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Digging into the ancestral stocks of Jurassic lineages: ostracods (Crustacea) from Carnian (Late Triassic) sponge mounds from the Maantang Formation (South China)[☆]

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Abstract – Microbial-sponge reef mounds of the Carnian, Late Triassic, Maantang Formation crop out along the northwestern margin of the Sichuan Basin in South China. Samples from three mounds have been investigated and their ostracod assemblages are here described for the first time. Thirty-three species are present, distributed into 19 genera, including five newly described species: *Carinobairdia cabralae* n. sp., *Hiatobairdia senegasi* n. sp., *Hiatobairdia zhengshuying* n. sp., *Hungarella gommerii* n. sp., *Pontocyprilla goussardi* n. sp. While most of the encountered genera are already known from the Carnian stage worldwide, the Maantang assemblages are precursors in providing the oldest occurrences of the family Schulerideidae, typical of the Middle and Late Jurassic of Europe, and of the genus *Carinobairdia*, which was until now restricted to the Norian-Rhaetian interval. These records demonstrate the underestimated importance of the easternmost Tethys in the early Mesozoic evolution of marine ostracods. Some important Jurassic European taxa might have originated on the eastern margin of the Tethys during the Carnian, migrated to the western Tethys later during the Late Triassic and diversified there up to the record known for the European Jurassic. Microbioerosion trace fossil analysis of associated brachiopod shells revealed *Orthogonum giganteum* as the sole identifiable ichnotaxon and represents the first record of this ichnospecies in Triassic strata. The complete absence of microborings produced by phototrophic trace makers points towards aphotic depths for the deposition of the Maantang Formation, providing independent evidence suggesting that typical shallow water ostracods (*Carinobairdia*, Schulerideidae) radiated in relatively deep settings.

Keywords: ostracods / Carnian / microbial-sponge mounds / Maantang Formation / South China

Résumé – À la découverte des stocks ancestraux de lignées jurassiques : ostracodes (Crustacea) des massifs d'éponges du Carnien (Trias supérieur) de la Formation Maantang (Chine du Sud). Les édifices récifaux d'éponges siliceuses et de microbes de la Formation Maantang (Carnien, Trias supérieur) affleurent le long de la marge nord-ouest du Bassin du Sichuan en Chine du Sud. Des échantillons de trois de ces édifices ont été étudiés et leurs assemblages d'ostracodes sont ici décrits pour la première fois. Trente-trois espèces sont présentes, distribuées en 19 genres, dont cinq espèces nouvellement décrites: *Carinobairdia cabralae* n. sp., *Hiatobairdia senegasi* n. sp., *Hiatobairdia zhengshuying* n. sp., *Hungarella gommerii* n. sp., *Pontocyprilla goussardi* n. sp. Alors que la plupart des genres présents sont déjà connus pendant le Carnien à l'échelle globale, les assemblages de la Formation Maantang sont précurseurs en documentant les plus anciennes occurrences de la famille Schulerideidae, typique du Jurassique moyen et supérieur d'Europe, et du genre *Carinobairdia* qui jusqu'à présent n'était connu que pendant l'intervalle

[☆] This contribution was first published in 2019 but to comply with the 2012 Amendment to the International Code of Zoological Nomenclature regarding availability, all newly described taxa have been registered in ZooBank and the registration numbers are added. This article was updated in 2020.

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Norien-Rhétien. Ces occurrences démontrent l'importance sous-estimée de la Téthys extrême-orientale dans l'évolution des ostracodes marins au Mésozoïque inférieur. Certains taxons jurassiques importants pourraient y avoir trouvé leur origine au Carnien, migré vers l'ouest de la Téthys plus tard au Trias supérieur et s'y être diversifiés, donnant lieu à l'enregistrement connu du Jurassique européen. L'analyse des traces fossiles de microbiéroserion sur les brachiopodes associés révèle *Orthogonum giganteum* comme seul ichnotaxon identifiable et représente le premier enregistrement de cette ichnoespèce dans le Trias. L'absence complète de traces produites par des phototrophes met en évidence les conditions aphotiques de dépôt de la Formation Maantang, apportant une évidence indépendante que la radiation d'ostracodes typiques d'eaux peu profondes (*Carinobairdia*, Schulerideidae) a eu lieu dans des zones relativement profondes.

Mots clés : ostracodes / Carnien / récifs microbes-éponges / Formation Maantang / Chine du Sud

1 Introduction

Comprehensive research on Triassic marine ostracods has been carried on mainly in the 1960s and 1970s and established the baseline of our understanding of their global distribution (Kristan-Tollmann, 1988). However, their Middle and Late Triassic record is strongly biased towards the European Tethys (e.g. Gümbel, 1869; Kollmann, 1960, 1963; Kristan-Tollmann, 1969, 1970, 1971a, b, 1978; Kozur, 1970a, b, 1971a–c; Bolz, 1971a, b; Bunza and Kozur, 1971; Urlichs, 1972; Kozur *et al.*, 1974; Lieberman, 1979; Kolar-Jurkovsek, 1988/89, 1990; Kristan-Tollmann *et al.*, 1991a, b; Bizzarini, 1993; Crasquin-Soleau and Grădinaru, 1996; Crasquin-Soleau *et al.*, 2000; Monostori and Tóth, 2013, 2014; Sebe *et al.*, 2013; Mette *et al.*, 2014; Tóth and Monostori, 2015; Crasquin *et al.*, 2018; Forel and Grădinaru, 2018). Although a number of assemblages from Alaska (Sohn, 1964, 1987), Australia (Kristan-Tollmann, 1986; Dépêche and Crasquin-Soleau, 1992; Kristan-Tollmann and Gramann, 1992), China (Zheng, 1976; Ye *et al.*, 1977; Kristan-Tollmann, 1983; Wei *et al.*, 1983; Guan, 1985), India (Pant and Azmi, 1981; Goel *et al.*, 1984; Kristan-Tollmann and Gupta, 1988); Indonesia (Kristan-Tollmann *et al.*, 1987; Kristan-Tollmann and Hasibuan, 1990), Iran (Kristan-Tollmann *et al.*, 1979, 1980; Kristan-Tollmann, 1991; Crasquin-Soleau and Teherani, 1995), Israel (Sohn, 1968), Jordan (Basha, 1982), Japan (Chablais *et al.*, 2011), Russia (Gramm, 1972, 1975, 1995), Thailand (Ketmuangmoon *et al.*, 2018) and Turkey (Forel *et al.*, 2018, 2019) have been reported, the diversity of eastern Tethys assemblages during the Triassic is still poorly understood. Our knowledge of the emergence of Mesozoic taxa is consequently largely dominated by western-Tethys localities and the importance of the eastern-Tethys might be underestimated, as was already hypothesized by Bate (1977) and Lord (1988). To fill in this gap, we report on the first assemblages of ostracods of Carnian (Late Triassic) age from siliceous sponge-microbe reef mounds of the Maantang Formation of Sichuan Province, South China.

The Sichuan Basin hosts a thick Middle to Upper Triassic sedimentary succession deposited in a foreland basin related to the Indosinian orogenesis (e.g. Luo and Long, 1992; Enos *et al.*, 1998; Li *et al.*, 2003, 2014a). During the Late Carnian, a hexactinellid-thrombolite reef mound tract developed along the northwestern margin of the Sichuan Basin, at the transition between the Chuan Dian Shelf in the east and the Songpan-Ganzi deep marine Trough in the west, which was connected with the Tethys. These mounds were discovered during geologic mapping in 1974–1976 (Wu *et al.*, 1977) and have been studied thoroughly since then (e.g. Wu *et al.*, 1979, 1985; Wu and Zhang, 1982, 1983; Wu, 1984, 1989; Wu and

Reinhardt, 1987; Wendt *et al.*, 1989; Wendt, 2001; Wang *et al.*, 2012, 2015; Zhang *et al.*, 2015; Shi *et al.*, 2017; Jin *et al.*, 2018, 2019). In the recent years, they have attracted an increasing interest aiming at the characterisation of the Carnian Pluvial Event in the Eastern Tethys (e.g. Zhang *et al.*, 2015; Shi *et al.*, 2017; Jin *et al.*, 2018, 2019). Ostracods within the Maantang Formation have been noticed in thin-sections from the mounds and inter-mounds areas but they were never studied in detail (Wendt *et al.*, 1989; Shi *et al.*, 2017; Jin *et al.*, 2018). For the present analysis, ostracod assemblages have been obtained from samples of three mounds of the Maantang Formation exposed in the Sichuan Province, South China, and their taxonomic composition and significance are described and discussed for the first time. The principal aim of this analysis is to add to the scientific understanding of marine ostracods during the Carnian stage, Late Triassic, by reporting on the still poorly known eastern tethyan fauna. We record the earliest occurrence of the family Schulerideidae, which is an important component of the Middle and Late Jurassic assemblages of Europe (e.g. Bate, 1977). This occurrence is in line with other fossil groups such as crinoids (Hagdorn, 2011) and microbiéroserion trace fossils reported here: they provide an important support to the assumption of Bate (1977) and Lord (1988) that ancestral stocks of Jurassic lineages might have been introduced into the northwest Europe from the eastern Tethys during the Late Triassic.

2 Geological setting and studied samples

2.1 Geographical and paleogeographical context

During the Triassic, the South China Block was located between the Panthalassa to the east and the seas and seaways of the Paleo- and Neo-Tethys to the west. The Yangtze Platform corresponds to most of the present-day Guizhou Province as well as parts of Sichuan, Yunnan, Guangxi, and Hunan provinces. The Sichuan Basin is located on the northern margin of the South China Block: it belongs to the western Yangtze Platform and was bathed by the eastern Tethys. From the Late Precambrian to the Middle Triassic, it was the place of shallow-water carbonate deposition (e.g. Luo and Long, 1992; Enos *et al.*, 1998; Li *et al.*, 2003, 2014b). On the eastern margin of the Longmen Mountains situated in the northwestern part of the Sichuan-Chongqing district (Fig. 1A), Middle Triassic platform peritidal carbonates culminated in lower Carnian facies of siliceous sponge-microbe reef mounds. At the Middle-Late Triassic transition, most of the Yangtze Platform sited in the Yunnan, Guizhou, Guangxi and southern Sichuan provinces became emerged, with the northwestern margin of

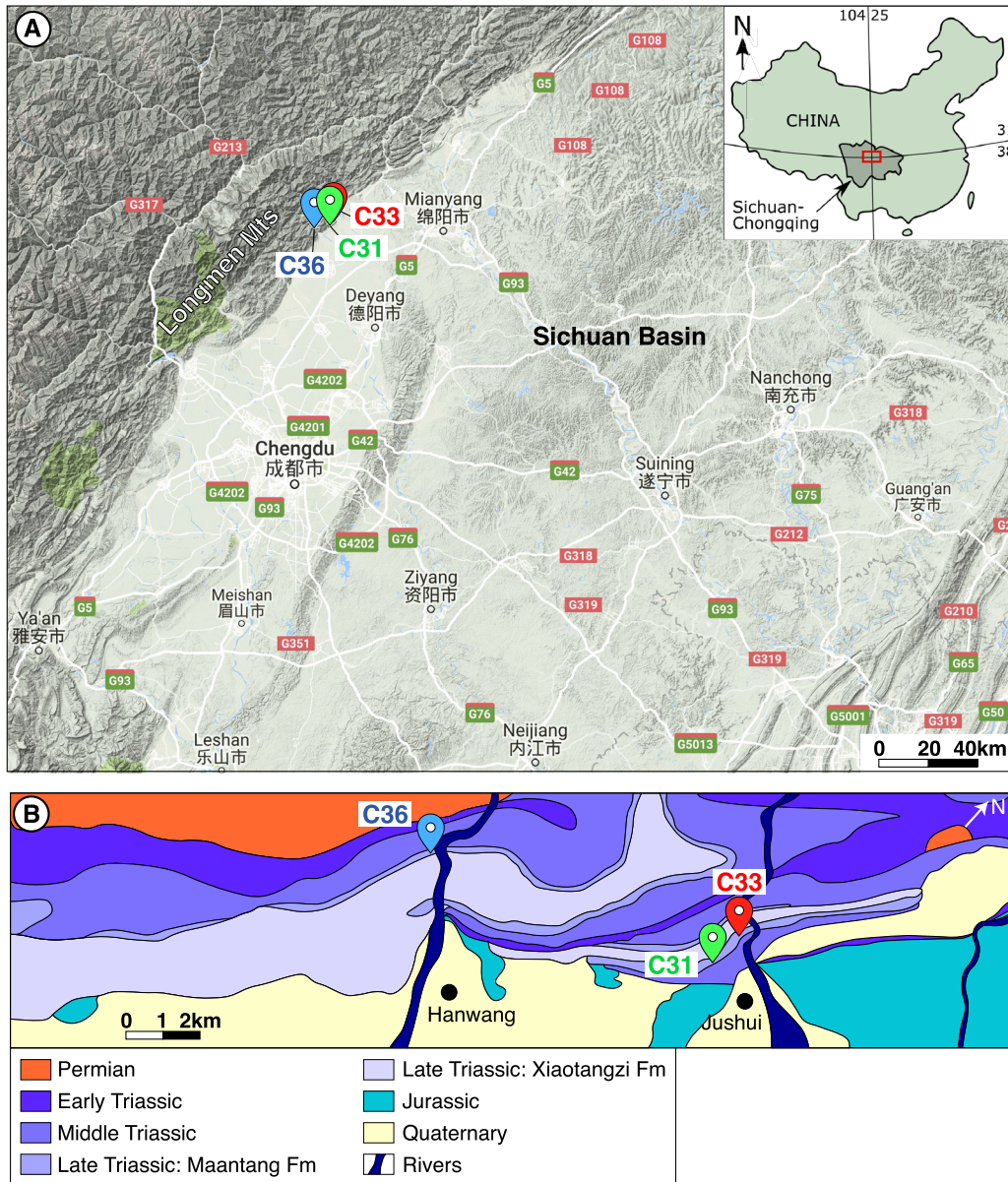


Fig. 1. A. Geographical and topographical map of the northwestern margin of the Sichuan Basin, South China (Google Maps, 2018), showing the locations of the three studied mounds (C31, C33 and C36). B. Simplified geological map showing the position of the studied mounds (redrawn for Wu, 1989 and Jin *et al.*, 2018).

northern Sichuan remaining drowned and covered with dark mudstones (*e.g.* Liu and Xu, 1994). The Yangtze Platform was terminated by the Carnian and never resumed so that the overlying Norian deposits are typically braided river systems emptying into coastal swamps (*e.g.* Lehrmann *et al.*, 2015; Minzoni *et al.*, 2015). A detailed synthesis of the Triassic facies history in the studied area is provided in Feng *et al.* (1997) and Enos *et al.* (2006).

The palaeogeography of northwestern Sichuan during the Carnian-Norian time interval is shown in Figure 2. During this interval, the deep marine Songpan-Ganzi Trough, located in Ganzi-Aba region in the west of Sichuan, was connected with the northern Tibet oceanic basin of the Tethys. From the beginning of the Carnian onwards, a marine transgression took place from the northwest to the southeast and led to the

development of a shallow marine gulf farther east (Fan, 1979). This embayment was limited by the Qinling-Daba Old Land in the north and the Kangdian Old Land in the south (Wu, 1989; Wang *et al.*, 2012). The siliceous sponge-microbe reef mounds were located at the transition between the Chuan Dian Shelf in the southeast and the Songpan-Ganzi Trough in the northwest (Figs. 1A and 2). The disappearance of the microbial-sponge mounds coincides with a sharp transition to terrigenous sedimentation, which has been correlated with the Carnian Humid Episode (Shi *et al.*, 2009, 2017; Wang *et al.*, 2015) corresponding to an increase in rainfall that caused input of terrigenous sediments and black shales deposition into sedimentary basins (*e.g.* Simms and Ruffell, 1989). A recent work on the Maantang Formation challenged this idea by showing that the sudden demise of the microbial-sponge mounds

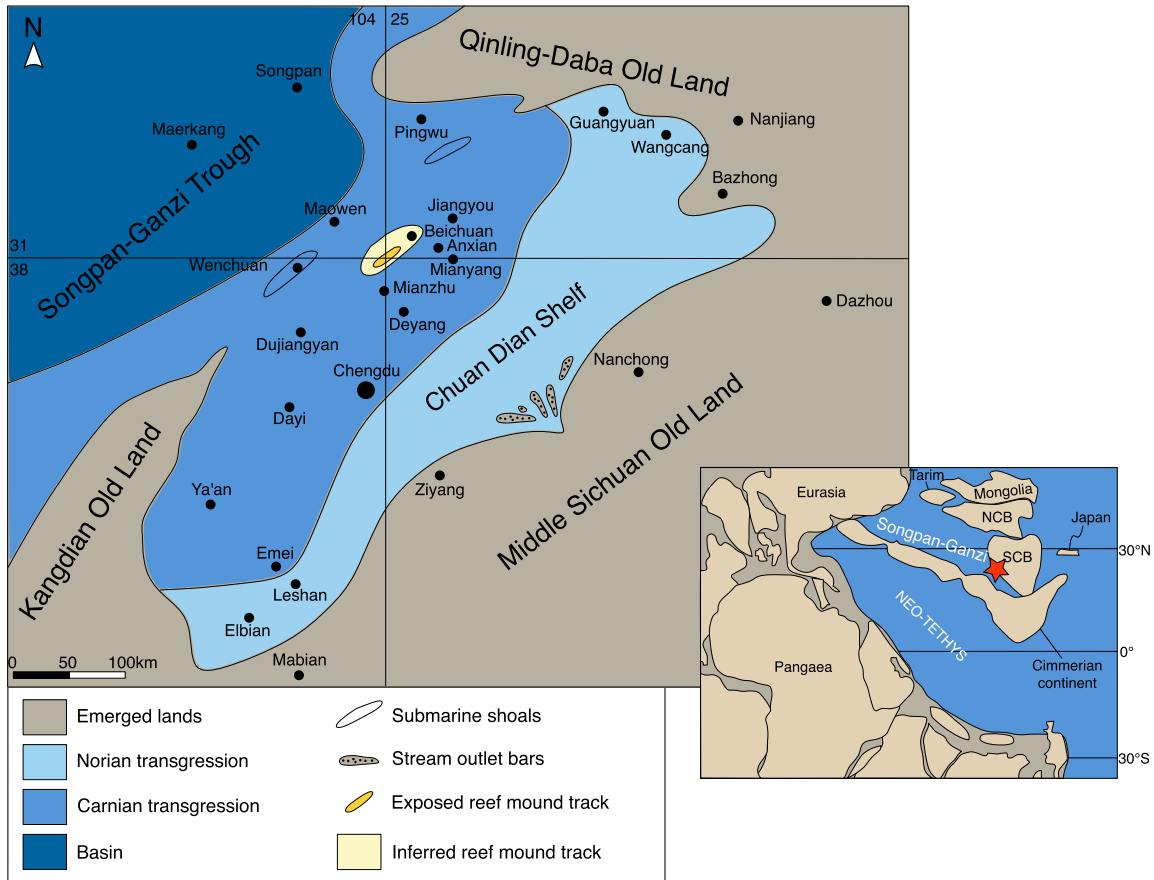


Fig. 2. Carnian to Middle Norian (Late Triassic) palaeogeography of the northwestern margin of the Sichuan Basin, South China (modified from Wu, 1989 and Wang *et al.*, 2012). Inset on the lower right part shows a Late Triassic reconstruction of the Tethyan area (modified from Besse *et al.*, 1998 and Golonka, 2007). SCB: South China Block, NCB: North China Block.

in the Hanwang area was related to paleoenvironmental changes due to the development of a foreland basin rather than to the Carnian Humid Episode (Jin *et al.*, 2018). The absence of distinctive palynological associations described in the western Tethys during the Carnian Humid Episode (*e.g.* Roghi, 2004; Roghi *et al.*, 2010; Mueller *et al.*, 2016) seems to further confirm that the succession in the Hanwang area is younger than the Carnian Humid Episode (Jin *et al.*, 2019).

2.2 Geological and stratigraphical contexts

The Middle and Upper Triassic deposits exposed in the northwestern Sichuan Basin are divided into the Tianjingshan, Maantang (sometimes written Ma'antang) and Xiaotangzi formations in ascending order (Figs. 1B and 3). The studied samples are issued from the Maantang Formation so that only general characteristics are given for the underlying Tianjingshan and overlying Xiaotangzi formations and the reader is referred to Wu (1989), Wang *et al.* (2012, 2015), Shi *et al.* (2017), Jin *et al.* (2019) and references therein for further details. It is worth noting that several articles discussing the hexactinellid-thrombolite reef mound tract developed in this region attribute it to the Upper Hanwang Formation (*e.g.* Wu, 1989; Wendt, 2001; Wang *et al.*, 2012, 2015) while more recent contributions attribute it to the Maantang Formation (*e.g.* Zhang *et al.*, 2015; Shi *et al.*, 2017;

Jin *et al.*, 2018, 2019). The Maantang Formation is subdivided into four sub-units, the mounds being part of the Unit 2 (*e.g.* Shi *et al.*, 2017) or Unit 3 (Jin *et al.*, 2019). This formation has been considered as the nearshore equivalent of the Hanwang Formation (Wu, 1989) and in recent contributions the Hanwang Formation has been considered as “approximately [...] corresponding to Maantang Formation” (Wang *et al.*, 2015, p. 188). The recent works of Shi *et al.* (2017) and Jin *et al.* (2018, 2019) scrutinized the Maantang Formation exposed at the Guanyinya section (sometimes written Guanyin Ya), which is one of the sections where a mound (labelled C36) attributed to the Hanwang Formation is analysed here (called Han II or Guanyinai in Wu, 1989 and Wendt, 2001). Furthermore, on the geological map of the studied area provided by Wu (1989), recently re-illustrated by Jin *et al.* (2018), the distribution of the Hanwang Formation has also been replaced by the Maantang Formation (Fig. 1B). For these reasons, we will therefore refer to the Maantang Formation. The sedimentary succession exposed at the Guanyinya section shown by Shi *et al.* (2017) is redrawn in Figure 3.

2.2.1 Tianjingshan Formation

The Tianjingshan Formation consists of light grey thin- to medium-bedded calcimicrobe-bearing wackestones and dolo-

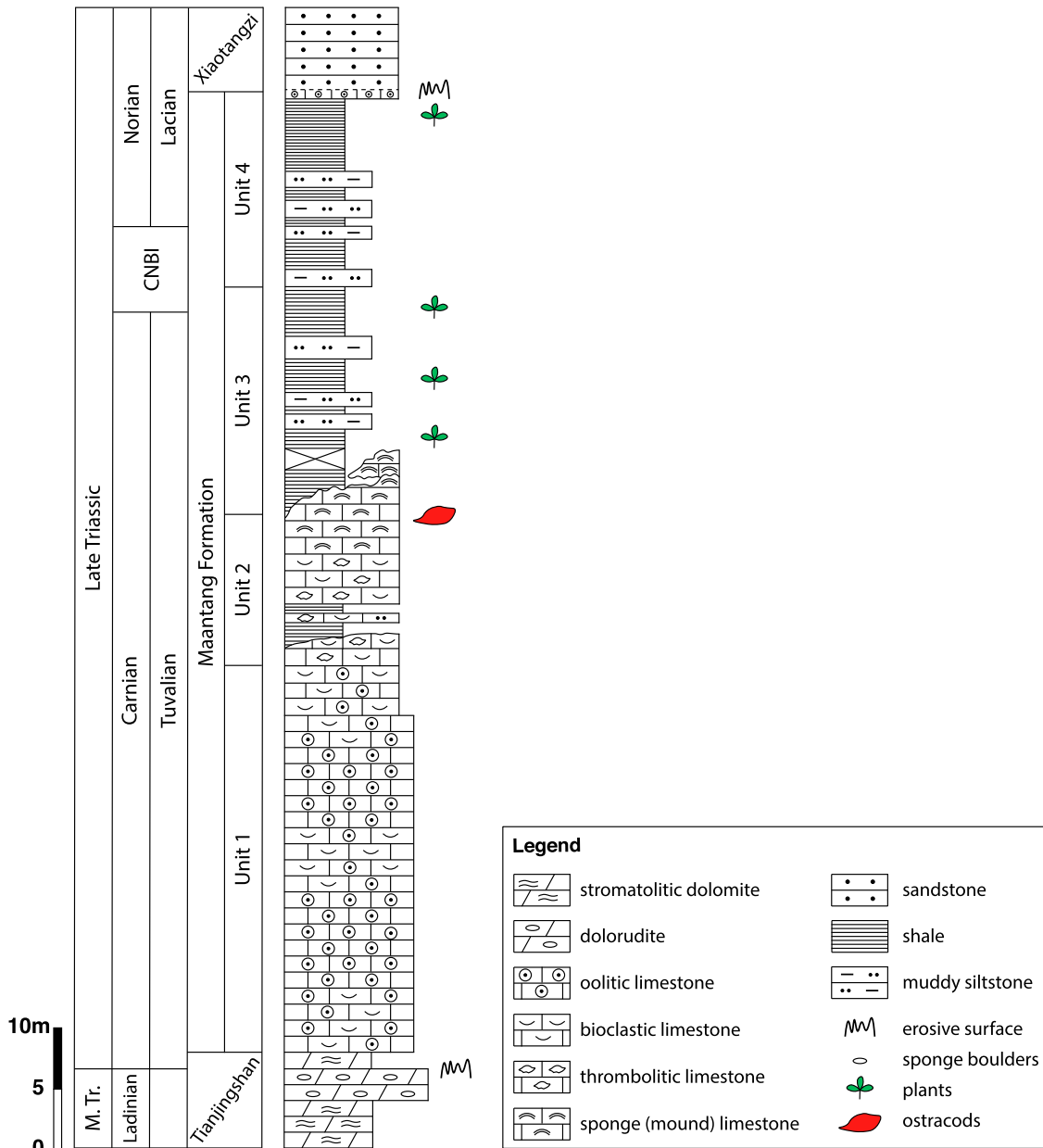


Fig. 3. Facies and lithologic units of the Upper Triassic Maantang Formation at Guanyinya section, Hanwang, Sichuan Province, in the central part of the western margin of Sichuan Basin (from Shi *et al.*, 2017 and Jin *et al.*, 2019). CNBI: Position of the Carnian-Norian boundary interval based on Jin *et al.* (2019).

mitic wackestones, with stromatolite at the top. Its thickness ranges from 77 to 150m in the southwestern part of the Sichuan-Chongqing district and reaches more than 600 m in the northeastern area. The contact with the overlying Maantang Formation is regarded as an unconformity by most of the researchers (e.g. Wu, 2009; Li *et al.*, 2014a, b; Shi *et al.*, 2017; Jin *et al.*, 2018) and as conformable by Wang (1992). This formation contains rare macrofossils, including only few ammonoid fragments for age attribution. A Ladinian age has been proposed based on pelecypods and brachiopods (Wu, 1989) and the Ladinian-Carnian boundary was placed at the transition from the Tianjingshan to the Maantang Formations by the discovery of the long-ranging Carnian conodont *Quadratella polygnathiformis* in the lower Maantang Formation

(Shi *et al.*, 2017). However, the occurrence of a Carnian foraminiferal association from the upper part of the Formation (He, 1980) and a revision of the conodonts in the closely located Jushui section both indicate that the uppermost Tianjingshan Formation should be assigned a Carnian age (Jin *et al.*, 2019). It represents an evaporitic tidal flat (Wu, 1989).

2.2.2 Maantang Formation

The Maantang Formation consists of oolitic limestones, bioclastic limestones and microbial-sponge mounds overlain by dark grey shales, calcareous silty mudstones and muddy siltstones. The Maantang Formation is subdivided into four lithological units labelled from 1 to 4 in ascending order, which

display high variability in the different regions (see details in Shi *et al.*, 2017).

The Unit 1 is mainly made of massive oolitic limestone with bryozoans, brachiopods, ostracods, echinoderms, bivalves, sponge spicules, gastropods and scarce algae. Ooids occur in grainstones or packstones, indicating changing hydrodynamic conditions. In Guanyinya section, grainstones with oncoids, fragments of thrombolites and bioclasts (brachiopods, ostracods, gastropods, echinoderms, bivalves and foraminifers) occur at the base of the Unit 1, indicating a high-energy environment. Another massive bioclastic limestone of about 4 m thick occurs in the middle part of Unit 1 in Guanyinya with abundant bioclasts (sponges, bryozoans, brachiopods, ostracods, echinoderms) and microcrystalline matrix, indicating low energy conditions (Shi *et al.*, 2017).

The Unit 2 (corresponding to Unit 3 in Jin *et al.*, 2018, 2019) corresponds to a bioclastic packstone and sponge mound facies. It is mainly composed of microbial-bioclastic limestone, sponge boundstone and interbedded shale. Individual mounds are up to 80 m thick, with inter-mound deposits being only one-fifth of the mound thickness. Close to the mounds, transported sponge skeletons are common. At the base of the mound sequence are some probably reworked ooids, while the upper part contains numerous hexactinellid sponges. The predominant skeletal components are hexactinellid sponges, most of which appear in their original growth position (*e.g.* Wendt, 2001). *Terebella* worm tubes encrust many sponge skeletons (Wendt *et al.*, 1989). The mound-dwelling fauna is dominated by pelecypods and brachiopods (mostly terebratulids), followed by gastropods and ammonoids. The marginal mound and inter-mound areas are dominated by crinoid remains (including holocrinids, isocrinids and some pentacrinids; see Thuy, 2013), brachiopods (mostly terebratulids), small ammonoids and other mollusc remains. Rare bryozoans, sponge spicules, miliolid foraminifers and ostracods were observed in thin sections (Wendt, 2001). In Guanyinya, the pervasive micritic matrix in the thrombolitic boundstone and sponge boundstone indicates that the mounds deposited in a low-energy environment (Shi *et al.*, 2017).

The Unit 3 is mainly composed of greyish black to dark grey sandy shale, mudstone and siltstone where plant remains and pyrite nodules are common. It represents a distinct marine flooding in the western Sichuan Basin during the Carnian (*e.g.* Li *et al.*, 2014b). Ammonoid taxa from a shale level above the sponge mounds in Jushui suggest an early Late Carnian age, *i. e.* early Tuvallian (Shi *et al.*, 2017). The upper part of the Unit 3 is poorly fossiliferous.

The Unit 4 mainly consists of shale with interbedded siltstone with common plant remains and pyrite nodules. It is not highly fossiliferous so that biostratigraphic context is complex to establish. In Guanyinya section, the topmost of the Maantang Formation is an oolitic grainstone, which is truncated by the erosive base of the Xiaotangzi Formation.

A magnetostratigraphic study at the Qingyangou section (also written Qingyan Gou, called Han I in Wu (1989) and Wendt (2001)), located 1.5 km east from Guanyinya section, concluded that the Maantang Formation might span the Julian 2 and that the transition to the Xiaotangzi Formation is at the Julian/Tuvallian boundary (Zhang *et al.*, 2015). This model was later revised to incorporate biostratigraphic information, leading to the attribution of the Units 1 and 2 to the Julian,

Early Carnian, and of the Units 3 and 4 to the Tuvallian, Late Carnian (Wu, 1989; Wang, 1992; Shi *et al.*, 2017). However, a recent work improved the determination of the ammonoid assemblage from the closely located Jushui section, which rather indicates a Late Tuvallian, Late Carnian, to early Norian age, in line with palynological associations (Jin *et al.*, 2019).

Overall, the facies succession of all sections studied so far document a carbonate drowning sequence (*e.g.* Shi *et al.*, 2017; Jin *et al.*, 2019), the Unit 3 representing an outer ramp (*e.g.* Wu, 2009; Wang *et al.*, 2015). The lithological change from the Unit 2 to the Unit 3 and the occurrence of neptunian dykes on top of the sponge-microbial build-ups have been interpreted as karst formed during subaerial exposure, and is considered as a chronostratigraphic boundary between the Lower and Upper Carnian, in line with biostratigraphic information (Shi *et al.*, 2017). In several localities including Qingyangou and Guanyinya sections, the karst is followed by the brief re-establishment of sponges (Shi *et al.*, 2017). The main sponge mound ecosystem developing during the Julian might have been terminated by an interval of subaerial exposure. The second period of mound development during the subsequent transgression might have been inhibited and ultimately terminated by freshwater and clay-rich sediment influx during the Carnian Pluvial Phase (Shi *et al.*, 2017). However, no erosive surface indicative of a hiatus was observed by Jin *et al.* (2018) and the conodont biostratigraphy rather implies that the Qingyangou section is younger than proposed by Zhang *et al.* (2015) and Shi *et al.* (2017) (Jin *et al.*, 2019). The conodonts, ammonoids and bivalves association in Qingyangou section imply a Tuvallian, Late Carnian age, for the microbial sponge mounds and that the Carnian-Norian boundary interval should be placed in the upper part of Unit 3 (Fig. 3).

2.2.3 Xiaotangzi Formation

The boundary between the Maantang Formation and the Xiaotangzi Formation is marked by a local unconformity (Zhang *et al.*, 2013). The Xiaotangzi Formation is widely distributed within the Sichuan Basin and consists of quartz arenite, coarse lithic arenite with calcite cement. These sediments are thought to have deposited between the littoral and a delta (Wu, 1989; Li *et al.*, 2003). It is tentatively dated to the Norian (Wu, 1989; Li *et al.*, 2003) but diagnostic fossils are missing (Deng *et al.*, 1982; Wu, 2009) so that its basal part could be of Tuvallian age (Shi *et al.*, 2017). The remaining part of the Xiaotangzi Formation is made of fluvial sandstone with common horizontal, cross and ripple bedding (Wu, 1989; Mei and Liu, 2017). This formation contains rare macrofossils and few ammonoid fragments for age attribution.

2.3 Material and methods

In the studied region, several active pits quarry the limestone and interbedded marlstone for the production of concrete. The marlstone intercalations within the microbial-sponge buildups are fossiliferous and yielded disarticulated echinoderms (mostly crinoids), articulate brachiopods, bryozoans, sponges and bivalves. For the present analysis, three samples (labelled C31, C33, C36) stored in the Muschelkalkmuseum Ingelfingen and described by Wendt *et al.* (1989) and Wendt (2001) have been studied. These samples of loose

material from weathered block surfaces were collected and simply washed and sieved under running water by Hans Hagdorn. The sample C31 originates from a mound exposed in a quarry in Jiancaogou, about 4 km northwest of Jushui (Wendt, 2001). Its coordinates are N31°28.925', E104°12.736' (Figs. 1A and 1B). Sample C33 originates from a mound exposed at a quarry in Muoziping, Shichanggou, about 2 km north of Jushui, which coordinates are N31°29.677', E104°13.623' (Figs. 1A and 1B). Sample C33 is extremely rich in fossils in all sieved fractions. Sample C36 originates from a mound exposed on the right bank of the Hanwang River, about 3 km northeast of Hanwang. It corresponds to a natural section of mound and underlying formations, also called Guanyinya or Guanyin Ya in Shi *et al.* (2017) and Jin *et al.* (2018), and Han II or Guanyinai in Wu (1989) and Wendt (2001). Its coordinates are N31°28.349', E104°08.834' (Figs. 1A, 1B and 3). It is dominated by articulate brachiopods, numerous mollusc fragments and echinoderms. The exact position of the sample C36 within the mound at Guanyinya is not known so it is placed in the middle of the major mound development in Figure 3. To characterize the palaeobathymetric setting of the studied samples, we performed an analysis of the microendolithic traces on brachiopods from two of the three studied mounds. For this purpose, eight brachiopods each from samples C31 and C33 were cleaned with hydrogen peroxide and an ultrasonic bath, before vacuum cast-embedding was performed to produce epoxy resin replicates of the positive infills of microborings (see Wisshak, 2012 for a detailed outline of this method). These were sputter-coated with gold and imaged with a Tescan VEGA3 XMU SEM.

3 Systematic paleontology (by Marie-Béatrice Forel)

In the present contribution, we follow the general classification of Moore (1961) and Horne *et al.* (2002). The taxonomy of the Cytheroidea, Cytheruridae, is based on the revisions of Whatley and Boomer (2000); Bythocytheridae taxonomy follows Schornikov (1990). Overall, the material recovered from the Maantang Formation is recrystallised and the preservation is relatively poor. Isolated valves are often weathered and the internal details are rarely observed. Because of the preservation state and low abundance, the diagnostic features of many species can not be fully appreciated so that many species are here kept in open nomenclature. In the systematic discussion, species left in open nomenclature, except for peculiar ones, are omitted but all species are illustrated to allow future comparison and understanding of these unique assemblages (Tab. 1; Plates 1–5). For morphological descriptions, we follow Maddocks (2015) in that the degree of slope of the antero-dorsal and postero-dorsal borders is measured on external lateral views of the carapaces or valves, with 0 being horizontal. The length convention is: < 0.40 very small, 0.40–0.50 small, 0.50–0.70 medium, 0.70–1.00 large, > 1.0 very large. In all height/length diagrams (Figs. 4 and 5), right and left valves are distinguished for both isolated valves and complete carapaces. This distinction allows accounting for difference of size between the valves and its possible variations through the ontogeny. It furthermore constrains the large dispersal of the H/L scatter plots when

specimens are plotted without distinction, including overlap intensity. For most of the species described here, left and right valves clearly plot separately (e.g. Figs. 4A, 4C, 4H and 5), illustrating the value of using such plotting methods. All specimens are deposited in the collections of the Muschelkalkmuseum Ingelfingen under the inventory numbers MHI2169/1 to MHI2169/73.

Abbreviations used in the text are as follow: L: length; H: height; W: width; AB: anterior border; VB: ventral border; PB: posterior border; DB: dorsal border; LV: left valve; RV: right valve; AV: antero-ventral border; PVB: postero-ventral border; ADB: antero-dorsal border; PDB: postero-dorsal border.

Class Ostracoda Latreille, 1806

Subclass Podocopa Müller, 1894

Superfamily Bairdioidea Sars, 1887

Family Bairdiidae Sars, 1887

Genus *Bairdia* McCoy, 1844

Type species. *Bairdia curta* McCoy, 1844 subsequently designated by Ulrich and Bassler (1923).

Bairdia anisicaforma Monostori, 1994

(Plates 1B and 1C)

1994 *Bairdia anisicaforma* Monostori: 315, figs. 3/6, 7.

? 2011 *Bairdia anisicaforma* Monostori; Forel and Crasquin: fig. 4D.

? 2011 *Bairdia anisicaforma* Monostori; Forel *et al.*: pl. 1, fig. 2.

2019 *Bairdia anisicaforma* Monostori, 1994 in Forel *et al.*: 10, 11, fig. 5T.

Material. Two right valves.

Dimensions. L = 868–880 µm, H = 433–460 µm (this material).

Occurrences. ? South Tibet, South China, Anisian, Middle Triassic (Forel and Crasquin, 2011; Forel *et al.*, 2011); Bakóny Mountains, Hungary, Late Carnian, Late Triassic (Monostori, 1994); Kilek section, Tavusçayiri Block, Sorgun Ophiolitic Mélange, southern Turkey, Huglu Tuffite, *Tetraporobrachia haeckeli* radiolarian Zone, Julian, Early Carnian, Late Triassic (Forel *et al.*, 2019); sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvallian, Late Carnian, Late Triassic (this work).

Remarks. The occurrence of *Bairdia anisicaforma* Monostori, 1994 from the Anisian, Middle Triassic, of Tibet (Forel and Crasquin, 2011; Forel *et al.*, 2011; the same specimen is illustrated in both contributions) is questioned because the illustrated specimen has a much shorter posterior margin than the type-material and because its ornamentation consists of concentric ridges rather than pits as described for *Bairdia anisicaforma*. This species is in need of revision to allow the clarification of its generic attribution, which seems close to *Hiatobairdia* Kristan-Tollmann, 1970. Only a re-examination of the type-material as well as new specimens, including complete carapaces, will allow the resolution of this issue.

Bairdia jiangyouensis Xie in Wei, Li, Jiang and Xie, 1983 (Plates 1D–1F)

1983 *Bairdia jiangyouensis* Xie in Wei *et al.*: 56, 57, pl. 15, fig. 8.

Material. One complete carapace, 2 right and 3 left valves.

Dimensions. See Figure 4A.

Occurrences. Kuahongdong Formation, Sichuan Province, South China, Norian, Late Triassic (Wei *et al.*, 1983);

Table 1. Taxonomic list of all ostracod species identified from the Maantang Formation, Hanwang and Jushui, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic.

Class **Ostracoda** Latreille, 1806
Subclass **Podocopa** Müller, 1894
Order **Podocopida** Sars, 1866
Suborder **Bairdiocopina** Gründel, 1967
Superfamily **Bairdioidea** Sars, 1865
Family **Bairdiidae** Sars, 1865
Acratia sp. 1 [C36]
Bairdia anisicaforma Monostori, 1994 [C36]
Bairdia jiangyouensis Xie in Wei *et al.*, 1983 [C36]
Bairdia cf. *peneovoidea* Bolz, 1971 [C33, C36]
Bairdia sp. 1 [C33, C36]
Bairdia? sp. 2 [C36]
Bairdia sp. 3 [C36]
Bairdia sp. 4 [C33, C36]
Bairdiacypris? sp. 1 [C36]
Bairdiacypris sp. 2 [C36]
Carinobairdia cabralae Forel n. sp. [C33, C36]
Carinobairdia sp. [C36]
Hiatobairdia senegasi Forel n. sp. [C33, C36]
Hiatobairdia zhengshuyingii Forel n. sp. [C36]
Isobythocypris sp. 1 [C36]
Isobythocypris sp. 2 [C36]
Ptychobairdia sp. [C36]
Superfamily **Cypridoidea** Baird, 1845
Family **Pontocypridae** Müller, 1894
Pontocyprilla goussardi Forel n. sp. [C36]
Superfamily **Cytheroidea** Baird, 1850
Family **Bythocytheridae** Sars, 1928
Monoceratina sp. [C33, C36]
Praebythoceratina sp. [C33]
Family **Cytheruridae** Müller, 1894
Eucytherura sp. [C36]
Family **Limnocytheridae** Klie, 1938
Simeonella sp. in Kristan-Tollmann *et al.*, 1991b [C33]
Family **Schuleriidae** Mandelstam, 1959
Schuleriidea? sp. [C36]
Family indet.
Cytheroidea gen. and sp. indet. 1 [C36]
Cytheroidea gen. and sp. indet. 2 [C36]
Cytheroidea gen. and sp. indet. 3 [C36]
Suborder **Metacopina** Sylvester-Bradley, 1961
Superfamily **Healdiidea** Harlton, 1933
Family **Healdiidae** Harlton, 1933
Hungarella gommerii Forel n. sp. [C31, C33, C36]
Hungarella postacuta Xie in Wei *et al.*, 1983 [C33]
Hungarella subtera Zheng, 1976 [C31, C33, C36]
Hungarella sp. 1 [C33, C36]
Hungarella sp. 2 [C36]
Order **Platycopida** Sars, 1866
Suborder **Platycopina** Sars, 1866
Superfamily **Cavellinoidea** Egorov, 1950
Family **Cavellinidae** Egorov, 1950
Bektasia sp. [C36]
Subclass **Myodocopa** Sars, 1866
Order **Myodocopida** Sars, 1866
Superfamily **Polycopoidea** Sars, 1866
Family **Polycopidae** Sars, 1866
Polycopa sp. [C36]

sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. Recently, Crasquin *et al.* (2018) noted that *Bairdia* sp. 3 from the Carnian of Sicily might be conspecific with *Bairdia* sp. 7 from the Rhaetian of the Northern Calcareous Alps (Mette and Mohtat-Aghai, 1999). These species are closely related to *Bairdia jiangyouensis* Xie in Wei *et al.*, 1983 as shown by their size, elongate posterior end, overlap of LV over RV along dorsal and ventral margins, ADB and DB straight and end of PDB very concave upward. However, the PB of the European species is more tapered with maximum of convexity located more ventrally, so that they are kept distinct from *Bairdia jiangyouensis* Xie in Wei *et al.*, 1983 until more material is obtained to clarify their relationship. Similarly, *Bairdia* sp. 1 from the Carnian of Turkey (Forel *et al.*, 2019) shows similar lateral outline but it is significantly smaller from the above-mentioned species. Based on the size difference of the specimens from the Maantang Formation, two ontogenetic stages are recognized for *Bairdia jiangyouensis* Xie in Wei *et al.*, 1983, in all likelihood A-1 and Adult (Fig. 4A). Although the material is not abundant in Wei *et al.* (1983) and in the present work, changes in the elongation of the carapaces as well as a lowering of the AB position are observed from A-1 to Adult stages. Changes in the elongation of the carapaces between these stages have also been recognized for several modern Bairdiidae (Smith and Kamiya, 2002; Yousef and Moustafa, 2017).

***Bairdia* cf. *peneovoidea* Bolz, 1971b**

(Plates 1G–1I)

Material. Five complete carapaces and one left valve.

Dimensions. See Figure 4B.

Occurrences. Samples C33, C36, Maantang Formation, Jushui and Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The present species is close to *Bairdia peneovoidea* Bolz, 1971b from the Late Norian-Rhaetian interval of the Alps (Bolz, 1971b) by its auriform and sub-rectangular massive morphology in lateral view. However, it differs by its less high and less convex dorsal margin, Hmax developed along all dorsal margin, anterior margin larger and dorsal margin tripartite at RV. It also differs from *Bairdia* cf. *peneovoidea* Bolz, 1971b in Kristan-Tollmann *et al.*, 1979 from the Rhaetian of Iran (Kristan-Tollmann *et al.*, 1979) which has a triangular dorsal overlap and a less uniformly rounded anterior margin. The present species might be new to science but its massive bairdiid morphology is quite frequent, so that more material is needed to clarify the conspecificity of these species or to clearly assess their diagnostic characters.

***Bairdia* sp. 3**

(Plates 1J and 1K)

Material. One posteriorly broken carapace, one left valve, several fragments.

Dimensions. L = 889 µm, H = 492 µm (dimensions of the left valve; Plate 1J).

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The present species is close to *Bairdia maantangensis* Xie in Wei *et al.*, 1983 from the Norian, Late Triassic of Kuahongdong Formation, Sichuan Province, South

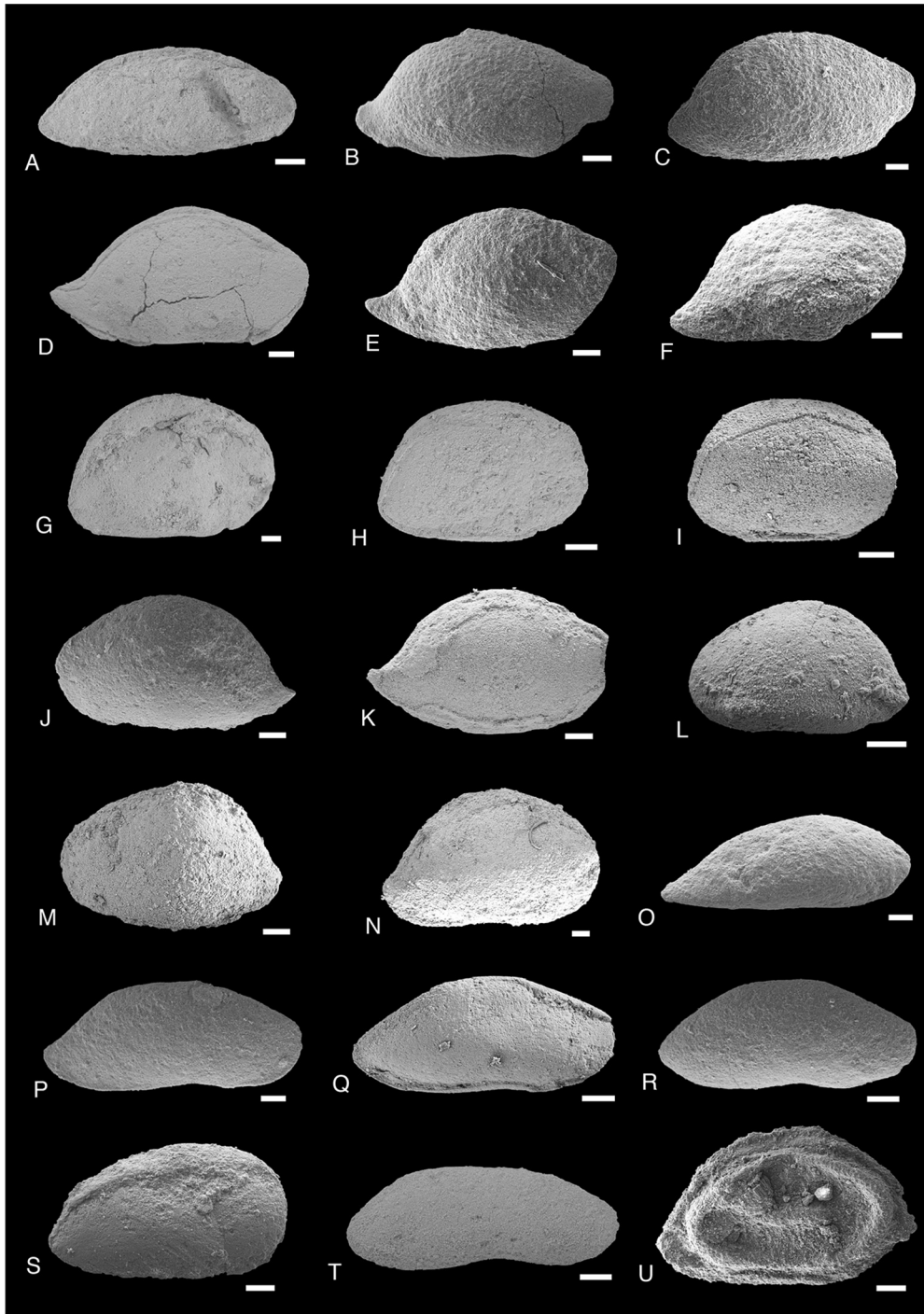


Plate 1. Ostracods from the Maantang Formation, Hanwang and Jushui, Sichuan Province, South China, Tuvlian, Late Carnian, Late Triassic. **A:** *Acratia* sp. 1, right lateral view of a complete carapace, sample C36, MHI2169/1; **B, C:** *Bairdia anisicaforma* Monostori, 1994, B: lateral view of a right valve, sample C36, MHI2169/2; C: lateral view of a right valve, sample C36, MHI2169/3; **D–F:** *Bairdia jiangyouensis* Xie in Wei *et al.*, 1983, D: right lateral view of a complete carapace, sample C36, MHI2169/4; E: lateral view of a right valve, sample C36, MHI2169/5; F: lateral view of a right valve, sample C36, MHI2169/6; **G–I:** *Bairdia* cf. *peneovoidea* Bolz, 1971b, G: right lateral view of a complete carapace, sample C36, MHI2169/7; H: right lateral view of a complete carapace, sample C36, MHI2169/8; I: right lateral view of a complete carapace, sample C33, MHI2169/9; **J, K:** *Bairdia* sp. 3, J: lateral view of a left valve, sample C36, MHI2169/10; K: right lateral view of a complete carapace, sample C36, MHI2169/11; **L–N:** *Bairdia* sp. 1, L: lateral view of a left valve, sample C33, MHI2169/12; M: lateral view of a left valve, sample C33, MHI2169/13; N: right lateral view of a complete carapace, sample C33, MHI2169/14; **O:** *Bairdia?* sp. 2, lateral view of a right valve, sample C36, MHI2169/15; **P:** *Bairdia* sp. 3, lateral view of a right valve, sample C36, MHI2169/16; **Q, R:** *Bairdia* sp. 4, Q: right lateral view of a complete carapace, sample C36, MHI2169/17; R: lateral view of a right valve, sample C36, MHI2169/18; **S:** *Bairdiacypris?* sp. 1, right lateral view of a complete carapace, sample C36, MHI2169/19; **T:** *Bairdiacypris* sp. 2, lateral view of a right valve, sample C36, MHI2169/20; **U:** *Carinobairdia cabralae* Forel n. sp., U: holotype, right lateral view of a complete carapace, sample C33, MHI2169/21. All scale bars are 100 μ m.

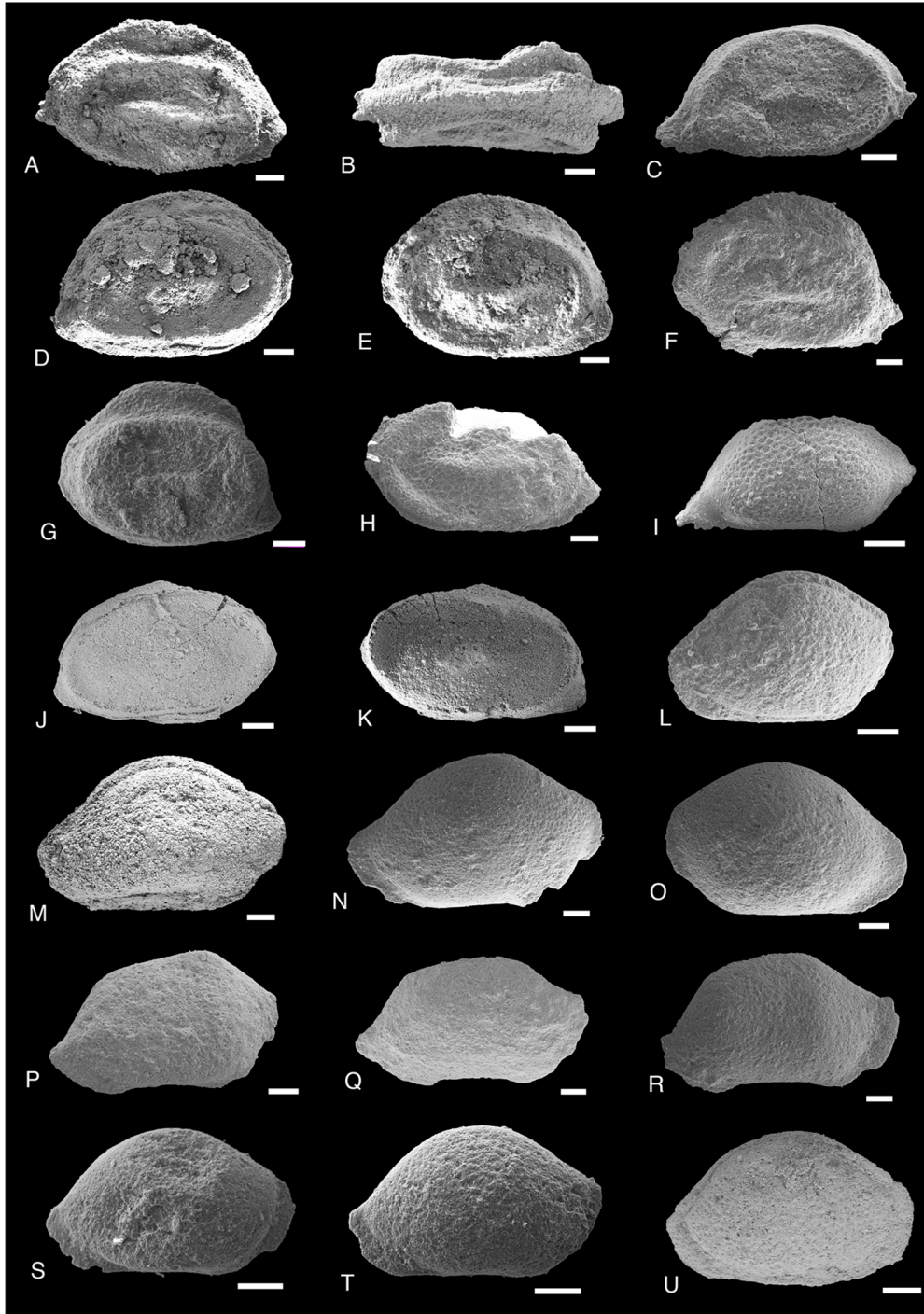


Plate 2. Ostracods from the Maantang Formation, Hanwang and Jushui, Sichuan Province, South China, Tuvlian, Late Carnian, Late Triassic. **A–I:** *Carinobairdia cabralae* Forel n. sp., A: holotype, same specimen as in [Plate 1U](#), left lateral view; B: same specimen, dorsal view; C: paratype 1, right lateral view of a complete carapace, sample C36, MHI2169/22; D: paratype 2, right lateral view of a complete carapace, sample C33, MHI2169/23; E: same specimen, left lateral view; F: lateral view of a left valve, sample C33, MHI2169/24; G: lateral view of a left valve, sample C36, MHI2169/25; H: lateral view of a left valve, sample C33, MHI2169/26; I: lateral view of a right valve, sample C36, MHI2169/27; **J, K:** *Carinobairdia* sp., J: right lateral view of a complete carapace, sample C36, MHI2169/28; K: same specimen, left lateral view; **L–R:** *Hiatobairdia senegasi* Forel n. sp., L: paratype, right lateral view of a complete carapace, sample C36, MHI2169/29; M: holotype, right lateral view of a complete carapace, sample C33, MHI2169/30; N: lateral view of a right valve, sample C36, MHI2169/31; O: lateral view of a left valve, sample C36, MHI2169/32; P: lateral view of a right valve, sample C36, MHI2169/33; Q: lateral view of a right valve, sample C36, MHI2169/34; R: lateral view of a right valve, sample C36, MHI2169/35; **S–U:** *Hiatobairdia zhengshuyingi* Forel n. sp., S: paratype 2, lateral view of a right valve, sample C36, MHI2169/36; T: paratype 1, lateral view of a right valve, sample C36, MHI2169/37; U: right lateral view of a complete carapace, sample C36, MHI2169/38. All scale bars are 100 μm .

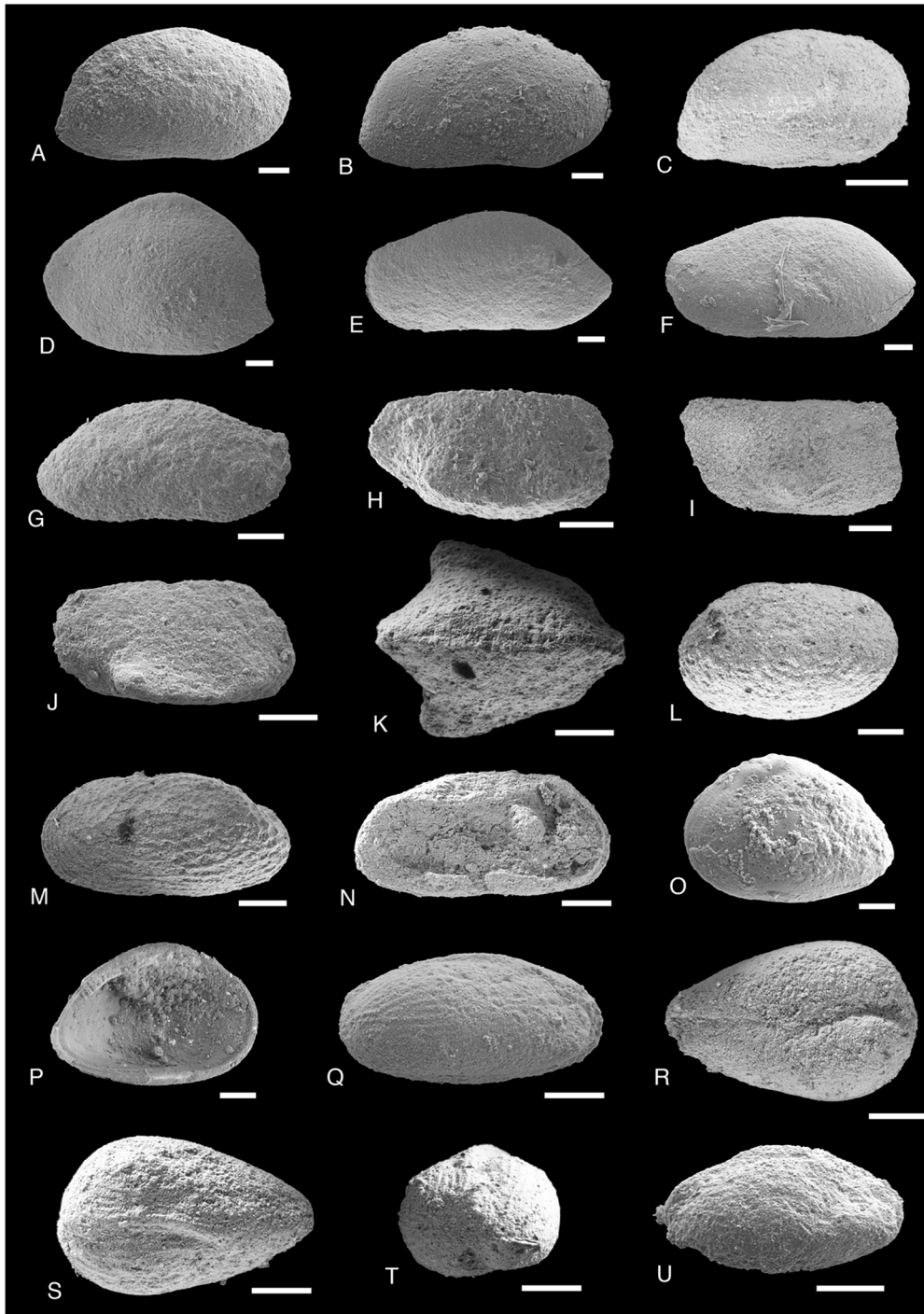


Plate 3. Ostracods from the Maantang Formation, Hanwang and Jushui, Sichuan Province, South China, Tuvlian, Late Carnian, Late Triassic. **A, B:** *Isobythocypris* sp. 1, A: lateral view of a right valve, sample C36, MHI2169/39, B: lateral view of a right valve, sample C36, MHI2169/40; **C:** *Isobythocypris* sp. 2, lateral view of a right valve, sample C36, MHI2169/41; **D:** *Ptychobairdia* sp., lateral view of a left valve, sample C36, MHI2169/42; **E–G:** *Pontocyprrella goussardi* Forel n. sp., E: holotype, lateral view of a left valve, sample C36, MHI2169/43; F: lateral view of a left valve, sample C36, MHI2169/44; G: paratype, right lateral view of a complete carapace, sample C36, MHI2169/45; **H:** *Monoceratina* sp., right lateral view of a complete carapace, sample C36, MHI2169/46; **I:** *Praebythoceratina* sp., lateral view of a right valve, sample C33, MHI2169/47; **J, K:** *Eucytherura* sp., J: right lateral view of a complete carapace, sample C36, MHI2169/48; K: same specimen, dorsal view; **L:** *Simeonella* sp. in [Kristan-Tollmann *et al.*, 1991b](#), lateral view of a left valve, sample C36, MHI2169/49; **M, N:** Cytheroidea gen. and sp. indet. 3, M: lateral view of a left valve, sample C36, MHI2169/50; N: same specimen, inner view; **O, P:** *Schuleridea?* sp., O: lateral view of a left valve, sample C36, MHI2169/51; P: same specimen, inner view; **Q–U:** Cytheroidea gen. and sp. indet. 1; Q: right lateral view of a complete carapace, sample C36, MHI2169/52; R: same specimen, ventral view; S: same specimen, dorsal view; T: same specimen, posterior view; U: right lateral view of a complete carapace, sample C36, MHI2169/53. All scale bars are 100 μm .

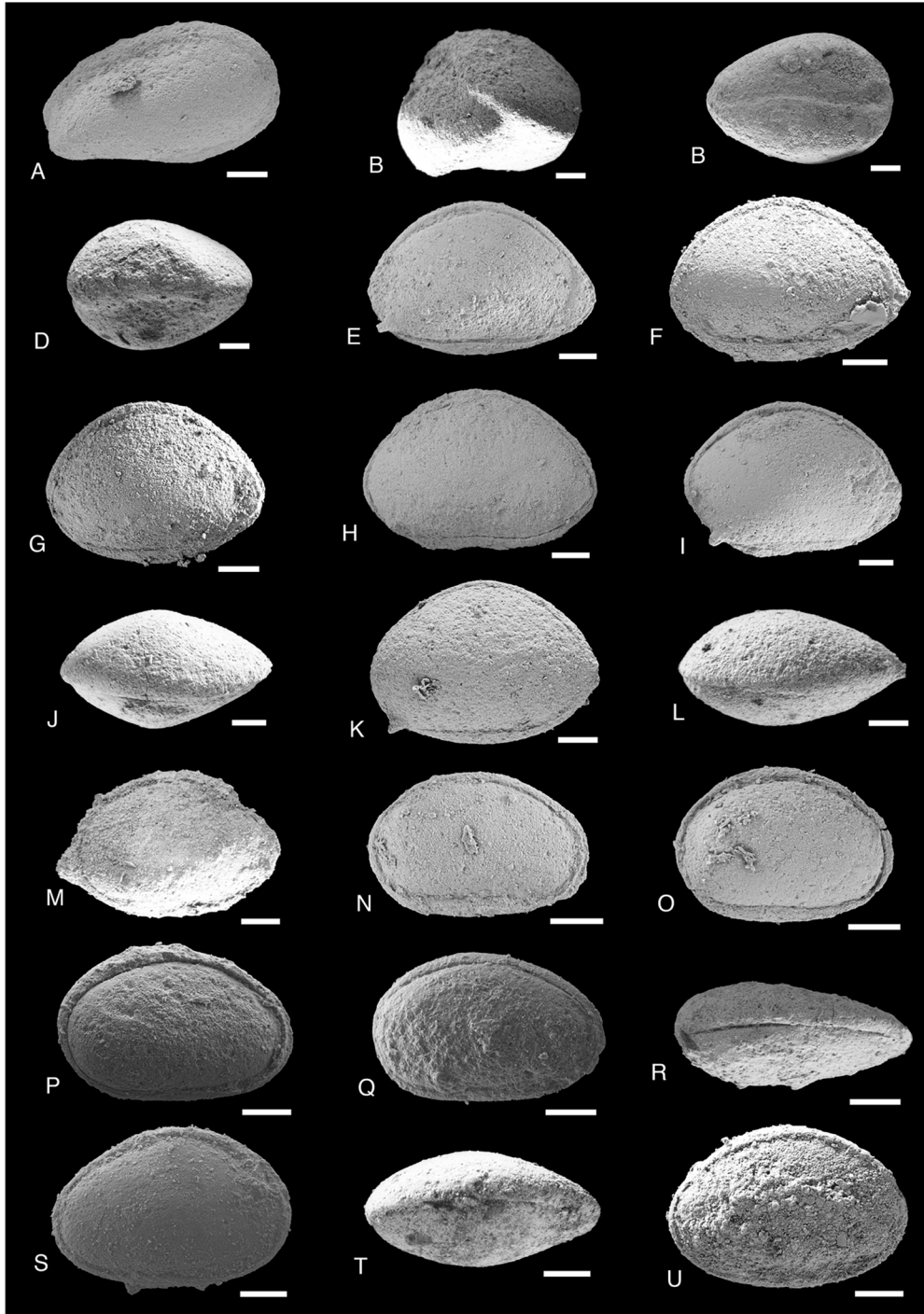


Plate 4. Ostracods from the Maantang Formation, Hanwang and Jushui, Sichuan Province, South China, Tuvlian, Late Carnian, Late Triassic. **A–D:** Cytheroidea gen. and sp. indet. 2, **A:** right lateral view of a complete carapace, sample C36, MHI2169/54; **B:** same specimen, posterior view; **C:** same specimen, ventral view; **D:** same specimen, dorsal view; **E–L:** *Hungarella gommerii* Forel n. sp.; **E:** holotype, right lateral view of a complete carapace, sample C36, MHI2169/55; **F:** right lateral view of a complete carapace, sample C33, MHI2169/56; **G:** paratype, right lateral view of a complete carapace, sample C33, MHI2169/57; **H:** right lateral view of a complete carapace, sample C36, MHI2169/58; **I:** right lateral view of a complete carapace, sample C33, MHI2169/59; **J:** same specimen, dorsal view; **K:** right lateral view of a complete carapace, sample C33, MHI2169/60; **L:** same specimen, dorsal view; **M:** *Hungarella postacuta* Xie in *Wei et al., 1983*, right lateral view of a complete carapace, sample C33, MHI2169/61; **N–U:** *Hungarella subtera* Zheng, 1976; **N:** right lateral view of a complete carapace, sample C36, MHI2169/62; **O:** right lateral view of a complete carapace, sample C36, MHI2169/63; **P:** right lateral view of a complete carapace, sample C36, MHI2169/64; **Q:** right lateral view of a complete carapace, sample C36, MHI2169/65; **R:** same specimen, dorsal view; **S:** right lateral view of a complete carapace, sample C33, MHI2169/66; **T:** same specimen, dorsal view; **U:** right lateral view of a complete carapace, sample C33, MHI2169/67. All scale bars are 100 μm .

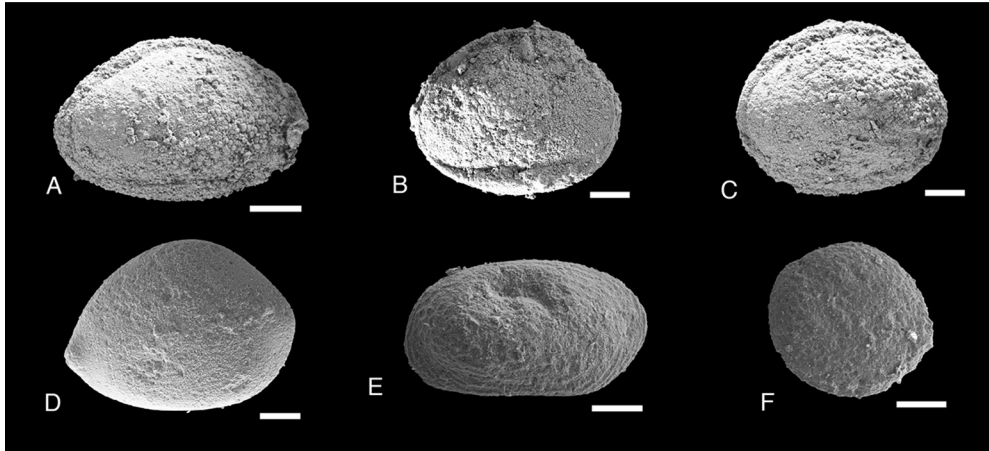


Plate 5. Ostracods from the Maantang Formation, Hanwang and Jushui, Sichuan Province, South China, Tuvlian, Late Carnian, Late Triassic. **A:** *Hungarella subtera* Zheng, 1976, right lateral view of a complete carapace, sample C33, MHI2169/68; **B, C:** *Hungarella* sp. 1; **B:** right lateral view of a complete carapace, sample C33, MHI2169/69; **C:** right lateral view of a complete carapace, sample C33, MHI2169/70; **D:** *Hungarella* sp. 2, lateral view of a left valve, sample C36, MHI2169/71; **E:** *Bektasia* sp., lateral view of a left valve, sample C36, MHI2169/72; **F:** *Polycoppe* sp., right lateral view of a complete carapace, sample C36, MHI2169/73. All scale bars are 100 μm .

China (Wei *et al.*, 1983) by its short and raised PB and long AVB. However, *Bairdia maantangensis* Xie in Wei *et al.*, 1983 is more elongate ($H/L = 0.50$ against 0.55 here) with a longer DB and a laterally compressed AVB. It can also be compared to *Bairdia weiyuanjiangensis* Hou and Gou in Ye *et al.*, 1977 from the Carnian, Late Triassic, Weiyuanjiang Formation of Jinggu county, Yunnan Province, South China (Ye *et al.*, 1977). However, *Bairdia* sp. 3 has a thinner and more pointed PB.

Bairdia sp. 4

(Plates 1Q and 1R)

Material. Two complete carapaces, two right and two left valves.

Dimensions. RV: $L = 731\text{--}812\ \mu\text{m}$, $H = 303\text{--}345\ \mu\text{m}$; LV: $L = 652\text{--}812\ \mu\text{m}$, $H = 290\text{--}365\ \mu\text{m}$.

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvlian, Late Carnian, Late Triassic (this work).

Remarks. *Bairdia* sp. 4 is close to *Bairdia liviae* Forel in Forel and Grădinaru, 2018 from the Bithynian, Anisian, Middle Triassic of Romania (Forel and Grădinaru, 2018) from which it differs by a more rounded AVB and a horizontal DB. *Bairdia* sp. 4 can also be compared to *Bairdia* cf. *humilis* Monostori, 1995 in Crasquin *et al.*, 2018 from the Carnian of Sicily (Crasquin *et al.*, 2018) but it is more elongate with a longer posterior end. We take this opportunity to point out that, as shown by Forel and Grădinaru (2018), *Bairdia humilis* Monostori, 1995 from the Illyrian, Anisian, Middle Triassic of Hungary (Monostori, 1995), is a junior primary homonym of *Bairdia humilis* Bushmina, 1970 from the Devonian-Carboniferous beds of the Eltsov Synclinorium (southwest Siberia; Bushmina, 1970). *Bairdia monostorii* has been introduced as a necessary new name (Forel and Grădinaru, 2018) so that *Bairdia* cf. *humilis* Monostori, 1995 in Crasquin *et al.*, 2018 is here replaced by *Bairdia* cf. *monostorii* in Crasquin *et al.*, 2018.

Genus *Carinobairdia* Kollmann, 1963

Type species. *Carinobairdia triassica* Kollmann, 1963 by original designation.

Preliminary remarks. The taxonomic history of *Carinobairdia*, and more generally of Triassic sculptured Bairdiidae, is complex with contrasting opinions on its validity. *Carinobairdia* was established by Kollmann (1963) to accommodate Late Triassic massive sculptured bairdiids with an annular ridge subparallel to the margins. Later, Bolz (1971b) considered that the morphology of the lateral sculpture of the valves should not be taken as a generic feature as it may be homeomorphic. Bolz (1971b) furthermore gathered *Nodobairdia* and *Carinobairdia* as subgenera of the genus *Triebelina*, considering that the morphology of their submarginal ornamentations (nodes and ridges respectively) has no taxonomic significance and that only the presence of marginal ornamentation is of generic importance, whatever its nature. For this reason, the genus *Carinobairdia* has sometimes been attributed to *Triebelina* (*Nodobairdia*; Bolz, 1971b; Urlichs, 1972; Mette and Mohtat-Aghai, 1999). Until a phylogeny of Triassic ornate Bairdiidae can be established, the classification of Kollmann (1963) is followed in considering primary ornamentation as relevant generic character, owing that ornamentation is widely used as generic marker for other families (e.g. Trachyleberididae; Moore, 1961; more recently Warne and Whatley, 2016 for the genera *Neohornibrookella*, *Tenedocythere*, *Bosasella*, *Hermanites*, *Jugocythereis* and *Thaerocythere*).

Carinobairdia cabralae Forel n. sp.

(Plates 1U and 2A–2I)

Etymology. The specific epithet honours Dr. Maria-Cristina Cabral, University of Lisbon, for her support to the first author and assistance in the taxonomic discussion on *Schuleridea*.

Material. Four complete carapaces, four left and five right valves, several fragments.

Holotype. One complete carapace, MHI2169/21 (Plates 1U, 2A and 2B).

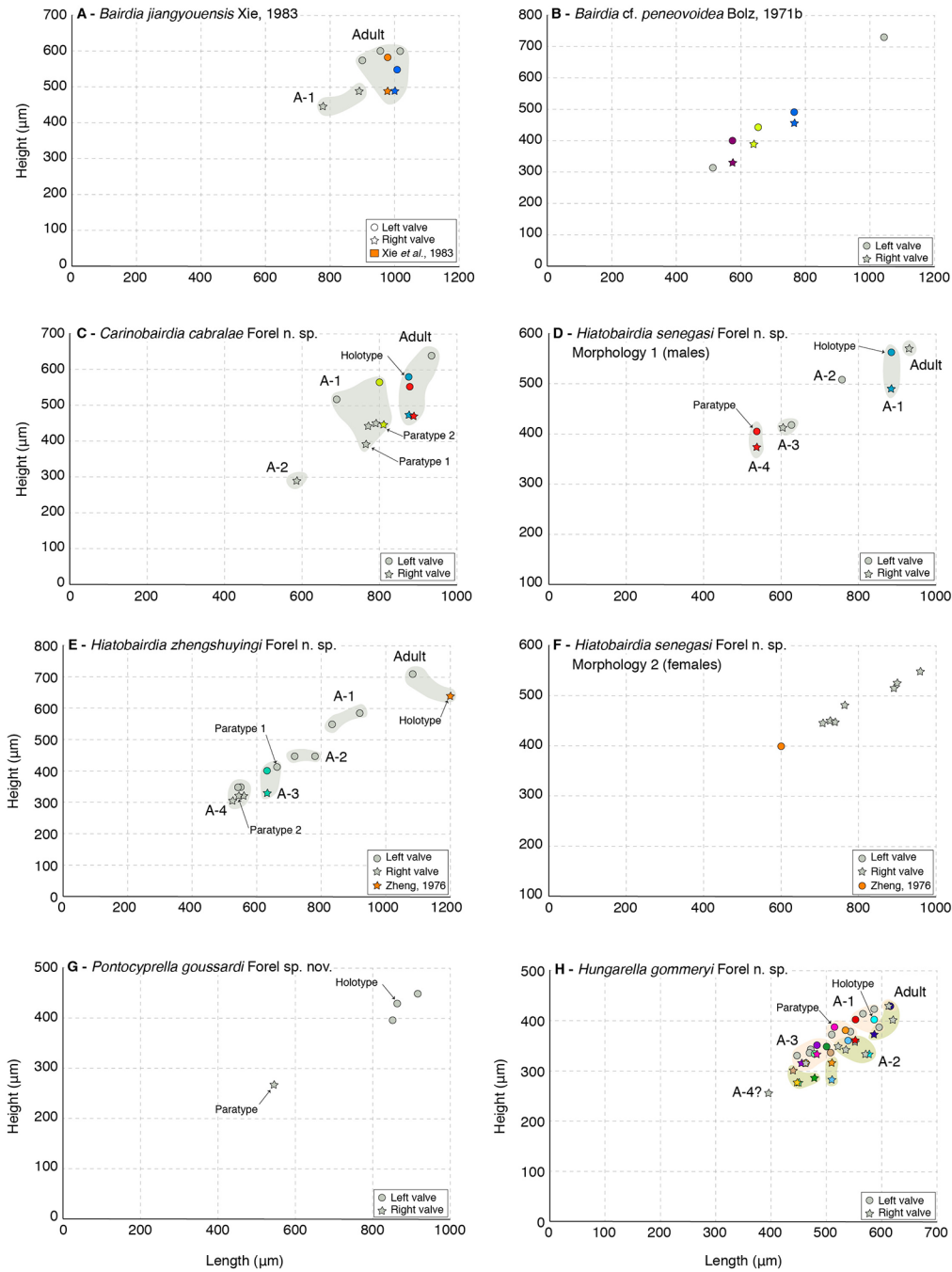


Fig. 4. Height/length scatter plots of species recovered from the Maantang Formation, Jushui and Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic. In all diagrams, the dimensions of right and left valves of complete carapaces are shown separately and illustrated in the same colour. **A:** *Bairdia jiangyouensis* Xie in Wei, Li, Jiang and Xie, 1983. All specimens are from Carnian and Norian of the Sichuan Province (Wei *et al.*, 1983; this work). **B:** *Bairdia* cf. *peneovoidea* Bolz, 1971b. All specimens are from the Sichuan Province (this work). **C:** *Carinobairdia cabralae* Forel n. sp. All specimens are from the Sichuan Province (this work). **D:** *Hiatobairdia senegasi* Forel n. sp., morphology 1 (males), all specimens are from Carnian and Norian of the Sichuan Province (Zheng, 1976; this work). **F:** morphology 2 (females). **E:** *Hiatobairdia zhengshuyingii* Forel n. sp. All specimens are from Carnian and Norian of the Sichuan Province (Zheng, 1976; Wei *et al.*, 1983; this work). **G:** *Pontocyprrella goussardi* Forel n. sp. All specimens are from the Sichuan Province (this work). **H:** *Hungarella gommerii* Forel n. sp. All specimens are from the Sichuan Province (this work).

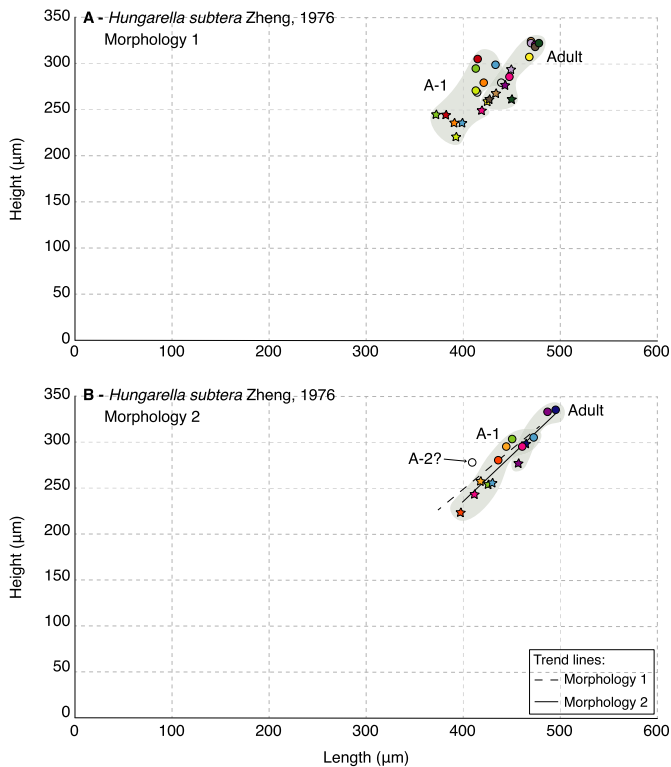


Fig. 5. H/L diagrams *Hungarella subtera* Zheng, 1976. All specimens are from Carnian and Norian of the Sichuan Province (Zheng, 1976; Wei *et al.*, 1983; this work). The dimensions of right and left valves of complete carapaces are shown separately and illustrated in the same colour.

Paratype 1. One complete carapace, MHI2169/22 (Plate 2C).

Paratype 2. One complete carapace, MHI2169/23 (Plates 2D and 2E).

Diagnosis. A species with dorsal border developed into a high and laterally compressed lamella, thick unbroken carina parallel to margins and central area always occupied by a thick horizontal bar.

Description. A thick-shelled large and massive species of *Carinobairdia* with subtriangular to subquadrate outline in lateral view; Hmax located at the antero-dorsal angulation and Lmax located below mid-H; all margins paralleled by a thick and unbroken carina only slightly removed from the edge; central area ellipsoidal occupied by an horizontal thick bar, which does not reach the sub-marginal carina; lateral surface of both valves evenly reticulated; in dorsal view, marginal carina depressed in its median area with Wmax located at the anterior extremity.

RV: dorsal margin tripartite with ADB-DB, DB-PDB angulations obtuse; PDB slightly concave posteriorly at some specimens; anterior margin rounded with ADB straight to slightly concave, AVB gently convex and maximum of convexity above mid-H, bordered by a thin lamella which extends horizontally, often only partially preserved; ventral margin straight with median concavity, PVB horizontal and denticulate; PB narrow and located close to the ventral margin.

LV: overlaps RV all around and overreaches it at DB; dorsal margin tripartite with PDB, DB and ADB straight and of

similar length; DB raised by a high laterally compressed lamella; anterior margin broadly rounded with maximum of convexity above mid-H, with AVB gently rounded and ADB straight; ventral margin long and straight with PVB short; posterior margin located close to ventral margin with narrow maximum of curvature.

Dimensions. See Figure 4C.

Occurrences. Samples C33, C36, Maantang Formation, Jushui and Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. *Carinobairdia cabralae* Forel n. sp. is related to *Carinobairdia alpina* Kollmann, 1963 emend. Kristan-Tollmann, 1970 from the Norian-Rhaetian of Austria (Kollmann, 1963; Bolz, 1971a, b) and Iran (Kristan-Tollmann *et al.*, 1979). The two species have similar lateral outlines and dimensions but the diagnosis of *Carinobairdia alpina* states that the median field area “seems to show a weak horizontal bulge in its central area” (translated from German; Kollmann, 1963), which is poorly visible on the originally illustrated specimens. On the other hand, all specimens of *Carinobairdia cabralae* Forel n. sp. display a well-defined horizontal central bar, which development is tracked through the ontogeny appearing in what is here interpreted as the A-2 stage. The possibility that *Carinobairdia alpina* might be juvenile of *Carinobairdia cabralae* is excluded because specimens lacking the horizontal median bar in *Carinobairdia alpina* have adult size and morphology. The horizontal bar in the median field area is therefore considered as a specific character differentiating the Norian-Rhaetian western tethyan population from the Carnian South Chinese species. As such, *Carinobairdia cabralae* Forel n. sp. might be considered as precursor of *Carinobairdia alpina*, proceeding through a simplification of the external ornamentation.

Genus *Hiatobairdia* Kristan-Tollmann, 1970

Type species. *Hiatobairdia subsymmetrica* Kristan-Tollmann, 1970 by original designation.

Preliminary remarks. *Hiatobairdia* was originally placed in the subfamily Bairdiinae Sars, 1923 by Kristan-Tollmann (1970, 1971a) and subsequently in the Bairdoppilatiinae Kristan-Tollmann, 1969 by Kristan-Tollmann (1978) and Kristan-Tollmann *et al.* (1980). The subfamily Bairdoppilatiinae Kristan-Tollmann, 1969 was erected to accommodate bairdiids with auxiliary bairdoppilatan denticles and sockets along the antero- and postero-dorsal positions in the selvage of the RV. Bolz (1971a, b) highlighted the functional significance of this auxiliary dentition and the probability that this character may be convergent. In parallel, Maddocks (1969) separated living Bairdiidae into two subfamilies: Bairdiinae, including the genus *Bairdoppilata*, and Bythocypridinae. Both subfamilies are diagnosed by characteristic adductor muscle-scars arrangement and substantiated by consistent patterns of carapace and appendages morphology (Maddocks, 1969). The absence of accessory bairdoppilate dentition in the present species might relate to the generally poor preservation of the material or to the weak development of this character as evoked by Maddocks (1969) to explain invisible Bairdoppilatan dentition on some modern specimens of *Bairdoppilata* (*Bairdoppilata?*) *hirsuta* (Brady, 1880).

Hiatobairdia senegasi Forel n. sp.

(Plates 2L–2R)

1976 *Bairdia* sp. Zheng: 80, 81, pl. 1, fig. 8.

Etymology. The specific epithet honours Dr. Frank Senegas (CNRS, CR2P, Paris, France) for his valued support to the first author of this work.

Material. Two complete carapaces, 10 right and two left valves (this work); one left valve (Zheng, 1976).

Holotype. One complete carapace, morphology 1, adult, MHI2169/30 (Plate 2M).

Paratype. One complete carapace, morphology 1, A-4, MHI2169/29 (Plate 2L).

Diagnosis. A species with very asymmetric preplete carapace, anterior maximum of convexity located high and posterior end truncated.

Description

Morphology 1 (males?; Plates 2L–2O): carapace laterally inflated, asymmetric subtriangular in shape with high dorsum; LV larger than RV, overlapping it along dorsal margin and VB; Hmax located at ADB-DB angulation with truncated posterior end; LV massive, highly arched with Hmax in front of mid-L without distinct angulations at dorsal margin, ventral margin straight; RV highly arched, dorsal margin tripartite with ADB long and concave anteriorly, sloping of $\approx 30^\circ$ towards AB, DB straight to slightly convex, gently sloping towards PDB-DB angulation ($\approx 10^\circ$), PDB concave terminally; VB long and straight to concave in its median portion; at both valves, anterior margin largely rounded with maximum of curvature located above mid-H, bordered with a laterally compressed thin flange extending along the upper 2/3rd of AVB; PB narrower than AB, with maximal curvature located in the lower 1/3rd of Hmax, AVB entirely bordered with a laterally compressed thin flange.

Morphology 2 (females?; Plates 2P–2R): RV asymmetric sub-rectangular in lateral outline with posterior end higher than in males; dorsal margin tripartite with ADB-DB and DB-PDB angulations more pronounced than in morphology 1, ADB straight to slightly concave anteriorly, DB straight to slightly convex, longer than in morphology 1, PDB more sloping (60°); AVB and PVB flanges similar to morphology 1; no female LV has been found.

Dimensions. See Figure 4D (morphology 1, males?), Figure 4F (morphology 2, females?).

Occurrences. Kuahongdong Formation, Sichuan Province, South China, Norian, Late Triassic (Zheng, 1976); samples C33, C36, Maantang Formation, Jushui and Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. Because of its very asymmetric lateral outline, *Hiatobairdia senegasi* Forel n. sp. differs from all known species of the genus *Hiatobairdia*. The specimens of *Hiatobairdia senegasi* Forel n. sp. are distributed into 5 ontogenetic stages, from A-4 to Adult (Fig. 4D). Several conclusions can be made, which are nonetheless only based on males: (1) the thickness of the overlap of LV over RV increases through the ontogeny as shown by the carapaces measured, (2) the relative increase of LV versus RV of complete carapaces corresponds to an increase in H, while L increases homogeneously in RV and LV, (3) the position of Hmax at RV moves backward through the ontogeny (from preplete in A-4 in Plate 1L, to close to amplete in A-1 in Plate 1M). In A-3 specimens, two different morphologies begin to show: the first one is stocky with PB truncated and PDB long and steeply sloping to PB (labelled Morphology 2), the second morpholo-

gy is elongate with longer posterior end, DB long and PDB shorter (labelled Morphology 1). This trend further develops up to the Adult stage. The female carapaces of recent Podocopida are generally larger, with a more inflated posterior end than males (e.g. *Cytherella*, *Metacypris*, *Neonesidea*, *Paranesidea*, *Uncicocythere*, *Xestoleberis*; Maddocks and Illiffe, 1986; Maddocks, 1991; Smith and Hiruta, 2004; Smith and Kamiya, 2005; Sato and Kamiya, 2007). Such pattern has also been recognized in the fossil record (e.g. Forel *et al.*, 2015; Yamaguchi *et al.*, 2017). Despite the differences in lateral outline, the consistency with which these two morphologic forms occur together in the same samples suggests a linkage between them, which could be explained as sexual dimorphism. Based on the uniformitarianist assumption that morphs displaying a stockier posterior end are females, Morphology 2 could be interpreted as females while the Morphology 1 could correspond to males. Based on this working hypothesis, sexual dimorphism might be visible as early as in A-3 juveniles for the species *Hiatobairdia senegasi* Forel n. sp. *Fabalicypis parva* Wang, 1978, distributed from the Carboniferous to the Late Permian worldwide, shows the onset of sexual dimorphism at A-3 stage (Forel *et al.*, 2015). The A-3 stage thus appears as an overall important stage for the establishment of sexual dimorphism in fossil Bairdioidea. Interestingly, the *Anlangen* of copulatory organs of modern Bairdioidea [*Neonesidea oligodontata* (Kajiyama, 1913) and *Neonesidea schulzi* (Hartmann, 1964)] form in the A-1 stage while previous stages are only affected by the formation of appendages and changes in their chaetotaxy (Smith and Kamiya, 2002; Yousef and Moustafa, 2017). This discrepancy might be related to adaptation mechanisms to peculiar and still unconstrained conditions. Until the 60's, it was considered that sexual dimorphism only becomes apparent in adult ostracods (Myodocopida and Podocopida; Van Morkhoven, 1962). Precocious sexual dimorphism has since been documented in recent Myodocopida (e.g. Kornicker, 1970) and Podocopida (e.g. Rohr, 1979; Ikeya and Ueda, 1988; Athersuch *et al.*, 1989; Kamiya, 1992). In the fossil record, Podocopida from the Middle Jurassic (Whatley and Stephens, 1977) or from the Permian-Triassic transition (Forel *et al.*, 2015), Myodocopida from the Silurian (Perrier *et al.*, 2007) display precocious sexual dimorphism as early as A-5 stage. However, these interpretations still need to be confronted with internal structures, such as marginal zones, to estimate the maturity of the growth stages.

Hiatobairdia zhengshuying Forel n. sp.

(Plates 2S–2U)

1976 *Bairdia* cf. *anisica* Kozur; Zheng: 80, pl. 1, fig. 7.

1983 *Bairdia* cf. *anisica* Kozur; Wei *et al.*: 80, pl. 14, fig. 4.

Etymology. The specific epithet honours Dr. Zheng Shuying (Nanjing Institute of Geology and Paleontology, China) who first recorded this species from the Norian Kuahongdong Formation, Sichuan, South China.

Material. One complete carapace, 2 right and 5 left valves (this work); one right valve (Zheng, 1976; Wei *et al.*, 1983; the same specimen is illustrated in both papers).

Holotype. One right valve, Kuahongdong Formation, Sichuan Province, collection number 31170 of the Nanjing Institute of Geology and Paleontology (pl. 1, fig. 7 in Zheng, 1976 and pl. 14, fig. 4 in Wei *et al.*, 1983).

Paratype 1. One right valve, MHI2169/37 (Plate 2T).

Paratype 2. One right valve, MHI2169/36 (Plate 2S).

Diagnosis. A large to very large symmetric species with inflated lateral surface, laterally compressed flange along antero-ventral and postero-dorsal borders and dorsal margin lacking angulations at the right valve.

Description. A large to very large species of *Hiatobairdia*, subtriangular symmetric in lateral view with Hmax at mid-L and Lmax around mid-H; LV larger than RV, overlapping it along dorsal and ventral margins; dorsal margin highly arched at both valves; ADB and PDB at the RV with subsymmetric slopes to AB and PB respectively ($\approx 30^\circ$), PDB steeper than ADB at the LV; VB long, straight to slightly concave at RV, straight at LV; at both valves, anterior margin largely rounded with maximum of curvature above mid-H, bordered with laterally compressed flange extending along the upper 2/3rd of the AVB; posterior margin narrower with maximum slightly below mid-H, bordered with laterally compressed flange extending all along the PVB; lateral surface of both valves inflated, reticulated except on the AV and PV flanges.

Dimensions. See Figure 4E.

Occurrences. Kuahongdong Formation, Sichuan Province, South China, Norian, Late Triassic (Zheng, 1976; Wei *et al.*, 1983); sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. *Hiatobairdia zhengshuyingi* Forel n. sp. differs from *Hiatobairdia yunnanensis* Gou in Ye *et al.*, 1977 from the Late Triassic of Yunnan Province (Ye *et al.*, 1977), which was the only known Late Triassic Chinese occurrence of the genus until the present record, by its more pointed posterior end with terminal concavity and Hmax at mid-L. The present species shares strong morphological similarity with *Hiatobairdia foveolata* Kristan-Tollmann, 1978 from the Early Carnian of Pralongia, Italy (Kristan-Tollmann, 1978) as shown by its arched dorsum, largely rounded anterior margin and laterally inflated LV where reticulation is visible. Noteworthy, the morphology of the RV of *Hiatobairdia foveolata* Kristan-Tollmann, 1978 is not described in its diagnosis and description: it is only known from drawings where its dorsal margin appears as tripartite and Hmax located at the ADB-DB angulation. Conversely, the dorsal margin of *Hiatobairdia zhengshuyingi* Forel n. sp. is uniformly rounded at RV without angulation and Hmax is located around mid-L. Furthermore, *Hiatobairdia zhengshuyingi* Forel n. sp. is much larger than *Hiatobairdia foveolata* Kristan-Tollmann, 1978, which holotype is 760 μm long and 470 μm high, corresponding to the A-3 to A-2 stage of the present species. *Hiatobairdia zhengshuyingi* Forel n. sp. is also close to *Hiatobairdia subsymmetrica* Kristan-Tollmann, 1970 from the Rhaetic of Austria (Kristan-Tollmann, 1970) but it is more highly arched, less elongate and lacks the ventral ridge characteristic of the Austrian species. Based on the H/L scatter plot in Figure 4E, four ontogenetic stages are recognized, from A-4 to Adult in ascending order. The ontogenetic development of this species is mainly marked by the increase of its dimensions.

Superfamily Cypridoidea Baird, 1845

Family Pontocyprididae Müller, 1894

Genus *Pontocyprrella* Mandelstam in Luebimova, 1955

Type species. *Bairdia harrisiana* Jones, 1849 by subsequent designation by Mandelstam in (Luebimova, 1955).

Pontocyprrella goussardi Forel n. sp.
(Plates 3E–3G)

Etymology. The specific epithet honours Dr. Florent Goussard (MNHN, CR2P, Paris, France) for his valued collaboration in promoting palaeontology with the first author of this work.

Material. One right and four left valves.

Holotype. One left valve, MHI2169/43 (Plate 3E).

Paratype. One right valve, MHI2169/45 (Plate 3G).

Diagnosis. A species with concave ADB, raised AB and PB located high for the genus.

Description. A large species of *Pontocyprrella* with a slender ovoid carapace, with Hmax at mid-L and Lmax at mid-H; dorsal margin low, uniformly rounded, with angulations poorly expressed to absent; ADB concave upward at RV and only slightly at LV; DB straight and only slightly sloping toward PDB-DB angulation ($\approx 5\text{--}10^\circ$) in specimens with visible dorsal angulations; PDB long, straight and steeper than ADB ($\approx 40^\circ$); anterior margin larger than posterior one, subrectangular, with maximum of curvature in the upper 1/3rd of H, AB raised upward and located very high; PB located in the lower 1/3rd of H, slightly rounded at RV, more pointed at LV, PVB short at both valves; ventral margin long and straight to slightly concave at LV, mid-concavity more pronounced at RV; AVB long, very steeply raised towards AB, vertical in some specimens; surface smooth.

Dimensions. See Figure 4G.

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. *Pontocyprrella goussardi* Forel n. sp. is not abundant in the present assemblage but its diagnostic characters are sufficient to discriminate it from species already known to science. It differs from all *Pontocyprrella* species recorded from the Carnian of Turkey (Forel *et al.*, 2019) by its antero-dorsal concavity, raised AB and angulate PB. Conversely, it shares close morphological similarity with *Pontocyprrella subaureola* Sheppard in Brand, 1990 from the Bathonian of Dorset, UK (Sheppard in Brand, 1990) but has a significantly shorter dorsal margin, a concavity at ADB and more rounded PB at RV. *Pontocyprrella goussardi* Forel n. sp. can also be compared to *Pontocyprrella* sp. from the Jurassic of the DSDP Leg 11 in Western Atlantic (sites 100 and 105; Oertli, 1972) but the Jurassic species has a larger posterior margin with higher PDB and lacks the AD concavity. It is also very close to *Paracypris?* sp. A *sensu* Whatley (1970) from the Callovian-Oxfordian of Scotland, Late Callovian of Southern England (Whatley, 1970) and Poland (Olempska and Blaszyk, 2001) but here again, this species lacks the typical AD concavity of *Pontocyprrella goussardi* Forel n. sp.

Superfamily Cytheroidea Baird, 1850

Family Cytheruridae Müller, 1894

Genus *Eucytherura* Müller, 1893 emend. Ayress, Whatley, Downing and Millson, 1995

Type species. *Cythere complexa* Brady, 1867 by subsequent designation by Müller (1893).

Eucytherura sp.

(Plates 3J and 3K)

Material. One complete carapace.

Dimensions. L = 400 μm , H = 207 μm .

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. *Eucytherura* sp. is closely related to *Gramella* (sic) species described from the Carnian-Norian interval of Austria and Hungary (Bunza and Kozur, 1971). The history of this genus is complex: the name, honouring Dr. M.N. Gramm, was misspelled for *Gramella* in the original diagnosis, description and discussion whereas the correct wording *Grammella* was used elsewhere in the text of Bunza and Kozur (1971). *Grammella* appeared to be a junior objective homonym of a bryozoan and was thus replaced by *Grammicythere* Kozur, 1972. More recently, Whatley and Boomer (2000) showed *Grammicythere* to be a junior synonym of *Eucytherura*. *Eucytherura* sp. recovered from the Maantang Formation differs from *Eucytherura hungarica* (Kozur in Bunza and Kozur, 1971) from the Carnian of Hungary (Bunza and Kozur, 1971) by its size (L/H = 1.68–1.75 for *Eucytherura hungarica* versus L/H = 1.93 for *Eucytherura* sp.), absence of surface reticulation and more pronounced dorsal angulations. The absence of spines along the posterior margin of *Eucytherura* sp. compared to *Eucytherura hungarica* (Kozur in Bunza and Kozur, 1971) can relate to the preservation state of our material. Noteworthy, *Eucytherura hungarica* (Kozur in Bunza and Kozur, 1971) is shown as a drawing (Tafel 1, fig. 1 in Bunza and Kozur, 1971) and as a photograph (Tafel 4, fig. 3 in Bunza and Kozur, 1971). However, the specimens illustrated differ by the position of the anterior maximum of curvature and by the elongation of the carapace so that they do not seem conspecific.

Family Limnocytheridae Klie, 1938

Genus *Simeonella* Sohn, 1968

Type species. *Simeonella brotzenorum* Sohn, 1968 by original designation.

***Simeonella* sp. in Kristan-Tollmann, Lobitzer and Solti, 1991**

(Plate 3L)

1991b *Simeonella* sp.; Kristan-Tollmann *et al.*: taf. III, fig. 8.

2019 *Simeonella* sp. in Kristan-Tollmann *et al.*; Forel *et al.*: fig. 20U.

Material. One left valve.

Dimensions. L = 491 μm , H = 307 μm .

Occurrences. Kössen Formation, Tyrol, Rhaetian, Late Triassic (Kristan-Tollmann *et al.*, 1991b); Kilek section, Tavuşçayırı Block, Sorgun Ophiolitic Mélange, southern Turkey, Huglu Tuffite, *Tetraporobrachia haeckeli* radiolarian Zone, Julian, Early Carnian, Late Triassic (Forel *et al.*, 2019); sample C33, Maantang Formation, Jushui, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The present species has first been recognized from the Rhaetian deposits of the Kössen Formation in Tyrol (Kristan-Tollmann *et al.*, 1991b) but was left in open nomenclature in all likelihood because of the lack of specimens. A unique specimen was also discovered recently from the Julian, Early Carnian of Turkey (Forel *et al.*, 2019). The present record of *Simeonella* sp. in Kristan-Tollmann *et al.*, 1991b is therefore the third known occurrence of this species worldwide, which spans from the Early Carnian to the Rhaetian. One specimen has been recovered from the C33 assemblage and more material is still needed to clearly define

the characters of this new species. Especially, the specimens have similar H/L ratio ranging from 0.62 to 0.64 but they differ by their dimensions: L = 271 μm , H = 171 μm for the Carnian specimen from Turkey (Forel *et al.*, 2019) and L = 610 μm , H = 391 μm for the Rhaetian specimen from Tyrol (Kristan-Tollmann *et al.*, 1991b). The smallest specimen has a more uniformly rounded anterior margin and smaller posterior margin than the larger specimens. These differences might relate to ontogeny, which will be clarified with more material.

Family indet.

Cytheroidea gen. and sp. indet. 3

(Plates 3M and 3N)

Material. One left valve.

Dimensions. L = 513 μm , H = 248 μm .

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The genus *Kinkelinella* is triangular to subrectangular in lateral view with compressed free margins, a very convex central part, eyespot and strong ridges with intermediate reticulation and ventral alar wing. Although very close, the present specimen differs from *Kinkelinella* because of its invaginated hinge line, ornamentation dominated ventrally by longitudinal ridges and latero-dorsal inflation and because it lacks the characteristic ventral alar wing. It is close to the Indet. gen. et sp. from the Jurassic of the DSDP Leg 11 in Western Atlantic (sites 100 and 105; Plate 3, fig. 44 in Oertli, 1972) but this Jurassic taxon lacks the intermediate ornamentation seen on the present specimen and on *Kinkelinella*, has a smooth and laterally compressed anterior margin underlined by a marginal ridge, a compressed AB, is rather latero-ventrally inflated and lacks the dorsal inflation. Only more material with well preserved internal structures will help clarify the attribution of this taxon.

Family Schulerideidae Mandelstam, 1959

Genus *Schuleridea* Swartz and Swain, 1946

Type species. *Schuleridea acuminata* Swartz and Swain, 1946 by original designation.

***Schuleridea?* sp.**

(Plates 3O and 3P)

Material. One left valve.

Dimensions. L = 578 μm , H = 410 μm .

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The present specimen bears strong similarities with the Jurassic genera *Schuleridea* Swartz and Swain, 1946 and *Praeschuleridea* Bate, 1963. Its sub-triangular outline with Lmax below mid-H, eyespot, sulcus and simple pitted ornamentation are rather typical of the genus *Schuleridea*, *Praeschuleridea* being more ovoid in lateral view with weaker ocular tubercle and sulcus. Except for these tenuous characters, *Praeschuleridea* and *Schuleridea* have similar outline, muscular arrangement, radial pore arrangement but differ by their hinge structures: in dorsal view, *Schuleridea* has a central bar on the RV while it is located on the LV in *Praeschuleridea* (Bate, 1963). The hinge elements of the present LV are weathered but no pronounced central bar is visible, which also points to the genus *Schuleridea*. The LV of *Schuleridea* generally has a central element longer than the terminal elements, while the central element is generally very short in

Praeschuleridea, with a small sulcus between two very long and crenulated sockets. In spite of the weathered condition of the present specimen, the length of the posterior socket, which is the best preserved, seems very elongate, possibly closer to *Praeschuleridea* (pers. comm. Dr. Maria-Cristina Cabral, University of Lisbon). Consequently, the unique weathered specimen found has morphological elements related both to *Schuleridea* and *Praeschuleridea*, but the similarity seems closer to *Schuleridea* so that it is attributed with doubt to the genus *Schuleridea*. A first questionable record of the genus *Schuleridea* was reported from the Late Triassic Weiyuanjiang Formation of Yunnan Province, South China (*Schuleridea?* sp.; Pl. 1, fig. 23 and Pl. 16, fig. 23 in [Ye *et al.*, 1977](#)). Although illustrations of the Yunnan specimens do not allow precise comparison, their elongate lateral outline is distinct from the shorter, plumper and triangular contour of the present *Schuleridea?* sp. The elongate carapace, tapered posterior margin and presence of posterodorsal angulation is rather reminiscent of the genus *Paracypris* [Sars, 1866](#) and more precisely of species described from the Norian-Rhaetian interval of Tyrol ([Kristan-Tollmann *et al.*, 1991b](#)) and from the Early Carnian of Turkey ([Forel *et al.*, 2019](#)). The description provided by [Ye *et al.* \(1977\)](#) does not mention any pitted ornamentation, eyespot or sulcus. For these reasons, the *Schuleridea* identification of the Yunnan specimen is rejected.

Suborder Metacopina [Sylvester-Bradley, 1961](#)

Superfamily Healdioidea [Harlton, 1933](#)

Family Healdiidae [Harlton, 1933](#)

Genus *Hungarella* [Méhes, 1911](#)

Type species. *Hungarella problematica* [Méhes, 1911](#) by original designation.

Preliminary remarks. It is out of the topic of the present contribution to discuss the generic status of *Hungarella* and its relationship with the typically Jurassic genera *Ogmoconcha* and *Ogmoconchella*. In the studied assemblages, specimens of the genus *Hungarella* are abundant and represented by complete carapaces and disarticulated valves. Most of the valves are complicated to identify at the species level so that only clearly identifiable material is considered. It is worth noting that several *Hungarella* species have been described from the Norian Kuahongdong Formation of Sichuan Province, South China: *H. ovata* [Zheng, 1976](#) (also found in [Wei *et al.*, 1983](#)), *H. subtera* [Zheng, 1976](#) (also found in [Wei *et al.*, 1983](#)), *H. subtriangulata* Hou and Gou, MS in [Zheng, 1976](#) [also found in [Wei *et al.*, 1983](#); at the time of writing [Zheng \(1976\)](#) contribution, Hou and Gou might have been in preparation or in press and is referred to as MS, with no corresponding reference], *H. emeiensis* Xie in [Wei *et al.*, 1983](#), *H. jiangyouensis* Xie in [Wei *et al.*, 1983](#), *H. postacuta* Xie in [Wei *et al.*, 1983](#), *H. subelliptica* Hou and Gou, 1977 in [Wei *et al.*, 1983](#). Additional species are also recorded from the Late Triassic of Yunnan Province, South China ([Ye *et al.*, 1977](#)): *H.? subelliptica* Hou and Gou in [Ye *et al.*, 1977](#), *H. subtriangulata* Hou and Gou in [Ye *et al.*, 1977](#), *H. subovata* Hou and Gou in [Ye *et al.*, 1977](#), *H.? sp. 1* in [Ye *et al.*, 1977](#) and *H.? sp. 2* in [Ye *et al.*, 1977](#).

Hungarella gommerii Forel n. sp.

(Plates 4E–4L)

Etymology. The specific epithet honours Dr. Dominique Gommery (CNRS, CR2P, Paris, France) for his treasurable support and friendship to the first author of this work.

Material. At least 12 carapaces, several right and left valves and fragments.

Holotype. One complete carapace, A-1, MHI2169/55 (Plate 4E).

Paratype. One complete carapace, A-2, MHI2169/57 (Plate 4G).

Diagnosis. A species of the genus *Hungarella* with triangular lateral outline, AB and PB located low, dorsal margin highly arched, anterior margin narrow and laterally compressed.

Description. A medium-size species with a triangular carapace in lateral view with Hmax slightly posterior to mid-L and Lmax below mid-H; dorsal margin highly arched with ADB and PDB straight to slightly convex at both valves; ventral margin gently convex, VB straight at RV with tenuous oral concavity, uniformly convex at LV; AVB and PVB short, close to symmetrical or with PVB slightly steeper than AVB and truncated at some specimens; anterior margin narrowly rounded with maximum of convexity located in the lower 3rd of Hmax, terminated by a large laterally compressed zone at the RV; posterior margin larger with maximum of convexity slightly higher than anterior one; LV smooth; RV with a short postero-ventral spine oriented backward and downward.

Dimensions. See [Figure 4H](#).

Occurrences. Samples C31, C33, C36, Maantang Formation, Jushui and Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The preservation state of the present material does not allow the observation of muscle scar patterns, which are highly important in the generic attribution of Triassic Healdiidae ([Kristan-Tollmann, 1971b](#)). However, external characters lead to the attribution to the genus *Hungarella* as the valves are not similar (postero-ventral spine only at RV). *Hungarella gommerii* Forel n. sp. is very close to *Hungarella? subtriangulata* Hou and Gou in [Ye *et al.*, 1977](#) from the Late Triassic Weiyuanjiang Formation of the Yunnan Province, South China ([Ye *et al.*, 1977](#)) by its overall triangular lateral outline. However, *Hungarella gommerii* Forel n. sp. is less highly arched and has a posteroventral spine as well as laterally compressed anterior margin, which are not present in *Hungarella? subtriangulata* Hou and Gou in [Ye *et al.*, 1977](#) and in the subsequent records ([Zheng, 1976](#); [Wei *et al.*, 1983](#)).

Hungarella postacuta Xie in [Wei, Li, Jiang and Xie, 1983](#) (Plate 4M)

1983 *Hungarella postacuta* Xie in [Wei *et al.*: 181, pl. 55, figs. 12, 13.](#)

Material. One complete carapace.

Dimensions. L = 563 μ m, H = 374 μ m.

Occurrences. Kuahongdong Formation, Sichuan Province, South China, Norian, Late Triassic ([Wei *et al.*, 1983](#)); sample C33, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. *Hungarella postacuta* Xie in [Wei *et al.*, 1983](#) has been described from the Norian Kuahongdong Formation exposed in Sichuan Province, South China ([Wei *et al.*, 1983](#)). The present record extends its temporal distribution down to the Late Carnian. In the current state of our knowledge, *Hungarella postacuta* is endemic to the Sichuan part of the Yangtze platform during the Late Triassic. This species appears as a minor component of the upper Triassic

assemblages as only two carapaces are known [one in Wei *et al.* (1983) and one in the present work]. Based on their respective sizes, the material illustrated in Wei *et al.* (1983) might represent a more mature stage than the present specimen.

***Hungarella subtera* Zheng, 1976**
(Plates 4N–4U and 5A)

1976 *Hungarella subtera* Zheng: 90, pl. III, figs. 42, 43.

1983 *Hungarella subtera* Zheng; Wei *et al.*: 182, pl. 55, fig. 15.

Material. 24 complete carapaces, several right and left valves.

Dimensions. See Figure 5.

Occurrences. Kuahongdong Formation, Sichuan Province, South China, Norian, Late Triassic (Zheng, 1976; Wei *et al.*, 1983); samples C31, C33, C36, Maantang Formation, Jushui and Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. *Hungarella subtera* Zheng, 1976 is endemic of the Late Triassic marine deposits of Sichuan as shown in the occurrences' list. The specimens from the Maantang Formation are distributed into two morphologies: the morphology 1 has a high and laterally inflated posterior end in lateral view, with Wmax in posterior half of the carapace in dorsal view (Plates 4N–4R), while the morphology 2 has a tapered posterior end in lateral view, and Wmax around mid-L in dorsal view (Plates 4S–4U, 5A). These morphologies of *Hungarella subtera* Zheng, 1976 could be related to sexual dimorphism with morphology 1 corresponding to females and morphology 2 to males. The H/L ratios of morphotypes 1 and 2 are shown in Figures 5A and 5B respectively. Their size distributions are close but specimens of the morphology 1 are located slightly above those of morphology 2 (Fig. 5B), being more slender. This distribution might be in line with our interpretation of morphology 1 being females and morphology 2 being males as is typically observed in modern marine taxa (e.g. Kamiya, 1992; Ozawa, 2009, 2013).

It is worth noting that the lateral outline of specimens of the morphology 2 is close to *Hungarella ovata* Zheng, 1976 from the Kuahongdong Formation of Sichuan Province, South China (Zheng, 1976; Wei *et al.*, 1983). However, the persistent posterior overlap of LV over RV observed in all specimens of the present work is a discriminating character between *Hungarella subtera* and *Hungarella ovata*. The H/L scatter plot in Figure 5 shows that LV and RV of males and females have approximate similar dimensions throughout the reconstructed portion of the ontogeny: no increase of the overlap intensity is observed. Two ontogenetic stages, A-1 and Adults, are documented for both females and males (Fig. 5).

Order Platycopida Sars, 1866

Suborder Platycopina Sars, 1866

Superfamily Cavellinoidea Egorov, 1950

Family Cavellinidae Egorov, 1950

Genus *Bektasia* Özdikmen, 2010

Type-species. *Reubenella avnimelechi* (Sohn, 1968) by original designation.

***Bektasia* sp.**

(Plate 5E)

Material. One left valve.

Dimensions. L = 475 µm, H = 269 µm.

Occurrences. Sample C36, Maantang Formation, Hanwang, Sichuan Province, South China, Tuvalian, Late Carnian, Late Triassic (this work).

Remarks. The oldest record of the genus *Bektasia* in South China is documented from the Late Anisian, Middle Triassic of Guizhou Province (Kristan-Tollmann, 1983). The present species is the second Late Triassic representative of this genus in South China, Yangtze platform: the first occurrence was questionably attributed to this genus from the Late Triassic Weiyuanjiang Formation of Yunnan Province (Ye *et al.*, 1977). Noteworthy, the ostracod genus *Reubenella* was defined in 1968 from the Middle and Late Triassic of Makhtesh Ramon, Israel (Sohn, 1968). This name was preoccupied by a valid trilobite genus defined by Lochman (1966) so that *Reubenella* Sohn, 1968 has been replaced by the name *Bektasia* (Özdikmen, 2010). The species *Reubenella* sp. identified by Kristan-Tollmann (1983) and *Reubenella? ovata* Hou and Gou in Ye *et al.*, 1977 described in Ye *et al.* (1977) are therefore renamed *Bektasia* sp. and *Bektasia? ovata*, respectively. *Bektasia* sp. identified from the Maantang Formation differs from *Bektasia* sp. in Kristan-Tollmann (1983) by its loosely reticulate surface, marked, large sulcus prolonged posteriorly by an incision directed downwards. It also differs from *Bektasia? ovata* (Hou and Gou in Ye *et al.*, 1977) by its asymmetrical and laterally compressed anterior and posterior margins, asymmetrical pit and surface ornamentation.

4 Results and discussion

4.1 Diversity and composition

Each of the three samples collected from the Carnian microbial-sponge mounds of the Maantang Formation in Sichuan Province, South China, yielded ostracods. In total, 33 species have been identified, belonging to 19 genera and 11 families: 7 species were previously known from the Late Triassic interval (including *Hiatobairdia senegasi* n. sp. and *Hiatobairdia zhengshuyingii* n. sp. being previously known under different identifications), 5 are new (*Carinobairdia cabralae* n. sp., *Hiatobairdia senegasi* n. sp., *Pontocyprella goussardi* n. sp., *Hungarella gommerii* n. sp. and *Hiatobairdia zhengshuyingii* n. sp.) and 24 are left in open nomenclature due to poor preservation and/or paucity of material (including *Simeonella* sp. in Kristan-Tollmann *et al.*, 1991b which is known from other localities). Table 1 provides a complete taxonomic list of the three assemblages from the Carnian Maantang Formation. The distribution of species within the 11 families is shown in Figure 6 (all specimens obtained from the sample C31 belong to *Hungarella* so that this assemblage is not displayed). The C36 assemblage is more diversified than C33 both in terms of families, genera and species (C36: 10 families, 17 genera, 30 species; C33: 4 families, 7 genera, 12 species). The assemblages C33 and C36 are both dominated by different proportions of Bairdiidae and Healdiidae, and for the sake of clarity, the composition of each assemblage is described separately.

The assemblage C36 is largely dominated by Bairdiidae (genera *Acratia*, *Bairdia*, *Bairdiacypris*, *Carinobairdia*, *Hiatobairdia*, *Isobrythocypris*, *Ptychobairdia*), representing 58% of the species. Healdiidae (genus *Hungarella*) is the second most important family with 13% of the species. The

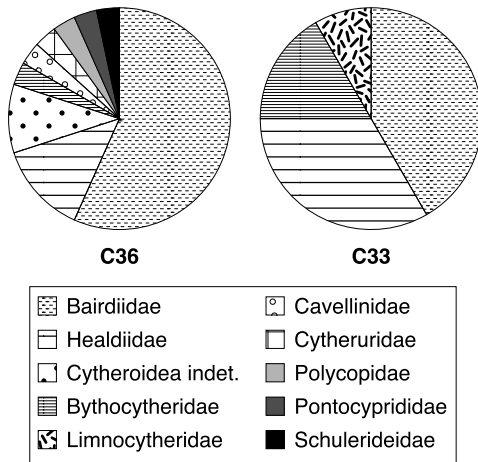


Fig. 6. Circular diagrams of faunal composition of ostracod assemblages C36 (about 300 specimens) and C33 (about 140 specimens) from the Maantang Formation, Tuvolian, Late Carnian, Late Triassic, South China.

third most important components are the indeterminate Cytheroidea (Cytheroidea gen. and sp. indet. 1-3), accounting for 10% of the assemblage. Pontocyprididae (genus *Pontocyprilla*), Bythocytheridae (genus *Monoceratina*), Cytheruridae (genus *Eucytherura*), Schulerideidae (genus *Schuleridea*?), Cavellinidae (genus *Bektasia*) and Polycopidae (genus *Polycope*) are represented by one species, each of which corresponds to about 3% of the assemblage. The assemblage C33 is also dominated by Bairdiidae (genera *Bairdia*, *Carinobairdia*, *Hiatobairdia*), which account for 42% of the species. Healdiidae (genus *Hungarella*) is the second most important family, being 33% of the species. Bythocytheridae (genera *Monoceratina*, *Praebythoceratina*) are the third family with 17% of the assemblage. Limnocytheridae (genus *Simeonella*) is represented by a monotypic genus, corresponding to 8% of the assemblage. Healdiidae are more or less diversified in the three assemblages but as a common rule, they are very abundant and dominate the assemblages in terms of specimens.

Most genera occurring in C33 are also present in C36, only *Praebythoceratina* and *Simeonella* are restricted to C33. Three species are only found in C33: *Praebythoceratina* sp., *Simeonella* sp. in Kristan-Tollmann *et al.*, 1991b and *Hungarella postacuta* Xie in Wei *et al.*, 1983.

4.2 Relation to other Triassic faunas

At the genus level, most taxa from the samples C31, C33 and C36 are already known from the classic literature on marine Carnian assemblages, as shown in the successive synonym lists and discussions in the Systematic paleontology part. Nevertheless, exceptions are the unknown Cytheroidea (gen. and sp. indet. 1-3) that might be new to science but for which the available material is not sufficient to clarify their systematic position and diagnostic characters. *Schuleridea*? and *Carinobairdia* are other exceptions, as discussed later, because the present assemblages witness their oldest occurrences to date.

At the species level, we were able to identify five previously known species (*Bairdia anisicaforma* Monostori, 1994; *Bairdia jiangyouensis* Xie in Wei *et al.*, 1983; *Simeonella* sp. in Kristan-Tollmann *et al.*, 1991b; *Hungarella postacuta* Xie in Wei *et al.*, 1983; *Hungarella subtera* Zheng, 1976), all other species are either new, indigenous or could only be compared (cf.) with described species. Of the previously described species, 5 are endemic to the Yangtze platform during the Late Triassic (*Bairdia jiangyouensis* Xie in Wei *et al.*, 1983; *Hiatobairdia senegasi* Forel n. sp.; *Hiatobairdia zhengshuyingii* Forel n. sp.; *Hungarella postacuta* Xie in Wei *et al.*, 1983; *Hungarella subtera* Zheng, 1976) and 2 are known from western localities during the Late Triassic: *Bairdia anisicaforma* Monostori, 1994, known from the Carnian of Hungary (Monostori, 1994) and Turkey (Forel *et al.*, 2019), and *Simeonella* sp. in Kristan-Tollmann *et al.*, 1991b, known from the Rhaetian of Tyrol (Kristan-Tollmann *et al.*, 1991b) and the Carnian of Turkey (Forel *et al.*, 2019). As discussed in the Systematic paleontology part, several species recorded from the Carnian microbial-sponge mounds of the Sichuan Basin show similarity to but not precise identity with known species from the Late Triassic-Jurassic western Tethys. Noteworthy, additional material will clarify the potential presence of *Bairdia jiangyouensis* Xie in Wei *et al.*, 1983 in the Carnian of Sicily (Crasquin *et al.*, 2018) and the Rhaetian of the Alps (Mette and Mohtat-Aghai, 1999).

4.3 Precursor fauna

The family Schulerideidae, first defined as a subfamily by Mandelstam (1959) and subsequently at the familial rank by Bate (1963), is abundant and diverse in the Middle and Late Jurassic of Europe (e.g. Bate, 1977). Without considering subgenera, it is composed of the genera *Amicytheridea* Bate, 1975, *Asciocythere* Swain, 1952, *Eoschuleridea* Bate, 1967, *Paraschuleridea* Swartz and Swain, 1946, *Pirileberis* Grekoff, 1963, *Praeschuleridea* Bate, 1963, *Schuleridea* Swartz and Swain, 1946. A literature survey shows that *Praeschuleridea* is the oldest representative of the Schulerideidae, first occurring during the Toarcian (Late Early Jurassic; Bate and Coleman, 1975). The origin of the Schulerideidae is still uncertain, with different opinions. In the first hypothesis, the *Pulviella*-group [corresponding to the Speluncellini according to Kozur (1973)] might be the origin of the Schulerideidae, which retain the same outline, sexual dimorphism and construction of the marginal zone (Kozur, 1973). The second hypothesis is that the earliest representative, *Praeschuleridea pseudokinkelinella* Bate and Coleman, 1975, might be the ancestor of the family (Bate, 1977). The third hypothesis is that the Jurassic genus *Ektypocythere* Bate, 1963 might have an ancestral position with respect to *Praeschuleridea* as shown by the nature of the hinge and of the anterior marginal pore canals (Boomer *et al.*, 2009). Here, the unique specimen in hand does not allow the clarification of these hypothesis but its morphological characters clearly tracks the roots of the Schulerideidae down to the Carnian. Additional findings of more abundant and well-preserved material will be a turning point in the understanding of the Triassic roots of these typical Jurassic ostracod taxa. It is nevertheless interesting to note that the genus *Praeschuleridea* has been tentatively identified in

multiple occasions in slightly younger sediments. First, juveniles from Pliensbachian-Sinemurian open marine deposits of Western Australia have been attributed to *Camptocythere/Praeschuleridea* (Lord *et al.*, 1993). These specimens are now considered as juvenile progonocytherids (Guzel, 2012). In older sediments from the Rhaetian of Ocean Drilling Program Leg 122, drilled on the northwestern margin of Australia, two species have been questionably attributed to the genus *Praeschuleridea*: *Praeschuleridea?* n. sp. 1 (Hole 761C), *Praeschuleridea?* sp. 2 (Hole 764A and 764B; Dépêche and Crasquin-Soleau, 1992). These specimens are not illustrated so that any comparison with the present material is precluded. The present study reports the oldest occurrence of the family Schuleriidae, with a specimen attributed with doubt to the genus *Schuleridea*, possessing characters related both to the genera *Schuleridea* and *Praeschuleridea*. Owing to the exceptional character of this specimen, it is essential to evaluate the possibility of contamination from younger layers. Upsection, the facies becomes siliciclastic and less diverse and has been interpreted as representing an outer ramp to basinal environment, under a water-depth of more than 300 m, that deposited into a foredeep (e.g. Yang *et al.*, 2008; Liu *et al.*, 2009; Li *et al.*, 2014a, b; Shi *et al.*, 2015). Samples from the uppermost Maantang Formation only contain internal moulds of gastropods (H. Hagdorn, personal observation; Jin *et al.*, 2018). The Jurassic deposits in the Sichuan Basin are terrestrial and famous for their prosauropod dinosaurs (e.g. Luo and Wang, 1999; Xing *et al.*, 2014). Hence, contamination from Jurassic material in the field and during the sample processing in the lab is excluded as it may have yielded freshwater taxa that are absent from the examined assemblages. The possibility of contamination from the uppermost siliciclastic Maantang layers is more complex. The preservation state of *Schuleridea?* sp. slightly differs from the other obtained taxa as it seems less recrystallized and it is the only specimen for which at least part of the inner structures could be satisfactorily observed. Contamination from the upper Maantang layers cannot be ruled out based on the only *Schuleridea?* sp. obtained. However, in the eventuality of contamination, this specimen might not be younger than Norian, Late Triassic, which might still represent the oldest known record of this family.

The precursor character of the present assemblages is also recognized among the Bairdiidae, which are parts of the samples C33 and C36. The genus *Carinobairdia* was defined from Rhaetian sediments of the Zlambach Formation in Austria (Kollmann, 1963) and has since then been documented from the Late Norian-Rhaetian interval of Tyrol (Kollmann, 1963; Bolz, 1971a, b; Urlichs, 1972; Kristan-Tollmann, 1988; Kristan-Tollmann *et al.*, 1991b; Mette and Mohtat-Aghai 1999; Hillebrandt *et al.*, 2007; Urlichs and Krystyn, 2016), Greece (Mercier, 1966) and Iran (Kristan-Tollmann *et al.*, 1979, 1980). A questionable occurrence is reported from the Ladinian of Nevada (*Carinobairdia?* sp.; Sohn, 1964, 1987) but because this generic attribution is only tentative and the specimen is not figured, this Middle Triassic occurrence is not considered. *Carinobairdia cabralae* Forel n. sp. is the oldest known representative of the genus *Carinobairdia*. As detailed in the Systematic paleontology part, *Carinobairdia cabralae* Forel n. sp. is very close to *Carinobairdia alpina* Kollmann, 1963, from the Norian-Rhaetian of Europe and Iran, from

which it differs by the constant occurrence of a well-defined horizontal central bar, which development is tracked through the ontogeny of the species. This specific character differentiates the Norian-Rhaetian population from the Carnian South Chinese species and *Carinobairdia cabralae* Forel n. sp. is considered a precursor of *Carinobairdia alpina* Kollmann, 1963, proceeding through a simplification of the external ornamentation as shown by the loss of the horizontal central bar.

The first occurrence of these two precursor taxa on the eastern side of the Tethys implies a westward migration until their first records in western areas, respectively during the Early Jurassic and the Late Norian-Rhaetian interval. They furthermore demonstrate that the importance of the eastern-most parts of the Tethys in the early Mesozoic evolution of marine ostracods is under-estimated, with the necessity to reconsider assessments such as “the European Province appears to have been the birth-place of the majority of the important Mesozoic families” (Bate, 1977; p. 233). These observations bring new elements to the hypothesis first made by Lord (1988) that typical Jurassic taxa might have originated on the eastern side of the Tethys, migrated to the western Tethys during the Late Triassic transgression and diversified there up to the record known for the European Jurassic. The present records furthermore revive the following statement that “[...] migration rather than evolutionary origination, accounts for the first stratigraphical appearances of most species in rock sections. It should therefore be stressed at the outset that comprehensive geographical coverage deserves as much priority as stratigraphical sampling interval.” (p. 872 in Cronin, 1988). It confirms the absolute necessity to increase the geographical coverage of the Triassic interval to better assess the radiation and changes through time of marine ostracods.

4.4 Paleoenvironmental implications

The depositional environment of the Maantang Formation and more particularly the growth conditions of the sponge-microbial mounds have been abundantly discussed since their discovery in the 1970's. This facies is generally interpreted as deposited in a relatively deep outer shelf (e.g. Wu, 1989, 2009; Wendt *et al.*, 1989; Wang *et al.*, 2015). The absence of phototrophic organisms (green algae or calcified cyanobacteria), the carbonate mud-rich facies, limited fragmentation of the skeletal grains of the Unit 2 as well as poor sorting support this conclusion and further suggest a deposition below the euphotic zone (Shi *et al.*, 2017). Furthermore, the amount of clay and quartz silt indicates that the mounds might have developed in turbid and muddy waters that may have provided nutrients for the development of sponges and heterotrophs (Wang *et al.*, 2012, 2015). The water-depth around the mounds was estimated to more than 150 m (Li *et al.*, 2014b).

The analysis of microbioerosion traces performed on brachiopods from samples C31 and C33 yielded only one identifiable microbioerosion trace fossil, *Orthogonum giganteum* Glaub, 1994 (Fig. 7). This ichnotaxon was previously only known from the Carboniferous, the Jurassic and the Recent (Glaub & Vogel, 2004; Thuy *et al.*, 2014; Hannon & Meyer, 2014), so that the Carnian occurrence provided by the

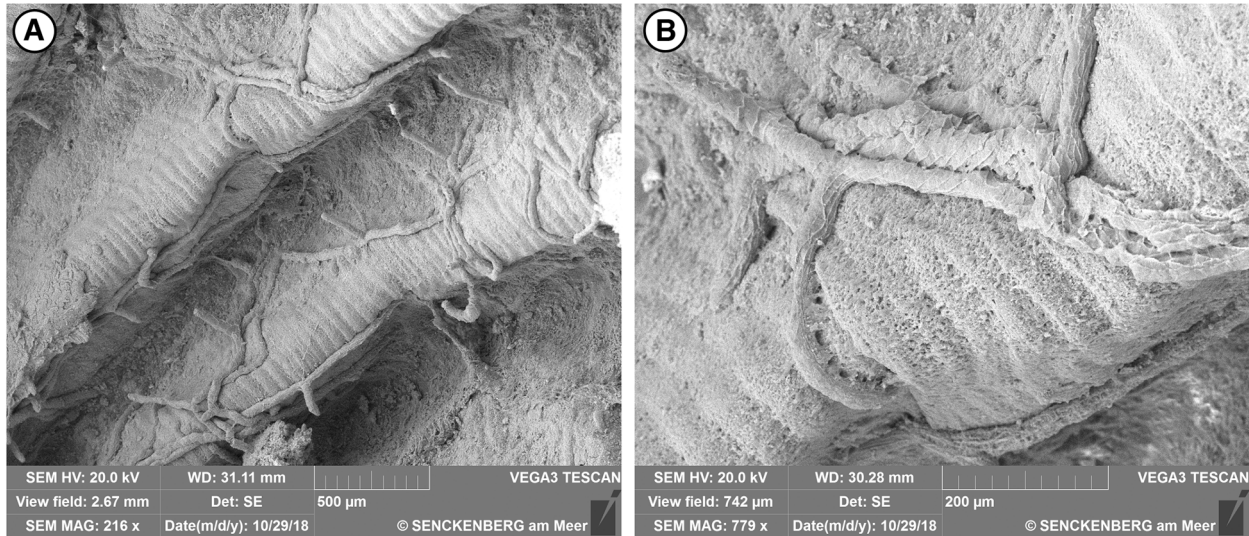


Fig. 7. A. Epoxy resin casts of the microboring *Orthogonum giganteum* Glaub, 1994, oriented closely parallel to the external substrate surface of an articulated brachiopod (sample C31). B. Close-up of A, showing the cylindrical tunnels and the characteristic rectangular branching pattern. The small ridges on the tunnel surface are a xenomorphic ornament reflecting the brachiopod's shell microstructure.

Maantang material adds the first Triassic record. The trace maker of *O. giganteum* is unknown, but considering that this trace is found in aphotic depths in modern oceans (unpublished observation MW), it is probably related to a marine fungus, analogous to other representatives of this ichnogenus (e.g. Radtke, 1991). In contrast, microborings considered to be produced by phototrophic trace makers (algae, cyanobacteria) that would in turn indicate dysphotic or euphotic conditions by their presence were not encountered in the studied samples from the Maantang Formation. Although we cannot prove their absence, the highly depleted microboring ichnofauna consisting of only one trace produced by an organotrophic trace maker neither conclusively implies aphotic conditions nor precludes a dysphotic or euphotic water depth. Nevertheless, our trace fossil analysis is in good accordance with previous palaeobathymetric reconstructions suggesting a deep sublittoral to upper bathyal depth (e.g. Wu, 1989, 2009; Wendt *et al.*, 1989; Wang *et al.*, 2015; Shi *et al.*, 2017).

With the exception of the sample C31 that is probably incomplete, two diverse ostracod assemblages have been obtained from the sponge-microbial mounds of the Maantang Formation (C33 and C36): they are indicative of marine shelf conditions as shown by the dominance of stenohaline taxa inhabiting fully marine waters (Bairdioidea and Healdioidea). Smooth-shelled ostracods dominate both assemblages, which may suggest that they represent outer shelf conditions, in line with previous palaeobathymetric conclusions. The influence of deep-waters is characterized by the persistent occurrence, although not abundant, of deep-sea Bythocytheridae. This picture is however balanced by the occurrence of shallow-water taxa such as the genus *Bektasia*, which tolerates important salinity variations (Kristan-Tollmann and Hamedani, 1973). Noteworthy, brackish water taxa typical of the Carnian salinity crisis such as *Renngartenella sanctaerucis* Kristan-Tollmann in Kristan-Tollmann and Hamedani, 1973 and *Simeonella brotzenorum nosterica* Monostori, 1994 (e.g. Gerry *et al.*, 1990; Monostori, 1994; Keim *et al.*, 2001) are

absent. This interpretation is also in line with the interpretation available from the literature (e.g. Wu, 1989, 2009; Wendt *et al.*, 1989; Wang *et al.*, 2015; Shi *et al.*, 2017) and with the microbioerosion analysis performed here. The influence of transportation from shallower and/or deeper areas seems to be relatively negligible on the scrutinized assemblages. The autochthonous or allochthonous nature of ostracod assemblages can be determined by the proportion of complete carapaces *versus* isolated valves and the demographic structure of populations (e.g. Boomer *et al.*, 2003). In the sponge-microbial mounds of the Maantang Formation, isolated valves are frequent but they do not dominate the assemblages, indicating that transportation might have occurred. However, the H/L diagrams in Figure 4 show that several of the species are composed of adults and successive ontogenetic stages, indicating that the transportation might have been very limited. The fact that ostracods' information are in line with those provided by the microbioerosion analysis strengthen this conclusion.

Thick-shelled Bairdiidae are generally considered as indicative of relatively high hydrodynamic conditions on the proximal platform (e.g. Urlichs, 1972). However, this claim was debated in the 1970's based on the occurrence of sculptured Bairdiidae in deep-water assemblages (Kozur, 1970a, 1971a, b, 1973; Urlichs, 1972; Kristan-Tollmann, 1978). Since then, this feature has been observed several times from the Middle and Late Triassic, (e.g. Mette *et al.*, 2014; Forel personal observation from the Carnian Pralongia section, Italy), including from the Carnian of Turkey where *Edithobairdia*, *Nodobairdia*, *Petasobairdia* and *Ptychobairdia* co-occur with Beecherellidae (*Acantoscapha*, *Gencella*), Rectoriidae, Berounellidae (*Paraberounella*) and diverse deep-water Bythocytheridae (Forel *et al.*, 2019). These observations are of extreme importance in calibrating the environmental reconstructions and unravelling the evolution of early Mesozoic marine ostracods. For this reason, the occurrence of *Carinobairdia* in the assemblages from the Maantang

Formation needs to be considered with extreme care for environmental reconstructions. To date, none of the *Carinobairdia* species known to science occurs in outer platform or deeper contexts (e.g. Kollmann, 1963; Bolz, 1971b; Kristan-Tollmann *et al.*, 1979; Mette and Mohtat-Aghai, 1999): *Carinobairdia cabralae* Forel n. sp. is therefore not only the oldest record of the genus but also its unique occurrence in deep-shelf settings. Similarly, *Praeschuleridea/Schuleridea* are euryhaline inner neritic forms (e.g. Damotte, 1988; Babinot, 1995; pers. comm. Dr. Maria-Cristina Cabral, University of Lisbon) but the record questionably attributed to *Schuleridea* in the present Maantang Formation implies a subsequent migration to shallow waters. Based on the independent proxy provided by the microbioerosion analysis, we propose that *Carinobairdia* and *Praeschuleridea/Schuleridea* radiated on the deep-shelf, later colonized and ultimately became restricted to shallow waters. It is necessary to precise that even in the case of a contamination from the uppermost Maantang siliciclastic layers, this hypothesis would still be valuable as these layers are attributed to outer ramp to basinal environment as detailed above. The ostracod records presented herein add to the growing evidence for the macroevolutionary importance of offshore origination in marine invertebrates (e.g. Lindner *et al.*, 2008; Thuy, 2013; Bribiesca-Contreras *et al.*, 2017; Hess and Thuy, 2018).

Taxa registration:

Carinobairdia cabralae: [urn:lsid:zoobank.org:act:08015D32-ABAD-4CA3-983F-8D4B941C7FCF](https://zoobank.org/urn:lsid:zoobank.org:act:08015D32-ABAD-4CA3-983F-8D4B941C7FCF)

Hiatobairdia senegasi: [urn:lsid:zoobank.org:act:ACE56DAC-660D-4531-94F3-D2F827B618EB](https://zoobank.org/urn:lsid:zoobank.org:act:ACE56DAC-660D-4531-94F3-D2F827B618EB)

Hiatobairdia zhengshuyingii: [urn:lsid:zoobank.org:act:16ACDDB8-8BDB-44E5-A4E2-D98D2086CC0F](https://zoobank.org/urn:lsid:zoobank.org:act:16ACDDB8-8BDB-44E5-A4E2-D98D2086CC0F)

Pontocyprilla goussardi: [urn:lsid:zoobank.org:act:FB73F885-25F4-4B19-AF2F-E98B97BF3B10](https://zoobank.org/urn:lsid:zoobank.org:act:FB73F885-25F4-4B19-AF2F-E98B97BF3B10)

Hungarella gommerii: [urn:lsid:zoobank.org:act:237AF6D6-2A06-48F8-95D4-398D1C42FD37](https://zoobank.org/urn:lsid:zoobank.org:act:237AF6D6-2A06-48F8-95D4-398D1C42FD37)

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