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Geological Society, London, Special Publications

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DOI: https://doi.org/10.1144/SP522-2021-102

To access the most recent version of this article, please click the DOI URL in the line above. When citing this article please include the above DOI.

Received 8 June 2021
Revised 11 November 2021
Accepted 12 November 2021

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All post- Cambrian ichnospecies of *Psammichnites* Torell, 1870 belong to *Olivellites* Fenton and Fenton, 1937a

Abbreviated title: the ichnogenus *Psammichnites* revisited

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Abstract

The ichnogenus *Psammichnites* herein restricted to *Psammichnites gigas* is based on comparison of morphology, feeding behaviour, contrast between the burrows and the host rock and possible producers. The record of siphonal activity as a "snorkel device" is discussed. The diagnosis of the ichnogenus *Olivellites* now is amended and includes all the records of *Psammichnites* in the post-Cambrian. *Olivellites* is now documented in successions other than the classical tidal flat deposits facies of the Carboniferous of the USA. We propose that the producer of *Olivellites* was an animal with capacity for displacement to different shallow infaunal levels for different feeding strategies. An interpretation of detritus feeding behavior with sediment displacement (pasichnia) is favoured here. The producer of *Olivellites* was likely to have been a bivalved mollusc–that evolved after the Late Ordovician mass extinction. It was euryhaline and lived in a broad bathymetric range, and is recorded in temperate to glacially related successions. The material of *Olivellites implexus* from western Argentina is the youngest record of the ichnogegenus from Western Gondwana.

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Keywords: marginal-marine, El Imperial Formation, molluscs, ichnofossils, pasichnia

In scientific use, Nomenclatorial actions in ichnology are regulated by the International Code of Zoological Nomenclature (ICZN), the first editions which, published in 1961 and 1964, became the cornerstone of modern ichnotaxonomy and the framework for ichnotaxonomy in the following years. In consequence, ichnotaxonomical changes affected the stability of ichnogenera and ichnospecies with amendments, reassignments of ichnospecies to other ichnogenera and new rules for the new names in a binomial nomenclature. Some well-known ichnogenera that were defined prior to the establishment of the ICZN were amended according to the rules of the ICZN, however, as pointed out by Bromley (1996), the International Commission on the Zoological Nomenclature strangely decided that names based on the work of an animal that were established after 1930 had to be accompanied by a statement suggesting the causative organism. Bromley (1996) also stated that "since the specific affinity of a trace fossil taxon is anonymous, post-1930 names became essentially unavailable", suggesting that with that decision the Dark Age of Ichnotaxonomy had begun. This age ended in the seventies with changes proposed by Häntzschel (1975). A new edition of the code by Ride *et al.* (1985) introduced some controversial changes. In this edition, for instance, a type ichnospecies is not required for an ichnogenus. The lastest version of the International Code of Zoological Nomenclature (ICZN, 1999) introduced holotypes as a fundamental change and restated the need for a type ichnospecies. Subsequently, recommendations from some ichnologists (Bertling *et al.* 2006) detailed the use and prevalence of different ichnotaxobases, while some of those recommendations are not incorporated into the ICZN, they are very useful in the process of making an ichnotaxonomical act. In recent years, Rindsberg (2018) provided a new, insightful view of ichnotaxonomy as a science, and by using several extreme examples he pointed out the problem of considering only pure morphology (geometry) of an ichnofossil in

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ichnotaxonomy and, indirectly, suggested a more holistic approach where the producer and the mechanism of creation of the structure of a trace fossil is relevant when addressing an ichnotaxonomic assignment, amending diagnoses and creating new ichnotaxa. Ichnologists have always pivoted between "lumpers" or "splitters", as extreme cases. An overly broad diagnosis permits lumping distinct ichnogenera together with the loss of relevant information, or a plethora of names representing very minor variations result when ichnotaxobases are incorrectly chosen, resulting in an excessively narrow diagnosis. The relationship of a trace fossil to its producer is something peculiar to the ichnotaxonomy of vertebrate ichnology but more difficult to apply in invertebrate ichnology, where an ichnofossil might be the result of different producers by behavioural convergence. The correct analysis of bioprint (Rindsberg and Kopaksa-Merkel, 2005) helps in dealing with this difficult task. Another important idea from Zonneveld (2016), notes that ichnologists usually work with other ichnologists, but as happens in neoichnology, ichnology as a science needs to be approached as an interdisciplinary science, incorporating aspects of sedimentology, palaeontology, biology, ecology and biogeochemistry.

The ichnotaxonomic framework is crucial to discuss some ichnotaxonomical actions taken in this paper. The revision of the ichnogenus *Psammichnites* by Mángano *et al.* (2002) was based on the Carboniferous ichnospecies of Laurasia, while the Cambrian ones of the same age of the type ichnospecies, were only discussed in some special aspects. *Psammichnites gigas* shows preservational variants like "*Aulichnites*", "*Olivellites*" and "*Laminites*" in the Carboniferous records, according to Seilacher and Hagedorn (2010). The more usual preservation is as positive epirelief, but less common negative epireliefs of the basal sections are also reported, thus explaining preservational variants. Partially eroded specimens permit observation of the internal structure, usually documentable only in polished sections and in a vertical plane.

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The revision by Mángano *et al.* (2002), which accurately amended the ichnogeneric diagnosis, concluded that *Psammichnites* is not part of the named "*Scolicia* group" (Häntzschel, 1975) and mentioned problems with the type material of *Psammichnites gigas* related to its internal structure and provenance, requesting a further revision. The restricted stratigraphic record of *Psammichnites gigas* to the Cambrian allowed Álvaro and Vizcaino (1999), and more recently MacNaughton *et al.* (2021), to suggest *P. gigas* as an ichnostratigraphic marker for the Cambrian. However, it is opportune to remark that Mángano *et al.* (2002) essentially focused on Carboniferous material from England, Ireland, Spain and the USA.

The consequences of the amendment of the diagnosis of *Psammichnites* affected the stability of other ichnogenera, and some ichnospecies were moved into *Psammichnites*. For instance, ichnogenera like *Plagiogmus* Roedel 1929 (but see MacNaughton *et al.* 2021) and *Olivellites* were regarded as junior synonyms. The latter was earlier consistent to be a junior synonym of *Psammichnites* by Chamberlain (1971) and D´Alessandro and Bromley (1987), and was formally synonymized by Mángano *et al.* (2002). Several authors, however, continued to use *Olivellites* as a valid ichnogenus (e.g., Yochelson and Schindel, 1978; Eagar *et al.*, 1985; Miller and Knox, 1985; Martino, 1989, 1996; Buckman, 1992; Greb and Chesnut, 1994). Moreover, *Olivellites plummeri*, type ichnospecies of the ichnogenus, was moved by Maples and Sutner (1990) to *Psammichnites*. The ichnotaxonomical status of some ichnospecies changed as they were reassigned to *Psammichnites*. Such is the case of *Uchirites implexus* Rindsberg 1994, while *Aulichnites parkerensis* Fenton and Fenton 1937b was considered to be a synonym of *Psammichnites plummeri* Fenton and Fenton 1937b by Mángano *et al.* (2002). Finally, *Psammichnites grumula* Romano and Meléndez 1979 completes the plexus of post-Cambrian ichnospecies analysed by Mángano *et al.* (2002).

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Almost 20 years later, *Psammichnites gigas* remains restricted to the Cambrian and with many unresolved problems around the type material. *Psammichnites plummeri* and *P. implexus*, were documented in Silurian to Early Permian strata, expanding the range that was originally restricted to the Carboniferous. The new records include those reported from Brazil in the Silurian of the Paranaiba Basin (Campelo *et al.* 2021) and Devonian of the Paraná Basin (Sedorko *et al*. 2019, 2021). In the latter case, it occurs in estuarine deposits with fluvial input. Davies and Shillito (2018) documented the ichnogenus in tidal deposits from the Silurian of Australia. The records in the Devonian of Bolivia by Gaillard and Rachebœuf (2006) are from shoreface deposits, while in the Devonian of Argentina they correspond to shallow marine deposits (Noetinger *et al.* 2016). The Devonian of Antarctica also contains records of the ichnogenus where a new ichnospecies was proposed (Bradshaw 2010). Outside of Gondwana *Psammichnites* was described in lagoon deposits of the Late Devonian in Belgium by Morelle and Denayer (2020) and in shoreface deposits of the Carboniferous in UK by Boyd (2016).

In the Carboniferous of North America the record corresponds to tidally related deposits and mouth bars in the USA (Mángano *et al.* 2002 and references therein), probably documenting salinity-stressed (hypersaline) conditions. In Europe, *Psammichnites* is reported from open estuarine deposits in the Italian-Austrian Alps (Baucon and Neto de Carvalho 2008), and prodelta marine deposits in Poland (Muzser 2020), showing a wider paleoenvironmental range distribution than in the USA.

In Western Gondwana, glacial stages or advances and retreats were frequent in the Carboniferous (Ezpeleta *et al.* 2020, Le Heron *et al.* 2021, López Gamundí *et al.* 2021). There, *Psammichnites* occurs in glacially related deposits of salinity-stressed deltaic facies in the Calingasta-Uspallata Basin in western Argentina (Mángano *et al.* 2003; Alonso-Muruaga *et al.* 2012, 2013). In Eastern Gondwana it has been documented in the Mississippian–

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Pennsylvanian open shelf deposits of the Himalayas (Singh *et al.* 2017). The youngest record of the ichnogenus is Early Permian, documented in tide-influenced, glacially related shoreface deposits from Australia (Luo *et al.* 2017) and also in deltaic facies (Austria and Italy) from Asselian–Sakmarian siliciclastic deposits (Baucon *et al.* 2015). Therefore, post-Cambrian records of *Psammichnites* include tidal, shelf to deltaic deposits and from hypersaline to hyposaline environments, suggesting a wide range of bathymetric conditions that confirm that the producer of *Psammichnites* was an euryhaline animal.

The new record analysed in this paper, which generally coincides with the diagnosis of *Psammichnites* (after Mángano *et al.* 2002), comes from the Pennsylvanian El Imperial Formation of the San Rafael Basin in Argentina. It is the first record of "*Psammichnites*" (see Systematic Ichnology) in the San Rafael Basin and its youngest record in Western Gondwana.

In order to address the ichnotaxonomic, as well as the ecological and the stratigraphic significance of the material recorded in the San Rafael Basin, the paper has several objectives: I) to suggest an ichnotaxonomic assignment of the studied material; II) to discuss the stability of post-Cambrian ichnospecies of *Psammichnites;* and III) to analyse the bathymetric range, autecology of the producer and stratigraphic position material herein described with other records in Argentina and the rest of the world.

Geological Setting

The San Rafael Basin is one of the western vergence late Palaeozoic basins in Argentina (Fig. 1), situated in the San Rafael Block. This block is a part of the composite Cuyania Terrane that collided with the western margin of Gondwana during the Ordovician (Thomas and Astini 1996) and also includes the Precordillera and Las Matras Block. The stratigraphic and geological evolution of the San Rafael Block was recently addressed by Cingolani (2017) and Cingolani and Ramos (2017). The lithostratigraphic scheme includes

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several units in the Atuel River Canyon, where the study locality is situated, and neighbouring areas (Fig. 2a, b) from the Precambrian up to the Ordovician. The Silurian–Devonian Río Seco de los Castaños Formation, the older unit exposed in the Atuel River Canyon (Fig. 2b), is a low-grade metasedimentary unit (Manassero *et al.* 2009; Tickyj *et al.* 2017) composed of turbidite-like deposits containing a rich ichnofauna dominated by *Nereites* MacLeay 1839 and *Dictyodora* Weiss 1884 (Pazos *et al.* 2015a, b). The stratigraphy and sedimentology and new ichnological characteristics of the unit have recently been addressed by Gutiérrez *et al.* (2021).

During the Middle–Late Devonian the collision of the Chilenia Terrane from the west (Ramos *et al.*, 1986) is responsible for a new tectonic event (Chanic Phase) that produced the folding and faulting of previous sedimentary and volcanic units, which constitute the basement of the San Rafael Basin. The overlying El Imperial Formation exposed along the Atuel Canyon documents the beginnings of a Pennsylvanian succession in the basin. It is in angular unconformity with the underlying Río Seco de los Castaños Formation. This unconformity was spectacularly figured by Manassero *et al.* (2009, fig. 4a). The El Imperial Formation has a lectostratotype at the homonymous “Arroyo El Imperial”, or type section, where it reaches more than 1600 metres in thickness. There, the succession is notably thicker than at locality studied for this paper, Cañón del Atuel (Fig. 2c), section logged earlier by Arias and Azcuy (1986) and *A*zcuy *et al.* (1987), who reported a thickness of 320 metres. Vázquez *et al.* (2020) recently revised the type locality to study its facies and palynological content. They also clarified some stratigraphic uncertainties pointed out by Espejo (1993) and Espejo and López Gamundí (1994) concerning the thickness of the unit and the nature of the basal contact. Several transgressive episodes were recognised and a new correlation with the Cañón del Atuel locality − different from another previously proposed by Pazos *et al.* (2017) − was suggested by Vázquez *et al.* (2020). The basal stratigraphic levels, in the type locality,

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are rich in marine fauna which confirms the Carboniferous age originally suggested by Dessanti (1956).

In the Cañón del Atuel, the unit was divided into two members: a) a lower one or Glacigénico, and b) an upper one or Cabecera del Cañón, with an erosional unconformity between them (Pazos *et al.* 2017). The material studied in this paper occurs in the upper member, whose ichnofauna was previously documented by Pazos *et al.* (2013), Pazos and Krapovickas (2014) and Pazos *et al.* (2017). The age of this member is still a matter of debate based on invertebrate biozones (compare Cisterna, 2011 and Taboada *et al.*, 2021).

Taboada *et al.* (2021) studied the marine fauna of the upper member, and proposed a correlation with the type locality integrating new palynological data. They determined a Moscovian age for the transgressive interval containing the ichnofauna studied here (but see below).

The El Imperial Formation is gently folded and covered above an angular unconformity by the Cisuralian volcano-sedimentary Cochicó Group. The unconformity is the result of a compressional event and associated volcanism known as the San Rafael Tectonic Phase (Kleiman and Japas, 2009). In some areas, cannibalized Carboniferous deposits with progressive unroofing of older units overlie the unconformity, which were observed in the region (Pazos *et al.* 2011). The geological record continues with Late Triassic rift-related deposits (Ottone *et al.* 2014) and ends with early Miocene Andean deposits (Fig. 2a, b) analysed by Forasiepi *et al.* (2015) as well as modern unconsolidated deposits.

The Cabecera del Cañón Member: sedimentology and ichnology

The unconformity (Fig. 3a) at the base of the upper member is covered by conglomeratic deposits containing angular to subrounded cobbles and scarce boulders (Fig. 3b). These deposits contrast with fine- to medium-grained sandstones of the underlying glacial deposits and deltaic deposits studied in detail by Pazos *et al.* (2007) and Henry *et al.*

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(2014). The unconformity is an irregular surface carved into the underlying deposits, and the conglomerates are restricted to the more incised areas at the base of the succession. Pazos *et al.* (2017) pointed out that the lithological composition of clasts and boulders includes metamorphic and metasedimentary rocks that are exposed exclusively to the east of the basin and beyond the basin border. This denotes a gap between members, including exposure and denudation of older units, constituting new supply areas. Thus, the basal unconformity of the upper member was related to tectonism rather than to eustatic sea level changes (Pazos *et al.* 2017). Overlying the coarsest levels, the lower part of the succession continues with gravelly sandstone beds, and sandstones showing clustered gravels (Fig. 3c). The succession is arranged in thinning-upward packages. Each bed is internally structureless or exhibits normal grading, with the participation of horizontal stratification, ripples and scarce crossbedding. The entire lower part of the succession is easily identifiable in the field by the whitish tones that contrast with the underlying brownish lower member (Fig. 3a). The succession continues with a dark fine-grained interval, visible in several parts of the canyon (Fig. 3d) and constituting a reliable stratigraphic local marker. It contains abundant plant remains like *Cordaites* (Fig. 3e); and also partially coalified trunks. The entire interval was interpreted as fluvial in origin with powerful flows and negligible fluvial plains in a braided fluvial system, while the fine-grained interval represents the end of the first depositional cycle with the extended fluvial plains with ponds (Pazos *et al.* 2017).

The overlying succession is varicoloured with dominant violaceous tones (Fig. 3d) and abundant amalgamated cosets of trough cross-stratification. In this interval, conglomerates and even coarse-grained basal lags, as well as fine-grained deposits, are absent. Notably, cross-stratification includes large, laterally extended structures that suggest bars of a sandy braided fluvial system and reactivation with respect to the end of the lower cycle. Relict silt-clay beds, laterally extended only locally, occur on top of sandy bars. This

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nonmarine lower part of the upper member has been interpreted as a lowstand system tract in a sequence stratigraphy analysis by Loss and Pazos (2006) and Pazos *et al.* (2017).

Stratigraphically higher beds are exposed in a faulted zone where fine-grained intervals are usually covered. The lower part contains laterally continuous medium- to coarse-grained sandstone beds. Some amalgamated intervals up to 2 metres in thickness exhibit slightly asymmetrical cross-stratification (Fig. 3f), occasionally with symmetrical ripples overlying them. The structures were produced by combined and oscillatory flows (Pazos *et al.* 2017). In those beds, abundant biogenic structures called *Zoophycos*-like forms (Pazos *et al.* 2013). These intervals are interbedded with gray to blackish shales up to 2 metres thick. The combination of sandstones and shales was the reason for the seminal interpretation of a meandering fluvial system by Arias and Azcuy (1986). It was analysed in detail by Pazos *et al.* (2017) and reinterpreted as marine in origin based mainly on the aforementioned ichnological record. Heterolithic deposits, sigmoidal structures and rhythmites are also frequent in this interval. Scarce sigmoidal structures indicate palaeocurrents directed to the east (flood) and record tidal flows with E-W axes. Stratigraphically upward, heterolithic deposits are composed of sandstones and siltstones to mudstones. The sandstone beds show almost symmetrical ripples separated by abundant mud drapes. These intervals evidence oscillatory flows (Fig. 3g), while mud drapes indicate settling by suspension. The beds contain escape biogenic structures, *Diplocraterion* Torell 1870 (Fig. 4a) and *Rhizocoralllium* Zenker 1836 (Fig. 4b) figured by Pazos *et al.* (2017). *Teichichnus* Seilacher 1955 (Fig. 4c) was also documented (Pazos and Krapovickas 2014), and the first mention of *Psammichnites* in the basin is attributable to those authors. Levels with abundant *Planolites* Nicholson 1873 (Fig. 4d) are documented in some coarse-grained sandstone beds. They resemble Palaeozoic records of *Macaronichnus segregatis* Clifton and Thompson 1978, where there is no grain size contrast between the host rock and the trace

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fossil. This occurs in quartzose rocks that obscure the diagnosis of the ichnogenus (Nara and Seike 2019, p. 292).

The invertebrate fauna of the El Imperial Formation is mainly composed of bivalves, but also brachiopods and fish scales among other groups (Taboada *et al.* 2021), suggesting stenohaline marine intervals, at least for the fossil-bearing levels. In terms of sequence stratigraphy, Pazos *et al.* (2017) reanalysed the proposal of Loss and Pazos (2006) and extended the transgressive system tract for this part of the succession. The uppermost exposed levels of the unit in the Cañón del Atuel contain shales and sandstone intervals with *Zoophycos*-like forms (Fig. 4e) that indicate the marine succession extended that far there.

Ichnology

The ichnogenus *Psammichnites:* an overview

The ichnogenus *Psammichnites* has been ichnotaxonomically reviewed by Mángano *et al.* (2002), who discussed valid ichnospecies, producers, palaeonvironmental framework for their occurrences, and autecology. Therefore, they amended the ichnogeneric diagnosis and stated that several ichnospecies remain valid within the ichnogenus *Psammichnites*. The type ichnospecies *Psammichnites gigas* is notably the only one almost exclusively restricted to the Cambrian; it has been recorded in Canada, Finland, France, India, Mongolia, Norway, Sardinia, Sweden, Spain and the United States (e.g. Hofmann and Patel 1989; Seilacher and Gámez-Vintaned 1996; McIlroy and Hayes, 1997; Álvaro and Vizcaino 1999; Seilacher-Drexler and Seilacher 1999; MacNaughton *et al.* 2021), and probably in China (Crimes and Jiang 1986). Kennedy and Droser (2011) mentioned *Psammichnites* in Cambrian fluvial deposits,–preserved as a doubly furrowed negative epirelief, but this morphology is not diagnostic of the ichnogenus. The other valid ichnospecies studied by Mángano *et al.* (2002), plus material described in open nomenclature as *Psammichnites* isp., are well documented in Carboniferous deposits of Austria, Belgium, Italy, Ireland, Poland, the UK and the USA in

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Laurasia and in Australia, Antarctica, Argentina, Bolivia, Brazil and India in Gondwana. Only one new ichnospecies has been erected in the last twenty years *Psammichnites devonicus* Bradshaw 2010 from Antarctica.

Mángano *et al.* (2002) pointed out two important problems with the type ichnospecies of *Psammichnites*. One of them is that the type material of *Psammichnites gigas* does not show the internal morphology usually documented in other specimens of the ichnospecies, as illustrated by Hofmann and Patel (1989). The other one is that the nature of such type material is also questionable due to morphological differences resulting from variable preservation.

Mángano *et al.* (2002) considered *Plagiogmus arcuatus* to be a probable junior synonym of *Psammichnites plummeri*. Similar synonymy with *Psammichnites* was proposed previously by Zhu (1997) and included *Taphrhelminthopsis circularis* Crimes *et al.* 1977. However, McIlroy and Hayes (1997) also documented similarities between *Psammichnites* and *Plagiogmus arcuatus* but retained them as separate ichnogenera based mainly on features like the transverse bars, the consistently present central groove rather than a ridge, and a more complex internal structure, but also the contrast in grain size between the biogenic structures and the surrounding sediment, that reflects other modes of construction in the last one. Moreover, they rejected the halkieriids as possible producers of *Plagiogmus* due to a lack of a structure attributable to siphon, and suggested other molluscs or a worm-like producer. These important differences cast doubts on the synonymy between *Psammichnites* and *Plagiogmus*. Later, Seilacher and Hagadorn (2010) placed *Plagiogmus arcuatus* in the informal ichnofamily of psammichnitids that includes several ichnogenera. McIlroy and Brasier (2017) suggested that *Plagiogmus arcuatus* appeared in the Cambrian Stage 2 and extended to the early part of the Cambrian Stage 3, differently than *Psammichnites gigas*, that appeared in the Fortunian. The material documented in the Cambrian of China exposes the problem between

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Psammichnites gigas and *Plagiomus* very well. The occurrence of *Psammichnites* and *Plagiogmus?* is mentioned by Crimes and Jiang (1986) referring to material described by Zunyi *et al.* (1982) even though the last ones did not mention *Psammichnites* but *Scolicia.* Zhang *et al.* (2017) proposed a flattened tubular annelid-like animal as a possible producer of *Plagiogmus*-like preservation of *Psammichnites* in the earliest Cambrian in China, as had been suggested by McIlroy and Hayes (1997).

Recently, the new ichnogenus *Parapsammichnites pretzeliformis* Buatois *et al.* 2018 was described in the Ediacaran of Namibia. Some resemblance with *Nereites saltensis* Aceñolaza and Durand 1973 is clear. A problem persists with the relocation of *Nereites saltensis* from the Cambrian of northern Argentina into *Psammichnites* by Seilacher *et al.* (2005). These trace fossils were documented as a record of undermat mining (Aceñolaza and Durand 1973), which were produced after the trilobite's undertracks (Seilacher and Hagadorn 2010) which were not deformed, only lifted and not eroded. The idea of a siphonate producer was earlier suggested by Yochelson and Schindel (1978) for *Olivellites* and later strongly supported by Mángano *et al.* (2002), but only following the interpretation of Seilacher (1997). But an undisturbed microbial mat precludes the existence of a siphon and suggests a crucial difference between *Nereites saltensis* and *Psammichnites*. The main function of a siphon is respiration, and permitting the entrance of sand to avoid the collapse of the structure (Seilacher and Hagadorn 2010), in a mechanism not well explained. It is well known that a microbial mat isolates the underlying low-oxygenated levels from the overlying surface (Porada and Bouougri 2007). The energy involved in crossing the mat to obtain oxygen, which is deficient under microbial mats (Gingras *et al.* 2011), points to a different producer of *Psammichnites saltensis* that in the other ichnospecies included in the ichnogenus. An infaunal siphonal animal requires a permanent or regular connection with the surface for respiration. Microbial mats have never been associated with *Psammichnites* in the geological

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record. It was probably for this reason plus the absence of diagnostic features of *Psammichnites*, including the evidence for a siphon, that the ichnospecies was later moved to *Nereites* (Aceñolaza and Aceñolaza 2006; Aceñolaza *et al.* 2009).

New Carboniferous records around the world attributed to *Psammichnites* are not all from tidal flats, suggesting more permanent subaqueous conditions (e.g. Mángano *et al.* 2003; Baucon and Neto de Carvalho 2008; Alonso-Muruaga *et al.* 2013; Baucon *et al.* 2015; Singh *et al.* 2017; Muszer 2020). However, records in the Devonian of South America are also in non-tidal deposits (Gaillard and Rachebœuf 2006; Boyd 2016; Noetinger *et al.* 2016; Sedorko *et al.* 2019).

Different possible producers have been suggested for *Psammichnites*, particularly referring to post-Cambrian ichnospecies. For instance, siphonal bivalves are considered to be the most likely producers. The evidence of a siphon in some ichnospecies like *P. grumula* is indisputable. However, vermiform animals or arthropods have likewise been proposed as producers (but see Mángano *et al.* 2002). Ethologically, a dominantly deposit feeding animal with locomotion (pasichnion) is the most accepted behaviour, related to an opportunistic strategy. Nevertheless, specimens forming aggregates (patches) were related to oxygen-deficient tidal flats, where chemosymbiosis has also been suggested (Mángano *et al.* 2002).

Systematic Ichnology

Olivellites Fenton and Fenton 1937a

1937a. *Olivellites* Fenton and Fenton: 452–453, fig. 1.

1937b. *Aulichnites parkerensis* Fenton and Fenton: 1078–1080, figs. 1–2.

1979. *?Olivellites* - Romano and Meléndez: 323, pl. 1, 2.2–3.

1982. '*Scolicia*' De Quatrefages 1849- Okolo: 252–253, pl. 143A–B.

1983. *Scolicia* isp. De Quatrefages 1849- Seilacher: 22, figs. 11–12.

1994. *Uchirites implexus* Rindsberg: 55–56, pl. 15B–D, 20D–E, 22A, C–D.

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2002. *Psammichnites* Torrell 1870- Mángano *et al.*: 3, figs. 1–9.

2002. *Scolicia* isp. De Quatrefages1849- Sequeira Fernandes *et al.*:141–142, figs.130–132.

2010. *Psammichnites* -Bradshaw: 97–99, figs. 25a–f.

2006. *Psammichnites* isp. Torell 1870- Gaillard and Rachebœuf: 1209, figs. 5.1, 5.2.

2015. *Psammichnites* - Baucon *et al.*:750, figs. 9 a,c.

2016. *Psammichnites isp*.- Noetinger *et al.*: 11, fig.7d 1,e–f.

2017. *Psammichnites* isp.- Singh *et al*.: 474. Fig. 9 i.

2018. *Psammichnites* isp. - Davis and Shillito: 679, figs. 1c–e.

2019. *Psammichnites* isp. - Sedorko *et al.*: 46, fig. 2I.

Type ichnospecies: *Olivellites plummeri* Fenton and Fenton 1937a

Emended diagnosis: Sinuous, to meandering, or contorted, mainly horizontal bilobed burrows. Width of specimens can be regular or variable. In full preserved convex epireliefs a central positive ridge or depressed groove sometimes with holes is present. The upper surface is smooth or present transverse striations, while basal concave epireliefs exhibit a median furrow, either alone or with transversal arcuate menisci. The cross section is usually subtriangular or lensoidal. It is rarely preserved as a convex hyporelief with a central furrow.

Comparison: *Olivellites* deserves comparison with several ichnogenera. It is excluded from *Psammichnites* due to distinctive features at all levels of exposure. The outline of *Psammichnites gigas* (type ichnospecies) is frequently cylindrical, with sharp external borders and only straight to curved courses. Its surface presents the expression of internal curved menisci or a smooth surface with a central ridge or groove. The external borders are sharp and linear in both *Psammichnites gigas* and *Aulichnites*, but irregular in *Olivellites* in most cases, particularly in the type ichnospecies. The ridges do not affect the morphology of menisci (see MacNaughton *et al*. 2021). The internal structure is variable and is usually the

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expression of the arcuate menisci tangential at the base and vertical on top (see Hoffman and Patel, 1989, MacNaughton *et al.* 2021). The basal section of *Psammichnites* with *Plagiogmus*-like preservation exhibits transversal ridges (McIlroy and Hayes, 1997) that are never observed in *Olivellites*. The transverse ridges are attributable to the activity of a soft muscular foot of some modern molluscs (Seilacher-Drexler and Seilacher 1999). Seilacher and Hagadorn (2010) suggest that transverse corrugation (striation) is similar to those left behind by extant quasi-infaunal molluscs traversing dry sediment.

A contrast between the host rock and the ichnofossil is documented in *Psammichnites gigas* (Álvaro and Vizcaino 1999) and in *Plagiogmus arcuatus* (McIlroy and Hayes, 1997), but this contrast is absent in *Olivellites.* Intriguingly, a feature that is never mentioned in *Psammichnites gigas* or *Plagiogmus arcuatus*, when they are compared with *Olivellites*, is the maximum width and length. For instance, in *Psammichnites* the burrows are wider and longer than in the former reaching several metres in length and up to 4.5 cm in width (Hoffmann and Patel, 1989; Jago and Gatehouse, 2007; Singh, 2011) or wider (Álvaro and Vizcaino, 1999). In short, several diagnostic different features between *Psammichnites gigas* and *Olivellites* exist.

Aulichnites was considered a preservational variant of *Psammichnites* by D´Alessandro and Bromley (1987), and formally relocated in *Psammichnites* by Mángano *et al.* (2002). *Aulichnites parkerensis* presents several problems (see Hakes 1977). The type material shown in the original draws features of *Olivellites*, like transversal striations or crenulations and a central ridge. The ichnogenus "*Aulichnites"* is also used informally by Mikuláš *et al.* (2017) to assign a flattened specimen without transverse striation that was produced by a Carboniferous chiton (mollusc, Polyplacophora). They left the material in open nomenclature and remarked that the holotype of *Aulichnites* is in fact a poorly preserved specimen of *Psammichnites*, as was previously stated by other researchers (Mángano et al

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2002). Simple non-striate forms are mentioned by Frey (1990), among others, mainly for records in the post-Palaeozoic. *Aulichnites* is a well-known name in the literature, and is still in use but the replacement of the old types with new ones is only possible with the approval of the ICZN.

The producer of *Psammichnites gigas* is attributed to halkieriids (e.g., Álvaro and Vizcaino, 1999). It is important to note the conclusion of McIlroy and Hayes (1997) that halkieriids had no siphon to explain the snorkel interpretation in *Psammichnites-Plagiogmus* variants. Halkieriids were restricted to the Cambrian (Morris and Caron 2007) and do not satisfy the suggestion of Seilacher-Drexler and Seilacher (1999) that they produced the central groove, its straight or undulating course relating to the depth of the infaunal activity of the producer. We favour a vermiform producer for *Plagiogmus arcuatus* an idea agreed by Zhang *et al.* (2017) when mentioning *Psammichnites-Plagiogmus* similarities. The validity of *Olivellites* when compared with *Plagiogmus* and *Psammichnites gigas*, is now surprisingly clear.

Olivellites plummeri **Fenton and Fenton 1937a**

1937a. *Olivellites plummeri* Fenton and Fenton: 452–453, fig. 1.

2002. *Psammichnites plummeri* Fenton and Fenton 1937a- Mángano *et al.*: 5–6, figs 1A–C, 2A–D, 3A–D, 4A, B, and cumulative synonymy.

2003. *Psammichnites plummeri* - Mángano *et al.*: 602, figs. 3a–e.

2008. *Psammichnites* cf. *plummeri* – Baucon and Neto de Carvalho: 102, fig. 14

2013. *Psammichnites plummeri* -Alonso-Muruaga *et al.*: 232, figs. 3e, 4a–b.

2017. *Psammichnites plummeri.* - Luo *et al.*: 459, figs 6 c – d, 7a – d.

2020. *Psammichnites plummeri* -Muszer: 9, figs 4F, 5A–F, 6, 7G–H.

2021. *Psammichnites plummeri*- Memoria *et al.*: 12, fig.11A.

Olivellites grumula **Romano and Melendez 1979**

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1979. ?*Olivellites grumula* Romano and Meléndez : 323, pl. 1, pl. 2.2–3

2002. *Psammichnites grumula* - Mángano *et al*.:10, figs. 2C–D, 5A–D; 6A, B; 7, and cumulative synonymy.

***Olivellites implexus* (Rindsberg 1994) (Fig. 5a-c)**

1982. *Olivellites* isp. Fenton and Fenton 1937a - Okolo: 248, Pl.126, 137, l38A–B, 139, Figs. 17, 140, 141, l42A–B.

1994. *Uchirites implexus* Rindsberg: 55–56, pl. 15B–D, 20D–E, 22A, C–D.

2002. *Psammichnites implexus* Rindsberg 1994- Mángano *et al*.: 604, figs. 4A–C, and cumulative synonymy.

2003. Psammichnites implexus - Mángano *et al.*: 604, fig. 4 a–c.

2003. *Psammichnites plummeri* - Mángano *et al.*: 605, fig. 3d.

2010. *Psammichnites devonicus* Bradshaw: 97–99, figs. 25 c–d.

2013. *Psammichnites implexus* - Alonso-Muruaga *et al.*:232–233, fig. 4 c–d.

2015. *Psammichnites plummeri* - Baucon *et al.*: 254, fig. 9 a,c.

2020. *Psammichnites implexus* - Morelle and Denayer: 11, fig. 8 f,g.

2021. *Psammichnites plummeri* - Campelo *et al.*: 12, fig. 11A

Description

The material described in this paper includes several (4–6?) uncollected–specimens that were photographed at the field. The exact number is unclear as all of them were documented in the horizon in a fine- to medium-grained, highly micaceous sandstone, where overcrossing of specimens was frequent and some parts of the courses were re-used (Fig. 5a, b), behaviour already mentioned by Yochelson and Schindel (1978) in *Olivellites*.

In the best-preserved material, the external shape is subtriangular with a subtly marked median ridge. However, transversal striae and, in some lateral parts, fringes can be

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observed (Fig. 5a). No differences in grain size are documented between successive transversal striae, and they are only visible due to weathering exposing the upper surface resembling a *mille-feuille* (Fig. 5 c). The friable nature of the sandstones precluded any attempt to collect them for slicing and analysing internal structure. Specimens occur in small patches or aggregates and show no differences either in grain size or colour compared with the ichnofossiliferous horizon or with the under- or overlying levels.

The most complete specimens are observed in convex positive epireliefs, the width ranges between 0.9 and 1.1 cm, and overcrossing and self-crossing of specimens are documented as well as a tendency to scribble rather than create guided meanders. Abrupt, tightly contorted turns sometimes continue with irregular courses. In some parts, the producer used the same previously bioturbated area producing a "double bioturbation" along the same course. The width is almost constant but increased on turns with lateral fringe striate (Fig. 5b). The only documented accompanying trace fossils are *Lingulichnus*? Hakes 1976, that were produced after *Psammichnites*, as they cross-cut some of them.

Remarks

The material described is confidently assignable to *Olivellites implexus;* it contains such diagnostic features of the ichnogenus as a subtle median ridge and transversal striation in convex epireliefs, and a subtriangular epichnial morphology that centrally divides the trace fossil in a bilobed structure. It has some particular features, such as the tendency to "scribble" and also the reduced size compared to other ichnospecies (*Olivellites plummeri*, *O. grumula* and *O. devonicus*). With the exceptions of regular meanders all the features are diagnostic of the ichnospecies *P. implexus* in the studied material. Reduced size is included in the diagnosis of the ichnospecies although it is not a encouraged ichnotaxobase (Bertling *et al.* 2006). However, the size matches the range mentioned in the emended diagnosis by Mángano *et al.* (2002), although at its widest limit. The lateral fringe (Fig. 6a) with striate is a feature

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previously documented in *P. grumula* by Mángano *et al.* (2002, fig. 6b) but not mentioned in any other ichnospecies until now. Regardless of this feature, the absence of holes and a subtle median ridge, attributed to a siphon device, preclude any assignment to *O. grumula*. The ichnospecies *P. plummeri* presents simpler, straight to curved courses rather than scribbling or meandering tendencies, as well as being larger than *O. implexus* (Mángano *et al.* 2002). In this regard, some of the specimens assigned to *P. plummeri* by Muzner (2020) are strongly sinuous and meandering to looping, and probably fit better in *P. implexus. O. devonicus,* documented in marine facies with fluvial influence in the Early Devonian of Antarctica (Bradshaw 2010), is distinguishable from the studied material only by its basal section (Bradshaw 2010, fig. 25 b), which presents median sand-filled strings, while the upper positive epireliefs are almost indistinguishable from those of *O. plummeri,* and the width is in the range of the former. The absence of basal sections in the material described in this paper and the smaller size allows disregarding the assignment to this ichnospecies. The basal sections in some eroded specimens of *O. plummeri* are almost indistinguishable from *O. devonicus,* therefore *O. devonicus* is probably a variant of *O. implexus,* particularly considering that upper and basal sections did not pertain to the same specimen (Bradshaw, 2010).

Olivellites implexus has also been documented by Mángano *et al.* (2003) and Alonso-Muruaga *et al.* (2013) in Carboniferous deposits of Argentina. They also documented the different size ratio between the ichnospecies *O. implexus* and *O. plummeri* previously stated by Mángano *et al.* (2002). In Europe, *O. implexus* has been documented in Late Devonian lagoon deposits of Belgium, where the specimens show unclear transverse striation but a robust median ridge and a divagant or clearly meandering courses (Morelle and Denayer 2020). The Luo *et al.* (2017, figs. 6c, 7a-d) material documented in the Permian of Australia as *Psammichnites plummeri,* but the contorted and meandering trails are similar to *O.*

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implexus rather than *P. plummeri*. It is probable that, due to its abnormally great width (20−30 mm) and the existence of an internal core not previously mentioned, the material is retained in the suggested ichnospecies.

Some *Olivellites* recorded in the Lower Devonian of South America (western Gondwana) and documented by Sedorko *et al.* (2019, 2021) do not show clear diagnostic features of the ichnogenus. However, these authors documented other decorticated specimens with menisci, where a median ridge is observable and the assignment is more consistent with the ichnogenus. In the Lower Devonian of Bolivia, the specimens of *Olivellites* isp. are relatively wide, up to 30 mm, and no transversal striate are reported by Gaillard and Rachebœuf (2006). However, they seem to appear in the specimen figured by Gaillard and Rachebœuf (2006, fig. 5.1), and possible holes are also observable. An axial tube exposed in decorticated specimens that connects with the median upper ridge is also visible (Gaillard and Rachebœuf 2006, fig. 5.2). Thus, in the future it might be relocated in *O. grumula*. In the Lower Devonian of Argentina Noetinger *et al.* (2016) described specimens preserved as positive epireliefs and exhibiting a medial ridge, but each side lobe shows convex downward rounded mounds, unusual in the ichnogenus; they were nevertheless assigned to *Olivellites* isp. The material described by Baucon *et al.* (2015, fig. 9a, c) in the Permian as *Psammichnites plummeri* referred to *O. implexus* based on its external morphology.

***Olivellites* isp.**

(Fig. 6a, b)

Simple epirelief specimens (two) with a subtriangular outline (Fig. 6a, b) divided into two lobes by a fairly well-preserved median ridge. One of the specimens shows a sinuous course and the other high density of over crossing. Transversal striation is lacking in both specimens and the short length specimens prevent full knowledge of the course of the trail. The poor quality of specimens precludes any assignment to any ichnospecies.

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The producer and autecology of *Olivellites*

Previous to any in-depth discussion about the potential producer of the ichnogenus, it is necessary to point out some aspects related to the ethological category of the ichnogenus, as well as the lifestyle of the producer. The existence of some certain organs is required to support the observed morphology in some specimens and to be in agreement with the suggested shallow infaunal interpretation that is indisputable (Mángano *et al.* 2002). The idea of a siphon for respiration was originally based on Cambrian ichnospecies of *Psammichnites gigas*, and on *Plagiogmus arcuatus*. For instance, McIlroy and Hayes (1997) in a polished section documented a structure left by a respiratory organ. Mángano *et al.* (2002) interpreted the spaced dorsal holes in *O grumula* as evidence of a siphon that was periodically connected to the surface. Following the idea of Seilacher-Drexler and Seilacher (1999) that at different depths of movement the surficial expression of a snorkel device is straight or undulating, the producers of *Olivellites* occupy a similar very shallow infaunal tier, as undulating ridge or grooves are absent. Mángano *et al.* (2002) documented transitions between *Psammichnites grumula* and *P. plummeri* (=*Olivellites*), confirming evidence of the respiration device in both ichnospecies, but at different tier positions.

Mángano *et al*. (2002) analogised the snorkel interpretation of *O. implexus* with that of *Dictyodora* Weiss 1884, particularly Rindsberg (1994, Plate 15b) and Mángano *et al.* (2002 fig. 8d). They documented the ridge that transitionally passes to the full relief of *O. implexus*, suggesting vertical movements of the producer. But the comparison with *Dictyodora* is not particularly satisfactory. *Dictyodora* presents as a diagnostic ichnotaxobase a “wall” filled with contrasting grained-size material between the infill and the host rock. Also, the basal section is fine-grained compared with the host rock (Pazos *et al.* 2015a; Zhang *et al.* 2020; Gutiérrez *et al.* 2021). The producer and the life styles are different

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in each ichnogenus. The material analysed by Muszer (2020, fig. 7g) exhibits a basal and upper bilobed shape, but no internal structure possible produced by siphon is evident.

An alternative interpretation of the device in *Psammichnites gigas* was suggested by Seilacher and Hagadorn (2010, p. 568) due to the absence of different grain sizes observed between the burrows and the host rock. The sediment was not digested and was passively moved behind and packed, which explains the fact that the structure did not collapse, introducing sand from the surface as a consequence of the activity of a respiratory organ. It is an explanation only in cases not overlain by silt or clay. In the cross section of the outcrops in the Marsdenian (Carboniferous) of the Pennine Basin in England, Okolo (1982) figured specimens as *Olivellites* isp. Some of them are very similar to the material described here, but even well-exposed vertical sections exhibit no evidence of a prolongation of a vertical siphon. Yochelson and Schindel (1978) documented fine-grained sediments that settled by suspension overlying the trace-fossil bearing levels and suggest that the producer moved up and down in the same way that is visible in the material figured by Rindsberg (1994), where the ridge is sometimes visible and *O. implexus* emerges progressively.

A mollusc is a more likely producer of *Olivellites* (see Mángano *et al*. 2002), an interpretation that is also supported by the lateral fringe in *O. grumula*, now documented in *O. implexus*. It was interpreted as sediment transported backward and the fringes were controlled by compaction of the sediment. The thicker fringes are suggestive of shallow infaunal positions with less compaction (Mángano *et al.* 2002). In the specimens analysed in this paper, the fringes are on the turns not on both sides of the burrow, and possibly result from lateral displacement of the producer. Regarding molluscs, Bradshaw (2010) suggested that *O. devonicus* could be produced by Monoplacophora, taking into account their abundance in the studied unit. However, they have no siphon device, but ctenidia. Moreover,

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the *Plectonotus* identified by Bradshaw (2010) as monoplacophorans are part of the epifauna and are gastropods (Bouchet *et al.* 2017).

The scribbling course of the traces is indicative of a simple feeding pattern and abundant detritus availability for a detritus feeder. Common overcrossing specimens are usually indicated in this regard. For instance, Hauck *et al.* (2009) analysed the relationship between total organic carbon (TOC) content and the course of the traces produced by isopods in a modern tidal flat and concluded that their complexity increases with food availability. In cases where overcrossing and looping are common, strophotaxis is frequent and probably useful in explaining morphological variation in *Olivellites*. The producer of *Olivellites* was able to deal with salinity stress and probably some oxygen restrictions, and lived in a broad bathymetric range. The complete absence of *Olivellites* in the Ordovician and its notable difference with Cambrian *Psammichnites gigas* probably suggest that the producer is different and that the producer of *Olivellites* appeared after the Ordovician mass extinction.

The age of *Olivellites* in Argentina

The record of *Olivellites* in the upper member of the El Imperial Formation permits discussion of its age in western Argentina. *Olivellites* occurs in regressive facies, postdating a postglacial transgression (Mángano *et al.* 2003; Alonso-Muruaga *et al.* 2013) in the Calingasta-Uspallata Basin and in non-glacially related deposits (this paper) in the San Rafael Basin. In the first case, it was documented in the coarsening-upward deposits overlying postglacial black shales. The age of the glaciation is envisaged as Serpunkovian to Baskirian by Taboada *et al.* (2021). The archetypic unit for this episode is in the northeastern sub-basin (Paganzo Basin; Fig. 1). There, in the Guandacol Formation the end of the glaciation has been dated at 319.57 ± 0.086 Ma (middle Bashkirian; Gulbranson *et al.* 2010). This unit presents ichnological elements that favour the correlation of the glacial event with at studied by Mángano *et al.* (2003) and Alonso-Muruaga *et al.* (2013). Taboada (2010) mentioned

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Orchesteropus atavus Frenguelli 1950 in the postglacial transgression. It is an arthropod-produced ichnofossil only documented in the early postglacial deposits of the Paganzo Basin, in the Guandacol Formation and equivalent units (e.g., Pazos 2002a, b; Buatois and Mángano 2003). The glacial records of the Hoyada Verde, Guandacol and the El Imperial formations have all been recently assigned to glacial stage IV (López-Gamundí *et al.* 2021). The biostratigraphic correlation scheme using invertebrate biozones is rather controversial. In the Calingasta-Uspallata Basin *Olivellites* is documented overlying the upper *Levipustula* Zone (Alonso-Muruaga *et al.* 2013), which Taboada (2010) called the *Marginovatia-Maemia* (M-M) Zone. However, in other schemes the upper *Levipustula* Zone is equivalent to the *Aseptella-Tuberculatella*/*Rhipidomella-Micrapheli* fauna (Cisterna and Sterren 2016; Cisterna *et al.* 2017). According to Sterren *et al.* (2021) the lower and upper faunas are coeval but document different palaeoecological conditions, in contrast to the proposal of Taboada *et al.* (2021) that still assigns a younger age to the upper *Levipustula* records. A very late Bashkirian age is reasonable for the levels bearing *Olivellites*, regardless of the scheme followed. Ichnofossils were recorded in shoreface deposits in the regressive phase following the postglacial transgression (Mángano *et al.* 2003) and pre-dating an unconformity. The salinity variations in the *Olivellites*-bearing horizons acted as a stressor, according to Alonso-Muruaga *et al.* (2013), can be attributed to fluvial discharges related to a fluvial system. However, the fluvial system overlies a regional unconformity that in places carves into glacial deposits (Taboada 1997; López Gamundí and Martínez 2003), suggesting an allocyclic control, and a Moscovian to Kasimovian age (Henry *et al.* 2008, fig. 3). This implies a notable gap between both units and a nongenetically related origin (López Gamundí and Martínez 2003).

The stratigraphic relationship with a gap is similar to that suggested for the El Imperial Formation by Pazos *et al.* (2017) between both members. Unlike other records,

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Olivellites is documented here as overlying the unconformity in the San Rafael Basin. The tectonic event involved in the gap is probably coeval in the Calingasta-Uspallata and San Rafael basins. In that case, their *Olivellites* is younger than described by Mángano *et al.* (2003) and Alonso-Muruaga *et al.* (2013). In the El Imperial Formation Taboada *et al.* (2021) suggested a Moscovian age was for the invertebrate fauna. The possibility that this fauna could reach the Kazimovian (e.g. Balseiro and Halpern 2016) or Gzelhian is not completely ruled out taking into account radiometric ages in of 307.2 ± 5.2 Ma (Moscovian–Ghzelian) in the southern Precordillera (Lech 2002). In consequence, the *Olivellites* studied in this paper is considered to be the youngest in Western Gondwana.

The trace fossils recorded in the El Imperial Formation indicate escape, grazing, dwelling and feeding behaviours including detritus and deposit feeders. The ichnofauna represents a dominance of shallow- and deep-tier deposit-feeders (*Planolites*, *Psammichnites*, *Rhizocoralllium*, *Zoophycos*-like forms, *Teichichnus*) followed by suspension-feeders (*Diplocraterion*, *Lingulichnus?*). The ethological categories and feeding mechanisms are relevant for the assignment to particular ichnofacies (MacEachern *et al.* 2007, 2012). This ichnological assemblage could point to a record of the Palaeozoic *Cruziana* Ichnofacies, while still deviating from the archetypal model. Although ichnogenera such as *Diplocraterion* and *Lingulichnus* are typical of the *Skolithos* Ichnofacies, their low abundance together with few escape structures, the dominance of deposit feeders, and the presence of *Teichichnus:* which is a typical constituent of the *Cruziana* Ichnofacies, are inconsistent with an archetypal *Skolithos* Ichnofacies assignment. However, a *Cruziana–Skolithos* Ichnofacies transition is not completely ruled out.

The presence of *Diplocraterion* and *Zoophycos*-like forms suggest marine conditions. Although trace fossils may indicate the existence of animals with some tolerance to salinity

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changes; the presence of brachiopods even though they might evidence transport, indicates intervals with stenohaline salinity conditions, as mentioned above.

Balseiro and Halpern (2016) recognised a faunal change after the glacial episode (*Levipustula* zone) with related to climatic amelioration, and a major increment in diversity of bivalve families and gastropods over brachiopods (Sterren and Cisterna 2010). It is clear that for the Devonian–Permian records of *Olivellites*, climate did not restrict its producers, as was the case in a low-latitude belt in Laurasia, and in mid-high latitudes in Gondwana (Fig. 7).

Conclusions

The revision of the ichnogenus *Psammichnites* 20 years after the previous one permits us to arrive at several salient conclusions, which are reflected in ichnotaxonomic acts in this paper. The differences between the type ichnospecies *Psammichnites gigas* and the remaining ichnospecies comprise several aspects that are relevant as ichnotaxobases at the ichnogenus level. Those contrasting features include more than pure morphological differences with the post-Cambrian documented ichnospecies attributed to the ichnogenus. In the Cambrian, specimens are straight or gently curved burrows, usually flattened or cylindrical in shape. Contrast in grain-size between the burrow and the host rock is frequent and reflects deposit-feeding behaviour, with backward- packed faeces and inorganic detritus. The width and length are notably higher than in post Cambrian records, and the internal structure, which includes menisci and basal ridges, is different. The existence of the siphon was proved in vertical thin sections, particularly in specimens with *Plagiogmus*-like preservation. The producers of the Cambrian records may include halkieriids, or sluglike molluscans in the sense of Seilacher-Drexler and Seilacher (1999), and vermiform animals for other researchers. It is the main difference with the post-Cambrian records, as halkieriids did not survive the Cambrian (McIlroy and Hayes, 1997), and were not siphonate. The post-Cambrian ichnospecies were earlier documented in tidally related deposits mainly in the

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USA, and restricted to the Carboniferous at the time of the revision made by Mángano *et al.* (2002).

In the last twenty years, new records attributed to *Psammichnites* in Gondwana and Laurasia successions, expanded the palaeoenvironmental distribution to mouth bars, shoreface, deltaic systems, and tidally-related deposits from the Silurian to the Permian. These points to a producer adapted to different bathymetric ranges, salinities and climatic conditions. Younger than the Cambrian counterparts, these records exhibit burrows with a tendency to form meanders, scribbled, self-crossing and contorted, and also the use of a previous course is proved. No contrast in grain size between the host rock and the burrow is evident. These features are considered a good indicator of a detritus-feeder (pasichnion producer), in which the complexity of the courses is related to food availability. The external morphology of the burrows is flattened, subtriangular, lensoidal, but rarely cylindrical. The basal section is planar or concave-upward, and is related to the erosion level and the possible preservation of a central furrow. A siphonate bivalve is the candidate producer as was earlier suggested by Mángano *et al.* (2002); producers lacking siphons like monoplacophorans and arthropods are unlikely. The abundance of documented differences between the *Psammichnites* documented in the Cambrian with the post-Ordovician records are considered sufficient to reassign all the post-Cambrian ichnospecies (*O. devonicus*, *O. grumula*, *O. implexus* and *O. plummeri)* to the ichnogenus *Olivellites* Fenton and Fenton 1937a. In particular, the material studied in this paper documented in the San Rafael Basin (western Argentina) in the El Imperial Formation of Moscovian or younger age is assigned to *Olivellites implexus* (Rindsberg, 1994), where lateral fringes are observed for the first time in this ichnospecies. The studied material constitutes the youngest record in Western Gondwana. It contrasts bathymetrically, palaeonvironmentally and climatically with previous records in Argentina from glacially-related deposits in the Calingasta-Uspallata Basin

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(Mángano *et al*. 2003, Alonso-Muruaga *et al*. 2013), which are older in age. The validity of *Olivellites devonicus* is doubtful and it might be a preservational variant of *O. implexus*, although a complete synonymy is premature. The *Psammichnites* isp. (= *Olivellites*) in the Devonian of Bolivia (Gaillard and Rachebœuf, 2006) needs to be re-examined to test whether they contain holes along the ridge that are typical of *O. grumula*. The analysis in this paper of a siphon used as a "snorkel device", frequently mentioned in the literature, is the indisputable result when a central ridge, sometimes with regularly spaced holes, is preserved. A connection with the surface is necessary, at least intermittently, for respiration. Besides, when a microbial mat exists, and any evidence of disturbance of the mat by a vertical structure is observed, a different mechanism of respiration and producer is envisaged for the trace fossils than for the producer of *Psammichnites*. For this reason, the material from northwestern Argentina, assigned to *Psammichnites saltensis* but later placed in *Nereites*, is considered as significantly different from *Psammichnites*. Finally, the ichnotaxonomical status of *Olivellites* turns out to be more robust than that of the pre-Ordovician ichnogenera and ichnospecies and is not a junior synonym of *Psammichnites.*

Acknowledgments This paper was benefited with the insightful reviews by Andrew Rindsberg, University of West Alabama (USA) and Andrea Baucon, Università di Milano (Italy) and, the editorial insightful comments of the Editor Duncan McIlroy (Memorial University, Newfoundland (Canada). The language improvement is the result of the help by Dr. Gerardo Ameri (Aerolineas Argentinas) and Lawrence Wheeler, translator, interpreter and regional Cambridge advisor for Latin America. The revised version benefited from insightful comments by Dr. Diana E. Fernández (Universidad de Buenos Aires). This is contribution number R 404 of the IDEAN and was financed by UBACyT 2020-2022 and PIP 2016 to Dr. Pablo Pazos. The final version is completely the responsibility of the authors.

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Figure Captions

Figure 1. Paleogeographic map of the Carboniferous–Permian in the western Gondwana margin.

Figure 2. Geological framework: a) Simplified chronostratigraphic chart of the San Rafael Block (modified from Cingolani, 2017). RBT: Rodeo de la Bordalesa Tonalite. b) Geology of the Atuel river and the study area is highlighted. Modified from Manassero *et al*. (2009) and Cingolani (2017). c) Google Earth image of the outcrops where *Olivellites* was documented.

Figure 3. Geological features of the El Imperial Formation in the Cañón del Atuel. a) Contact between the lower and upper members. Note the whitish colour of the upper member (A). Basal conglomerates (1) and the overlying section (B). A dotted line marks the limit between the fluvial sections b) Detail of the coarse-grained levels (1). c) Sandstones with clustered gravels. d) Detail of the coaly level (arrows). e) Sandstone with *Cordaites* remains. f) Slightly asymmetrical cross-stratification. g) Detail of oscillatory flow deposits in heterolithic intervals.

Figure 4. Field photograph of trace fossils: a) *Diplocraterion*. b) *Rhizocoralllium*. c) *Teichichnus*. d) *Planolites*. e) *Zoophycos*-like forms.

Figure 5. Field photographs and line drawing of epichnial *Olivellites implexus*. a) *Olivellites implexus* patches. a´) Details observed in a). Transversal striation not well-developed, and on some turns lateral fringes are observed (white arrow); also *Lingulichnus*? (orange arrows). Specimens are marked with different colours to indicate crossing and self-crossing. b) Another patch of *Olivellites implexus.* b´) Trail courses denoting overcrossing and arrows indicate direction of movement. The use of the same course is observed in some cases with opposite directions.

Figure 6. a-b) Field photographs of *Olivellites* isp. Simple epireliefs of two specimens with a subtriangular outline divided into two lobes by a poorly preserved median ridge.

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Figure 7. Location of *Olivellites* records in the Silurian, Devonian, Carboniferous and Permian. The palaeogeographic reconstruction is from the Late Carboniferous. (Pennsylvanian; modified after Torsvik and Cocks, 2004).

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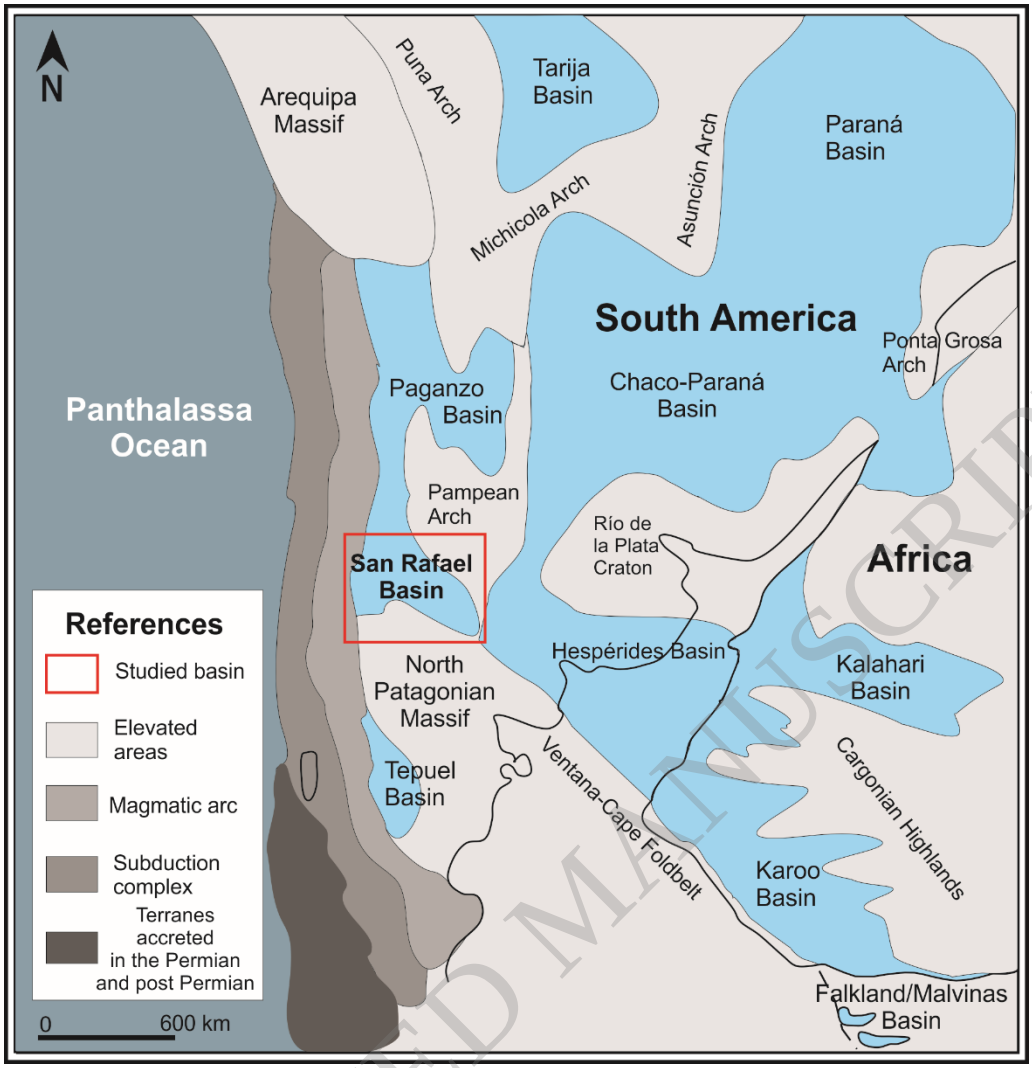

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Figure 1

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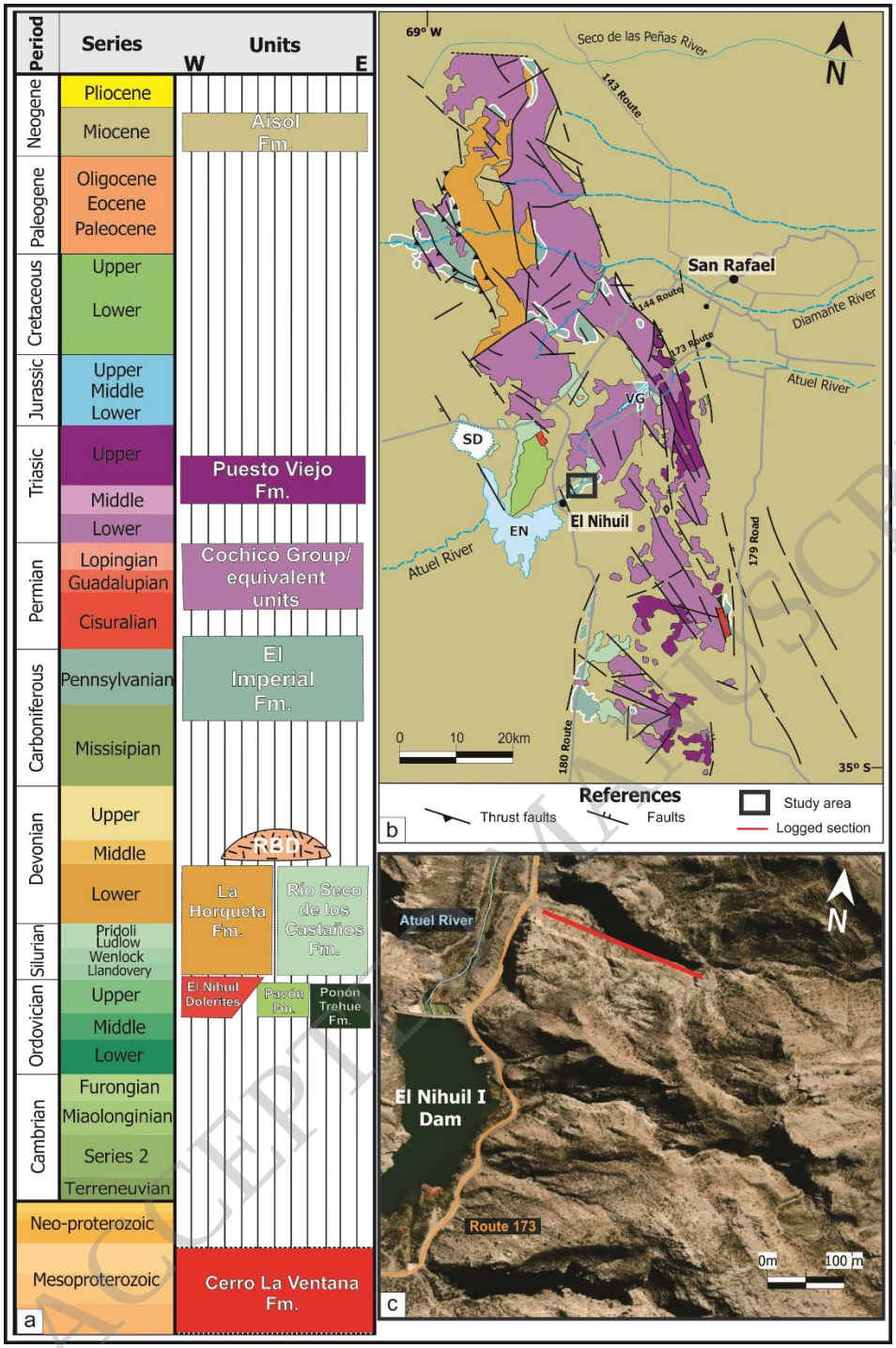

Figure 2

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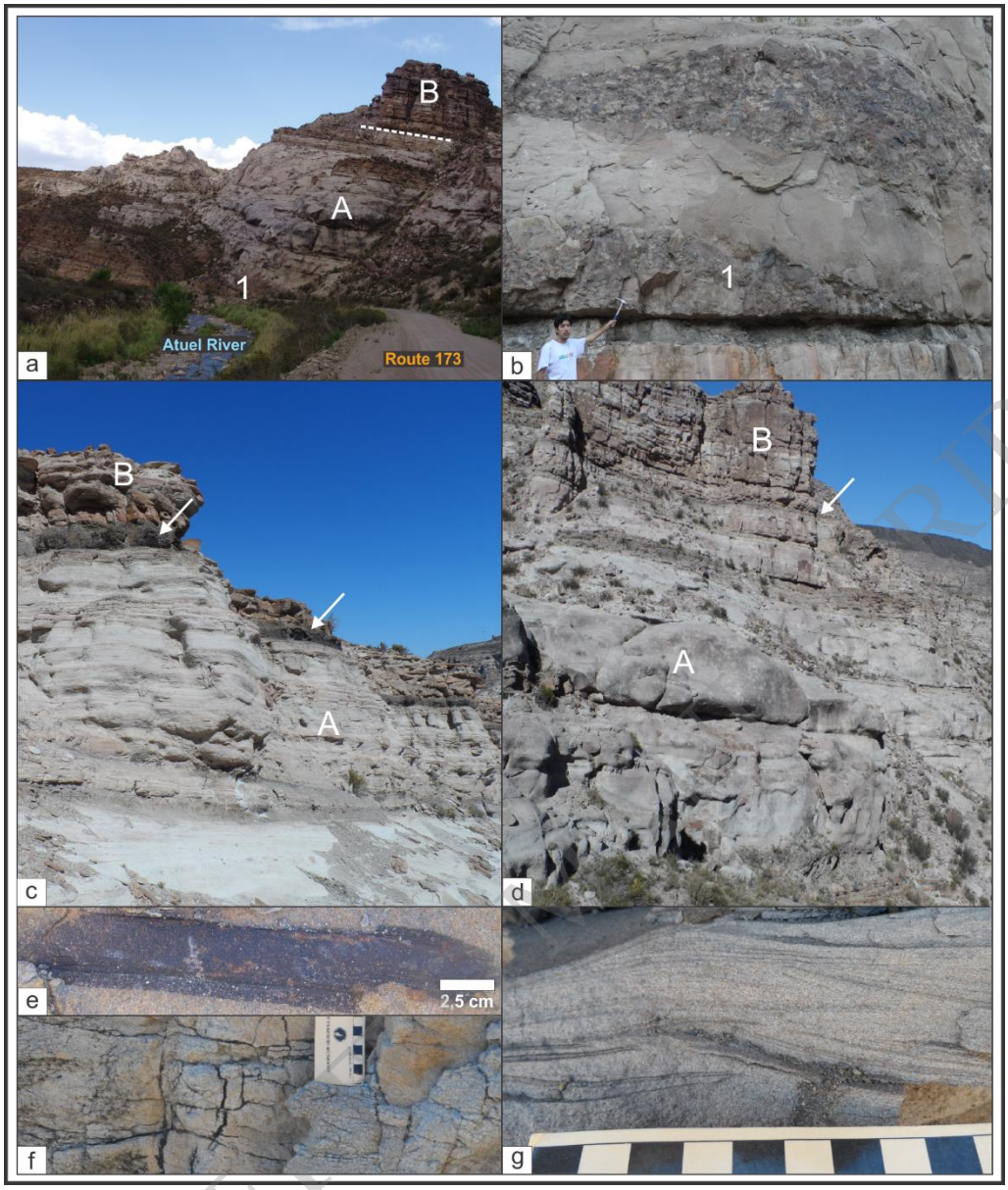

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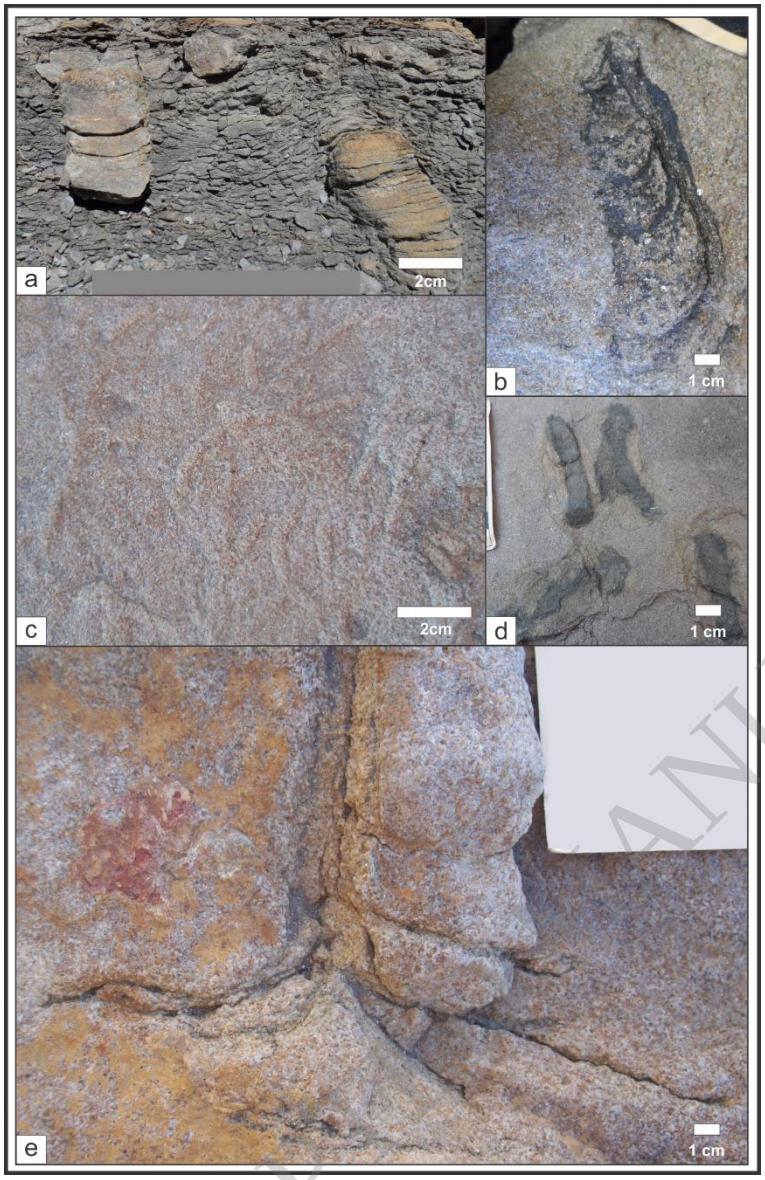

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Figure 4

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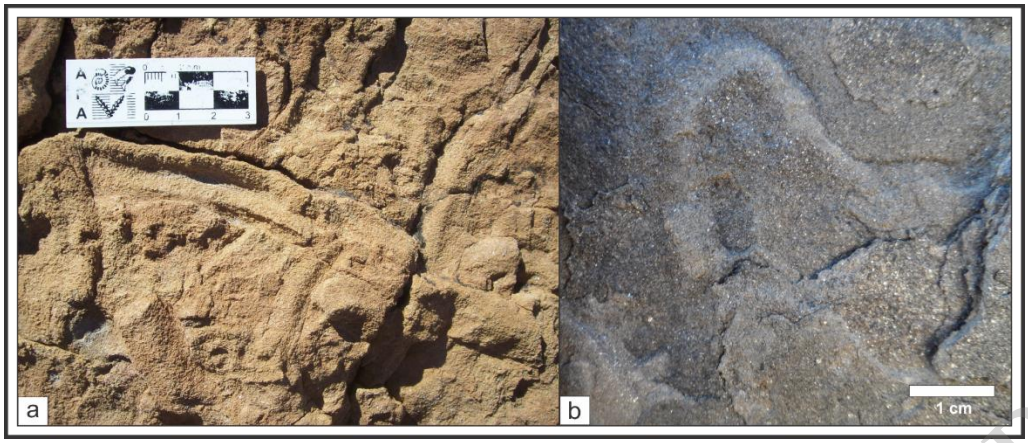

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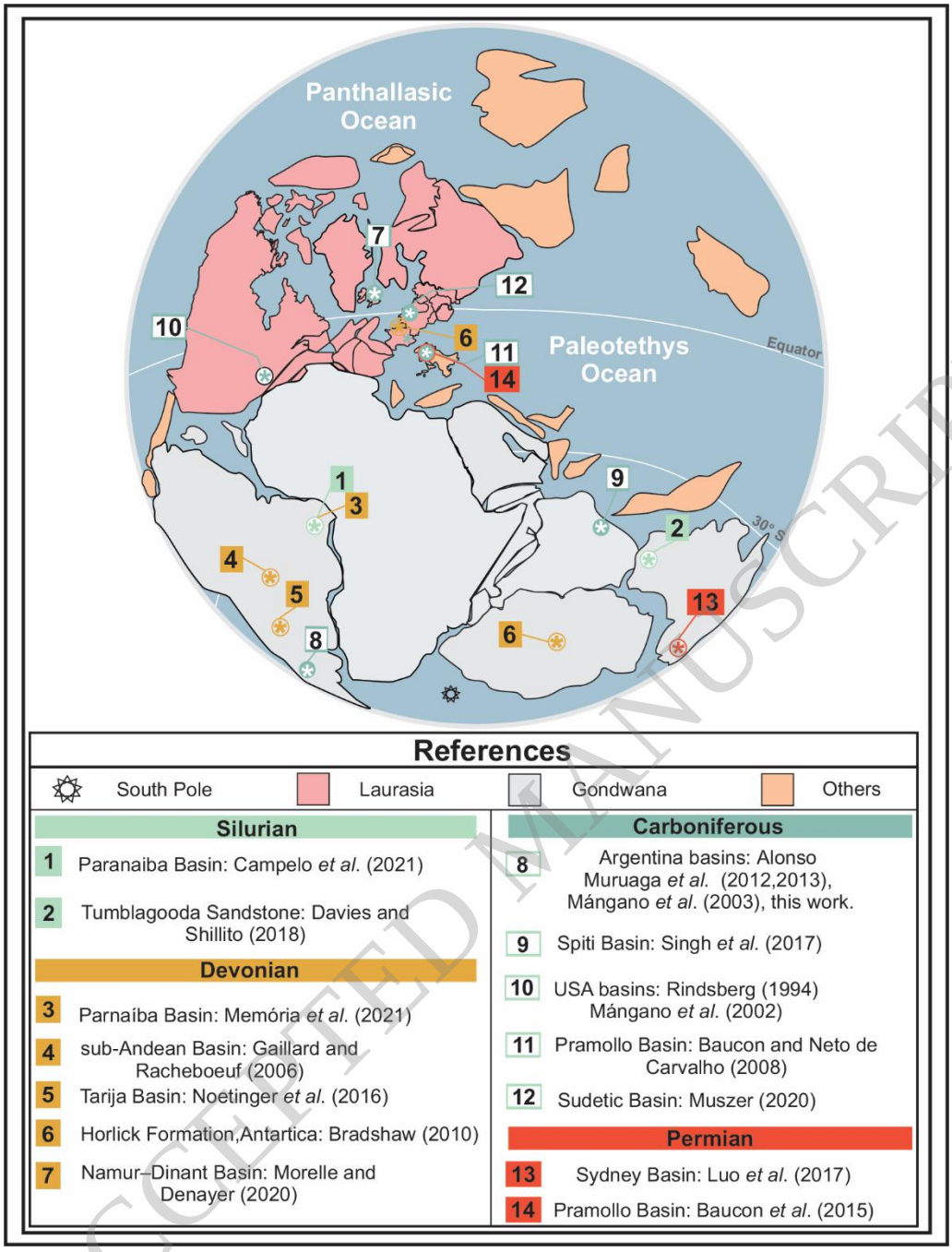

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Figure 7