

BRACHIOPOD ASSEMBLAGES OF THE *EURYDESMA* FAUNA IN GLACIAL-DEGLACIAL SEQUENCES FROM ARGENTINA AND AUSTRALIA

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Abstract. The *Eurydesma* Fauna characterizes the Late Pennsylvanian-Permian glacial-postglacial sediments recorded in several Gondwanan basins during the Late Paleozoic Ice Age (LPIA). Brachiopods, as one of the most significant components of this fauna, are herein analyzed along with the associated bivalves, in two key sections from western and eastern Gondwana (Bonete Formation in the Sauce Grande Basin, eastern Argentina, and the Wasp Head Formation in the southern Sydney Basin, eastern Australia). The preliminary quantitative analysis indicates a high compositional similarity in both regions but occupancy exhibits important differences: brachiopod-dominated faunas can be found in eastern Australia (*Tomiopsis* and *Trigonotreta* are the most frequent taxa), and bivalve-dominated faunas are characteristic in eastern Argentina, where the brachiopods are poorly represented with the genera *Tivertonia* and *Tomiopsis*. In this locality, the development of r-strategy taxa, such as the bivalve *Eurydesma*, during the end of a glacial episode would adversely affect brachiopods' abundance. This is also consistent with previous studies that indicate that brachiopods already showed a decrease in importance in Pennsylvanian communities from Argentina. Relative abundances of brachiopods and bivalves in both localities may reflect differences in the regional environmental conditions but, unfortunately, eastern Argentina lacks younger records to compare the faunal turnover with that of the Australian sequences. Despite the ecological structural differences identified (i.e. brachiopod:bivalve ratio), the post-glacial *Eurydesma* fauna flourished in western and eastern Gondwana and it is striking that two faunas located on the opposite margins of this paleocontinent show such high compositional similarity during the development of a global postglacial event. This is particularly significant considering that the type of the basins (i.e. restricted vs open basins), biological features, paleoenvironmental conditions directly related to glacial dynamics, and also the diachronism of the transgression, can be controlling the composition of this fauna.

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INTRODUCTION

The Late Paleozoic Ice Age (LPIA) was characterized by a number of simultaneous global environmental changes (e.g., atmospheric chemistry, continental configuration, climate regime) and biotic changes (Shi & Waterhouse 2010; Gastaldo et al. 1996). However, few regional studies have been published to show how Late Paleozoic biotic communities were directly affected by the glacial-deglacial events, particularly those for the marine ecosystem.

The response of brachiopods and bivalves to the climate changes associated with the LPIA has been studied at different scales in western Argentina (Cisterna & Sterren 2010; Balseiro 2016; Balseiro & Halpern 2016, 2019; Cisterna et al. 2017), but it remains unknown in the eastern region, the Sauce Grande Basin. Such analyses have been also performed in the Permian sequences of eastern Australia (Clapham & James 2008, 2012). However, comparative studies to gain a broader understanding of how marine benthic communities responded to glacial/interglacial dynamics remain scanty. This is despite the fact that in both western Argentina and eastern Australia there are well known and relatively complete records of the Late Paleozoic glacial-deglacial events where the effects of climate regime changes on the marine benthic faunas can be evaluated.

In Argentina, two different scenarios are suggested for the postglacial transgressions following the glacial episodes in the early Late Carboniferous-Early Permian interval (López-Gamundí 1997): (a) to the west, the Late Carboniferous Paleopacific transgression, related to the Glacial Episode II represented in the Andean basins (Fig. 1), is characterized by a well-diversified brachiopod fauna (Cisterna et al. 2017 and references therein) that developed in arc-related and retroarc basins (Ramos & Palma 1996; Limarino & Spalletti 2006); and (b) to the east, the most widespread Late Carboniferous-Early Permian transgression associated with the Glacial Episode III (Fig. 1), is documented in the Sauce Grande Basin. This transgression can be distinguished by fossil assemblages dominated by bivalves (*Eurydesma* Fauna) with a low-diversity brachiopod fauna, which inhabited epeiric seas generated by flooding over an intraplate basin (Ramos & Palma 1996; Limarino & Spalletti 2006).

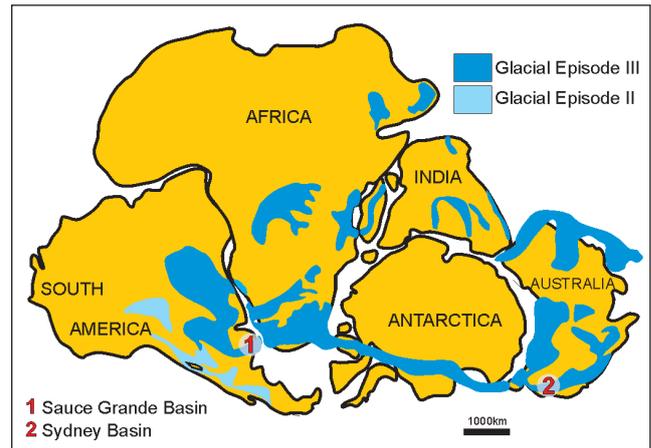


Fig. 1- Reconstruction of Gondwana supercontinent with simplified outlines of principal basins during the Late Carboniferous-Early Permian (Glacial episodes II and III of López-Gamundí 1997). Modified from López-Gamundí & Buatois (2010).

Geological and paleontological evidences of the glacial-postglacial transition are well exposed in eastern Australia, particularly in the Permian succession of the southern Sydney Basin (Dickins 1996; Tye et al. 1996; Eyles et al. 1997, 1998; Fielding et al. 2008; Rygel et al. 2008). Many authors have suggested that these records consist of a number of even shorter (1 to 8 Myr), discrete glacial intervals separated by non-glacial periods of similar duration (Jones & Fielding 2004; Montañez et al. 2007; Fielding et al. 2008). The Wasp Head Formation encloses the record of the first of these glacial intervals identified for eastern Australia (Fielding et al. 2008), which also contains the typical *Eurydesma* Fauna. The associated brachiopod assemblages are characterized by a group of diagnostic species whose diversity and stratigraphic occurrences in relation to sedimentary facies reflect the transition from an intra-glacial interval to post-glacial conditions (Cisterna & Shi 2014).

This paper aims to analyze the biotic composition and paleoecological features of the brachiopod assemblages of the *Eurydesma* Fauna in two key sections from western and eastern Gondwana (i.e., the Bonete Formation in the Sauce Grande Basin, eastern Argentina, and the Wasp Head Formation in the southern Sydney Basin, eastern Australia). Brachiopods, one the most significant components of the postglacial *Eurydesma* Fauna, are herein quantitatively analyzed, along with the associated bivalves, in order to understand their different response to postglacial conditions on both sides of Gondwana.

THE *EURYDESMA* FAUNA

The *Eurydesma* Fauna characterizes the Late Pennsylvanian-Permian glacial-postglacial sediments that have been recorded in several Gondwanan basins during the Late Paleozoic Ice Age (LPIA) (López-Gamundí et al. 1997; Isbell et al. 2008; Fielding et al. 2008; Shi & Waterhouse 2010). This invertebrate fauna is mainly distinguished by *Eurydesma* Morris, a well-known psychrophilic bivalve characteristic of glacial deposits over Gondwana, and especially typical of the Australian Permian faunas (Runnegar 1979; Waterhouse & Shi 2010). The *Eurydesma* Fauna is generally comprised of a number of cold-water bivalve and brachiopod genera (e.g., *Eurydesma*, *Deltopecten*, *Trigonotreta*, *Tomioopsis*, *Cyrtella*, *Bandoproductus*, *Strophalosia*, *Lyonia*, *Gilledia*, among other genera) and it is commonly found in strata associated with beds containing the *Glossopteris* Flora (Archangelsky et al. 1996 and references therein provided; Dickins 1985, 1992, 1996; González & Diaz Saravia 2007, among other authors).

In addition to *Eurydesma cordatum* Morris, 1845, first described from eastern Australia (Mitchell 1838; Morris 1845), several other *Eurydesma* species have been recorded in the Lower Permian glacial deposits of Australia, India, South Africa and South America (Johnston 1887; Reed 1932, 1936; Harrington 1955; Sahni & Srivastava 1956; Dickins 1957; Sahni & Dutt 1959; Waterhouse 1987). The wide distribution of this genus across Gondwana has allowed it to be considered an important paleobiogeographic tool. However, from a biostratigraphic viewpoint, *Eurydesma* is not a precise marker because its species are described throughout the Cisuralian interval, from Asselian to Kungurian. Furthermore, radiometric ages of the sections containing the *Eurydesma* Fauna are only known from a few localities in South Africa, South America (Bangert et al. 1999; López-Gamundí et al. 2013) and Australia, as will be discussed later.

From an ecological point of view, the genus *Eurydesma* has been interpreted as an opportunist bivalve with preferences for hard, clean, sublittoral substrates, which rapidly colonized sediments derived from rocky shorelines (Runnegar 1979). However, the species of this genus are frequently found in different onshore-offshore biofacies across the bathymetric gradient. In the context of the sequence stratigraphic framework, this fauna can be found in different parts of the systems tract (López-Gamundí 2010): in

South Africa, *Eurydesma* was recorded at the top of the deglaciation sequences of the Dwyka Formation, deposited in the lowstand systems tract (LST); in the Talchir Formation, India, it was found in the transgressive systems tract (TST), and in the Bonete Formation, Argentina, it appears in the highstand systems tract (HST). Records of *Eurydesma* in South America are restricted to eastern Argentina, in the Sauce Grande Basin (Bonete Formation, Pillahuincó Group), where it appears associated with species of the genera *Atomodesma*, *Promytilus*, *Allorisma*, *Stutchburia*, *Myonia*, *Vacunella*, *Leptodesma*, *Deltopecten*, *Heteropecten* and the brachiopods *Tomioopsis* and *Tivertonia*, as detailed below. Most of these bivalve genera have been also described from the glacial sequences of the Paraná Basin in Brazil (Simões et al. 2012; Neves et al. 2014). However, characteristic members of the cold-water bivalve faunas (i.e., *Eurydesma* and *Deltopecten*) recorded from Australia and Argentina, have not been found in this basin up to the present time. Neves et al. (2014) studied the bivalves from the postglacial interval of the Taciba Formation, Itararé Group (Pennsylvanian-early Permian, Holz et al. 2010; Pennsylvanian, Cagliari et al. 2014, Griffis et al. 2018), in Teixeira Soares, state of Paraná, Brazil. These authors described *Myonia argentinensis* (Harrington, 1955), *Heteropecten paranaensis* Neves et al. (2014) and *Atomodesma* (*Aphanaia*) *orbirugata* (Harrington, 1955) (named MHA horizon by Taboada et al. 2016), suggesting a correlation with faunal assemblages of the Bonete Formation from the Sauce Grande Basin. Brachiopods identified in this assemblage were recently described as *Lyonia*, *Langella*, *?Streptorhynchus*, *?Cyrtella*, *Tomioopsis*, *Quinquenella* and *Biconvexiella* which would integrate the *Eurydesma*-*Lyonia* Fauna (Taboada et al. 2016). These authors defined the Subzone MAH (*Myonia*-*Atomodesma*-*Heteropecten*) in the upper part of the proposed new fauna (Taboada et al. 2016, fig. 4). Moreover, they notice the absence of members of the icehouse-style *Eurydesma*-*Trigonotreta* biota, and attribute it to environmental conditions or sampling bias, rather than differences in age with the Argentine and Australian faunas.

Invertebrate assemblages of the *Eurydesma* Fauna identified the Karoo Basin, South Africa (Reed 1932; Dickins 1961), are only composed of mollusks with the bivalves *Eurydesma mytiloides* Reed, 1932, *Atomodesma* (*Aphanaia*) *haibensis* (Reed, 1936) and the gastropod *Peruvispira vipersdorfensis* Dickins (1957) (Dickins 1961, 1985).

Elements of the Early Permian *Eurydesma* Fauna have been found and published from numerous localities across several Permian sedimentary basins of eastern Australia (Bowen, Sydney, Cranky Corner and Tasmania) (Etheridge & Dun 1910; Runnegar 1969, 1979; Archbold 2003). Several *Eurydesma* species are distributed from the Tiverton Formation (Sakmarian), in the north (Bowen Basin), to the southern Sydney Basin. These latter records include the Wasp Head Formation (late Asselian-early Sakmarian, Cisterna & Shi 2014), Pebbly Beach Formation (Sakmarian-Artinskian), and from the base of the Snapper Point Formation (Kungurian, Shi et al. 2010). In the Tasmanian Basin, considered by Clarke (1987) as “the most extreme example of cold-water Gondwanan faunas known”, the genus reaches the Kungurian horizon, representing the youngest record of *Eurydesma* (Clapham & James 2008). Other bivalves associated with the Eastern Australian *Eurydesma* Fauna are: *Myonia*, *Atomodesma*, *Leptodesma*, *Stutchburia*, *Deltopecten* and *Vacunella*.

The eastern Australian Permian brachiopods (mainly from the Tasmanian and Sydney basins) that can be included in the *Eurydesma* Fauna are characterized by the genera *Arctitreta*, *Strophalosia*, *Trigonotreta*, *Sulcipleca*, *Tomiopsis*, ?*Cyrtella*, *Fletcherithyris*, *Gilledia*, *Lichareviella*, *Kelsovia*, *Lyonia* and *Bandoproductus* (Archbold 1996, 2000 and references therein provided; Cisterna & Shi 2014; Waterhouse 2015). In particular, the Tasmanian faunas represent the best preserved and the most abundant and diverse brachiopod assemblages within the oldest parts of the characteristic Gondwanan cold-water *Eurydesma* Fauna anywhere in eastern Australia and probably in the world (Clarke 1990).

Eurydesma records in western Australia are much scarcer, with occurrences of *E. playfordi* in the Lyons Group, Carnarvon Basin (Dickins 1956, 1957, 1961) and in the Carrandibby Formation near Callytharra Springs area (Dixon & Haig 2004). In this region other characteristic bivalves are *Myonia*, *Stutchburia*, *Promytilus*, *Vacunella* and *Deltopecten* (Dickins 1956, 1957, 1961). The brachiopod faunas associated with *Eurydesma* have been mostly recognized in the Perth and Carnarvon basins. These faunas are characterized by the cold water genera *Lyonia*, *Cyrtella*, *Arctitreta*, *Tomiopsis*, *Trigonotreta*, *Neilotreta*, *Rhynchopora* and *Kiangsiella* (Archbold 1996 and references provided therein).

The genus *Eurydesma* was also recorded in the Asselian-Sakmarian glacial-postglacial successions of some Asian basins. Several species of *Eurydesma* were identified from India (Salt Range, Talchir Formation, Reed 1936; Kashmir, Agglomeratic Slate Formation, Reed 1932); Himalaya and Tibet (Gungri Formation, Srikantia et al. 1978; Zhanjin Formation, Sahni & Srivastava 1956; Liu & Cui 1983), accompanied by *Leptodesma* (*Leiopteria*) and *Deltopecten*, *Praeundolomya*, *Pachymyonia*, and *Megadesmus* among others genera (Sahni & Dutt 1959; Archbold & Gaetani 1993; Ghosh 2003). Brachiopods such as *Semilingula*, *Arctitreta*, *Etherilosia*, *Strophalosia*, *Aulosteges*, *Bandoproductus*, *Cyrtella*, *Neospirifer*, *Crassispirifer*, *Tomiopsis* and *Gilledia*, have been described from Peninsular India (Manendragarh, Umaria, Badhaura) by Archbold et al. (1996), while from the eastern Himalaya (Garu Formation), species of the genera *Tivertonia*, *Costatumulus*, *Cyrtella*, *Subansiria*, *Tomiopsis*, and *Trigonotreta* have been studied (Singh & Archbold 1993).

Eurydesma was documented in Afghanistan along with *Atomodesma*, *Heteropecten* and *Megadesmus*, as the most characteristic elements (Wardak Formation, Termier et al. 1974; Ghosh et al. 2003). The brachiopod genera *Cyrtella* and *Tomiopsis* have been also identified from these sequences (Termier et al. 1974). In addition, *Eurydesma* has been reported from Pakistan in the Asselian sequences of the Gircha Formation (western Karakorum), with the bivalves *Etheripecten* sp., *Deltopecten* sp., accompanied by the brachiopod genera *Lyonia*, *Rhynchopora*, *Punctospirifer*, *Trigonotreta*, *Spirelytha* and *Tomiopsis* (Angiolini 1995; Angiolini et al. 2005).

While the bivalves of the *Eurydesma* Fauna were widely studied in some basins (Pagani 2000; Neves et al. 2014), a modern taxonomic revision of *Eurydesma* species, that includes the different parts of Gondwana is also necessary, since the last works date from the 20th century (Etheridge & Dun 1910; Reed 1932, 1936; Harrington 1955; Dickins et al. 1969; Runnegar 1969, 1979; Nilsen 1982, among other authors).

Key brachiopods of the *Eurydesma* Fauna

Among the brachiopod genera that usually appear associated with *Eurydesma*, *Tomiopsis* Benediktova is the only genus common to all the Gondwanan localities. It has also been recorded from the Carboniferous (Visean) to Permian (Cisuralian) in Russian and Asian sequences. *Tomiopsis*

can be considered an antitropical genus (i.e., a pattern of biotic distribution in which forms of life “shun the Tropics”, Hubbs 1952) with particular combined bipolar (s.s.) and bitemperate distribution patterns described by Shi & Grunt (2010). These authors proposed that *Tomioopsis* belongs to a group of genera with paleogeographical ranges extending from the paleotemperate to paleopolar zones in each hemisphere. The occurrence of *Tomioopsis* in the *Eurydesma* Fauna of the Bonete Formation, Sauce Grande Basin, and Wasp Head Formations, southeastern Sydney Basin, represents the earliest record (Asselian) of this genus from Gondwanaland. Then, in the Sakmarian-Kungurian interval, *Tomioopsis* appears to show a clear antitropical distribution with species occurring extensively in the high-palaeolatitudinal zones of both hemispheres (Shi & Grunt 2010), being particularly well represented in eastern Australia with species that even reach the Late Permian in the Tasmania and Bowen basins. *Tomioopsis* would have had a broader environmental tolerance or it was better able to adapt to the changing conditions and remained present in moderate abundance in the warmer conditions of the Kungurian (Clapham & James 2008).

Trigonotreta Koenig, a characteristic Asselian-Sakmarian Gondwanan brachiopod genus, with most of its records from localities in eastern Gondwana, can be also considered diagnostic of the *Eurydesma* Fauna. *Trigonotreta* was described as a typical cool-adapted fauna (Clarke 1990; Archbold 1996; Shi & Archbold 1993), being a particularly important component of the Early Permian faunal assemblages from the eastern Australian basins. Paleocological studies in the marine communities of these basins suggest that *Trigonotreta* and *Eurydesma* were dominant during the last stages of the glaciation (Sakmarian), but during the Kungurian climate warming, *Eurydesma* became extinct and *Trigonotreta* persisted at low abundance levels (Clapham & James 2008).

Trigonotreta has not been identified in the *Eurydesma* Fauna of western Gondwana, i.e., Paraná and Sauce Grande basins, in South America. The species from Late Paleozoic western Argentinian basins that were once described as belonging to this genus (Cisterna & Simanaukas 2000; Cisterna et al. 2002) have been reassigned to *Pericospira* (Cisterna & Archbold 2007), a very close genus of the Trigonotretidae.

The spiriferinids *Cyrtella* Fredericks and *Punctocyrtella* Plodowski are also conspicuous in the *Eurydesma* Fauna, with an important distribution during the lower-middle Cisuralian in Gondwanaland (particularly in Australia), the peri-Gondwanan regions and the Cimmerian blocks (Angiolini et al. 1997; Angiolini et al. 2003; Shen 2018). ?*Cyrtella* sp. has been recently described, in the upper part of the Taciba Formation, Paraná Basin, Brazil (Taboada et al. 2016), where it appears associated to the bivalves *Atomodesma* and *Heteropecten* in the same horizon.

The genus *Lyonia* Archbold, associated with *Eurydesma*, is widely distributed in the earliest Permian of eastern and western Australia. This brachiopod has also been reported from the Taciba Formation indicating affinities with the western Australian basins during the late Asselian-early Sakmarian (*Eurydesma-Lyonia* Fauna, Taboada et al. 2016), but it should be noted that the genus *Eurydesma* has not been reported from Brazil.

Although the genus *Tivertonia* Archbold does not have a wide distribution across Gondwana, it has been recorded from the Sauce Grande Basin, eastern Argentina, where it appears typically associated with *Eurydesma* (Pagani 1998; Taboada et al. 2016; Cisterna et al. 2018). Also, in the Garu Formation, eastern Himalaya, *Tivertonia* has been identified in the cold-water *Eurydesma* Fauna (Singh 1987; Singh & Archbold 1993). However, in eastern Australia (Bowen and Sydney basins), the genus has been described in the more diversified Artinskian faunas that indicate an increase in temperatures (Archbold 1986, 1996). In addition, in west-central Argentina *Tivertonia* characterizes the Late Carboniferous (Moscovian) *Tivertonia-Streptorhynchus* Fauna (Cisterna & Simanaukas 2000; Cisterna et al. 2002; Cisterna 2010; Cisterna et al. 2011); the development of these faunas is associated with an important climatic amelioration recorded in the western Argentinian basins (Sterren & Cisterna 2010).

***EURYDESMA* FAUNA IN THE SAUCE GRANDE BASIN, ARGENTINA**

Fossil assemblages of the *Eurydesma* Fauna from the Sauce Grande basin have been identified in the lower part of the Bonete Formation exposed in the Sierras Australes Foldbelt of eastern

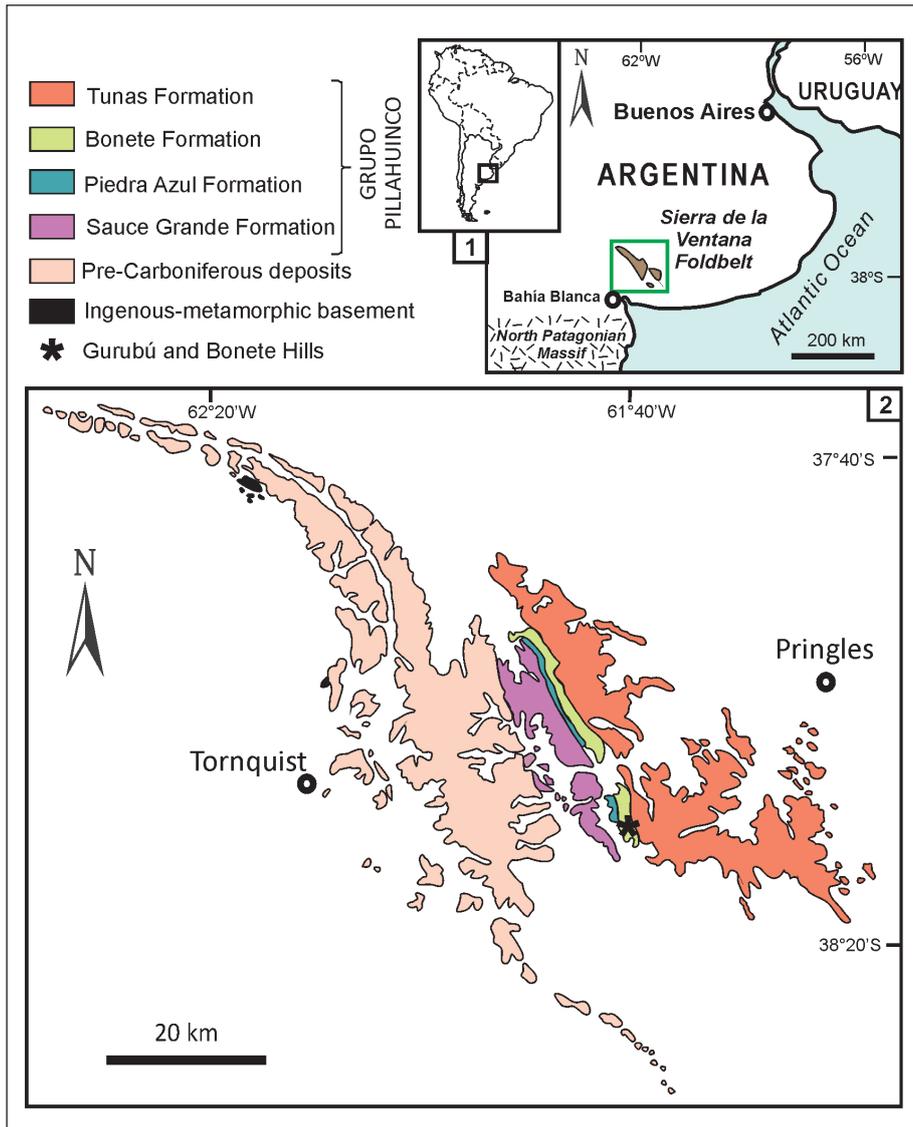
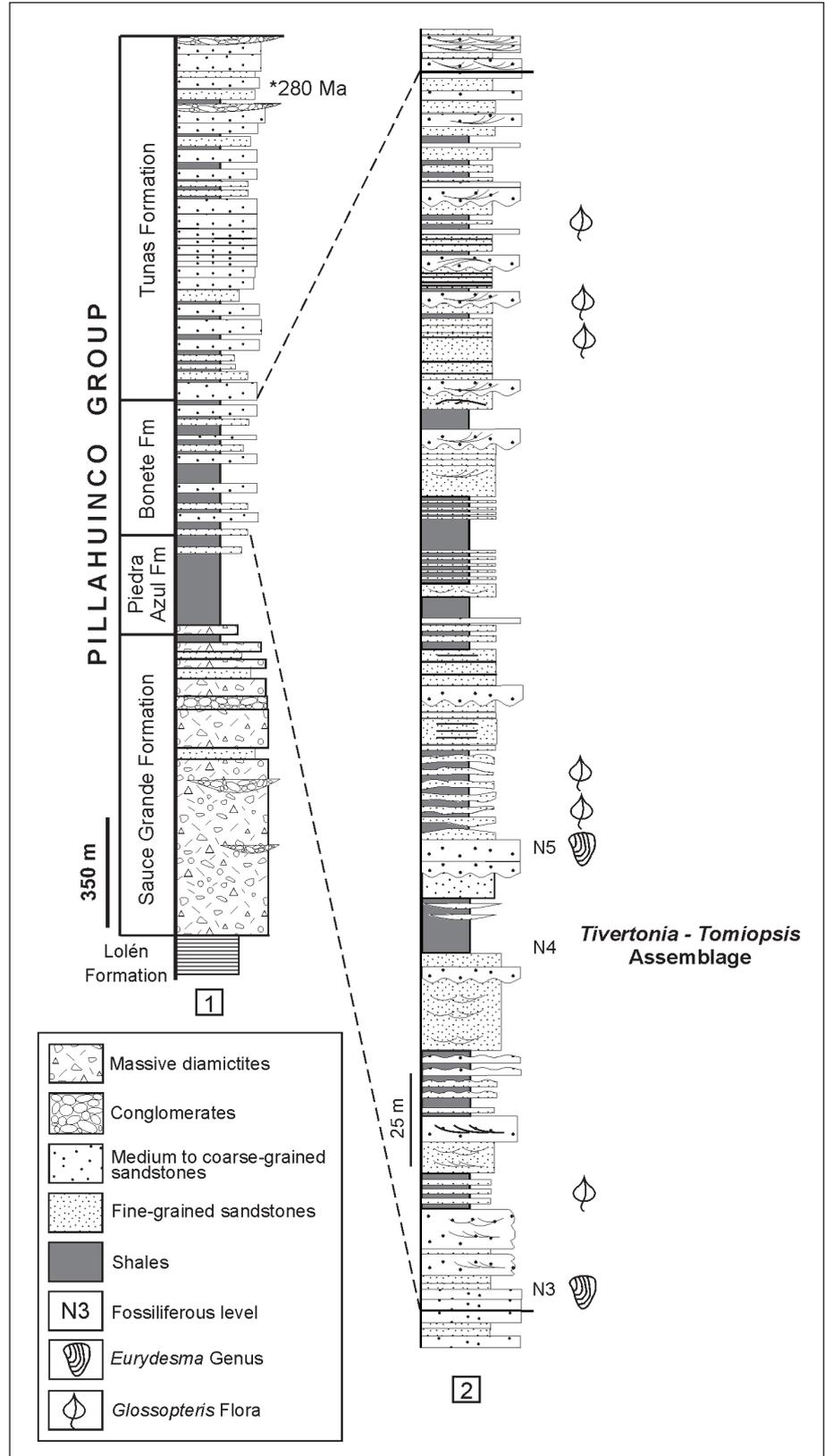


Fig. 2 - 1) Geographic location of Sierra de la Ventana Foldbelt in the Sauce Grande Basin, eastern Argentina; 2) Sierra de la Ventana Foldbelt outcrops with emphasis on the Upper Paleozoic units (Pillahuincó Group) and the fossil localities (Gurubú and Bonete Hills). Modified from López-Gamundí et al. (2013).

central Argentina (Fig. 2.1). The main outcrops of this unit are located to the east of Sierras Australes (Fig. 2.2), and they are included in the Pillahuincó Group (Harrington 1947); it represents the Gondwanan succession in the Sauce Grande Basin and has been subdivided into four formations. These are, in ascending stratigraphic order: Sauce Grande, Piedra Azul, Bonete and Tunas formations (Fig. 3). The Bonete Formation along with the underlying Sauce Grande and Piedra Azul Formations show an integrated depositional history which can be explained in terms of glaciomarine sedimentation (Sauce Grande Formation) and postglacial transgression (Piedra Azul and Bonete Formations) (López-Gamundí et al. 1995). The Sauce Grande Formation (Pennsylvanian-Cisuralian, Di Pasquo et al. 2008), lies atop a regional unconformity on Devonian basement and is characterized by mas-

sive to crudely stratified glacial-marine diamictites with subordinate gravity flows deposits and channelized, slumped conglomerates and sandstones. Isolated ice-rafted horizons and rhythmites have also been recognized (López-Gamundí et al. 1995, 2013). This unit grades up to outer shelf shales of the Piedra Azul Formation which pass upward to the heterolithic facies of fine-to medium-grained outer to inner shelf sandstones and bioturbated shales with fossils of *Eurydesma* that characterize the Bonete Formation (a stratigraphic succession about 400 meters thick), which also contain the *Glossopteris* Flora (Fig. 3.2). Increasing amount of sandstone toward the top of the Pillahuincó Group has been also identified by López-Gamundí et al. (1995, 2013). These authors have studied the Tunas Formation, the last formation of the Pillahuincó Group, which is characterized by deltaic mouth

Fig. 3 - 1) Stratigraphic column of the Upper Paleozoic Pillahuincó Group at the Ventana foldbelt (modified from López-Gamundí et al. 2013); 2) Detail of the fossiliferous Bonete Formation and the stratigraphic distribution of the brachiopod assemblage and of the genus *Eurydesma* (modified from Andreis & Japas 1991).



bar/distributary channel sandstones arranged in coarsening-upward sequences. The occurrence of the *Glossopteris* Flora in the lower half of this unit would suggest a Sakmarian-Artinskian age according to Archangelsky et al. (1996).

SHRIMP radiogenic isotope dating on zircons in the levels tuffaceous intercalated in the upper half of the Pillahuincó Group confirms a Cisuralian age (280.8 ± 1.9 Ma) for the uppermost section of the Tunas Formation; besides it indicates that the

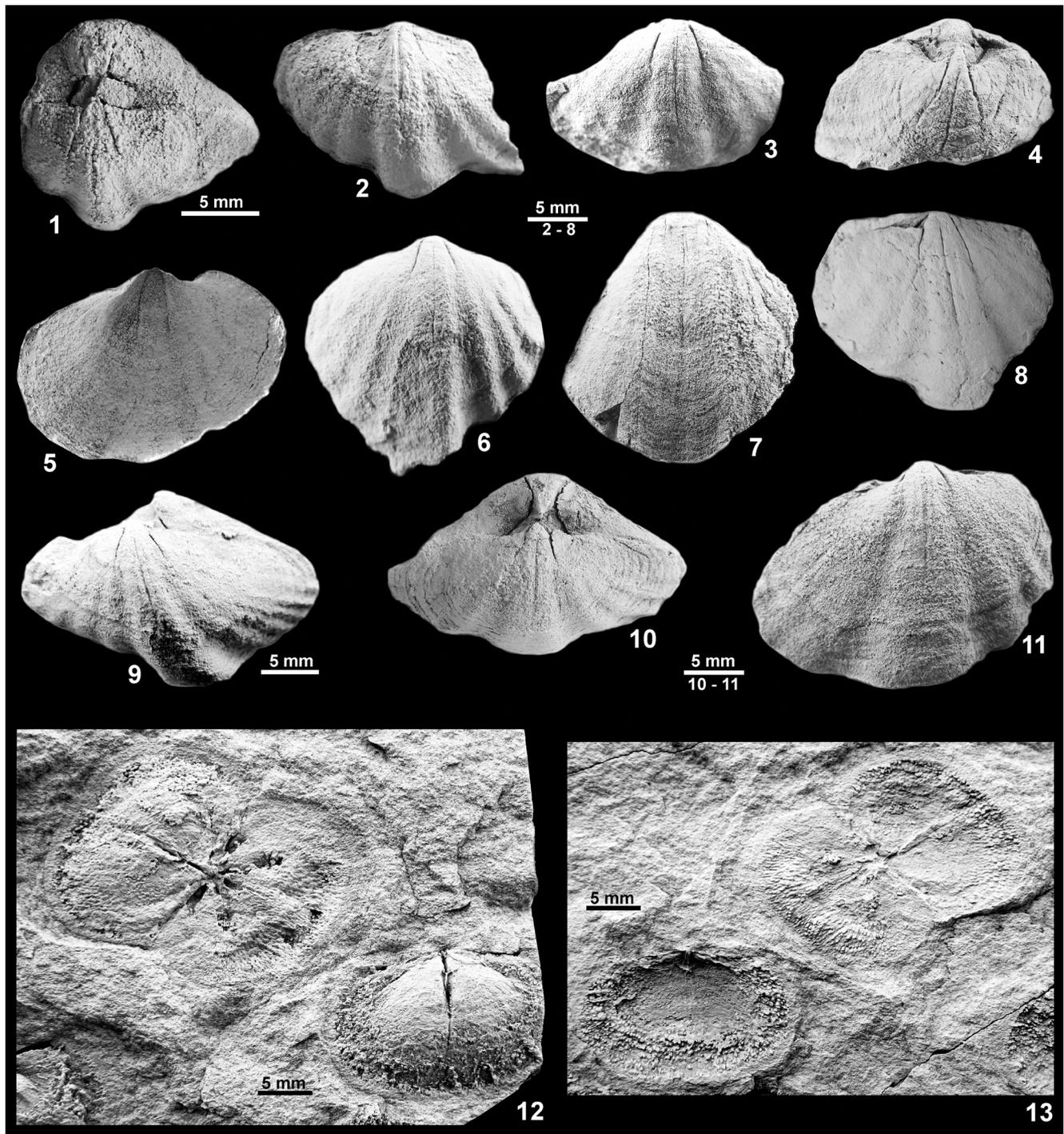


Fig. 4 - *Tivertonia* -*Tomiopsis* assemblage from the Bonete Formation, Sauce Grande Basin (Argentina). 1-11) *Tomiopsis harringtoni* Archbold & Thomas. 1: MLP 35904, internal mould of articulate specimen, dorsal view; 2: MLP 35905, internal mould of dorsal valve; 3: MLP 35906, internal mould of dorsal valve; 4: MLP 35907, internal mould of articulate specimen, ventral view; 5: MLP 35908, external mould of ventral valve; 6: MLP 35909, internal mould of dorsal valve; 7: MLP 35910, internal mould of ventral valve; 8: MLP 35911, internal mould of dorsal valve; 9: MLP 35912, internal mould of articulate specimen, dorsal view; 10: MLP 35913, internal mould of articulate specimen, dorsal view; 11: MLP 35914, internal mould of articulate specimen, dorsal view; 12-13) *Tivertonia pillabutuensis* (Harrington), internal and external mould of an articulate specimen (MLP 35920a-b) and a ventral valve (MLP 35921a-b). Materials figured are registered by the prefix MLP, Museo de la Plata.

glacial conditions ceased in the Sauce Grande basin by the early Artinskian and it constrains the marine fauna of the Bonete Formation to the Asselian-Sak-

marian interval (López-Gamundí et al. 2013).

The first descriptions of brachiopods and bivalves from the Bonete Formation were made by



Fig. 5 - 1) *Eurydesma cordatum* Morris, internal mould of right valve, MLP 35939; 2) *Eurydesma hobartense* (Johnston) internal mould of right valve, MLP35940, Bonete Formation, Sauce Grande Basin (Argentina); 3, 5) *Eurydesma* shell bed from the *Trigonotreta* - *Tomioopsis* assemblage, Wasp Head Formation, Sydney Basin, Australia, 4) *Eurydesma* shell bed from N5 level, Bonete Formation, Sauce Grande Basin (Argentina), MLP 35943.

Harrington (1955), who recognized five fossiliferous levels throughout the Pillahuincó Group. The lower, Level 1, in the Sauce Grande Formation, with *Astartella? pusilla* Harrington and the second, Level 2, in the Piedra Azul Formation, with gastropods indet. The three upper fossiliferous levels are in the Bonete Formation, and they are characterized by bivalves and brachiopods of the *Eurydesma* Fauna: Level 3, with *Eurydesma cordatum* Morris; Level 4 with “*Chonetes*” *pillabuincensis* Harrington, *Notospirifer darwini* (Morris), *Stutchburia? argentinensis* Harrington, *Allorisma inflectoventris* Harrington, *Aphanaia? orbirugata* Harrington and *Liopteria? dutoiti* Harrington; and Level 5 with *Eurydesma altum* Harrington, *E. mytiloides* Reed, *E. hobartense* (Johnston), *Liopteria? bonaerensis* Harrington, *Schizodus cycloliratus* Harrington and *Promytilus acinaciformis* Harrington. Rocha Campos & de Carvalho (1975) also described from Level 4 the bivalves *Deltopecten harringtoni* and *Vacunella camachoii*.

Archbold & Thomas (1986) redescribed the brachiopod *Notospirifer darwini* (Morris) as the new species *Tomioopsis harringtoni*, and Pagani (1998) re-assigned the species *Chonetes pillabuincensis* to the genus *Tivertonia* Archbold, and studied the gastropod *Peruvispira* sp. of the Piedra Azul Formation. Also, Pagani (2000) described *Heteropecten* sp. and *Myonia* sp. from the Bonete Formation, reviewed the Harrington species and re-assigned *Leptodesma* (*Liopteria?*) *bonaerensis* Harrington, *Leptodesma* (*Liopteria?*) *dutoiti* (Harrington) and *Atomodesma* (*Aphanaia*) *orbirugata* Harrington.

The recent fieldwork in the Sierra de la Ventana Foldbelt (Fig. 2B) has allowed us to identify, in the fossiliferous interval of the Bonete Formation, two faunal assemblages spanning the *Eurydesma* Fauna interval (Fig. 3): the *Tivertonia* - *Tomioopsis* assemblage (Fig. 4) in the lower part, and the *Eurydesma* assemblage in the upper, both associated with sandstones beds. The first (N4, Fig. 3.2), which is probably equivalent

to “Level 4” of the section described by Harrington (1955: 113), is dominated by the brachiopods *Tivertonia pillabuincensis* (Harrington) and *Tomioopsis barringtoni* Archbold & Thomas, accompanied by scarce bivalves (*Heteropecten* sp., *Allorisma?* sp. and *Bivalvia* indet. spp. which are still under study). Fossil concentrations occur as shell beds. *Tomioopsis* shells, that usually appear in ‘nests’, show a low degree of fragmentation, a high percentage of articulate specimens, and include many different ontogenetic stages. A predominance of *Tivertonia* and the absence of bivalves have been observed in some levels. The second assemblage recognized (N5, Fig. 3.2), equivalent to “Level 5” from the section described by Harrington (1955:113), we preliminary identified *Eurydesma cordatum?* Morris, *E. hobartense* (Johnston) and *Bivalvia* indet. (Fig. 5); the material is still under study by one of the authors (AFS). These bivalves are preserved as internal moulds and appear scattered and occasionally concentrated in cm-thick beds.

Harrington (1955) described five bivalve species from the Bonete Formation but he suggested that the correct identification of the different species assigned to *Eurydesma* Morris is a difficult task because the genus has a wide range of specific variability. Harrington also suggests that the species distinguished until that moment showed an equally wide range of individual variation. In addition, Japas & Amos (1986) noted that the specimens of the Bonete Formation assigned to the different species of *Eurydesma*, would have been subjected to tectonic deformation, which leads to overestimate the number of species. These authors questioned the validity of the species *E. altum* defined by Harrington, which would be a deformed specimen of *E. hobartense*, and proposed that *E. mytiloides* and *E. hobartense* belong to the same taxon. Based on the new material reviewed by us, we agree that the number of *Eurydesma* species might have been overestimated due to deformation.

The material herein studied was assigned to *Eurydesma cordatum?* Morris mainly by the size and shape of the shell (large, inflated and subcircular) with relatively high umbones and pronounced umbonal slopes (Fig. 5.1) and to *E. hobartense* (Johnston) because of its medium size, general outline obliquely elongate and comparatively low umbones (Fig. 5.2). However, a modern taxonomic revision of the group is required.

EURYDESMA FAUNA IN THE SOUTHERN SYDNEY BASIN, AUSTRALIA

Fossil assemblages of the *Eurydesma* Fauna from the southern Sydney Basin have been studied in a key section, the Wasp Head Formation, a shallow marine sandstone dominated unit that encloses records of the first Permian glacial interval suggested for eastern Australia (Fielding et al. 2008). Outcrops of the Wasp Head Formation (up to 100 meters thick) are exposed along the coast between Myrtle Beach and Depot Beach on the south coast of New South Wales, southeastern Australia (Fig. 6). The unit, widely studied in terms of stratigraphy and sedimentology (Gostin & Herbert 1973; Tye et al. 1996; Eyles et al. 1997, 1998; Rygel et al. 2008), is unconformably overlying the lower Paleozoic Wagonga Group, and is characterized by a basal part

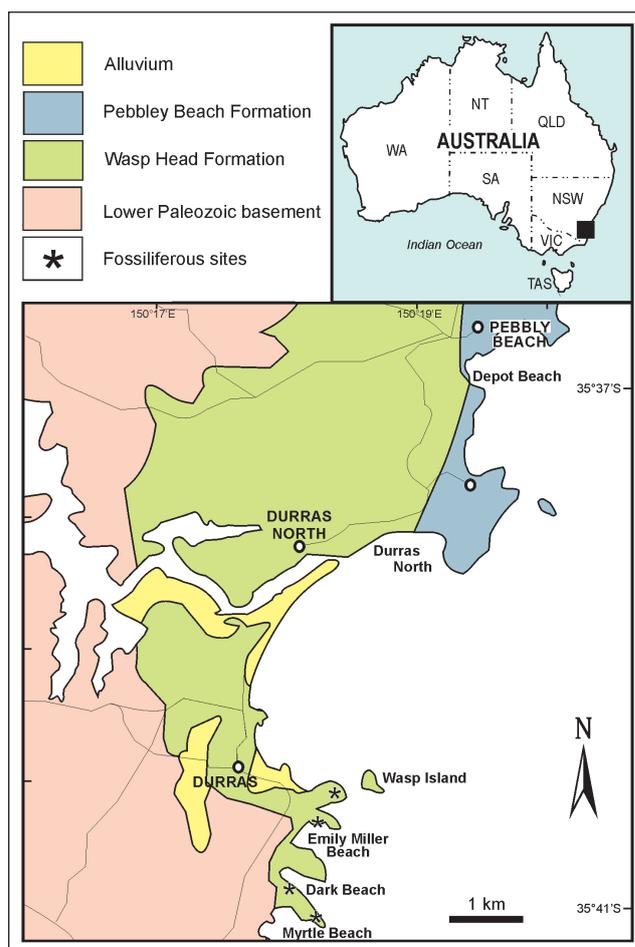


Fig. 6 - Location map showing the distribution of the Wasp Head Formation and the fossiliferous localities studied (modified from Rygel et al. 2008).

dominated by massive breccias, passing upwards to sandstone, mudstone, thin conglomerate, and admixed sandstone and mudstone (Gostin & Herbert 1973). Rygel et al. (2008) indicated that ice-rafted debris is present throughout the formation but the amount and size of the clasts generally decrease upwards through this unit. These authors have also proposed a depositional model for the Wasp Head Formation suggesting that its basal part records a gradual deepening upward trend from upper to middle shoreface water depths, and that the upper part consists of alternations between shoreface to offshore deposits that reflect a response to relatively rapid (glacioeustatic) sea level rises. According to Rygel et al. (2008) this unit was deposited during a transition to a nonglacial period following the late Asselian to early Sakmarian glaciation in eastern Australia.

Previous paleontological studies of the Wasp Head Formation, particularly those of its brachiopod faunas, have been widely discussed by Cisterna & Shi (2014). In relation with the occurrence of the *Eurydesma* genus in this section, only two species have been described from the Wasp Head Formation, i.e. *Eurydesma cordatum* Morris and *Eurydesma* sp. indet. (Runnegar 1969; Dickins et al. 1969; Nilsen 1982), but there are no more recent works that have reviewed the taxonomy of this group.

Cisterna & Shi (2014), identified three brachiopod assemblages containing typical genera of the *Eurydesma* Fauna throughout the Wasp Head Formation (Fig. 7): the lower assemblage *Strophalosia concentrica* Zone that appears associated with the breccia horizons in the basal part of the section (Mb2/Db2, Fig. 7) is bivalve-dominated. *Tomiopsis konincki* (Etheridge) is, based on abundance, the most common species among the brachiopods, and is accompanied by *Arctitreta* sp., *Pseudosyrinx*? sp. and *Strophalosia concentrica* Clarke that characterizes the *Strophalosia concentrica* Zone Briggs (1998). Bivalve species of the genera *Promytilus*, *Merismopecteria*, *Etheripecten*, *Streblopecteria*? and *Pyramus* have been described in this assemblage (Nilsen 1982).

The second assemblage *Strophalosia subcircularis* Zone in the middle part of the section (GRS1, Fig. 7) is usually associated with conglomeratic horizons in an interval of fine-grained to coarse-grained sandstone with conglomeratic beds that characterize the middle shoreface facies association (Rygel et al. 2008). This assemblage is also bivalve-dominated

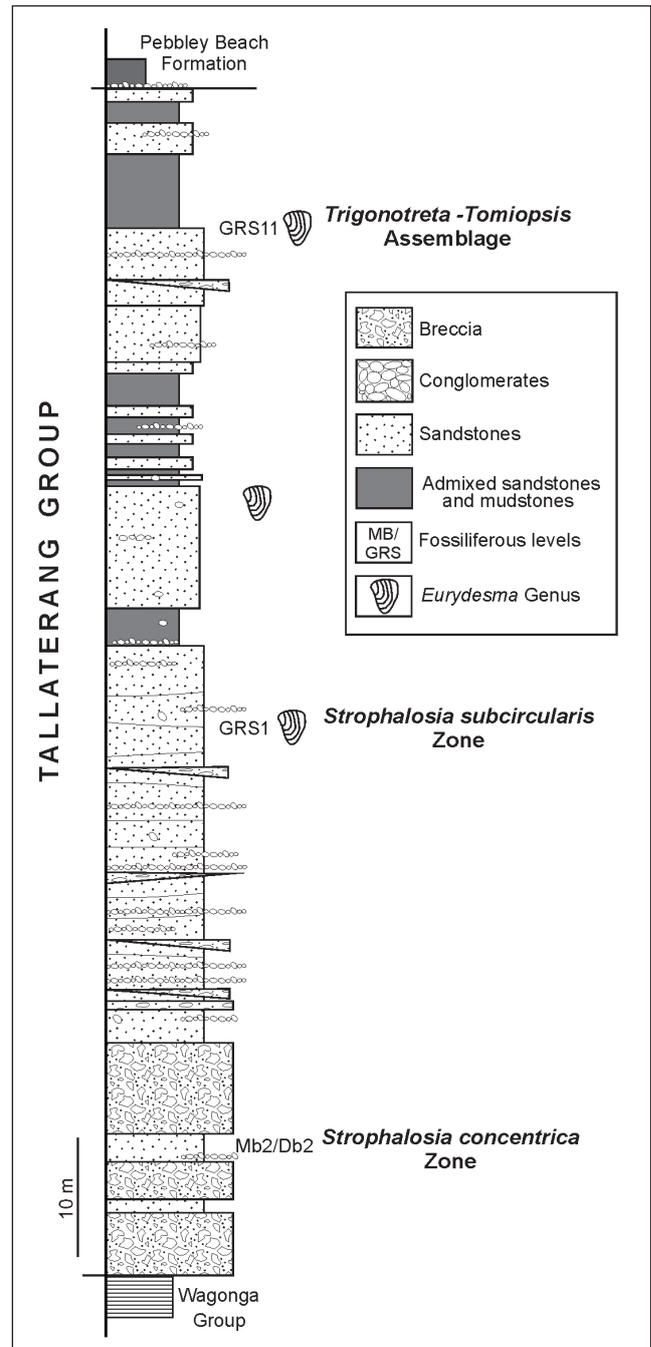


Fig. 7 - Stratigraphic column of the Wasp Head Formation and stratigraphic distribution of the brachiopod assemblages and of the *Eurydesma* genus (modified from Rygel et al. 2008).

and the brachiopods are very rare and fragmentary. However, the diagnostic brachiopods *Strophalosia subcircularis* and *Tomiopsis konincki* of the *Strophalosia subcircularis* Zone have been recognized. The bivalve fauna identified in this assemblage by Nilsen (1982), includes species of *Kaibabella*, *Astartila*, *Permophorus*, *Megadesmus* and *Myonia*. In addition, from this interval Runnegar (1969) described *Eurydesma cordatum*, *Neoschizodus australis* and *Australomya hillae*.

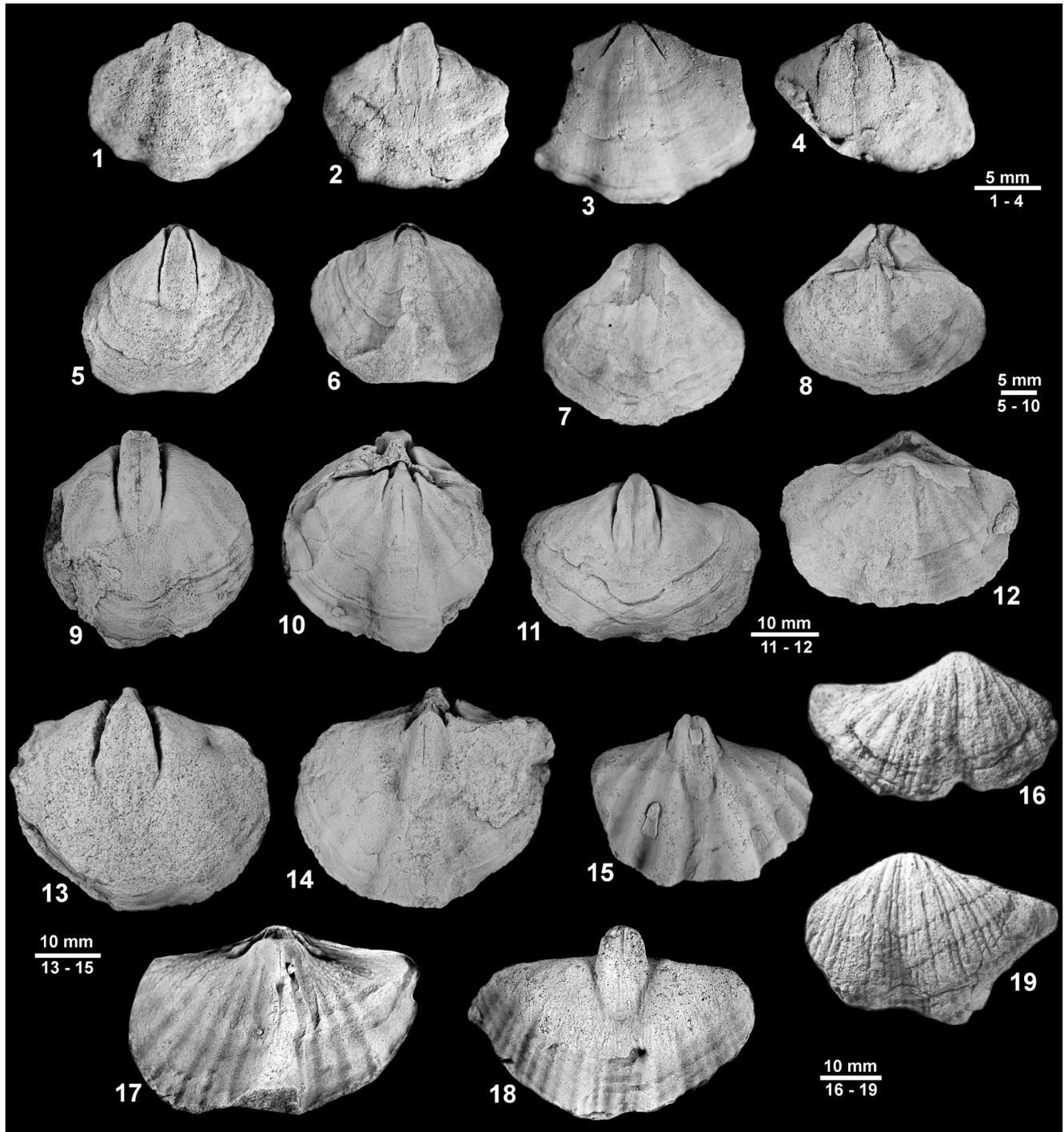


Fig. 8 - *Trigonotreta* - *Tomiopsis* assemblage from the Wasp Head Formation, Sydney Basin, Australia. 1-4) *Tomiopsis konincki* (Etheridge). 1: UQF 73041, dorsal internal mould; 2: UQF 73032, ventral internal mould; 3: UQF 73036, ventral internal mould; 4: UQF 73047, ventral internal mould. 5-10) *Tomiopsis* sp. aff. *T. konincki* (Etheridge). 5-6: NMV P309911, internal mould of articulate specimen, ventral and dorsal views; 7-8: NMV P309912, articulate specimen, ventral and dorsal views; 9-10: NMV P309897, internal mould of articulate specimen, ventral and dorsal views. 11-14) *Tomiopsis piersoni* Cisterna & Shi. 11-12: NMV P309931, internal mould of articulate specimen, ventral and dorsal views; 13-14: NMV P309932, internal mould of articulate specimen, ventral and dorsal views. 15) *Tomiopsis?* sp., NMV P309941, ventral internal mould. 16-19) *Trigonotreta stokesi* Koenig. 16: NMV P309946, ventral valve; 17: UQF 73022, dorsal internal mould; 18: UQF 73023, ventral internal mould; 19: NMV P309954, ventral valve. Materials figured are registered by the prefix NMV P, housed in the paleontological collections of Museum Victoria, Melbourne, Australia, and UQF, housed in the Queensland Museum, Brisbane, Australia.

The third of the brachiopod assemblages (*Trigonotreta-Tomiopsis*) appears in the uppermost

part of the formation (GRS11, Fig. 7), commonly associated with admixed pebbly sandstone and

mudstone rocks, abundant dropstones, and conglomerate layers. This interval has been interpreted as the product of alternating shoreface and offshore environments (Rygel et al. 2008). Two brachiopod-dominated subassemblages have been recognized in this assemblage: the lower, in a conglomerate layer, is dominated by *Trigonotreta stokesi* Koenig, accompanied by very scarce *Trigonotreta* sp., *Trigonotretidae* indet., *Tomiopsis* sp. aff. *Tomiopsis konincki*, and *Pseudosyrinx?* sp. The associated fauna is mainly represented by the bivalve *Eurydesma cordatum* Morris but species of the genera *Myonia*, *Etheripecten*, *Elimata*, *Stutchburia* and *Vacunella* have also been described (Nillsen 1982). The bioclasts appear concentrated in matrix-supported beds, chaotically oriented and with different fragmentation degrees. Immediately above the conglomerate layer, the second brachiopod subassemblage has been identified (Cisterna & Shi 2014). It is represented by a relatively high-diversity fauna (Fig. 8), dominated by *Tomiopsis* spp. (*Tomiopsis* sp. aff. *Tomiopsis konincki* (Etheridge), *Tomiopsis piersoni* Cisterna & Shi and *Tomiopsis?* sp.), accompanied by *Pseudosyrinx?* sp. and the terebratulids *Fletcherithyris?* sp. and *Gilledia?* sp.). Some bivalves and very rare gastropods were also identified. For this subassemblage Cisterna & Shi (2014) described, the taphonomic and paleoecologic features (i.e., fossil concentrations occur as shell beds; *Tomiopsis* shells usually appear in ‘nests’; bioclasts show poor sorting and a random distribution; shells show low degree of abrasion, fragmentation and very high percentage of articulate specimens; a high degree of shell size mixing involving shells of different ontogenetic stages), that indicate a paraautochthonous to autochthonous origin.

PRELIMINARY QUANTITATIVE ANALYSIS

Paleoecological studies of brachiopods represent an important tool to understand the complex paleoenvironmental conditions related to the glacial-deglacial events of the LPIA (Balseiro 2016; Cisterna et al. 2017). Therefore brachiopods, as one of the most significant components of the postglacial *Eurydesma* Fauna, are herein quantitatively analyzed, along with the bivalves associated, in two key Gondwanan sections from Argentina (Bonete Formation, Sauce Grande Basin) and Australia (Wasp Head Formation, Sydney Basin).

The analyses were based on 56 collections (bulk samples from single beds scale) with 172 occurrences of 36 genera of Asselian-Sakmarian brachiopods (13) and bivalves (23) from the Bonete Formation (19 collections) and Wasp Head Formation (37 collections). An occurrence is the presence of certain taxa recorded in a bed or at section scale (i.e.: collection scale, see Supplementary Data 1). In order to evaluate the compositional differences between the Bonete and Wasp Head faunas, we carried out an ordination analysis and a PERMANOVA. For the ordination, we performed a Nonmetric Multidimensional scaling (i.e., NMDS) using Forbes distance (Alroy 2015). The NMDS has shown to be very powerful for recognizing underlying gradients in fossil data (Bush & Brame 2010), and the Forbes distance can minimize compositional differences caused by differences in sample size alone (Alroy 2015). We further used a PERMANOVA to test compositional differences. PERMANOVA has shown to be more robust than similar methods (i.e. ANOSIM) relative to differences in multivariate dispersion (Warton et al. 2012) with *metaMDS* and *adonis* functions of the package ‘vegan’ (Oksanen et al. 2018).

The occupancy is considered a good estimate for relative abundance (Hsieh et al. 2019). Herein, it represents the proportion of the available collections where a given genus occurs. In other words, it is expressed as the total number of occurrences of a taxon relative to the total number of samples. We calculated taxa occupancies for each region separately. We then built occupancy – rank plots in order to assess brachiopods and bivalves dominance in the postglacial *Eurydesma* Fauna.

The compositional similarity between Australian and Argentinian samples can be observed in the Figure 9. The wide distribution of the samples in the NMDS (stress= 0.2) with a total overlap of the hulls suggests a lack of compositional differences between the regions. A PERMANOVA test confirms this pattern of no significant differences between Wasp Head and Bonete formations ($R=0.31$, $df=1$, $p=1$).

On the other hand, occupancies exhibit differences between the two regions. The Wasp Head Formation has a higher proportion of brachiopods than Bonete Formation. In fact, out of the 13 brachiopods genera represented in both areas, 12 are recorded in the Wasp Head Formation and only 2 can be found in the Bonete section. Moreover, the most

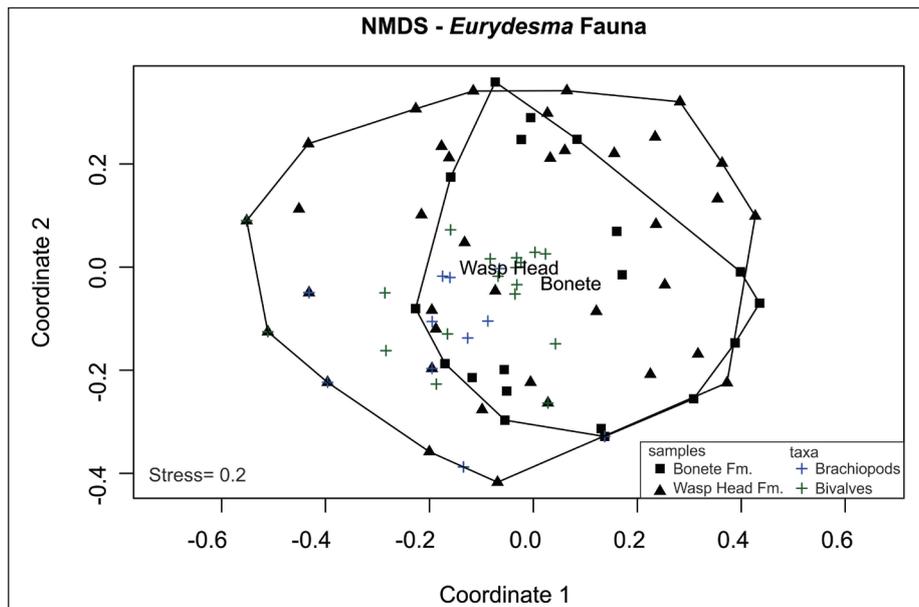


Fig. 9 - Non-Multidimensional Scale Analysis using Forbes distance (Alroy 2015) showing compositional variation between samples from the Wasp Head (black triangles) and Bonete (black squares) formations. Brachiopods and bivalves genera are represented with blue and green crosses, respectively. Convex-hulls (black lines) arrangement exhibits the similitude between both localities.

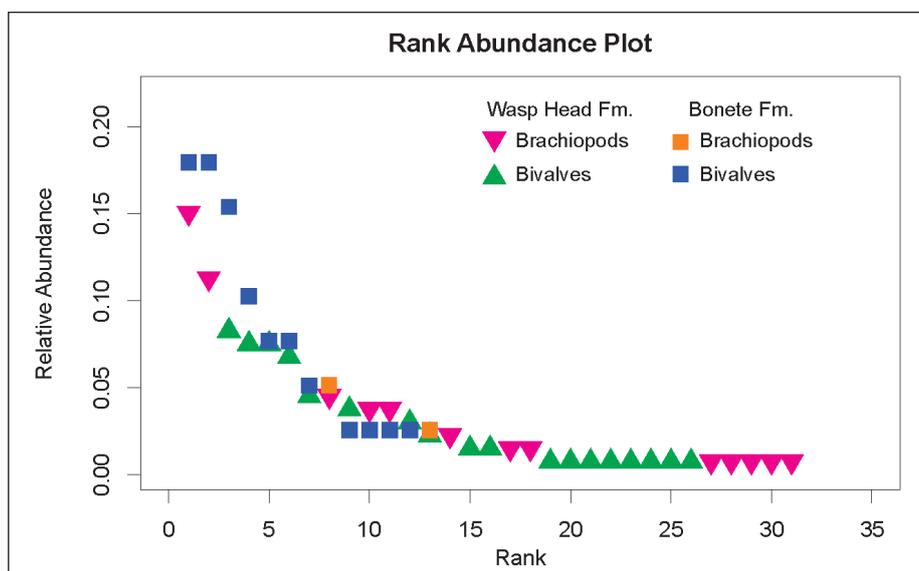


Fig. 10 - Proportional occupancy-rank plot showing the variation of taxa distribution in the Wasp Head (triangles) and Bonete (squares) formations. Note that brachiopods (fuchsia triangles) and bivalves (green triangles) dominate in the Wasp Head Formation whilst only bivalves (blue squares) dominate in the Bonete Formation.

frequent taxa recorded in Wasp Head Formation are *Tomiopsis* and *Trigonotreta*, followed by three bivalves: *Megadesmus*, *Eurydesma*, and *Pyramus* (Fig. 10). In contrast, the Bonete Formation is characterized by high dominance of bivalves: *Eurydesma*, *Promytilus*, and *Heteropecten* together with *Myonia* and *Atomodesma* while brachiopods are poorly represented in these faunal assemblages (Fig. 10).

TIMING OF THE TRANSGRESSION WITH THE *EURYDESMA* FAUNA

The diachronism of the glacial deposits in the LPIA, as a result of the wandering of Gondwana through the pole, is widely accepted, so that some authors (López-Gamundí 1997; Isbell et al. 2003)

have suggested three glacial episodes, from the early Carboniferous to the early Permian. The *Eurydesma* Fauna was associated with the more extensive of these glacial episodes, Episode III (late Carboniferous-early Permian), widespread from South America across Africa to India and to Australia (López-Gamundí 1997, 2010 and references therein). The stratigraphic record indicates that large ice sheets previous to this episode were never present (Isbell et al. 2003). In eastern Australia, in particular, stratigraphic and sedimentological data from New South Wales and Queensland suggest that the LPIA consisted of at least eight discrete glacial intervals, with durations from ~1 to several m.y., but they were not necessarily coeval in different parts of Gondwana (Fielding et al. 2008).

On the other hand, the timing of onset and demise of each glacial episode of the LPIA remains controversial. With relation to the Episode III in particular, radiometric data are available from South America (Argentina and Brazil), Australia and South Africa. In the glacial deposits of the Dwyka Group in Namibia, Karoo Basin, tuff horizons associated with the upper part of the Hardap Shale Member, and the top deglaciation sequence III of Bangert et al. (2000), revealed a SHRIMP age of 297.1 ± 1.8 Ma, i.e. early Permian Asselian (Stollhofen et al. 2008). The post-glacial sequences dated contain the *Eurydesma* Fauna and they have been correlated with the Gondwana-wide *Eurydesma* transgression by Stollhofen et al. (2008). These authors also stressed the importance of this datum to calibrate the age of a well-established global event, the *Eurydesma* transgression, which has been reported from South America, India and Australia.

In the Paraná Basin, Brazil, U–Pb SHRIMP ages obtained from the coal-bearing deposits of the Rio Bonito Formation (Matos et al. 2001; Rocha Campos et al. 2006, 2007, 2019; Mori et al. 2012; Simões et al. 2012), have constrained the beds with marine invertebrates of the underlying Taciba Formation (upper part of the Itararé Group) to pre-Artinskian. However, LA-ICP-MS U–Pb radiometric age provided by Cagliari et al. (2014), suggests that deposition of the post-glacial coal-bearing deposits of the Rio Bonito Formation was probably initiated before the Early Permian. It conflicts with the palynomorphs and plant fossils data, and would constrain the deposition of the entire Itararé Group between Bashkirian–Moscovian times (Taboada et al. 2016). Also, Cagliari et al. (2016) presented new U–Pb radiometric ages for glacial (307.7 ± 3.1 Ma at the topmost glacial deposits of the Itararé Group) and post-glacial deposits (298.8 ± 1.9 Ma at the base of the Rio Bonito Formation) of the Paraná Basin that constrain the glaciation to the Pennsylvanian. These authors compared the glacial and post-glacial deposits of the southern Paraná Basin with the Paganzo and Karoo basins, indicating that the end of the LPIA is asynchronous. It is remarkable, however, that they did not include the neighboring Sauce Grande Basin in the comparison with the Paraná Basin, considering that both record the *Eurydesma* transgression. The SHRIMP age of 280.8 ± 1.9 Ma from the upper part of the Tunas Formation, in the post-glacial section of the Pillahuincó Group, would con-

firm that the glacial conditions in the Sauce Grande Basin ceased by the Artinskian (López-Gamundí et al. 2013). Recently, Griffis et al. (2018) reexamined the previously dated coal interval of the Paraná Basin, using the CA-TIMS (chemical abrasion–thermal ionization mass spectrometry) analysis of individual zircons, and suggest that that terminal deglaciation in this basin occurred near the Permian–Carboniferous boundary.

In the Sydney Basin radiometric ages that would constrain the timing of the *Eurydesma* transgression in eastern Australia, have been provided by Roberts et al. (1996). SHRIMP zircon dating from tuff of the lower Branxton Formation had an age of 272.2 ± 3.2 Ma (i.e., the Kungurian–Guadalupian boundary). The lower part of the Branxton Formation contains brachiopods probably referable to the upper part of the *Echinalosia maxwelli* Zone and *Echinalosia discinia* (Roberts et al. 1996; Briggs 1998; Fielding et al. 2008; Waterhouse 2008), allowing the biostratigraphical correlation with the Snapper Point and Wandrawandian formations. Thus, the presence of *Eurydesma* in these units (Dickins et al. 1969; Runnegar 1979; Roberts et al. 1996; Shi et al. 2010) can be considered the youngest records of the genus. The occurrences of *Eurydesma* in the Branxton section has been also reported by Raggatt (1930), however, this datum could not be confirmed by further studies. The information currently available indicates that from eastern Australia the *Eurydesma* Fauna is clearly related with the glacial episodes P1 and P2 proposed by Fielding et al. (2008) and could be also associated with the youngest episode P3. In western Australia, the glacial deposits containing the *Eurydesma* Fauna have not been dated by radiometric methods; the documentation of these sequences is mainly based on biostratigraphic markers by the key ammonoids *Juresanites jacksoni* (Etheridge) and *Uraloceras irvinense* (Teichert & Glenister), and by palynoflora data (Archbold 1999, 2001; Leonova 1999, 2011; Haig et al. 2014).

The diachronism and the controversial timing of the end of deglaciation prevent a precise biostratigraphic correlation of the postglacial *Eurydesma* Fauna. However, comparative analyses of this fauna throughout the Gondwanan localities, in terms of its composition and paleoecological parameters, are necessary in order to understand the paleoenvironmental conditions that could have been controlling its distribution.

PALEOECOLOGY OF *EURYDESMA* FAUNA IN THE STUDIED SECTIONS

The preliminary quantitative analysis of the postglacial *Eurydesma* Fauna in the two key sections that record the earliest Permian glacial episode [episode P1 of Fielding et al. (2008)] from western and eastern Gondwana, indicate that they show high compositional similarity (Fig. 9). However, as outlined above, occupancies exhibit important differences between the two studied regions: dominance of brachiopods can be found in eastern Australia, and dominance of bivalves is characteristic of eastern Argentina (Fig. 10). *Eurydesma* is a frequent taxon in the two analyzed regions (Fig. 10), but it does not seem to be highly diversified [(the number of species proposed for the Bonete Formation, in particular, is probably overestimated due to tectonic deformation as suggested by Japas & Amos (1986)].

In the Bonete Formation where the postglacial *Eurydesma* Fauna occurs in outer to inner shelf deposits (López-Gamundí et al. 1995, 2013), the brachiopods are poorly represented with the genera *Tivertonia* and *Tomioopsis*. Species of the genus *Tivertonia*, like other Late Paleozoic chonetids from Argentina usually associated with sandstone beds, have been identified as opportunists (Simanaukas 1991; Simanaukas & Muzón 1991; Simanaukas & Cisterna 2000; Cisterna et al. 2017). The morphology of this type of free-lying brachiopods (e.g. the flat or very slightly convex shape) has been interpreted to be a response to increase stability in higher energy conditions (Simanaukas & Cisterna 2000). The local dominance of this genus with respect to the spiriferid *Tomioopsis* in the Bonete Formation has been recognized in some beds of the sandstone interval containing the *Tivertonia-Tomioopsis* assemblage.

Tivertonia was also regionally dominant during the climate amelioration intervals that affected the western Gondwana margin (Sterren & Cisterna 2010). Hence, an increase in *Tivertonia*'s abundance at a sample scale in the Bonete section could represent brief rise of the temperature. Nevertheless, its low abundance at a regional scale in the Sauce Grande Basin (Fig. 10) could be restrained by other environmental factors (i.e., turbulence, substrate preference) or/and by biological factors (i.e., competition with bivalves or low dispersion rate) (Peck 2008). Most likely, the development of r-strategy taxa, such as *Eurydesma* (Runnegar 1979) during the

end of a glacial episode would negatively affect brachiopods' abundance. Opportunist (or r-strategy) taxa are broadly tolerant to environmental changes; they can rapidly increase their numbers and dominate rather stable communities or colonize new substrates (Levinton 1970). Moreover, for having been densely recorded in a variety of depth and substrate settings, from shoreface to below fair weather wave base facies (Runnegar 1979). *Eurydesma* could be considered as an opportunist taxon characteristic of this postglacial fauna. Other than bivalves, brachiopods can be bathymetric or substrate specialists (Topper et al. 2015; Balseiro & Halpern 2019), namely during their larval settlement in glacial environments (Peck & Robinson 1994). Both ecological features could have a synergistic effect in a poor representation of brachiopods in this region. Nevertheless, brachiopods already showed a decrease in importance in Pennsylvanian communities from Argentina, despite they presented no differences relative to bivalves in environmental preferences nor in environmental breadth (Balseiro 2016; Balseiro & Halpern 2016, 2019). Unfortunately, eastern Argentina lacks younger records to compare the faunal turnover with the Australian sequences.

In the Wasp Head Formation, the postglacial *Eurydesma* Fauna is characterized by a higher proportion of brachiopods with respect to that of the Bonete Formation. *Tomioopsis* and *Trigonotreta* are the most frequent taxa and mainly occur in the upper part of the section, an alternation between shoreface and offshore deposits that reflect the response to relatively rapid (glacioeustatic) sea level rises (Rygal et al. 2008). This postglacial interval is characterized by the brachiopod-dominated assemblage *Tomioopsis-Trigonotreta* mainly composed of spiriferids. Productid brachiopods are scarce in the Wasp Head Formation (only *Strophalosia* has been identified) and it occurs from the lower to middle part of the section; the latter is distinguished by bivalve-dominated assemblages, that records a gradual deepening upward trend from upper to middle shoreface water depths (Rygal et al. 2008).

The analyzed localities exhibit differences in the brachiopod:bivalve ratio through their occupancies. As it was outlined above brachiopod-dominated faunas can be found in eastern Australia and bivalve-dominated faunas are characteristic in eastern Argentina (Fig. 10). Hence, because bivalves are less vulnerable taxa and rhynchonelliformean brachio-

pods have more restricted ecological preferences (Peck 2008), their relative abundances could be reflecting differences in regional environmental conditions.

In eastern Australia, during the last stages of the early Permian glaciation, the benthic communities seem to have been dominated by the brachiopods *Trigonotreta* and *Tomioopsis*, and the bivalve *Eurydesma*. However, James and Clapham (2008) suggest that these cold-water adapted taxa had different responses during the warming climate change, and later they would be replaced by productoid brachiopod faunas. These authors recognized that *Trigonotreta* had a dramatic loss in its ecological dominance, whilst *Tomioopsis* remained practically stable and *Eurydesma* became a relict fauna in cooler waters. Instead, Percival et al. (2012) related the absence of productoids in previous records to environmental availability. The faunal turnover was then most probably controlled by environmental attributes, such as water depth together with substrate characteristics, rather than driven by climate (Percival et al. 2012).

CONCLUSIONS

- The analysis of the biotic composition and distribution of the brachiopod assemblages in two key sections from western and eastern Gondwana (i.e., the Bonete Formation in the Sauce Grande Basin, eastern Argentina, and the Wasp Head Formation in the southern Sydney Basin, eastern Australia, Fig. 11), suggests a high compositional similarity between the regions. However, the occupancies show significant differences: brachiopod-dominated faunas can be found in the Wasp Head Formation (*Tomioopsis* and *Trigonotreta* are the most frequent taxa), and bivalve-dominated faunas are characteristic of the Bonete Formation, where the brachiopods are poorly represented by the genera *Tivertonia* and *Tomioopsis*.

- The genus *Eurydesma* would have been a cold-adapted r-strategist as a response to environmentally stressed conditions. The high occurrence of this bivalve during the postglacial episode recorded in the Sauce Grande Basin would have adversely affected brachiopods abundance. This feature has not been observed in eastern Australia where the *Eurydesma* Fauna is clearly related to at least two gla-

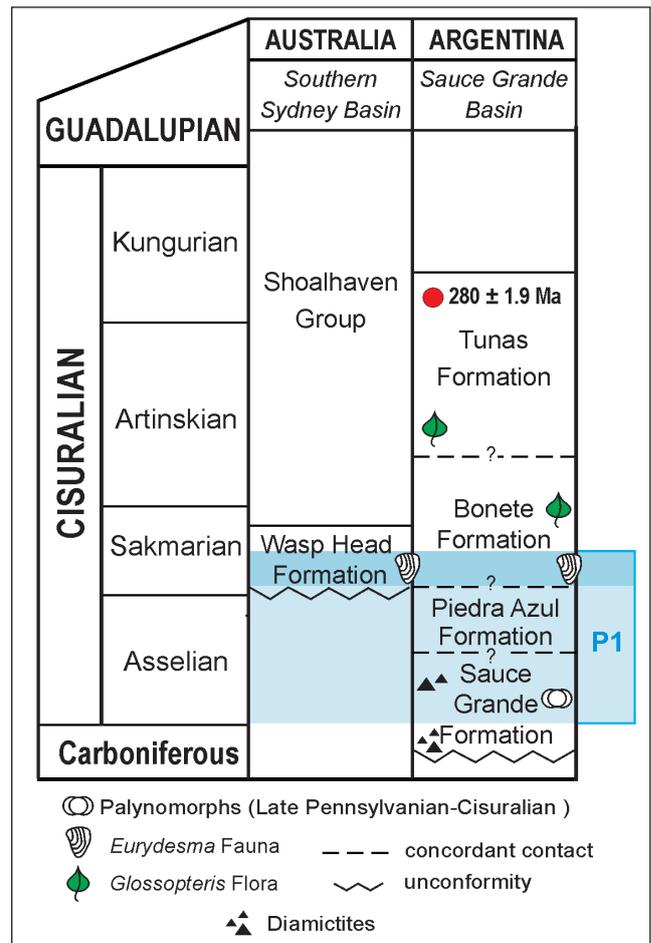


Fig. 11 - Biostratigraphic framework of the Permian postglacial faunas in the Sauce Grande Basin (Argentina) and Southern Sydney Basin (Australia), indicating the glacial episode proposed by Fielding et al. (2008).

cial episodes, and perhaps three (P1, P2 and probably P3, Fielding et al. 2008), extending over a longer period of time (Cisuralian).

- The low brachiopod abundance in the Sauce Grande Basin is also consistent with previous studies which indicate that in Pennsylvanian communities from Argentina this group already showed a decrease in importance, despite they presented no differences relative to bivalves in environmental preferences nor in environmental breadth (Balseiro 2016; Balseiro & Halpern 2016, 2019).

- Although the ecological structural differences identified (i.e., brachiopod:bivalve ratio), the postglacial *Eurydesma* Fauna flourished in western and eastern Gondwana and it is noticeable that two faunas located in opposite margins of this paleo-continent show such high compositional similarity during the development of a global postglacial event.

- The radiometric data available from the different sections containing the *Eurydesma* Fauna across Gondwana, indicate that the diachronism and the controversial timing of the end of the deglaciation prevent its precise biostratigraphic correlation. However, compositional and paleoecological comparative analyses of this fauna throughout the Gondwanan localities are feasible and necessary with a view to improving knowledge of the paleoenvironmental conditions that could be controlling its distribution.

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