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The trace fossil *Circulichnis* as a record of feeding exploration: New data from deep-sea Oligocene–Miocene deposits of northern Italy

Trace fossile de Circulichnis*, un enregistrement de la recherche de nourriture : nouvelles données obtenues à partir de dépôts oligo-miocènes du Nord de l'Italie*

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ABSTRACT

Circulichnis is a puzzling, ring-like trace fossil preserved on bedding planes. It is represented mostly by its type ichnospecies *C. montanus*, which is characterized by an evenly circular or elliptical course. A new ichnospecies, *C. ligusticus*, is distinguished based on material from deep-sea Oligocene–Miocene deposits of the Tertiary Piemonte Basin, NW Italy. It shows a winding or irregular course. A new model of *Circulichnis* is proposed as an exploration burrow produced mostly by the trace makers of *Helminthoidichnites*, *Gordia*, or *Helminthopsis*, as it moved to a different sediment layer to checking its feeding utility. This type of behaviour occurred already by the Ediacaran and is common in marine, mostly deep-sea bedded sediments. The trace makers belong mostly to polychaetes in marine sediments and to oligochaetes in continental sediments.

RÉSUMÉ

Circulichnis est une curieuse trace fossile de forme annulaire, préservée sur les plans de stratification. Elle représente, la plupart du temps, son espèce type *C. montanus*, qui se caractérise par un parcours régulièrement elliptique ou circulaire. Une nouvelle ichnoespèce, *C. ligusticus*, s'en distingue, sur la base d'un matériel en provenance de dépôts oligo-miocènes de mer profonde, du Bassin piémontais tertiaire du Nord de l'Italie, par un parcours enroulé ou irrégulier. Un nouveau modèle de *Circulichnis* est proposé, de type fouissage exploratoire, produit la plupart du temps par des auteurs de traces de type *Helminthoidichnites*, *Gordia* ou *Helminthopsis*, car il se déplace vers un lit sédimentaire différent pour en tester l'utilité alimentaire. Ce type de comportement a déjà été observé à l'Édicarien et est commun dans les sédiments déposés en milieu matin, de mer profonde le plus souvent. Les auteurs de traces sont pour la plupart des polychètes dans les sédiments marins et des oligochètes dans les sédiments continentaux.

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1. Introduction

Circulichnis Vialov, 1971 is a trace fossil in the form of a ring preserved on bedding surfaces. It is known since the Ediacaran in marine and since late Palaeozoic in nonmarine sediments. Its behavioural explanation causes some problems because (1) its tracemaker should appear somehow in the place of production of the trace, but the traces of entering and exiting are usually not present, and (2) it is hard to explain why the tracemaker burrowed along a circular path. Even its name became ambiguous because the spelling *Circulichnus* has been proposed in the meantime (Keighley and Pickerill, 1997).

New material of *Circulichnis* from the Monastero Formation (Oligocene) and additional material from the Rocchetta Formation (upper Oligocene–Aquitanian), both in NW Italy, shed some light on the outlined problems. This is an opportunity to present the material, which includes a new ichnospecies, and to make a review of *Circulichnis* in general. These aims are undertaken in the paper.

2. Geological setting

The Monastero Formation (Bellinzona et al., 1971; Marroni et al., in press; Mutti et al., 1995) is a lithostratigraphic unit in the lower part of the fill of the Tertiary Piemonte Basin, which is located in the suture between the northern Apennines and the Alps. The formation overlies the Savignone Conglomerate and is covered by the Gremiasco Formation. The Monastero Formation is about 1000 m thick and is dominated by turbiditic sandstones and mudstones, which overlie fan-delta conglomerates of the Savignone Conglomerate (Gelati, 1977; Ghibaudo et al., 1985). In the lower part, the sandstones are locally conglomeratic, while pelitic facies prevail in the upper part. Locally, pebbly mudstones and slump deposits are present. Calcareous nannoplankton date this unit to the NP23 or NP24 zones (upper Rupelian to lower Chattian) (Marroni et al., in press).

Circulichnis was found at the following localities (Fig. 1): Grondona 1 (44°41.673–772'N; 008°58.524'E), Grondona 2 (44°44.806'N; 008°58.699'E), Liveto (44°42.884'N; 008°58.035'E), Variana (44°41.696'N; 008°56.855'E), and Molo Borbera Nord (44°44.817'N; 008°58.672'E).

The Rocchetta Formation (Upper Oligocene to Aquitanian) is also a lithostratigraphic unit in the lower part of the fill of the Tertiary Piemonte Basin. This is a clastic unit composed mostly of mudstones interbedded with sandstones or more rarely with limestones. These deposits accumulated as pelagic and turbiditic sediments and prodelta muds (Artoni et al., 1999; Gelati, 1968). This formation overlies the Molare Formation, the basal unit of the Tertiary Piemonte Basin in its western part, and is followed by the Monesiglio Formation. The Rocchetta Formation is 100–550 m thick and is time-transgressing; it is Rupelian to Chattian in age in the eastern part and Chattian to Aquitanian in the western part (d'Atri et al., 1997; Gelati, 1968; Gelati et al., 1993). The Rocchetta Formation and the Monesiglio Formation are considered together as the Rocchetta–Monesiglio Group or the Rocchetta–Monesiglio Formation (Gelati et al., in press).

Circulichnis was found in the middle part of the formation at Mombaldone in the Bormida Valley, within the upper part of the so-called Molino di Mombaldone Erosional Depression (lower Aquitanian), which is an erosional canyon whose upper part is filled by diluted turbidites and hemipelagites of a prograding slope (Ghibaudo et al., 2014). The locality is on the western side of the road from Mombaldone to Vengore (44°34.738'N; 008°19'590'E; Fig. 1).

3. Systematic ichnology

Ichnogenus *Circulichnis* Vialov, 1971

Type ichnospecies. *Circulichnis montanus* Vialov, 1971.

Emended diagnosis. Horizontal, approximately circular to oval, cylindrical ring.

Remarks. Keighley and Pickerill (1997) proposed correction of the original ichnogeneric name *Circulichnis* to *Circulichnus* (see also Blisset and Pickerill, 2004) because of its improper ending. The name *Circulichnus* was also used before but without any formal decision (e.g., Uchman, 1992; Yeh, 1987). However, according to Art. 33.2 of the International Code of Zoological Nomenclature, they created *Circulichnus* Keighley and Pickerill, 1997, which is a younger objective synonym of *Circulichnis* Vialov, 1971. Therefore, *Circulichnus* is not recommended for further use. Irrespective of the arguments, several authors still use the original name.

Originally, Vialov (1971, p. 91) defined *Circulichnis* as "Koltzevoi sled pochti krugloi (ili ovalnoi) formi, obrazovanyi odnim valikom" can be translated as "Ring trace, almost circular (or elliptical) developed in one cylinder". This definition reflects the shape of this trace fossil, but information on its horizontal orientation is lacking. The translation of this original diagnosis by Fillion and Pickerill (1984) and Blisset and Pickerill (2004), which reads "Annular track of almost round (or oval) shape, formed by one cylinder", is rather unfortunate. In particular, the phrase ". . . formed by one cylinder" sounds awkward, probably from unfortunate translation from the Russian. It suggests a mode of formation by a cylindrical object. The diagnosis by Häntzschel (1975, p. W52), viz. "Ring-shaped trace, almost circular (or oval), formed by some cylindrical object" is also unfortunate for the same reason. The diagnosis by Fillion and Pickerill (1990) is closer to the original: "Circular to oval, unbranched horizontal trail or burrow". However, the distinction between trails and burrows is interpretative and the horizontal orientation is also unmentioned. Therefore, the diagnosis is emended.

Circulichnis is sometimes considered as a monospecific ichnogenus, but several ichnospecies have been distinguished under this name. *Circulichnus ngariensis* Yang and Song, 1985 from the Middle to Upper Triassic flysch of the SW Tibet was included in *C. montanus* by Yang (1986). However, this trace fossil is a winding, open loop that conforms better to *Gordia marina* Emmons, 1844, according to Fillion and Pickerill (1990). Also, *Circulichnis spiralis* Li, 1993 from the Ordovician of Inner Mongolia, China, is composed of distinct loops and should be ascribed to *Gordia*. *Circulichnis sinensis* Yang, 1990 in Yang et al., 2004 from the Ordovician of China, 20–40 mm in diameter, is a ring that shows lateral, tangential branches, which are

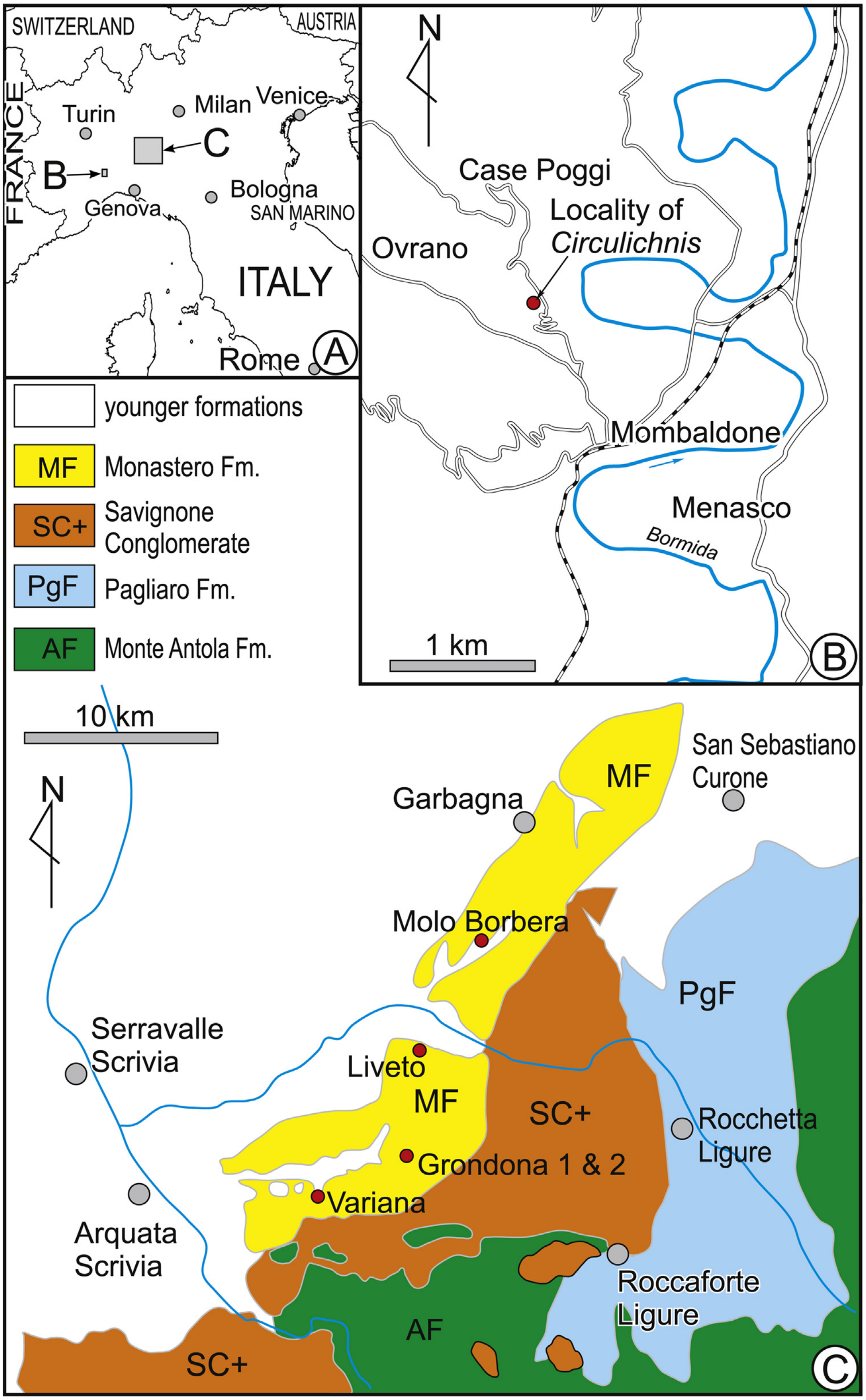

Fig. 1. Location map. **A.** Location of the study area in NW Italy. **B.** Map of locality with *Circulichnis ligusticus* in the Rocchetta Formation near Mombaldone. **C.** Localities of *C. ligusticus* in the Monastero Formation.

Fig. 1. Carte de localisation. **A.** Localisation de la zone étudiée dans le Nord-Ouest de l'Italie. **B.** Carte de la localité à *Circulichnis ligusticus* dans la formation Rocchetta, près de Mombladone. **C.** Localités à *Circulichnis ligusticus* dans la formation Monastero.

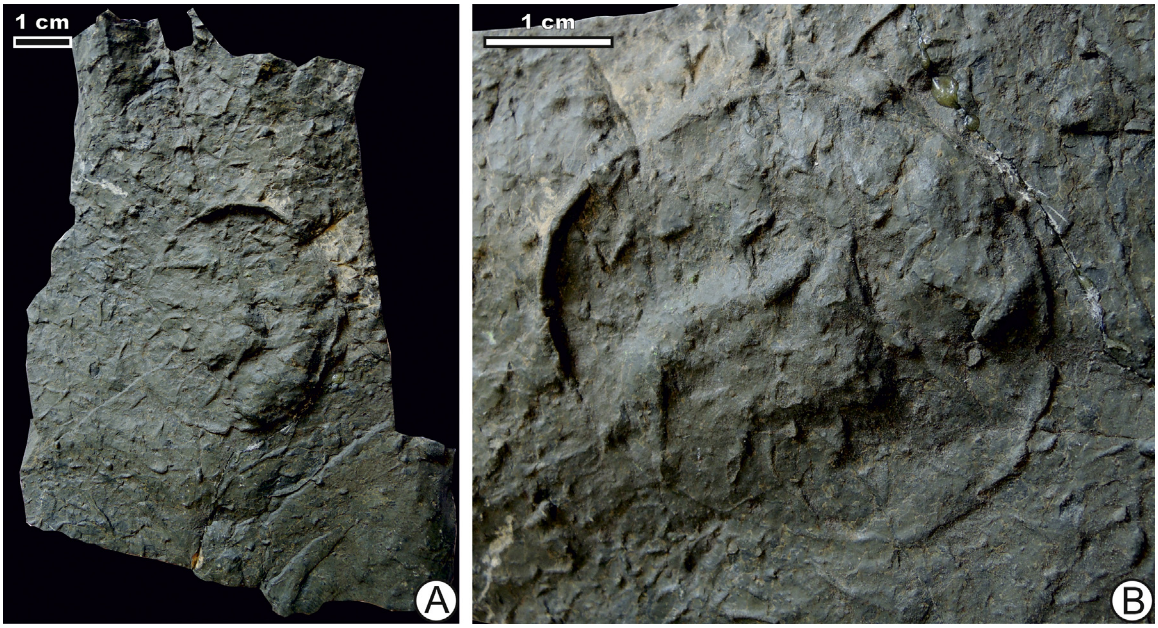

Fig. 2. The holotype of *Circulichnis montanus* Vialov, 1971, specimen 5816, Chernyshev Central Geological Research Museum (CNIGR Museum) of the VSEGEI Institute, St. Petersburg, Russia, Istyksk Suite (Norian–?Rhaetian), Yuzhnaya Akdzhilga river, SW Pamir, Russia. **A.** General view of the specimen. **B.** Detail of A.

Fig. 2. Holotype de *Circulichnis montanus* Vialov, 1971, spécimen 5816, Chermishev Central Geological Research Museum (CNIGR Museum) de l'Institut VSEGEI, Saint-Pétersbourg, Russie, Suite Istyksk (Norien–?Rhétien), rivière Yuzhnaya Akdzhilga, Sud-Ouest du Pamir, Russie. **A.** Vue générale de l'échantillon. **B.** Détail de A.

not features of *Circulichnis.*

Circulichnis montanus Vialov, 1971

Fig. 2

*1971 *Circulichnis montanus* Vialov sp. n. – Vialov, p. 91, pl. 1, fig. 1. [fig. 2].

1975 *Circulichnis montanus* – Häntzschel, p. W52, fig. 31.4 [figure labelled as *Circulichnus* (sic!)].

1981 *Circulichnis montanus* Vialov, 1971 – Pickerill and Keppie, p. 131, fig. 3a–d.

1983 *Circulichnis montanus* Vialov, 1971 – Gureev, p. 31, fig. on p. 31.

1984 *Circulichnis montanus* Vialov, 1971 – Fillion and Pickerill, p. 9, fig. 7g.

1984 *Circulichnis montanus* Vialov, 1971 – Pickerill et al., p. 419, fig. 5E.

partim 1986 *Circulichnis montanus* Vialov – Gureev, p. 43, fig. 3e [non fig. 3d].

partim 1986 *Laevicyclus* – Pieńkowski and Westwalewicz-Mogilska, p. 58, fig. 4c [non fig. 4D, E].

1988 *Circulichnis montanus* Vialov, 1971 – McCann and Pickerill, p. 334, fig. 3.4.

1989 *Gordia arcuata*? Książkiewicz, 1977 – Gibson, p. 2, fig. 3.1.

1990 *Circulichnis montanus* – McCann, p. 245, fig. 4b.

non 1990 *Circulichnis* ichnosp. – Uchman, p. 111 [*Gordia*].

1991 *Circulichnis montanus* Wiałow–Uchman, p. 209.

1991 *Circulichnis montanus* Wiałow–Uchman, p. 431.

1993 *Circulichnis montanus* Vyalov 1971–Buatois and Mángano, p. 240, fig. 3B.

non? 1992 *Circulichnis montanus* Vyalov, 1971 – Mikuláš, p. 223, pl. 5, fig. 1.

? 1993? *Circulichnis* ichnosp. – Miller, p. 16, fig. 4C. non?

1993 *Circulichnus montanus* Vyalov 1971 – Li, pl. 93, pl. 1, fig. 1.

1993 *Circulichnis montanus* Vialov, 1971 – McCann, p. 41, fig. 4B.

? 1996 *Circulichnis*? *montanus* Vyalov – Pickerill et al., p. 224, fig. 2c.

?non 1996 *Circulichnis* isp. – Tunis and Uchman, p. 3, fig. 1A.

1998 *Circulichnis montanus* – Buatois and Mángano, fig. 4G.

1998a *Circulichnis montanus* Vyalov – Buatois et al., p. 6, fig. 20.

1998b *Circulichnis montanus* Vyalov – Buatois et al., p. 155, fig. 4.1.

1999 *Circulichnus montanus* Vialov, 1971 – Pickerill and Fyffe, p. 220, fig. 2a, c.

1999 *Circulichnus montanus* Vialov, 1971 – Tchoumatchenco and Uchman, p. 174, fig. 3A.

? 1999 *Circulichus* isp. [sic] – Tian et al., fig. 4.

? 2000 *Circulichnus* – Fang and Liu, p. 69, pl. 1, fig. 6.

? 2001 *Circulichnus montanus* Vialov, 1971 – Buatois et al., p. 27, fig. 2.2.

2002 *Circulichnis* isp. – Fernandes et al., p. 33, fig. 29. [Mentioned also in Fernandes, 1999].

?partim 2002 *Circulichnus montanus* (Vyalov, 1971) – Kim et al., p. 46, fig. 3G. [not fig. 3H–*Gordia*]

? 2003 *Circulichnis montanus* Vialov, 1971 – Kappel, p. 30, pl. 4, fig. 7.

? 2003b *Circulichnis montanus* – Buatois and Mángano, p. 107, fig. 2E. [Illustrated also in Buatois and Mángano, 2012, fig. 6A; taxonomic assignment questioned by Aceñolaza and Aceñolaza, 2007].

2007 *Circulichnis montanus* Vialov, 1971 – Wetzel et al., p. 571, fig. 6 [part].

2010 *Circulichnus* – Davies et al., p. 534, fig. 5O.

2013 *Circulichnis montanus* Vialov – Bekker, p. 63, pl. 1, fig. 9.

?non 2014 *Circulichnis montanus* – Knaust et al., p. 2225, fig. 7B. [A loop–probably *Gordia*].

non 2015 *Circulichnus* isp. – Solanki et al., p. 33, fig. 3a. [Incomplete, uneven half-ring].

2015 *Circulichnis montanus* (Vyalov, 1971) – Zhao et al., p. 107, fig. 5D, E.

? 2016 *Circulichnus* – Bhatt et al., p. 81, pl. 1, fig. 8.

2016 *Circulichnus montanus* Vialov – Jackson et al., p. 270, fig. 4D.

Feng et al., 2017; 2017 *Circulichnus* Keighley and Pickerill, 1997 – Feng et al., p. 129, fig. 6C, D.

Diagnosis. Horizontal, cylindrical burrow, which shows a course along a regular circle or ellipse.

Holotype. Specimen 5816, Chernyshev Central Geological Research Museum (CNIGR Museum) of the VSEGEI Institute, St. Petersburg, Russia, collected by B.K. Kushlin in 1968, Istyksk Suite (Norian To?Rhaetian), Yuzhnaya Akdzhilga River, SW Pamir.

Remarks. *Circulichnis montanus*, the type ichnospecies of *Circulichnis*, should be limited for circular and regularly elliptical forms. The holotype is 35–41 mm wide, 0.7–1.5 mm wide, up to 1.5 mm high.

Circulichnis ligusticus isp. nov.
Figs. 3 and 4

1990 knotted circular burrow – Narbonne and Aitken, p. 974, fig. 7B.

?partim 1997 *Circulichnus montanus* Vialov, 1971 (nom. correct.) – Keighley and Pickerill, p. 184, figs. 2A [non? figs. 22B, 10F].

? 2003a?*Circulichnis montanus* Vyalov 1971 – Buatois and Mángano, p. 57, fig. 3A.

2004 *Circulichnus montanus* Vialov, 1971 (nom. correct.) – Blisset and Pickerill, p. 348, pl. 2, fig. B.

? 2007 *Circulichnus montanus* Vialov, 1971 – Metz, p. 3, fig. 3.

2011 *Circulichnis montanus* Vyalov, 1971 – Avanzini et al., p. 98, fig. 2.2.

2015 *Circulichnus* isp. – Khaidem et al., p. 1098, fig. 6c.

Derivation of name. From Latin adjective of Liguria–*ligusticus*, in relation to the Ligurian Apennines.

Diagnosis. Horizontal, cylindrical ring, which shows a winding or irregular course.

Holotype and other material. Holotype INGUJ149P109 is the (Fig. 3A; Monastero Formation, Grondona 1); paratype INGUJ149P114 (Fig. 3B; Monastero Formation, Grondona 1); and one additional specimen INGUJ149P116 (Monastero Formation, Grondona 1). All are housed in the Nature Education Centre of the Jagiellonian University (CEP)–Museum of Geology; plus one specimens (no. 2717) from the Rocchetta Formation housed in the Crocefischi Museo (Crocefieschi, north of Genova, Italy).

Description. Hypichnial, horizontal, cylindrical ring, which shows winding or irregular course. Usually, the path is closed or shows one, rarely more, breaks. Exceptionally, a short lateral, cylindrical tunnel runs outside the ring. Cylinder of the ring is more or less of uniform width, which ranges from 0.8 to 1.4 mm, with differences up to 0.2 mm in a single ring. The tunnel is mostly smooth, except for some specimens, which may display some local nodes and slight vertical undulations. The ring is at maximum 8–25 mm wide. The maximum to minimum width ratio ranges from 1 to 1.3. Some morphometric parameters are presented in Fig. 5.

The trace fossil is preserved in semirelief in mostly very thin and thin turbiditic beds of very fine-grained or fine-grained, quartz-dominated sandstone with muscovite and ophiolitic detritus. The beds show graded bedding and ripple cross and parallel lamination (Tc, Td). Usually, *Circulichnis ligusticus* co-occurs with *Helminthoidichnites* isp. in the same bed package or on the same bedding plane, where they generally display the same cylinder width and appearance.

Remarks. *Circulichnis ligusticus* differs from *C. montanus* by its winding and irregular course. The described material shows very close morphometric parameters (Fig. 5) and comes from deep-sea turbiditic sediments. *Circulichnus* isp. from late Eocene–early Oligocene flysch sediments of NE India described by Khaidem et al. (2015) is also included in *C. ligusticus*, similarly to *C. montanus* from the lower Miocene basinal limestones of Jamaica by Blisset and Pickerill (2004). The same morphological basic features and close morphometric parameters are presented by specimens from nonmarine Carboniferous–Triassic sediments, including some specimens of *C. montanus* from Carboniferous nonmarine deposits of SE Canada (Keighley and Pickerill, 1997) and *C. montanus* from Permian marginal lacustrine deposits on North Italy (Avanzini et al., 2011). Possibly, specimens determined as ?*C. montanus* from nonmarine (fjord?) sediments of Argentina (Buatois and Mángano (2003a) and *C. montanus* from the Late Triassic marginal marine deposits in NE USA (Metz, 2007) belong to *C. ligusticus*. Their different age and environment need not prevent their assignment to this ichnospecies, because such features are not recommended as ichnotaxobases (Bertling et al., 2006).

The most problematic is the specimen described by Narbonne and Aitken (1990) as "knotted circular burrow" from the Ediacaran of western Canada, and associated with "arcuate burrows", which can be ascribed to *Helminthoidichnites* (their *Helminthoida* sp. and *Helminthopsis*? sp.). This is a hypichnion showing features of *Circulichnis ligusticus*, but its size (up to 31–71 mm) is much larger than other specimens ascribed to this ichnospecies (see also Fig. 5). Nevertheless, size as a single criterion is also not recommended as a ichnotaxobase (Bertling et al., 2006).

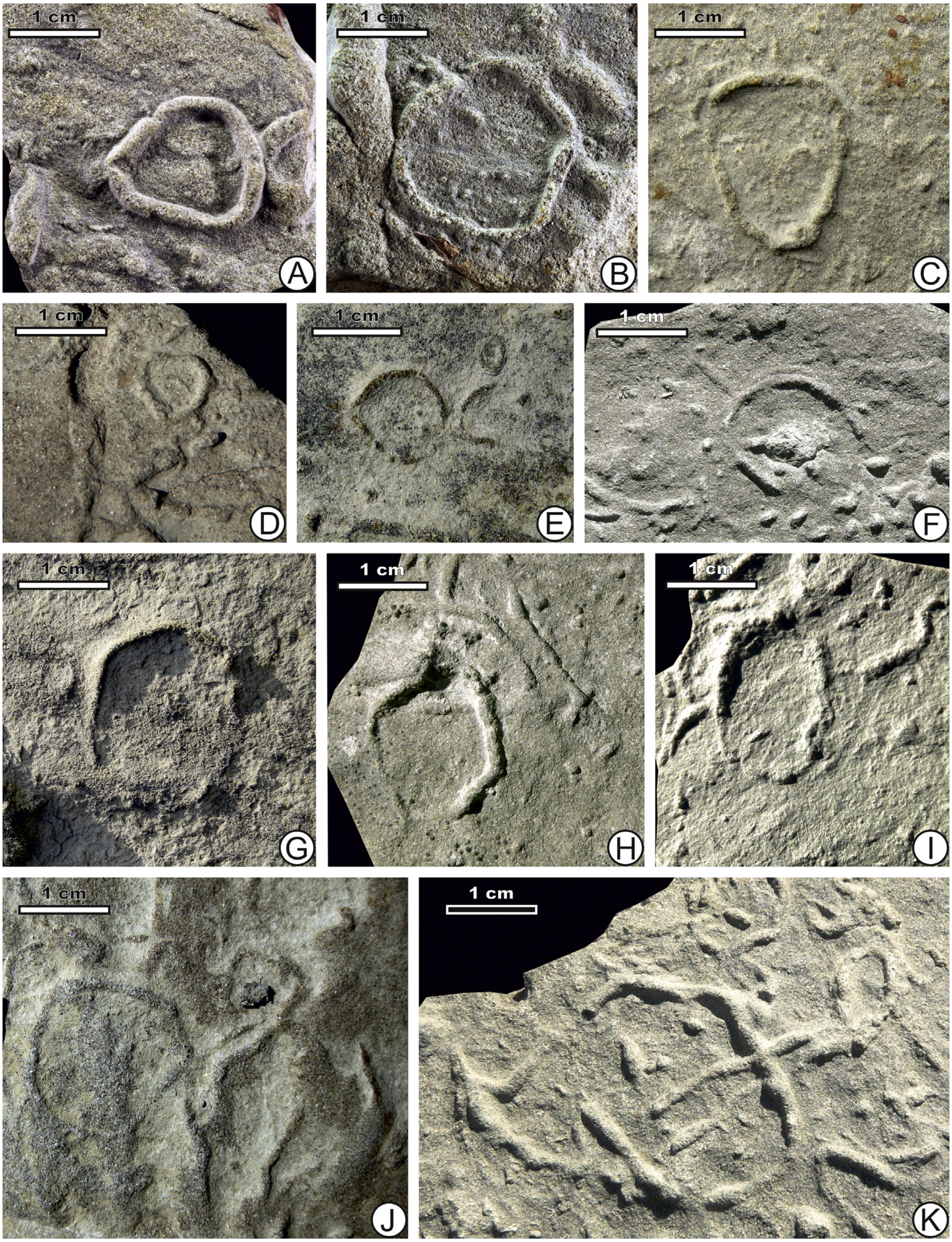

Fig. 3. *Circulichnis ligusticus* from the Monastero Formation (Oligocene). Hypichnia on turbiditic sandstone beds. Note a short lateral cylindrical tunnel in A–C, F. **A.** INGUJ149P109, holotype, Grondona 1. **B.** INGUJ149P114, paratype, Grondona 2. **C.** Liveto, field photograph. **D.** Grondona 1, field photograph. **E.** Liveto, field photograph. **F.** INJGUJ149P103, Grondona 1. **G.** Liveto, field photograph. **H. and I.** Grondona 1, field photograph. **J.** Liveto, field photograph. **K.** A transitional form to *Gordia*, Grondona 1, field photograph.

Fig. 3. *Circulichnis ligusticus* de la formation Monastero (Oligocène). Hypichnia sur des lits turbiditiques gréseux. À noter un étroit tunnel cylindrique latéral en A–C, F. **A.** INGUJ149P109, holotype, Grondona 1. **B.** INGUJ149P114, paratype, Grondana 2. **C.** Liveto, photographie de terrain. **D.** Grondona 1, photographie de terrain. **E.** Liveto, photographie de terrain. **F.** UNGUJ149P103, Grondana1. **G.** Liveto, photographie de terrain. **H. and I.** Grondana 1, photographie de terrain. **J.** Liveto, Photographie de terrain. **K.** Forme de transition vers *Gordia*, Grondana 1, photographie de terrain.

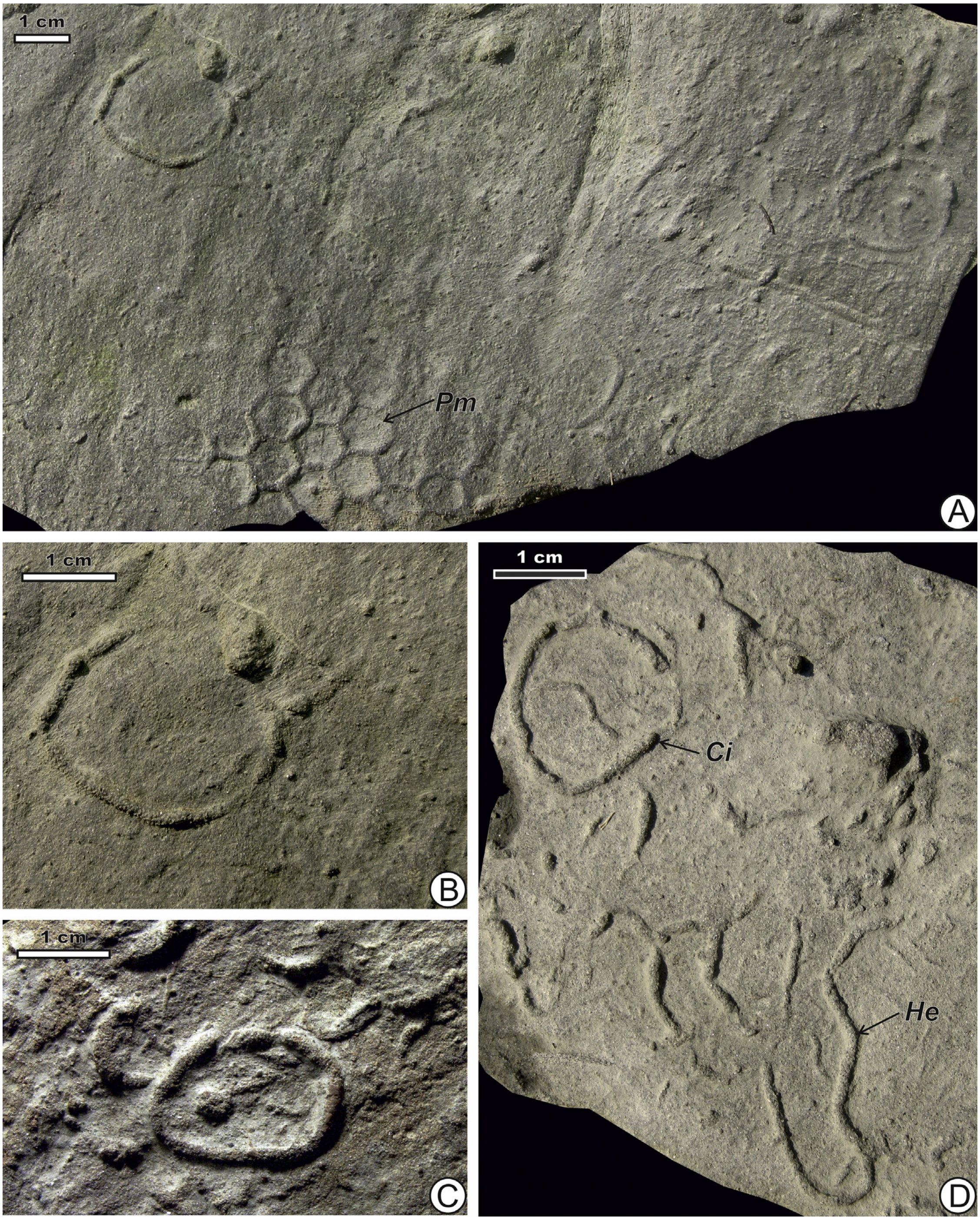

Fig. 4. *Circulichnis ligusticus* and associated trace fossils. Hypichnia on turbiditic sandstone beds. **A.** *C. ligusticus* and *Paleodictyon majus* (*Pm*), Variana, Monastero Formation, field photograph. **B.** Details of A, whose ring shows a short, side cylindrical tunnel. **C.** Mombaldone, Rocchetta Formation, specimen 2717. **D.** *C. ligusticus* and *Helminthoidichnites* isp., Liveto, Monastero Formati on, field photograph.

Fig. 4. *Circulichnis ligsusticus* et traces fossiles associées. Hypichnia sur lits turbiditiques gréseux. **A.** *C. ligusticus* et *Paleodictyon majus* (*Pm*), Vatiana, formation Monastero, photographie de terrain. **B.** Détails de A, dont l'anneau montre un étroit tunnel cylindrique sur le côté. **C.** Mombaldone, formation Rocchetta, specimen 2717. **D.** *C. ligusticus* et *Helminthoidichnites* isp. Liveto, formation Monastero, photographie de terrain.

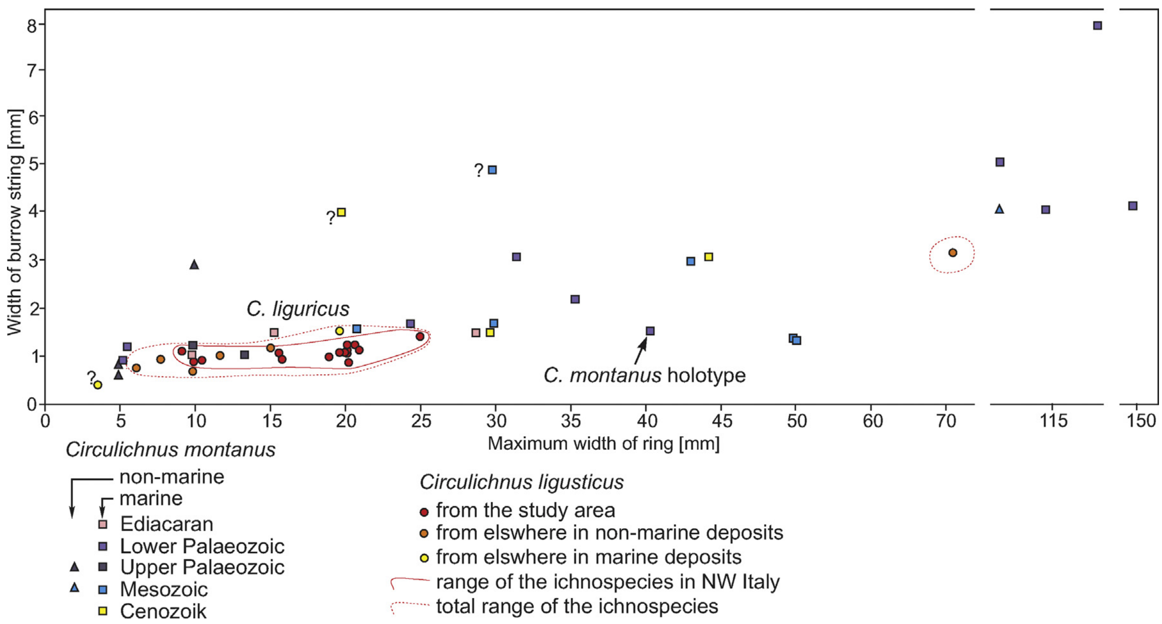

Fig. 5. Diagram with plotted maximum diameter of the ring and diameter of the burrow string for *Circulichnis*.

Fig. 5. Diagramme avec, en abscisse, la largeur maximum de l'anneau (en mm) et, en ordonnée, la largeur maximum du trou de fouissage (en mm).

4. Discussion

4.1. Ethology and tracemaker

Vialov (1971) ascribed *Circulichnis montanus* together with *Laevicyclus* to the Circulichnidii Vialov, 1968 and Circulichnidae Vialov, 1971, and regarded the former trace fossil as a crawling trace produced by a worm, which after completion of its circle, moved up from the bottom or perhaps plunged into the sediment. *Circulichnis* is usually preserved as a convex hyporelief, but Pickerill et al. (1988) reported also concave epirelief structures. Fillion and Pickerill (1990) discussed the problem of the generally missing entry or exit branch and noted that the trace was not necessarily produced on the sediment surface. However, a side branch was noted by Pickerill and Keppie (1981), who suggested a "worm" producer. Keighley and Pickerill (1997) regarded that *Circulichnis* could be either a burrow (subsurface structure) or a trail (surface structure).

Buatois et al. (1998a, 1998b) considered *Circulichnis* as a fodinichnion produced by annelids, or an unspecialized grazing trail (also Buatois et al., 2006; Mángano et al., 1997). Fillion and Pickerill (1990) speculated that the ring tunnel served for storage of food; they pointed to pustulose sediment within the ring in specimens they analysed, which may be referred to primary mucous layer encircled by the ring. However, no proof has been provided to support such a view.

Pickerill and Keppie (1981) reported *Circulichnis montanus* and *Helminthopsis* isp. in the same bed, both showing the same appearance except for their course. These authors concluded that the aforementioned trace fossils were produced by the same trace maker; they also invoked a picture in Häntzschel (1975, fig. 44.2a, p. W71) showing *Helminthopsis* isp. together with a ring-like trace fossil.

A new ethological model of *Circulichnis ligusticus* and *Circulichnis* in general is proposed in this paper. Its function is interpreted as an exploration by the trace maker of *Helminthoidichnites* in the investigated Monastero Formation. In other formations *Circulichnis* could be also produced by the trace maker of *Gordia* or *Helminthopsis*. In this model, *Helminthoidichnites*, *Gordia* and *Helminthopsis* are feeding-locomotion or locomotion burrows or trails, and their trace makers tried to recognize the environment on deeper or shallower sediment levels, mostly for feeding, usually along bedding interfaces. Hiding or other purposes for change in sediment level are also not excluded. Energetically, the most economical way to make such an exploratory burrow is to drive a shaft through nutritionally less attractive sediment, to make a ring burrow in a more interesting horizon and, if the horizon is not suitable for the expected purpose, to return through the same shaft (Fig. 6A).

The rejoining to the shaft can be exactly at the point of the vertical to subvertical shaft connection with the ring, or with the shaft bent to the horizontal position near the ring, or with the shaft diverging in the lower part and transit to an imperfect ring that is not closed on the same level (Fig. 6B). Depending on these differences, the ring can be complete without branches, have a short side branch, or be incomplete (Fig. 6B, variants A, B and C, respectively). However, the incomplete ring may result also from uneven scouring before casting in the case of specimens preserved in semireliefs. The shaft connecting the ring with other level is mostly speculative. It has never been traced, except for the short side branches referred to as subhorizontal near the ring.

Geometry of the burrows suggests a trace maker having flexible, elongate body with no evidence of body appendages making "fingerprints" in the trace. The broad

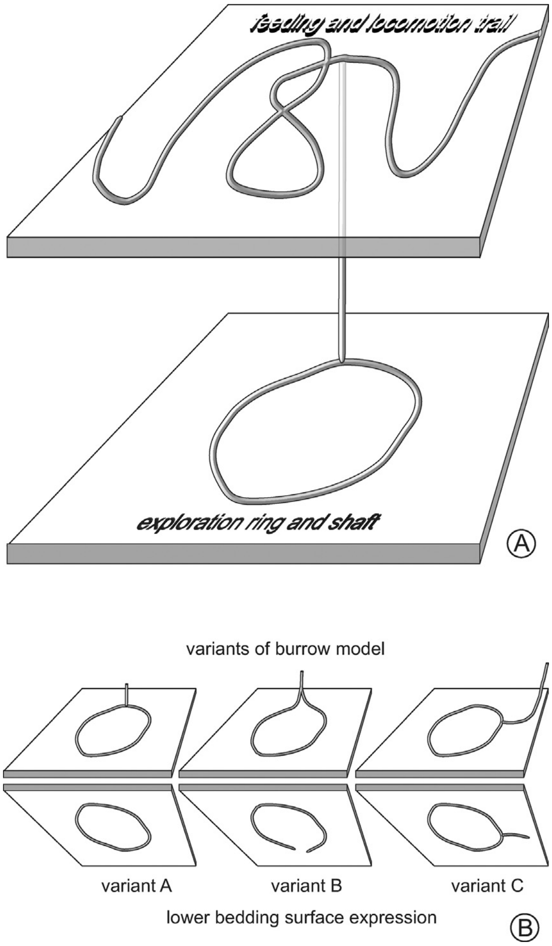

Fig. 6. Model of *Circulichnis ligusticus*. **A.** Model of the burrow. **B.** Models of burrow variants A, B and C and their preservation on the lower bedding surface.

Fig. 6. Modèle de *Circulichnuis ligusticus*. **A.** Modèle du fouissage. **B.** Modèles de variantes de fouissage. A, B et C et leur conservation sur la surface inférieure du litage.

stratigraphic and environmental range (see further discussion) points to a common, evolutionary successful group of invertebrates. Presumably, they are polychaetes, which display a wide plasticity of behaviours (Jumars et al., 2015) and have been abundant throughout the Phanerozoic. In nonmarine environments, the makers could be oligochaete annelids as suggested by Buatois et al. (1998a, 1998b). The differences in morphometric parameters of *Circulichnis* from different areas and ages are significant (Fig. 5). *C. ligusticus* is generally much smaller than *C. montanus*. Large forms of *Circulichnis* are especially common in the lower Palaeozoic, which can be up 600 mm wide and 10 mm thick, have also been noted (Keighley and Pickerill, 1997). The large differences suggests that the group of trace makers was taxonomically diverse, even if all were polychaetes. The small differences in morphometric parameters of *C. ligusticus*, especially in the thickness of tunnel, which may express the body size, may be related to ontogenetic development.

4.2. Taxonomic status and problems

The close relationships (probably the same trace maker) among *Circulichnis*, *Helminthoidichnites*, *Gordia*, and *Helminthopsis* and their common co-occurrence in the same or adjacent beds pose a question as to of their ichnotaxonomic distinction. The known transitions between *Gordia* (commonly looping, mostly feeding behaviour) and *Helminthoidichnites* (mostly irregularly winding, occasionally looping, more locomotory than feeding) are proved (Hofmann, 1990; Hofmann and Patel, 1989), but it is worthwhile to keep them separate as two end members illustrating different behaviours. Some loops of *Gordia* can be mistaken for *Circulichnis* and some transitional forms between them may be present (Fig. 3K). Nevertheless, the loops in such specimens are closed by intersecting burrow segments. Incompletely preserved loops can pose a problem in proper identification. In many cases, *Circulichnis* does not co-occur with *Helminthoidichnites*, *Gordia*, or *Helminthopsis* on the bedding surface. The shaft joining the ring and the aforementioned burrows is mostly an interpretative structure. Still, the ring expresses different behaviour than feeding and/or locomotion and feeding, i.e. it can be considered as an exploration trace. Therefore, the distinction of *Circulichnis* as a separate ichnogenus is sufficiently grounded.

The separation of *Circulichnis montanus* (circular or elliptical, even ring-like structure) and *C. ligusticus* (ring with winding, irregular course) is arbitrary. Transitional forms may exist, but they seem to be rare; they should be determined as *C.* cf. *montanus* or *C.* cf. *ligusticus*. Hagadorn and Waggoner (1990) suggested that preservational variants of the problematic, globular, Ediacaran organism *Nimbia* may be very similar to *Circulichnis*. Also, *C. montanus* can be mistaken for a preservational variant of medusae as shown in material from the Cambrian of Spain (Mayoral et al., 2004, 2008).

Similarly, ring-like Lebensspuren from recent deep-sea photographs (grooves and ridges) have been compared to *Circulichnis*. For instance, Kitchell et al. (1978, fig. 3.17) presented circular ridges 30–45 cm in diameter in the Arctic Alpha Cordillera. Kitchell and Clark (1979, pl. 4.2) reported a slightly undulating, unclosed ring from the deep-sea floor of the Arctic. Young et al. (1985, fig. 8) presented a circular ridge formed by rotation of the oweniid polychaete *Myriochele* protruding from a vertical shaft in the middle, and grooves originated in a similar fashion. They referred also to Heezen and Hollister (1971, figs. 6.28, 6.30), who illustrated "circle scribers" in a crater-like depression or concentric grooves. However, all of these are similar in origin to scratch circles produced by rotating objects (cf. Jensen et al., 2002; Uchman and Rattazzi, 2013). *Circulichnis* displays no concentric structures or central shaft. Therefore, the comparisons are rather misguided.

4.3. Environment and age

Circulichnis shows a wide environmental range (Fillion and Pickerill, 1984; Buatois et al., 1998b), from different continental to deep-sea settings, with a preference for the latter. The ichnogenus is known from the *Mermia* ichnofacies, which is typical of lakes (Buatois and Mángano, 1995, 2004, 2007), less frequently from shelf settings and more frequently from turbiditic deposits (e.g., Pickerill and Keppie, 1981, this study). In the studied deposits, this is the *Nereites* ichnofacies as evidenced by the presence of graphoglyptids (Sacco, 1888; personal observations). The more frequent occurrence in deep-sea turbiditic sediments can be an effect of feeding along bedding interfaces, which exploration seems to be important strategy.

The oldest occurrences of *Circulichnis* are from the Ediacaran (e.g., Bekker, 2013; Fedonkin, 1988; Gureev, 1983, 1986; Narbonne and Aitken, 1990). It is possible that their trace makers explored sediments under microbial mats as evidenced by many other Ediacaran trace fossils (e.g., Jensen et al., 2005). Making an exploratory loop seems to be an appropriate behaviour in such situation. Larger *Circulichnis* seems to be more frequent in the lower Palaeozoic than in younger rocks (Fig. 5). The known continental occurrences of *Circulichnis* are so far no older than Carboniferous.

The wide environmental and stratigraphic range of *Circulichnis* results probably from necessity of exploration of different levels, mostly for food, which was invented very early in the history of burrowing, i.e. in the Ediacaran. This was a successful adaptation changing animal behaviour.

5. Conclusions

Circulichnis represents a distinct behaviour, i.e. exploration burrowing within different horizons in the sediment, presumably for feeding. In most cases, it was produced by the trace makers of *Helminthoidichnites*, *Gordia*, or *Helminthopsis*, probably by several taxa of polychaetes in marine sediments and oligochaetes in continental sediments. *Circulichnis montanus* is characterized by an evenly circular or elliptical ring. *C. ligusticus*, newly distinguished on the basis of material from Oligocene–Miocene turbiditic sediments of the Tertiary Piemonte Basin, NW Italy, shows a winding or irregular course and usually a relatively small size. Minor differences in morphology within this ichnospecies resulted from primary differences of burrow geometry or from preservational processes. The exploration behaviour recorded as *Circulichnis* appeared already during the Ediacaran and continued throughout the Phanerozoic. *Circulichnis* is most frequent in bedded deep-sea sediments.

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