First occurrence in life position of two Triassic brachiopod species (Thecideida) from NE Italy: Paleoecological considerations

Primer registro en posición de vida de dos especies de braquiópodos triásicos (Thecideida) del NE de Italia: Consideraciones paleoecológicas

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ABSTRACT

The San Cassiano Formation from the Dolomites, NE Italy, is a Ladinian–Carnian (Middle – Upper Triassic) lithostratigraphic unit belonging to the Western Tethys domain. In this formation numerous groups of marine invertebrates from reef communities have been reported. In particular, brachiopods are represented by different orders. Thecideids are the most abundant and diverse, with different species of the genus *Thecospira*. Despite the apparent abundance, only one report exists of a thecideid of the genus preserved in life position: *Thecospira tyrolensis*. In this study, we describe and discuss the first finding of *Thecospira semseyi* and *Thecospira tenuistriata* in life position based on the study of thin sections of Cipit boulders. Seemingly, the *Th. semseyi* shells were not firmly attached to the substrate by a small cementation surface; therefore, they could have lived embedded into the biogenic matrix. By contrast, *Th. tenuistriata* displays an umbonal region modified in a cementation area, allowing the attachment to the bio-builder. Most samples don't show any signal of transport since all specimens are articulated and are still attached to the substrate. Besides, the commissures are partially opened, free of any encrustation of sponge or bryozoan growing. The preservation of brachiopods suggests that the samples of both species were fossilized in life position. Moreover, *Th. semseyi* and *Th. tenuistriata* continued to live although the host's fabric was imbibing the brachiopods' ventral valve. This shows that thecideids were important components of Tethys reef communities.

Keywords: Thecideid brachiopods, San Cassiano Formation, paleoecology, Triassic, Italy.

RESUMEN

La Formación San Cassiano de las Dolomitas, NE de Italia, es una unidad litoestratigráfica del Ladiniano-Carniano (Triásico Medio Superior) que pertenece al dominio del Tethys Occidental. En esta formación se han reportado numerosos grupos de invertebrados marinos de comunidades arrecifales. En particular, los braquiópodos están representados por diferentes órdenes. Los tecideidos son los más abundantes y diversos, con distintas especies del género Thecospira. A pesar de la aparente abundancia, solo existe un reporte de un tecideido del género conservado en posición de vida: Thecospira tyrolensis. En este estudio, describimos y discutimos el primer hallazgo de Thecospira semseyi y Thecospira tenuistriata en posición de vida, basado en el estudio de láminas delgadas elaboradas a partir de olistolitos Cipit. Aparentemente, las conchas de Th. semseyi no estaban firmemente adheridas al sustrato por medio de una pequeña superficie de cementación; por lo tanto, pudieron haber vivido incrustados en la matriz biogénica. Por el contrario, Th. tenuistriata muestra una región umbonal modificada en un área de cementación, lo que permite la unión al bioconstructor. La mayoría de las muestras no presentan señal alguna de transporte, ya que todas las muestras están articuladas y aún están adheridas al sustrato. Además, las comisuras están parcialmente abiertas, libres de cualquier incrustación de crecimiento de esponjas o briozoos. La preservación de braquiópodos permite corroborar que los ejemplares de ambas especies fueron fosilizados en posición de vida. Adicionalmente, Th. semseyi y Th. tenuistriata continuaron con vida a pesar de que el tejido del huésped absorbía la valva ventral de los braquiópodos. Dicha información muestra que los tecideidos fueron componentes importantes de las comunidades del arrecife del Tethys.

Palabras clave: Braquiópodos tecideidos, Formación San Cassiano, paleoecología, Triásico, Italia.

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1. Introduction

The San Cassiano Formation is well-exposed in the vicinity Cortina d' Ampezzo, a town within the Dolomites, NE Italy. It is considered a lithostratigraphic unit belonging to the Western Tethys domain (Feist-Burkhardt *et al.*, 2008). The formation was deposited in the Middle–Late Triassic, particularly in the Ladinian–Carnian, when the climate and paleogeography of the Earth changed drastically. In addition, the increase of volcanic activity during the late Anisian–Ladinian forced pluvialization was causing a substantial decrease in annual mean temperature over the Western Tethys domain (Szulc, 2000, Feist-Burkhardt *et al.*, 2008). Such alterations strongly influenced the marine biotas of the world, especially reef communities. Thus, an important transition in marine faunas' composition and structure can be observed during this time interval, from relatively low species diversity (Ladinian–early Carnian) to a higher diversity during the late Carnian and Norian (Fagerstrom, 1987; Flügel, 2002). In the Late Triassic, a significant renovation of reef invertebrates took place, from sponge-dominated frameworks during the Carnian to coral-dominated associations during the Norian and Rhaetian (Dagys, 1974; Fagerstrom, 1987; Flügel, 2002). In both stages, thecideid brachiopods were already present (Benigni and Ferliga, 1989; Dagys, 1993).

In this context, the San Cassiano Formation is well-recognized by its diversity of reef communities in which numerous marine taxa have been identified and recorded, such as foraminifera, sponges, corals, polychaete galleries, ostracods, gastropods, bivalves, scaphopods, cephalopods, bryozoans, brachiopods, echinoids, holothuroids, ophiuroids, and crinoids (Fürsich and Wendt, 1977; Reitner, 1987; Benigni and Ferliga, 1989; Russo, 2005; Nützel and Kaim, 2014; Hausmann and Nützel, 2015; Sánchez-Beristain and Reitner, 2016, 2017; Roden *et al.*, 2020).

Brachiopods are moderately common in this stratigraphic unit, with specimens from the orders Athyridida, Thecideida, and Terebratulida (Bittner, 1900; Benigni and Ferliga, 1989; Nützel and Kaim, 2014; Hausmann and Nützel, 2015). Thecideids are mainly represented by different species from the genus *Thecospira*. Despite the apparent abundance of these brachiopods in the San Cassiano Formation reported by Benigni and Ferliga in 1989, there is currently only one report of a thecideid from this formation preserved in life position. It is the most abundant species in the unit, namely *Thecospira tyrolensis* (Benigni and Ferliga, 1989). This suggests that preservation is very uncommon. Such information is important since it contributes to the paleoecological knowledge of these Triassic brachiopods, allowing us to know how they were deposited and attached to the substrate in reef environments.

Brachiopods of the Western Tethys domain had a high degree of latitudinal migration in the Tethyan ocean during the Middle-Late Triassic (Dagys, 1993). This work represents the first record of preservation of *Thecospira semseyi* and *Th. tenuistriata* in life position, thus providing more paleoecological knowledge of thecideids as components from Tethys reef communities.

2. Geological setting

The San Cassiano Formation (Ladinian-Carnian,) belongs geographically to the Dolomites. Its type locality can be found in the vicinity of the town of San Cassiano (Figure 1). It was first identified by Münster (1834, 1841), who named it *'Cassianer Schichten'* (i.e., Cassian Beds) referring to San Cassiano, located in the province of Alto Adige. This formation was firstly recognized by von Hauer (1858). It is made up by two members: a Lower Member (Ladinian-Carnian) and an Upper Member (Carnian). Both notably outcrop at the localities of Seelandalpe and Misurina (Figure 1), with a similar lithology, namely strata consisting of interbedded marl and limestone. These strata are considerably rich in fossils (e.g. Fürsich and Wendt, 1977; Russo *et al.*, 1997; Sánchez-Beristain and Reitner, 2016, 2018, 2019; Roden *et al.*, 2020),

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which preservation is extraordinary. Many of them preserve their original mineral composition (Neuweiler and Reitner, 1995; Sánchez-Beristain and Reitner, 2016, 2018), in such an extent that certain localities where this formation outcrops are labelled as Fossil-Lagerstätten (Fürsich, 2000), as well as Liberation Fossil-Lagerstätten according to Roden *et al.* (2020).

Despite the exceptional degree of preservation in the deposits of the San Cassiano Formation (e.g. Hausmann and Nützel, 2015; Roden *et al.*, 2020), it is even higher in the "Cipit" olistoliths, commonly named Cipit boulders in the English language literature (Sánchez-Beristain and Reitner, 2016), and whose etymology derives from the altered toponym of the Tschapit creek (von Richthofen, 1860). These boulders come, for the most part, from patch reefs (e.g Wendt, 1982) and from platform facies -mostly dolomitized- from both the Lower and Upper Cassian Dolomite (Figure 2), which were subjected to subsequent processes of emersion and karstification (Biddle, 1981; Russo *et al.*, 1997). These processes aided the settlement of the olistoliths coming from the platform margins into the San Cassiano basin. (Russo *et al.*, 1997). The boulders subject of this study come entirely from the Upper Member of the San Cassiano Formation (Figure 2), and are mainly composed by automicrite (up to 75%), allomicrite (up to 50%), framestones made up of skeletal components (up to 50%) and primary or secondary cements (up to 10%) as dominant facies. As a rule, automicritic facies and skeletal framestones are mutually exclusive, or, given the dominance of one of them, the other tends to decrease significantly (Sánchez-Beristain and Reitner, 2016, 2017).

The exceptional state of preservation of the "Cassian Patch Reefs" (Wendt, 1982) and their derived Cipit boulders has allowed a broad scope of studies, such as the evaluation of diagenetic pathways (Russo *et al.*, 1991), the determination of palaeotemperatures by means of stable isotopes (Stanley and Swart, 1995) and the finding of almost unaltered organic matter (Neuweiler and Reitner, 1995; Sánchez-Beristain and Reitner, 2012). These erratic reef boulders can be collected at, among other localities, both the Seelandalpe ("Alpe di Specie") or in Misurina, where preservation state is at its best (Sánchez-Beristain and Reitner, 2012).

For further details concerning the geology and stratigraphy of the region, readers are referred to the works of Bosellini and Rossi (1974) and Müller-Wille and Reitner (1993).

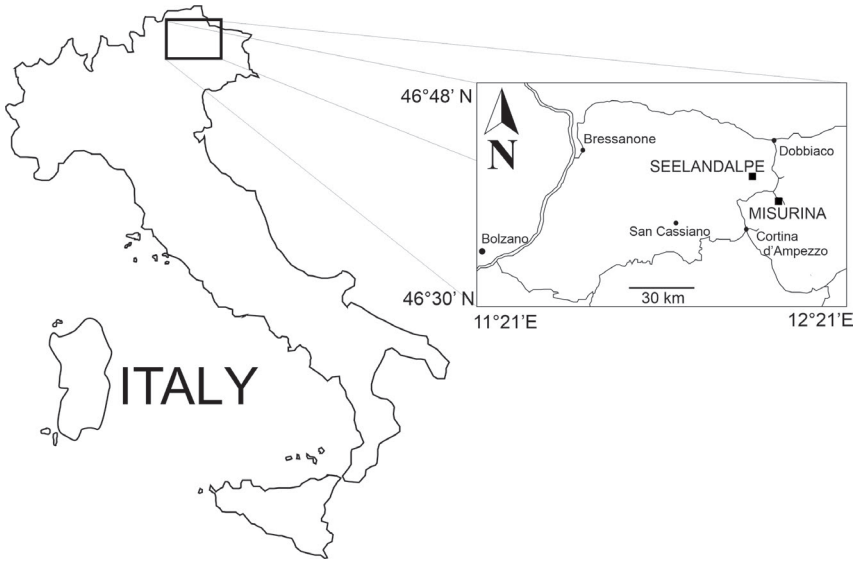

Figure 1 Geographic position of the two localities where material comes from: the Seelandalpe and Misurina near to the town of San Cassiano and to the city of Cortina d'Ampezzo in Alto Adige (modified from Müller-Wille and Reitner 1993).

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3. Material and methods

The material consists of seven complete specimens preserved in thin sections of carbonate rocks from the Triassic (Ladinian-Carnian) of the San Cassiano Formation. The samples are housed in the collections of the Geowissenschafltiches Museum der Universität Göttingen (GZG), and were photographed using a Zeiss Axioplan Microscope with Plan Neofluar Objectives 2.5x, 5x and 10x, and a mounted photographic equipment VISICOL made by Visitron Systems GmbH, Germany.

Supraspecific morphological features were corroborated by means of the Treatise on Invertebrate Paleontology, specifically the chapter of the order Thecideida (Baker, 2006). Analyzed material was identified in the following thin sections: JR X1, FSM XXVI-2, JR III- 19, JR III-66 and JR III-11.

4. Systematic Paleontology

Order Thecideida Elliot, 1958
Superfamily Thecospiroidea Bittner, 1890
Family Thecospiridae Bittner, 1890
Genus *Thecospira* Zugmayer, 1880

Type species. *Thecidea haidingeri* Suess, 1854. Rhaetian (Kitsberg, Austria).

Thecospira semseyi Bittner, 1900
Figures 3A and 3B
Synonymy
Thecospira Semseyi Bittner, 1900, p. 41, pl. 4, figs. 40-65; pl. 5, fig. 1.
Thecospira aff. *Semseyi* Bittner. Scalia, 1910, p. 23, pl. 2, figs. 19, 20.
Thecospira semseyi Bittner. Dagys, 1972, p. 90, 91, 96, text-fig. 2.
Thecospiropsis semseyi (Bittner). Dagys, 1974, p. 75, pl. 27, figs. 1-5, text-figs. 28, 46.
Thecospira semseyi Bittner. Benigni and Ferliga, 1989, p. 521-527, 529-535, 545-547, pl. 57, figs. 4-7; pl. 58, fig. 6; pl. 62, figs. 1-3; text-figs. 4, 7-9, 15, 17B, 25.

Remarks. Brachiopods observed in two thin sections display the typical features of the species *Th. semseyi*. The rectimarginate and plano-convex shell; ventral valve strongly convex; interarea elongated; umbonal region affected by a small cementation surface, with well-defined umbo; and the dorsal valve with reduced inter-area and pointed umbo are traits that allow relating the samples with the species referred. Besides, our specimens coincide in size (shells up to 6.5 mm in length) with those samples described by Benigni and Ferliga (1989) from the San Cassiano Formation. Contrary to previous records of the species, in which have only been reported material detached (e.g. Bittner, 1900; Dagys, 1972, 1974; Benigni and Ferliga, 1989), our specimens are observed as autochthonous components of their depositional environment, preserved in life position.

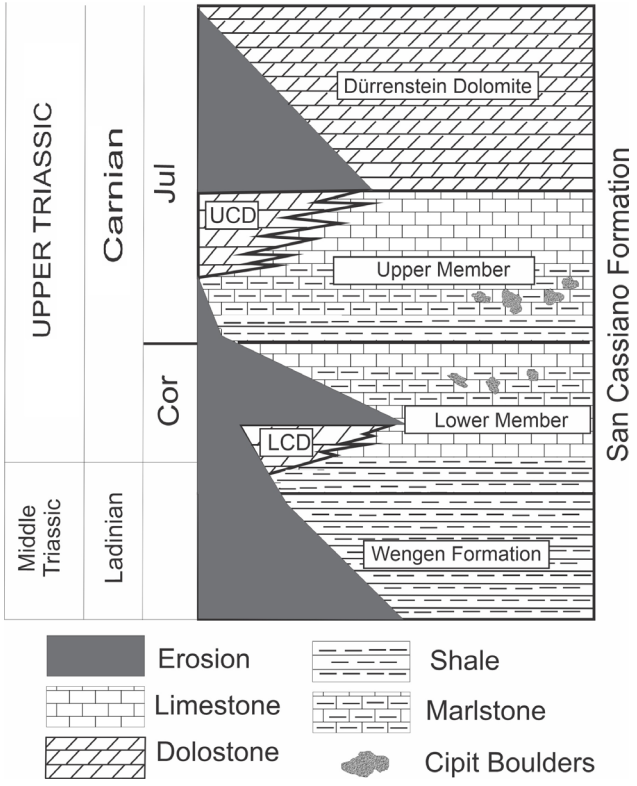

Figure 2 Stratigraphic section of the San Cassiano Formation at the Seelandalpe. LCD: Lower Cassian Dolomite; UCD: Upper Cassian Dolomite. Cor: Cordevolian. Jul: Julian. Modified from Sánchez-Beristain and Reitner (2017).

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Occurrence. Upper Member of the San Cassiano Formation (lower Carnian, Upper Triassic) of the Seelandalpe (Alpe di Specie) and Misurina; Alto Adige, Dolomites, NE Italy.

Thecospira tenuistriata Bittner, 1890
Figures 3C-F

Synonymy
Thecidium sp. Penecke, 1884, p. 383.
Thecospira sp. Bittner, 1888, p. 128.
Thecospira tenuistriata Bittner, 1890, p. 143, pl. 38, figs. 27-31.
Thecospiropsis tenuistriata (Bittner). Dagys, 1974, p. 75.
Thecospira tenuistriata Bittner. Benigni and Ferliga, 1989, p. 518-520, 524, 525, 528, 529, 534-536, 542-545, pl. 57, figs. 8, 9; pl. 58, fig. 4; pl. 61, figs. 1-4; text-figs. 5, 11, 17C, 23, 24.

Remarks. The material displays the traits described for *Th. tenuistriata* from the Carnian (Upper Triassic) of Cortina d' Ampezzo, Italy (Benigni and Ferliga, 1989). The uniplicate and biconvex shell; shells up to 0.75 cm in length; ventral valve moderately convex; umbonal region totally modified in a cementation area, with poorly developed interarea; dorsal valve lesser convex than the opposite valve; in addition to the umbo small and interarea minute are features that allow associating our specimens with this species of the genus *Thecospira*. The samples of *Th. tenuistriata* also were observed in life position, encrusting other invertebrates.

Occurrence. Upper Member of the San Cassiano Formation (lower Carnian, Upper Triassic) of the Seelandalpe (Alpe di Specie) and Misurina; Alto Adige, Dolomites, NE Italy.

5. Discussion

The San Cassiano Formation is a Triassic (Ladinian-Carnian) unit characterized by its high diversity of marine benthic faunas, mainly related to massive reefs and patch reef areas corresponding to the coeval Cassian Dolomite (Wendt, 1982; Sánchez-Beristain and Reitner, 2017). An important part of the San Cassiano Formation is composed of the Cipit boulders, which consist of facies dominated either by microbialites or by distinct reef builders (Reitner, 1987; Russo, 2005; Sánchez-Beristain and Reitner, 2016, 2017). Although sponges are the most common group of the Cipit boulders, other benthic groups have also been recorded as important bio-builder organisms, though in minor proportion, such as scleractinian corals and bryozoans (Fürsich and Wendt, 1977; Russo, 2005; Nützel and Kaim, 2014; Hausmann and Nützel, 2015). Apart from serving as base for the reef structures, these taxa also were a very valuable substratum to different encrusting taxonomical groups such as foraminifera, sponges, corals, serpulids, bivalves, and bryozoans, as well as craniid and thecideid brachiopods (Nebelsick *et al*., 2011). Thus, in these environments proliferated a diverse number of protists and invertebrates, represented by numerous taxa.

In particular, thecideids are abundant in specific localities where Cipit boulders occur. Both complete specimens and dissociated valves can be found. These brachiopods probably descended from the order Spiriferida (Williams *et al*., 2000), and are the last order that appeared in the fossil record. Thecideids are characterized by small shells (though some exceptions), which can cement on hard substrates, especially in cryptic habitats (Simonet Roda *et al*., 2021). They have even been considered brachiopods representing cryptic relicts from the past (Nebelsick *et al*., 2011). Particularly, thecideids are well-recognized in the Carnian of the San Cassiano Formation, highlighting the genus *Thecospira* because of its abundance and specific diversity, represented by *Thecospira tyrolensis, Thecospira semseyi, Thecospira tenuistriata, Thecospira haidingeri* and *Thecospira davidsonii* (Benigni and Ferliga, 1989; Hausmann and Nützel, 2015).

Thecospira samples are frequent in the Cortina d' Ampezzo area, and it is common to find disarticulated valves or complete specimens separated from the substrate. The occurrence of individual valves can be attributed to the abnormally wide gape that facilitates postmortem disarticulation of valves. However, in the case of complete samples,

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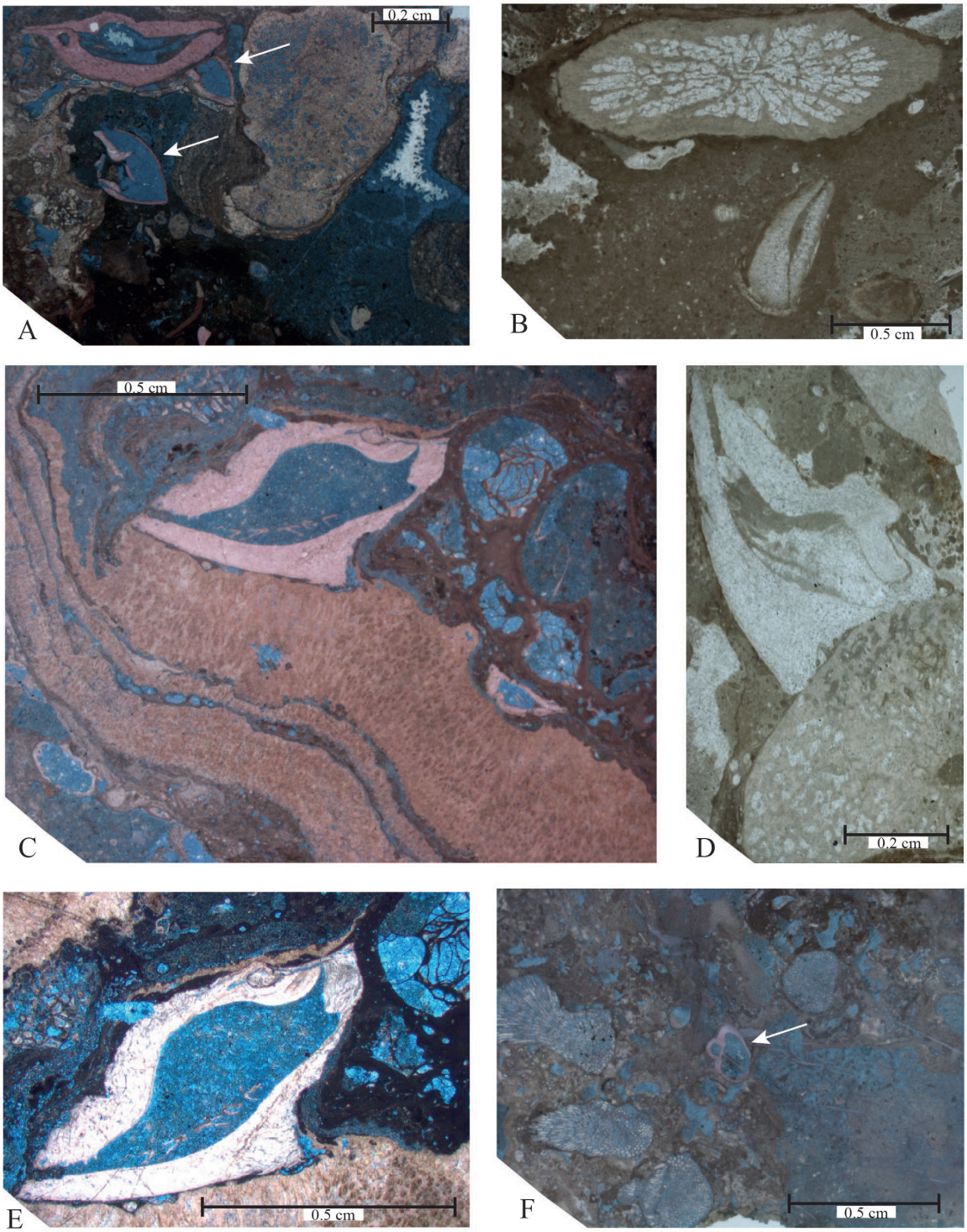

Figure 3 A) *Thecospira semseyi* (arrows) in life position. Specimens are surrounded by an association composed by thick microbialite (dark grey) and frame-building sponges. Sample JR-X1. B) *Th. semseyi* (below) as a part of an association made up of microbialite (dark grey) and scleractinian corals. Sample FSM XXVI-2. C) T*h. tenuistriata* in life position as an encruster/dweller of a framework (the "*Ceratoporella-Tubiphytes*" association; Sánchez-Beristain and Reitner, 2016). Sample JR III-19. D) *Th. tenuistriata* in life position, on top of a frame building sponge. E) Close-up of *Th. tenuistriata* from sample JR III-19, showing part of the spiralia. F) *Th. tenuistriata* in life position within a microbialitic matrix. Sample JR III-11. See text for further details.

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cemented shells could have detached from the substrate (calcareous sponges or coral associations) due to the high energy environment (Benigni and Ferliga, 1989; Baker, 2006). The study made by Benigni and Ferliga (1989) proves this. Their prospection and results included about 273 complete specimens and 719 isolated dorsal valves of all species mentioned. It is worth noting that only one sample of *Th. tyrolensis* was attached to its original substrate, displaying a life position (Benigni and Ferliga, 1989, pl. 60, fig. 3). Even though it has been reported that these brachiopods preferred encrusting calcareous sponges and, to a lesser extent, bivalves and other thecideids, the record of these brachiopods in situ is scarce and uncommon. Given that the different species of *Thecospira* display dissimilar interareas, cementation areas, and shell shapes, added to the poor record of specimens in situ, the finding of *Th. semseyi* and *Th. tenuistriata* in life position in thin sections of calcareous rocks from the San Cassiano Formation allows knowing how these taxa encrusted in biogenic substrates from the Triassic.

In the case of *Th. semseyi*, the shells were apparently not firmly attached to the substrate like in other species of the genus, mainly by the small cementation surface. In Figure 3A two specimens embedded in fabric composed by microbialite and a calcareous sponge are observed, whereas another juvenile brachiopod is encrusting the ventral valve of the larger thecideid. Because *Th. semseyi* inhabited reef environments, it should be strongly joined to any hard substrate; however, it is probable that its cementation surface was not enough. Therefore, apart from being cemented, such brachiopods could have lived embedded into the biogenic matrix, becoming trapped in the host fabric while it was growing (e.g., calcareous sponge). This process may have helped the species resist the high energy high environment. Nonetheless, it is probable that the tissue of the bio-builder had not covered all brachiopods in such a way that shells would be completely uprooted from the substrate and deposited in the calcareous mud (Figure 3B). On the contrary, *Th. tenuistriata* displays an umbonal region totally modified in a cementation area, allowing brachiopods to be attached firmly to the bio-builder. This can be observed in Figure 3D, where the cementation region of the thecideid is evident. Regarding Figures 3C and 3E, apart from the large attachment area, the calcareous sponge fabric is present, growing next to the brachiopod.

It is worth noting that shells studied herein do not show any transport signal, since all specimens are articulated and are still attached to the substrate (except Figure 3B). In addition, the commissures are partially opened, free of any encrustation of sponge or bryozoan growing. In Figure 3A, there is even a complete juvenile specimen encrusting another one. Considering that epibionts are always preserved in situ with respect to their substrate (Torres-Martínez *et al.*, 2021), the features of brachiopods allow corroborating that the samples of both species were fossilized in life position. Given that the finding of these specimens makes it possible to identify the arrangement of the biotic association to the moment of the sedimentary deposit, we noticed that *Th. semseyi* and *Th. tenuistriata* continued alive despite the fabric of the sponge was imbibing the ventral valve of the encrusting brachiopods.

As mentioned above, these brachiopods are common in the Cipit boulders, and are characterized by their facies related to cryptic marine environments. This habitat preference has been associated with their small to minute size, since this feature has allowed them to feed and survive in relatively shallow water (Harper, 2002), avoiding predation by other invertebrates (e.g., echinoids) (Asgaard and Stentoft, 1984). From the Triassic, thecideids began to diversify in cryptic environments, becoming one of the most important encrusters, along with sponges, serpulids, oysters, and bryozoans during the Jurassic and Cretaceous (Nebelsick *et al.*, 2011).

6. Conclusions

Thecideids, and especially the genus *Thecospira*, have been recorded in different localities from the Triassic of the San Cassiano Formation, repre-

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sented by the species *Th. tyrolensis, Th. semseyi, Th. tenuistriata, Th. davidsonii*, and *Th. haidingeri*.

Although the material of these brachiopods is common with both complete specimens and dissociated valves, until now only one specimen of *Th. tyrolensis* had been recorded in life position, being still attached to the original substrate. This study reports the first preservation in life position of *Th. semseyi* and *Th. tenuistriata*.

Apparently, the *Th. semseyi* shells were not firmly attached to the substrate, mainly by the small cementation surface. Hence, apart from being cemented, such brachiopods could have lived embedded into the biogenic matrix, becoming trapped in the host fabric while it was growing. In contrast, *Th. tenuistriata* displays an umbonal region totally modified into a cementation area, allowing brachiopods to be attached firmly to the bio-builder.

Most shells studied do not show any transport signal since all specimens are articulated and are still attached to the substrate. Furthermore, the commissures are partially opened, free of any encrustation of sponge or bryozoan growing. The preservation of the brachiopods suggests that both species were fossilized in life position. Moreover, *Th. semseyi* and *Th. tenuistriata* continued to live despite the fabric of the host was covering the ventral valve of the brachiopods.

Contributions of authors

Miguel A. Torres-Martínez: conceptualization, paleontological descriptions and paleoecological interpretations, writing of the original manuscript. Francisco Sánchez-Beristain: paleoecological interpretations, methodology, writing of the original manuscript, fieldwork, funding. Joachim Reitner: fieldwork, methodology, funding, correction and edition of the manuscript.

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Conflicts of interest

The authors have no conflicts of interest to declare.

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