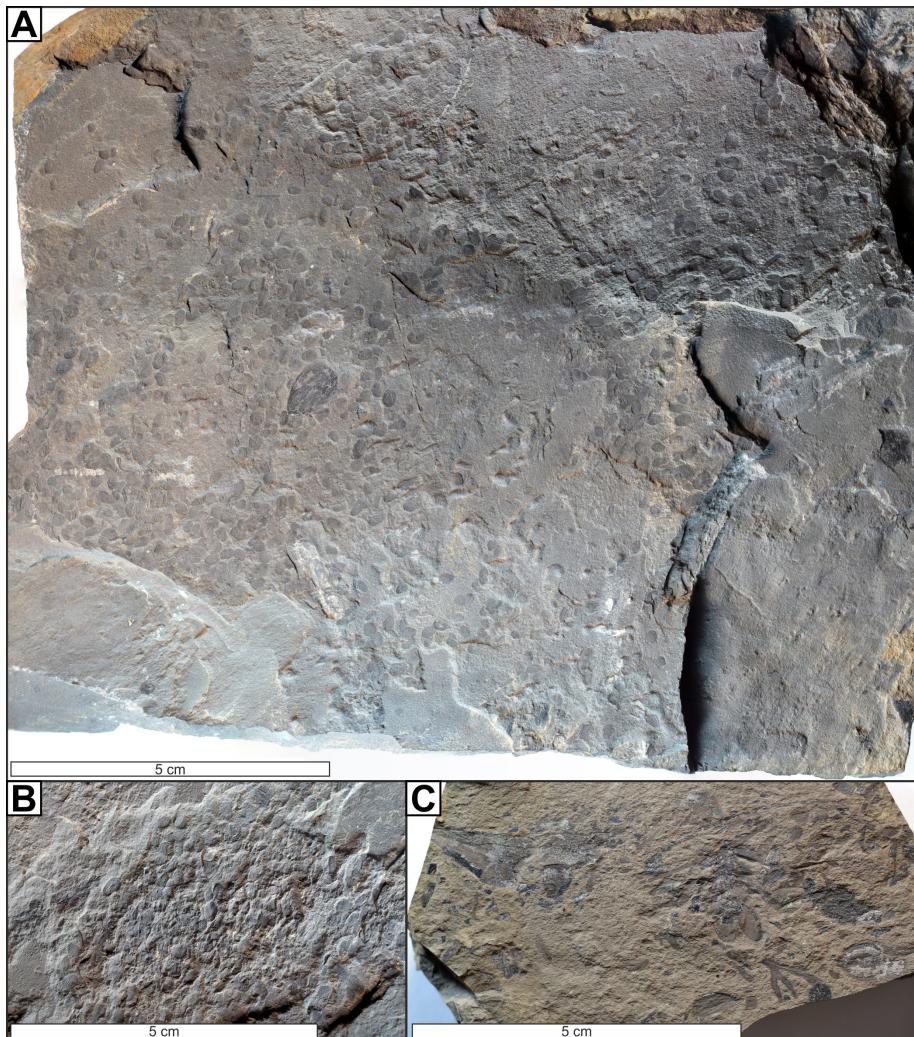
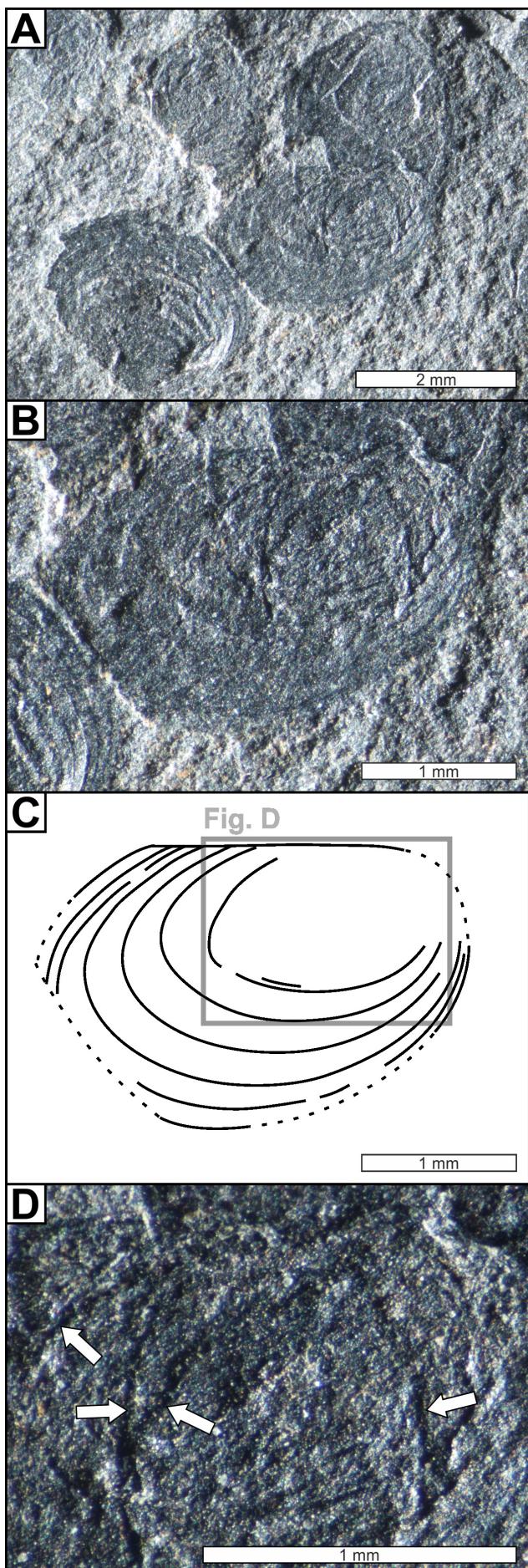


Fig. 5 - Slabs of grey coloured, horizontally bedded, fine-grained (predominantly silty) siliciclastics from the Tregiovo Formation (Kungurian, early Permian) in the Le Fraine outcrop section. A, B) mass-occurrence of conchostracan carapace valves assigned to *Pseudestheria* form Le Fraine. C) Bedding plane yielding detritus and larger fragments of plants.

Le Fraine locality

In the Tregiovo Formation, the studied conchostracan occurrence is restricted to fine-grained siliciclastics. In cross section, slabs containing the conchostracans show alternating bedding between clayey and silty layers. Frequently, distinct layers with a higher proportion of silt may also yield plant fragments (Fig. 5C). The samples from the Le Fraine section (upper part of the Tregiovo Formation) show bedding planes bearing mass-occurrences of conchostracan carapace valves. The material consists approximately of several hundred individuals. Comparing carapace valves within a mass-occurrence enables first observations of deformation that has affected most individuals. In particular, respective valves from the Le Fraine section show frequently elongated shapes in various degrees, probably due to post-sedimentary (i.e., tectonically induced), plastic deformation. A grey, glossy, tissue-like shell substance or its derivate is more or less present. The most prominent structures are concentric lines that can be seen cover-

ing the carapace valves in lateral view (Fig. 6). These concentric lines represent either margins of growth bands and/or concentric ribs; however, they are apparently less distinct due to a high degree of compaction of the carapaces. Towards the umbonal area of the valves, these concentric lines are decreasingly preserved or even apparently missing (Fig. 6B). Problematically, if growth lines are not preserved in the umbonal region resulting in an apparently large larval valve, those individual could show “*Lioestheria*-similar forms”. On the contrary, other individuals from such samples of mass-occurrence show more completely preserved umbonal growth lines demonstrating a primary smaller larval valve and, therefore, should be determined taxonomically as *Pseudestheria* form Le Fraine. Additionally, a few slightly curved to almost straight, very thin structures occur sporadically in the umbonal area (Fig. 6D), which might correspond primarily to weekly preserved appendages of the crustacean body (i.e., potential antennules, antennal rami or isolated trunk appendages).



SYSTEMATIC PALAEONTOLOGY

Dimensions of valve parameters are exclusively based on absolute measurements of the fossil specimens in lateral view, regardless of whether or not individual valves show indications for tectonic deformation. This involves parameters, and their ratio calculation, as follows: H (=total height of the valve), L (=total length of the valve), l (=length of the dorsal margin), h (height of the larval valve), H/L, l/L, h/H, and GL (=total number of preserved growth lines).

For taxonomy, a form-based classification is used for determinations on the substituted species level. The respective name results from the designation of the outcrop section. This follows a careful approach that had been applied previously by Schneider et al. (2005, 2022) and Schneider & Scholze (2018) to conchostracan valves from either particularly small numbers of specimens or single occurrences. Thus, instead of formalizing species names, this careful approach prevents defining species based potentially on incompletely understood valve morphologies. When more data become available through future studies of both new samples and better preserved specimens, the form-based classification used preliminarily in the present study can be replaced by formalized designations at the species level.

Class **BRANCHIOPODA** Lamarck, 1801
 Subclass **PHYLLOPODA** Preuss, 1951
 Order **Diplostraca** Gerstaecker, 1866
 Family **Lioestheriidae** Raymond, 1946
 emend. Holub & Kozur, 1981
 Genus **Pseudestheria** Raymond, 1946

Type species: *Pseudestheria brevis* Raymond, 1946, from Noble County (Oklahoma, U.S.A.) in the Wellington Formation, Leonardian regional stage (late Artinskian Stage, early Permian).

Diagnosis: see Raymond (1946: p. 243), Martens (1983: p. 14), Scholze et al. (2019: p.76), Martens (2020: p. 74).

Fig. 6 - Stereomicroscopic photographs and line drawing of conchostracans from the Le Fraine section (Tregiovo Formation; Kungurian, early Permian); collection no. MUSE-pn20. A) Lateral view on carapace valves marked by concentric lines. B, C) Close-up view and microscopic drawing, showing reduced preservation of concentric (growth) lines towards the umbo. D) Indistinctly preserved structures visible in the umbonal area of the valve that might represent crustacean body appendages (marked by white arrows).

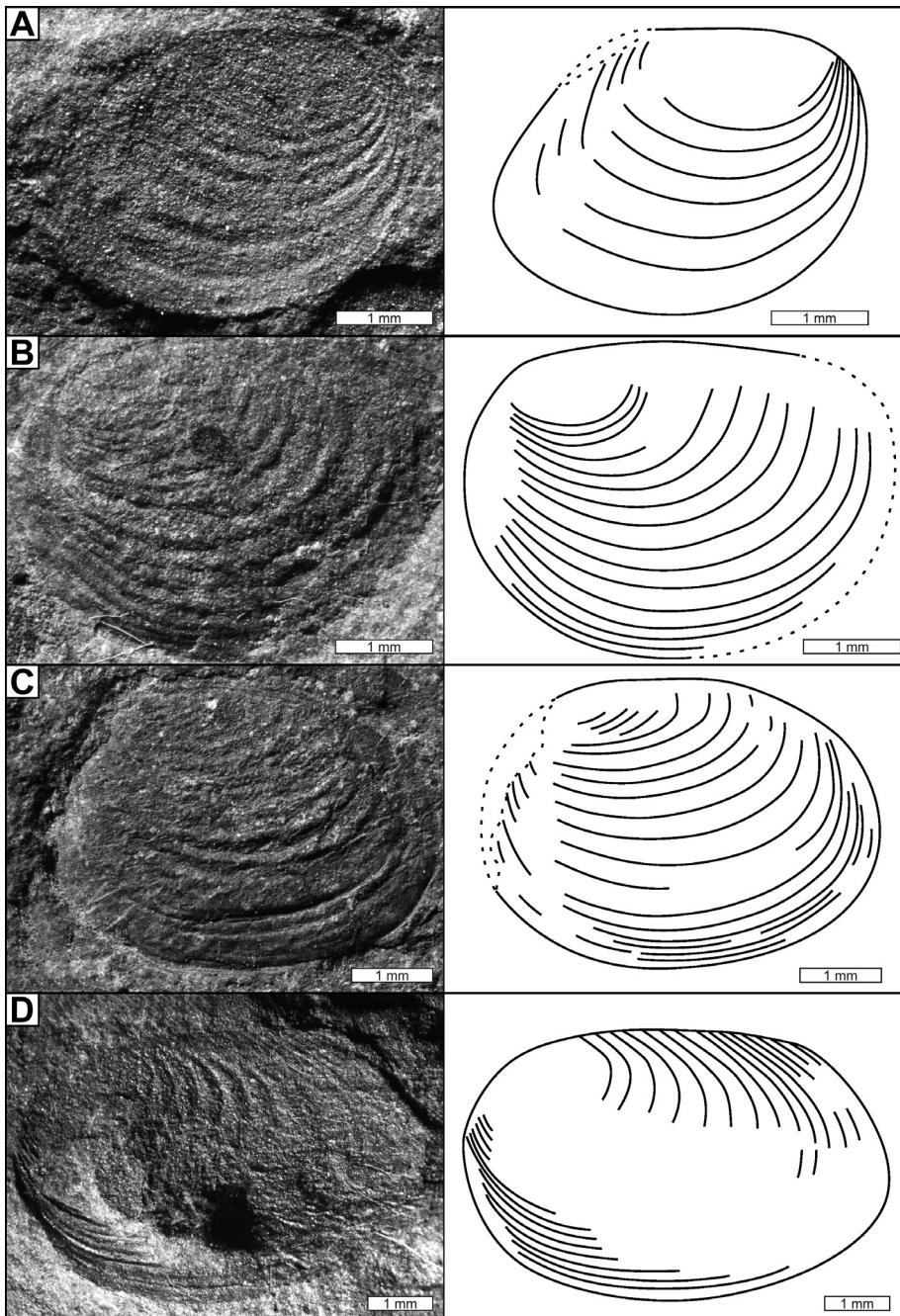


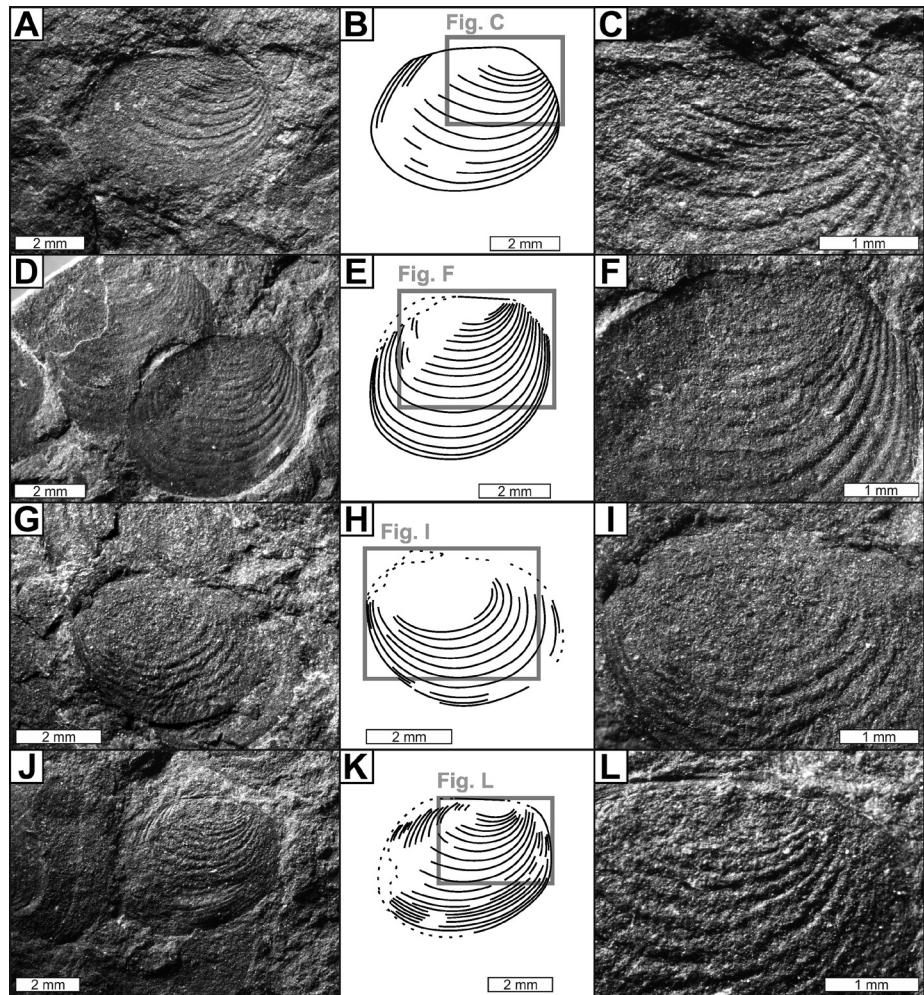
Fig. 7 - Photomicrographs and line drawings showing carapace valves of *Pseudestheria* form Oberbozen from the Guncina Formation (late Kungurian, Early Permian) in the Oberbozen section (N-Italy). A) external side of a right valve; collection number MCSNBS PA-00067d. B) external side of a left valve; MCSNBS PA-00084b. C) external side of a left valve; MCSNBS PA-00061. D) internal side of a right valve; tectonic deformation is evident by the plastic elongation; MCSNBS PA-00067c.

Description. Raymond (1946) described the carapace valves of *Pseudestheria* as oval in shape and having concentric lines or ribs (“lirae or costellae” in Raymond, 1946: p. 243). In general, the genus is poor in distinct morphological characteristics; instead, it includes multiple morphologies ranging between small to very large valves, oval to round shapes of the valves, and straight to slightly curved dorsal margins (Scholze et al. 2019). According to Holub & Kozur (1981: p. 49), the growth bands variable in number reach up to the umbo. Anterior and posterior margins of the carapace valves were described by Holub & Kozur (1981: p. 49) as weak-

ly and strongly rounded, respectively. Based on the original description of this genus, its type species *Pseudestheria brevis* is lacking a distinct ornamentation, but a “punctuation” (Raymond 1946: p. 243) in microstructure can be present.

Remarks. In the opinion of Martens (2020: p. 30), other critical features of the genus *Pseudestheria* are 1) a gutter-like ridged dorsal margin with two dorsal ribs and tightly fanned internal growth lines and 2) a relatively small larval valve with a small sculpture. However, attempts to recognize such tightly fan-like bundled lines on the dorsal margins running towards the umbo would require

Fig. 8 - Microscopic photographs, drawings, and close-ups on the umbonal area of *Pseudestheria* form Oberbozen; all from the Guncina Formation (late Kungurian, early Permian), Oberbozen section (N-Italy). A–C) internal side of a left valve; collection number MCSNBS PA-00067b. D–F) internal side of a left valve; its apparently stout shape is caused by compressive, plastic deformation of the valve; MCSNBS PA-00067a. G–I) external side of a left valve; decreased preservation of both growth lines and concentric ribs towards the umbo results in an apparently large larval valve; MCSNBS PA-00067f. J–L) external side of a right valve; the preservation of growth lines in the umbonal area proves that the larval valve was primary very small; MCSNBS PA-00073a.



a top view on well-preserved dorsal margins, which is not available when studying fossil valves in lateral view.

In some species of *Pseudestheria*, their microstructures are designated as a pitted (e.g., Zharinova et al. 2018; Scholze et al. 2019) or punctate (e.g., Li 2020) ornamentation. More recently, Scholze et al. (2021: fig. 5) also observed microstructures exclusively on the inner side of a carapace valve of *Pseudestheria* sp. aff. *P. limbata* (Goldenberg, 1877) from the Kinney Brick Quarry section (New Mexico, U.S.A., Atrasado Formation, Late Carboniferous) that appear as finely dotted ornamentation.

Besides the records of *Pseudestheria* in the Carboniferous (e.g., Schneider et al. 2022) and Permian (e.g., Schneider & Scholze 2018), this genus name has also been ascribed to conchostracans from Devonian (e.g., Liao & Shen 2022) and Triassic (e.g., Zharinova et al. 2020a, 2020b) rocks. Thus the genus *Pseudestheria* has a wide stratigraphic and geographic distribution.

Pseudestheria form Oberbozen

Figs. 4C, 7, 8

Referred material: MCSNBS PA-00073b (Fig. 4C), MCSNBS PA-00067d (Fig. 7A), MCSNBS PA-00084b (Fig. 7B), MCSNBS PA-00061 (Fig. 7C), MCSNBS PA-00067c (Fig. 7D), MCSNBS PA-00067b (Fig. 8A–C), MCSNBS PA-00067a (Fig. 8D–F), MCSNBS PA-00067f (Fig. 8G–I), MCSNBS PA-00073a (Fig. 8J–L).

Occurrence: Oberbozen outcrop section (Fig. 3A) (also called Soprabolzano section) in the Südtirol Province (also called Alto Adige Province), northern Athesian Volcanic Group, Guncina Formation; upper Kungurian Stage (upper Cisuralian).

Dimensions: H=2.9–4.6 mm, 3.8 mm on average; L=3.8–6.5 mm, 5.1 mm on average; H/L=0.63–0.92, 0.76 on average; l=1.8–4.6 mm, 2.8 mm on average; l/L=0.44–0.73, 0.55 on average; h=0.4–1.5 mm, 0.7 mm on average; h/H=0.09–0.42, 0.21 on average; GL=8–20, 15 on average.

Description. *Pseudestheria* form Oberbozen is characterized by medium- to large-sized carapace valves that are oval to round in shape; the length of the dorsal margin varies between short and apparently long; the umbo is located in median-anterior to slightly anterior-median position, not overtop-

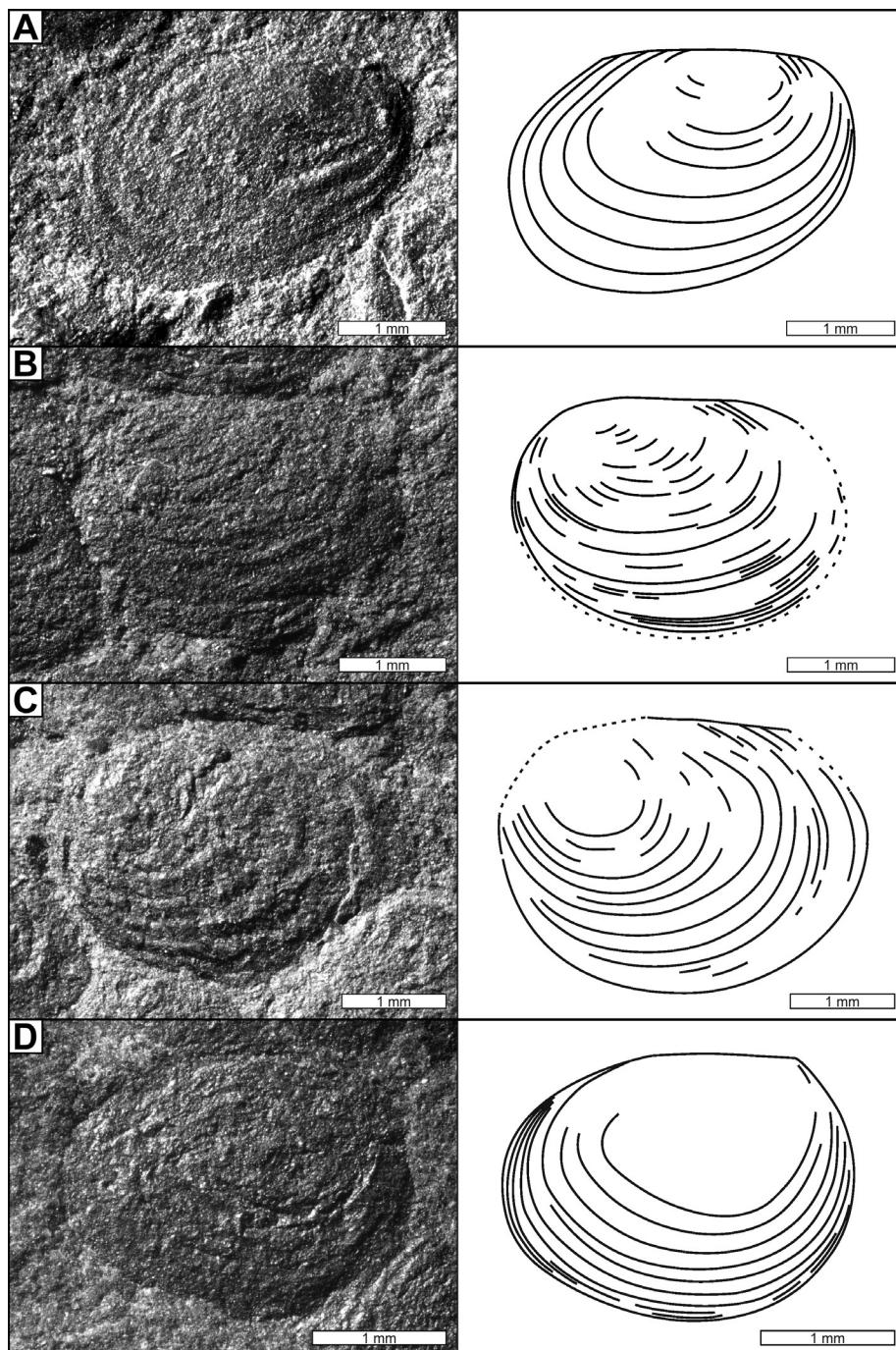


Fig. 9 - Microscopic photographs and line drawings showing carapace valves of *Pseudestheria* form Le Fraine from the Tregiovo Formation (late Kungurian, Early Permian) in the Le Fraine section (Tregiovo Basin, N-Italy). A) external side of a right valve; collection number MUSE-pn23. B) external side of a left valve; MUSE-pn7. C) external side of a left valve; MUSE-pn6. D) external side of a right valve; the seemingly large larval valve is due to reduced preservation of growth lines in the umbonal area; MUSE-pn5.

ping the dorsal margin; the size of the larval valve is very small to small; ornamentation is not visible.

Remarks. The documented wide ranges of the total valve height (H) and total valve length (L), length of the dorsal margin (l), height of the larval valve (h), and respective ratio values (in particular H/L and l/L) indicate a remarkably high degree of morphologic variation in *Pseudestheria* form Oberbozen. Possibly, this is an effect of rock deformation caused by tectonics, resulting in more or less intensive elongation or compression of individual carapace valves.

Pseudestheria form Le Fraine

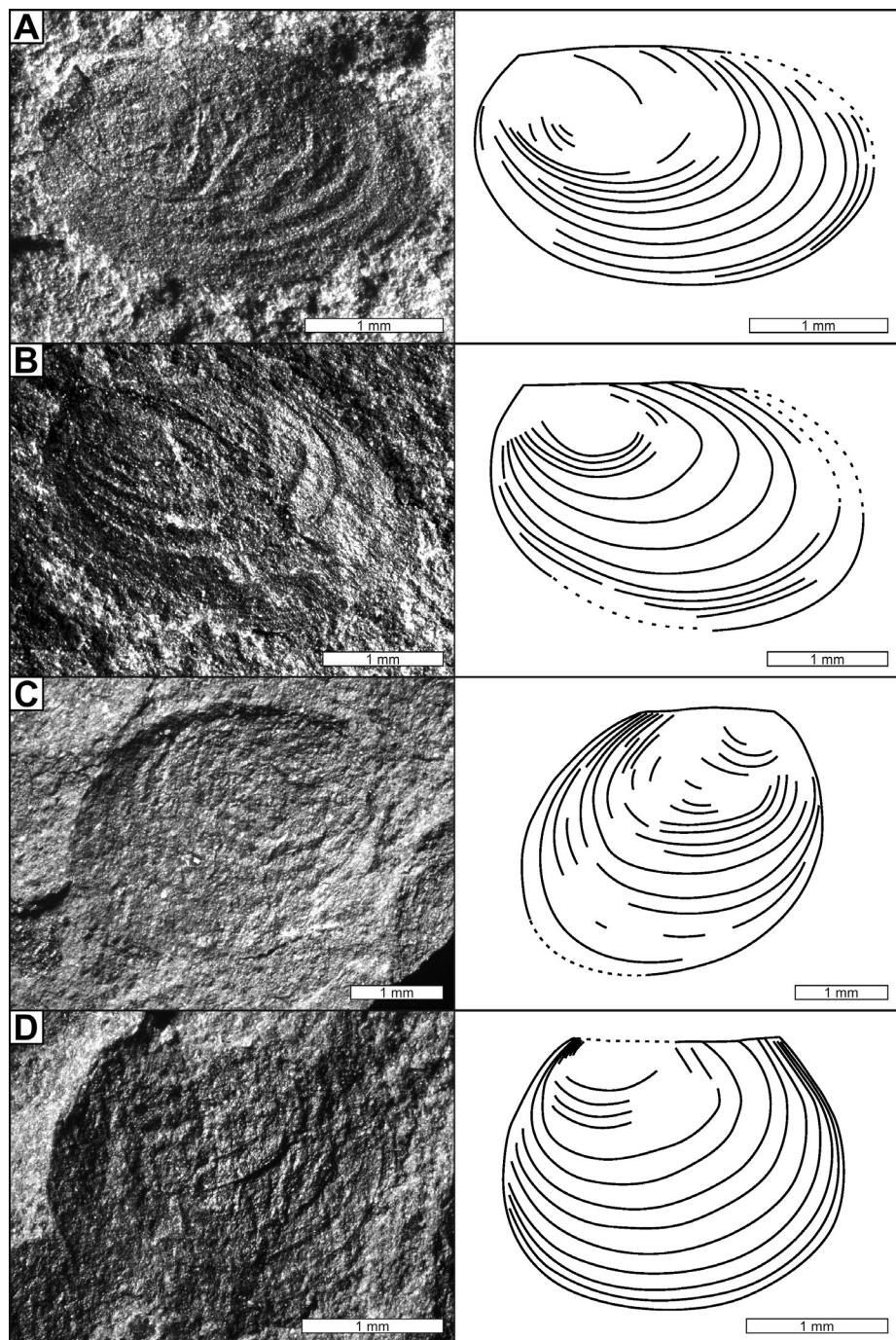
Figs. 6, 9, 10

Referred Material: MUSE-pn20 (Fig. 6), MUSE-pn23 (Fig. 9A), MUSE-pn7 (Fig. 9B), MUSE-pn6 (Fig. 9C), MUSE-pn5 (Fig. 9D), MUSE-pn15 (Fig. 10A), MUSE-pn19 (Fig. 10B), MUSE-pn1 (Fig. 10C), MUSE-pn3 (Fig. 10D).

Occurrence: Le Fraine section (Fig. 3B, C) in the Trentino Province, in the Tregiovo Basin, from the Tregiovo Formation; upper Kungurian Stage (upper Cisuralian).

Dimensions: H=2.0–3.0 mm, 2.4 mm on average; L=2.8–3.9 mm, 3.4 mm on average; H/L=0.59–0.83, 0.70 on average; l=1.4–2.5 mm, 2.1 mm on average; l/L=0.47–0.66, 0.60 on average; h=0.2–1.3 mm, 0.8 mm on average; h/H=0.20–0.62, 0.33 on average; GL=6–18, 11 on average.

Fig. 10 - Microscopic photographs and drawings showing the variation of shape in *Pseudestheria* form Le Fraine; all from the Tregiovo Formation (late Kungurian, Early Permian), Le Fraine section (Tregiovo Basin, N-Italy). A) internal side of a right valve; remnants of growth lines in the umbral area are preserved indistinctly; shape of the valve became elongated secondarily, due to plastic deformation; collection number MUSE-pn15. B) external side of a left valve; slightly elongated deformation towards the postero-ventral margin; MUSE-pn19. C) internal side of a left valve; a slight compressive deformation is evident by the stout shape of the valve; MUSE-pn1. D) internal side of a right valve; stout form of the valve due to compression; well-preserved growth lines, whereas concentric ribs are apparently absent in this valve; MUSE-pn3.



Description. *Pseudestheria* form Le Fraine is characterized by medium- to large-sized carapace valves that are oval to round in shape; the length of the dorsal margin varies between very short and long; the umbo is located in median-anterior to slightly anterior-median position, not overtopping the dorsal margin; the size of the larval valve is very small to large; ornamentation is not visible.

Remarks. Both the total valve height (H) and total valve length (L) of *Pseudestheria* form Le Fraine are less variable than in *Pseudestheria* form Oberbozen. However, pronounced variations in the

ratio values of both the dorsal margin length (l/L) and the larval valve size (h/H) within *Pseudestheria* form Le Fraine has been caused either by tectonic deformation (i.e., elongation or compression of the carapace valves) or by decreased growth line preservation towards the umbo.

DISCUSSION

Taxonomy

The results show that in some individuals

the growth lines are apparently absent (see Figs. 6B–D, 8G–I, 9D, 10A), due to a decrease in fossil growth line preservation towards the umbonal area; therefore, a potentially observed larval valve can incorrectly appear larger than it really was. In such cases, *Pseudestheria* can be easily mistaken for the genus *Lioestheria* Depéret & Mazeran 1912. First conchostracan finds from the Tregiovo Basin were mentioned to share some morphological similarities with the genus *Lioestheria*, but the low amount of specimens was composed of tectonically deformed, taxonomically indeterminable carapace valves (Marchetti et al. 2015: page 186). However, the analysis of multiple individuals from layers of mass-occurrences (e.g., Fig. 5A, 5B) allows for a more complete understanding of the preservational variability, especially along the umbonal areas of both *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine. Both forms show on well-preserved umbonal areas the presence of a larval valve that has been primarily smaller than one-third of the total valve length, and therefore, is in agreement to their determination as *Pseudestheria* following Holub & Kozur (1981: p. 47). On the contrary, larval valves in *Lioestheria* would be expected to be larger than one-third of the total valve size (also following the convention of Holub & Kozur 1981: p. 47). Thus, regarding the genus taxon level, discussions on morphologic similarities between *Lioestheria* (Marchetti et al., 2015) and the studied conchostracan material from the Oberbozen (e.g., Figs. 7, 8) and Le Fraine (e.g., Figs. 9, 10) localities in the Tregiovo Basin are no longer supported, due to their primary small- to very small-sized larval valves. Additionally, larval valves in the present study are lacking both a convexly shaped node and a radial sculpture, but a presence of these larval sculptures would be characteristic for the genus *Lioestheria* (e.g., Martens 1983).

On the species level, *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine can be differentiated from other species or morphotypes in *Pseudestheria* that were described recently by Martens (2020) from Lower Permian deposits in Texas (U.S.A.). The material had been collected by Martens (2020) from the upper Waggoner Ranch Formation and the lowermost Vale Formation, which were discussed by Martens (2020: therein fig. 56) to be of Kungurian age. Therein, a higher number of growth lines and a stronger convexly curved dor-

sal margin in *Pseudestheria brevis* described by Martens (2020: plate 15) from the Mitchel Creek Flats locality, upper Waggoner Range Formation, differ from *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine. Additionally, both a hemispherical sculpture on the larval valve and distinctly sculptured growth bands in *Pseudestheria brevis* (reported by Martens 2020: p. 74) are missing in *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine. Another species, *Pseudestheria megaangulata* Martens, 2020, described by Martens (2020: therein plate 14, figs. 1–7) from the Mitchel Creek and “concho cutbank” localities, upper Waggoner Range Formation, seem to be lacking concentric ribs and are larger than *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine. Finally, a morphotype designated as “*Pseudestheria* sp. V1” by Martens (2020: plate 16) from the Sid McAdams locality, lowermost Vale Formation, is more strongly elongated in shape and smaller in total valve size than *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine.

Another morphotype designated as *Pseudestheria* form Wilhelmsthal by Schneider & Scholze (2018: see therein fig. 2/no. 26; based on “*Pseudestheria* n. sp. W” defined originally by Martens, 1983: p. 29) (Fig. 11) occurs in the Eisenach Formation (Rotliegend Group) of the Thuringian Forest Basin (central Germany). It resembles in its size and shape the valves of *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine, respectively. In comparison, characteristic concentric ribs that can be observed in both *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine are absent in *Pseudestheria* form Wilhelmsthal (see Martens 1983: plates 21, 22); probably, the latter represents a morphologically similar but taxonomically different species.

Another morphotype, designated as *Pseudestheria* form Sentyak (see Schneider et al. 2020: therein fig. 4; for its description see Silantiev et al. 2015: p. 167) (Fig. 11), occurs in the Sentyak outcrop section (Belebey Formation; Kazanian regional stage, lower Roadian, lower Guadalupian) of the Volga-Kama region (Tatarstan, East European Platform). In its carapace valve size and shape, it is very similar to *Pseudestheria* form Oberbozen (Figs. 4, 7, 8). Also the intensity in relief of both growth lines and concentric ribs on the carapace valves are remarkably similar between *Pseudestheria* form Sentyak and *Pseudestheria* form Oberbozen. Possi-

Ma	Period/Age	conchostracan index species/morphotypes	biostratigraphic zones/faunas (from Schneider et al., 2020)
255	Lopingian	<i>Pseudestheria chatangensis</i> 1 mm	" <i>Pseudestheria petri</i> "– <i>Pseudestheria chatangensis</i> fauna
260	Guadalupian	<i>Pseudestheria petri</i> 1 mm	<i>Pseudestheria graciliformis</i> – <i>Palaeolimnadiopsis</i> form Rhinow– <i>Pseudestheria</i> form Lieth assemblage zone
265	Roadian	<i>Pseudestheria exiguia</i> 1 mm	<i>Pseudestheria</i> form Sentyak– <i>Pseudestheria exiguia</i> – assemblage zone
270	Wordian	<i>Curvacornutus mashaensis</i> 1 mm	
275	Kungurian	<i>Hemicycloleaia</i> cf. <i>rhodendorfi</i> 1 mm	
280	Artinskian	<i>Pseudestheria</i> form Oberbozen 1 mm	<i>Lioestheria andreevi</i> – <i>Pseudestheria</i> form Wilhelmsthal assemblage zone
285	Sakmarian	<i>Pseudestheria</i> form Le Fraine 1 mm	
290	Asselian	<i>Lioestheria</i> <i>andreevi</i> 1 mm	
295	Cisuralian	<i>Lioestheria</i> <i>oboraensis</i> 1 mm	<i>Lioestheria extuberata</i> – <i>Lioestheria oboraensis</i> – <i>Pseudestheria</i> form Oberhof assemblage zone
		<i>Pseudestheria</i> form Wilhelmsthal 1 mm	
		<i>Pseudestheria</i> form Oberhof 1 mm	
		<i>Palaeolimnadiopsis</i> <i>obenaueri</i> 3 mm	
		<i>Lioestheria</i> <i>paupera</i> 1 mm	<i>Lioestheria paupera</i> – <i>Pseudestheria</i> palaeoniscorum assemblage zone
		<i>Pseudestheria</i> palaeoniscorum 1 mm	

Fig. 11 - Conchostracan biostratigraphic subdivisions for the Early Permian in Western and Central Europe, and the Middle to Late Permian in Central and Eastern Europe (excerpt from Schneider et al. 2020: therein fig. 4). Positions of *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine (both highlighted in red colour) are based on results of the present study (exemplified individuals shown; cf. Figs. 8B, 9C). Grey coloured intervals of biostratigraphic zones/faunas mark a lack of significant index taxa/morphotypes in the proposed biostratigraphic schema of Schneider et al. (2020).

bly, both valve morphologies represent closely related species. However, neither form is formalized on species level, so far, due to a low number of individuals and limitations in knowledge on the intraspecific and preservational-caused variabilities in the carapace valve morphologies.

Biostratigraphy

On a regional scale, only little data exists from literature, so far, on conchostracan occurrences in the Cisuralian units of the Southern Alps other than the material described in the present study. In particular, Conti et al. (1991: plate 1.4) figured a single frag-

ment of a conchostracan valve assigned informally to “*Esteria*” from the locality Malga Dasdana Busa, Val Dorizzo Member of the Collio Formation. The Collio Formation in the Collio Basin of the Brescian pre-Alps region forms an up to 1500 m thick succession that is divided lithostratigraphically into two members (Cassinis et al. 2012). The lower one, called the Pian delle Baste Member, shows a fining- and thinning-upward trend that ranges from massive coarse-grained sandstones to tabular fine-grained sandstones and laminated mudstones, which represent a lithofacies transition from alluvial fans to sand flats and lacustrine deposits. The upper one, which is called the Val Dorizzo Member, is characterized by sandstones with local intercalations of volcanoclastic deposits (i.e., “Dasdana beds”). Further volcanic rocks both underlying (“Lower Quartz Porphyries”) and overlying (“Auccia Volcanite”) the Collio Formation have been isotopically (U/Pb) dated to 283.1 ± 0.6 Ma and 279.8 ± 1.1 Ma, respectively (Schaltegger & Brack 2007). Thus, the age of the Collio Formation is constrained to the early Kungurian. This makes the sequences of the Collio Formation highly useful for potentially collecting further conchostracan samples through future fieldwork, in order to perform comparisons to the slightly younger aged *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine of the present study. Despite this, neither their palaeogeographic distributions nor their biostratigraphic ranges are fully understood at present, because their respective records are restricted to single localities.

At a larger scale, conchostracan occurrences correlated stratigraphically to the Kungurian Stage are very rarely known from the literature (e.g., Martens 2020). In particular, a “*Lioestheria andreevi*–*Pseudestheria* form Wilhelmsthal assemblage zone” in Schneider & Scholze (2018: p. 376) of late Artinskian to Kungurian age (Early Permian, or even younger; see Schneider et al. 2020: figs. 3, 4) cannot be applied for biostratigraphic correlation, because the index taxon *Pseudestheria* form Wilhelmsthal (Fig. 11) differs morphologically from both *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine. *Pseudestheria* form Wilhelmsthal (= “*Pseudestheria? wilhelmthalensis*” in Martens 2020) had been described from the Eisenach Formation of the Thuringian Forest Basin (central Germany); however, it is poorly constrained to the “late Artinskian–Rodian/Wordian” (Schneider & Scholze 2018: p. 376) or “later? Permian” (Martens 2020: p. 40).

CONCLUSIONS

As demonstrated by previous studies (e.g., Schneider & Scholze 2018; Schneider et al. 2005, 2020, 2022; Martens 2020), conchostracans can be a useful tool for intra- to inter-regional biostratigraphic correlations, especially when using assemblage zones that include several index forms or species (Fig. 11). On the contrary, any single taxon/morphotype from single localities, as it is the case for *Pseudestheria* form Oberbozen and *Pseudestheria* form Le Fraine of the present study, should be handled biostratigraphically with caution. The present study was able to show for the first time some initial arguments for a potential phylogenetic relationship between *Pseudestheria* form Oberbozen (Figs. 4, 7, 8; late Kungurian in age) and *Pseudestheria* form Sent-yak (Schneider et al. 2020; early Roadian in age). Thus, further records of corresponding valve morphologies can be expected from different regions within the critical late Early Permian to early Middle Permian interval. Successive studies seem necessary, for developing an understanding of their full biostratigraphic ranges. Consequently, systematic (bed-by-bed) sampling of tectonically undeformed specimens is recommended in order to formalize the taxonomic names at the species level. Moreover, the combination of both geochronological data (e.g., Avanzini et al. 2007; Marocchi et al. 2008; Cassinis et al. 2012) and conchostracan occurrences from the Southern Alps basins bear high potential for refining the conchostracan biostratigraphic subdivisions (Fig. 11) within the late Early Permian time interval.

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