Chapter 4

Palaeoichnology

Network theory demonstrated to be an extremely efficient tool in describing and analyzing modern ichnological systems, therefore a question might arise: is it applicable to the study of trace fossils (palaeoichnology)? This section aims to answer to this question by considering the Pramollo ichnolagerstätte (Carboniferous-Permian; sections 4.1, 4.2, 4.3) and the Nurra succession (Permian-Triassic; sections 4.4), both of which are characterized by a rich, diverse and well-preserved ichnological heritage. The aforementioned ichnosites allow to test the ichnonetwork method on a wide, fluvial-influenced environmental gradient comprising continental to fully marine terms.

In particular, this chapter aims to model the studied ichnological systems as ichnonetworks and, based on their topological patterns, reconstitute the palaeoenvironment of the studied ichnosites. This approach allows to consider the response of ichnological systems to global environmental dynamics and establish a connection between network topology, ecological space and the spatial structure of the environment. In this regard, an alternative approach – fractal analysis – is proposed in order to study the spatial structure of low-diversity ichnoassemblages (section 4.5).

Chapter index

Chapter 4

4.1 Architectures of behavioural complexity: ichnonetwork analysis of the Meledis and Pizzul Formations (Pramollo, Italy-Austria)

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Architectures of behavioural complexity: ichnonetwork analysis of the Meledis and Pizzul Formations (upper Carboniferous; Pramollo ichnolagerstätte, Italy-Austria)

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Abstract. Networks - sets of nodes and links - are efficient tools for describing and analyzing complex systems. This paper aims to describe theory and application of network theory for the study of fossil ichnological systems, illustrating basic concepts, graphical methods and quantitative techniques for analyzing ichnological networks (ichnonetworks). For this purpose, the Meledis and Pizzul Formations (upper Carboniferous; Italy-Austria) of the Pramollo ichnolagerstätte represent the ideal ground for applying ichnonetwork analysis because of their abundant, diverse and well-exposed ichnological heritage. According to the ichnonetwork approach, a given stratigraphical log is modelled as a network by representing trace fossil types (ichnotaxa) as nodes and association relationships as links. Based on a central *tenet* of ichnology – traces are manifestations of biological behaviour – ichnonetworks are behavioural networks and, for this reason, ichnonetwork analysis finds application in the study of ethology. For the same reason, ichnonetwork analysis is important for (palaeo)ecology, given that environmental parameters, such as hydrodynamics, oxygenation and sedimentation rate, have a crucial influence on biologic behaviour. In light of this perspective, ichnonetwork architecture is structured by environmental processes and, for this reason, its analysis allows palaeoenvironmental reconstitution. This approach is integrated with new theoretical insights provided by ichnonetwork analysis, which provides a new basis for the concepts of ichnoassociation, ichnoassemblage, ichnofacies and introduces the ideas of habitat and niche in ichnology. Based on these assumptions, the here considered upper Carboniferous ichnological system is investigated by network analysis, revealing the following major findings: (1) at a coarse scale, the palaeoenvironment was continuous; (2) at a fine scale, the palaeoenvironment was inhomogeneous, with different habitat types grading one into another; (3) specific ichnotaxa (i.e. *Cylindrichnus, Helminthoidichnites*) bridged different ecological domains; (4) ichnoassociations correspond to delta front and prodeltaic/open marine habitats; (5) a dysoxic episode, driven by tectonics, characterized the palaeoenvironmental evolution of the Pramollo ichnolagerstätte.

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1. Introduction

Networks – sets of nodes and links – are among the crucial tools for studying complex systems (Boccaletti *et al.* 2006). In fact, many natural, social and technological systems can be modelled as networks, which have been important in understanding the structure and dynamics of food webs, internet, circles of friends, among others (Boccaletti et al. 2006; Junker and Schreiber 2008).

The application of network theory to ethology is not new (Makagon *et al.* 2012), but only recent studies applied it to the study of traces, which indeed represent evidences of biologic behaviour (Seilacher 2007). In this regard, two major levels of scale have been inspected: (a) individual-trace level, according to which the morphology of a single burrow is modelled as a network; typical studies involve modern nests of social insects (Buhl *et al.* 2006; Perna *et al.* 2008) (b) ichnosite-level, according to which entire ichnological systems have been modelled as ichnonetworks – sets of individual traces linked by association relationships (Baucon and Felletti 2013; Baucon et al. 2014*a*, *b*).

The latter approach proved to be particularly efficient for reconstituting the palaeoenvironment, given that the environmental characteristics, such as hydrodynamics, oxygenation and sedimentation rate, have a crucial influence on biologic behaviour.

In light of these observations, ichnonetwork analysis is the focus of this paper, which primarily aims to illustrate methods and concepts of network theory for the study of trace fossils. For this purpose, the Pramollo ichnolagerstätte represents the ideal ground for applying ichnonetwork analysis because of its abundant, diverse and well-exposed ichnological heritage (Baucon and Carvalho 2008). In this context, the aim is to go from ichnological patterns to (palaeo)environmental processes – including both environmental factors and landscape structure. Finally, theory and application of ichnonetwork analysis encourage to consider the implication of network theory for the theoretical background of ichnology.

2. Geological setting

2.1. Pontebba Supergroup

The study area is located in the surroundings of the Pramollo Pass (Italy-Austria; Fig. 1). Here a

Permian-Carboniferous sequence known as to the Pontebba Supergroup (Moscovian p.p.-Artinskian p.p.) deposited within a narrow N120°E elongated trough, known as the Pramollo Basin (Venturini 1983, 1990*a*). The entire succession reaches a maximum thickness of 1500 m in the surroundings of the Pramollo Pass, whereas the minimum thickness (about 100 m) is found in the Monte Cavallo-Valbertad sector (Venturini 1990*b*).

The Pontebba Supergroup comprises siliciclastic and carbonatic facies, mostly indicating deltaic to shelfal environments (Venturini 1990*a*, *b*). From a stratigraphic perspective, the Pontebba Supergroup consists of a very basal unit (Bombaso Formation), which is unconformably overlying the Variscan Basement, and three major units (Venturini 2002): the lower Pramollo Group (P), the middle Rattendorf Group (R) and the upper Trogkofel Group (T; Fig. 2). At the group scale, carbonates increase in frequence and thickness from the base to the top, well-conforming with the documented timing of the Late Paleozoic glaciation (Roscher and Schneider 2006; Tabor and Poulsen 2008; Allen et al. 2011).

Since at least the middle 1900s, researchers noted the abundant and well-preserved ichnological heritage of the Pramollo Basin (Selli 1963; Venturini 2006), although only few studies dealt specifically with ichnology (Mietto et al. 1985; Barbiero et al. 1990; Conti et al. 1991*a*). Baucon and Carvalho (2008) provided the first general overview of the ichnosite and, in light of the preservation, diversity and abundance of trace fossils, established Pramollo as an ichnolagerstätte. More recently, Baucon, Venturini, et al. (2013) applied network analysis to the Val Dolce Formation of the Rattendorf Group, therefore there is the need of using the same approach to the lower units of the Supergroup. Hence, this study focuses on the Pramollo Group and, in particular, to the Meledis-Pizzul Formations.

2.2. Pramollo Group

The basal unit of the Supergroup is represented by siliciclastic sediments with radiolaritic, arenitic, volcanic clasts and limestone pebbles (Bombaso Formation; upper Moscovian). Progressive intercalation of quartz-rich conglomerates marks the transition with the Pramollo Group, suggesting that the source area shifted towards western metamorphic reliefs (Fenninger and Stategger 1977; Fontana and Venturini 1982). The Pramollo Group is represented by conglomerates, sandstones, pelites and limestones (Tab. 1), mostly corresponding to fluvio-deltaic and shelfal settings. It is stratigraphically subdivided into five units on the basis of the frequency of limestone layers: Meledis, Pizzul, Corona, Auernig and Carnizza Formations. According to fusulinid biostratigraphy, the upper part of the group is accompanied by the increase in sedimentation rate, shifting from about 50 mm/10^3 y (Meledis Fm-lower Pizzul Fm.) to about 800 mm /10^3 y (upper Pizzul Formation- Carnizza Formation; Venturini, 1983, 1990a, 2006).

This study focuses on the first, low-sedimentation interval and, in particular, to the Meledis and Pizzul Formations.

2.3. Meledis and Pizzul Formations

Overall, the Meledis and Pizzul Formations comprise predominantly terrigenous sediments with less common carbonatic bodies. In the prevailing view, these units collectively represent marine and fluvio-deltaic environments (Venturini, 1990a, 1990b, and references therein).

More specifically, the Meledis Formation (Upper Moskovian – Lower Kasimovian) is dominated by arenitic and pelitic facies (facies S4 and P1; Tab. 1; Fig. 3A, B) and rarer dolomitic algal limestones (facies L1), which are corresponding to quiet offshore environments (Venturini 1990*b*). Higher-energy processes are represented by tempestitic and turbiditic deposits (facies S5, S6) , while slumped horizons (facies L4) are locally found. Quartz-conglomerates and planar-bedded sandstones (facies C1, S3) are rarer.

The overlying Pizzul Formation (Kasimovian – upper Ghzelian) is predominantly represented by pelites with abundant plant fragments (facies P1; Tab. 1; Fig. 3C, D). Locally, decimetric sandstone layers (facies S7) are interbedded within the pelitic intervals; in light of their sedimentary structures (flute casts, parallel lamination), they are likely to represent turbiditic deposition. Quartz-rich conglomerates (facies C1), interpreted as fluvio-deltaic environments, are especially common in the middle-upper parts of the Pizzul Formation, as well as limestone bodies (facies L1 and L3).

The Meledis Formation is distributed at the scale of the entire basin, while the Pizzul Formation is mostly lacking from the central area of the basin (Monte Cavallo-Valbertad). This aspect suggests a tectonic uplift which has precluded deposition on the central sector since the Lower Ghzelian

(Venturini 1983, 1990*b*). This hypothesis is supported by a breccia horizon ('Malinfier Horizon') formed by reworked limestone clasts deriving from the Devonian-Lower Caroniferous basement (Venturini 1983, 1990*a*). For this reasons, during the Lower Ghzelian, the Pramollo Basin was divided into two subsiding sectors divided by a central horst (Venturini 1990*a*). This tectonic pulse was anticipated by minor erosional episodes, mostly developed on the immediate surroundings of the uplifting horst (Venturini 1990*b*).

The Meledis and Pizzul Formations are well-exposed in the surroundings of the Pramollo and Val Dolce areas (Venturini 1990*a*, *b*, 1991), which have been thoroughly explored in this study (Fig. 1). In particular, an unnamed stream near Casera For, located in the surroundings of the Pramollo Pass, has been selected for network analysis, since it preserves the transition between the Meledis and Pizzul Formations. The stream is here referred as 'Rio Romanino' (Fig. 1), named after the fossil researcher Romanino Azzola who has explored the area since the 1970s; it corresponds to the 'stream SW of Casera For' informally indicated in Baucon and Carvalho (2008).

3. Method

In analogy with ecological network analysis (Jordán and Scheuring 2004) ichnonetwork analysis aims to provide insight on how ichnodiversity is structured, highlighting prominent ichnotaxa, organization patterns and their environmental significance. In order to model an ichnological system as a network, the fundamental step is to describe a traditional stratigraphical log of the succession to be studied, along which presence/absence of each ichnotaxon is noted (Fig. 4). The idea is to represent ichnotaxa as nodes, and connect with a link those that are co-occurring; links can be weighted based on the strength of the association relationships (Baucon and Felletti, 2013; Baucon, Ronchi, et al., 2013).

The aforementioned process can be conveniently performed by digital tools in three steps (Fig. 5):

1. *Spreadsheet recording.* The first step is to digitally store the stratigraphical log to be analyzed, which represents the source data of the ichnonetwork. For this purpose, the stratigraphical log has to be recorded as a spreadsheet in which rows correspond to stratigraphic units (i.e. layers) and columns to ichnotaxa; accordingly, each cell stores presence/absence of each ichnotaxon. In this paper, the sampling unit is the bedset, intended

as a set of beds with uniform ichnological and sedimentological features (similarly to Reineck and Singh, 1986). It should be noted that intensity of bioturbation, recorded semiquantitatively and referred to the bedding plane bioturbation index (BPBI; Miller and Smail, 1997; Fig. 4), is not recorded in the ichnonetwork.

2. *Calculation of the adjacency matrix.* The ichnological information stored in the spreadsheet allows to derive ichnotaxon-vs-ichnotaxon relationships, to be recorded as a matrix in which there is a row and a column for each ichnotaxon (adjacency matrix; see Wassermann and Faust, 1994). Each cell of the adjacency matrix records whether two ichnotaxa are associated or not, that is, in network terms, whether two nodes are linked or not (Wassermann and Faust 1994). The adjacency matrix can be binary (i.e. entries record presence/absence of a link) or valued (i.e. entries record presence/absence of a link and its strength). In this study, association strength is quantified by the Jaccard index (Jaccard 1901, 1912; Hammer and Harper 2006), which measures the probability of finding two co-occurring ichnotaxa if at least one of them is present in the sample (Baucon and Felletti 2013).

3. *Network visualization.* The adjacency matrix contains exactly the same information as a network, therefore it can be rendered graphically by graph visualization software.

4. Trace fossils of the Meledis and Pizzul Formations

This section documents the results of the ichnological survey of the study area, reporting the major trace fossil types (ichnotaxa) of the Meledis and Pizzul Formations. Overall the Meledis and Pizzul Formations are characterized by a mixture of vertical (i.e. *Cylindrichnus*), horizontal (i.e. *Curvolithus*) and spreite (i.e. *Zoophycos*) structures (Fig. 6). With few exceptions, the ichnotaxa of the Meledis and Pizzul Formations have already been discussed in detail in the previous ichnological review of the Pramollo ichnolagerstätte (Baucon and Carvalho 2008). For this reason, ichnotaxa are concisely reported in Tab. 2, while the reader is addressed to Baucon and Carvalho (2008) for a more comprehensive taxonomical and ethological discussion on individual ichnotaxa.

5. Ichnonetwork analysis

The ichnological data of the studied stratigraphical section are represented as a network by mapping ichnotaxa as nodes and association relationships as links (Fig. 7), following the previously described procedure (chapter 5). Consequently, the studied ichnological system can be explored by concepts, graphical techniques and metrics proper of network analysis.

In the following sections, each concept, graphical technique and metric is first described under a graph-theoretical perspective (‘description’), then its ichnological significance is presented (‘ichnological significance’). Similar terms (‘synonyms’) and subject-specific observations (‘remarks’) are optionally reported. If applicable, level of ichnological analysis is expressed by the terms ichnotaxon-level (i.e. concerning individual trace fossil types), ichnoassociation-level (i.e. focusing on groups of ichnotaxa) and ichnosite-level (i.e. concerning the whole ichnological system). Finally, application to the studied network is synthetically presented and commented in the ‘results’ subsection; quantitative results are thoroughly listed in Tab. 3, Tab. 4,

5.1. Basic network concepts

This section describes the key notions of network theory, forming the conceptual basis for the following metrics and graphical techniques. The reader is addressed to previous works (Wassermann and Faust 1994; Réka and Barbási 2002; Boccaletti et al. 2006; Fortunato 2010) for a detailed mathematical treatment of network theory.

5.1.1. Network

Description. A network consists of two sets of information: a set of nodes and a set of links between pair of nodes (Wassermann and Faust 1994). Such information can be represented in a graphical manner or, alternatively, in a matrical form (Wassermann and Faust 1994; Boccaletti et al. 2006).

Synonyms. Formally, a complex network can be represented as a graph (Boccaletti *et al.* 2006), but these terms are often used interchangeably (i.e. Newman, 2011).

Remarks. Networks are abstractions of real-world systems, therefore several representation rules are available for depicting a given system. The representation norms for depicting an ichnological system as an ichnological network (ichnonetwork) are the following: (a) links have no orientation (undirected network) (b) a number is associated to each link (weighted network) (c) there are no loops (i.e. a node cannot be linked with itself) (d) a pair of nodes can be connected by no more than one line. In light of these features, ichnonetworks are simple graphs as defined by Wassermann and Faust (1994).

Ichnological significance. Network represents the whole ichnological system.

Level of analysis. Ichnosite- to ichnotaxon-level.

Results. .The network of the studied stratigraphical section is shown in Fig. 7.

5.1.2. Node

Description. Nodes are the fundamental units of a network, representing the objects to be studied. They are commonly represented as circles.

Remarks. Location of nodes on the page has no meaning (Wassermann and Faust 1994).

Synonyms. Vertex, point (Boccaletti *et al.* 2006).

Ichnological significance. Ichnotaxon.

Level of analysis. Ichnotaxon-level.

5.1.3. Link

Description. Links are fundamental constituents of a network as they establish relationships between nodes or, more formally, they can be seen as pairs of nodes (Boccaletti *et al.* 2006).

Remarks. When visualizing a network, link length has no meaning (Wassermann and Faust 1994). In the studied ichnonetwork, links are weighted according to the intensity of the association relationship, which is visualized as edge thickness (e.g. Fig. 7).

Synonyms. Edge, line (Boccaletti *et al.* 2006).

Ichnological significance. In parallel to Wassermann and Faust (1994), a link with two nodes indicates that the corresponding ichnotaxa are found in the same layer. For this reason, a link represents the association relationship between two ichnotaxa and its intensity.

Level of analysis. Pairs of ichnotaxa.

5.1.4. Number of nodes

Description. This aspect quantifies the total number of nodes of a given network.

Ichnological significance. Since nodes correspond to ichnotaxa, the number of nodes correspond to the number of different ichnotaxa, that is, ichnodiversity (*sensu* Bromley, 1996; Buatois and Mángano, 2011).

Level of analysis. Ichnosite-level.

Results. The studied network consists of 10 nodes, implying a moderate ichnodiversity.

5.2. Graphical techniques

A common approach to network analysis is to graphically represent the information stored in a matrical form. In fact, graphical visualization of networks makes it easier to analyze the data than if they were viewed in a matrical form, possibly revealing internal relationships and structures that were otherwise hidden (Purchase 2000).

In this regard, it should be highlighted that the network visualization displays the same information stored in the corresponding adjacency matrix, therefore the two representations are equivalent. In parallel to the matrical representation, relational data are the crucial information, hence link length and position of nodes on the page have no meaning, while aspect of nodes and links does not influence the relational data. For this reason, these attributes can be manipulated to better explore the network under study. In particular, four classes of graphical tools are of particular interest for ichnological purposes, being therefore the focus of this section: node aspect, link aspect, filtering and layout.

5.2.1. Node aspect tools.

Description. Graphical aspect of nodes can be changed to highlight structural properties or relationship features (Makagon *et al.* 2012). In this regard, each node can be sized according to its topological position; groups of nodes can be highlighted by colour; node shape can indicate special nodes.

Level of analysis. Ichnotaxon-level.

Results. In order to analyze the studied ichnosite, it is important to determine the role played by individual ichnotaxa and how they are embedded in the whole system. Consequently, in this paper, node sizing and colouring is used to emphasize the topological properties of individual ichnotaxa. For instance, nodes can be sized and coloured according to the number of incident links to them (node degree; Fig. 8), thus highlighting the tendency to associate with other ichnotaxa. In the analysis of the Rio Romanino ichnonetwork, node sizing and colouring are widely used in the visualization of other quantitative properties (section 5.3).

5.2.2. Link aspect tools.

Description. The relationships between node pairs are expressed by links, therefore relational properties can be evidenced by changing line thickness and colour.

Level of analysis. Pairs of ichnotaxa.

Results. In the graphical rendering of the studied ichnonetwork, line width is used to represent link weight, following the conventions of network visualization (Makagon *et al.* 2012). This allows to visually detect strong ties, such as those existing between *Ancorichnus* and *Beaconites, Beaconites and Curvolithus* (Fig. 7). For the same aim, link colouring can be used in parallel to link sizing. This allows to note other strong links, such as the ones connecting *Palaeophycus* and *Cylindrichnus, Archaeonassa* and *Ancorichnus* (Fig. 8B).

Interpretation of these observations derives from the ichnological nature of links (section 5.1.3): nodes connected by strong ties are ichnotaxa with intense association relationships.

5.2.3. Filtering

Description. Networks are often graphically intricate, therefore data exploration can be facilitated by focusing on subsets of nodes and/or links. In other words, data can be filtered in order to highlight structural features of interest, such as high-weight links or ego networks, that are subnetworks consisting of a given node and the nodes directly linked with it. Similarly, attention can be focused on given behavioural properties, such as deposit-feeding ichnotaxa.

Level of analysis. Ichnosite- to ichnotaxon-level.

Results. Filtering is a useful tool to explore the Rio Romanino ichnonetwork. For instance, intense association relationships are highlighted by filtering out links with weight inferior than network average (Fig. 9A). Similarly, the ego network of *Zoophycos* shows that the traces associated to *Zoophycos* are associated to each other (Fig. 9B).

5.2.4. Layout tools

Description. Network layout - intended as the mapping of the nodes and edges into the plane (Fleischer and Hirsch 2001) - can be adjusted in order to better visualize relational data. For this purpose, nodes can be positioned manually or, alternatively, network layout algorithms can be applied for automatically positioning nodes on the page (Huang *et al.* 2013). Four groups of automatic layouts are of particular interest for ichnological studies:

- Random layouts position nodes at random (Fig. 10A).
- Geometric layouts distribute nodes according to a fixed geometric shape. For instance, circular layout algorithm positions nodes on the perimeter of a circle (Fig. 7).
- Dimensionality reduction layouts aims to project the data stored into the adjacency matrix onto lower-dimensional spaces. In this regard, multidimensional scaling algorithms are widely used in network drawing, aiming to spatially represent the similarity between nodes (Wassermann and Faust 1994). The idea is to position the nodes so that the higher the degree of association, the closer the distance between nodes, and vice versa (Baucon and Felletti 2013) (Fig. 10B).
- Force-directed methods interpret a network as a physical system with forces between the nodes, then trying to minimize the energy of the system (Fleischer and Hirsch 2001). The algorithm of Fruchterman and Reingold (1991) models the network as a system of springs between linked nodes, while repulsive electrical forces push all the nodes away (Hu 2005) (Fig. 10C). A similar approach is followed by the algorithm of Hu (2005), combining a multilevel method with an octree technique (Fig. 10D).

Level of analysis. Ichnosite.

Results. Application of different layout algorithms results in very different visualizations of the Rio Romanino ichnonetwork (Fig. 7, Fig. 10). Despite the contrasting visual appearance, these visualizations are topologically equivalent because they represent the same relational data. In this context, application of random layout (Fig. 10A) favours an unbiased observation of the ichnonetwork, although its readability is difficult. In fact, random positioning could result in node overlapping, as shown by the nodes *Zoophycos* and *Cylindrichnus* in Fig. 10A.

On the other hand, circular layout (Fig. 7) prevents node overlapping and facilitates unbiased observation of the network, but it does not emphasize the topological properties of individual nodes nor their organization. In contrast, multidimensional scaling (Fig. 10B) distributes nodes according to their association relationships, therefore it reflects the structural organization of the studied system. In fact, nodes (ichnotaxa) are positioned so that the higher the degree of association, the closer the distance between nodes (Baucon and Felletti 2013). According to this approach, *Zoophycos, Nereites* and *Palaeophycus* are distant from *Ancorichnus, Beaconites, Planolites* and *Archaeonassa*, implying that these groups of traces are environmentally separated. A similar interpretation is suggested by the application of the Hu (2005) layout, showing the same structural domains (Fig. 10D). The interpretation of the Fruchterman and Reingold (1991) layout is more difficult, as most nodes are placed onto the perimeter of a circle (Fig. 10C).

In sum, analysis of the studied network shows a coarse-grained organization in two groups of traces, but further analysis has to be performed to move to finer level of details.

5.3. Quantitative techniques

In agreement with Wassermann and Faust (1994), network theory offers numerous metrics and techniques to characterize topological properties of networks. Three major properties, thoroughly described by previous authors (Wassermann and Faust 1994; Fortunato 2010; Makagon et al. 2012), are of particular interest for ichnological analysis:

1. Prominence refers to the existence of ‘important’ nodes within the network (Wassermann and Faust 1994; Makagon et al. 2012);
2. Range refers to the extent of the network (Makagon *et al.* 2012);
3. Cohesion focus on the grouping of nodes according to strong common relationships (Makagon *et al.* 2012). Following Makagon et al., 2012, the notion of community structure, dealing with the organization of nodes in modules (Fortunato 2010), is a related concept.

Prominence, range and cohesion can be characterized by specific metrics and techniques, which are the focus of this section. It should be noted that most of the metrics of and techniques of this section are unweighted, i.e. association intensity is not taken into account.

5.3.1. Measures of prominence

5.3.1.1. Node degree

Description. The degree of a node is the number of links incident with the node, therefore it can be seen also as the number of nodes linked with it (Boccaletti *et al.* 2006).

Ichnological significance. In ichnological terms, degree quantifies the number of ichnotaxa associated to a given one, therefore it measures the 'associatedness' of a given ichnotaxon. It should be noted that nodes with degree=0 correspond to strictly monoichnospecific ichnotaxa, being never associated with others.

Level of analysis. Ichnotaxon-level.

Results. Helmithoidichnites presents the highest degree of the network (Fig. 11), being associated to 9 other ichnotaxa (degree=9) . On the other hand, *Zoophycos* and *Palaeophycus* show the lowest degree, being linked to 3 nodes (degree=3).

5.3.1.2. Node betweenness

Description. Node betweenness indicates 'how between' a node is by considering the shortest paths passing through a given node (Wassermann and Faust 1994). More precisely, betweenness of a node is the total number of shortest paths in the graph divided by the number of shortest paths passing through a node (Boccaletti *et al.* 2006).

Ichnological significance. Environment-crossing. High betweenness nodes lie between many others, connecting distinct structural areas of the network. For this reason, high-betweeness ichnotaxa act as bridges among distinct structural units of the ichnological system. Thus, 'bridge ichnotaxa' are likely to occur in different environmental contexts, being poor environmental indicators (Baucon and Felletti 2013).

Level of analysis. Ichnotaxon-level, although node betweenness depends on the global connection pattern.

Results. The studied network is characterized by four nodes with high betweenness, *Helminthoidichnites, Cylindrichnus, Nereites* and *Curvolithus* (Fig. 11). These high-betweeness ichnotaxa are bridges connecting different structural units, being therefore poor environmental indicators. This result well conforms with the application of multidimensional scaling and Hu layouts (Fig. 10B, C), which place these ichnotaxa between the others. On the other hand, *Zoophycos, Planolites* and *Palaeophycus* are characterized by betweenness=0, implying that they are restricted to specific structural areas of the network and, therefore, they are environment-specific.

5.3.2. Measures of range

5.3.2.1. Distance

Description. The distance between two nodes is the minimum number of links that must be traversed to get from one node to the other (Humphries and Gurney 2008) (Fig. 13A). More specifically, distance is the length of the shortest path (geodesic) between two nodes, given that the length of a path is the number of links in it (Wassermann and Faust 1994).

Synonyms. Geodesic distance (Wassermann and Faust 1994).

Remarks. Two nodes are said to be adjacent or neighbouring if they are connected by a link (distance=1); the set of nodes with distance=1 from a given node is known as its neighbourhood (Wassermann and Faust 1994; Humphries and Gurney 2008).

Ichnological significance. Distance measures the degrees of separation between nodes, hence it quantifies the environmental incompatibility between ichnotaxa.

Level of analysis. Pairs of ichnotaxa.

Results. A visual inspection of the studied ichnonetwork reveals directly connected nodes (distance=1) and nodes separated by two links (distance=2):

- Distance=1 indicates that the given nodes are separated by only one link, implying that the corresponding ichnotaxa are environmentally compatible. This is the case of *Archaeonassa* and *Ancorichnus*, *Nereites* and *Zoophycos,* among others.

- Distance=2 suggests environmentally incompatible ichnotaxa, since they are indirectly linked through a common node. This is the case of *Nereites* and *Ancorichnus, Curvolithus* and *Planolites*, among others.

Tab. 4 shows distance for each pair of nodes, including the trivial case distance=0 (that is, the distance from a node to itself).

5.3.2.2. Node eccentricity

Diameter. The eccentricity of a node is the largest distance between that node and any other node (Wassermann and Faust 1994).

Synonyms. Association number (Wassermann and Faust 1994).

Remarks. If a node is directly connected (adjacent) to all other nodes, its eccentricity is minimum (eccentricity=1; Wassermann and Faust, 1994).

Ichnological significance. Eccentricity summarizes how far a node is from the node most distant from it (Wassermann and Faust 1994), therefore it indicates the degree of incompatibility with the most environmentally incompatible ichnotaxon.

Level of analysis. Ichnotaxon-level.

Results. With the exception of *Helminthoidichites,* nodes have an eccentricity equal to 2.

5.3.2.3. Diameter

Description. Diameter is the largest distance between any pair of nodes in a network, that is, the largest node eccentricity (Wassermann and Faust 1994).

Remarks. If all possible links are present (complete network), the diameter is minimum (diameter=1) as all pairs of nodes are directly connected (Wassermann and Faust 1994).

Ichnological significance. Diameter indicates how far are the farthest nodes in the network, hence it indicates the maximum ichnological incompatibility in the system.

Level of analysis. Ichnosite-level.

Results. The diameter of the studied ichnonetwork is 2, therefore the most environmentally incompatible ichnotaxa are separated by an intermediary ichnotaxon.

5.3.3. Measures of cohesion

5.3.3.1. Density

Description. The number of nodes determines the maximum possible number of links (Wassermann and Faust 1994), therefore the completeness of a network is a measurable parameter. Density is the ratio of the number of links present to the maximum possible (Wassermann and Faust 1994).

Remarks. The density of a network ranges from 0 (no links are present) to 1 if all possible links are present (Wassermann and Faust 1994). In the second case, a network is said to be complete: density is maximum and each node is connected to all others (Wassermann and Faust 1994).

Ichnological significance. Together with link weights, diameter and average clustering coefficient, ichnonetwork density is dependent from environmental uniformity. In fact, the traces of a uniform environment are expected to form a complete ichnonetwork because they are mutually associated. However, complete ichnonetworks are not necessarily corresponding to uniform environments, especially if link weights are uneven (Baucon et al. 2014*a*).

Level of analysis. Ichnological system.

Results. The density of the Rio Romanino ichnonetwork is 0.644, implying that the 64.4% of the possible links are present.

5.3.3.2. Clustering coefficient

Description. Clustering coefficient measures the degree to which nodes tend to cluster together by considering if the nodes connected with a given one are also connected to each other (Wassermann and Faust 1994). More precisely, the clustering coefficient of a node is quantified as the number of links between the neighbours of a node divided by the maximum number of connections (Bhadra *et al.* 2009).

Remarks. Clustering coefficient quantifies the density of connections between the direct neighbours of a node, reaching the maximum value of 1 when all the neighbours of a node are connected to each other (Bhadra *et al.* 2009).

Ichnological significance. In parallel to Bhadra et al., (2009), clustering coefficient measures the density of connections between the traces associated to a given one. For this reason, high-clustering ichnotaxa (core ichnotaxa *sensu* Baucon and Felletti, 2013) occupy central positions in ichnoassociations and have few association relationships towards other groups of traces

Level of analysis. Ichnotaxon-level.

Results. In the studied network, *Planolites, Palaeophycus* and *Zoophycos* present the maximum clustering coefficient and consequently they lie at the core of a group of co-occurring traces (Fig. 14). This topological feature can be also highlighted by producing ego-centered networks through filtering: for instance, all the nodes linked to *Zoophycos* are linked to each other (Fig. 9B). In contrast, the lowest clustering coefficient corresponds to *Helminthoidichnites.*

5.3.4. Community structure

Many real-world networks are not regular, but they are objects where order coexists with disorder (Fortunato 2010). In fact, network structure is commonly organized in groups of tightly connected nodes forming dense subnetworks within a larger network (Newman and Girvan 2004; Fortunato 2010; Newman 2011). This topological feature is known as community structure, the knowledge of which is of crucial importance because it characterizes the large-scale structure of the network under study (Fortunato 2010; Newman 2011).

Communities are best understood as groups of densely interconnected nodes, and low concentrations of links between these groups; hence, their constituting elements are likely to share common properties (Fortunato 2010). In ichnological terms, communities are ichnoassociations and the shared property is the environmental range (Baucon and Felletti 2013; Baucon et al. 2014*a*).

The idea of community is intuitive, but many methods exist for their detection (Newman and Girvan 2004; Boccaletti et al. 2006; Fortunato and Barthélemy 2007; Fortunato 2010; Coscia et al. 2011; Newman 2011). The concepts and algorithms presented in the following sections have been selected for their immediate ichnological application.

5.3.4.1. Component

Description. A component of a network is a maximal connected subnetwork (Wassermann and

Faust 1994; Scott 2000) (Fig. 13B).More specifically, it is a maximal entity because a component may not be included in another component; it is connected, because all pairs of nodes are reachable through a continuous chain of links. Consequently, a component can also be seen as a group of nodes in which there is a link between all pair of nodes and there is no link directed outside from the component (Wassermann and Faust 1994).

Remarks. A network with a single component is said to be connected, while a network with multiple components is said to be disconnected (Wassermann and Faust 1994; Scott 2000).

Ichnological significance. A component is a coherent group of nodes, but it is less restrictive than other community concepts (i.e. cliques). For this reason, a component is an ichnoassociation but at a very coarse scale. In addition, the degree of habitat fragmentation is measured by the number of components of the network. In fact, nodes are ichnotaxa, each of which has a specific environmental range, therefore a single-component network reflects a continuous environmental scenario. In contrast, disconnected networks suggest abrupt variations in environmental properties, typical of a fragmented environment.

Level of analysis. Ichnoassociation-level.

Results. Given its coarse-grained resolution, the concept of component is useful in delineating the gross organization of the Rio Romanino network but, for the same reason, it fails to detect fine association patterns. In this regard, the studied network is constituted by a single component, therefore it represents a continuous environment rather than a fragmented one.

5.3.4.2. Clique

Description. A clique is a maximal complete subnetwork (Scott 2000) (Fig. 13C). More specifically, it is maximal because a clique should not be contained in another clique; it is complete, because its link density is maximum. In other words, a clique is a subset of nodes all of which are connected to each other, and such that no other nodes are connected to all of them (Boccaletti *et al.* 2006).

In light of these features, the concept of clique is the simplest definition of community but also the most restrictive one (Boccaletti et al. 2006; Yan and Gregory 2009).

Remarks. The aforementioned definition conforms with the commonest usage in network analysis, according to which a clique is a maximal concept; in graph theory, cliques can be also non-maximal (Evans 2010). In addition, in ichnological studies, the recommendation of Wassermann and Faust (1994) can be relaxed so that cliques can be also composed of node pairs.

Ichnological significance. Ichnoassociation. The concept of clique requires that all pairs of clique members are linked to each other (Boccaletti *et al.* 2006), therefore it corresponds to the idea of ichnoassociation at a finer scale than the concept of component. In fact, while a component is maximal and connected, a clique is maximal and complete (Scott 2000).

Level of analysis. Ichnoassociation-level.

Results. The studied ichnonetwork consists of the following cliques (Fig. 15):

1. *Ancorichnus Archaeonassa Beaconites Cylindrichnus Helminthoidichnites Planolites*
2. *Ancorichnus Beaconites Curvolithus Cylindrichnus Helminthoidichnites*
3. *Archaeonassa Cylindrichnus Helminthoidichnites Nereites*
4. *Curvolithus Cylindrichnus Helminthoidichnites Nereites*
5. *Cylindrichnus Helminthoidichnites Nereites Palaeophycus*
6. *Curvolithus Helminthoidichnites Nereites Zoophycos*

This results show the methodological advantages of the concept of clique. First, it allows to detect overlapping communities, in which a node can belong to more than one community (Coscia *et al.* 2011; Newman 2011). For instance, *Cylindrichnus* and *Helminthoidichnites* are shared among several associations. Second, the logical properties of a clique are of immediate interpretation: clique members are associated each to the other. This allows a meaningful interpretation of the corresponding ichnoassociations.

Nevertheless, the application of clique-finding on the studied network reveals also its shortcomings. In fact, the studied network consists of several small, largely overlapping cliques. This feature, well-known by network analysts (Wassermann and Faust 1994; Yan and Gregory 2009), makes the interpretation of the corresponding ichnoassociations difficult. This shortcoming derives from the strictness of the clique concept: the absence of a single link will prevent a subnetwork from being a clique, therefore a dense network is likely to consist of many overlapping cliques (Wassermann and Faust 1994; Yan and Gregory 2009). On the other hand, the concept of clique ignores link weight, therefore it does not picture the intensity of co-occurrence relationships between ichnotaxa. Consequently, a pair of ichnotaxa may be included in the same clique even if they are loosely associated.

5.3.4.3. Modularity optimization

Description. The problem of community detection requires the partition of a network into communities of tightly knit nodes (Blondel *et al.* 2008) and modularity is a quantitative criterion to assess the goodness of individual graph partitions (Fortunato 2010). Specifically, the modularity of a partition measures the density of links inside communities as compared to links between communities (Blondel *et al.* 2008). For this reason, modularity has been used to evaluate the quality of the partitions obtained by different methods, but also to find communities through its optimization (Blondel *et al.* 2008; Fortunato 2010).

Ichnological significance. Ichnoassociation.

Level of analysis. Ichnoassociation-level.

Results. Modularity optimization reveals two communities in the Rio Romanino ichnonetwork:

- *Curvolithus, Helminthoidichnites, Ancorichnus, Beaconites, Archaeonassa, Planolites*
- *Zoophycos, Nereites, Palaeophycus, Cylindrichnus*

From a methodological perspective, modularity optimization has the advantage of considering edge weights in the community-finding process, but it does not find overlapping communities. In addition, small modules may not be resolved through modularity optimization (Fortunato and Barthélemy 2007).

*5.3.4.4. Infomap***.**

Description. The Infomap algorithm is based on finding an efficient description of how information flows (Rosvall and Bergstrom 2008). A random walk is adopted to model the process of information diffusion, aiming to find the subnetworks that minimize the length of its description (Yang *et al.* 2013). This approach is similar to the process of designing a geographical map, as it attempts to simplify the structure of a network by describing groups of well-connected nodes as single, well-connected modules (Rosvall and Bergstrom 2008).

Ichnological significance. Ichnoassociation.

Level of analysis. Ichnoassociation-level.

Results. Application of the Infomap method on the studied network does not reveal community structure. This result is surprising not only for the efficiency of the algorithm (Fortunato 2010), but also because Infomap already found successful application in ichnology (Baucon and Felletti 2013). This result could be explained by the moderate link density of the studied network, together with its small diameter and few nodes. In fact, Infomap revealed to be sensitive to the number of inter-community links (Tibély 2012)

6. Discussion

Ichnonetwork analysis aims to answer one of the fundamental questions of ecology: "What are the processes responsible for existing patterns?" (Wu 2008). In fact, in ichnological terms, patterns are embedded in the ichnonetwork, whereas the processes are the environmental factors which structured the palaeoenvironment, being rensponsible for the existing topological patterns. In light of this philosophy, this section discusses the pattern-process relationships of the Rio Romanino ichnonetwork, aiming to reconstitute the environmental factors (section 6.1) and the structure (section 6.2) of the palaeoenvironment, as evidenced by the topological patterns of the ichnonetwork. Such analysis allows to consider the evolution of the environment in time (section 6.3) and to tackle the nomenclature of trace fossil groups (section 6.4).

6.1. Ichnonetwork analysis

Concepts, graphical techniques and topological measures account for three major domains of scale, each of which is considered in the following subsections.

6.1.1. Ichnosite-level

At the ichnosite level, the studied ichnonetwork is represented by 10 nodes and 29 links, corresponding to a moderate ichnodiversity. Since only the 64.4% of the maximum possible number of links is present (network density=0.644), a question might arise: how is ichnodiversity structured?

This question may be approached by considering the number of connected components. In this regard, the studied network is constituted by a single connected component, therefore traces are organized as a continuous chain of association relationships. This suggests that the environment was continuous: if the environment had been fragmented, several, disconnected subnetworks would have been expected. In this regard, the continuous palaeoenvironment delineated by coarse-scale network architecture might have been:

1. uniform, with environmental variables constant in space;
2. non-uniform, with environmental variables gradually changing in space.

The presence of high-betweenness ichnotaxa (bridge ichnotaxa) supports the second hypothesis, as the existence of bridges requires the presence of different structural areas in the ichnonetwork. In fact, an inhomogeneous association pattern indicates that groups of traces associated preferentially, mirroring a non-uniform distribution of environmental parameters. Network inhomogeneity can be identified by considering the degree distribution (Solé and Valverde 2004), which characterizes the probability that a node chosen uniformly at random has a given degree (Boccaletti *et al.* 2006). However, the studied network is characterized by a very small number of nodes, therefore inhomogeneity is here tested by comparing the studied network with known models of homogeneous networks. In this regard, homogeneity in the interaction structure means that almost all nodes are topologically equivalent, like in regular lattices or in random graphs (Boccaletti *et al.* 2006). In regular networks, each node is connected to the same number of nodes, for which reason both average clustering coefficient and average distance are high (Bhadra *et al.* 2009). In contrast, some nodes of the studied network (i.e. *Helminthoidichnites, Cylindrichnus*) are connected to a large number of nodes, being characterized by high degrees, while other nodes present a relatively low degree (i.e. *Zoophycos*, *Palaeophycus*). In parallel, the average clustering coefficient of the studied network is high (0.8) but the average path length is low (0.1356). Consequently, the nodes of the studied network tend to cluster together (like in a regular mesh) but, similarly to a random network, there are shortcuts between different regions of the network. Consequently, the studied network is inhomogeneous as it falls between regular and random networks, being suggestive of the 'small-world model' (Watts and Strogatz 1998). Following Humphries and Gurney (2008), a network is a small world if it has a similar path length but greater clustering of nodes than an equivalent random network with the same number of nodes and links. For this reason, the small-world-ness of the studied network can be measured by comparing the studied network to a random network, leading to the small-world-ness index (Humphries and Gurney 2008). The studied network present a significant small-worldness index (2.5), therefore is not regular like a mesh nor disordered like a random network: paraphrasing Boccaletti et al., (2006) it is an object where order coexists with disorder.

6.1.2. Ichnoassociation-level

The distribution of links in the studied ichnonetwork is locally inhomogeneous. In fact, as shown by many real-world networks (Boccaletti *et al.* 2006), it presents high concentrations of links within special groups of nodes, and low concentrations between these groups. In other words, the network is characterized by community structure. Network communities are, in ichnological terms, ichnoassociations, which are of crucial interest for reconstituting the palaeoenvironment because, in parallel to species associations (Legendre 2005), they provide a conceptual framework to synthesize environmental characteristics. In fact, groups of ichnotaxa are usually more sensitive environmental indicators than individual ichnotaxa (Buatois and Mángano 2011). Consequently, following the approach of Legendre (2005) the idea is to detect ichnoassociations first and then find the ecological requirements common to most or all members of an ichnoassociation instead of having to consider each ichnotaxon individually.

At a very coarse scale, the ichnonetwork is constituted by a single connected component, representing a macro-ichnoassociation. It is characterized by dominance of horizontal traces (i.e. *Nereites, Curvolithus, Helminthoidichnites*), subordinate presence of vertical ones (*Cylindrichnus*), predominance of deposit feeding structures produced by mobile fauna (i.e. *Nereites, Helminthoidichnites*), locally high bioturbation intensity. These features are corresponding to the Cruziana ichnofacies, which is reflecting accumulation of organic detritus in the sediment under moderate- to low-energy hydrodynamics (Buatois and Mángano 2011). Suspension-feeding structures are virtually absent, suggesting (a) paucity of suspended food resources, precluding suspension-feeding or (b) significant turbidity, unsuitable for suspension-feeding strategies (MacEachern *et al.* 2005). Overall, ichnofaunal composition is compatible with those of other Permo-Carboniferous deltas (Chakraborty and Bhattacharya 2005). A finer scale of analysis is needed to provide a more detailed palaeoenvironmental interpretation. In this regard, the network texture is locally inhomogeneous, revealing a modular organization at a finer scale. In fact, modularity optimization algorithm (Blondel *et al.* 2008) revealed two communities in the studied ichnonetwork:

- *Curvolithus, Helminthoidichnites, Ancorichnus, Beaconites, Archaeonassa, Planolites*
- *Zoophycos, Nereites, Palaeophycus, Cylindrichnus*

From an ichnological perspective, this organization seems to reflect the biological response to increasing depth, which is accompanied by decreasing hydrodynamics and freshwater influence. In fact, some ichnotaxa of the first group (i.e. *Ancorichnus, Archaeonassa*) are commonly found in salinity-stressed environments, whereas *Zoophycos* and *Nereites* are more typical of deeper, quieter fully-marine settings (Frey et al. 1984; MacEachern et al. 2005; Buatois and Mángano 2011; Uchman and Wetzel 2011; Melchor et al. 2012). The aforementioned modularity-based groups are likely to reflect the natural organization of the system, since other methods have provided analogous results. In fact, a similar bipartite architecture is highlighted by multidimensional scaling and Yifan Hu algorithms, which position nodes on the basis of their association relationships (Fig. 10).

Despite the coherent topological and ichnological significance of modularity-based communities, modularity optimization has some limitations with regard to their ichnological application. In fact, overlapping communities are not found by the modularity optimization algorithm (Blondel *et al.*

2008), which is also affected by resolution limits (Fortunato and Barthélemy 2007). In contrast, the idea of clique is very strict, allowing to find overlapping cliques at a very detailed resolution. The studied network is constituted by the following clique-based ichnoassociations:

1. *Ancorichnus Archaeonassa Beaconites Cylindrichnus Helminthoidichnites Planolites*
2. *Ancorichnus Beaconites Curvolithus Cylindrichnus Helminthoidichnites*
3. *Archaeonassa Cylindrichnus Helminthoidichnites Nereites*
4. *Curvolithus Cylindrichnus Helminthoidichnites Nereites*
5. *Cylindrichnus Helminthoidichnites Nereites Palaeophycus*
6. *Curvolithus Helminthoidichnites Nereites Zoophycos*

Cliques 3-6 are characterized by a higher marine affinity with respect to cliques 1-2, given the presence of typical full-marine ichnotaxa such as *Nereites* and *Zoophycos* (Uchman 1995; Buatois and Mángano 2011). However, it is difficult to attribute a distinct palaeoenvironmental significance to each clique because cliques are numerous and largely overlapping, implying that clique-based ichnoassociations are sharing many ichnotaxa with each other. This issue is both a strength and a limitation of the clique approach, which detects communities at a very fine scale; for instance, a dense network with 20 nodes may approach 2000 overlapping cliques (Scott 2000). For this reason, it is necessary to study ichnoassociations at a coarser scale than that of cliques, but at a finer scale than that of connected components. For this aim, the study of clique overlapping is a useful approach in network analysis (Wassermann and Faust 1994; Scott 2000; Evans 2010).

In line with Evans (2010), the pattern of clique overlap is conveniently represented as a network, which can be successively analyzed by community-finding methods in order to find groups of similar cliques. More specifically, the idea is to translate the original network into a clique network, the nodes of which represent the cliques in the original network (Evans 2010). Because cliques are ichnoassociations, a clique network represents an ichnoassociation network, derived from the original ichnonetwork. Whereas the nodes of the original ichnonetwork are traces, the nodes of the ichnoassociation network are the ichnoassociations of the original ichnonetwork. Similarly, whereas the links of the original ichnonetwork connect co-occurring traces, the links of the ichnoassociation network connect ‘similar’ (overlapping) ichnoassociations. This process is represented by a toy network in Fig. 16.

The practical process for producing an ichnoassociation network is analogous to that of producing a standard network (section 3). In fact, the first step is to record the ichnofaunal composition of each clique-based ichnoassociation as a spreadsheet in which rows correspond to ichnotaxa and columns to ichnoassociations. Successively, the adjacency matrix is calculated, with each cell corresponding to the Jaccard index of a clique pair. While in the original ichnonetwork the Jaccard index measured the probability of co-occurrence of two ichnotaxa, in this case it measures the ichnofaunal similarity of ichnoassociation pairs. In other words, it corresponds to the number of shared ichnotaxa divided by the total number of ichnotaxa (Hammer and Harper 2006), that is proportional to the percentage of clique overlap. The third step is to visualize the network, in parallel to chapter 3.

Similarly to the approach of Evans (2010), the ichnoassociation network of the Rio Romanino ichnonetwork (Fig. 17) can be studied by the same community-finding methods applied to the original ichnonetwork. In this regard, the ichnoassociation network consists of a single connected component, which is also a clique because of its homogeneous link distribution (density of the ichnoassociation network=1). In contrast, link weight is inhomogeneous, as revealed by the co-existence of strong (i.e. nodes 1-2) with weak ties (i.e. 1-5). Modularity optimization algorithm reveals two ichnoassociations in the ichnonetwork, which are referred as to ‘ichnoassociation groups’ for underlining their hierarchical relationship with respect to ichnoassociations 1-6. In particular, these ichnoassociation groups are:

1. Ichnoassociation group A, consisting of ichnoassociations 1, 2: *Ancorichnus, Archaeonassa, Beaconites, Curvolithus, Cylindrichnus, Helminthoidichnites, Planolites*
2. Ichnoassociation group B, consisting of ichnoassociations 3, 4, 5, 6: *Archaeonassa, Curvolithus, Cylindrichnus, Helminthoidichnites, Nereites , Palaeophycus, Zoophycos*

The same groups are revealed by multidimensional scaling, confirming the aforementioned community structure (Fig. 17). Ichnofaunal composition of the ichnoassociation group A, integrated with field observations, allows to define its environmental significance. In fact, the predominance of horizontal structures and the absence of suspension feeding burrows are significant of nutrients in deposition and, at the same time, noxious conditions for suspension feeders (Pemberton *et al.* 2001; MacEachern *et al.* 2005; Tonkin 2012). Smooth but well-defined burrow margins and the presence of meniscate trace fossils are indicative of unconsolidated substrates (softgrounds; Buatois and Mángano, 2011). These conditions are common in deltaic environments, which are also suggested by the presence of *Cylindrichnhnus* and *Curvolithus* (Tonkin 2012). In addition, most occurrences of this ichnoassociation are characterized by low diversity, low and fluctuating bioturbation (BPBI 1-2). These features are frequently associated to brackish-water settings (Pemberton et al. 2001; Buatois and Mángano 2011). In sum, ichnoassociation A reflects deltaic settings with freshwater-influence, softground substrates, significant turbidity. These features are consistent with the delta front, which is the area where sediment-laden fluvial currents enter the basin and interact with basinal processes (Reading 1996).

This interpretation is also suggested by the bioprint of *Planolites,* which is resembling the one of *Pramollichnus;* this ichnotaxon is almost invariably distributed in deltaic, storm-influenced environments (Baucon and Carvalho 2008). Although *Cylindrichnus* is not restricted to brackish, shallow-marine environments, its abundant occurrence is suggestive of storm-influenced environments (Sarkar *et al.* 2009). In addition, sedimentological features co-occurring with this ichnoassociation (parallel lamination, plant fragments) agree with a delta front environment.

In parallel to ichnoassociation group A, ichnofaunal composition and field observations allows to interpret the palaeoenvironment of ichnoassociation group B. Ichnofaunal composition is relatively similar to that of ichnoassociation group A, since the high-betweenness ichnotaxa *Curvolithus, Helminthoidichnites* and *Cylindrichnus* are shared among these groups, together with *Archaeonassa.* Nevertheless, this ichnoassociation is characterized by *Zoophycos*, which is a common indicator of normal marine salinity (Buatois and Mángano 2011). In this context, the presence of *Curvolithus* is apparently contrasting because it is commonly reported from shallow deltaic environments with high sedimentation rate (Tonkin 2012); however, the studied individuals are small sized (width 0.4-0.8 cm:

'*Curvolithus* small form' of Baucon and Carvalho, 2008), suggesting suboptimal conditions for this ichnotaxon. Normal marine settings are also supported by the abundant pascichnial form of *Nereites* (similar to *Nereites missouriensis*), which is commonly reported from shelf to deep-sea environments (Uchman 1995; Seilacher 2007). In addition, the presence of *Nereites* and *Zoophycos* in modern sediments is compatible with monsoon-influenced climate (Wetzel 2002; Lowemark and Schafer 2003), although it is does not constitute a conclusive proof *per se.* Nutrients in deposition and noxious conditions for suspension feeders are suggested by the predominance of horizontal structures related to deposit-feeding strategies (Buatois and Mángano 2011).

Overall, ichnological characteristics of ichnoassociation group B suggest a marine environment with normal marine salinity and low to moderate hydrodynamics. For this reasons, the ichnoassociation group B is reflecting offshore conditions, being also compatible to the prodelta, which is the part of the delta unaffected by wave or tidal processes (Reading 1996). This interpretation is supported by high ichnodiversity, high and constant bioturbation (BPBI 4-5), which are typical of normal-marine conditions (Buatois and Mángano 2011). Frequent presence of marine fossils (i.e. crinoids) agrees with this interpretation.

6.1.3. Ichnotaxon-level

At the ichnotaxon-level, *Helminthoidichnites* and *Cylindrichnus* are characterized by the highest betweenness, indicating that these traces are poor environmental indicators. This interpretation agrees with the detected community structure, as *Helminthoidichnites* and *Cylindrichnus* are shared between the two ichnoassociations A and B. Being environmental generalists, they appear in both ichnoassociations, which are corresponding to different environmental contexts. In addition, the high-betweenness of *Helminthoidichnites* and *Cylindrichnus* is in line with the wide environmental distribution of these ichnotaxa, as deduced from their occurrence in several depositional contexts (Minter *et al.* 2007; Wetzel *et al.* 2007; Tonkin 2012).

The low environmental specificity of *Helminthoidichnites* is also supported by its low eccentricity. In fact, its eccentricity=1 implies that *Helminthoidichnites* is directly associated to all the other ichnotaxa,

therefore its occurrence – alone - is not informative about the environmental setting.
In contrast, typical environment-crossing ichnogenera (i.e. *Planolites, Palaeophycus*) present lower values of betweenness with respect to *Nereites* and *Curvolithus,* which are usually more precise environmental indicators (Pemberton et al. 2001; Uchman and Wetzel 2011; Tonkin 2012). This apparent contradiction is explained by site-specificity: values of betweenness refer to the Rio Romanino network, hence they may express local rather than global trends. In addition, betweenness is not influenced by edge weights, hence it does not take into account association strength.

6.2. Ichnoassociation overlaps reveal the structure of the palaeolandscape

The previous section explored network architecture, interpreting the palaeoenvironmental significance of the studied network, from the scale of individual ichnotaxa to the entire network. Consequently, a question might arise: how are these levels of scale related? In addition, the question of how the palaeolandscape was structured remains unanswered.

6.2.1. Ecological significance of ichnonetworks: the niche concept in ichnology

In order to answer the aforementioned questions, the ecological significance of an ichnonetwork has to be better delineated. In this context, the basic principles of ichnology (Bromley 1996; Pemberton et al. 2001; Seilacher 2007; Buatois and Mángano 2011), coupled with network theory, delineate the ecological meaning of ichnonetworks through three fundamental aspects:

1. Behavioural significance. Trace fossils are evidence of fossil behaviour (Bromley 1996; Seilacher 2007; Buatois and Mángano 2011), therefore an ichnoetwork – made of traces and their association relationships - is a behavioural network.

2. Spatial significance. Trace fossils represent the in-situ record of biogenic activity because, almost invariably, they have not been transported (Buatois and Mángano 2011). For this reason, the co-occurrence relationships expressed in the rock record mirror the association relationships existed in the palaeoenvironment. Consequently, since co-occurrence relationships are expressed by links, an ichnonetwork expresses the original spatial relationships existed between ichnotaxa.

3. Environmental significance. Being expressions of biologic behaviour, which can be influenced by the environment, trace fossils bear an environmental significance (Bromley 1996; Pemberton et al. 2001; Seilacher 2007; Buatois and Mángano 2011). Consequently, an ichnonetwork expresses the architecture of the original palaeoenvironment as reflected by traces and their association relationships.

In light of these points, the spatial distribution of an ichnotaxon (spatial significance) derives from the environmental parameters (environmental significance) favouring the corresponding behaviour (behavioural significance). This observation is similar to the niche perspective, according to which the distribution of an organism is determined by the environmental conditions in which it can persist, that is, its ecological niche (Helaouët and Beaugrand 2009; Schoener 2009). More specifically, the Hutchinsonian niche of an organism describes the set of environmental conditions which allow its persistence, being conceptualized as an abstract space with dimensions corresponding to the environmental factors (Helaouët and Beaugrand 2009; Holt 2009; Schoener 2009). Because more than three environmental factors may define the environmental range of an organism, the niche is an n-dimensional hypervolume in which in which n ideally corresponds to all the environmental factors (Helaouët and Beaugrand 2009).

The concept of Hutchinsonian niche provides an interpretative framework for ichnonetworks and, in a broader sense, for any ichnological system (Baucon et al. 2014*a*). In fact, paraphrasing Lewis (2009), an ichnological niche consists of all the combinations of environmental attributes that are favourable to the persistence of a given ichnotaxon. Consequently, in line with the Hutchinsonian concept, the niche of an ichnotaxon is represented by an n-dimensional hypervolume, the axes of which correspond to environmental factors, i.e. oxygen content, salinity, hydrodynamic energy, among others (Fig. 18). In this regard, the niche of ichnotaxon is a subset of the ecological space and includes the combinations of environmental attributes favourable to its persistence.

The niche approach allows to answer to the question of how the levels of scale of an ichnonetwork are related. In this regard, the levels of organization of an ichnological system – as represented by an ichnonetwork – are described as follows:

- *Ichnotaxon-level.* In network terms, nodes are ichnotaxa, each of which is characterized by its environmental range, that is, its Hutchinsonian niche (Fig. 18).
- *Ichnoassociation-level.* If a pair of nodes are linked, the corresponding ichnotaxa are co-occurring in space and, for this reason, their environmental ranges are overlapping. Consequently, their niches are intersecting. This concept can be extended for any number of mutually interlinked nodes, including the members of a clique. In this context, the environmental range of a clique-based ichnoassociation correspond to the intersection of the niches of its members (Fig. 19). Given that an intersection is equal or smaller than the intersecting sets, this idea conforms with the principle that an ichnoassociation is usually a more precise environmental indicator than an individual ichnotaxon (Buatois and Mángano 2011).
- *Ichnosite-level.* In light of the previous points, an ichnonetwork can be seen as the expression of niche interrelationships, with links corresponding to niche overlaps. Paraphrasing Cranston et al., (2011), an ichnonetwork can be seen as an intersection representation, that is, a family of niches corresponding to the ichnotaxa so that the corresponding nodes are connected if and only if their assigned niches intersect.

The niche perspective relates the three different level of scale of an ichnonetwork, providing the theoretical basis for studying the overlap pattern of ichnoassociations, allowing to understand environmental structure from network architecture. For this purpose, the basic tool is the ichnoassociation network, which represents the cliques of the original ichnonetwork as nodes and their overlapping relationships as links. Based on the preliminary observations of Baucon et al. (2014), two basic node-to-node relationships are found in an ichnoassociation network:

1. Linked nodes (overlapping ichnoassociations): In the ichnoassociation network, two nodes are linked if the corresponding ichnoassociations share at least one ichnotaxon. For this reason, in the ecological space, the environmental ranges of the two linked ichnoassociations are bridged by the niches of the shared ichnotaxa. This topological relationship is exemplified by the linked ichnoassociations 1-3 and 2-3 in Fig. 20.
2. Disjoint nodes (disjoint ichnoassociations). Two nodes of the ichnoassociation

network are disjoint when the corresponding ichnoassociations have no ichnotaxon in common. If disjoint nodes are members of the same connected component, their environmental ranges are reachable through a continuous chain of niches. This topological relationship is exemplified by the disjoint ichnoassociations 1-2 in Fig. 20. On the other hand, if disjoint nodes are members of disconnected components, there are no niches covering the gap between two ichnoassociations, implying that there are no continuous environmental corridors among the disjoint ichnoassociations. The ichnoassociation network of the ichnonetwork in Fig. 21A would exemplify this topological relationship.

All node pairs of the Rio Romanino ichnoassociation network (Fig. 17) follows the first case, as shown by maximum link density (density =1). In other words, all possible links are present in the ichnoassociation network, which is therefore complete. Consequently, there is a niche between each of the environmental ranges defined by ichnoassociations and, for this reason, the environmental ranges of ichnoassociations 1-6 are part of a continuous ecological gradient existing in the abstract ecospace.

6.2.2. Ichnonetworks in physical space: the habitat concept in ichnology

After elucidating the relationship between the topological space (containing networks) and the abstract ecospace (containing niches), a question might arise: what is the relationship between the abstract ecospace and the physical space?

In ecology, the concept of habitat is one of the fundamental logical tools for understanding species distribution in the physical space. In fact, the habitat of an organism generally indicates the place where an organism lives (Dennis *et al.* 2003; Dennis 2010). Consequently, the concept of habitat represents a promising tool for analyzing the spatial distribution of ichnotaxa, which can be synthesized as a set of ichnological habitats. Among the various definitions of habitat (Dennis *et al.* 2003; Bunce *et al.* 2013), the functional, resource-based definition provides a direct connection with the concept of Hutchinsonian niche: “habitat is a zone (area) comprising a set of resources, consumables and utilities, for the maintenance of an organism” (Dennis *et al.* 2003; Dennis 2010).

According to this approach, the habitat of an organism is delimited by the environmental controls which define its Hutchinsonian niche (Whittaker *et al.* 1973; Dennis *et al.* 2003; Dennis 2010; Bunce *et al.* 2013). This functional, resource-based approach can be extended to the ichnological realm: the habitat of an ichnotaxon (or a set of ichnotaxa) is a zone comprising a set of environmental resources for the maintenance of an ichnotaxon (or a set of ichnotaxa). Consequently, paraphrasing Dennis et al. (2003), the habitat of an ichnotaxon is to the physical space as niche is to the abstract ecospace; the same idea is extended to any set of co-occurring ichnotaxa, including ichnoassociations. For these reasons, it is possible to derive landscape structure from ichnological data since topological, ecological and physical spaces are related each to the other (Fig. 20). This relationship allows to interpret the small-world-ness of the studied network as an expression of the spatial heterogeneity of the palaeoenvironment represented by the Rio Romanino section.

In light of the relationship between topological, ecological and physical space, the ichnoassociation network – derived from the original ichnonetwork – describes how different types of habitats are related. In fact, each node of the ichnoassociation network is an ichnoassociation, which – in the abstract ecospace – delimits a niche intersection, which, in turn, marks a habitat type in the physical space. Consequently, in the ichnoassociation network, a pair of linked nodes are two habitat types grading one into another. In light of the maximum density of the studied ichnoassociation network (Fig. 17), the bioturbated habitats of the Rio Romanino section graded one into another.

Whereas configuration of habitat types is revealed by the ichnoassociation network, habitat size and shape are not described in the topological space. In addition, clique-based ichnoassociations depict habitat types with maximal local ichnodiversity and, for this reason, low-ichnodiversity habitats may be underrepresented in the corresponding ichnoassociation network. More specifically, the concept of clique is maximal (a clique should not be contained in another clique; Wassermann and Faust, 1994), therefore the cliques of an ichnonetwork represent the largest groups of mutually associated ichnotaxa (Fig. 16). Consequently, the habitats of the corresponding ichnoassociations – represented as nodes in the corresponding ichnoassociation network – present high ichnodiversity. Similar conditions are reached in spatially wide habitats (Fig. 22A), especially those with stable and predictable environmental conditions (Buatois and Mángano 2011); this is the case of the habitat of ichnoassociation 6, the field occurrences of which are laterally continuous. However, local peaks of ichnodiversity may be also reached in transitional habitats, regardless of their spatial extent. For instance, the narrow transitional zone between two wider habitats may comprise ichnotaxa from both of the habitats which separate (Fig. 22B), paralleling the ecotone concept in landscape ecology (Harding 2002; Yarrow and Salthe 2008). Consequently, ichnodiversity will be higher in the transitional habitat, the ichnofaunal composition of which will be probably detected as a clique-based ichnoassociation. If all the ichnotaxa of the bordering habitats are shared in the transitional habitat, their specific ichnofaunal composition will be not detected as a clique. In addition, a transitional habitat may provide particular environmental conditions, being potentially characterized by specific ichnotaxa.

The topological features of the ichnoassociation network of Fig. 17 are reflected at a coarser level, since ichnoassociation group A is overlapping with the ichnoassociation group B. This pattern of overlap may be represented with an ichnoassociation network consisting of two nodes – ichnoassociation groups A and B – connected by a link. In light of the aforementioned observations, this linked topology corresponds to a gradient of environmental ranges, the end-members of which are ichnoassociations A and B themselves. Consequently, the corresponding habitats were part of a continuum: the delta front habitat (ichnoassociation group A) was adjacent to the prodelta/open marine habitat (ichnoassociation B).

6.3. A new hierarchy for groups of traces

In ecology, associations of taxa allow to predict environmental characteristics (Legendre 2005), therefore associations of ichnotaxa (ichnoassociations) are useful conceptual tools for reconstituting the palaeoenvironment. For this reason, the palaeoenvironmental evolution of the Rio Romanino section may be interpreted by attributing field data to the previously described ichnoassociations.

For this purpose, a terminological problem arise: there is no present consensus on the term ichnoassociation itself (Buatois and Mángano 2011). In this regard, this study has followed an operational definition of ichnoassociation, based on the approach of Legendre (2005) to species associations: “an ichnoassociation is a group of ichnotaxa recognized as a cluster following the application of a clearly stated set of rules”. For instance, in the case of ichnoassociations 1-6, the rules are represented by the concept of clique. In line with the definition of species association (Legendre 2005) from which derives, the aforementioned definition of ichnoassociation agrees with the general concept of taxa association, that is a group of taxa that are significantly found together; in statistical terms, it represents a recurrent group of co-occurring (for presence-absence data) or correlated (for abundance data) taxa (Legendre and Legendre 2003).

For these reasons, a given ichnoassociation is conveniently regarded as the generalization of a set of field occurrences of traces (Fig. 20). In this regard, the term ichnoassemblage conveniently indicate any of these field occurrences (Baucon et al. 2014*a*) because it does not imply assumptions about recurrence in the stratigraphic record (Buatois and Mángano 2011). More specifically, an ichnoassemblage is any group of traces in the field (Baucon et al. 2014*a*).

In sum, according to the proposed terminology, an ichnoassociation is derived from a set of ichnoassemblages, whereas an ichnoassemblage may be attributed to a specific ichnoassociation on the basis of the similarity of ichnological features. This approach can be extended to the Seilacherian ichnofacies, which are therefore regarded as generalizations at the higher hierarchical level. In fact, following other authors (Buatois and Mángano 2011; MacEachern et al. 2012), a given ichnofacies derives from the distillation of recurring characteristics from numerous case studies. Consequently, a given ichnofacies is the generalization of many ichnoassemblages (Fig. 20).

6.4. Differences between ichnoassociations and ichnoassemblages

Since ichnoassociation detection is a process of generalization, it implies that generalized patterns (ichnoassociations) may differ from field occurrences (ichnoassemblages). For instance, the Rio Romanino ichnonetwork does not account for all traces and association relationships of the Meledis and Pizzul Formations. In fact, *Kouphichnium* (Conti et al. 1991*b*), large *Archaeonassa*-like traces, *Schaubcylindrchnus* and *Phymatoderma* have been not documented in the Rio Romanino section, hence they do not compare in the ichnonetwork. Similarly, *Beaconites* has been found with *Nereites* (Fig. 21A) and *Zoophycos* (Baucon and Carvalho 2008), but only in loose material; consequently, the ichnonetwork of the Rio Romanino section – based on outcrop data – does not depict the corresponding association relationships. For this reason, *Beaconites* is likely to be not exclusive of the delta front ichnoassociation A, but it could also indicate deeper, open marine settings, which are typical of *Nereites* and *Zoophycos* (Uchman 1995; Seilacher 2007; Buatois and Mángano 2011).

Another difference between generalized patterns (ichnoassociations) and field occurrences (ichnoassemblages) concerns ichnodiversity. In fact, ichnoassemblages of the study area commonly consist of a fewer number of traces with respect to clique-based ichnoassociations. This phenomenon is explained by the concept of clique, which detect the largest groups of co-occurring traces and, for this reason, tends to include in the same ichnoassociation groups of co-occuring traces with similar ichnofaunal composition (Fig. 22C). In addition, the ichnofaunal composition of clique-based ichnoassociations may reflect transitional habitats where ichnodiversity is maximum due to the edge effect (section 6.2.2).

6.5. Networks in time: local or global causes?

The Rio Romanino section is characterized by two peaks in bioturbation intensity (BPBI 3-5), both of which are followed by a marked decrease in bioturbation intensity (BPBI 1-2). Since changes in bioturbation intensity are paralleled by changes in ichnodiversity, ichnofaunal composition and sedimentary facies, they allow to define environmentally-significant intervals in the studied section (Fig. 25A):

1. Interval 1 is characterized by high and constant bioturbation (BPBI 5). Overall, ichnodiversity is moderate, while the ichnofaunal composition is consistent with the open marine/prodeltaic ichnoassociation group B. A *Beaconites*-bearing horizon appears in the upper part of the interval but, in light of the observations of section 6.4 and the high, constant bioturbation intensity, it reflects the same environmental setting of ichnoassociation B. In sum, this interval is interpreted to reflect open marine/prodeltaic conditions.

2. Interval 2 is characterized by intermediate bioturbation intensities (BPBI ranging between 3 and 4) with respect to the highly bioturbated interval 1 and the sparsely bioturbated interval 3. For this reason, it is interpreted to reflect transitional conditions between the open marine/prodeltaic settings of interval 1 and the delta front environments of interval 3. This interpretation is suggested by ichnofaunal composition, presenting ichnotaxa shared by both ichnoassociation groups, although elements of the ichnoassociation group A are numerically dominant. These features highlight the transitional character of this interval, which is also suggested by the high ichnodiversity. In sum, this interval represent the transition from marine to delta front conditions.

3. Interval 3 is dominated by low bioturbation intensities (BPBI 1-2), being therefore consistent with high sedimentation rates (Gingras *et al.* 2011). Trace fossils are sporadically distributed, indicating persistent, spatio-temporal variability in physico-chemical conditions (Gingras *et al.* 2011). The ichnoassociation group A, attributed to delta front settings, is dominant. Overall, this interval reflects delta front settings, as confirmed by the presence of coal and plant fragments.

4. Interval 4 is marked by an increase in bioturbation intensity (BPBI 4-5). Ichnoassociation group B is dominant, while ichnodiversity is moderate. These features show an increased marine influence with respect to the underlying interval 2 and is confirmed by the presence of marine body fossils (crinoids).

5. Interval 5 is characterized by an extreme scarceness of distinct burrows, although isolated layers with *Cylindrichnus, Nereites* and *Palaeophycus* may be present (typical BPBI is 1-2 with isolated horizons characterized by higher bioturbation intensities). Ichnofaunal composition is suggestive of the prodeltaic ichnoassociation group B, although the low bioturbation intensity and the sporadic bioturbation distribution differ from the typical occurrences of the ichnoassociation. In this regard, the overall low bioturbation intensity and the low ichnodiversity suggest significant environmental stress (Buatois and Mángano 2011; Gingras et al. 2011). According to the dark sediment colour, good preservation of body fossils, low oxygen conditions are interpreted to be the major environmental stressor. This interpretation

is supported by bioturbation distribution itself, since fluctuations in oxygenation may be responsible for intense bioturbation along horizons characterized by oxygenation events, but otherwise absent (Gingras *et al.* 2011). In sum, the palaeoenvironment of the interval 5 is interpreted to be a dysoxic prodelta.

In light of the aforementioned interpretation, the depositional environment was first characterized by a shallowing phase expressed as the transition from prodeltaic to delta front settings (intervals 1-3). Successively, marine conditions re-established (intervals 4-5) but, in contrast to the oxygenated prodelta of interval 1, oxygenation was poor (interval 5).

With respect to the dysoxic prodelta represented by interval 5, similar environmental conditions are expressed at the scale of the entire Pramollo basin. In fact, the lower parts of the Pizzul Formation are characterized by sedimentary indicators of low oxygenation, including dark sediment colour and excellent preservation of body fossils (Fig. 26A, B). This interpretation is supported by ichnological evidences of low oxygenation, including the presence of *Phymatoderma* (Fig. 24C) and monoichnospecific occurrences of *Zoophycos*, both of which are reported from dysoxic environments (Buatois and Mángano 2011; Izumi 2012). Overall, bioturbation intensity is low, being in line with low oxygen conditions (Buatois and Mángano 2011). Intensely bioturbated horizons are sporadically distributed within these low-bioturbation sediments and are characterized by low diversity ichnoassemblages, which are indicative of a stressed environment (Buatois and Mángano 2011; Gingras et al. 2011). These intensely bioturbated horizons are commonly dominated by monoichnospecific assemblages of pyritized *Cylindrichnus* (Fig. 26C). This peculiar preservation is likely to indicate low-oxygen settings, since low oxygen environments favour the precipitation of pyrite and prevent its oxidation (Walther 2009); in addition, Fe shows a large degree of pyritization in euxinic conditions, which are characterized by high concentrations of hydrogen sulphide and commonly evolve from anoxic settings (Meyer and Kump 2008).

The total thickness of the low-oxygen interval has not been measured with accuracy because the upper part of the Rio Romanino section is covered with vegetation. However, according to field observations, the low-oxygen interval is estimated to measure at least 25 metres, therefore it is both laterally and vertically extensive.

According to these observations, the interval 5 of the Rio Romanino section reflects a basin-scale decrease in bottom oxygen, possibly accompanied by free hydrogen sulphide. Consequently, a question might arise: what is the process responsible for the Pizzul dysoxic event?

This question is approached by considering which factors favours low oxygen conditions. At the basin scale, modern environments characterized by low oxygen conditions and free hydrogen sulphide are typically characterized by restricted circulation, are deep relative to their surface area, and support high primary productivity because of elevated nutrient concentrations (Meyer and Kump 2008). With regard to the Pramollo Basin, the deposition of the Meledis and Pizzul Formation is accompanied by major changes in basin geometry which are likely to have influenced water circulation and the depth/area relationship. More specifically, deposition of the Meledis Formation was homogeneous at the basin scale, although a slightly erosive surface, documented in the upper part of the Meledis Formation, suggests a first tectonic event (Venturini 1983, 1990*b*, 1991). Significant variations in thickness of the Pizzul Formation and the deposition of a breccia horizon (Malinfier Horizon) mark a second tectonic event, after which the M. Cavallo-Valbertad horst emerged and separated two lateral subsiding sectors (Venturini 1983, 1990*b*, 1991).

The tectonic phase delimited by the above mentioned events correspond to the intervals 3-5 of the Rio Romanino section (Fig. 25). In fact, in light of the ichnological and sedimentological features of the the Rio Tratte, Rio Cordin, Rio das Barbacis, Rio del Museo sections (Venturini et al. 1982; Venturini 1990*a*, 1991), the first erosive, tectonically-driven event is correlated with the slightly erosive base of the interval 3 of the Rio Romanino section (Fig. 25B); similarly, the second, major event is placed near to the top of interval 5.

For these reasons, the Pizzul dysoxic event is interpreted as the effect of tectonically-related changes in basin geometry, which restricted both the surface area and the water circulation of the Pramollo Basin. In line with modern anoxic and euxinic basins (Meyer and Kump 2008), these phenomena promoted nutrient trapping and favoured widespread dysoxia and, locally, euxinia. Vertical stratification and local changes in productivity may have played an additional role, although clear evidences of these phenomena are lacking.

In addition, the Pizzul dysoxic event may have been favoured by global phenomena such as the crisis of Carboniferous rainforests (Carboniferous Rainforest Collapse) (Cleal and Thomas 2005; Montañez et al. 2007; Falcon-Lang and Dimichele 2010; Sahney et al. 2010), which possibly influenced nutrient dynamics; the upper Carboniferous continental configuration, favourable to nutrient-trapping (Meyer and Kump 2008); the reduced tidal mixing, possibly controlling coastal circulation (Wells *et al.* 2005). Although global events may have played a secondary role, local causes are sufficient to explain the Pizzul dysoxic event. In this regard, further studies are required for estimating which global events influenced the Pizzul dysoxia and for evaluating its relationship with the major euxinic (Meyer and Kump 2008) and anoxic basins (Wells *et al.* 2005) from the upper Carboniferous.

7. Conclusions

This paper described the analytic framework for ichnonetwork analysis of fossil ichnological systems, presenting its application on the Rio Romanino stratigraphic section (Meledis-Pizzul Formations, upper Carboniferous; Pramollo ichnolagerstätte). Ichnonetwork analysis allowed to reconstruct the palaeoenvironment and analyze its evolution in time, providing a new theoretical basis to the concept of ichnoassociation.

These results encourage the application of network theory on other ichnological systems, both fossil and modern. In the specific case of the Pramollo ichnolagerstätte, the Meledis, Pizzul (this paper) and Val Dolce Formations (Baucon et al. 2014*a*) have been studied, whereas Corona, Auernig and Carnizza Formations are lacking an ichnonetwork approach. In addition, application of network theory for studying the morphology of individual traces (Perna *et al.* 2008) is a promising application of network theory to ichnology, but an application to broader domains of scale is still lacking. For instance, network theory could synthesize ichnological data concerning several ichnosites in order to find recurring patterns at a regional or global scale.

From a methodological perspective, several important direction for further work are identified. First, weighted metrics should be better integrated in ichnonetwork analysis, which is mostly using unweighted concepts and techniques. Second, a framework for identifying monoichnospecific ichnoassociations has to be developed, as the application of the Jaccard index produces an adjacency matrix where the entries of the main diagonal are all equal to 1. Third, the influence of sampling on ichnonetwork topology has to be better defined, including aspects concerning sampling error and ichnotaxonomical resolution.

Finally, this paper explored – through the network perspective – the conceptual background of ichnology and proposed new concepts. In fact, the ideas of ichnoassociation and ichnofacies have been presented as different levels of generalization based on ichnoassemblages. In addition, the concept of ichnological niche have been linked to the idea of habitat, allowing the reconstitution of the palaeolandscape structure. This approach allowed to recognize the of the edge effect on trace fossil diversity, suggesting new perspectives in the palaeoenvironmental interpretation of ichnodiversity.

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FIGURES

Fig. 1. Study area.

Fig. 2. Geological setting.

Fig. 3. Sedimentary features of the Meledis and Pizzul Formations. A – Planar bedded sandstones (facies S1). Meledis Formation. B – Micaceous sandstone (facies S4) with a specimen of *Zoophycos.* Meledis Formation. C – Pelitic interval (facies P1) in the Pizzul Formation. D – Plant fragments in the pelitic facies (facies P1) of the Pizzul Formation.

Fig. 4. Stratigraphical section of the Rio Romanino stream.

Fig. 5. From data to the network.

Fig. 6. Ichnological heritage of the study area. (A) *Beaconites.* (B) Bedding plane intensely bioturbated by meniscate traces (*Beaconites*?; *Ancorichnus*?) and *Cylindrichnus.* (C) Particular of B.

Fig. 7. Ichnonetwork of the Rio Romanino section.

Fig. 8. Aspect tools. (A) Nodes are sized and coloured on the basis of the number of incident links (node degree). (B) Links are sized and coloured on the basis of their weight.

Fig. 9. Filtering. (A) Strong links, evidenced by links with weight higher or equal to the network average. (B) Ego network of *Zoophycos,* consisting of *Zoophycos* and the nodes associated to it (neighbours).

Fig. 10. Layout tools.

Fig. 11. Node degree of the Rio Romanino ichnonetwork.

Fig. 12. Node betweenness of the Rio Romanino ichnonetwork.

Fig. 13. Toy networks illustrating measures of range and community structure. (A) Concept of distance. Length of the shortest path (dashed) between the highlighted nodes equals to 2, whereas the length of the dotted path equals to 5. Distance is the length of the shortest path, that is 2. (B) Concept of component. A network consisting of two disconnected components. (C) Concept of clique. The four highlighted nodes are part of a clique because they are mutually interconnected.

Fig. 14. Clustering coefficient of the Rio Romanino ichnonetwork.

Fig. 15. Clique-based ichnoassociations for the studied ichnonetwork.

Fig. 16. From ichnonetwork to the ichnoassociation network. (A) Toy ichnonetwork, consisting of nodes (ichnotaxa) and links (association relationships). (B) Cliques of the toy ichnonetwork in A; two are the nodes shared among cliques, which represent ichnoassociations. (C) Ichnoassociation network of the toy ichnonetwork shown in A. In particular, the ichnoassociation network consists of nodes (ichnoassociations, that are cliques in B) and links (clique overlapping in B).

Fig. 17. Ichnoassociation network. Nodes represent the clique-based ichnoassociations in Fig. 15.

Fig. 18. The concept of ichnological niche.

Fig. 19. Niche concept and levels of organization of an ichnological system. (A) Toy ichnonetwork consisting of three nodes (a, b, c), each of which correspond to a given ichnotaxon. Being mutually interconnected, a, b and c form a clique (clique-based ichnoassociation). (B) In the ecological space, the toy ichnonetwork of A correspond to a group of intersecting niches.

Fig. 20. Node-to-node relationships in an ichnoassociation network. (A) Toy ichnonetwork formed by three, partially overlapping cliques (ichnoassociations). (B) Ichnoassociation network derived from the toy ichnonetwork in A. Ichnoassociation 1 is disjoint from ichnoassociation 2, while ichnoassociations 1 is linked to ichnoassociation 3, as well as ichnoassociation 3 and 2. (C) In the ecological space, the toy ichnonetwork of A is represented as a set of habitats.

Fig. 21. A toy ichnological system represented in the topological (A), ecological (B) and physical (C) space.

Fig. 22. Habitat distribution and ichnonetwork architecture. Habitat 1 is typified by the presence of ichnotaxa a, b, habitat 2 is characterized by the presence of ichnotaxa a, b, c, d, habitat 3 is characterized by ichnotaxa c, d. (A) Wide habitat with maximal local ichnodiversity and two marginal, narrower habitats. The ichnonetwork of the figured ichnological system is constituted by a single clique-based ichnoassociation which is comprising ichnotaxa a, b, c, d. Consequently, habitat 2 is reflected by the ichnofaunal composition of the clique-based ichnoassociation, whereas habitats 1 and 2 are suggested by link weights. (B) Narrow, transitional habitat bridging two wider habitats with lower ichnodiversity. The ichnonetwork is constituted by a single clique, being equivalent to the ichnonetwork figured in A. (C) Discontinuously distributed habitats.

Fig. 23. Hierarchical definition of ichnoassemblage, ichnoassociation and ichnofacies.

Fig. 24. Ichnological variability not depicted in the ichnonetwork. (A) *Beaconites* (Be) associated to *Nereites* (Ne), Meledis Formation. (B) *Archaeonassa*-like (Ar) traces, Meledis Formation. (C) *Phymatoderma* (Ph), Pizzul Formation.

Fig. 25. Environmental evolution of the Rio Romanino section. (A) Environmental evolution of the Rio Romanino section. (B) Correlation with other sections. Integrated and simplified from Venturini (1990*a*); sedimentary structures not illustrated.

Fig. 26. Low-oxygen indicators in the lower Pizzul Formation. (A) Well-preserved crinoid. (B) Monoichnospecific occurrence of *Zoophycos* (Zo) together with a well-preserved brachiopod (Br) and a crinoid fragment (Cr). (C) Pyritised *Cylindrichnus.*

Fig. 27. Turbidite-related structures from the lower part of the Pizzul Formation. (A) Flute casts. (B) Groove casts with wings.

	Lithology	Major structures	Color	Body Fossils	Organization	Code
Conglomeratic facies	medium- to coarse grained quartz-conglomerate	Massive, trough-bedding, graded-bedding	White	Very rare plant fragments	Plurimetric units, often deriving from amalgamated bodies; common erosive base	C1
Arenitic facies	fine- to medium-grained sandstone	Planar-lamination dominant with sparse hummocky-cross laminated horizons. Water escape structures locally abundant	Light brown to rusty brown	Very rare shell coquina	plurimetric bodies with planar or wavy bedding	S1
	fine- to medium-grained sandstone	Massive	Light to dark brown	Bioclastic horizons are frequent (mainly brachiopods and crinoids)	interbedded in pelitic sequences. Thickness: 10-30 cm.	S2
	Medium-grained sandstone	Massive	Grey to pale brown	absent	Plurimetric bodies with planar bedding	S3
	Medium-grained, mica-rich sandstone	Massive; common concretions	Grey to greenish	Rare shell coquina	Plurimetric bodies	S4
	Fine sandstone to siltstone	Hummocky-cross lamination	Grey to greenish	absent	Plurimetric bodies	S5
	Bioclastic sandstones	Sole marks	Pale brown	Brachiopods, crinoids, gastroppds, bryozoans	Decimetric bodies interbedded in pelitic sequences	S6
	Sandstones	Planar lamination, sole marks	Dark grey	Plant fragments	Decimetric bodies interbedded in pelitic sequences	S7
Pelitic facies	siltstone and sandy siltstone	Discontinuous planar and wavy lamination	Light grey to bluish	bryozoans, brachiopods, gastropods, crinoids	Plurimetric bodies with occasional sandstone layers (facies S2).	P1
	siltstone	Discontinuous planar and wavy lamination	Brown to light grey; metallic shine	Plant remains	Metric to plurimetric units	P2
Carbonatic facies	Wackestone or packstone. Coated grains and algae common.	Massive	Light grey	fusulinids, brachiopods, gastropods, echinoderms and bryozoans.	Decimetric layers	L1
	Packstone to rudstone, usually dolomitic		Light grey	Articulated algae	Decimetric layers	L2
	Packstone or grainstone		Light grey			L3
	sandstone or limestone	Slump folds	Various colors		Metric layers	L8

Table 1. Major sedimentary facies of the Pramollo Group, based on field observations and previous works (Baucon & Carvalho, 2008; Venturini, 1990, 1991).

Ichnotaxon	Abbreviation	Description	Diameter	Behavior	Ichnoguild data			Reference	Figure
					Bauplan	Trophic strategy	Use of space		
Ancorichnus	An	Horizontal, unbranched, winding cylindrical full relief burrow having gentle annulations on the surface.	0.4-0.8 cm		Transitory structure		2	A	10B
Archaeonassa	Ar	Horizontal, straight or gently winding trail constituted by two symmetrical lobes separated by a central furrow.	0.6-1-6 cm	Locomotion	Transitory structure	Predation, detritus feeding	0-1	A	
Beaconites	Be	Horizontal or slightly oblique meniscated trace preserved as full-relief. Micaceous, light menisci are separated by thin arcuate segments of sediment, darker in colour. Thin wall.	0.5-2 cm	Feeding	Transitory structure	Deposit feeding	2	A	
Curvolithus	Cu	Unbranched, winding sub-horizontal structures with a central lobe flanked on both sides by a lateral string.	0.4-1.8 cm	Locomotion	Transitory structure	Predation	0-1	A	
Cylindrichnus	Cy	Vertical or inclined unbranched burrows, circular or elliptical on bedding plane; lining concentrically laminated and surrounding a central core representing the burrow fill.	0.3-0.8 cm	Feeding	Permanent burrow	Detritus feeding, suspension feeding and predation	1-2	A	
Helminthoidichnites	He	Small, simple and unbranched, winding traces preserved as positive hyporeliefs.	0.1-0-2 cm	Feeding	Transitory structure	Deposit feeding	0-1	A	
Kouphichnium	-	footprints with five imprints, resulting in a Y-shaped morphology	0.4-1.2 cm	Locomotion	Transitory structure		0	B	
Nereites	Ne	Simple, horizontal, unbranched burrow constituted by a central meniscate ribbon surrounded by a lobate zone of reworked sediment	0.4-0.8 cm	Feeding	Transitory structure	Deposit feeding	1	A	
Palaeophycus	Pa	Simple, horizontal, unbranched burrow lacking a wall lining. Fill different to the host rock.	0.4-1.2 cm	Feeding	Transitory structure	Predation	1	A	
Planolites	Pl	Simple, horizontal, unbranched burrow lacking a wall lining. Fill similar to the host rock.	0.3-0.5 cm	Feeding	Transitory structure	Deposit feeding	1	A	
Zoophycos	Zo	Helically coiled spreite burrows, constituted by numerous structures revolving around a central axis	15-40 cm	Feeding	Permanent burrow	? deposit feeding	2-3	A	

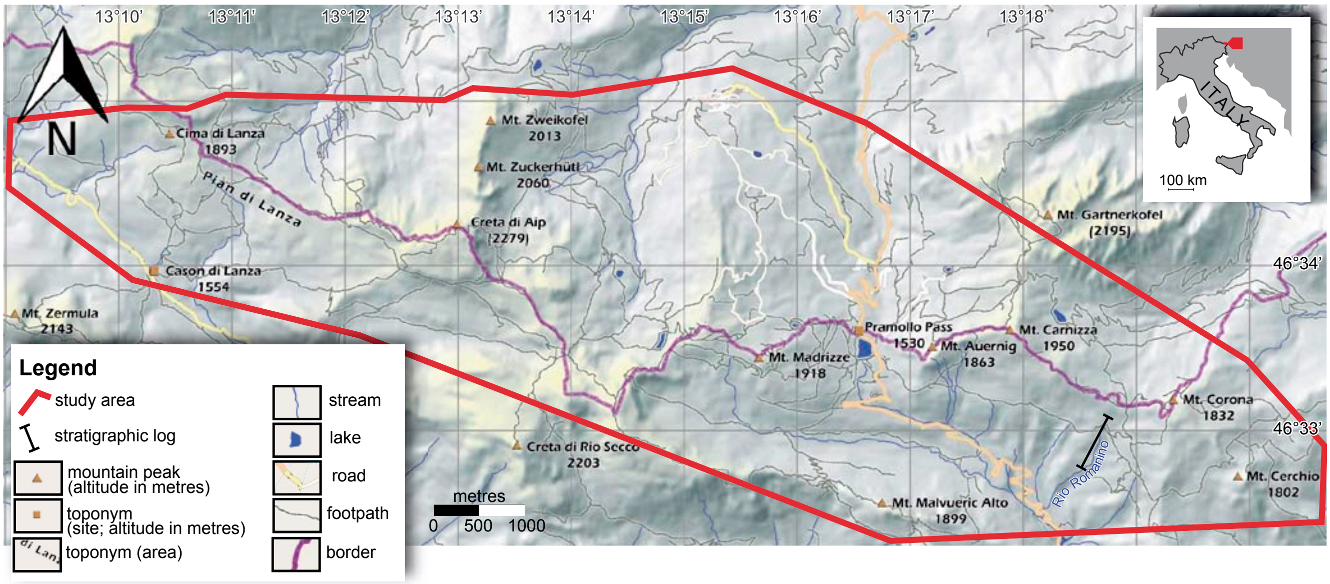
Table 2. Trace fossils of the Meledis and Pizzul Formations. In line to the ichnoguild approach, bauplan, trophic strategy and use of space are indicated on the basis of field observation and previous works (Conti et al., 1991; Pemberton et al., 2001; Baucon and Carvalho, 2008). In

Node	**Degree**	**Betweenness**	**Eccentricity**	**Clustering Coefficient**
Helminthoidichnites	9	6.7833333333	1	0.5555555556
Cylindrichnus	8	3.45	2	0.6428571429
Ancorichnus	6	0.45	2	0.8666666667
Archaeonassa	6	0.8333333333	2	0.8
Beaconites	6	0.45	2	0.8666666667
Curvolithus	6	1.8333333333	2	0.6666666667
Nereites	6	2.2	2	0.6
Planolites	5	0	2	1
Zoophycos	3	0	2	1
Palaeophycus	3	0	2	1
MNIMUM	3	0	1	0.5555555556
AVERAGE	5.8	1.6	1.9	0.7998412698
MAXIMUM	9	6.7833333333	2*	1

Tab. 3. Topological measures of the Rio Romanino ichnonetwork. Network diameter is the maximum node eccentricity (*).

	Ancorichnus	*Archaeonassa*	*Beaconites*	*Curvolithus*	*Cylindrichnus*	*Helminthoidichnites*	*Nereites*	*Palaeophycus*	*Planolites*	*Zoophycos*
Ancorichnus	0	1	1	1	1	1	2	2	1	2
Archaeonassa	1	0	1	2	1	1	1	2	1	2
Beaconites	1	1	0	1	1	1	2	2	1	2
Curvolithus	1	2	1	0	1	1	1	2	2	1
Cylindrichnus	1	1	1	1	0	1	1	1	1	2
Helminthoidichnites	1	1	1	1	1	0	1	1	1	1
Nereites	2	1	2	1	1	1	0	1	2	1
Palaeophycus	2	2	2	2	1	1	1	0	2	2
Planolites	1	1	1	2	1	1	2	2	0	2
Zoophycos	2	2	2	1	2	1	1	2	2	0

Tab. 4. Node-to-node distances in the studied ichnonetwork.


13°10'
13°11'
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13°15'
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ITALY
100 km
Cima di Lanza 1893
Pian di Lanza
Mt. Zweikofel 2013
Mt. Zuckerhütl 2060
Creta di Aip (2279)
Cason di Lanza 1554
Mt. Zermula 2143
Mt. Gartnerkofel (2195)
Pramollo Pass 1530
Mt. Madrizze 1918
Mt. Auernig 1863
Mt. Carnizza 1950
Mt. Corona 1832
Creta di Rio Secco 2203
Mt. Malvueric Alto 1899
Mt. Cerchio 1802
Rio Romanino
metres
0 500 1000
Legend
study area
stratigraphic log
mountain peak (altitude in metres)
toponym (site; altitude in metres)
toponym (area)
stream
lake
road
footpath
border

Fig. 1.

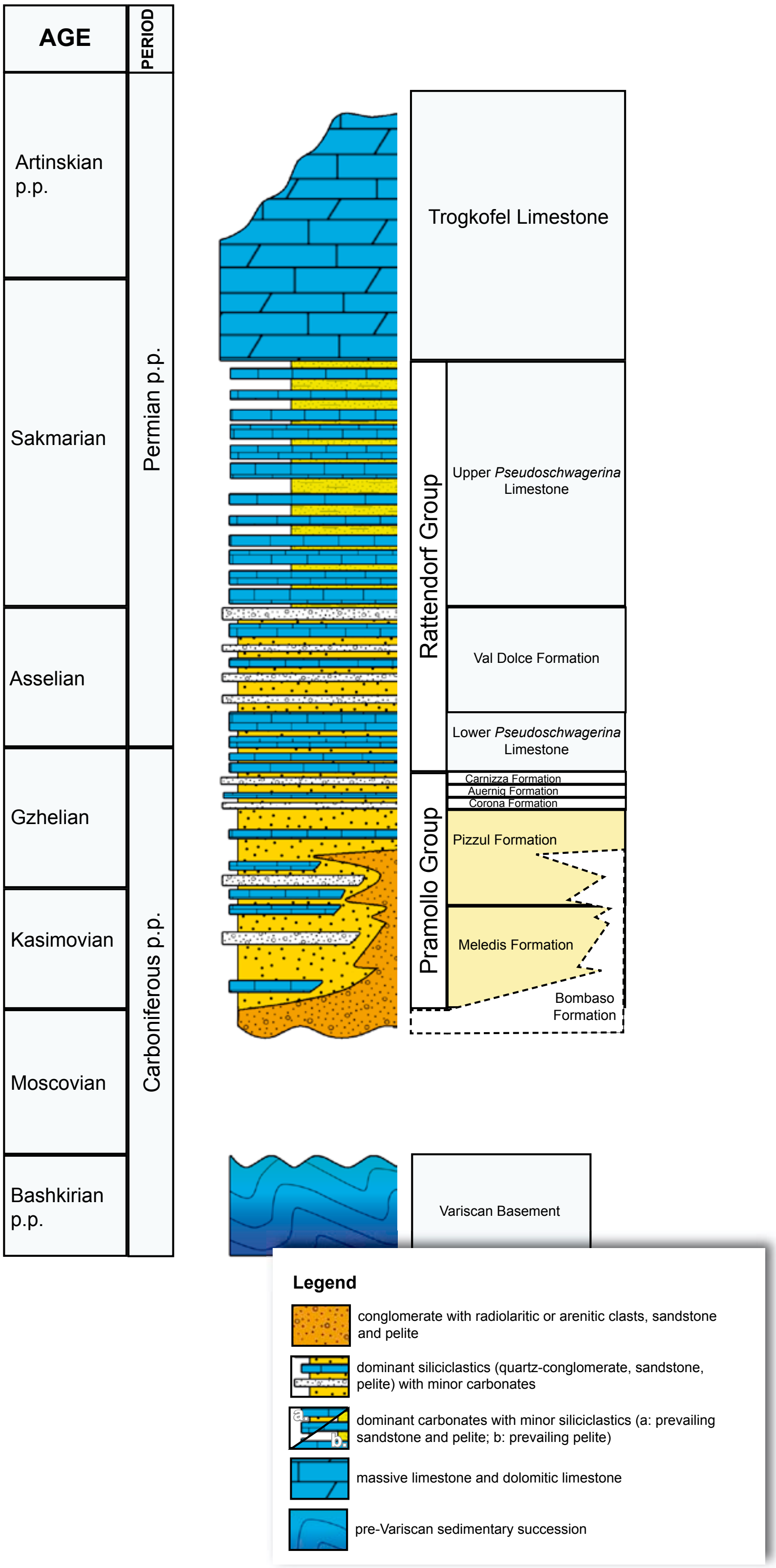

AGE
PERIOD
Artinskian p.p.
Sakmarian
Asselian
Gzhelian
Kasimovian
Moscovian
Bashkirian p.p.
Permian p.p.
Carboniferous p.p.
Trogkofel Limestone
Rattendorf Group
Upper Pseudoschwagerina Limestone
Val Dolce Formation
Lower Pseudoschwagerina Limestone
Pramollo Group
Carnizza Formation
Auernig Formation
Corona Formation
Pizzul Formation
Meledis Formation
Bombaso Formation
Variscan Basement
Legend
conglomerate with radiolaritic or arenitic clasts, sandstone and pelite
dominant siliciclastics (quartz-conglomerate, sandstone, pelite) with minor carbonates
a
b
dominant carbonates with minor siliciclastics (a: prevailing sandstone and pelite; b: prevailing pelite)
massive limestone and dolomitic limestone
pre-Variscan sedimentary succession

Fig. 2.

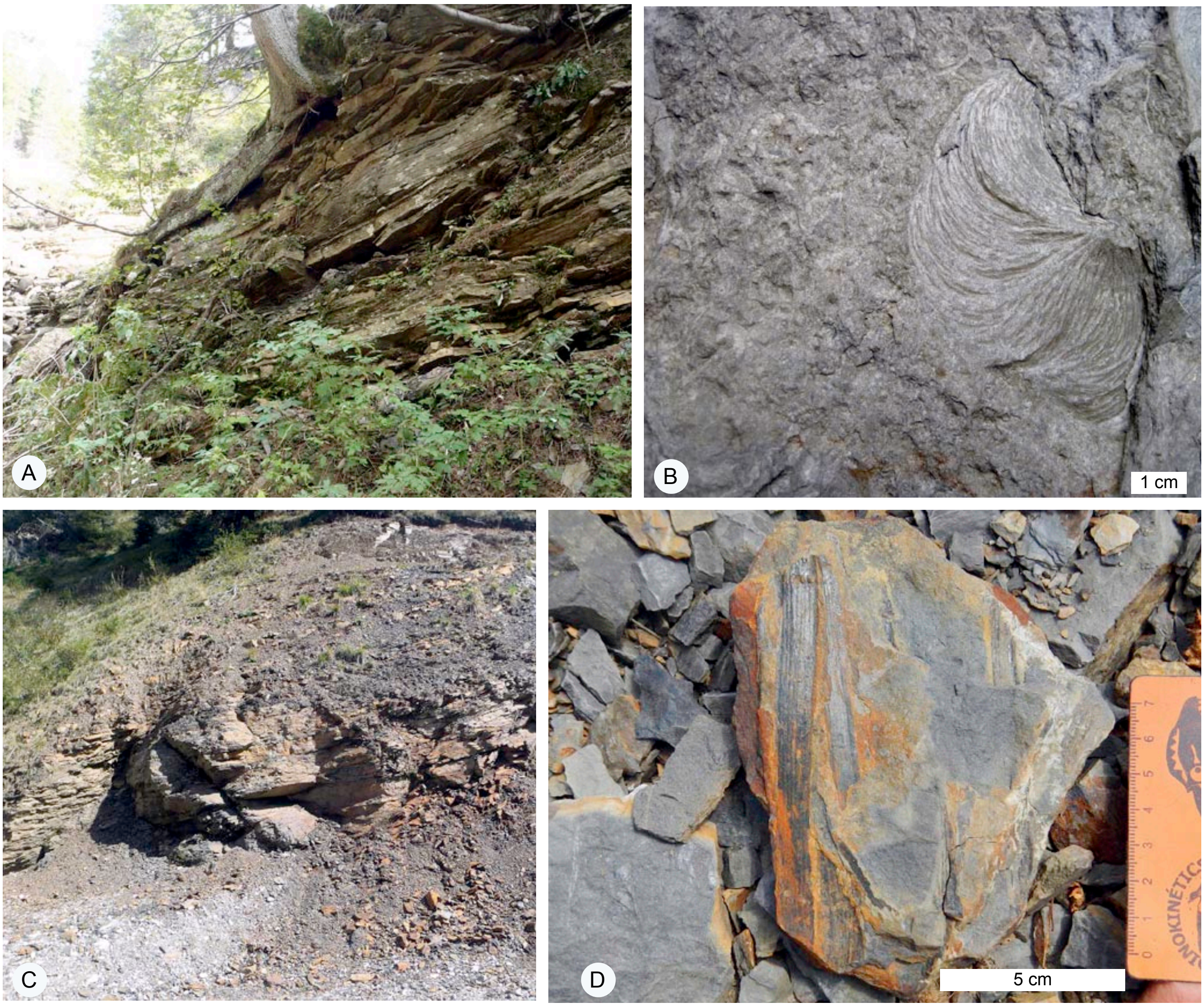
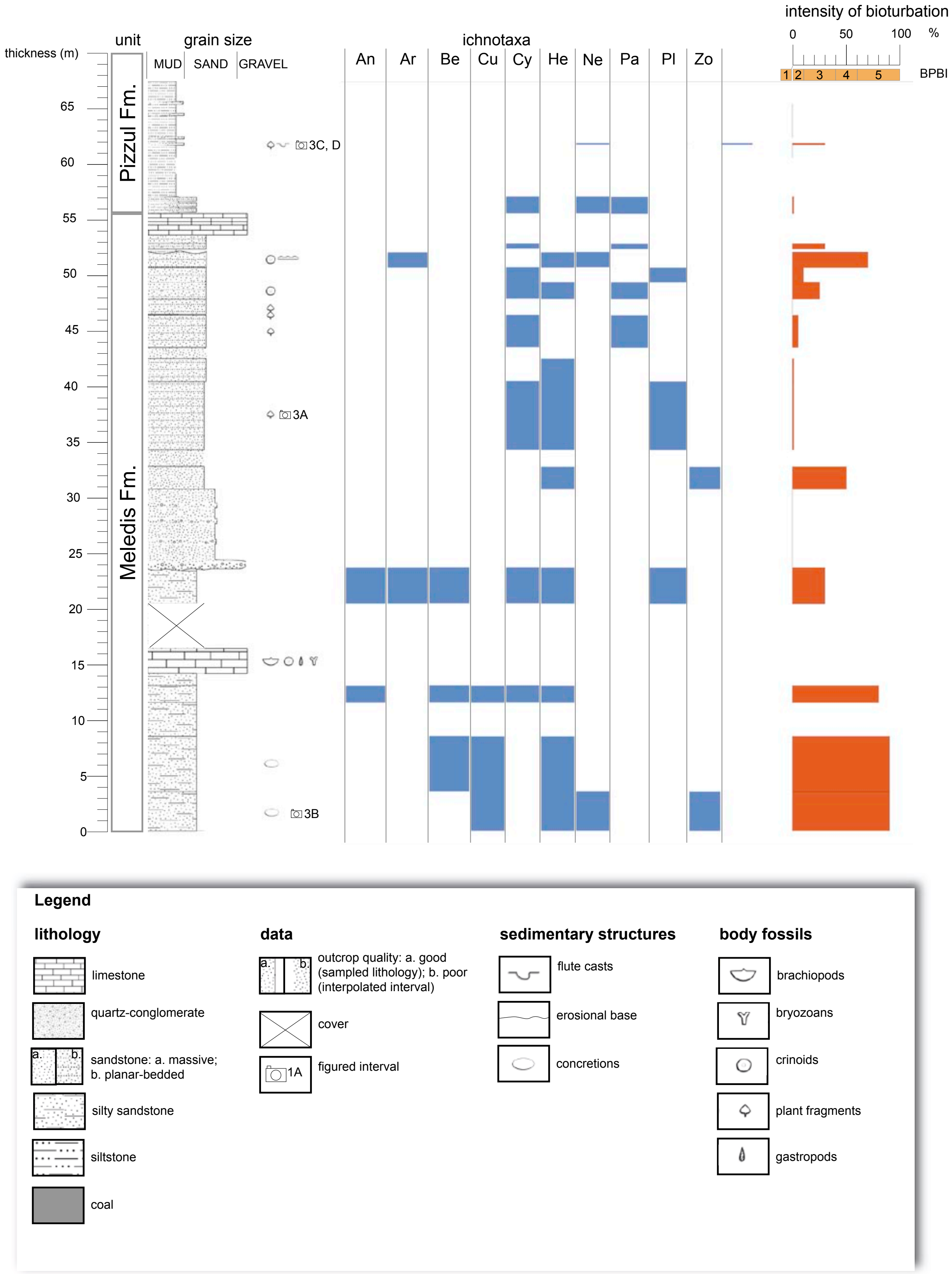


Fig. 3.


thickness (m)
unit
grain size
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Zo
intensity of bioturbation
0
50
100
%
1
2
3
4
5
BPBI
65
60
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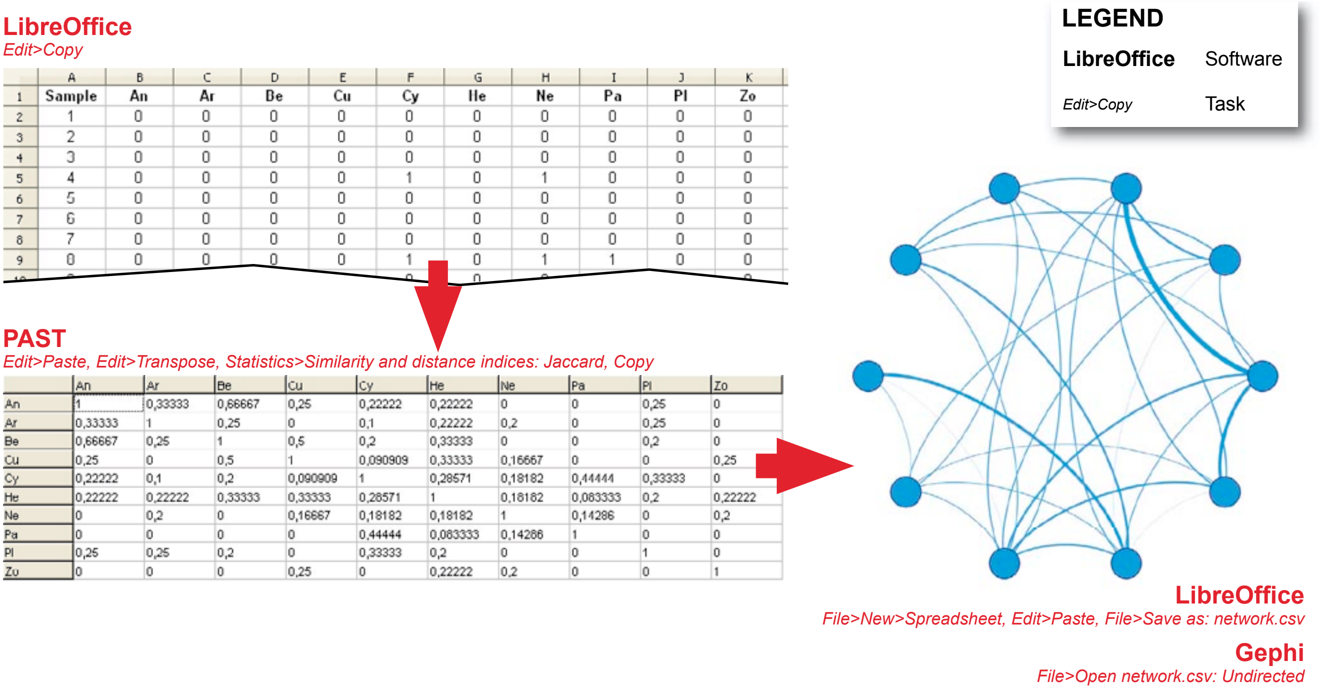
50
45
40
35
30
25
20
15
10
5
0
Pizzul Fm.
Meledis Fm.
3C, D
3A
3B
Legend
lithology
limestone
quartz-conglomerate
a.
b.
sandstone: a. massive; b. planar-bedded
silty sandstone
siltstone
coal
data
outcrop quality: a. good (sampled lithology); b. poor (interpolated interval)
cover
1A
figured interval
sedimentary structures
flute casts
erosional base
concretions
body fossils
brachiopods
bryozoans
crinoids
plant fragments
gastropods

Fig. 4.



LEGEND	
LibreOffice	Software
Edit>Copy	Task

LibreOffice

Edit>Copy

	A	B	C	D	E	F	G	H	I	J	K
1	Sample	An	Ar	Be	Cu	Cy	He	Ne	Pa	Pl	Zo
2	1	0	0	0	0	0	0	0	0	0	0
3	2	0	0	0	0	0	0	0	0	0	0
4	3	0	0	0	0	0	0	0	0	0	0
5	4	0	0	0	0	1	0	1	0	0	0
6	5	0	0	0	0	0	0	0	0	0	0
7	6	0	0	0	0	0	0	0	0	0	0
8	7	0	0	0	0	0	0	0	0	0	0
9	8	0	0	0	0	1	0	1	1	0	0

PAST

Edit>Paste, Edit>Transpose, Statistics>Similarity and distance indices: Jaccard, Copy

	An	Ar	Be	Cu	Cy	He	Ne	Pa	Pl	Zo
An	1	0,33333	0,66667	0,25	0,22222	0,22222	0	0	0,25	0
Ar	0,33333	1	0,25	0	0,1	0,22222	0,2	0	0,25	0
Be	0,66667	0,25	1	0,5	0,2	0,33333	0	0	0,2	0
Cu	0,25	0	0,5	1	0,090909	0,33333	0,16667	0	0	0,25
Cy	0,22222	0,1	0,2	0,090909	1	0,28571	0,18182	0,44444	0,33333	0
He	0,22222	0,22222	0,33333	0,33333	0,28571	1	0,18182	0,083333	0,2	0,22222
Ne	0	0,2	0	0,16667	0,18182	0,18182	1	0,14286	0	0,2
Pa	0	0	0	0	0,44444	0,083333	0,14286	1	0	0
Pl	0,25	0,25	0,2	0	0,33333	0,2	0	0	1	0
Zo	0	0	0	0,25	0	0,22222	0,2	0	0	1

LibreOffice

File>New>Spreadsheet, Edit>Paste, File>Save as: network.csv

Gephi

File>Open network.csv: Undirected

Fig. 5.

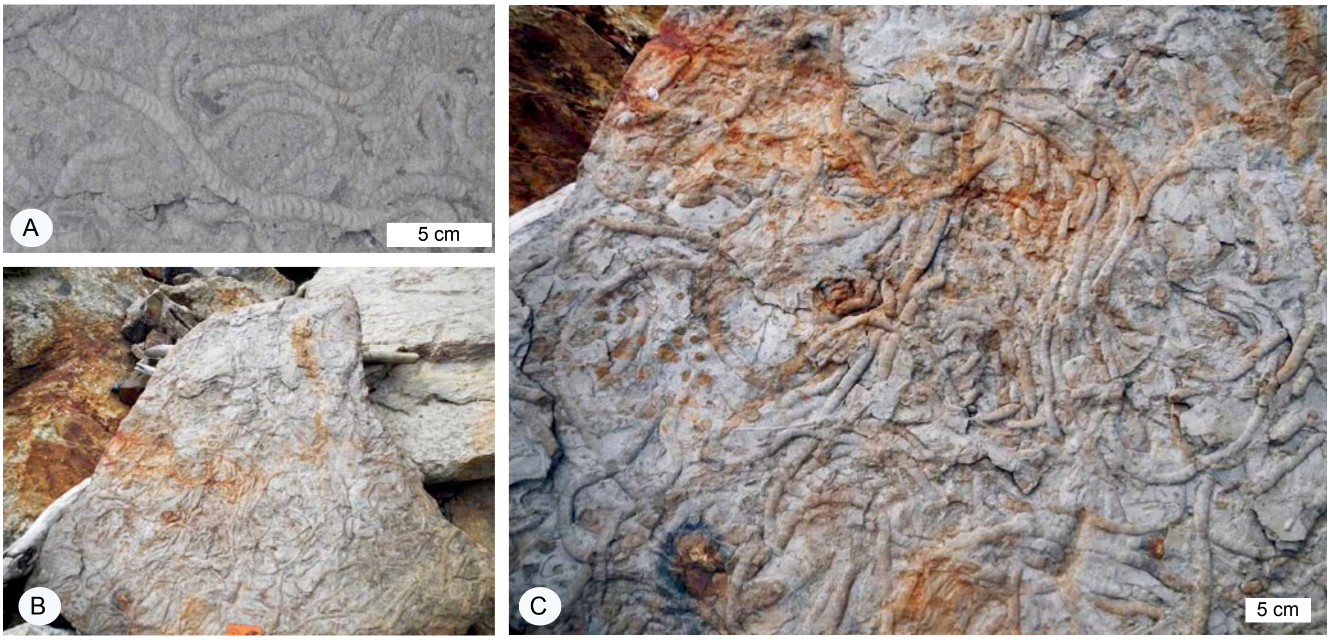


Fig. 6.

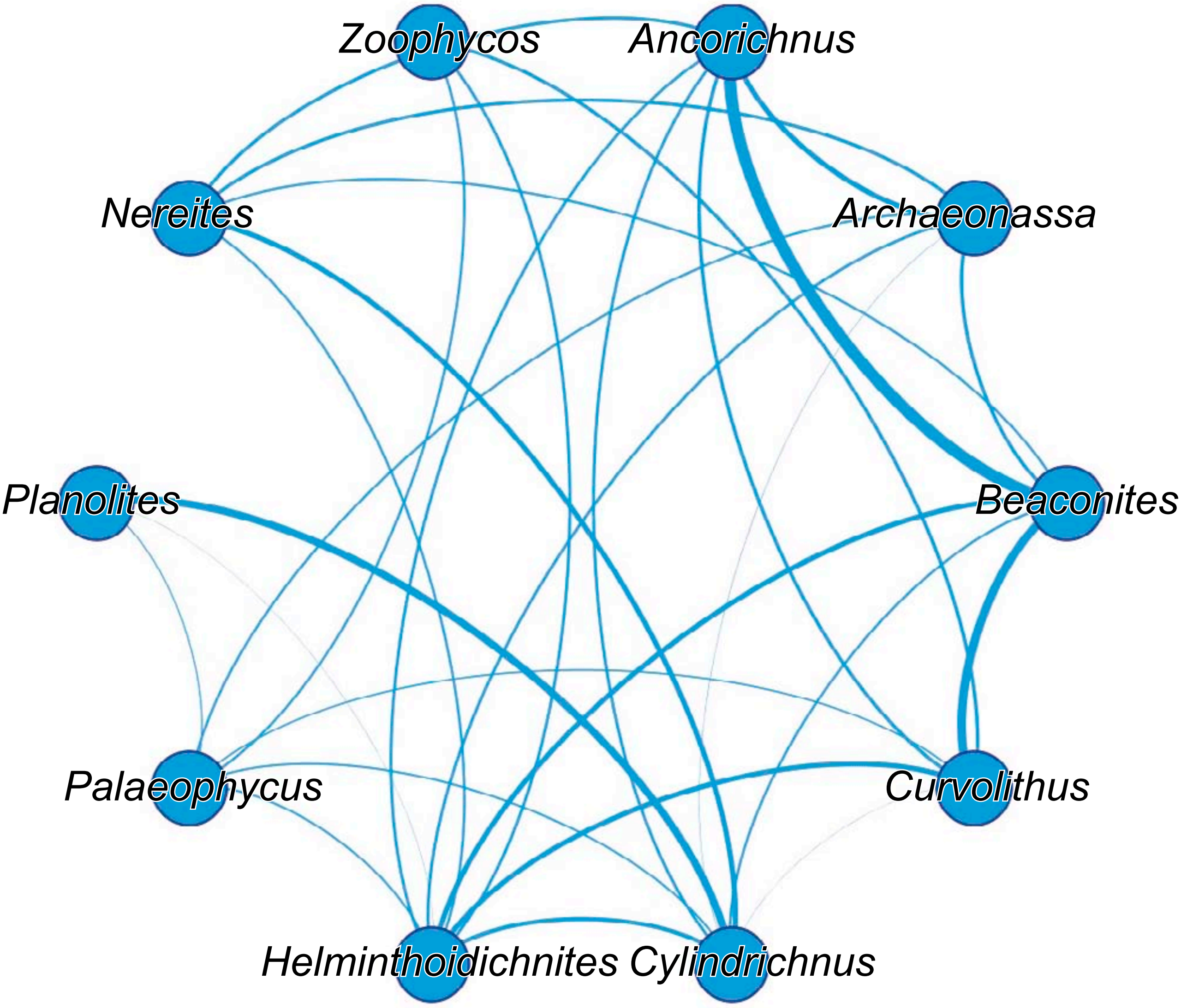

Zoophycos
Ancorichnus
Nereites
Archaeonassa
Planolites
Beaconites
Palaeophycus
Curvolithus
Helminthoidichnites
Cylindrichnus

Fig. 7.

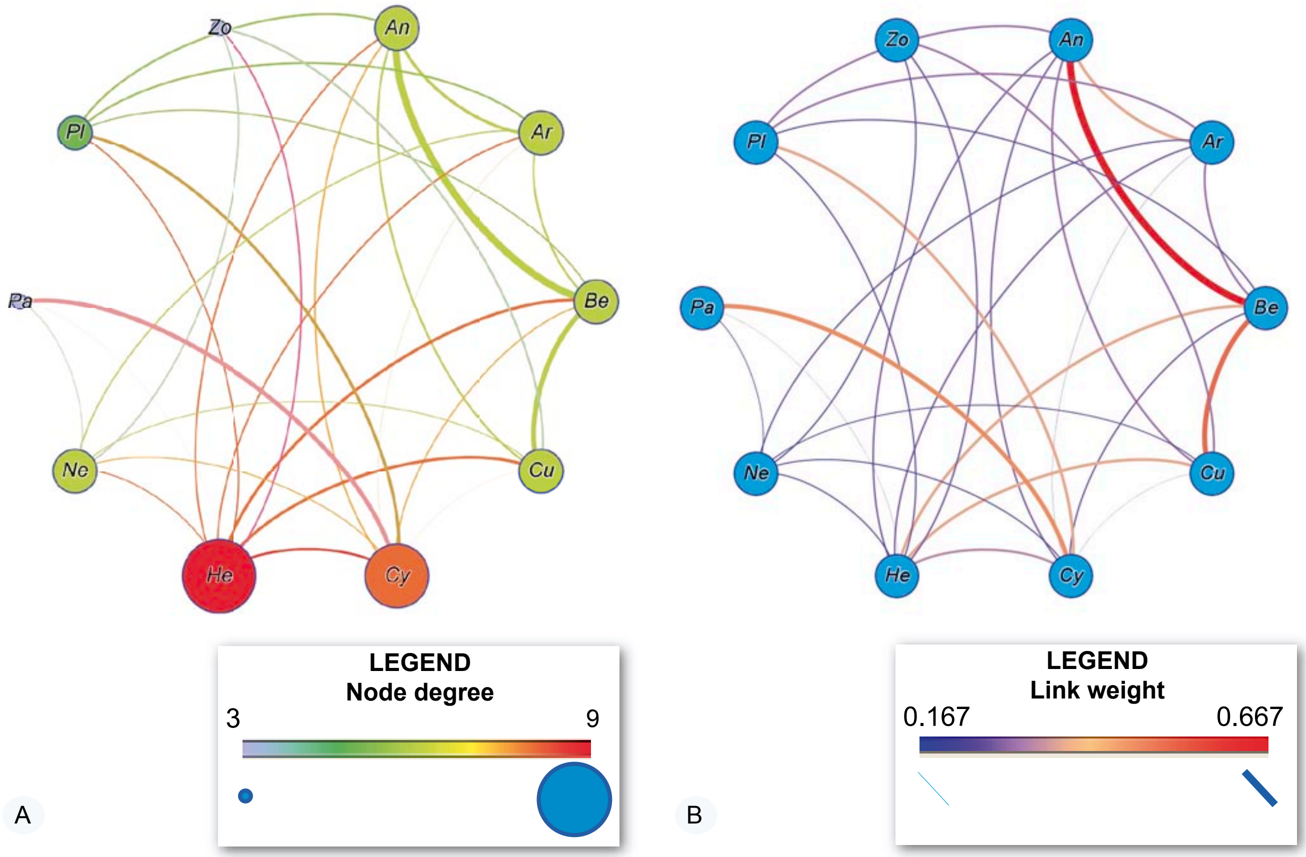

Zo
An
Pl
Ar
Pa
Be
Ne
Cu
He
Cy
LEGEND
Node degree
3
9
A
Zo
An
Pl
Ar
Pa
Be
Ne
Cu
He
Cy
LEGEND
Link weight
0.167
0.667
B

Fig. 8.

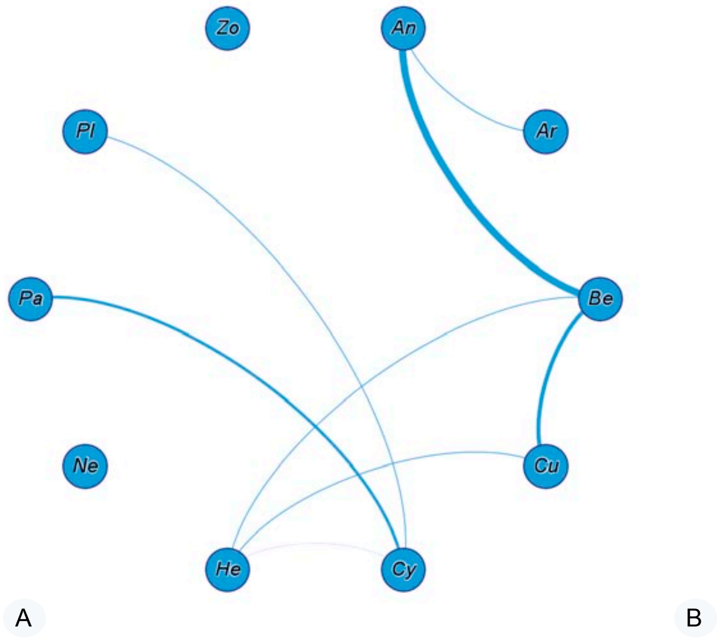


Fig. 9.

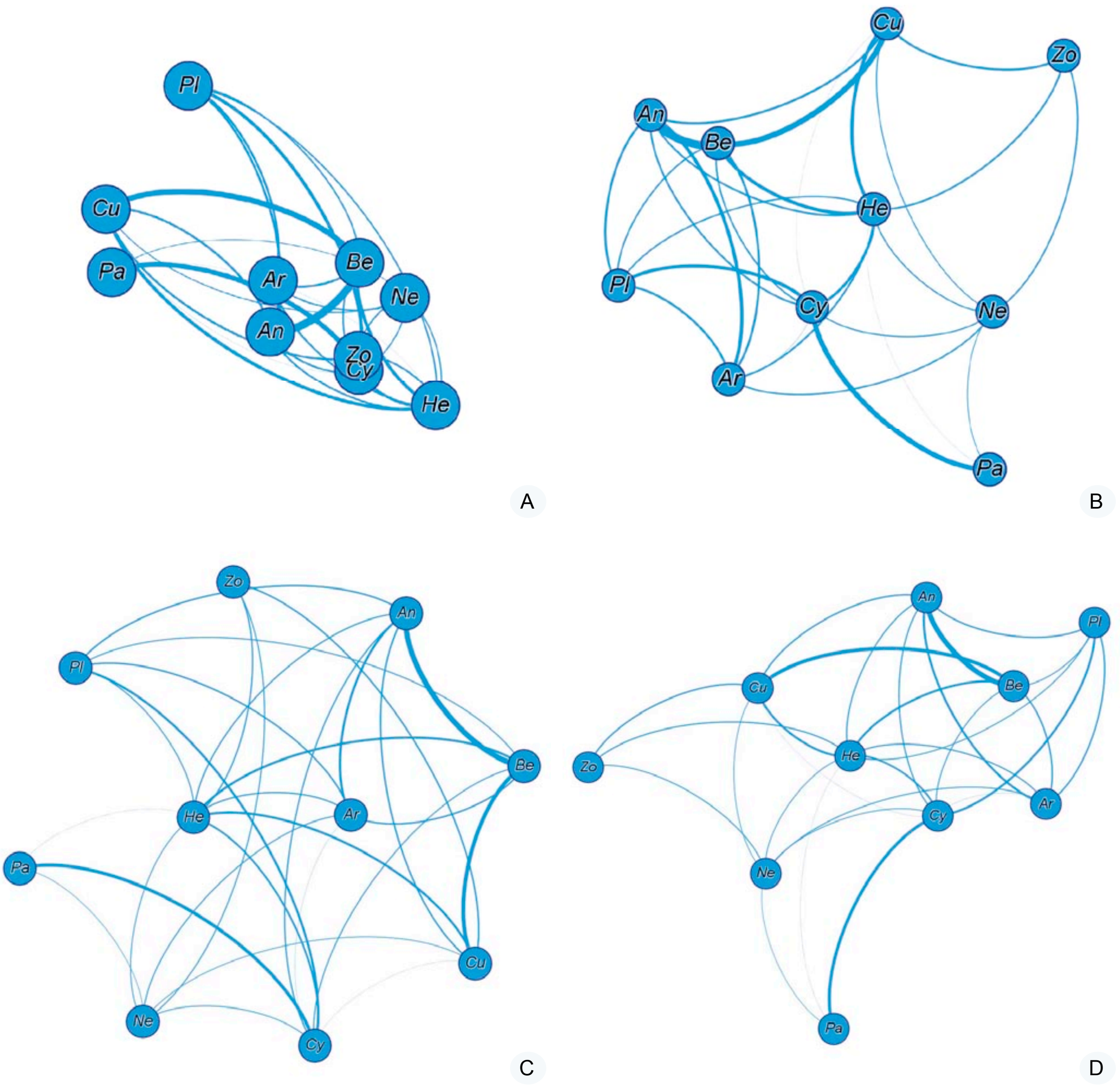

Pl
Cu
Pa
Ar
Be
Ne
An
Zo
Cy
He
A
Cu
Zo
An
Be
He
Pl
Cy
Ne
Ar
Pa
B
Zo
An
Pl
Be
He
Ar
Pa
Cu
Ne
Cy
C
An
Pl
Cu
Be
Zo
He
Ar
Cy
Ne
Pa
D

Fig. 10.

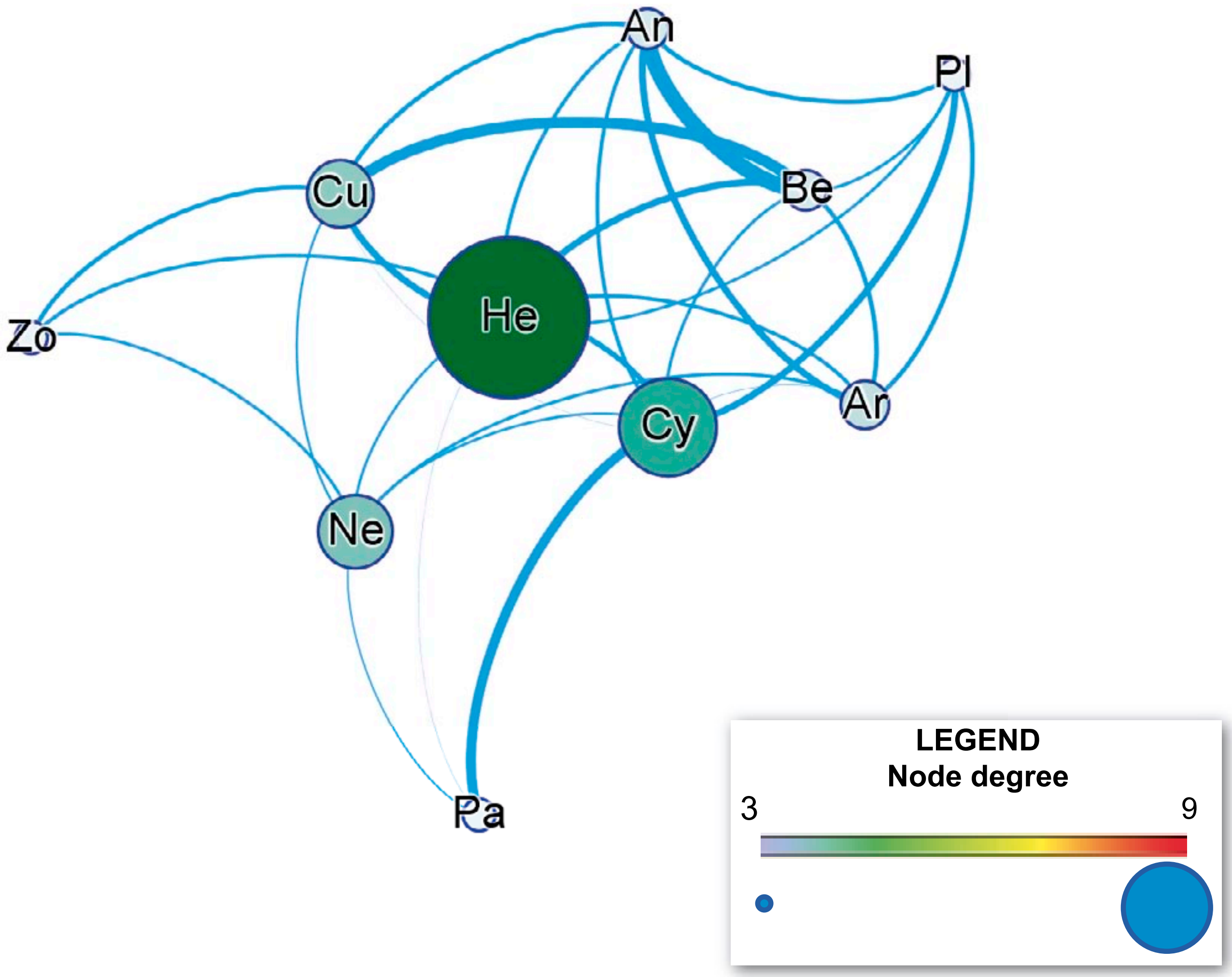


Fig. 11.

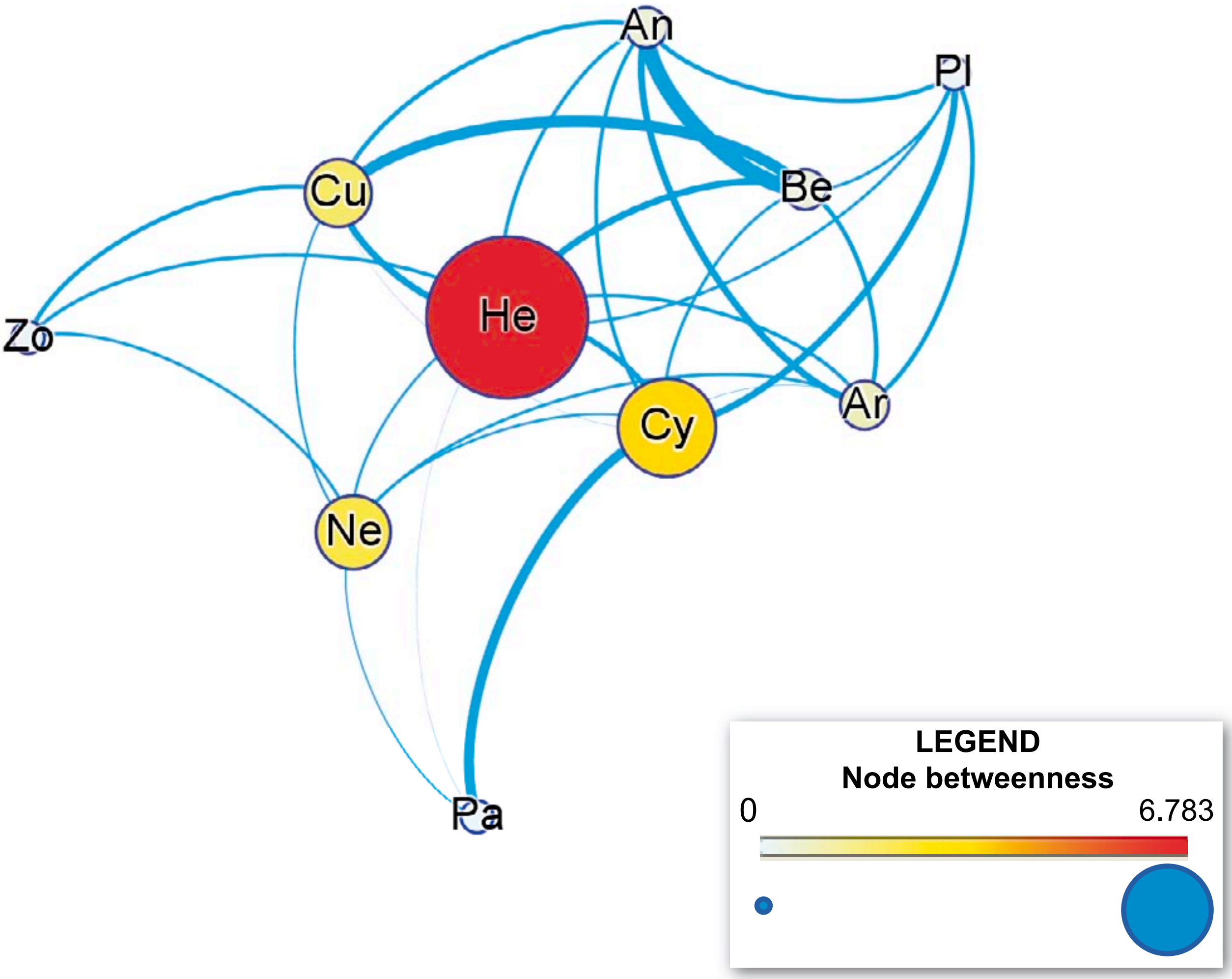


Fig. 12.

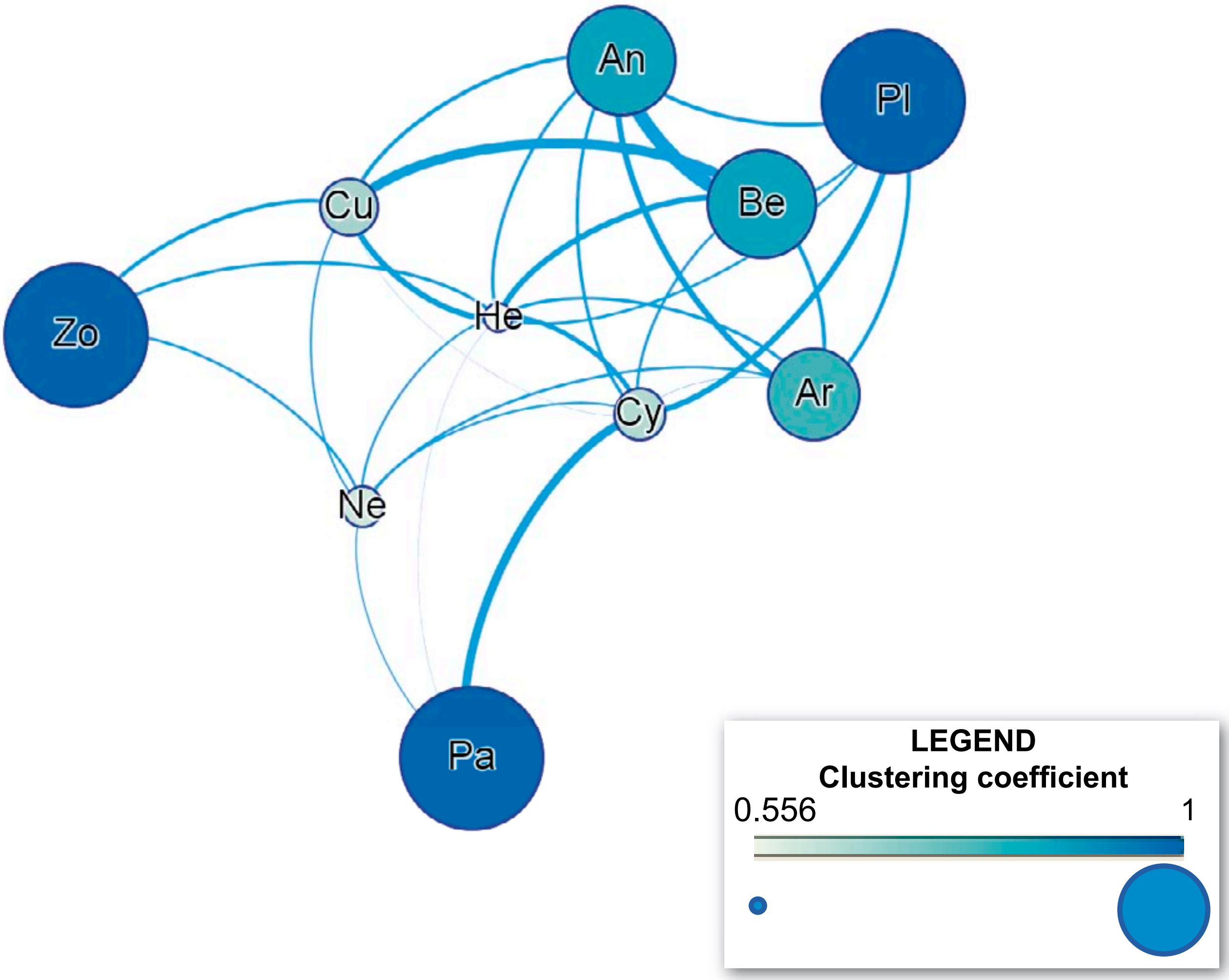

An
Pl
Cu
Be
Zo
He
Cy
Ar
Ne
Pa
LEGEND
Clustering coefficient
0.556
1

Fig. 13.

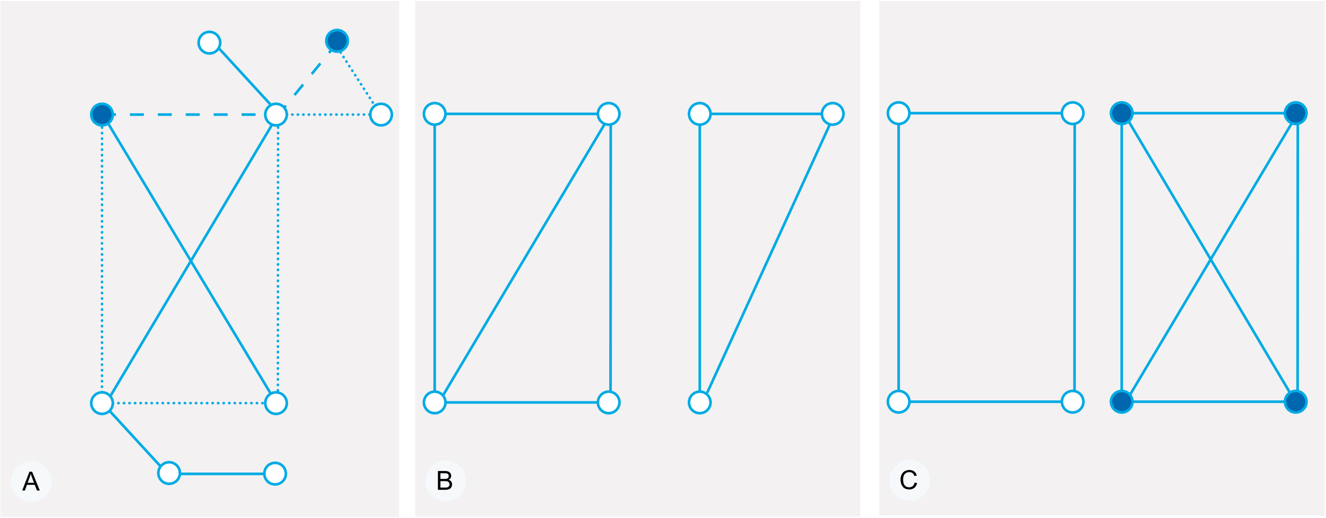


Fig. 14.

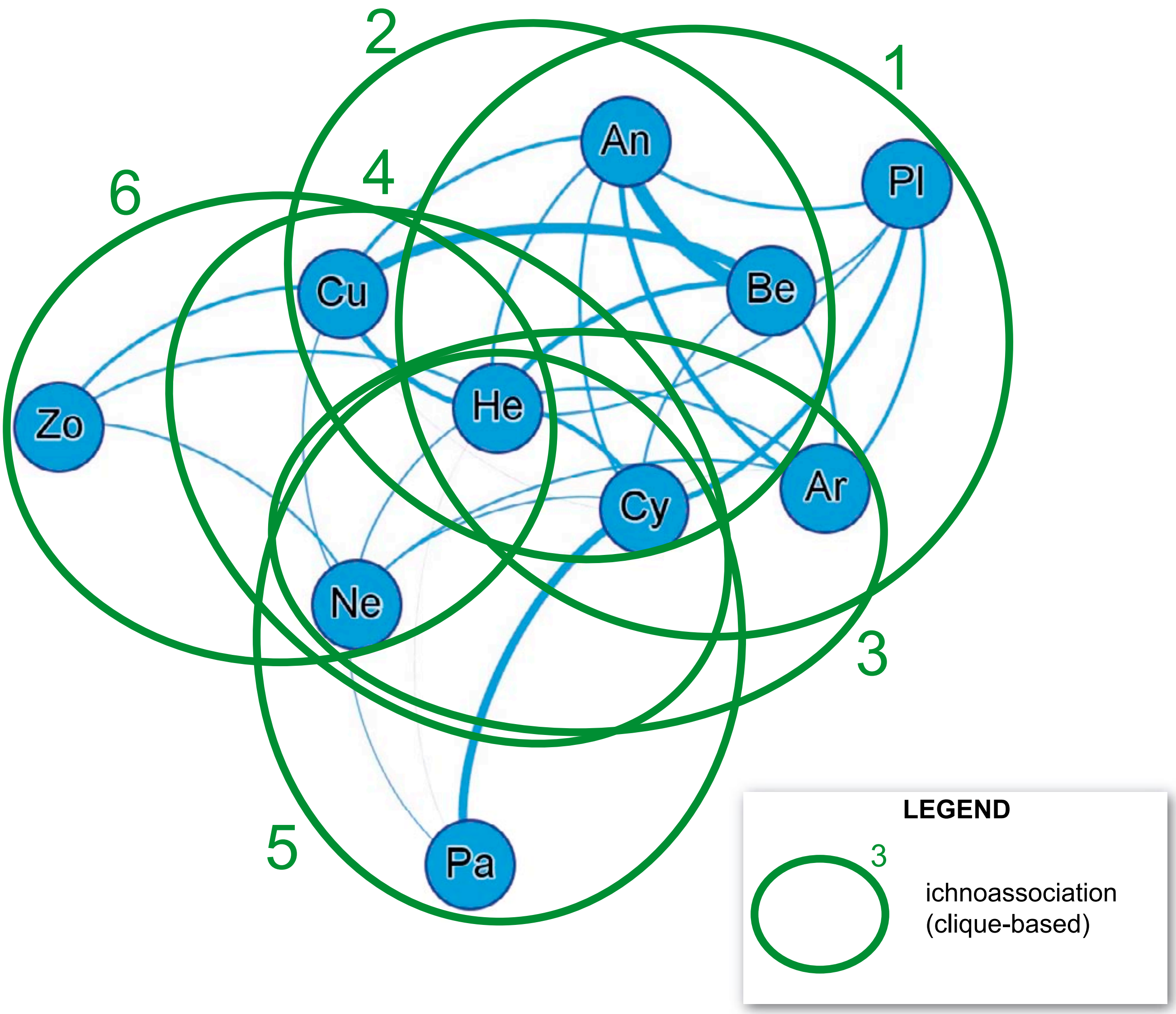

2
1
An
Pl
6
4
Cu
Be
Zo
He
Ar
Cy
Ne
3
5
Pa
LEGEND
3
ichnoassociation
(clique-based)

Fig. 15.

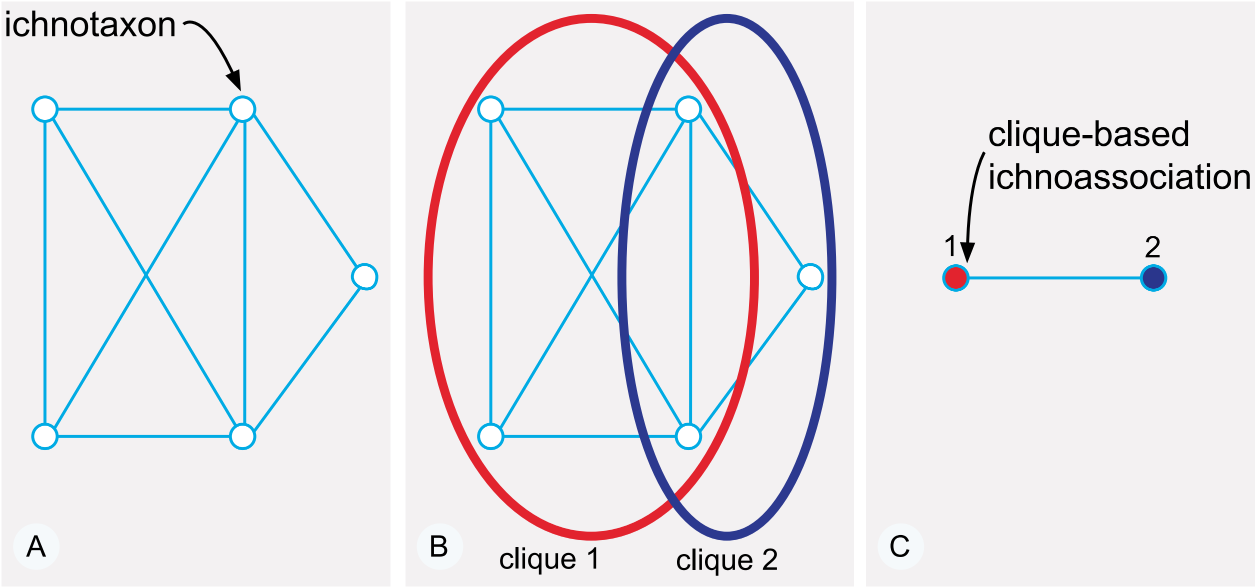

ichnotaxon
A
B
clique 1
clique 2
C
clique-based
ichnoassociation
1
2

Fig. 16.

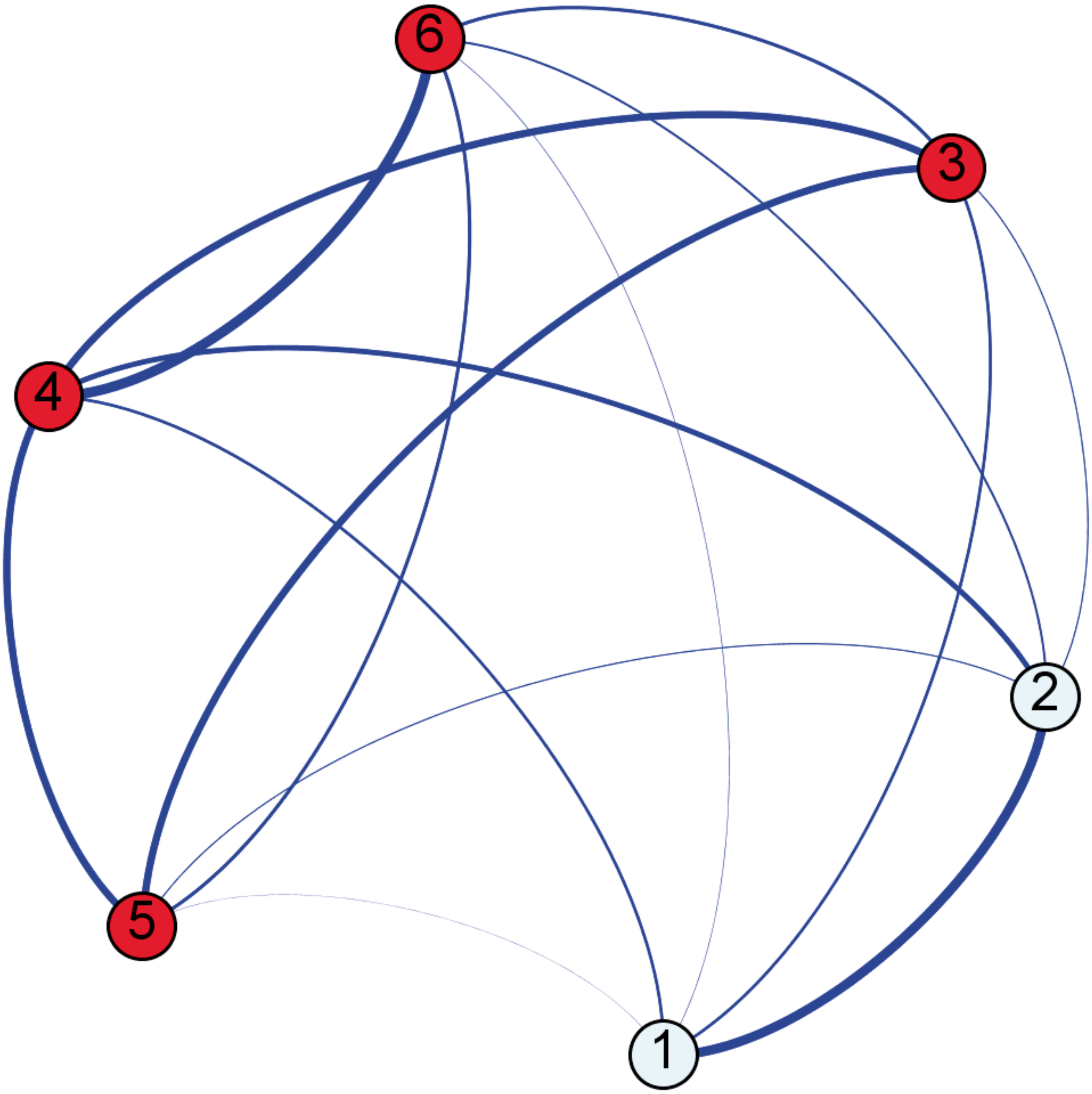


Fig. 17.

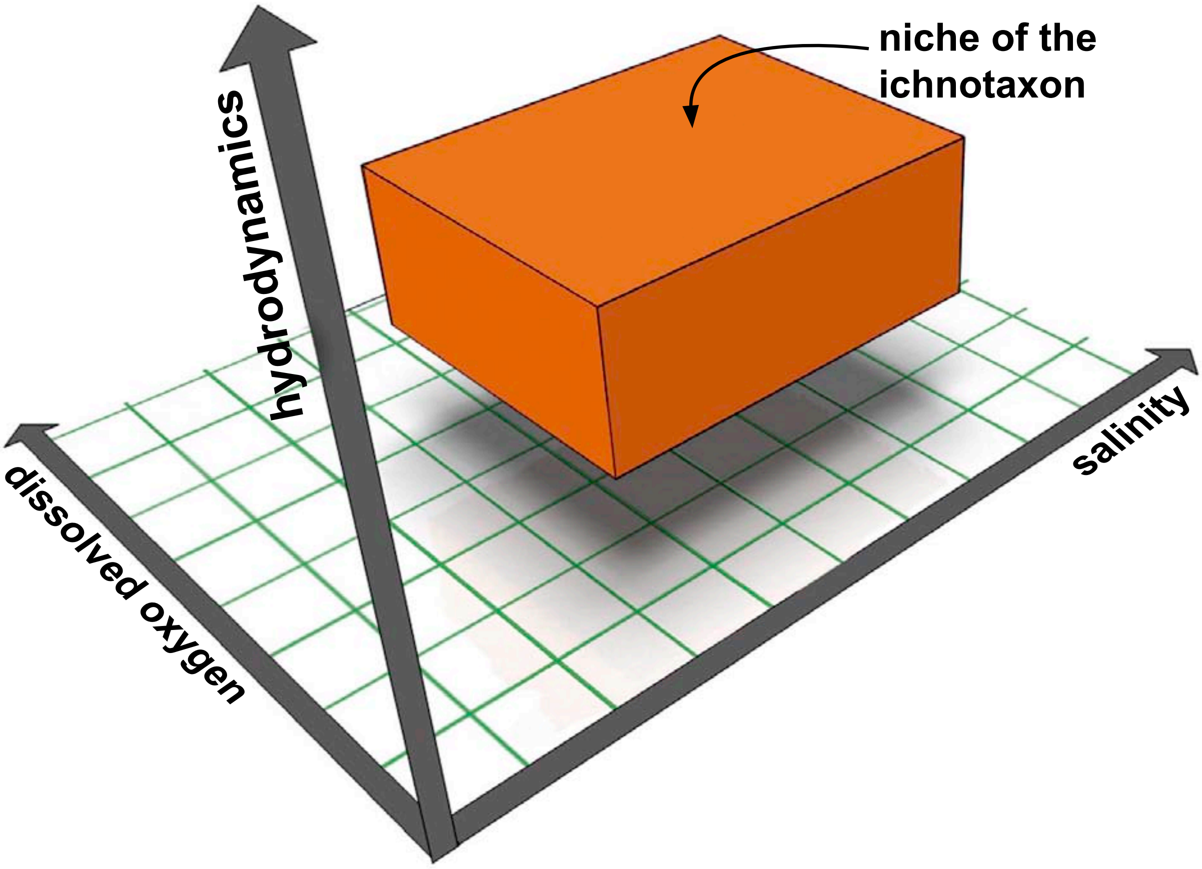

niche of the ichnotaxon
hydrodynamics
dissolved oxygen
salinity

Fig. 18.

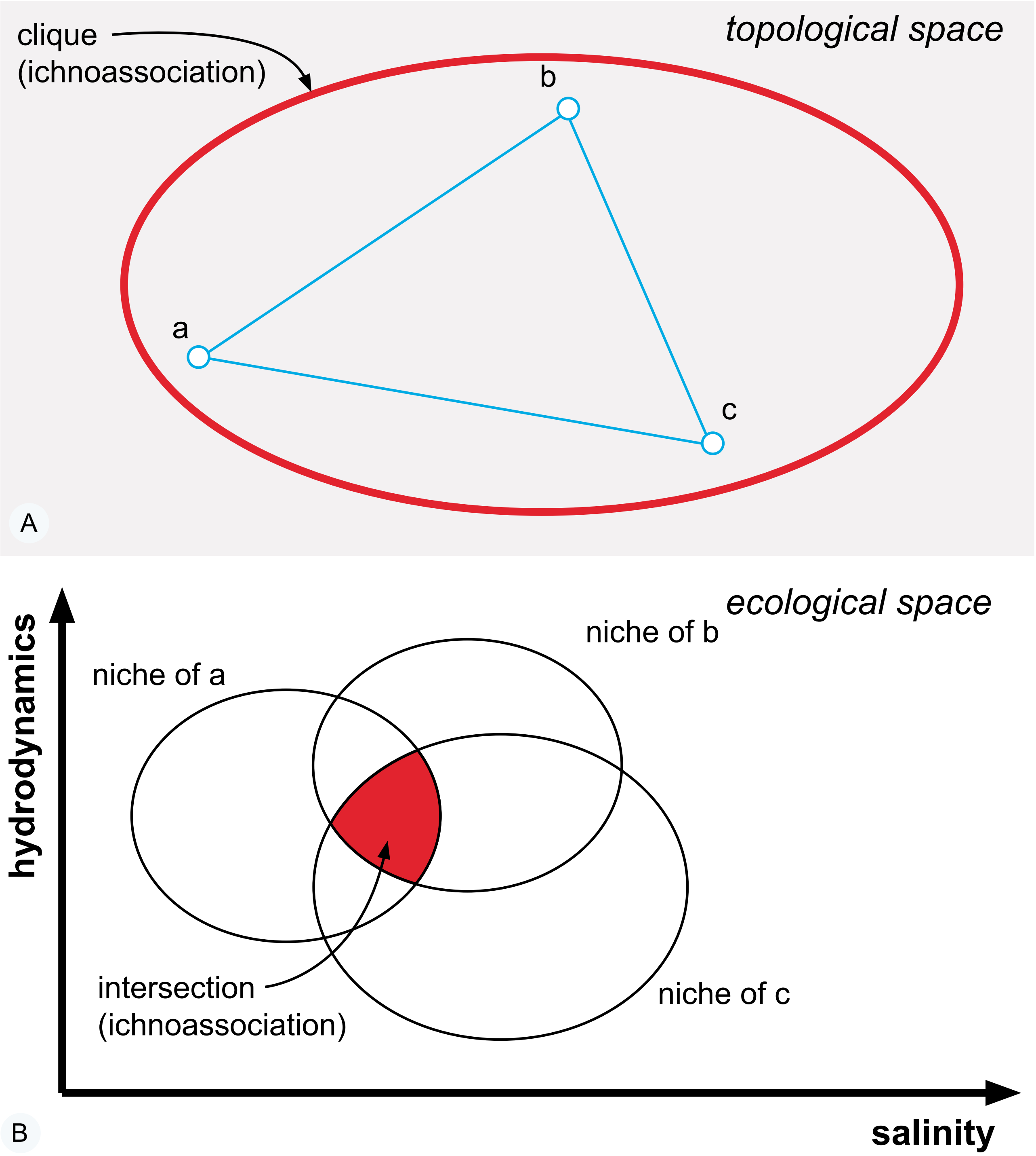

clique
(ichnoassociation)
topological space
b
a
c
A
ecological space
hydrodynamics
niche of b
niche of a
intersection
(ichnoassociation)
niche of c
salinity
B

Fig. 19.

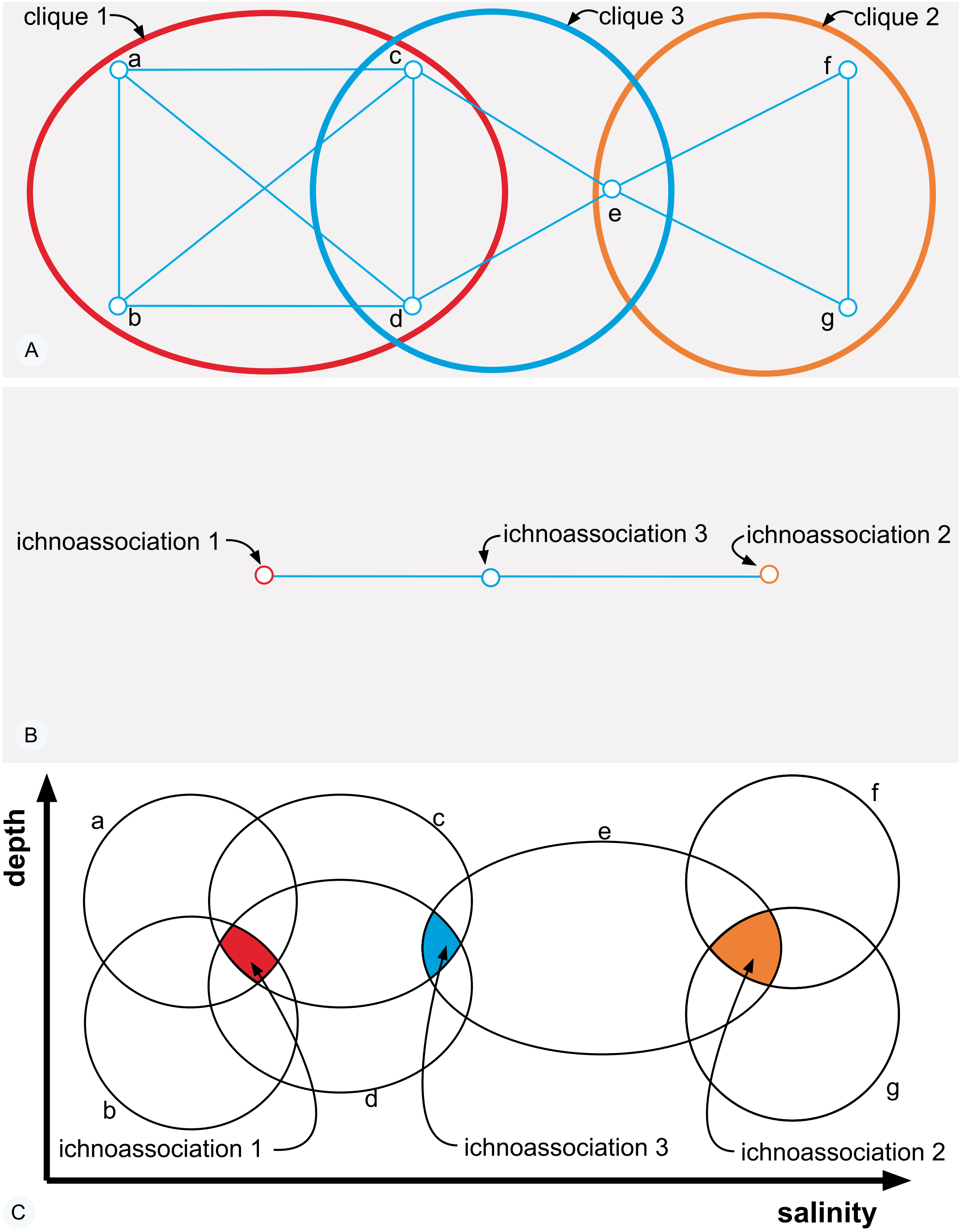

clique 1
clique 3
clique 2
a
c
f
e
b
d
g
A
ichnoassociation 1
ichnoassociation 3
ichnoassociation 2
B
depth
a
c
e
f
b
d
g
ichnoassociation 1
ichnoassociation 3
ichnoassociation 2
C
salinity

Fig. 20.

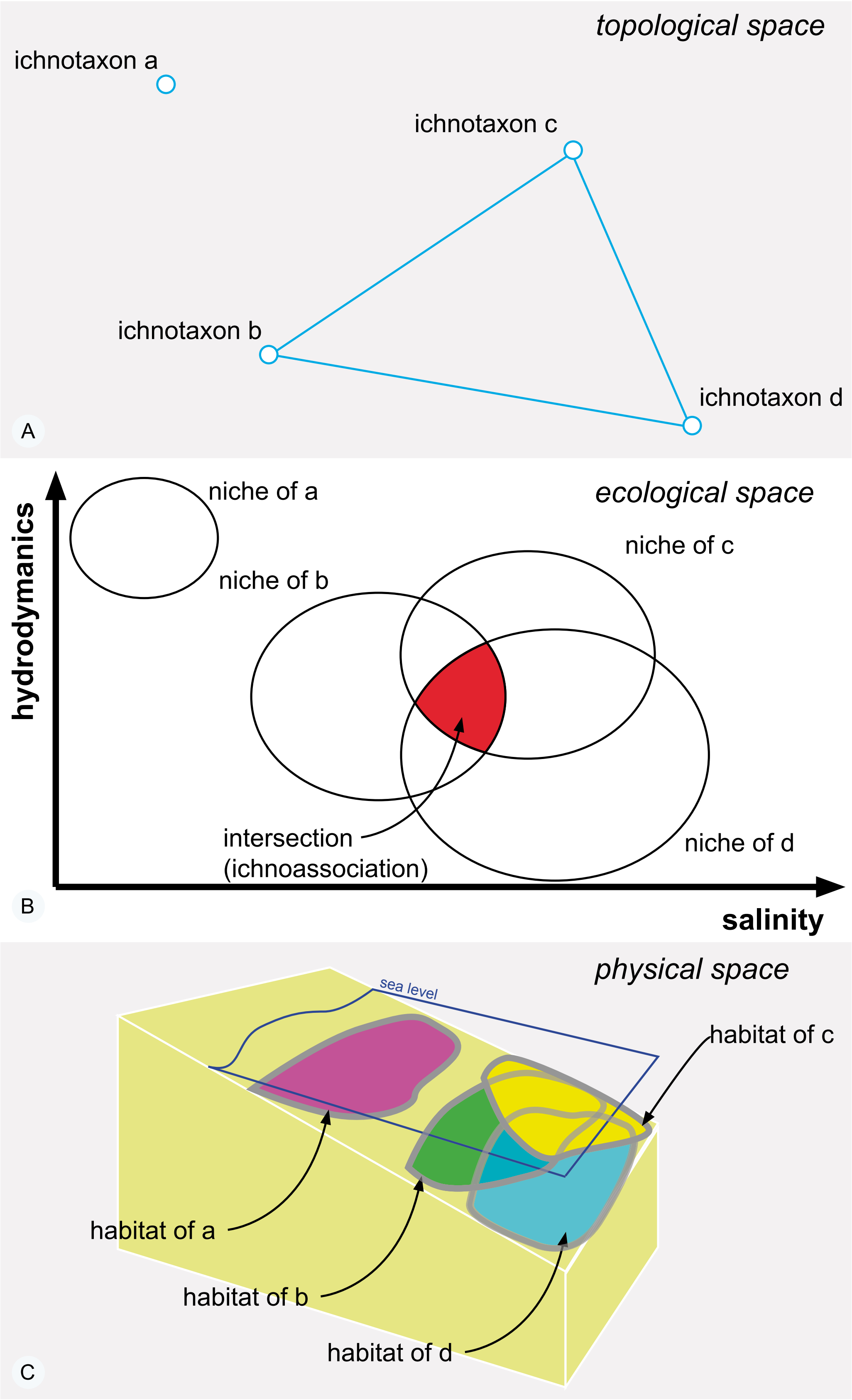

topological space
ichnotaxon a
ichnotaxon c
ichnotaxon b
ichnotaxon d
A
hydrodymanics
niche of a
ecological space
niche of c
niche of b
intersection
(ichnoassociation)
niche of d
B
salinity
physical space
sea level
habitat of c
habitat of a
habitat of b
habitat of d
C

Fig. 21.

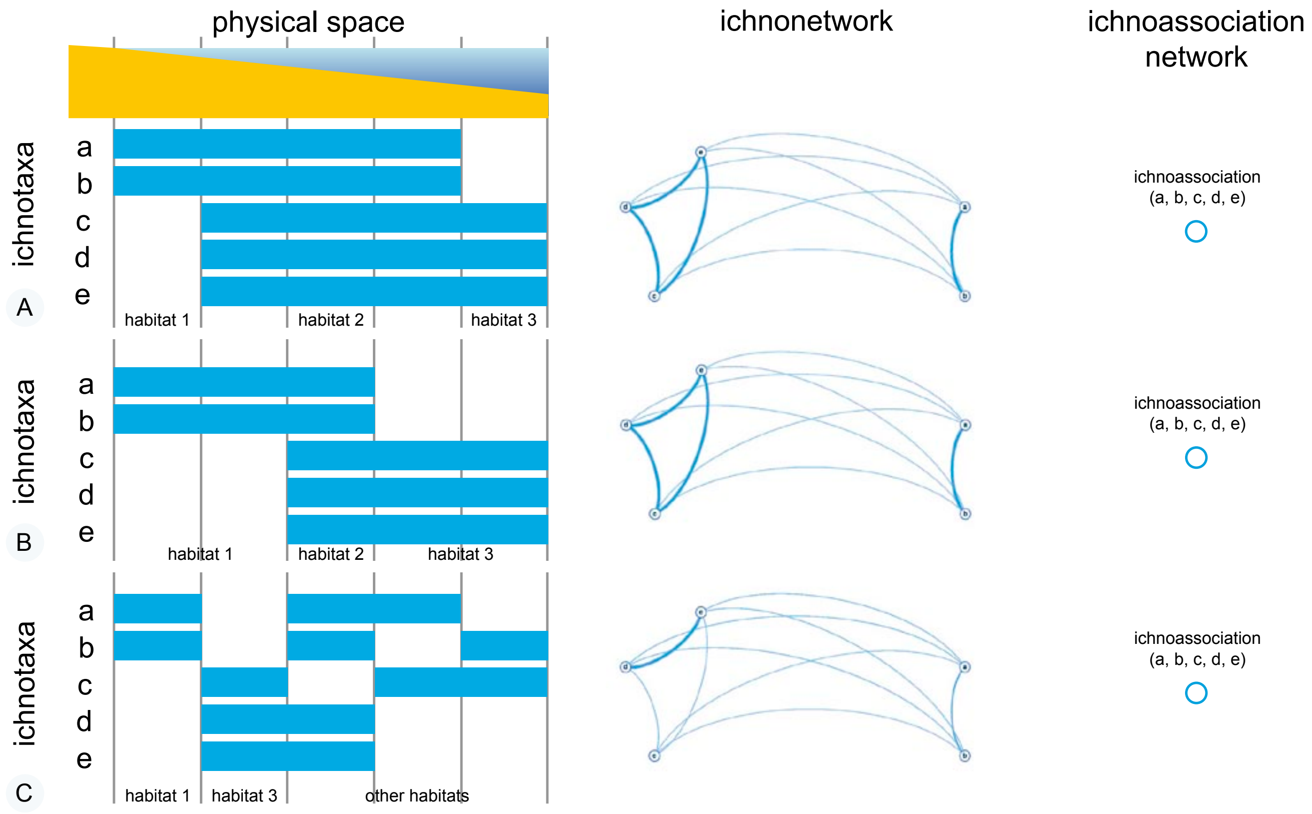

physical space
ichnonetwork
ichnoassociation network
ichnotaxa
a
b
c
d
e
A
habitat 1
habitat 2
habitat 3
ichnoassociation (a, b, c, d, e)
ichnotaxa
a
b
c
d
e
B
habitat 1
habitat 2
habitat 3
ichnoassociation (a, b, c, d, e)
ichnotaxa
a
b
c
d
e
C
habitat 1
habitat 3
other habitats
ichnoassociation (a, b, c, d, e)

Fig. 22.

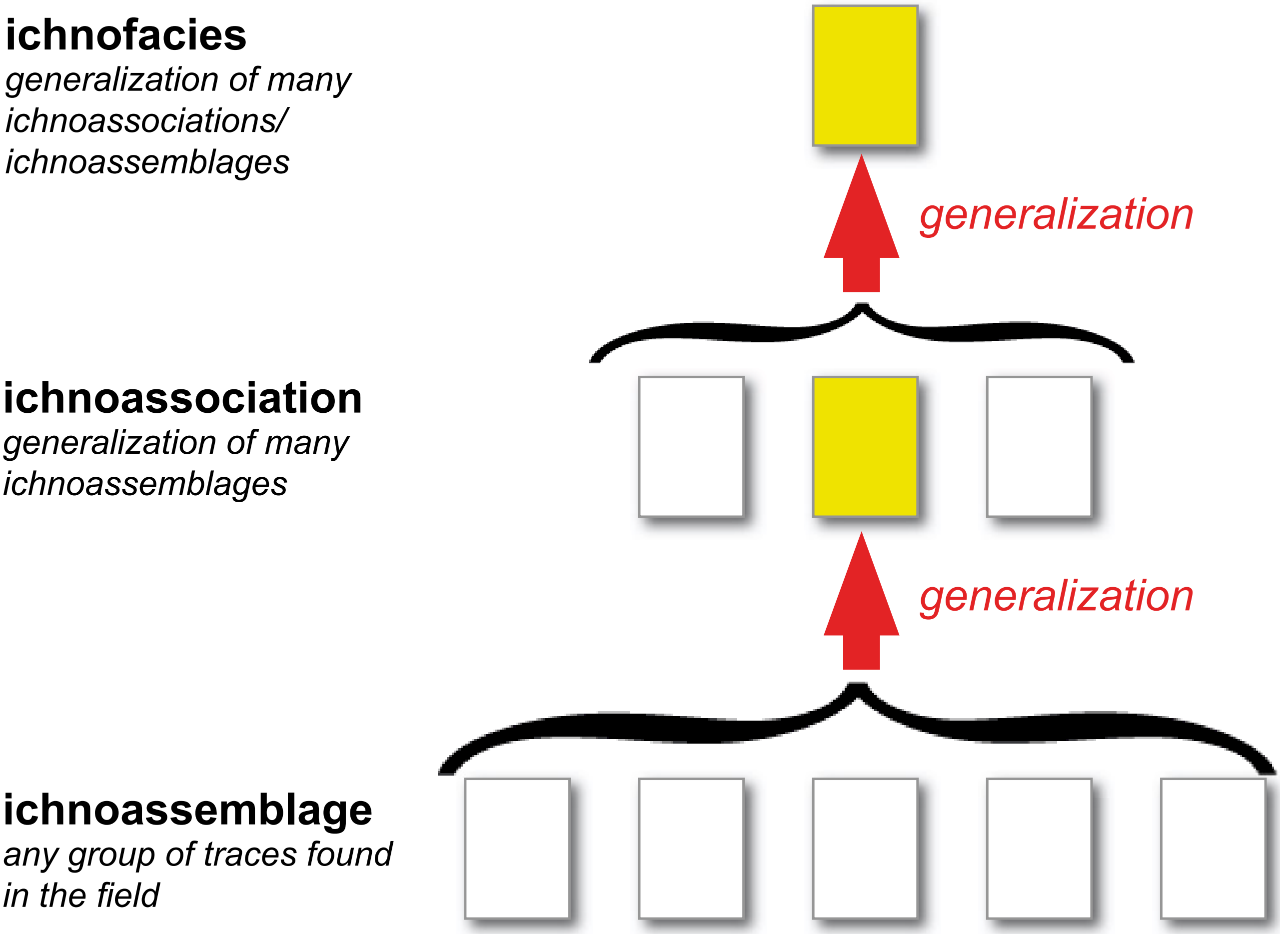

ichnofacies
generalization of many ichnoassociations/ ichnoassemblages
generalization
ichnoassociation
generalization of many ichnoassemblages
generalization
ichnoassemblage
any group of traces found in the field

Fig. 23.

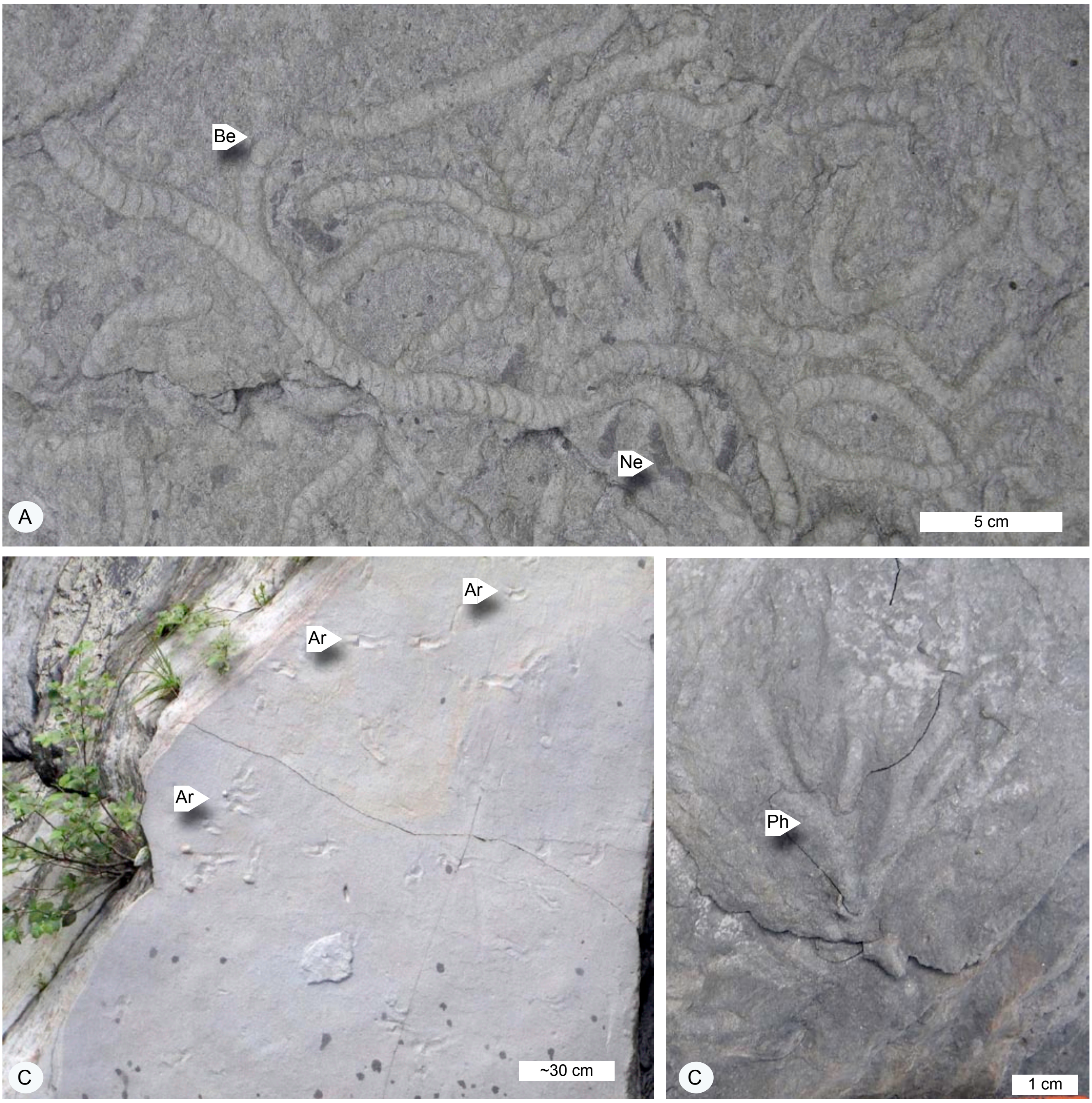


Fig. 24.

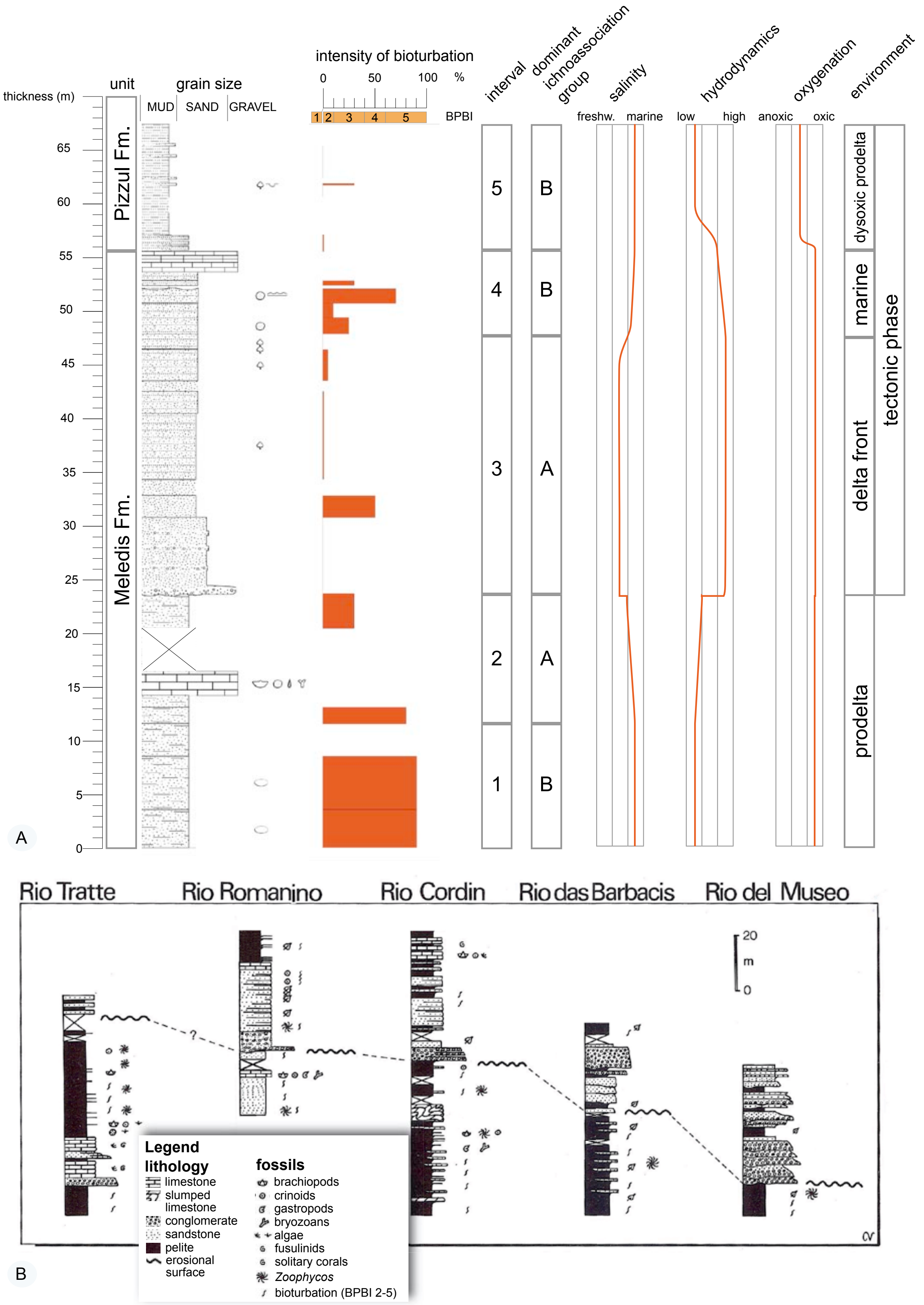

thickness (m)
unit
grain size
MUD
SAND
GRAVEL
intensity of bioturbation
0
50
100
%
1
2
3
4
5
BPBI
interval
dominant ichnoassociation group
salinity
freshw.
marine
hydrodynamics
low
high
oxygenation
anoxic
oxic
environment
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Pizzul Fm.
Meledis Fm.
5
4
3
2
1
B
B
A
A
B
dysoxic prodelta
marine
delta front
prodelta
tectonic phase
A
Rio Tratte
Rio Romanino
Rio Cordin
Rio das Barbacis
Rio del Museo
20
m
0
?
Legend
lithology
limestone
slumped limestone
conglomerate
sandstone
pelite
erosional surface
fossils
brachiopods
crinoids
gastropods
bryozoans
algae
fusulinids
solitary corals
Zoophycos
bioturbation (BPBI 2-5)
B

Fig. 25.

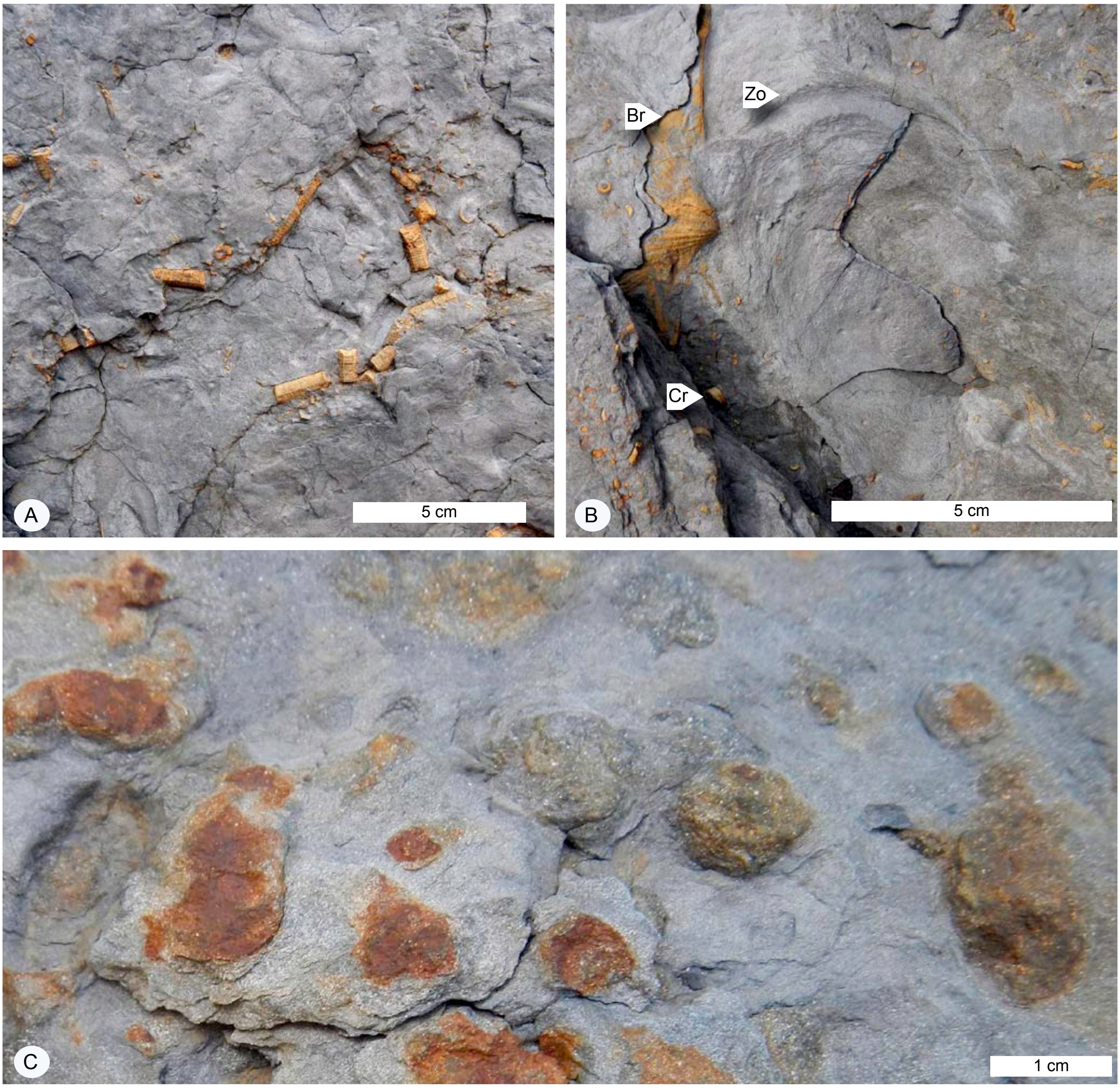


Fig. 26.

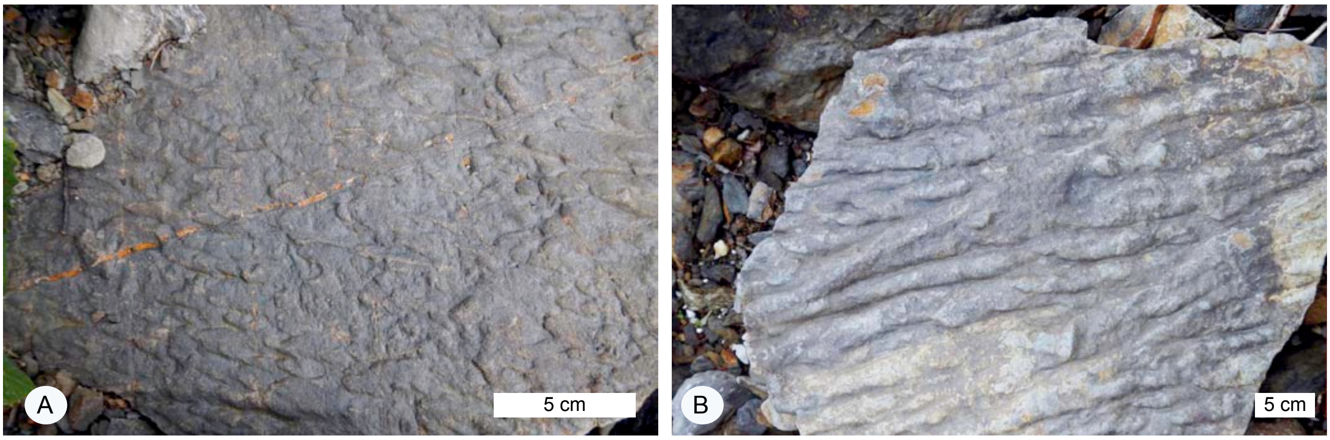


Fig. 27.

Chapter 4

4.2 Behaviours mapped by new geographies: ichnonetwork analysis of the Val Dolce Formation (Lower Permian; Italy-Austria)

From: Baucon, A., Venturini, C., Neto de Carvalho, C., Felletti, F., Mattoni, G. 2014. Behaviours mapped by new geographies: ichnonetwork analysis of the Val Dolce Formation (Lower Permian; Italy-Austria). Geosphere (submitted)

Behaviours mapped by new geographies: ichnonetwork analysis of the Val Dolce Formation (Lower Permian; Italy-Austria)

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Abstract

The Pramollo Basin (Italy-Austria) is one of the richest body and trace fossil sites of the Alps, exhibiting a well-preserved Permian-Carboniferous fluvio-deltaic and marginal-marine sedimentary succession. Despite the exceptionally abundant and well-preserved ichnological heritage, the trace fossils of the Pramollo Basin are understudied, with particular regard of the Permian units.

This study focuses on the ichnofauna of the Val Dolce Formation (Permian; Asselian p.p.-?Sakmarian p.p.), aiming to document its ichnological heritage and reconstruct its palaeoenvironment. These research questions are addressed by applying network theory, an emerging field of complexity science which focuses on web-like systems made of interconnected entities. In fact, an ichnological system can be seen as a set of interlinked ichnotaxa, the topology of which depends on the organism-environment interactions.

The following ichnotaxa are documented from the Val Dolce Formation: *Archaeonassa* isp., *Curvolithus simplex, Cylindrichnus* isp., *Helminthoidichnites tenuis, Nereites missouriensis, Planolites* isp., *Phymatoderma* isp., *Pramollichnus pastae, Psammichnites plummeri, Taenidium, Zoophycos* isp. Network analysis indicates that the Val Dolce ichnological system is structured, with ichnotaxa organized in environment-driven ichnoassociations: *Cylindrichnus-Planolites* (proximal delta front), *Phymatoderma-Zoophycos* (prodelta with dysoxic porewaters), *Cylindrichnus-Helminthoidichnites-Curvolithus-Zoophycos* (distal delta front-proximal prodelta), *Helminthoidichnites-Taenidium-Curvolithus-Nereites-Zoophycos* (prodelta). Furthermore, the delta-front-prodelta gradient is accompanied by increasing bioturbation intensity and diversity, reflecting the decreasing intensity of major environmental stressors (hydrodynamics, freshwater input, turbidity). Centrality measures, proper of network analysis, allow to discern the topological position of traces within the studied system, detecting the palaeoenvironmental resolution of individual ichnotaxa.

As intersections of sets can be described by networks, the studied ichnoassociations can be considered as intersecting behavioural niches. In fact, in analogy with the concept of Hutchinsonian niche, an ichnotaxon's niche exists in a multidimensional abstract space defined by environmental parameters, which are expressed as spatial variables in the (palaeo)landscape. Consequently, ichnoassociations are not just association patterns, but they represent spatial, environmental and topological entities.

keywords: network theory, ichnoassociation, ichnoassemblage, niche, Pramollo Basin

INTRODUCTION

> "In addition to that branch of geometry which is concerned with distances, and which has always received the greatest attention, there is another branch, hitherto almost unknown, which Leibniz first mentioned, calling it the geometry of position"
>
> - Euler, *Solutio problematis ad geometriam situs pertinentis* (Euler, 1736)

The process of describing real-world phenomena as networks – sets of nodes connected by links – is rooted into the 18th century, when Euler used an abstract representation of the city of Königsberg (Lewis, 2009; Barbasi, 2002; Euler, 1736). Since then, network theory has emerged as an efficient framework for describing and analyzing complex systems, from food webs to the Internet. In fact, many natural and artificial systems can be seen as web-like groups of interconnected entities, the topology of which can be analyzed by graphical and mathematical tools. Consequently, network theory finds application in the most disparate disciplines, including biology, computer science and physics

(Réka and Barbási, 2002). In particular, social sciences greately benefited from the network approach, according to which individuals are embedded in webs of interpersonal relationships (Borgatti et al., 2009). The corresponding graphs have been rightfully considered "geographies of emotion" because they map social relationships, while a vast set of analytical tools allows to explore network topology, recognize groupings and discern critically important individuals (Wassermann and Faust, 1994).

In parallel to sociology, network theory inspired a new approach in the study of fossil and modern traces (ichnology) (Baucon and Felletti, 2013b). In fact, traces such as burrows, footprints and borings, are manifestations of biological behaviour (Seilacher, 2007; Buatois and Mángano, 2011; Bromley, 1996; Knaust, 2012; Baucon et al., 2012), hence ichnological systems are behavioural networks recording the biological response to the surrounding environment. Ichnological networks are therefore "geographies of behaviour" which can shed light on the organism-environment relationship in fossil and modern ecosystems.

In light of these assumptions, this paper aims to apply network theory for understanding the ecosystem of the Pramollo Basin (Italy-Austria), known as an ichnolagerstätte for the exceptional quality and quantity of Palaeozoic trace fossils (Baucon and Carvalho, 2008). In particular, the focus is on the ichnology of the Val Dolce Formation (Lower Permian), which has been comparatively understudied with respect to the underlying Carboniferous units. Specifically, three major questions are posed:

1) What are the trace fossils of the Val Dolce Formation?
2) How was organized the ichnological system?
3) How was structured the palaeoenvironment?

Geological Framework

The Pramollo Basin is located in the Carnic Alps (Italy-Austria) and exhibits a Carboniferous to Permian succession (Moscovian p.p.-Artinskian p.p.) referred to as the Pontebba Supergroup (Fig. 2), which is unconformably overlying Lower Carboniferous basement (Venturini, 1990; Venturini, 2002a; Venturini, 1991). The evolution of the Pramollo Basin is framed within the transtensional tectonic regime that characterized the Southern Alps during the late Palaeozoic, opening as a pullapart basin between Moscovian and Kasimovian (Vai, 1991; Venturini, 1983; Venturini et al., 1982). The corresponding fault-delimited trough has been initially filled by coarse conglomerates (Bombaso Formation), followed by prevailing siliciclastic supply with minor limestone deposits (Pramollo Group). These units are overlain by carbonates and minor siliciclastic deposits (Rattendorf Group and Trogkofel Groups). According to petrographic and sedimentological studies (Venturini, 1990; Venturini, 1991; Fontana and Venturini, 1982), the source area of the Bombaso Formation was dominated by carbonates and siliciclastics, whereas the Pramollo and Rattendorf Groups were related to the erosion of a phyllitic basement located northwest of the Pramollo Basin.

Overall, the Pontebba Supergroup reflects fluvio-deltaic and marginal-marine deposition strongly controlled by tectonics (Venturini, 1983). Consequently, the Pramollo Basin is one of the few peri-Tethyan sites recording marine and deltaic conditions (Venturini, 2002b; Vai and Venturini, 1997).

This peculiarity is accompanied by a rich body fossil heritage, which has been documented since the 19th century (Venturini, 1991). In fact, the fossil record of the Pontebba Supergroup includes brachiopods, trilobites, cartilaginous fishes, corals, bryozoans, fusulinids, crinoids and a well-preserved paleoflora (Venturini, 2006). Although the trace fossil record of the Pramollo Basin has been known since the 1960s (Selli, 1963; Vai et al., 1979; Barbiero et al., 1990; Mietto et al., 1985; Conti et al., 1991), the ichnosite has been qualified only recently as an ichnolagerstätte for its exceptional ichnological content (Baucon and Carvalho, 2008). For these reasons, Pramollo and its surroundings constitute one of the most spectacular body and trace fossil sites of the Alps (Baucon and Carvalho, 2008; Venturini, 2006).

This paper focus on the Val Dolce Formation, which received less ichnological attention with respect to the Pramollo Group. There is general consensus that the Permian-Carboniferous boundary is near to the base of the Val Dolce Formation, which is mostly of Asselian age (Vai and Venturini, 1997; Forke, 2002); some authors extend it to basal Sakmarian (Forke, 2000). The Val Dolce Formation, known as Grenzland Formation by German-speaking authors (Forke, 2000), is well exposed in the surroundings of Cason di Lanza, where it is represented by prevailing siliciclastic deposits and minor bioclastic limestones. This unit is organized in shallowing-up cycles which are commonly comprising brachiopod-rich pelites, trough-/planar-/hummocky-stratified sandstones and quartz-conglomerates

(Vai and Venturini, 1997; Venturini, 1990; Fig. 3). Table 1 includes a general facies description; the reader is addressed to previous works (Vai and Venturini, 1997; Venturini, 1991; Forke, 2000) for a more detailed sedimentological analysis. In line with the general setting of the Pontebba Supergroup, the Val Dolce Formation represents fluvio-deltaic to marginal-marine deposition (Venturini, 1990).

Materials and Methods

Field survey was performed during 2012 for defining the ichnofaunal composition of the Val Dolce Formation. The study area is shown in Fig. 1. Based on optimal outcrop quality, the stream intersecting Pian di Lanza (Fig. 1) was selected for realizing a standard stratigraphical section in which trace fossil distribution was noted (Fig. 4). This section records the lower and middle part of the Val Dolce Formation, although the contact with the underlying lower Pseudoschwagerina Formation is not exposed. Nevertheless, comparison with previously studied stratigraphic sections (Forke, 2002; Venturini, 1990; Schönlaub and Forke, 2007) shows that the Pian di Lanza section is one of the most integer and continuous exposures of the Val Dolce Formation. This dataset represents the source for drawing the ichnonetwork, following the methodology described in previous works (Baucon et al., 2013; Baucon and Felletti, 2013b).

The idea is to represent ichnotaxa as nodes, and connect those pairs that co-occur together. The strength of each association relationship is described by link weight, which corresponds to the Jaccard index and is related to the probability of co-occurrence of ichnotaxa pairs (Hammer and Harper, 2006; Jaccard, 1901; Jaccard, 1912). In practical terms, free and open-source software allows to derive an ichnonetwork from stratigraphical data in three steps (Fig. 5):

1. store stratigraphical data into a spreadsheet (i.e. LibreOffice Calc);
2. calculate Jaccard index for each ichnotaxa pair. Statistical software (i.e. PAST (Hammer et al., 2001)) allows to calculate and save results in a matrical form (adjacency matrix);
3. Render the adjacency matrix as a network. Network analysis software (i.e. Gephi (Bastian et al., 2009)) allows to draw and analyze the network and perform network analysis;

The process for obtaining an ichnonetwork from a stratigraphic log with free and open-source software is thoroughly described in previous works (Baucon and Felletti, 2013b; Baucon et al., 2013).

RESULTS

Trace fossils of the Val Dolce Formation

This section describes the types of trace fossils of the Val Dolce Formation, named after a well-established parataxonomical nomenclature based on morphological characters (Knaust, 2012). According to this practice, trace fossils are placed into taxonomical units (ichnotaxa); more in detail, two ranks of ichnotaxa are generally used: ichnogenus (igen.) and ichnospecies (isp.) (Bromley, 1996).

During field survey, 11 ichnogenera have been recognized in the study area. With the exception of *Phymatoderma,* all of the observed ichnotaxa received ichnotaxonomic treatment in the previous ichnological review of the Pramollo Basin (Baucon and Carvalho, 2008). The vertebrate footprint *Limnopus,* previously reported from the same study area (Mietto et al., 1985), is probably to be included in the Val Dolce ichnofauna, although further records are needed to confirm this hypothesis.

This section documents the ichnofauna noted during field survey, providing amended descriptions of the morphology, behaviour, tracemaker and environmental range of each ichnotaxon:

Archaeonassa isp. Winding trails consisting of a central furrow and two parallel lobes. Trail width: 0.8-1 cm. In light of the comparison with modern gastropod trails (Baucon and Felletti, 2013a), *Archaeonassa* is interpreted as the surface trail produced by locomoting invertebrates. *Archaeonassa* is reported from both marginal-marine and continental environments (Buatois and Mangano, 2002; Knaust et al., 2012).

Curvolithus simplex. Unbranched, straight or winding structures consisting of a central lobe flanked by two smaller lateral lobes (Fig. 6). Burrow width: 0.3-1.5 cm. The ichnogenus is interpreted as the locomotion trace of infaunal carnivores, including flatworms, nemerteans and gastropods (Buatois et al., 1998). *Curvolithus* is a typical component of shallow marine and, especially, deltaic environments with rapid sand deposition in quiet settings ('*Curvolithus* ichnofacies': (Tonkin, 2012)).

Cylindrichnus isp. Dominantly vertical, curved unbranched burrows with circular cross-section.

Lining concentrically laminated (Fig. 6). Burrow diameter: 0.3-1 cm (Fig. 6, Fig. 7). There is no complete consensus on the trophic strategy of *Cylindrichnus,* which is interpreted as the burrow of an ambush predator, a suspension-feeder or a detritus-feeder (Sarkar et al., 2009; Głuszek, 1998). However, strong analogies exist between *Cylindrichnus* and the burrow of the modern terebellid polychaete *Amphitrite ornata,* which feeds on detritus and bacterial cultures (Głuszek, 1998). *Cylindrichnus* is frequently reported from storm-influenced environments, ranging from middle shoreface to middle offshore (Sarkar et al., 2009). *Cylindrichnus* is also common in, but not exclusive to, brackish-water settings (Gingras, MacEachern, et al., 2012). In this context, *Cylindrichnus* typically characterizes delta front settings, including mouth bars (Tonkin, 2012).

Helminthoidichnites tenuis. Horizontal, irregularly winding traces without branches and self-overcrossings. Weathered specimens shows dark fill. Burrow diameter: 0.1-0.2 cm (Fig. 7). The presence of dark fill suggests sediment processing, indicative of deposit-feeding. *Helminthoidichnites* is an environment-crossing ichnogenus, being reported in continental and marine settings; typical producers include nematodes and insects (Uchman et al., 2009).

Nereites missouriensis. Simple, horizontal, unbranched burrow constituted by a central meniscate ribbon surrounded by a lobate zone of reworked sediment (Fig. 8). The menisci can be spaced (thick-meniscate form *sensu* Uchman, 1995) or tightly packed, resulting in a homogeneous string (‘fecal ribbon’ *sensu* Uchman, 1995). The lobate zone has a low contrast with respect to the host sediment (‘*Scalarituba*’ preservation: Seilacher, 2007) , therefore this ichnotaxon is easily confused with *Palaeophycus* or *Taenidium.* Burrow width 0.4-0.8 cm.

Two models have been invoked for explaining the morphology of *Nereites:*

1. Pascichnial model. A worm-like organism fed successively within each lobe and left a faecal string preserved as the central ribbon (Uchman, 1995; Martin and Rindsberg, 2007). Pascichnial forms of *Nereites* are generally documented from shelf to deep-sea environments (i.e. *Nereites missouriensis, Nereites irregularis;* Seilacher, 2007; Uchman, 1995).
2. Repichnial model. An arthropod producer moved at the surface, producing lobed pressure-

release structures with legs (Martin and Rindsberg, 2007). This model is accounted for modern xiphosurans (Martin and Rindsberg, 2007) and hermit crabs (Baucon and Felletti, 2013a) inhabiting intertidal and shallow subtidal settings, respectively. Similar environmental settings are attributed to Ordovician forms of *Nereites jacksoni (Neto de Carvalho and Baucon, 2010)*.

The presence of a well-developed fecal string is consistent with a combination of locomotion and feeding (pascichnia) rather than locomotion only (repichnia). *Nereites missouriensis* is an eurybathic form, documented from shelf (Seilacher, 2007) and, especially, turbiditic settings (Uchman, 1995). Modern *Nereites* ichnofabrics, comprising *N. missouriensis,* have been reported from deep-sea softgrounds and soupgrounds influenced by upwelling (Wetzel, 2002).

Planolites isp. Simple, horizontal, unbranched burrow lacking a wall lining. Fill similar to the host rock. Burrow width: 0.3-0.5 cm. The bioprint is similar to the one of *Pramollichnus,* suggesting similar worm-like tracemakers. *Planolites* is regarded as an environment-crossing ichnogenus corresponding to deposit-feeding strategies (Pemberton and Frey, 1982).

Phymatoderma isp. Horizontal or inclined burrows with multiple palmate lobes. Fill contrasting in color with the host rock; pelletted fill rarely preserved. Burrow width: 0.4-0.8 cm (Fig. 8A). *Phymatoderma* is interpreted as a deposit-feeding burrow (Uchman and Gaździcki, 2010).

Analysis of large Pliocene specimens (Miller III and Vokes, 1998) revealed that the *Phymatoderma* producer fed on surface sediments and excreted fecal pellets at depth as a food cache. This behaviour allowed to revisit tunnels succesively, in response to a fluctuating trophic regime. Carbon-isotope data confirm that the *Phymatoderma* producer ingested the surface sediments and subsequently excreted fecal pellets at depth (Izumi, 2012).

Phymatoderma occurs mostly in outer shelf or deeper environments (Uchman and Gaździcki, 2010), especially from deep glaciomarine settings (Lima and Netto, 2012). The ichnogenus is interpreted to reflect oxygenated bottomwater (Lima and Netto, 2012; Izumi, 2012) but is commonly found within black shale facies, hence indicating low-oxygen porewater.

Pramollichnus pastae. Crescent-shaped structures resulting from juxtaposed spaghetti-like burrows that connect two apical points; tight meanders may be present (see (Venturini, 2006) fig. 9.3c). Burrow diameter: 0.3-0.7 cm (Fig. 8). *Pramollichnus* is interpreted as a deposit-feeding structure produced by worm-like organisms (Baucon and Carvalho, 2008). In the study area, *Pramollichnus* occurs at the top of hummocky-cross-stratified intervals, therefore reflecting opportunistic colonization of storm-deposited sandbodies. The present data extends the previous record of *Pramollichnus (Baucon and Carvalho, 2008)* into the Permian.

Psammichnites plummeri. Horizontal, unbranched traces with a median string. Traces follow a straight, winding, meandering or looping course. Trace width: 0.8-1.2 cm (Fig. 9). *Psammichnites* is interpreted as the trace of an infaunal deposit-feeder (probably a mollusc) with a snorkel-like device (Seilacher and Hagadorn, 2010; Alonso-Muruaga et al., 2013; Seilacher, 2007). Psammichnites is a common component of the *Psilonichnus* and *Cruziana* ichnofacies, being reported from intertidal flats (MacEachern et al., 2012). In addition, Psammichnites is documented from deltaic environments as a component of the *Cruziana* ichnofacies (Alonso-Muruaga et al., 2013).

Taenidium isp. Horizontal, unbranched, unwalled burrow consisting of dark, arcuate menisci alterning with thinner menisci, which are concordant in texture with the host rock. Burrow width: 0.4-1 cm. Nature of the fill suggest that the tracemaker backfilled its burrow by excreting digested sediment (‘ingestion and excretion backfill’ sensu Baucon et al., 2013). For this reason, a deposit-feeding strategy is likely.

Taxonomy of meniscate traces is disputed, in particular the distiction between *Beaconites* and *Taenidium.* According to (Keighley and Pickerill, 1994), Beaconites is walled, *Taenidium* not. For this reason, the studied structure is attributed to *Taenidium,* which is typically documented from continental environments but appears also in marine settings (Uchman et al., 2013; Buatois and Mángano, 2011).

Zoophycos isp. Helically coiled spreite structures, consisting of individual burrows revolving around a central axis. Outline circular. Two morphotypes are distinguished on the basis of the presence of lobes (Fig. 10A, B). Specimens without lobes often present a well-preserved apex (Fig. 10C). Lobed specimens commonly show a marginal tube contrasting in colour with respect to the host rock (Fig. 11), suggesting the presence of oxidised iron minerals. Trace diameter: 15-30 cm.

Several hypotheses has been proposed for the ethology of the *Zoophycos* producer, including deposit-feeding, detritus feeding, caching, refuse dump and gardening of microorganisms (Bromley, 1991; Lowemark and Schafer, 2003).

Although general consensus is still to be reached, the cache model conveniently explains the major features of the ichnogenus (Buatois and Mángano, 2011; Baucon and Avanzini, 2008; Bromley, 1991). According to this model, the *Zoophycos* producer fed at the sediment/water interface and excreted fecal pellets at depth in order to maintain a food source for periods of scarce nutrient flux (Bromley, 1991). In analogy with *Zoophycos rhodensis* (Bromley and Hanken, 2003), the function of the marginal tube of lobed specimens could be linked with chemosymbyosis.

Zoophycos shifted from shallow to deep settings across the Phanerozoic (Bottjer et al., 1988; Baucon and Avanzini, 2008; Neto de Carvalho and Rodrigues, 2003), being commonly associated to quiet-water conditions and dysoxia (Martin, 2004; Lowemark and Schafer, 2003; MacEachern et al., 2012). Recent *Zoophycos* are particularly abundant in upwelling-controlled areas (Lowemark and Schafer, 2003). Evidences from Quaternary sediments relate *Zoophycos* to seasonal fluctuations in food supply deriving from monsoonal climate (Löwemark et al., 2005). In this regard, recent *Zoophycos* were produced during times of strong summer monsoon, in particular during interglacial times (Wetzel et al., 2011).

Ichnonetwork analysis

A network is a set of nodes (or ‘vertices’) connected by links (or ‘edges’) of a specified type, such as social, trophic or co-occurrence relationships (Borgatti and Halgin, 2011). For instance, a friendship network can be described by persons (nodes) linked by friendship relationships (links), while trophic networks comprise biological taxa connected by trophic relationships (‘who eats whom’). These examples confirm that the strength of the network approach is its simplicity and generality, as it can describe almost any system with multiple components (Krause et al., 2009). As anticipated by Euler (Euler, 1736), the reciprocal position of these components – defined by their links – plays a central role in understanding the studied system. In this regard, network theory provides measures to describe the position of individual components and the architecture of the whole system, which can be both related to real-world phenomena (Borgatti and Halgin, 2011). Regardless of the network type, structure is central in network analysis (Borgatti et al., 2009).

Network theory demonstrated to be an extremely powerful tool in the study of fossil and recent traces (Baucon and Felletti, 2013b; Baucon et al., 2013). In fact, ichnological systems can be described as behavioural networks (ichnonetworks) consisting of mutually interconnected elements. In this case, nodes represent ichnotaxa, while links picture the association relationships between ichnotaxa pairs.

This section provides an overview of the topographical features of the ichnonetwork under study, which has been derived from the stratigraphic section of the Pian di Lanza stream (Fig. 1).
The corresponding ichnonetwork (Fig. 12; Supplemental File 1) shows ichnotaxa, association relationships and their intensity.

The studied ichnonetwork is constituted by a single component, i.e. all pairs of nodes are reachable through a continuous chain of links (connected network *sensu* Wassermann and Faust, 1994; Fig. 13A, B). Edges have variable weight, displaying strong association relationships between *Zoophycos* and *Curvolithus, Curvolithus* and *Palaeophycus*, *Helminthoidichnites* and *Palaeophycus*, *Zoophycos* and *Helminthoidichnites*.

Graphic inspection shows that not all node pairs are directly connected (i.e. *Phymatoderma* and *Cylindrichnus;* Fig. 12), hence some ichnotaxa are never co-occurring with some-others. For this reason, the ichnonetwork is not complete as only a part of the maximum possible number of links is present. In fact, two nodes can be linked by no more than one link, therefore an ichnonetwork can have only a given number of links which is determined by the number of nodes (Wassermann and Faust, 1994). It is possible to quantify the completeness of the studied ichnonetwork by computing graph density, that is the ratio of the links present to the maximum possible (Wassermann and Faust, 1994). According to this measure, only the 53.6% of the possible links are present.

In light of this result, it is interesting to see if some nodes (ichnotaxa) have more connections than others. In order to reach this aim, the number of links that are incident with a given node is considered. This measure, known as node degree (Wassermann and Faust, 1994), corresponds to the number of ichnotaxa that are directly associated with a certain ichnotaxon. *Zoophycos, Helminthoidichnites, Curvolithus* are among the highest degree ichnotaxa, while *Planolites* and *Phymatoderma* are associated only to one ichnotaxon (degree=1). Degree is represented by node size in Fig. 12.

Node degree provides information on local network structure, because it quantifies the number of direct connections, but it ignores any indirect link. For instance, *Curvolithus* and *Phymatoderma* are not directly connected, but it it takes at least two 'steps' to get from one to the other. The same can be said for the highlighted nodes in Fig. 13C. These examples show the concept of path length, which is the number of 'steps' (links) necessary to get from one node to another (Scott, 2000). As many paths are likely to connect a pair of nodes, it is important to consider the shortest path length among them (geodesic distance; Fig. 13C). In fact, the concept of distance allows to discern the structural position of a node within the network by calculating how close a node is to all other nodes (node closeness; (Wassermann and Faust, 1994)). More specifically, closeness is the inverse of the sum of the shortest paths (or distances) from a given node to the others (Wassermann and Faust, 1994). Accordingly, closeness allows to discern zones in the network, in the same way that central bus stations are recognized because they are at a few stops from the others. Based on their low closeness scores, *Phymatoderma* and *Planolites* lie at the periphery of the studied network because they are 'far' from the other nodes. In contrast, the centre of the network is occupied by *Zoophycos, Curvolithus, Helminthoidichnites* and *Cylindrichnus.* These high-closeness nodes are close to a large number of other nodes (Wassermann and Faust, 1994).

In light of these results, a 'geography' of the studied ichnonetwork is recognized. Accordingly, the structure of the network can be better understood if nodes are arranged in a way that highlight their topological geography. Nodes can be arranged manually, although there exist many algorithms to display nodes in order to facilitate interpretation. Among these, the Yifan Hu method is a force-directed algorithm which models the graph drawing problem by a physical system of bodies, with forces acting between them (Hu, 2005). The resulting layout (Fig. 15) finds a good placement of nodes by minimizing the energy of the system (Hu, 2005). It should be noted that changing layout does not change the connection pattern of the network, therefore Fig. 14 and Fig. 15 are topologically equivalent.

Visual inspection of Fig. 15 reveals that some nodes act as a 'bridge' and connect central to peripheral areas of the networks. This subject can be approached by considering node betweenness, which measures the extent to which a particular node lies 'between' the others (Scott, 2000). This measure is proportional to the number of shortest paths passing through a node (Wassermann and Faust, 1994). In fact, the communication of indirectly connected nodes depends on the nodes lying between them, therefore a measure of the relevance of a node is the number of shortest paths going through it (Boccaletti et al., 2006). *Zoophycos* and *Cylindrichnus* are the highest betweenness ichnotaxa, being the 'intermediaries ' of the network.

The ichnological significance of betweenness is important, because it is related both to the palaeoenvironmental resolution of the ichnotaxon and the existence of network inhomogeneities:

1. High-betweenness ichnotaxa are likely to be poor environmental indicators. In fact, if a node lies between many others, it bridges different structural islands of the network (bridge ichnotaxa *sensu Baucon and Felletti, 2013b*).
2. The existence of bridges implies that the network texture is not regular like a lattice, but is structured. In fact, nodes with non-zero betweenness connect areas of the network that would otherwise be sparsely or not connected at all (Martín González et al., 2010). For instance, in a friendship network, high betweenness nodes are hubs between otherwise disconnected groups; this could be exemplified by rugby players and ballet dancers with a single common friend.

The structured organization of the network is also suggested by clustering coefficient, which offers a measure of the interconnectivity between nodes linked to a given one (Ravasz et al., 2002; Boccaletti et al., 2006). In sociological terms, the clustering coefficient of a node indicates how likely a person's friends are friends of each other. In ichnological terms, clustering coefficient of a node is maximum (1) if the node lies at the center of a fully interconnected cluster, i.e. when all the traces associated to a given one are also associated together (Fig. 17).

Consequently, if the network structure is modular, the clustering coefficient averaged over all nodes will be high (Ravasz et al., 2002). In this context, the considerable average clustering coefficient

(0.772) of the studied network is suggestive of community structure. In more formal terms, this property is characterized by high concentrations of edges within special groups of nodes, and low concentrations between these groups, which are termed communities or modules (Fortunato, 2010). In the social context, friendship circles exemplify the concept of community while, in ichnological terms, communities are cohesive groups of closely associated ichnotaxa, and, therefore, they represent ichnoassociations (Baucon and Felletti, 2013b; Baucon et al., 2013).

Communities have important implications in network analysis, because they represent groups of nodes which are likely to share common properties (Fortunato, 2010). In ichnological networks, environmental parameters are the properties shared among ichnoassociation members. In fact, biologic behaviour depends on the surrounding environment, therefore the formation of groups of associated behaviours (i.e. ichnoassociations) is likely to be driven by environmental properties.

Although the concept of community is intuitive, community detection is not straightforward and many algorithms have been proposed to approach the problem (Boccaletti et al., 2006; Fortunato, 2010). In this regard, the concept of clique is among the most immediate and stringent (Boccaletti et al., 2006). In fact, a clique is a subset of nodes in which every possible pair of nodes is directly connected by a link, and the clique is not contained in any other (Scott, 2000) (Fig. 12D). This definition implies that (a) cliques may partially overlap and (b) a clique has the maximum possible link density (Yan and Gregory, 2009; Boccaletti et al., 2006). For instance, in a friendship network, a clique is a group of persons all of which are linked by friendship. In ichnology, a clique consists of a group of traces all of which are associated to each other. As stated in previous research (Baucon et al., 2013), in ichnology is necessary to relax the reccomandation of (Wassermann and Faust, 1994) and consider also cliques formed by node pairs. In light of these assumptions, four cliques have been found in the studied ichnonetwork (Fig. 18):

- C_1: *Cylindrichnus-Planolites*
- C_2: *Phymatoderma-Zoophycos*
- C_3: *Cylindrichnus-Helminthoidichnites-Curvolithus-Zoophycos*
- C_4: *Helminthoidichnites-Taenidium-Curvolithus-Nereites-Zoophycos*

As stated before, these cohesive subgroups represent ichnoassociations.

DISCUSSION

The topological attributes described in the previous section derive from the structure of the environment, in the measure in which it influenced the biological behaviour recorded by trace fossils. These attributes account for various domains of scale, ranging from individual nodes to the whole network:

1. Network-level scale
2. Group-level scale
3. Node-level scale

These different observation levels reflect different scales of environmental structure. Network-level attributes (i.e. average clustering coefficient) refer to the ichnological system as a whole, and therefore consider the system at the level of the depositional environment; group-level attributes (i.e. network communities) account for ichnoassociations, hence they consider subenvironments; node-level attributes (i.e. node degree) refer to the role of individual ichnotaxa within the ichnological system.

Network-level scale

General features of the Val Dolce Formation show the ichnological signature of deltaic environments:

1. dominance of deposit feeding behaviours. Deltaic environments are characterized by high suspended loads which clog filter-feeding structures and therefore preclude suspension feeding (MacEachern et al., 2005; Buatois and Mángano, 2011). In the Val Dolce Formation, absence of suspension-feeding structures is documented even in sandy facies (i.e. facies S1), where suspension-feeding behaviours would be expected in nondeltaic analogues (MacEachern et al., 2005).

2. presence of opportunistic trophic generalists. Harsh environments are commonly inhabited by nonspecialized r-selected animals, adapted to high levels of stress (Buatois and Mángano, 2011). The studied unit comprise opportunistic, facies crossing-ichnotaxa such as Planolites, Helminthoidichnites and *Cylindrichnus.*

3. evidences of freshwater influence. The Val Dolce ichnofaunas are commonly (but not exclusively) characterized by forms typically found in marine environments, mixture of horizontal and vertical structures from the *Cruziana* and *Skolithos* ichnofacies, dominance of infaunal traces, presence of monospecific assemblages and small size. These features are typical of brackish-water conditions (Buatois and Mángano, 2011; Pemberton et al., 1982; Gingras, Maceachern, et al., 2012).

Network texture has no abrupt discontinuities, as manifested by the existence of a single connected component in which all nodes are reachable through a continuous chain of links. As trace fossils distribution is driven by the environment, this means that individual ichnotaxa are part of the same environmental *continuum*. It should be noted that evidence of an environmental *continuum* at a broad scale does not exclude smaller-scale fluctuations in environmental conditions. In fact, patchy distribution of traces and fluctuating bioturbation index is commonly recognized at the outcrop scale, suggesting local variations in environmental variables.

Similarly, at an intermediate scale, the *continuum* of the network is not homogeneous as a regular lattice. In fact, nodes have varying number of connections (degree) and the network is characterized by a relatively high average clustering coefficient. As the clustering coefficient of a node is related to its interconnectivity pattern, the average clustering coefficient of the network is a measure of its potential modularity (Solé and Valverde, 2004; Ravasz and Barabási, 2003). This aspect bridges the network-level scale of analysis to the scale of groups, the ichnological significance of which is to be found.

Group-level analysis

Ichnologists, as well as ecologists, are interested in finding groups of taxa that are significantly found together (Legendre, 2005). For instance, ecologists look for taxa associations as a conceptual framework to synthesize environmental features or to predict environmental characteristics (Legendre, 2005). In line with the use of the term ‘association’ in ecology (Legendre, 2005), an ichnoassociation can be regarded as a group of ichnotaxa recognized as a cluster following the application of a clearly stated set of rules. In this paper the clique rule has been used, but other techniques may be employed.

In parallel to community ecology (Legendre, 2005), this section aims to find the ecological requirements common to the members of each ichnoassociation. These ecological requirements allow to define a corresponding depositional subenvironment, which is named after the well-established process-based zonation of deltas (Reading, 1996):

Cylindrichnus-Planolites* *ichnoassociation **(C_1).** This ichnoassociation is characterized by low ichnodiversity and patchy, low bioturbation intensity (BI 1-3). Monoichnospecific manifestations of *Cylindrichnus* (Fig. 19) are commoner than the presence of both components of the ichnoassociation.

Low ichnodiversity is commonly associated to stressed settings (Buatois and Mángano, 2011) and, in deltaic environments, monoichnospecific assemblages are usually indicative of high energy, high sedimentation rate and lowered salinity (Tonkin, 2012). In particular, dominance of deposit-feeding strategies and absence of suspension-feeding behaviours suggests noxious conditions for suspension-feeders. This phenomenon may be explained by (a) quiet waters with low sedimentation rate, providing low concentrations of suspended nutrients or (b) high suspended loads, clogging filter-feeding structures (Buatois and Mángano, 2011; MacEachern et al., 2005; Tonkin, 2012). The latter hypothesis is more convenient, as ichnological and sedimentological evidences (facies S1) point to a high-energy setting. In fact, vertical or steeply inclined forms of *Cylindrichnus* have been interpreted as indicators of high-hydrodynamics (Frey, 1970). *Cylindrichnus* is commonly found in association with shifting substrates and event-bed deposition (Tonkin, 2012). Sedimentological features support this interpretation, as ichnoassociation C_1 occurs within facies S1, showing evidences of traction (parallel laminae in sandstone) and storm-deposition (hummocky-cross stratification; Fig. 20A). For this reason, maximum depth of this ichnoassociation coincides with storm wave base, which commonly ranges between 25 and 50 metres in modern environments (Immenhauser, 2009).

In line with previous works on brackish-water ichnofaunas (Buatois and Mángano, 2011; Pemberton et al., 1982; Gingras, Maceachern, et al., 2012), this ichnoassociation displays typical signatures of freshwater input in marine settings: marine forms (i.e. *Cylindrichnus*), dominance of infaunal traces rather than epifaunal trails, simple structures produced by trophic generalists, variable abundance, low ichnodiversity and monoichnospecific occurrences.

In sum, the ecological requirements of this ichnoassociation are: high suspended load, freshwater input into seawater and relatively high hydrodynamics. These features are characteristically associated to the delta-front, which is the area where sediment-laden fluvial currents enter the basin and interact with basinal processes (Reading, 1996). More specifically, significant freshwater input and hydrodynamics are indicative of proximal bar subenvironments (i.e. bar back and bar crest areas; Reading, 1996).

Phymatoderma-Zoophycos ichnoassociation **(C_2).** Low ichnodiversity and homogeneous, moderate to high intensity of bioturbation (BI 3-5) characterize this ichnoassociation.

In contrast to the *Cylindrichnus-Planolites* ichnoassociation, there are no evidences of freshwater influence. In fact, homogeneous, high bioturbation intensities are commonly regarded as signatures of normal-marine salinity conditions (Buatois and Mángano, 2011). This interpretation is in line with the distribution of the individual components of the ichnoassociation. In fact, *Zoophycos* is commonly associated to quiet-water environments with low sedimentation rates, while *Phymatoderma* occurs mostly in outer shelf or deeper environments (Uchman and Gaździcki, 2010; Lima and Netto, 2012). Consequently, the *Zoophycos-Phymatoderma* ichnoassociation is thought to represent seafloors below the fairwater wave.

While freshwater influence is insignificant, availability of oxygen seems to be the limiting factor. In fact, in light of the oxygenation model of Ekdale and Mason (Ekdale and Mason, 1988), intense bioturbation indicates that the bottom seawater was sufficiently oxygenated for supporting infaunal communities; at the same time, the predominance of burrows connected to the seafloor (*Phymatoderma* and *Zoophycos*) suggests that porewaters were poorly oxygenated. In fact, a permanent connection with the seafloor allows to exploit poorly oxygenated substrates by ventilating the burrow with more oxygenated water (Ekdale and Mason, 1988; Baucon and Felletti, 2013a). Nevertheless, caution must be exercised in interpreting ichnodiversity because intense bioturbation by deep-tier burrows (Zoophycos, Phymatoderma) may have obliterated shallower tier structures.

The resemblance with the *Zoophycos-Chondrites* ichnoguild, which is typically documented from low-oxygen environments (Bromley, 1996; Martin, 2004), supports the idea of poorly oxygenated porewaters. Furthermore, the shift from Phymatoderma-Zoophycos ichnoassociation to the rest of the network shows an increase in ichnodiversity and a shift from dominant surface deposit-feeding

(*Phymatoderma, Zoophycos*) to mixed surface (*Zoophycos*) and subsurface (*Taenidium, Nereites*) deposit feeding. A similar shift from subsurface deposit feeding to surface feeding accompanies declining levels of oxygen in modern environments, alongside with decreasing burrow diameter and ichnodiversity (Smith et al., 2000). In addition, Phymatoderma and *Zoophycos* are commonly (but not exclusively) reported from substrates with lowered interstitial oxygen (Izumi, 2012; Bromley, 1996).

The ichnological evidences for quiet, fully marine settings with poorly oxygenated porewaters are confirmed by sedimentological and palaeontological features. In fact, the *Phymatoderma-Zoophycos* ichnoassociation is commonly found with low oxygen indicators (pyrite, well-preserved body fossils) within facies P1 (Tab.1; Fig. 20B).The trophic strategies represented by *Zoophycos* and *Phymtoderma* suggest a seasonally fluctuating environmental regime. In fact, a cache model has been proposed for both *Zoophycos* and *Phymatoderma* (Uchman and Gaździcki, 2010; Miller III and Vokes, 1998; Wetzel et al., 2011; Miller III and D'Alberto, 2001); according to this interpretation, during periods of high food flux the tracemakers fed on surface sediment and excreted fecal pellets at depth, in order to revisit them during periods of reduced food supply.

In sum, the *Phymatoderma-Zoophycos* ichnoassociation indicates normal-marine salinity, quiet hydrodynamics, low-oxygen porewaters, oxic to dysoxic bottom waters and seasonal fluctuations in food flux. Overall, these features are compatible with prodelta, which is the part of the delta unaffected by wave or tidal processes (Reading, 1996).

Seasonality of food flux and low-oxygen conditions can be both explained by monsoons, that are seasonal reversals of atmospheric circulation (Jacques et al., 2013). In fact, marine productivity is seasonally enhanced by monsoons, which control both river runoff and upwelling (Jyothibabu et al., 2008). As a consequence, increased deposition of organic carbon may led to low-oxygen conditions. This hypothesis fits very well with the record of recent *Zoophycos*, which has been reported from monsoon-influenced areas with upwelling and seasonal pulses in food flux (Wetzel et al., 2011). Although a direct link has not been established, *Phymatoderma* occurs abundantly within the monsoon-influenced Posidonia Shale (Röhl et al., 2001; Izumi, 2012).

Despite the coherent explanation offered by monsoonal climate, other climatic phenomena (i.e. summer water stratification: Eldridge and Morse, 2008; Tyson and Pearson, 1991) are able to produce low-oxygen conditions, therefore further studies are required to confirm influence of monsoons in the Val Dolce Formation.

***Cylindrichnus-Helminthoidichnites-Curvolithus-Zoophycos* ichnoassociation (C_3).** With respect to the partially overlapping ichnoassociation C_1, this ichnoassociation marks an increase in ichnodiversity, intensity (BI 3-4) and homogeneity of bioturbation. These aspects are likely to reflect the decreasing role of the major environmental stressors (freshwater input, hydrodynamics, suspended load). In fact, homogeneous and intense bioturbation is typical of fully marine conditions, in contrast with the sparse bioturbation characterizing brackish settings (Buatois and Mángano, 2011). This ichnoassociation covers a gradient in bioturbation homogeneity and intensity (Fig. 19B, C), corresponding to freshwater-influenced to fully marine settings. Moderate diversity of deposit-feeding strategies indicates that nutrients were largely available onto and within the sediment. For this reason, relatively low hydrodynamics is necessary to settle fine organic particles.

The ichnofauna does not show evidence of low-oxygen conditions. Although oxygen levels stayed in the range of oxic waters, they should have been low enough to avoid total oxidation of the organic matter exploited by deposit feeders. In this regard, the presence of *Zoophycos* could indicate seasonal fluctuations in food flux (Wetzel et al., 2011; Miller III and D'Alberto, 2001).

Overall, the ecological requirements of this ichnoassociation are: freshwater-influenced to fully marine conditions, moderate to low hydrodynamics, oxic bottomwaters and seasonally fluctuating flood flux. These features are coherent with distal delta front (i.e. distal bars) and, especially, prodeltaic settings, where influence of wave and/or tidal processes is minimal (Reading, 1996).

***Helminthoidichnites-Taenidium-Curvolithus-Nereites-Zoophycos* ichnoassociation (C_4).** This ichnoassociation is characterized by homogeneous, intense bioturbation (BI4-5) and moderately diverse ichnofauna. Since the backfill of *Nereites* and *Taenidium* shows that no connection was maintained with the seafloor, bottom waters are interpreted as sufficiently oxygenated (Buatois and Mángano, 2011; Ekdale and Mason, 1988).

In light the common ichnological features, ichnoassociations C_3 and C_4 had a similar environmental significance. Nevertheless, ichnoassociation C_4 is likely to correspond to more distal environments in light of the more intense and homogeneous bioturbation and the presence of *Nereites missouriensis,* which is an ichnogenus with deep-marine affinity. In addition, the small size of *Curvolithus* (width <0.5 cm; Fig. 20D) indicates suboptimal conditions for the producer. As *Curvolithus* is commonly regarded as an indicator of rapid sand deposition (Tonkin, 2012), reduction in size support the idea of a quieter, more distal environment.

In conclusion, this ichnoassociation could represent a normoxic prodeltaic environment characterized by dominant marine influence. This interpretation is supported by the fine grain size (facies P1) and the presence of marine body fossils (Fig. 20D).

In light of neoichnological evidences (Wetzel, 2002; Wetzel et al., 2011), presence of *Zoophycos* and *Nereites* is compatible with monsoon-influenced climate, although it is does not constitute a conclusive proof *per se*. In this regard, further studies are required to demonstrate monsoonal climate in the Val Dolce Formation.

Unburrowed units. Sediment units without distinct burrows do not occur only as unbioturbated patches within sandy facies (facies S1, S2), but also as largely unburrowed sediments.

In fact, conglomerates (facies C1, C2) are unburrowed, probably because of their high-energy setting which prevented benthic colonization. In light of their sedimentological attributes, facies C1 is interpreted to represent distributary channels, mostly pertaining to the river-dominated delta plain, while facies C2 could represent beach deposits (Venturini, 1990).

The measured section does not present limestone layers, although they are present in the neignborhood. Distinct burrows have never been recovered from limestone facies, although indistinct bioturbational structures may be present. In light of their sedimentological features, these limestone facies have been attributed to shallow, open sea environments below the fairweather wave base (Sanders and Krainer, 2005; Venturini, 1990).

Interpretation of the aforementioned topological patterns (cliques) as ichnoassociations well conforms with a central *tenet* of ichnology, i.e. that trace fossil associations tend to be environmentally restricted (Buatois and Mángano, 2011). In fact, behaviour is a biological response to the surrounding environment, hence groups of associated behaviours – that are manifested by ichnoassociations – arise from common environmental drivers. This idea can be better understood by representing the potential environment of an individual ichnotaxon as an abstract space, the dimensions of which correspond to the major environmental factors. In parallel to the concept of Hutchinsonian niche (Holt, 2009), the environmental requirements of a given ichnotaxon define its environmental range ('niche'). This concept is exemplified by _, showing a three-dimensional space defined by three axes: salinity, oxygenation and depth. In this abstract space, the environmental niche of an ichnotaxon is defined by specific values of the mentioned environmental factors. Although the mentioned example is three-dimensional, it should be noted that the concept of niche can be extended for any n-dimensional space.

In the niche perspective, the co-occurrence of two or more ichnotaxa is verified where their niches meet (Fig. 23A). In fact, the intersection of different niches comprises the environmental requirements common to the corresponding ichnotaxa. This aspect can be demonstrated by translating the niche intersections (Fig. 23A) in the form of an ichnonetwork, which can be regarded as an intersection graph. In fact, an intersection representation of a network is a family of sets corresponding to the nodes so that nodes are linked if and only if their assigned sets intersect (Cranston et al., 2011). In ichnological terms, niche intersections are the association relationships which define the links of an ichnonetwork. From the ichnonetwork perspective, two ichnotaxa are linked if they are co-occurring, while co-occurrence is possible only if their niches overlap.

In this study, an ichnoassociation is recognized as a clique, which is corresponding to the intersection of mutually incident niches. For instance, the niches of ichnotaxa a, b and c are mutually intersecting (Fig. 23A), therefore they form a clique, that is, an ichnoassociation (Fig. 23B).

Since that an intersection is equal or smaller than the intersecting niches, an ichnoassociation delimit a relatively narrow environmental range (i.e. Fig. 23A). Consequently, the topological relationships among different cliques (ichnoassociations) provide information on how different subenvironments are related. In this regard, two major clique-to-clique relationships are distinguished: overlap and disjointness.

Intuitively, overlapping cliques are overlapping ichnoassociations, hence they are environmentally affine. However, a more specific significance is revealed by comparing the niche perspective (Fig. 24A) with the ichnonetwork one (Fig. 24B). In fact, overlapping cliques share common nodes (e.g. node e in Fig. 24B), the niches of which bridge the environmental ranges of the overlapping cliques (e.g. a-b-e and c-d-e in Fig. 24A). This means that a continuous environmental gradient connect overlapping ichnoassociations, since cliques are ichnoassociations.

Several overlapping relationships are seen in the studied ichnonetwork: for instance, ichnoassociation C_1 overlaps with ichnoassociation C_3 which overlaps with ichnoassociation C_4 (Fig. 19). In light of the aforementioned discussion, the environment of clique C_1 graded into the environment of clique C_3, which, in turn, transitioned into the environment of clique C_4. This hypothesis conforms with the environmental interpretation of ichnoassociations C_1 , C_3, C_4 , indicating proximal delta front, distal delta front to proximal prodelta and prodelta, respectively. Similarly, the overlap pattern of ichnoassociation C_2 may be part of an oxygenation gradient.

On the other hand, if two cliques are disjoint in the ichnonetwork, an environmental gap separates the corresponding environmental ranges (Fig. 25, Fig. 26). This gap may be:

- Empty. If there are no niches covering the gap between two ichnoassociations, there are no continuous environmental corridors among the disjoint ichnoassociations (Fig. 25A). In other words, there are no bioturbated environments bridging the disjoint environments represented by disjoint cliques. This configuration corresponds, for instance, to a network with disconnected components (Fig. 25B). Theoretically, disconnected components may be explained also with adjacency in the abstract space, although such sharp boundaries are unlikely in nature (Erdös et al., 2011).
- Covered. If, in the abstract space, two disjoint ichnoassociations are connected through a continuous chain of niches, these constitute the environmental corridors bridging the disjoint ichnoassociations (Fig. 26A). In other words, the environments represented by disjoint ichnoassociations are distinct, but they grade one into another through a set of bioturbated environments. The ichnonetwork equivalent of Fig. 26A is represented by two disjoint cliques both overlapping with a third one (Fig. 26B). In the studied network, the non-overlapping cliques C_1 and C_4 provide an analogue, being connected by clique C_3. Their environmental interpretation is coherent with this assumption, as C_1 and C_4 represent the proximal delta front and the prodelta,

respectively. In fact, these deltaic environments are separate zones of the same gradient, being connected by a transitional zone which corresponds to clique C_3.

Node-level analysis

The role of individual ichnotaxa (node-level attributes) is quantified by standard measures of node centrality (Boccaletti et al., 2006): degree, closeness and betweenness.

Node degree describes the local connectivity pattern of a node by measuring the number of incident links. Consequently, high-degree nodes such as *Curvolithus* and *Zoophycos* are associated to many other ichnotaxa (Fig. 12). Nevertheless, degree is a local measure of centrality, while nodes with similar degree may play different roles within the studied system. In the studied system, this aspect is exemplified by *Zoophycos* and *Curvolithus* themselves*,* which have similar degree (Fig. 12) but different betweenness (Fig. 16).

In fact, node betweenness describes the importance of a node as a connector between different parts of the network (Martín González et al., 2010) and, therefore, recognizes those behaviours that can compete in different environmental contexts. For this reason, betweenness measures the reliability of an ichnotaxon as a palaeoenvironmental indicator: the higher betweenness, the lower environmental specificity. In this regard, the studied ichnonetwork is generally consistent with global patterns of bioturbation. In fact, the high-betweenness ichnotaxa *Zoophycos* and *Cylindrichnus* have a characteristically wide environmental range at a global scale (Bottjer et al., 1988; Tonkin, 2012; Głuszek, 1998; Baucon and Avanzini, 2008), while low betweenness characterizes Curvolithus and *Nereites,* which are are keystone ichnogenera of environmentally sensitive ichnofacies (Buatois et al., 1998; Tonkin, 2012; MacEachern et al., 2012). Despite these results, it should be noted that betweenness describe the role of an ichnotaxon within the boundaries of the studied system, hence global patterns of bioturbation are not necessarily respected in all cases (i.e. low betweenness of the generalist Planolites).

The significance of betweenness can be approached by considering the niche perspective. According to this approach, each ichnotaxon is represented by a node with a corresponding niche (Fig. 23). Hence, the niches of high-betweenness ichnotaxa (bridge ichnotaxa) are expected to lie between many other niches. Similarly, the niches of bridge ichnotaxa tend to cover the abstract space separating disjoint ichnoassociations (Fig. 24). Conversely, low-betweenness and high-clustering ichnotaxa are likely to be environment-specific, playing a role similar to that of species which reflect some measure of the character of the habitat ('indicator species'; see Anas et al., 2013).

In the original paleolandscape, the spatial distribution of bridge ichnotaxa is expected to mirror the abstract space in which their niches are defined. In fact, each site of the landscape is characterized by a specific set of environmental parameters, which correspond to the axes of the abstract space. For instance, the spatial distribution of Fig. 27A corresponds to the ichnonetwork and the abstract space represented in Fig. 24. In this regard, the high-betweenness ichnotaxon (node e in Fig. 24B) covers the abstract space separating disjoint ichnoassociations (Fig. 24A) and, at the same time, it bridges two separate areas of the landscape (Fig. 27A). A similar spatial configuration explains coherently the high-betweenness of *Cylindrichnus* and *Zoophycos,* which occupy similar topological positions within the Val Dolce ichnonetwork.

This idea establishes the connection between the abstract space and the topographical one, from which the topology of the ichnonetwork derives. Consequently, ichnoassociations, as defined in this study, are environmental (abstract space), topographical (landscape space) and topological (network space) entities.

In parallel to Fig. 27A, which describes overlapping ichnoassociations, Fig. 27B represents the spatial manifestation of disjoint ones. In other words, Fig. 27B is the equivalent of Fig. 25. Again, network topology is influenced by both spatial relationships and environmental niche of individual ichnotaxa. In fact, the disjoint ichnoassociations of Fig. 27B reflect distinct spatial and environmental ranges.

The aforementioned examples (Fig. 27A, B) show cliques with homogeneous fabric. However, structural inhomogeneities may occur if several ichnotaxa with different environmental affinities reach their distributional limits within the same zone. For instance, if the upper and lower distributional limits of several ichnotaxa converge in the same belt, a clique will comprise all of these ichnotaxa (Fig. 27C). Such transition belt is analogous to the original definition of ecotone, which was proposed to indicate a narrow transition zone between two adjacent ecosystems with mixed characteristics of the two adjacent ecosystems (Di Castri et al., 1988; Dutoit et al., 2007; Basset et al., 2012; Erdös et al., 2011). In parallel, a peak in ichnodiversity is reached within the aforementioned belt (Fig. 27C), since it contains a mixture of traces from neighbouring zones. The corresponding ichnonetwork, shown in _C, will consist of a single clique, although finer levels of organization are seen in the spatial distribution of traces. In fact, 'shallow' ichnotaxa (a, b) and deep ichnotaxa (c, d, e) are clearly distinguished in the environmental distribution of Fig. 27C. Consequently, a question might arise: is it possible to recognize these finer patterns of organization from ichnonetwork analysis?

The answer can be found by confronting homogeneous trace distributions (Fig. 27D) with a converging pattern (Fig. 27C). If preferential association patterns are not manifested, the weight distribution will be tendentially homogeneous. On the other hand, link inhomogeneities arise when ichnotaxa are not homogeneously associated within the same ichnoassociation.

The latter scenario is consistent with the edge weights of clique $C_{3,}$ which are not homogeneously distributed, but they account for association relationships of different strength. For instance, the edge connecting *Zoophycos* with *Curvolithus* has a higher weight than the edge between *Zoophycos* and *Cylindrichnus* (Fig. 18). Consequently, finer patterns of association can be found within the ichnoassociation C_3. In order to better visualize these patterns, clique C_3 is isolated from the rest of the network and the corresponding subnetwork is filtered by average edge weight (Fig. 28A). As a consequence, two subcliques are evidenced: *Cylindrichnus-Helminthoidichnites* and *Curvolithus-Zoophycos-Helminthoidichnites.* This weight pattern can be coherently explained with the converging distribution depicted in Fig. 27C. More specifically, the subichnoassociation *Cylindrichnus-Helminthoidichnites,* which is frequently reported from the field (Fig. 28B), is interpreted to be more proximal in light of the lower ichnodiversity and the environmental affinity of individual ichnotaxa.

Whilst clique C_3 is markedly inhomogeneous, a more homogeneous situation is depicted by clique C_4. In fact, the links between *Helminthoidichnites*-*Curvolithus*-*Nereites*-*Zoophycos* have relatively homogeneous weights (Fig. 28C). Only the weight of the *Nereites-Zoophycos* link is lower than clique average, but the difference is not significant (clique average weight: 0.392; *Nereites-Zoophycos* weight: 0.363). In contrast, *Taenidium* has weaker links, possibly representing a rarer ichnotaxon.

From the outcrop to the model, and back

The results of the aforementioned analysis can be synthesized as a model in which individual traces and ichnoassociations are framed within a palaeoenvironmental setting. For this aim, topological patterns provide the constraints for reconstituting the spatial and environmental relationships of both ichnoassociations and individual ichnotaxa. At the same time, interpretation of ichnological features offers a perspective on the environmental processes controlling trace distribution.

The palaeoenvironmental model of the Lower Permian Val Dolce Formation (Fig. 29) explains and synthesizes coherently both the ichnological features and the topological patterns of the studied ichnonetwork, which is respected at the network-, group- and node-level.

This model finds potential application for understanding the palaeoenvironment from field occurrences of trace fossils. In this regard, it should be stressed that ichnoassociations arise from a pattern-finding process and, therefore, they represent a generalization of natural phenomena. As a such, field observations may not coincide exactly with the generalized ichnoassociations $C_{1\text{-}4}$. This observation is particularly true for shallow deltaic settings in which trace distribution is typically patchy.

This distinction between field observations and generalized patterns poses a terminological issue: if generalized patterns are named ichnoassociations, what term to use for any group of traces found in the field? An unequivocal answer is difficult to find, as few studies dealt with the terminology of groups of traces (Buatois and Mángano, 2011; Bromley, 1996). Despite numerous exceptions (i.e. Savary et al., 2004), the term ichnoassemblage could be adopted to indicate any field occurrence of traces as it is commonly used in a general sense (Buatois and Mángano, 2011).

CONCLUSIONS

This study documented the ichnological heritage of the Val Dolce Formation (Pontebba Supergroup) and applied ichnonetwork analysis for recognizing organism-environment interactions. A clear pattern found is the increase in bioturbation intensity and ichnodiversity with increasing distance from the (palaeo)river mouth. Specific ichnoassociations, revealed by ichnonetwork analysis, mark different subenvironments within deltaic depositional setting. Hydrodynamics, freshwater input and oxygenation are the main controlling factors on the Val Dolce ichnofauna.

In the study area, some groups of co-occurring traces have no correspondences in the studied ichnonetwork. For instance, isolated slabs with *Pramollichnus* and *Psammichnites* are commonly found in the easternmost part of the study area. This aspect is explained by the limits of the studied stratigraphical section, which is missing the uppermost part of the Val Dolce Formation. For this reason, further researches are needed to identify and study a section representing the final part of the Val Dolce Formation. In addition, this example shows that field occurrences may differ from generalized patterns, requiring to use different names (i.e. ichnoassemblage and ichnoassociation) to indicate these different aspects.

Ichnonetwork analysis revealed to be a powerful approach for studying fossil ichnological systems, providing a rich set of graphical and statistical tools for palaeoenvironmental analysis. Nevertheless, some open questions remains on monoichnospecific ichnoassociations. In fact, an adjacency matrix based on the Jaccard index does not represent well monoichnospecific ichnoassociations, because all elements on the main diagonal are equal to 1. Although the Jaccard index provided robust results, further investigation is required to define a framework to identify significant monoichnospecific assemblages.

As the number of ichnonetwork-based studies is growing, identification of superfamilies of ichnonetworks may be useful in finding general patterns in ichnological systems. In line with other applications of network theory, different network-forming phenomena may leave specific architectural signatures in the corresponding graphs. In this context, global network measures (Solé and Valverde, 2004) and network motifs (Milo et al., 2002) may be useful approaches for classifying neworks.

Finally, this paper approached quantitatively to the concept of ichnoassociation, which demonstrated to have a spatial, topological and environmental aspect. This result shows that ichnoassociations arise from simple association rules based on the environment, therefore it opens a question: are ichnoassociations artificial categories to describe natural patterns or are they emerging properties of the ecosystem?

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Figure captions

Fig. 1. Geographical setting.

Fig. 2. Stratigraphical setting of the Pontebba Supergroup, modified after (Venturini, 2002b). Studied unit (Val Dolce Formation) is highlighted.

Fig. 3. Major facies of the Val Dolce Formation; see Tab.1 for facies codes. A – Quartz-conglomerate (facies C1). B – Medium-grained sandstone (facies S1). Hammer for scale. C – Pelitic sequence (facies P1) with interbedded sandstone layers (facies S2). Hammer for scale. D – Algal limestone (facies L2). Note the well-preserved thalli in growth position, possibly *Anthracoporella.*

Fig. 4. Stratigraphical log of the Pian di Lanza stream.

Fig. 5. Process for rendering an ichnonetwork with free and open-source software: LibreOffice (http://www.libreoffice.org/), PAST (http://folk.uio.no/ohammer/past/), Gephi (https://gephi.org/). When saving to .csv format, it is recommenced to choose the semicolon as field delimiter and full stop as the decimal separator.

Fig. 6. *Curvolithus* and *Cylindrichnus.* A - Lower bedding plane with *Cylindrichnus* (Cy) and *Curvolithus* (Cu). B – Upper bedding plane densely bioturbated by *Curvolithus.*

Fig. 7. *Helminthoidichnites.* A - Upper bedding plane with *Cylindrichnus* (Cy) and *Helminthoidichnites* (He). B – *Helminthoidichnites* with dark fill. Upper bedding plane view.

Fig. 8. *Nereites, Phymatoderma, Pramollichnus.* A – *Nereites.* The dashed line highlights part of the lateral gill-like structure, while the solid line marks backfill menisci. Top view. B

– *Phymatoderma, upper bedding plane.* C – *Pramollichnus*, upper bedding plane.

Fig. 9. *Psammichnites* and *Taenidium.* A – Upper bedding plane with *Psammichnites* (Ps). Tick spacing 1 cm.B – Lower bedding plane densely bioturbated by *Psammichnites.* Tick spacing1 cm. C – Upper bedding plane with numerous, finely preserved *Psammichnites.* C - *Taenidium*; top view.

Fig. 10. *Zoophycos.* A – Circular morphotype of *Zoophycos*. Upper bedding plane view; tick scale = 1 cm. B – Lobate *Zoophycos.* Upper bedding plane view. C – *Zoophycos* with evident apex (arrowed). Lower bedding plane view.

Fig. 11. Zoophycos. A - *Zoophycos* (Zo) and *Phymatoderma* (Ph). B – Particular of a specimen of *Zoophycos* showing marginal tube (arrowed). C – *Zoophycos* is frequently associated with body fossils, such as bryozoans (Br) and plant fragments (Pl).

Fig. 12. Ichnonetwork of the Val Dolce Formation. Each node represent an ichnotaxon: *Cylindrichnus* (Cy), *Curvolithus* (Cu)*, Helminthoidichnites* (He)*, Palaeophycus* (Pa)*, Phymatoderma* (Ph)*, Planolites* (Pl)*, Taenidium* (Ta)*, Zoophycos* (Zo). Nodes have been scaled according to their degree, while thickness and colour of links refer to their weight (intensity of association relationship).

Fig. 13. Network concepts represented by toy networks. A – Connected network. The figured network consists of a single connected component. B – Disconnected network. The figured network is not connected, but consists of two components. C – The highlighted nodes are connected by various paths, among which the dotted and the slashed one. The dashed one has the shortest path length. D – Clique. The components of a clique have to be mutually interconnected: the highlighted nodes are part of the same clique, the non-highlighted ones are not. In the latter case, four dyadic cliques are found.

Fig. 14. Closeness centrality. Nodes have been colored and sized according to their closeness.

Fig. 15. Node arrangement according to the Yifan-Hu algorithm. The figured network is equivalent to Fig. 14.

Fig. 16. Node betweeness. Nodes have been colored and sized according to their betweeness.

Fig. 17. Clustering coefficient.

Fig. 18. Ichnoassociations as cliques.

Fig. 19. River mouth-offshore transition expressed as a bioturbation gradient, going from low (A) to intense (D) bioturbation. A – Monoichniospecific assemblages of *Cylindrichnus,* attributable to ichnoassociation $C_{1\,,}$ are characterized by low bioturbation intensity. Similar occurrences are interpreted to reflect proximal delta front settings. B – Low-bioturbation expression of ichnoassociation C_3 with *Curvolithus* (Cu), *Cylindrichnus* (Cy) and *Helminthoidichnites* (He); ichnological features are suggestive of distal delta front. C – Moderate-bioturbation manifestation of ichnoassociation C_3 with *Curvolithus* (Cu) and *Cylindrichnus* (Cy). Ichnological features indicate a proximal prodeltaic setting. D – Intense bioturbation by diminutive specimens of *Curvolithus* (Cu), attributable to ichnoassociation C_4, are suggestive of prodeltaic settings.

Fig. 20. Sedimentary features and ichnoassociations. A – Planar stratification and hummocky-cross stratification are commonly co-occurring with ichnoassociations C_1 and C_3. B – Brachiopods from an interval corresponding to the ichnoassociation C_2. C – The more distal expressions of the ichnoassociation C_3 and C_4 are usually accompanied by shell fragments. Note *Curvolithus* (Cu). D – Well-preserved body fossils, such as this large gastropod, co-occur with the ichnoassociation C_4. Note *Nereites* (Ne).

Fig. 21. *Phymatoderma* (Ph) - *Zoophycos* (Zo) ichnoassociation.

Fig. 22. The concept of niche in ichnology. Environmental parameters define the dimensions of a multidimensional space; here, three dimensions have been used for ease of visualization.

Fig. 23. From the niche concept to the ichnonetwork. A – Ichnotaxa a, b and c form an ichnoassociation in correspondence of the intersection of their niches. Salinity and depth have been considered the dimensions of the abstract space, but other parameters – in any number – would be valid examples as well. B – Ichnonetwork representation of Fig. 23A. The intersection of the niches of ichnotaxa a, b, c corresponds to a clique, that is, an ichnoassociation.

Fig. 24. Overlapping ichnoassociations. A – Environmental parameters define the dimensions of an abstract space in which niches of ichnotaxa a, b, c are represented. B – The figured ichnonetwork is equivalent to the niche arrangement of Fig. 24A. Ichnoassociations 1 and 2 correspond to cliques 1 and 2, respectively.

Fig. 25. Disjoint ichnoassociations with empty gap. A – Abstract environmental space in which two completely disjoint ichnoassociations are represented. B – Network equivalent of Fig. 25A.

Fig. 26. Disjoint ichnoassociations with covered gap. A – Disjoint ichnoassociations bridged by a third one. B – Network equivalent of Fig. 26A.

Fig. 27. Spatial configurations and their corresponding ichnonetworks. Node diameter and link size are proportional to betweenness and weight, respectively. A – Overlapping ichnoassociations, corresponding to Fig. 24. B- Disjoint ichnoassociations, corresponding to Fig. 25. C – Converging spatial ranges, corresponding to a single clique with inhomogeneous weight distribution.. D – Coinciding spatial ranges, corresponding to a single clique with homogeneous weight distribution.

Fig. 28. Patterns of association revealed by link weight. A – Ichnoassociation C_3, filtered by average link weight. Note the strong association relationships involving *Cylindrichnus-Helminthoidichnites* and *Curvolithus-Zoophycos-Helminthoidichnites.* B – The common co-occurrence of *Helminthoidichnites* (He) and *Cylindrichnus* (Cy) supports the association patterns detected by ichnonetwork analysis. C – Ichnoassociation C_4, filtered by average link weight. Note the relatively homogeneous link weight.

Fig. 29. Palaeoenvironmental model of the Val Dolce Formation, based on ichnonetwork analysis.

Fig. 30. New perspectives of study. *Psammichnites* and *Pramollichnus* have not been reported from the studied section, but they are commonly found within the study area.

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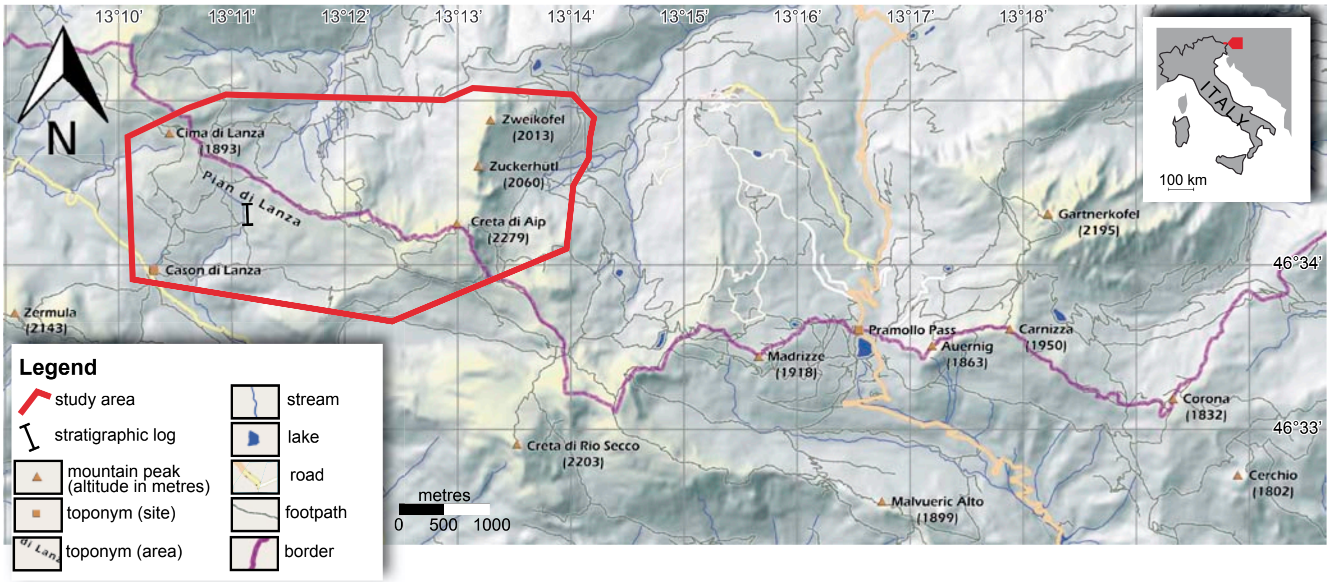
	Lithology	Major structures	Dominant color	Body Fossils	Organization	Code
Conglomeratic facies	medium- to coarse grained quartz-conglomerate	Massive, trough-bedding, graded-bedding	White	Very rare plant fragments	Plurimetric units, often deriving from amalgamated bodies; common erosive base	C1
	Fine- to medium-grained conglomerate		White	absent	Metric, cross-stratified units	C2
Arenitic facies	fine- to medium-grained sandstone	Planar-lamination dominant. Water escape structures locally abundant	Light brown to rusty brown	Very rare shell fragments	plurimetric bodies with planar or wavy bedding; hummocky-stratified horizons common	S1
	fine-grained sandstone or sandy siltstone with carbonatic cement	Massive	Light to dark brown	Bioclastic horizons are frequent (mainly brachiopods and crinoids)	interbedded in pelitic sequences. Thickness: 10-30 cm.	S2
	Medium-grained sandstone	Massive	Grey to pale brown	absent	Plurimetric bodies with planar bedding	S3
Pelitic facies	siltstone and sandy siltstone	Discontinuous planar and wavy lamination	Light grey to bluish	bryozoans, brachiopods, gastropods, crinoids	Plurimetric bodies with occasional sandstone layers (facies S2).	P1
	siltstone	Discontinuous planar and wavy lamination	Brown to light grey; metallic shine	Plant remains	Metric to plurimetric units	P2
Carbonatic facies	Wackestone or packstone. Coated grains and algae common.	Massive	Light grey	fusulinids, brachiopods, gastropods, echinoderms and bryozoans.	Decimetric layers	L1
	Packstone to rudstone	Massive	Light grey	Articulated algae	Decimetric layers	L2
	Packstone to grainstone	Massive	Light grey	Oncolites	Decimetric layers	L3

Table 1. Major sedimentary facies of Val Dolce Formation.


13°10'
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ITALY
100 km
Cima di Lanza (1893)
Plan di Lanza
Cason di Lanza
Zermula (2143)
Zweikofel (2013)
Zuckerhutl (2060)
Creta di Aip (2279)
Gartnerkofel (2195)
Pramollo Pass
Auernig (1863)
Carnizza (1950)
Madrizze (1918)
Corona (1832)
Creta di Rio Secco (2203)
Malvueric Alto (1899)
Cerchio (1802)
metres
0 500 1000
Legend
study area
stratigraphic log
mountain peak (altitude in metres)
toponym (site)
toponym (area)
stream
lake
road
footpath
border

Fig. 1.

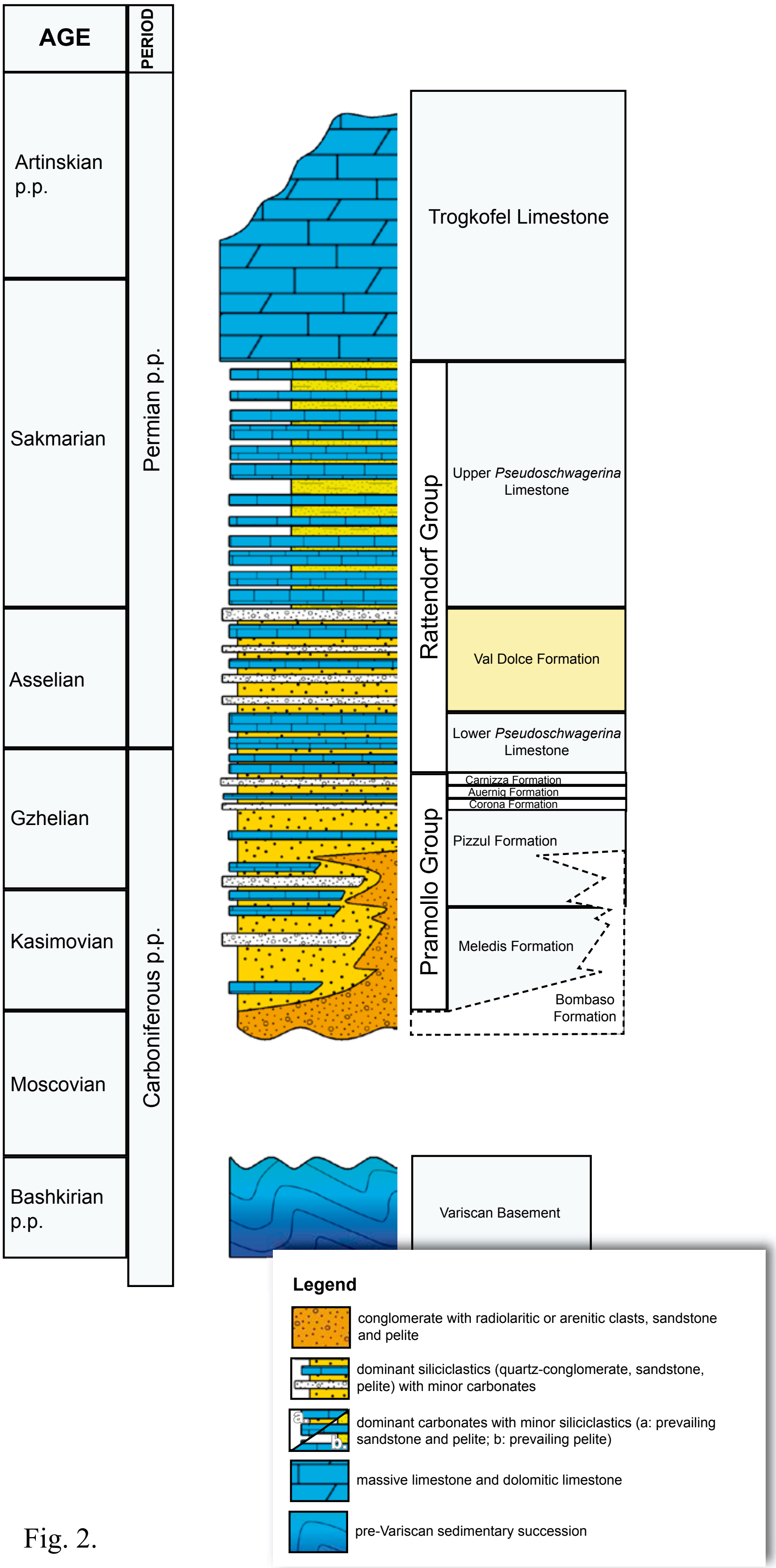

AGE
PERIOD
Artinskian p.p.
Sakmarian
Asselian
Gzhelian
Kasimovian
Moscovian
Bashkirian p.p.
Permian p.p.
Carboniferous p.p.
Trogkofel Limestone
Rattendorf Group
Upper *Pseudoschwagerina* Limestone
Val Dolce Formation
Lower *Pseudoschwagerina* Limestone
Pramollo Group
Carnizza Formation
Auernig Formation
Corona Formation
Pizzul Formation
Meledis Formation
Bombaso Formation
Variscan Basement
Legend
conglomerate with radiolaritic or arenitic clasts, sandstone and pelite
dominant siliciclastics (quartz-conglomerate, sandstone, pelite) with minor carbonates
a
b
dominant carbonates with minor siliciclastics (a: prevailing sandstone and pelite; b: prevailing pelite)
massive limestone and dolomitic limestone
pre-Variscan sedimentary succession

Fig. 2.

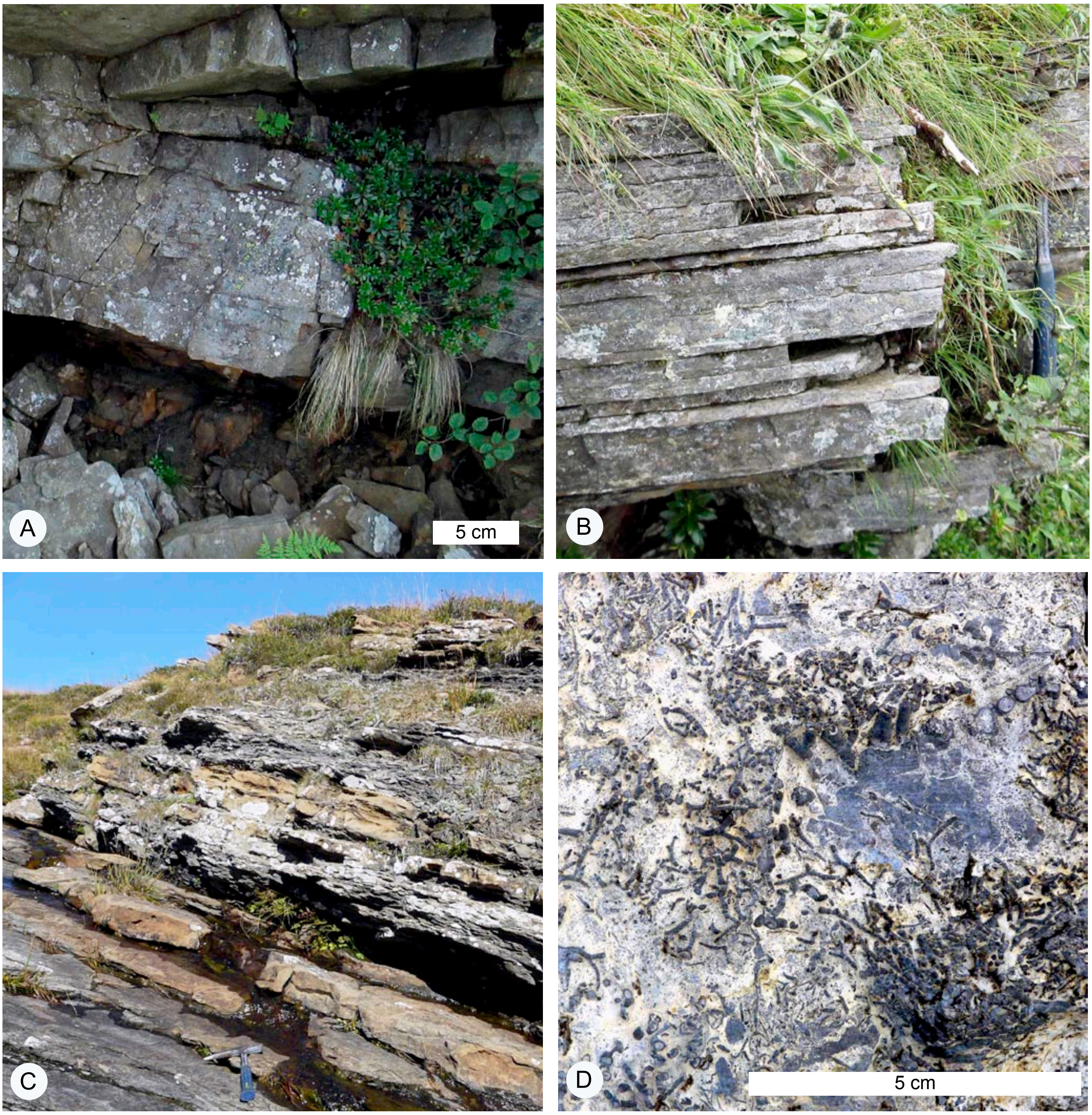


Fig. 3.

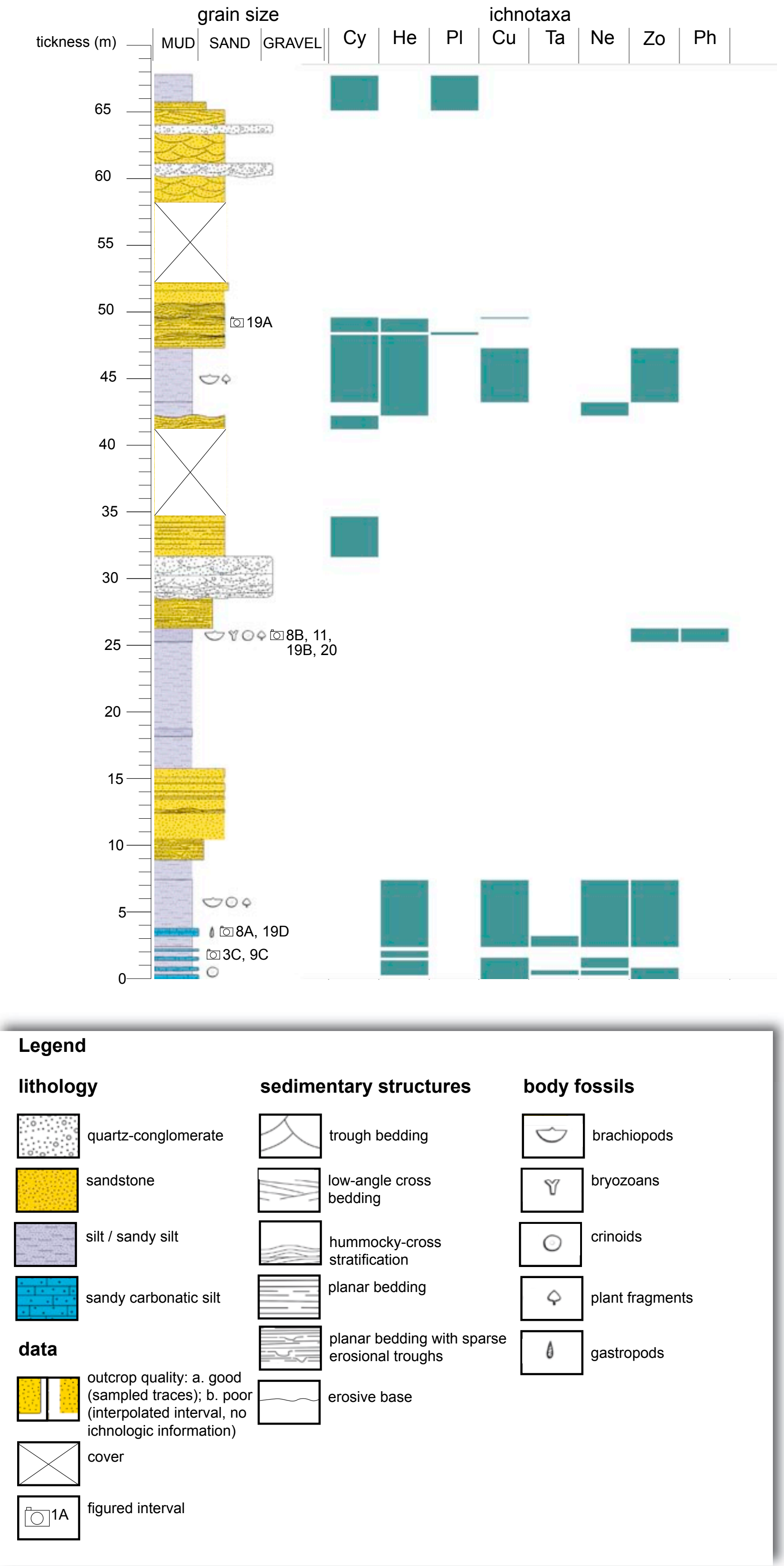
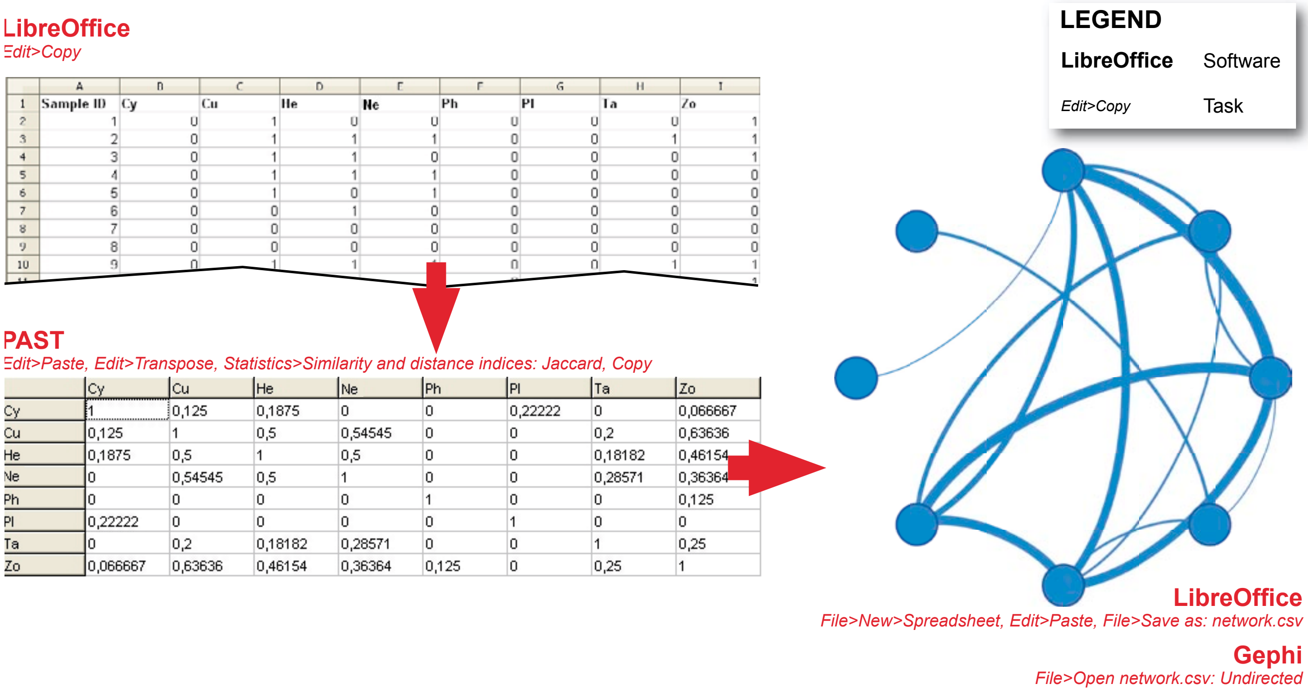

grain size
ichnotaxa
tickness (m)
MUD
SAND
GRAVEL
Cy
He
Pl
Cu
Ta
Ne
Zo
Ph
65
60
55
50
45
40
35
30
25
20
15
10
5
0
19A
8B, 11, 19B, 20
8A, 19D
3C, 9C
Legend
lithology
quartz-conglomerate
sandstone
silt / sandy silt
sandy carbonatic silt
data
outcrop quality: a. good (sampled traces); b. poor (interpolated interval, no ichnologic information)
cover
1A
figured interval
sedimentary structures
trough bedding
low-angle cross bedding
hummocky-cross stratification
planar bedding
planar bedding with sparse erosional troughs
erosive base
body fossils
brachiopods
bryozoans
crinoids
plant fragments
gastropods

Fig. 4.



LibreOffice
Edit>Copy

	A	B	C	D	E	F	G	H	I
1	Sample ID	Cy	Cu	He	Ne	Ph	Pl	Ta	Zo
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3	2	0	1	1	1	0	0	1	1
4	3	0	1	1	0	0	0	0	1
5	4	0	1	1	1	0	0	0	0
6	5	0	1	0	1	0	0	0	0
7	6	0	0	1	0	0	0	0	0
8	7	0	0	0	0	0	0	0	0
9	8	0	0	0	0	0	0	0	0
10	9	0	1	1	1	0	0	1	1

PAST
Edit>Paste, Edit>Transpose, Statistics>Similarity and distance indices: Jaccard, Copy

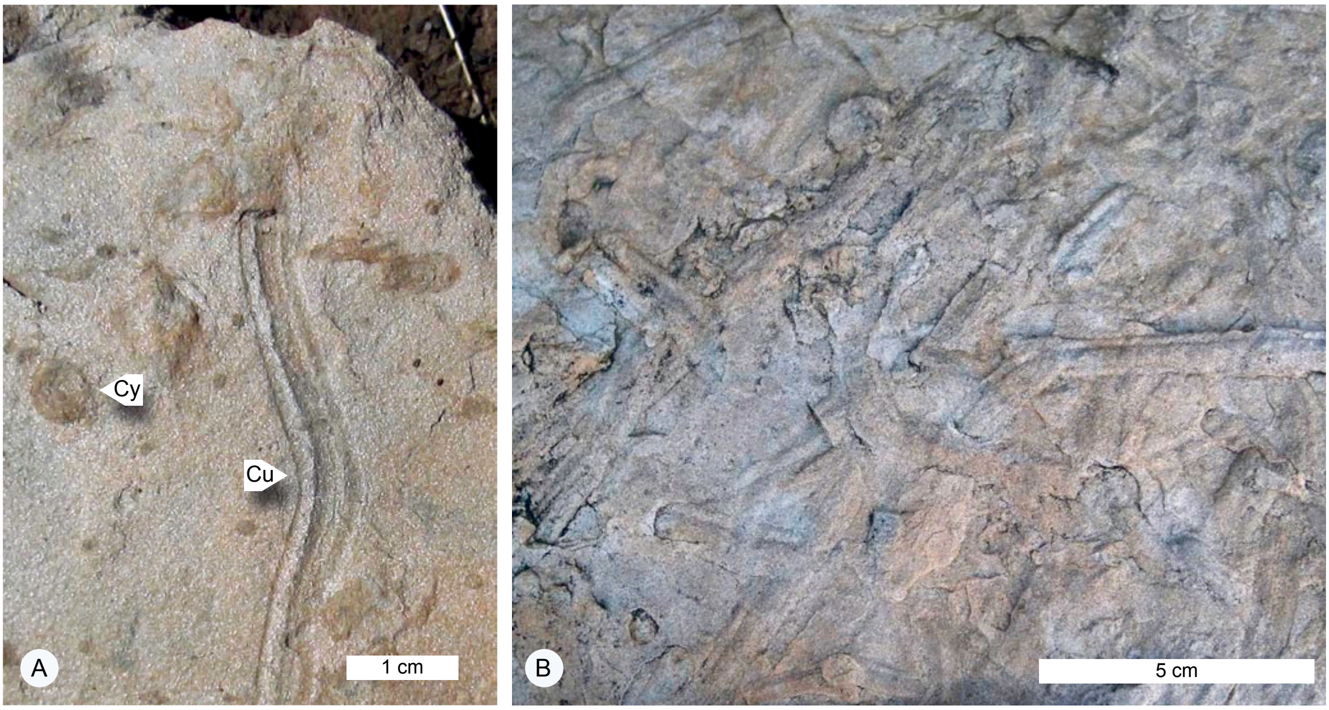
	Cy	Cu	He	Ne	Ph	Pl	Ta	Zo
Cy	1	0,125	0,1875	0	0	0,22222	0	0,066667
Cu	0,125	1	0,5	0,54545	0	0	0,2	0,63636
He	0,1875	0,5	1	0,5	0	0	0,18182	0,46154
Ne	0	0,54545	0,5	1	0	0	0,28571	0,36364
Ph	0	0	0	0	1	0	0	0,125
Pl	0,22222	0	0	0	0	1	0	0
Ta	0	0,2	0,18182	0,28571	0	0	1	0,25
Zo	0,066667	0,63636	0,46154	0,36364	0,125	0	0,25	1

LEGEND	
LibreOffice	Software
Edit>Copy	Task

LibreOffice
File>New>Spreadsheet, Edit>Paste, File>Save as: network.csv

Gephi
File>Open network.csv: Undirected

Fig. 5.



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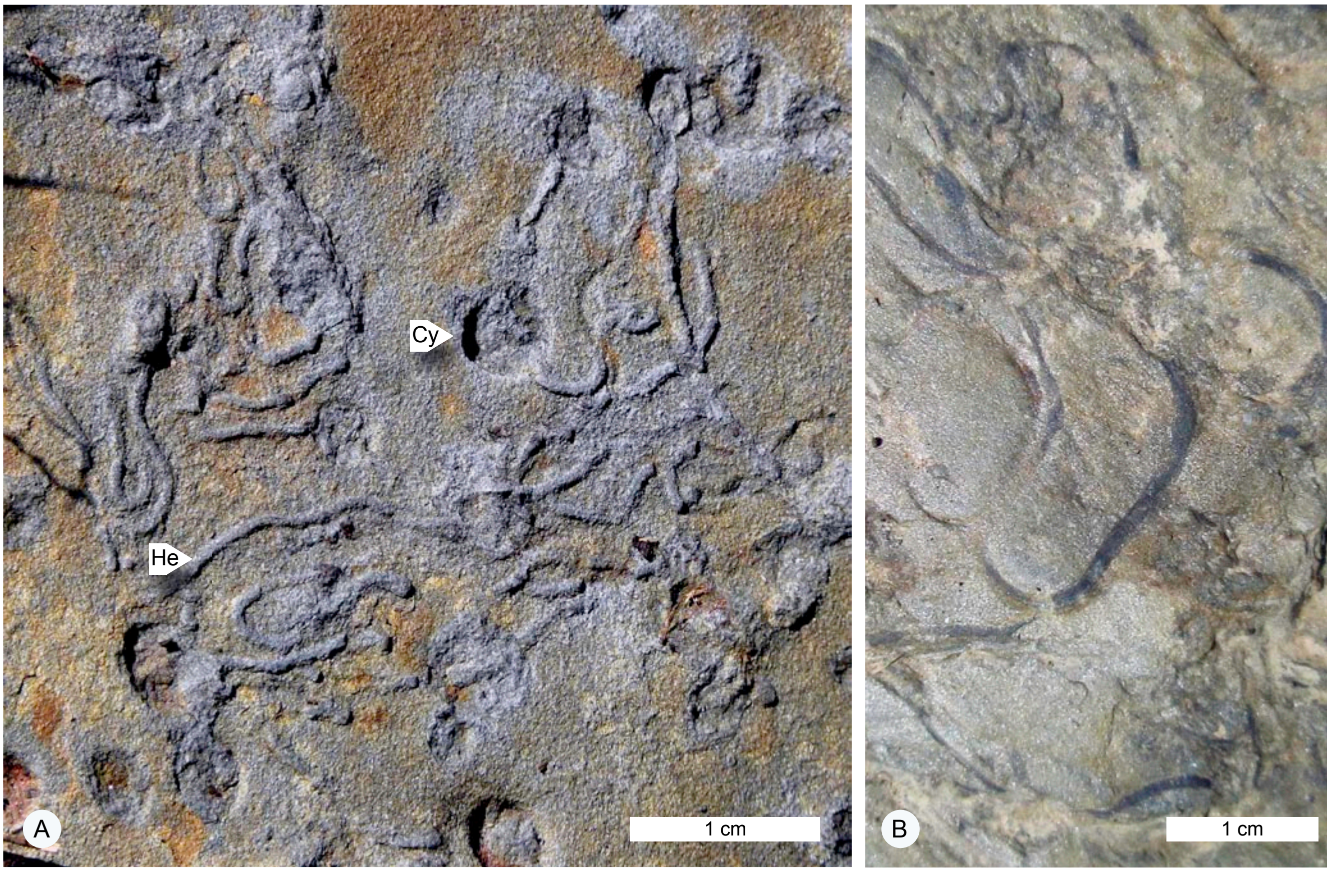

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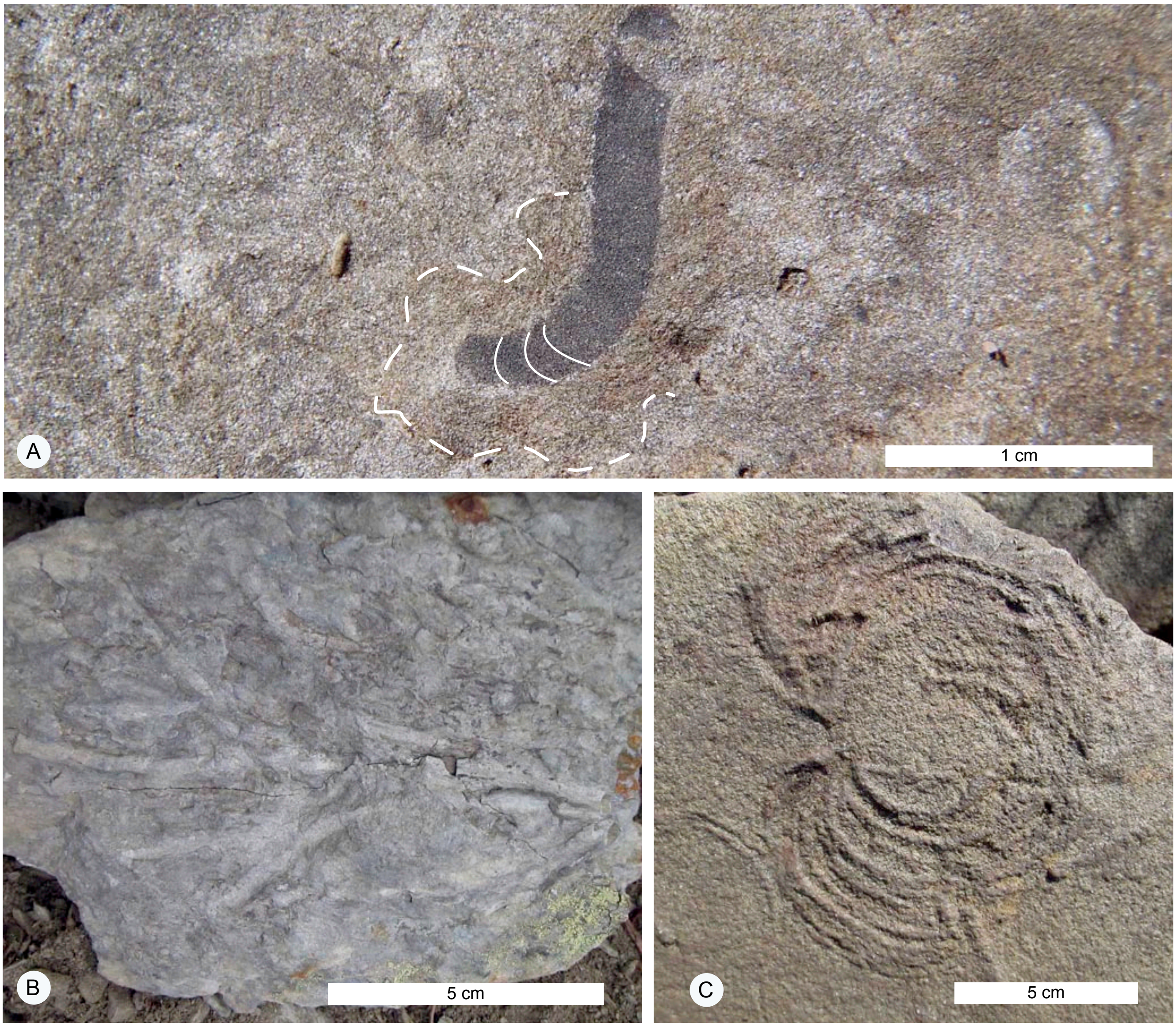

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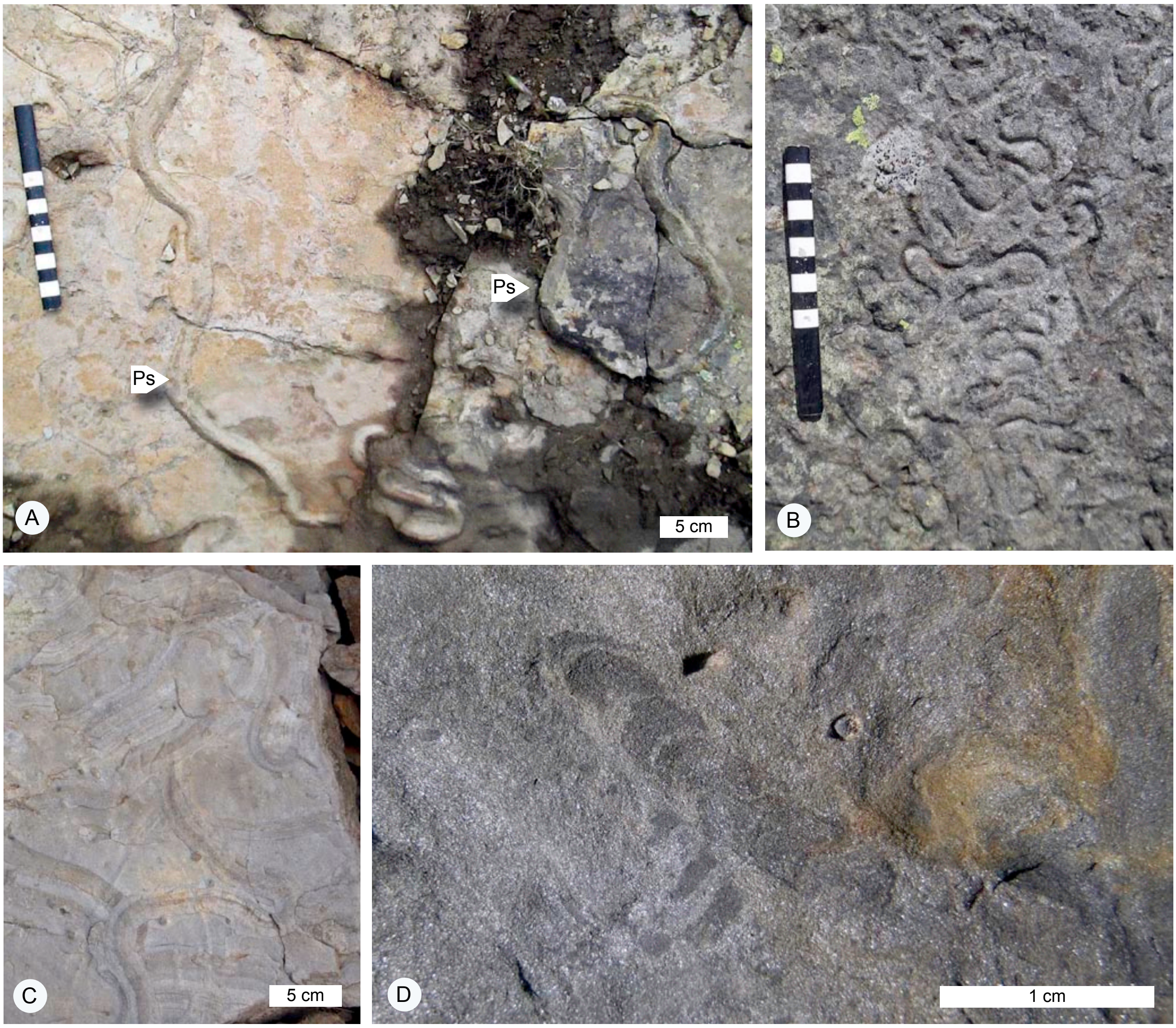


Fig. 9.

Fig. 10.

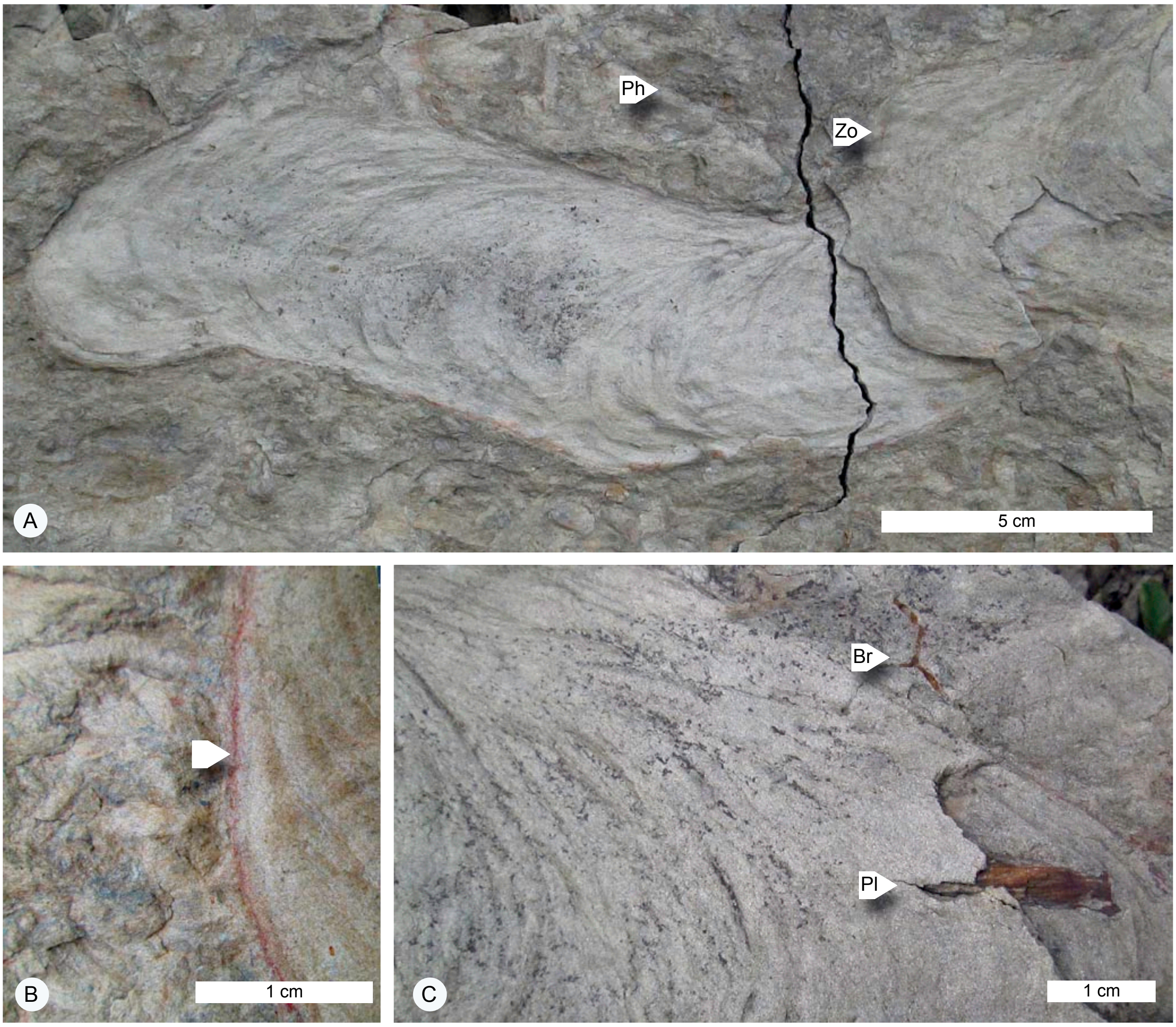


Fig. 11.

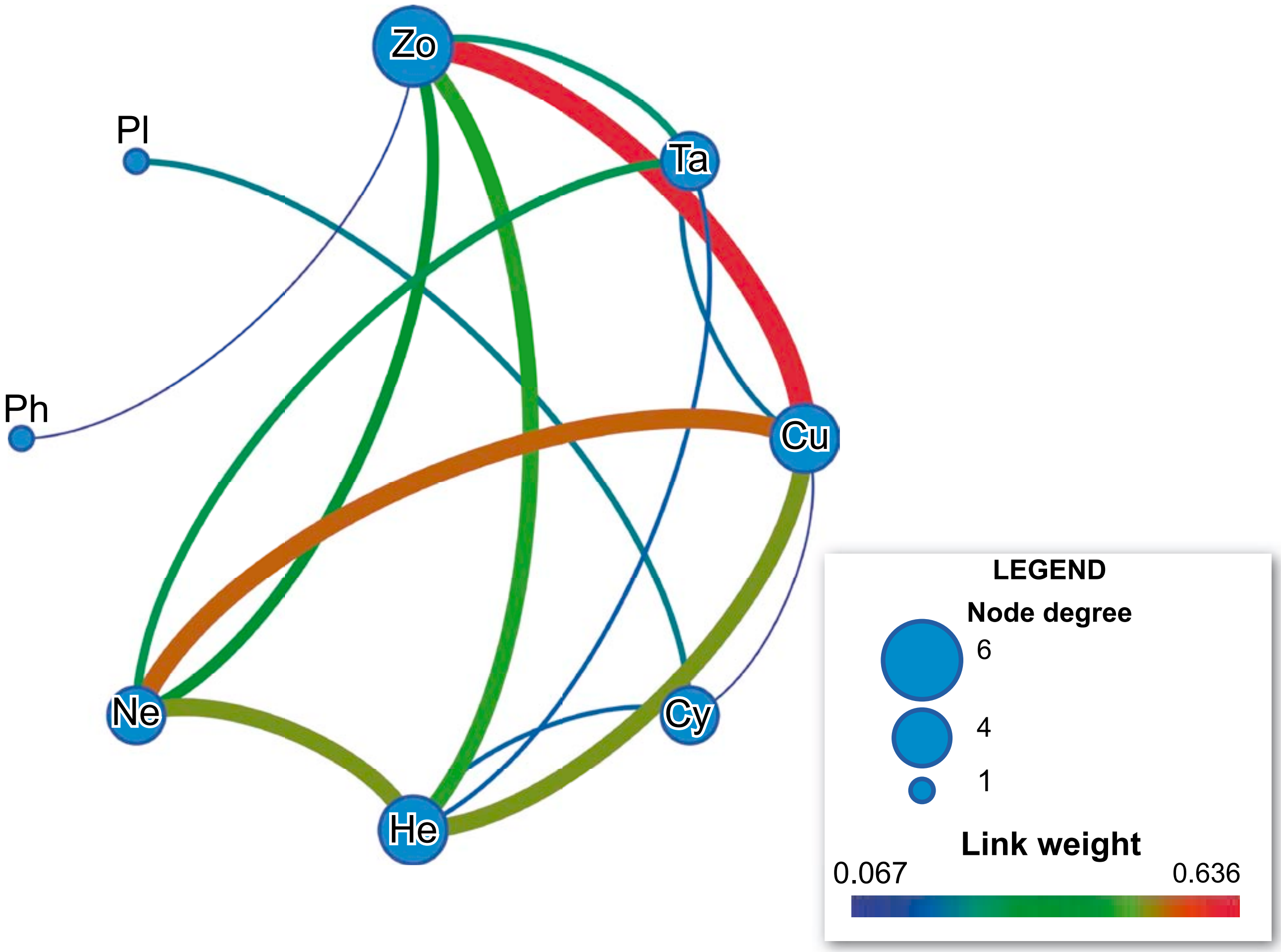

Zo
Pl
Ta
Ph
Cu
Ne
Cy
He
LEGEND
Node degree
6
4
1
Link weight
0.067
0.636

Fig. 12.

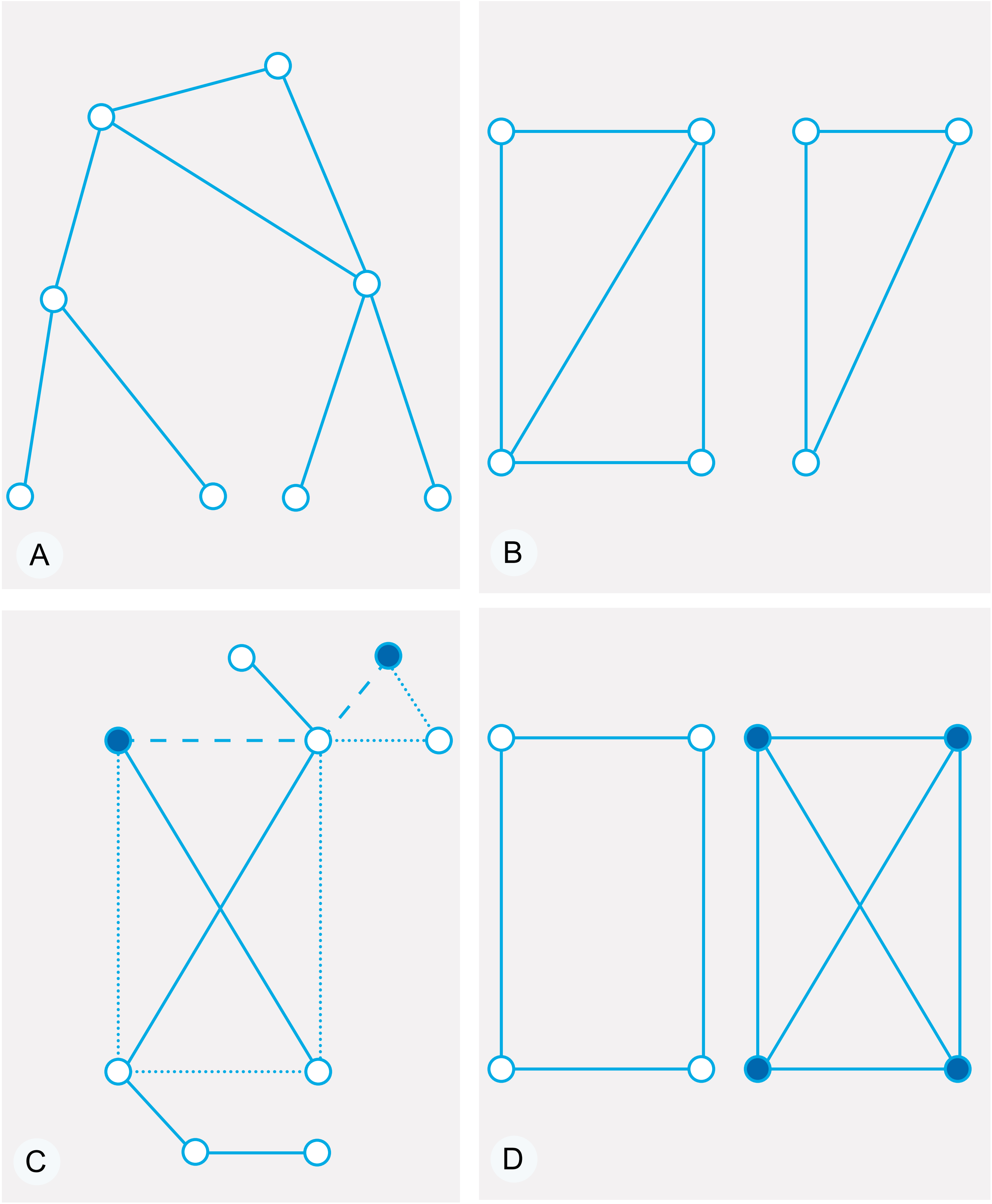
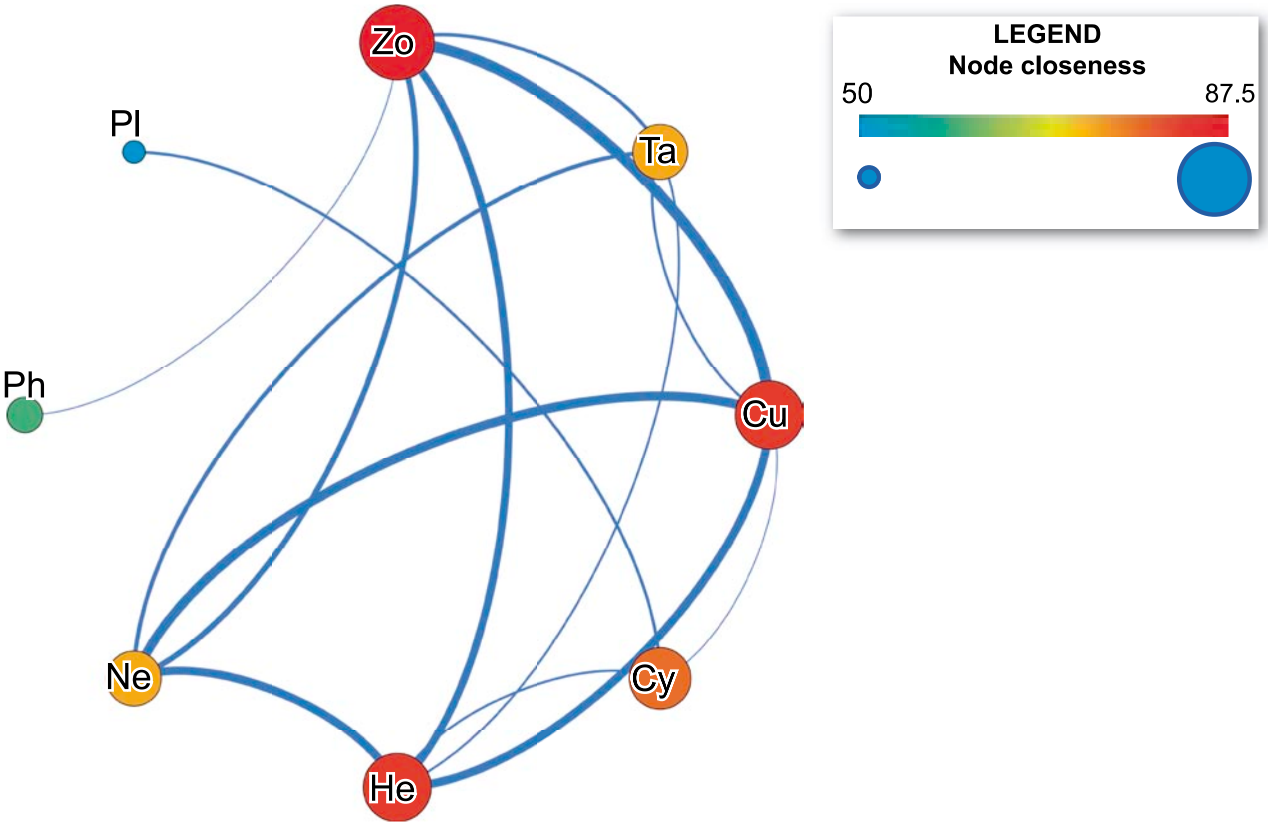


Fig. 13.



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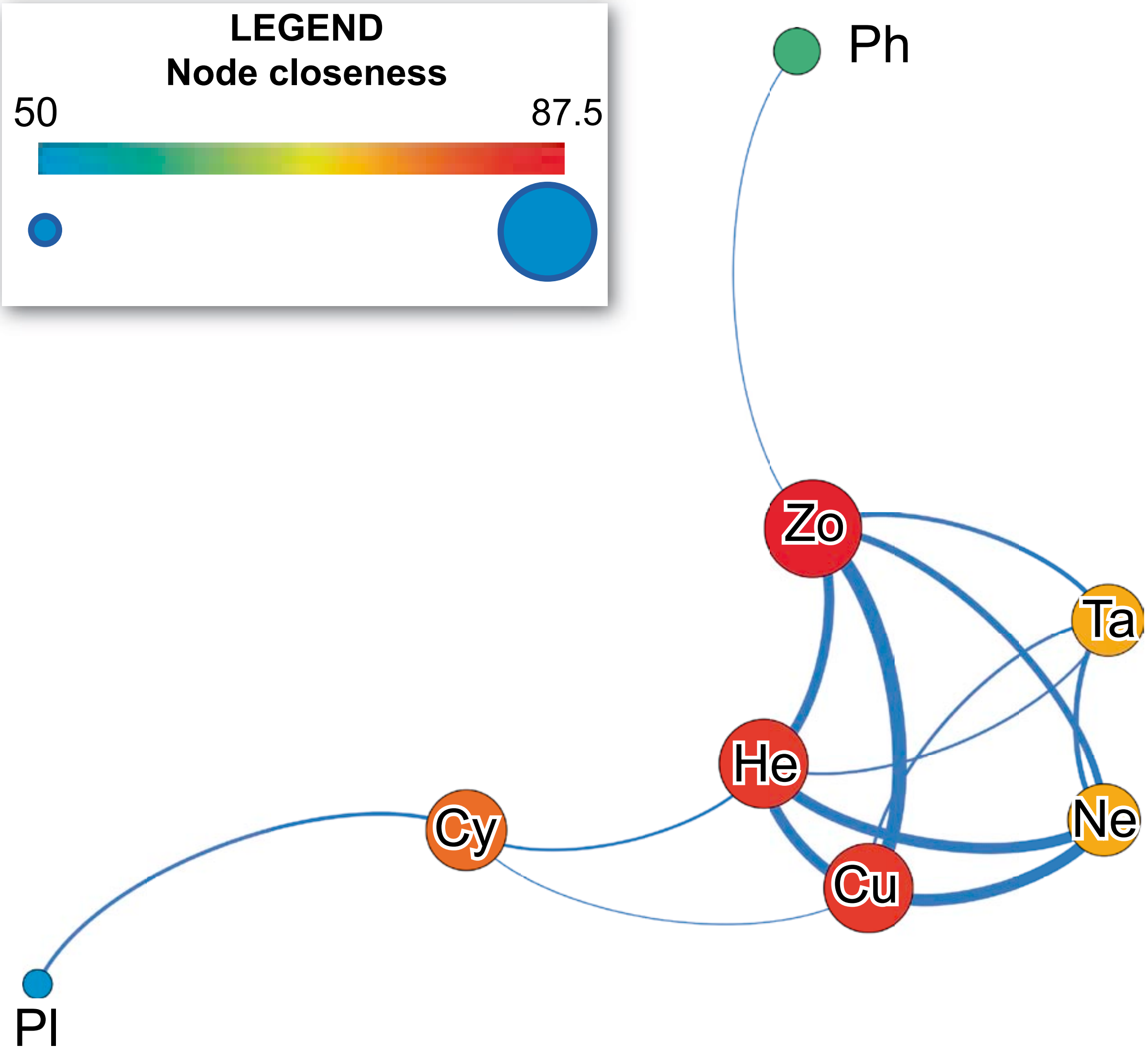

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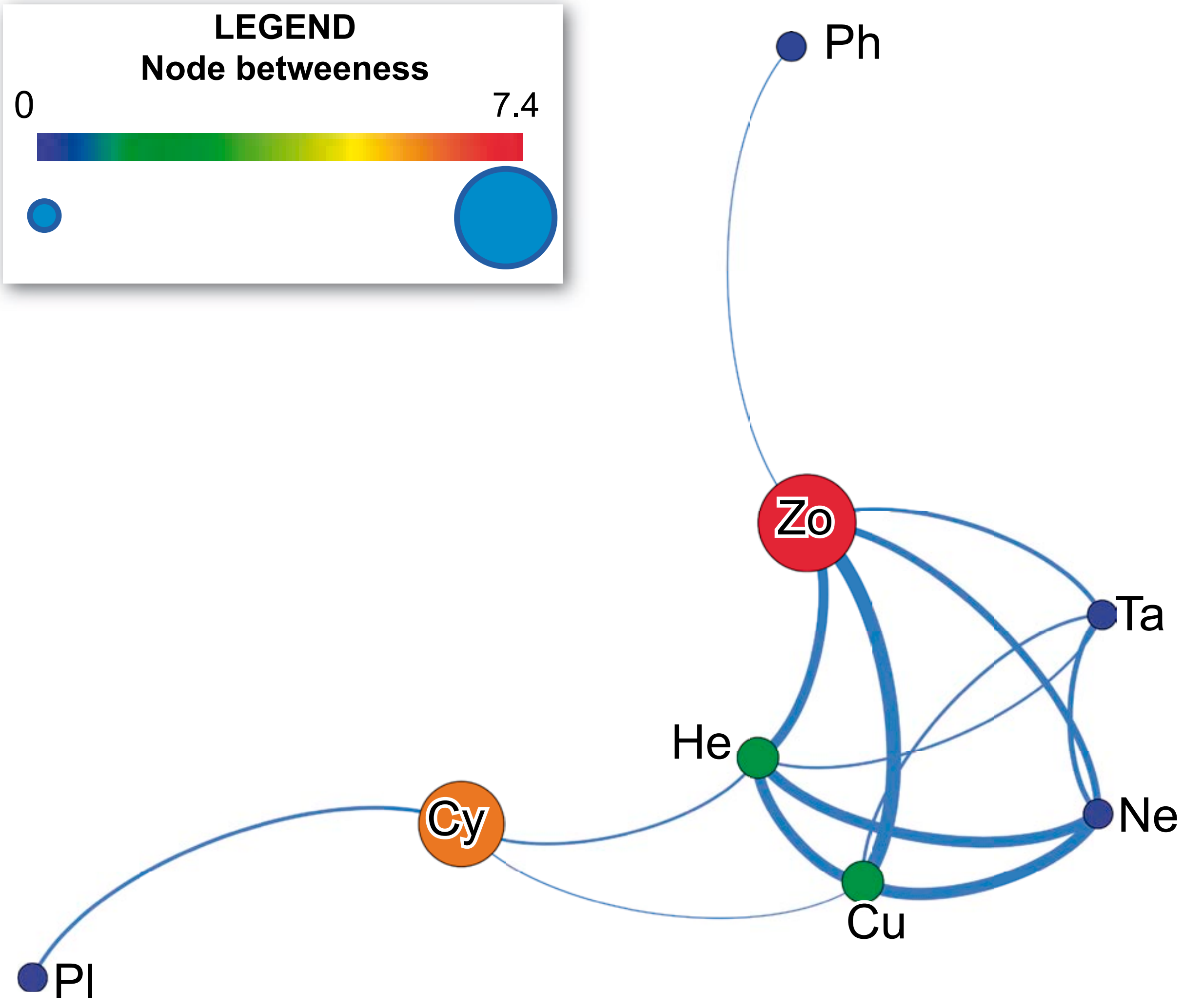


Fig. 16.

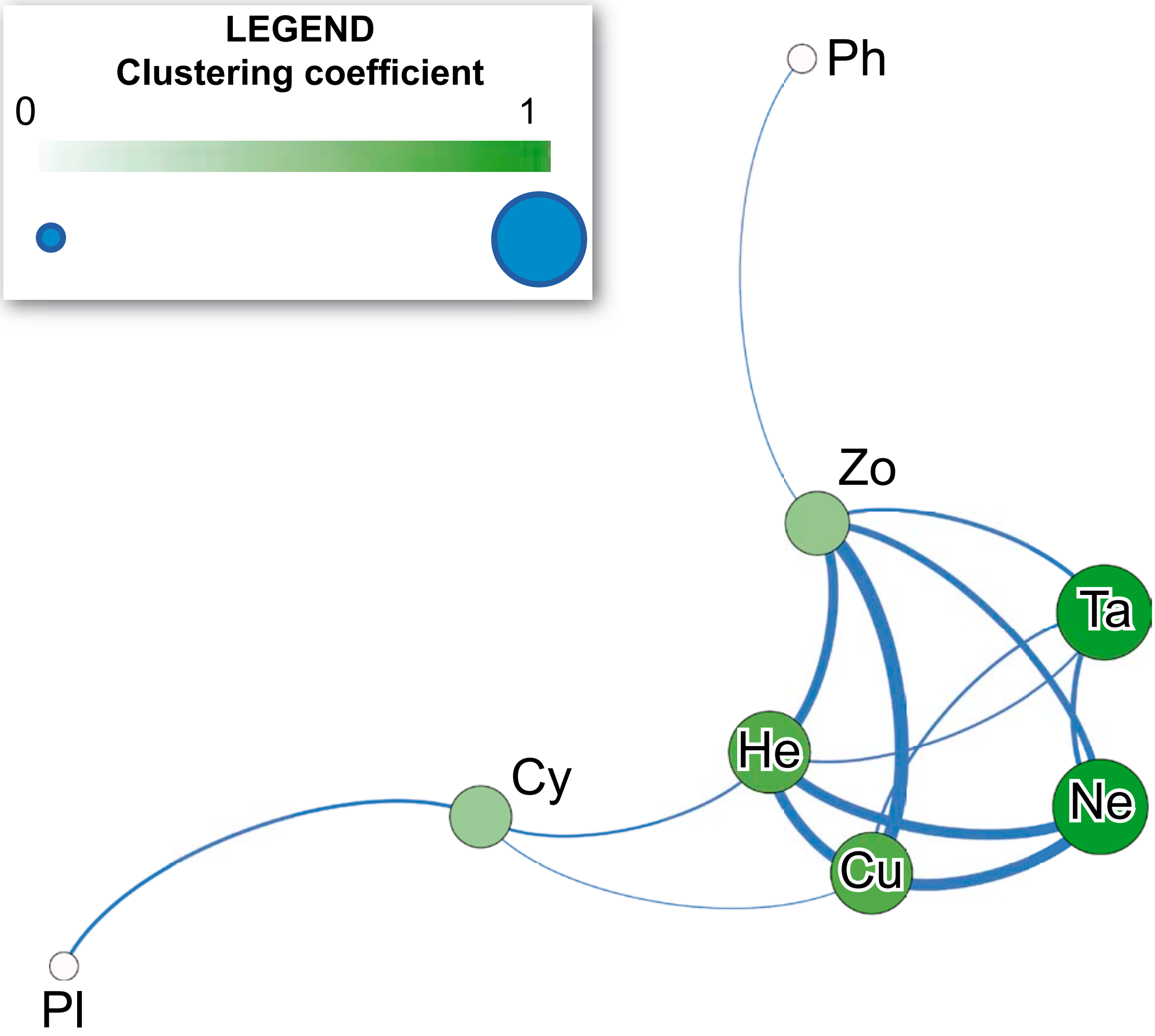


Fig. 17.

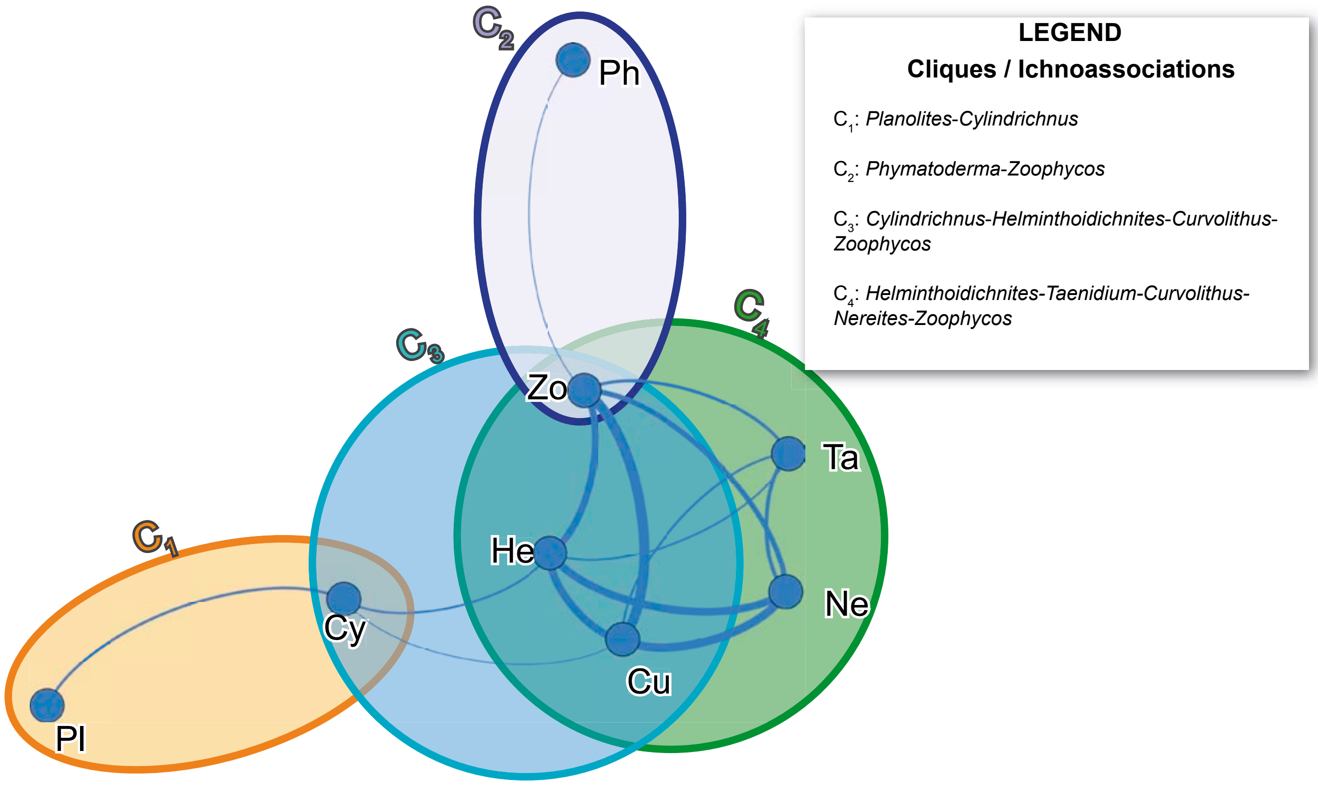

C_2
Ph
C_4
C_3
Zo
Ta
C_1
He
Ne
Cy
Cu
Pl
LEGEND
Cliques / Ichnoassociations
C_1: *Planolites-Cylindrichnus*
C_2: *Phymatoderma-Zoophycos*
C_3: *Cylindrichnus-Helminthoidichnites-Curvolithus-Zoophycos*
C_4: *Helminthoidichnites-Taenidium-Curvolithus-Nereites-Zoophycos*

Fig. 18.

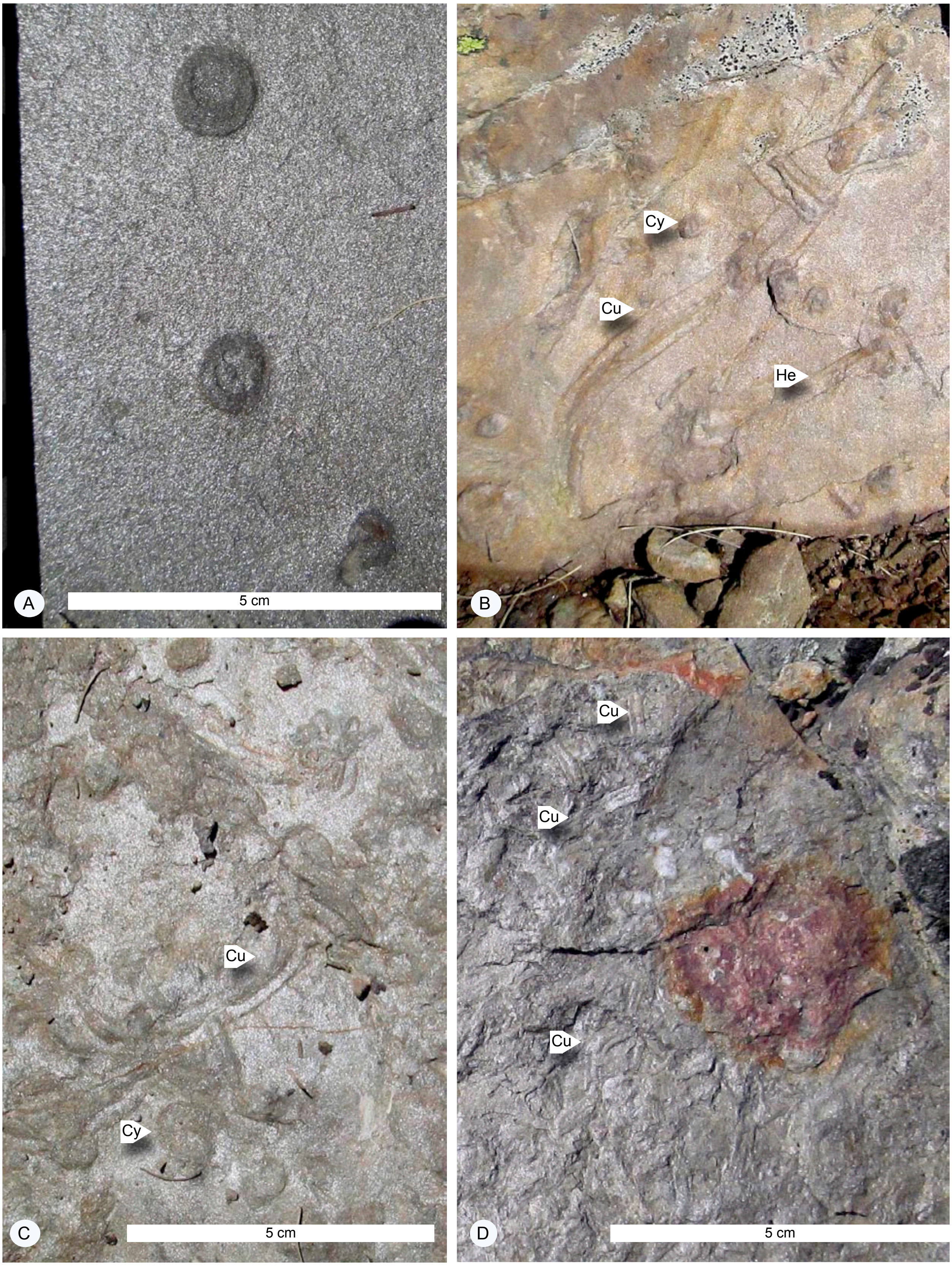


Fig. 19.

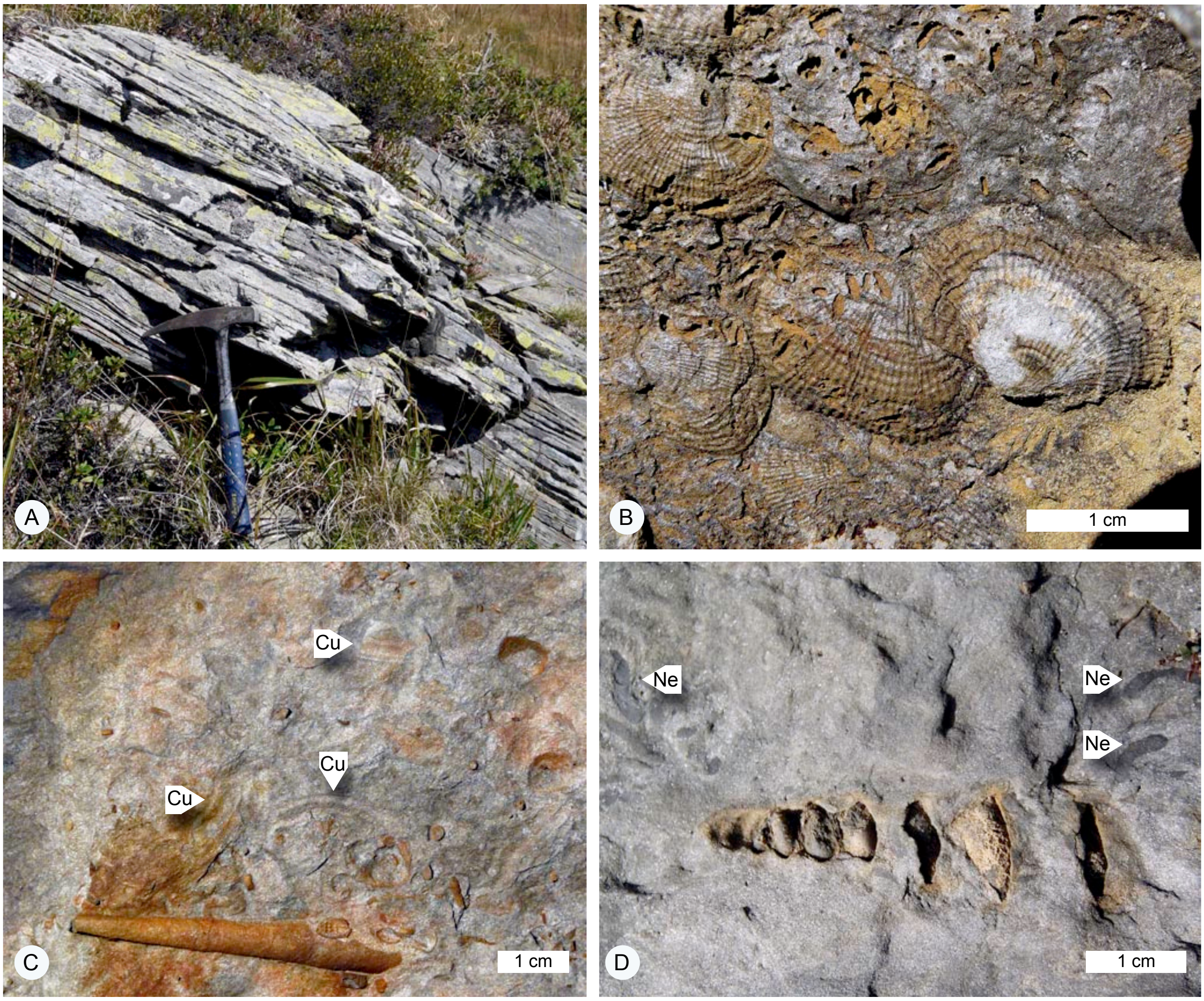
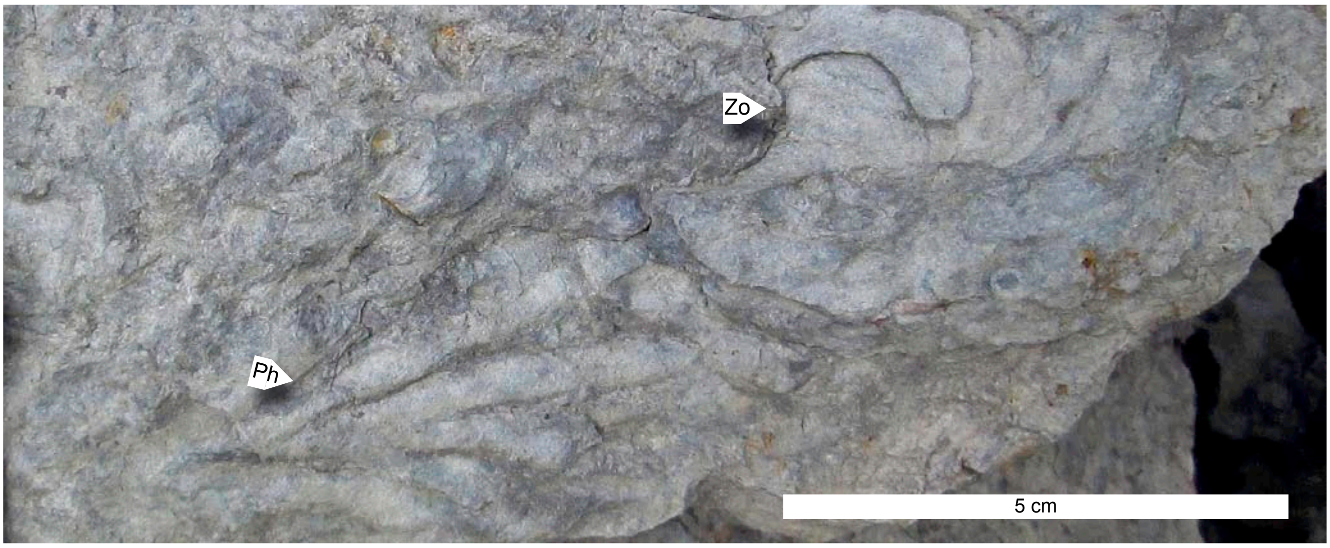


Fig. 20.



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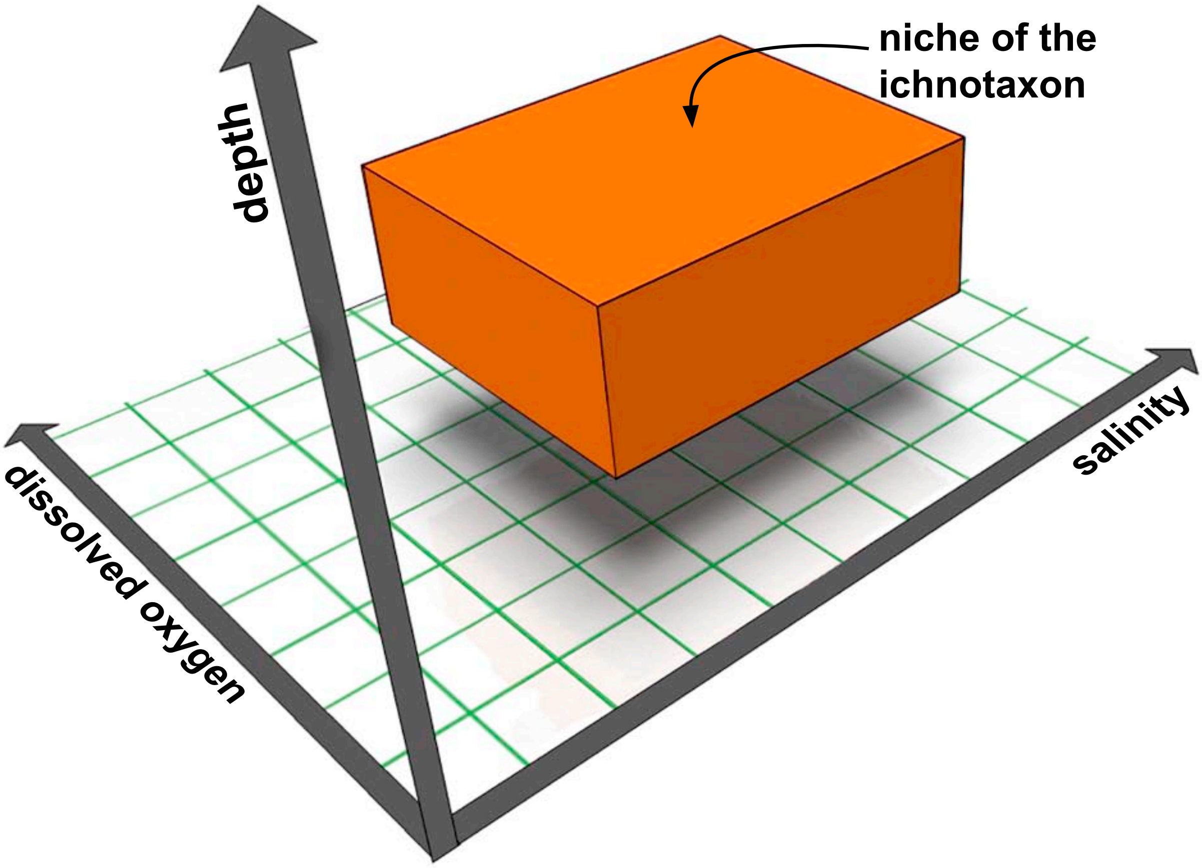

Fig. 22.

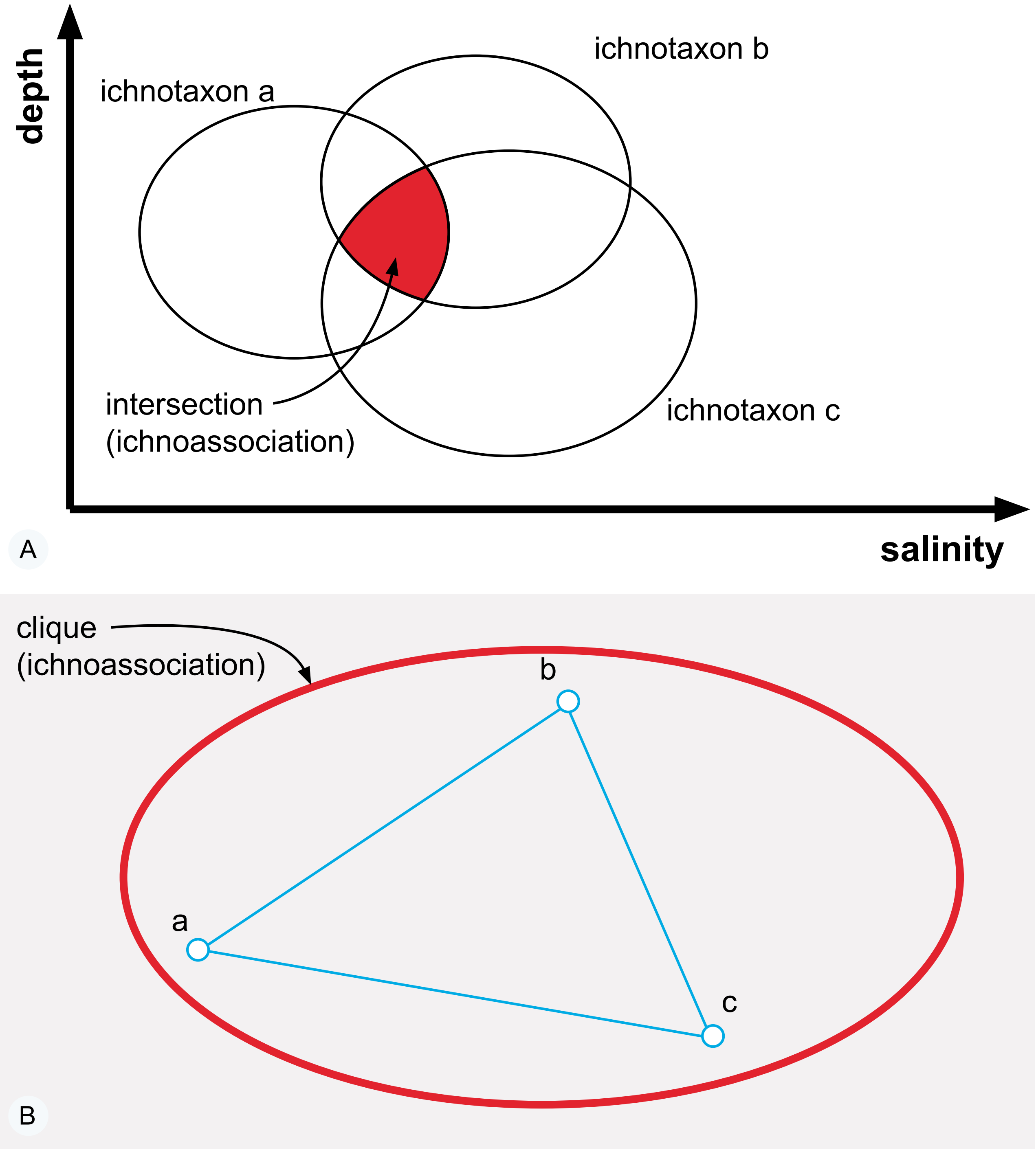
depth
ichnotaxon a
ichnotaxon b
ichnotaxon c
intersection
(ichnoassociation)
salinity
A
clique
(ichnoassociation)
a
b
c
B

Fig. 23.

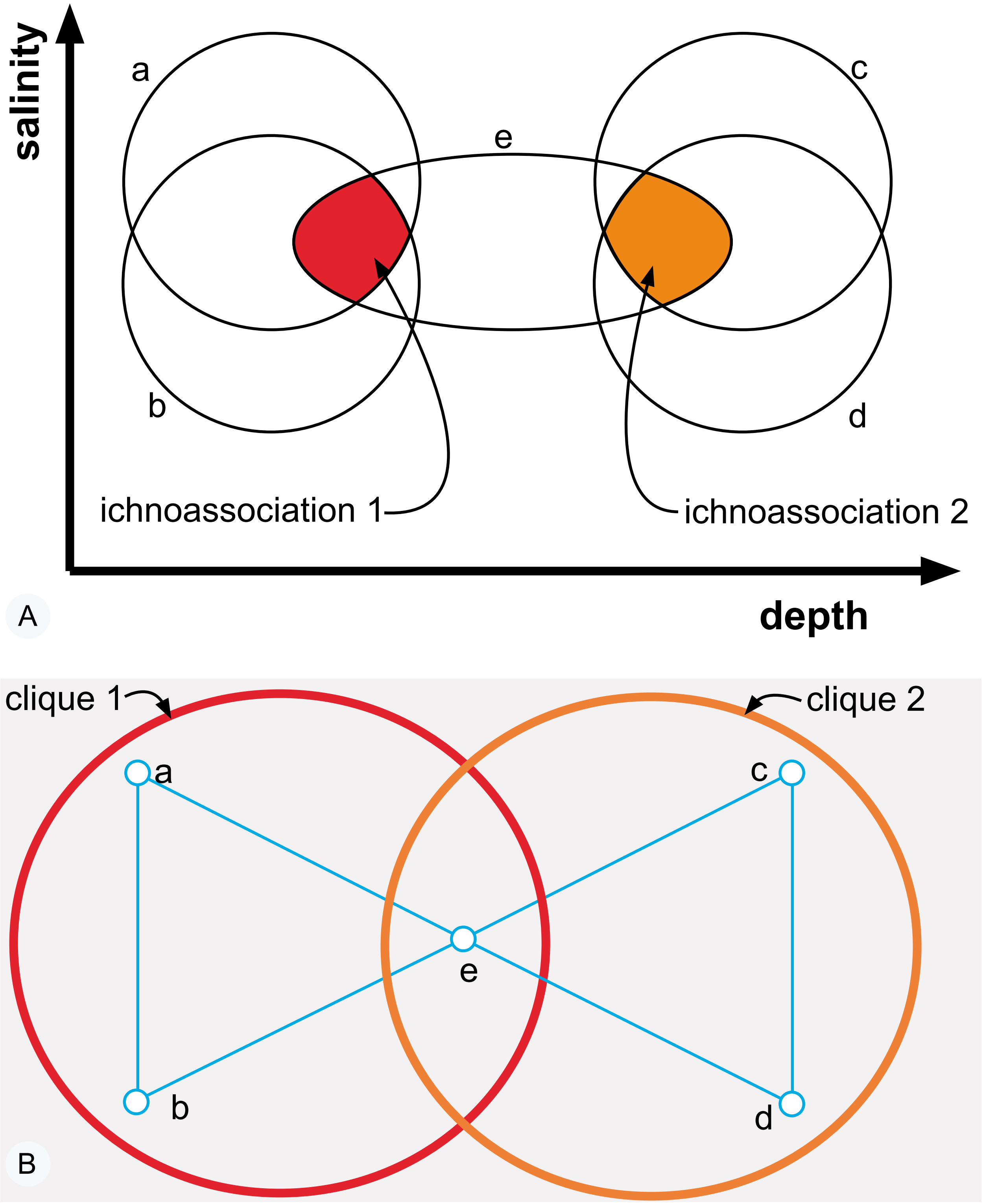
salinity
a
c
e
b
d
ichnoassociation 1
ichnoassociation 2
A
depth
clique 1
clique 2
a
c
e
b
d
B

Fig. 24.

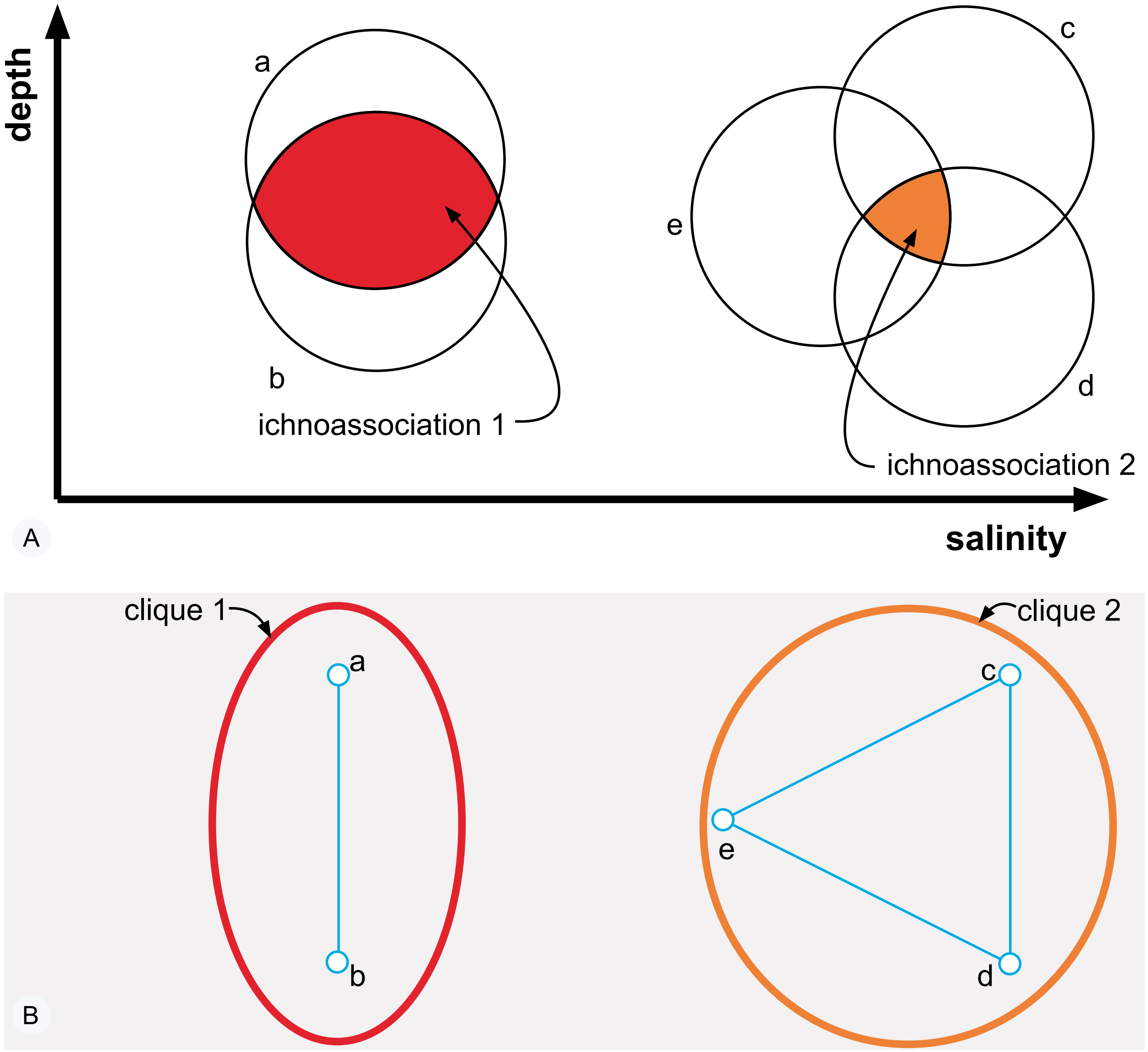
depth
a
b
ichnoassociation 1
c
e
d
ichnoassociation 2
A
salinity
clique 1
a
b
clique 2
c
e
d
B

Fig. 25.

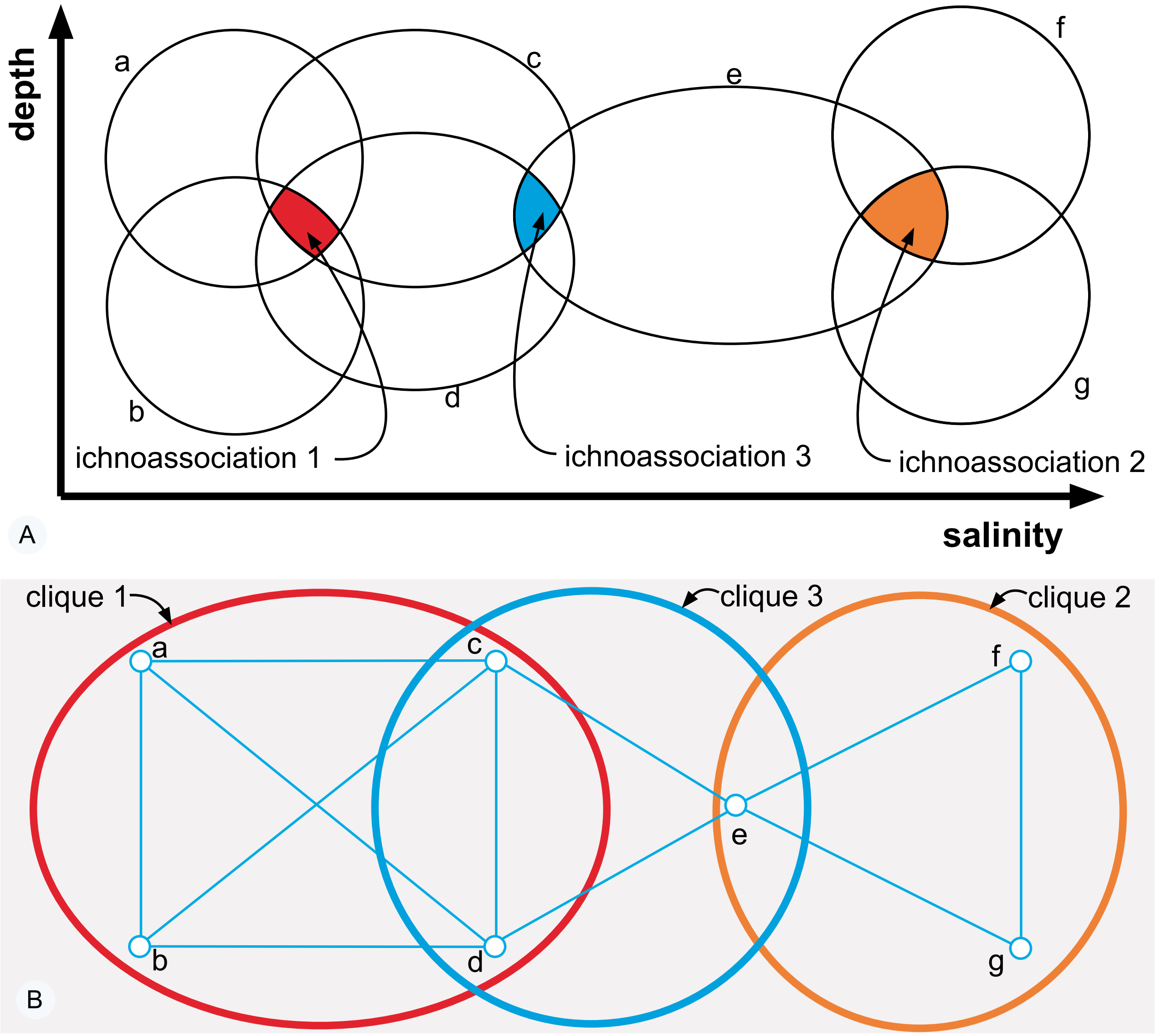
depth
a
c
e
f
b
d
g
ichnoassociation 1
ichnoassociation 3
ichnoassociation 2
A
salinity
clique 1
clique 3
clique 2
a
c
f
e
b
d
g
B

Fig. 26.

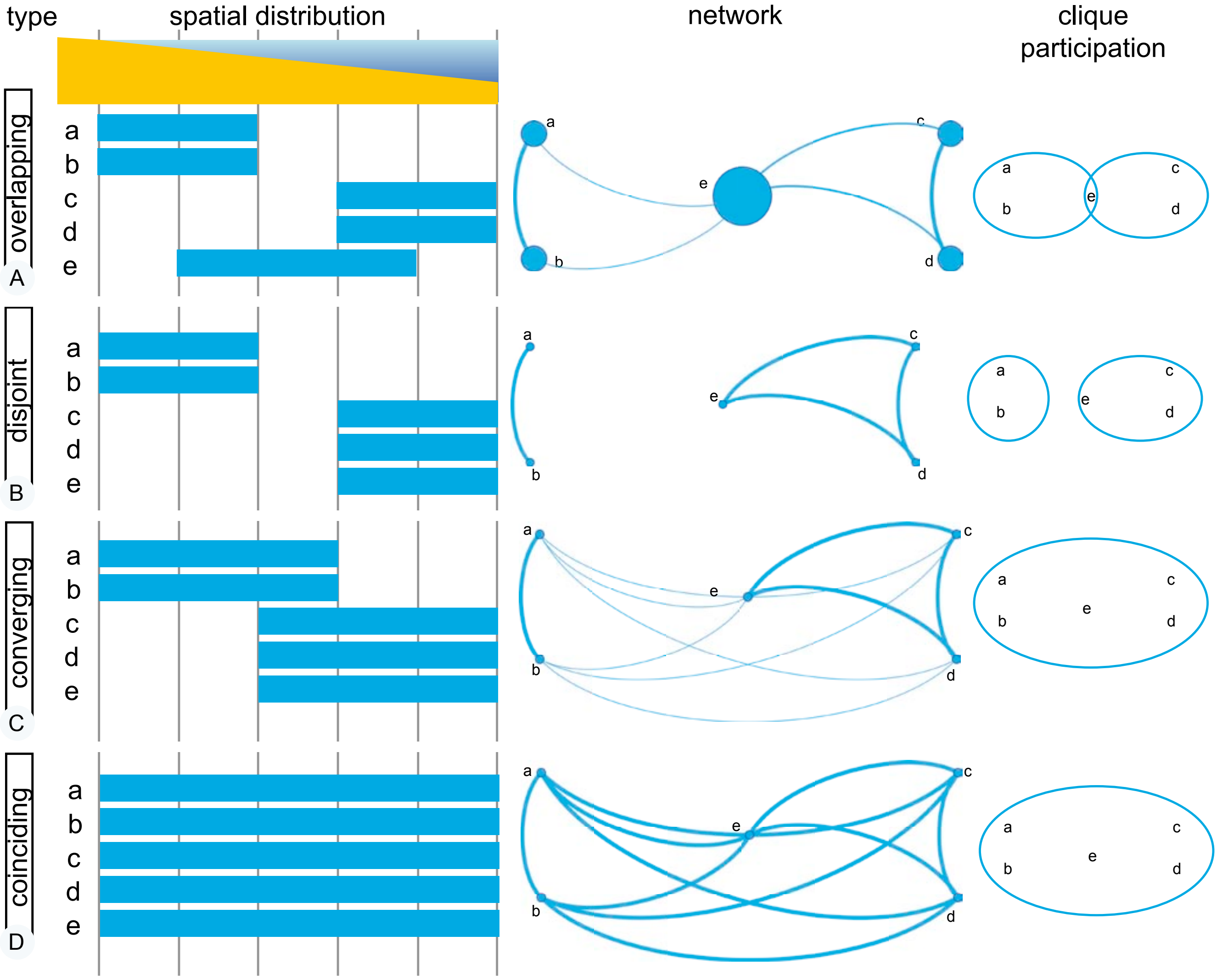
type
spatial distribution
network
clique participation
overlapping
A
disjoint
B
converging
C
coinciding
D
a
b
c
d
e

Fig. 27.

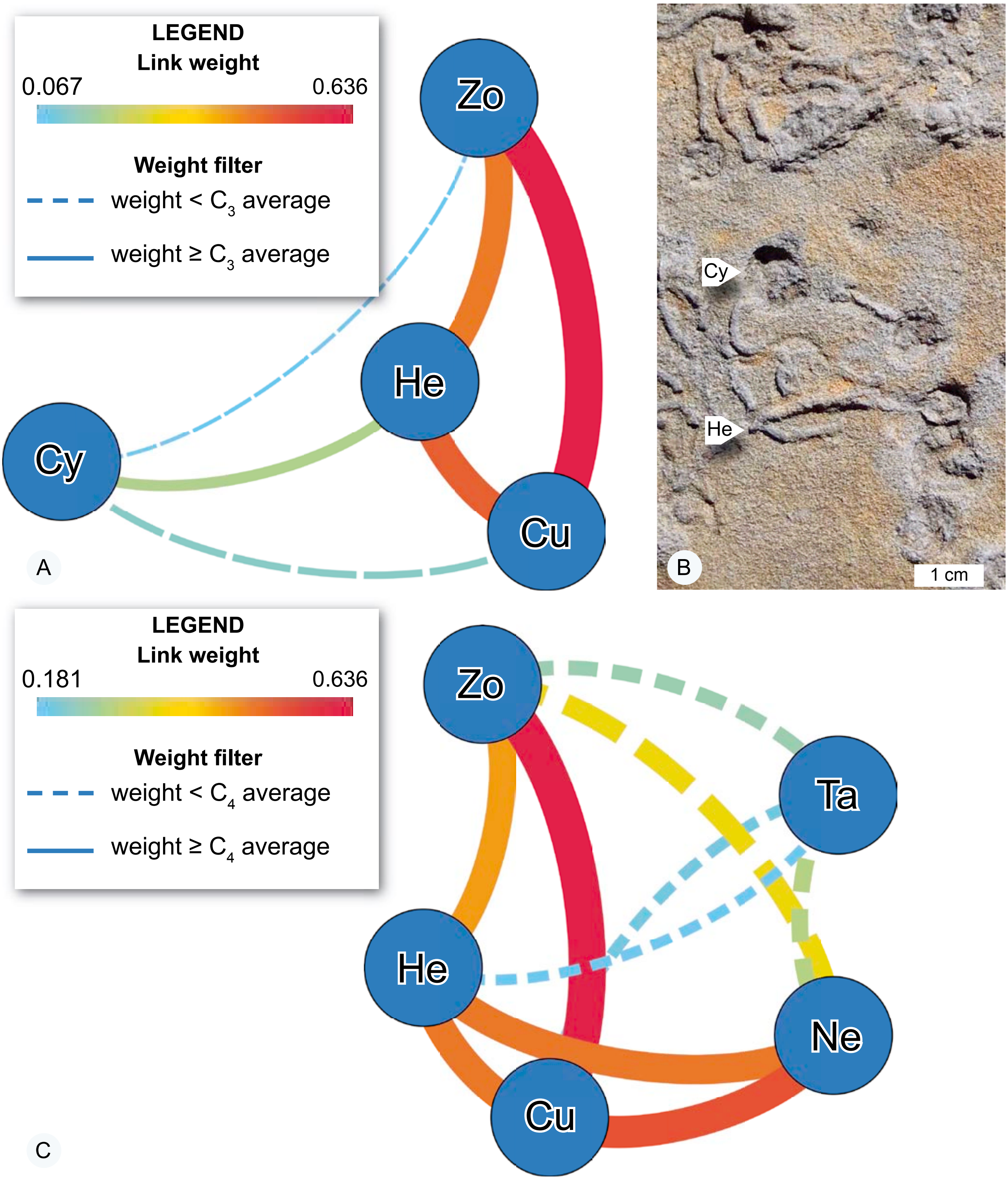
LEGEND
Link weight
0.067
0.636
Weight filter
weight < C_3 average
weight ≥ C_3 average
Zo
He
Cy
Cu
A
Cy
He
B
1 cm
LEGEND
Link weight
0.181
0.636
Weight filter
weight < C_4 average
weight ≥ C_4 average
Zo
Ta
He
Ne
Cu
C

Fig. 28.

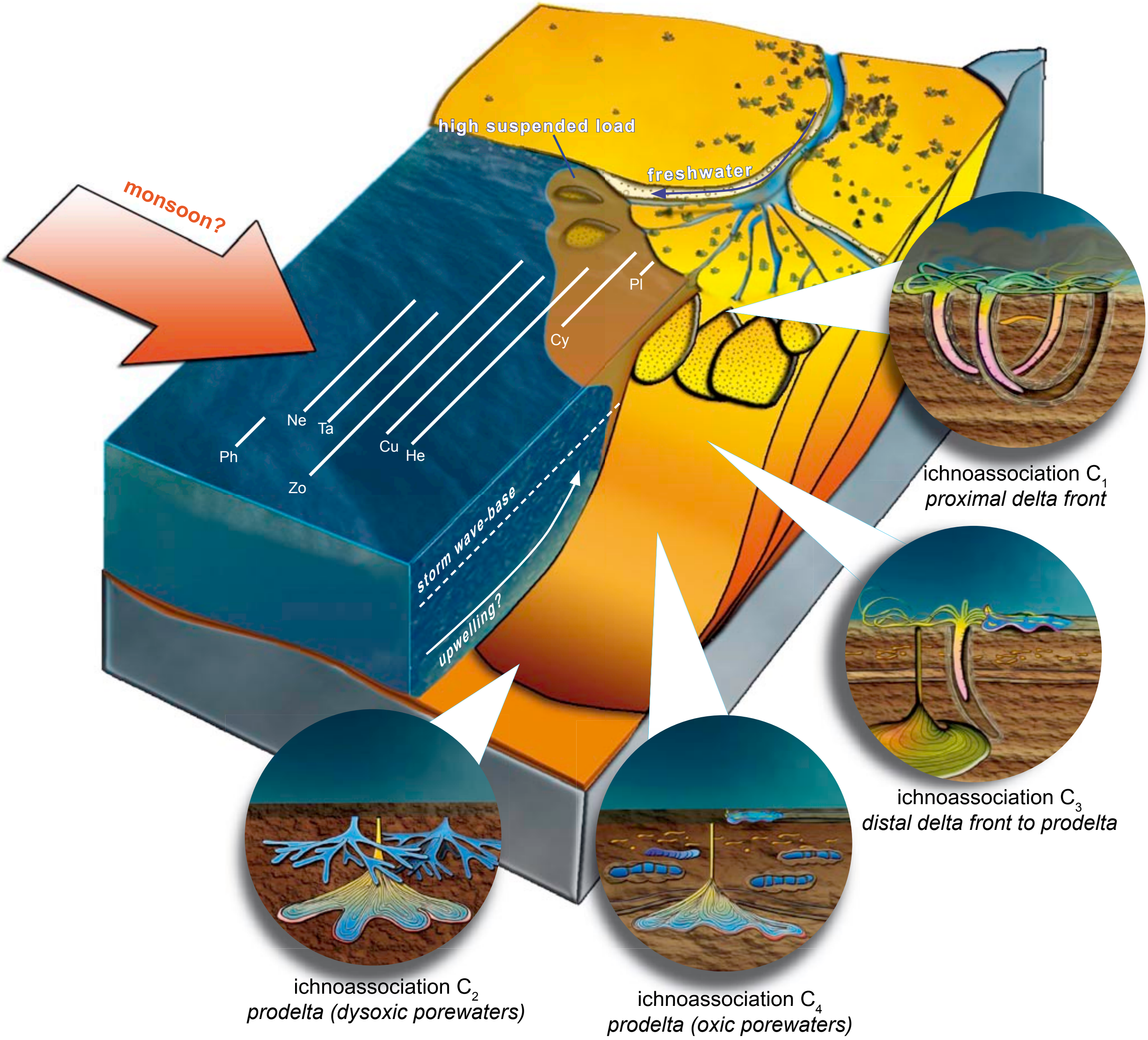
monsoon?
high suspended load
freshwater
Pl
Cy
Ne
Ta
Ph
Zo
Cu
He
storm wave-base
upwelling?
ichnoassociation C_1
proximal delta front
ichnoassociation C_3
distal delta front to prodelta
ichnoassociation C_2
prodelta (dysoxic porewaters)
ichnoassociation C_4
prodelta (oxic porewaters)

Fig. 29.

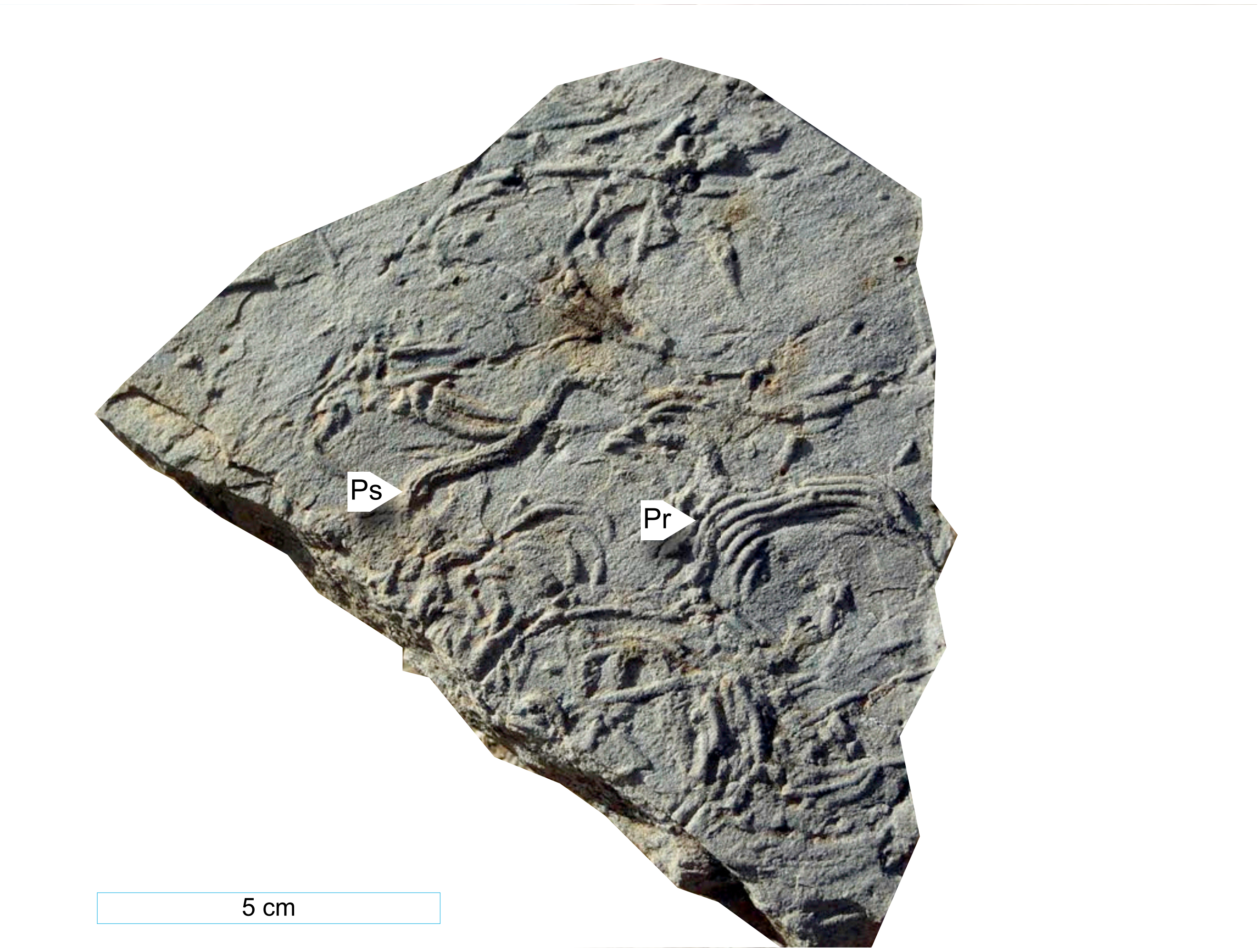

Fig. 30.

Chapter 4

4.3 Evolution of Crustaceans at the edge of the end-Permian crisis: ichnonetwork analysis of the fluvial succession of Nurra (Permian-Triassic, Sardinia, Italy)

From Baucon, A. Ronchi, A., Felletti, F., Neto de Carvalho, C. 2014. Evolution of Crustaceans at the edge of the end-Permian crisis: ichnonetwork analysis of the fluvial succession of Nurra (Permian-Triassic, Sardinia, Italy). Palaeogeography, Palaeoclimatology, Palaeoecology (submitted)

Evolution of Crustaceans at the edge of the end-Permian crisis: ichnonetwork analysis of the fluvial succession of Nurra (Permian-Triassic, Sardinia, Italy)

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ABSTRACT

Decapod crustaceans are among the most efficient ecosystem engineers of the Phanerozoic, but the path that led to their engineering success is poorly known. The Permian-Triassic succession of Nurra (Asselian-Anisian; Sardinia, Italy) sheds light on this obscure subject, because it preserves the oldest (Roadian) fluvial *Ophiomorpha* and *Camborygma,* ascribed to ghost shrimps (Decapoda: Axiidea, Gebiidea) and crayfishes (Decapoda: Astacidea, Parastacidea), respectively. These crustacean trace fossils are part of a well-preserved ichnofauna including *Arenicolites, Diplocraterion, Helminthoidichnites, Palaeophycus, Planolites,* rhizolites, *Skolithos, Spongeliomorpha, Taenidium, Treptichnus,* alongside with an undetermined tetrapod footprint, helical burrows and *Sinusichnus*-like traces.

In light of the abundance of crustacean trace fossils, the Cala Viola section (Roadian-Anisian) was selected for ichnonetwork analysis. This novel approach, focusing on the topology of the association relationships of ichnotaxa, revealed that *Camborygma* and *Ophiomorpha* colonized adjacent, partially overlapping fluvial subenvironments, ranging from active fluvial channels to periaquatic overbanks. As the Nurra occurrences are older of the astacid/thalassinid diversification (Carboniferous-early Permian) and coeval to the appearance of crayfishes (middle Permian), fluvial environments played an important role in the evolution of both crayfishes and ghost shrimps. The most parsimonious explanation of the observed scenario is that astacid/thalassinid diversification happened in fluvial environments between Carboniferous and early Permian, while ghost shrimps has invaded marine environments at the Permian/Triassic boundary. In addition, ichnonetwork analysis revealed that the ichnological system simplified across the Permian-Triassic boundary, accounting for a structured Permian ecosystem and fragmented, stressed habitats during early Triassic. This scenario is explained by a progressive drying trend which changed dramatically the hydrological features across the Permian-Triassic boundary. These evidences support the crucial role of global warming in driving the end-Permian crisis and its prolonged recovery.

keywords: *Camborygma, Ophiomorpha*, decapod evolution, Permian-Triassic extinction, ichnonetwork analysis

1. Introduction

Crustaceans are among the most dominant macro-organisms on Earth, in terms of distribution, diversity and centrality for the ecosystem. In fact, they colonize all of Earth's major habitats, from deep sea to mountains (Duffy and Thiel, 2007), and they count more than 65 000 extant species (Martin and Davis, 2006). Crustaceans occupy crucial positions in many food webs, controlling fluxes of energy and matter (Cartes et al., 2007; Moore, 2007). In many cases, the importance of crustaceans is so critical that involves structure and function of habitats themselves. In fact, many crustaceans are ecosystem engineers as they are able to create, modify and maintain habitats (Cuddington et al., 2007).

Decapod crustaceans are among the most efficient ecosystem engineers of the whole animal realm, changing the environment from the scale of geochemical processes (Vonk et al., 2008) to that of regional topography (Curran and Martin, 2003). Nowadays, ghost shrimps (Decapoda: Axiidea, Gebiidea; 'thalassinideans') are dominant ecosystem engineers in the marine realm, while crayfishes (Decapoda: Astacoidea, Parastacoidea; 'astacids') have a vital role in freshwater environments. In fact, recent studies evidenced that these groups of decapods are crucial geobiological and geomorphological agents, deeply affecting the environments in which they live (Pillay and Branch, 2011; Statzner, 2012). This key role is recognized since early Mesozoic times, when decapod burrows became conspicuous components of both marine and continental landscapes (Buatois et al., 1998; Buatois and Mángano, 2011). Despite the different environmental preferences of ghost shrimps and crayfishes, geographical, morphological and palaeontological data indicate that both groups differentiated from marine ancestors between 325 and 280 millions of years ago (upper Carboniferous-early Permian; Porter et al., 2005; Crandall et al., 2009; Schultz et al., 2009). Consequently, the path that led from decapod diversification to their engineering success is of vital importance for the study of biological evolution and ecology alike.

The Permian-Triassic succession of Nurra (North-Western Sardinia) provides an excellent opportunity to explore the mentioned path, as its trace fossil-bearing outcrops (Cassinis et al., 2002) record the time span between decapod diversification and their engineering success. In this context, this study aims to explore the scenario of crustacean radiation through the analysis of the ichnological heritage of Nurra.

2. Geological setting

Well-exposed outcrops of Permian-Triassic nonmarine strata, with intercalated volcanic deposits, characterize the Nurra region (North-Western Sardinia; Fig. 1). The entire volcano-sedimentary succession accounts for more than 600 m and can be considered rightfully as one of the best reference sections for the PT in the Western Mediterranean. This terrestrial megasequence covers unconformably the Variscan basement and is subdivided in three unconformity-bounded sequences or cycles (Fig. 2; Cassinis et al., 2002; 2003). A complete facies analysis is beyond the scope of this paper, therefore an amended description is presented in Table 1; for a more detailed sedimentological and stratigraphical background the reader is addressed to the above-cited works and to Gasperi and Gelmini (1980), Fontana et al. (2001), Sciunnach (2001), Ghinassi et al. (2009), Ronchiet al., (2011), Ronchi et al. (2011). The stacking pattern of units of the Nurra volcano-sedimentary succession is synthesized here below:

1. First Sequence (Asselian *p.p.* - Sakmarian *p.p.*)

– Punta Lu Caparoni Fm. This thin unit (0–15 m) is composed by black lacustrine fine deposits with conglomeratic and arenitic fluvial intercalations. Rich Early Permian paleofloras and sporomorphs are reported by various authors (Pecorini, 1962; Gasperi and Gelmini, 1980; Ronchi et al., 1998). This unit lies non-conformably over the Variscan basement and is locally overlain by quartz-rich ignimbrites (V1, Fig. 2).

2. Second Sequence (Sakmarian *p.p.* – Roadian *p.p.*):

– Pedru Siligu Formation. This 50 metre-thick unit is dominated by coarse-grained whitish sandstones and conglomerates with subordinated pelites. Such clastics are organized in thick channeled bodies showing trough cross-bedding and represent the deposition in a braided fluvial system. It covers with a slight angular unconformity the Punta Lu Caparoni Fm. below and is followed locally by ignimbrite deposits (V2, Fig. 2). A stratigraphic contact with the above Porto Ferro formation is never been observed.

– Porto Ferro Fm. These medium- coarse-grained deposits rich in porphyric and basement-sourced pebbles, are represented by up to 150-200 m of fossil-barren red beds characteristic of a braided-to-alluvial plain setting. Depositional structures are represented by metre-sized trough cross-beddings and tabular cross-beddings forming metre-sized sets. Typical facies is the stacking of several channelized units, characterized by minor internal erosive surfaces and an overall fining upward trend, marked by the transition from a pebbly conglomerate to medium-coarse sandstone and clay plugs. Point bars and sand bodies with lateral accretions are not rare among the main braided facies. The unit passes upwards and trough an angular unconformity to the Cala del Vino Fm.

– Cala del Vino Formation. This unit consists of stratified greenish to reddish sandstones and siltstones. Facies model indicates a meandering channel complex, and the thick dark red silty portions intercalated between channel-fills are interpreted as floodplain deposits on which pedogenic transformations took place. Sheet-like sandstone layers intercalated with siltstones are interpreted as crevasse-splay deposits. In the Porticciolo-Cala Viola area a very low lateral continuity of the arenitic bodies (ribbon-like channel-fills) and prevalence of pelites is observed. The alluvial plain fine sediments appear homogeneous and deeply bioturbated, while the latter bodies often have lenticular shape and erosive bases and, where not amalgamated, with internal trough cross− to plane parallel−stratification or fine ripple cross−lamination. The sandstone bodies often show lateral accretion (point bars). The lenticular sandstone at the top of these bars could represent the infill of small chute-channels cut at the bar top during the main floods (Ghinassi et al., 2009; Ronchi, Cassinis, et al., 2011). Such lithologies and fluvial architecture are typical of a meandering-channel alluvial system (Fontana et al., 2001; Ghinassi et al., 2009).

3. Third Sequence (Induan *p.p.* - Anisian *p.p.*):

– Porticciolo Conglomerate. This unit ranges from a few metres to 13 metres and evolves from a sheet-like, matrix-supported conglomerate bank up to coarse-grained fluvial-aeolian sandstones. This unit superimposes on the previous one through a sharp unconformity, marked by an impressive facies change. Such first Triassic deposits lie sub horizontally over the Middle Permian Cala del Vino Fm.: the corresponding angular unconformity can be seen in the area between il Porticciolo and Cala Viola. The conglomerate portion is internally subdivided into decimetre- to metre-thick sets with erosional bases. Planar and through cross-bedded sets of microconglomerates and coarse sandstones are intercalated. The upper part of the unit is composed of coarse-grained sandstones with planar-to-cross-beddings. Facies analysis suggests for the conglomeratic basal part of the unit a gravely braided river setting.

– Cala Viola Sandstone. This unit lies unconformably on the Porticciolo Conglomerate and is represented by dark-red medium-grained sandstones and, with subordinate siltstones, forms metre-sized climbing ripple sets, evolving into horizontal to low-angle laminated or through-bedded thin sandstone layers. The unconformity is marked by an abrupt facies change, which suggests very different climatic conditions with respect to the depositional style below. The Cala Viola Sandstone was laid in relatively sinuous channels emplaced in a terminal fan setting (Cassinis et al., 2003). These floodplain-to-playa deposits are rich in pedogenetic carbonate concretions (*in situ* or reworked).

3. Materials and methods

In this study, the Permian-Triassic succession of Nurra was ichnologically investigated, carrying out trace fossil analysis at two levels of scale. The first level involved the ichnological exploration of the major outcrops (Fig. 1) with the primary aim of recognizing the intervals rich in crustacean trace fossils. This level of analysis led to the systematic description of the trace fossils from the study area (section 4).

As a consequence of the first phase, the Cala Viola section (Fig. 2) has been chosen for a layer-by-layer analysis, given the optimal quality of the outcrops and the richness in crustacean trace fossils. Based on the idea that ichnological systems are behavioural networks consisting of mutually interconnected elements, ichnonetwork analysis (Baucon and Felletti, 2013) has been used to explore the subject. According to this approach, data collecting involved the description of a traditional stratigraphical log, including information on layer thickness, lithology and ichnofauna. These data provided the necessary information to describe the association relationships between different ichnotaxa, allowing to build a graph to be analyzed with visual and numerical techniques proper of network analysis. Given the specificity of the subject, more information on ichnonetwork analysis will be given in the corresponding section (section 5).

4. Trace fossils

Although previous studies accounted for the presence of trace fossils in the studied area (i.e. Fontana et al., 2001; Cassinis and Ronchi, 2002; Ronchi, Cassinis, et al., 2011; Ronchi, Sacchi, et al., 2011; Cassinis and Ronchi, 2002), a systematic analysis of the ichnofauna was lacking. Based on this consideration, this section describes the major ichnotaxa occurring in the Permian-Triassic layers of Nurra. Trace fossils are organized into morphological groups, partly based on the classification scheme by Książkiewicz (1977). Stratigraphic and sedimentologic information are given following the nomenclature of Fig. 2 and Tab. 1, respectively.

4.1. Simple structures

Palaeophycus tubularis

Description: Straight, unbranched burrows constituted by a horizontal segment, occasionally connecting two short vertical shafts. Lining very thin, and fill contrasting to the host rock. Burrow diameter: 0.4–1 cm; length of the horizontal segment: 5–10 cm.

Remarks: The studied specimens are consistent with the ichnogenus *Palaeophycus*, which is distinguished from the morphologically similar *Planolites* by the presence of a burrow lining; see Pemberton and Frey (1982) and Keighley and Pickerill (1995) for a complete review on the mentioned ichnogenera. Lack of ornamentation and thin lining are suggestive of *Palaeophycus tubularis* (see Uchman, 1995).

The trace is interpreted as an open burrow; the presence of a lining is possibly related to the necessity of stabilizing the tunnel within shifting substrates. As concerns environmental and behavioural significance, *Palaeophycus* is a facies-crossing ichnogenus produced by carnivorous and omnivorous organisms (Pemberton and Frey, 1982; Keighley and Pickerill, 1995).

Occurrence: Porticciolo Conglomerate; Facies S1, C1.

Helminthoidichnites tenuis

Description: lined, horizontal unbranched burrows with faint constrictions. Burrow diameter: 1–1.5 mm; burrow length: 10–50 mm; spacing of the constrictions: 2–3 mm.

Remarks: Morphology is reminescent of *Helminthoidichnites*, a simple horizontal unbranched burrow (Minter et al., 2007). *Helminthoidichnites* is known from marine and non-marine environments, being attributed to insects or worm-like tracemakers (Uchman et al., 2009). In the case of the Nurra structure, constrictions possibly account for peristalic contractions of a worm-like organism (Pemberton and Frey, 1982), although their faintness preclude a straightforward interpretation.

Occurrence: Cala Viola Sandstone; Facies C1.

Skolithos isp.

Description: Simple straight, unlined, vertical or oblique burrows. Massive fill may be present. Burrow section circular, diameter constant (0.8–1.5 cm), penetration depth 18–25 cm (Fig. 3).

Remarks: Although the studied specimens are consistent with the ichnogenus *Skolithos,* they markedly differ in size from its most typical occurrences (i.e. Häntzschel, 1975: W107). Consequently, the identity and behaviour of the tracemaker are difficultly assignable to suspension-feeding worms, which have been the most iconical tracemakers of *Skolithos* since the work of Richter (1920). This interpretation is supported by sedimentological attributes, consistent with freshwater-influenced terrestrial environments. Accordingly, two are the most convenient interpretations of the studied *Skolithos*:

1. *Skolithos* is commonly produced by insects, arachnids and other terrestrial arthropods (Netto, 2007). In particular, modern wolf spiders are known to produce straight vertical burrows with dimensions comparable to the here considered structures (Hasiotis, 2007; Suter et al., 2011). Modern counterparts present only slight morphological differences (tapered neck: Hasiotis, 2007; terminal enlargement: Suter et al., 2011), while they share a similar tendency to cluster in dense groups (Fernandez-Montraveta et al., 1991; Fernandez-Montraveta and Cuadrado, 2008).
2. Modern plant roots are known to produce incipient *Skolithos* (Gregory et al., 2006), while similar structures have been described as root traces (see Buatois and Mangano, 2012: fig.

10.5c).

The presence of a passive fill is more consistent with an open burrow produced by animals rather than a root-related structure. In addition, root traces are usually characterized by irregular diameter and tapering (Klappa, 1980). This interpretation suggests a climatic indication of *Skolithos,* as modern spider burrows are abundant in dry areas with sparse vegetation (Fernandez-Montraveta et al., 1991; Fernandez-Montraveta and Cuadrado, 2008). The studied occurrence improve the database compiled by Netto (2007, table 1) showing particular abundance of continental *Skolithos* during Permian-Triassic times.

Occurrence: Cala Viola Sandstone; Facies S4.

Taenidium barretti / Planolites montanus

Description: unlined, unbranched curved burrows. Burrow course horizontal, although burrow terminations may plunge into the sediment. Burrow fill is apparently structureless; however, well-preserved specimens show non-compartimentalized, tightly packed arcuate menisci. The fill presents the same grain size and mineralogy of the host rock. Two morphotypes are distinguished on the basis of burrow diameter: medium (0.3 – 0.8 cm; Fig. 4) and large (0.8 – 3.5 cm; Fig. 5).

Remarks: Identity and behaviour of tracemakers are revealed by defining the commonest dynamics of backfilling (Table 2):

1. Ingestion-and-excretion backfilling: many backfilled structures are the result of several cycles of ingestion and excretion. Although arthropods could be able to ingest-and-excrete sediment, this burrowing style is more typical of worm-like organisms. More precisely, worms can backfill only by processing the sediment, because they lack of strong skeletonized limbs to manipulate it. This interpretation is valid even for annelids with protruding locomotory organs, among which polychaetes are the most representative group. Indeed polychaetes use parapodia for slow locomotion on the substrate, but burrowing involves a very efficient mechanism: crack propagation (Dorgan et al., 2005; Moore, 2006; Che and Dorgan, 2010). Ingestion-and-excretion backfilling produces burrows with fill contrasting to the matrix, because it involves digestion and, occasionally, particle selection. For the same reason, fecal pellets may be present within the burrow fill.

2. Excavation backfilling: backfilled structures can be produced by actively manipulating the sediment with rigid limbs. Many organisms are able to backfill by excavation, but the major group is certainly represented by arthropods. Modern examples include cycada nymphs, masked chafer beetles and harvester ants (Smith and Hasiotis, 2008; Counts and Hasiotis, 2009; Halfen and Hasiotis, 2010). Because excavation backfilling do not involve ingestion, fill presents the same mineralogy and grain size of the host sediment.

The backfill of the studied specimens is similar to the host rock, therefore excavation backfilling is the most convenient mechanism to explain burrow morphology. Modern coleopterans display the same burrowing dynamics and similar burrow morphologies (Smith and Hasiotis, 2008), therefore they are the most probable tracemakers of the studied trace fossils.

The observed structures are placed into the ichnospecies *Taenidium barretti,* consisting of unwalled, cylindrical burrows with arcuate menisci (Keighley and Pickerill, 1994). However, the structures are easily confused with the ichnospecies *Planolites montanus*, because menisci are rarely well-preserved. Backfilled structures without ornamentation are characteristic elements of the pre-desiccation suite of the *Scoyenia* ichnofacies, indicating substrates that are periodically inundated or exposed (Buatois and Mangano, 2002). In particular, *Taenidium barretti* predominantly occurs in freshwater environments, including alluvial fan, fluvial, overbank, floodplain and lacustrine settings (Keighley and Pickerill, 1994).

Occurrence: Cala Viola Sandstone, Cala del Vino Fm., Porto Ferro Fm., Pedru Siligu Fm; Facies S2, S3, S4.

Treptichnus isp.

Description: burrow systems consisting of straight horizontal segments connected by infrequent angular turns (Fig. 6A). Short vertical shafts are found in correspondence of angular turns.

The burrow wall is rusty-coloured, unornamented or with two ornamentation types:

1. delicate arch-like annulations, irregularly spaced. Arch axis parallel (Fig. 6B) or inclined with respect to the burrow direction (Fig. 6C).

2. irregular crenulations resulting from alignment of small packets of sediment.

Intergradational forms between wall types are common. Burrow diameter: 1-3 mm; burrow length: 1–7 cm; annulations spacing: less than 1 mm; turning angle=50°–60°.

Remarks: Burrow colour usually differs from the matrix, but it is likely to reflect diagenetical rather than behavioural processes. Consequently, ornamentation is the signature of burrowing mechanics and therefore represents a fundamental clue for functional analysis. In this context, it is important to distinguish constrictions from annulations and crenulations, the first of which are the result of the peristaltic contractions of a worm-like organism. In contrast, the observed ornamentation is more conveniently explained by the syncopated burrowing mechanics of an elliptical-bodied organism. In fact, each arch represents the same behavioural phase, and the space between two successive arches another one. Furthermore, burrow diameter corresponds to the width of the tracemaker, which cannot be much longer than arch spacing. In light of these considerations, a three-phased burrowing cycle has been reconstituted (Fig. 7):

1. push-up phase: sediment is pushed upward after rotating the body in the vertical plane. This phase serves not only to force a passage through the sediment, but also to produce material failures, either by fracture or plastic deformation, to be followed during the last phase of the burrowing cycle.
2. stop phase: the tracemaker rotates its body to reach the horizontal plane.
3. tunnelling phase: the organism moves forward, displacing and compressing the sediment with its body.

After the last phase, burrowing cycle is repeated by pushing up again the sediment (push-up phase).

According to this interpretation, the whole burrows were produced mainly by compression and arches are the impressions left by a specific phase of the compression process (see also Bromley, 1996: p. 11). Eiseman et al. (2010) reported a similar burrowing cycle for modern heterocerid beetles, producers of shallow subsurface burrows along the edges of fresh or brackish waters.

Variations in the mentioned burrowing cycle account for unornamented and crenulated burrow margins. In particular, when there was no need of the push-up phase, the tunneling phase was predominant and was responsible for unornamented walls. Similarly, crenulations are explained by slight angular changes during the tunneling phase, when the organism moved on the horizontal plane.

The studied forms are reminiscent of *Palaeophycus crenulatus,* a lined open burrow with millimetre-scale annulations (Desjardins et al., 2010). Nevertheless, the infrequent angular turns place the structure in the ichnogenus *Treptichnus,* which consists of segments connected at their ends, each one to the next (Rindsberg and Kopaska-Merkel, 2005). More in detail, the specimens fall into the third group of Rindsberg and Kopaska-Merkel (2005), which include irregularly branching subsurface burrows similar to *Treptichnus bifurcus.* Typical of freshwater to brackish-water environments, these forms are characteristically attributed to insects (Rindsberg and Kopaska-Merkel, 2005; Uchman, 2005). As concern the studied specimens, functional interpretation, tracemaker size and neoichnological analogies are consistent with an insect tracemaker. Straight burrow course and angular turns are additional clues for identifying the producer, as evidenced by the morphology of incipient *Treptichnus* produced by insects (Uchman, 2005).

Occurrence: Cala del Vino Formation, Facies S2, S3.

4.2. U-structures

Arenicolites isp.

Description. Vertical U-shaped burrows without spreite. The traces are preserved as concave epireliefs (Fig. 8A) or convex hyporeliefs with fill similar to the casting medium (Fig. 8B). Burrow width 1.9–4.2 cm, burrow height 0.5–1 cm, tunnel diameter 0.2–0.3 cm.

Remarks. Burrow morphology is clearly consistent with the ichnogenus *Arenicolites*, although the studied specimens are less elongated with respect to the most iconical *Arenicolites* (e.g. Häntzschel, 1975: fig. 24a,b.). This morphological aspect, related to the high height/width ratio of the burrow, primarily derives from tracemaking processes because there are no evidences of severe preservational or diagenetic effects (i.e. erosion, compression, compaction). Thus, a question might arise: what is the significance of such ‘compressed’ *Arenicolites*?

Modern U-burrows allow to answer this question, because they enable to compare morphological parameters with their behavioural, environmental and functional significance. This approach is exemplified by Fig. 9, which collects information from 31 modern burrows described in previous literature. On the basis of the dominating architectural elements, five styles of U-burrows are recognized and named after the most representative tracemaker:

– Polychaete-style 1 (smooth): Flexible organisms usually produce highly curved burrows because they can significantly bend their body. A typical example is represented by the incipient *Arenicolites* produced by the modern polychaete *Chateopterus* (Bromley, 1996; Nishi et al., 2009). High curvature implies a characteristically high height/width ratio, as explained by a simple geometrical experiment. Let consider a theoretical U-burrow with constant curvature and fixed height: the higher curvature, the lower distance between burrow limbs (width; Fig. 8C).

– Mayfly-style: On the basis of the same geometrical experiment, organisms with limited body flexibility are likely to produce U-shaped burrows with low curvature and low height/width ratio. This is the case of many U-shaped burrows built by insects, i.e. larvae of Ephemeroptera (mayflies) and Anisoptera (dragonflies; Wallace and Merritt, 1980). This interpretation is supported by Carboniferous *Arenicolites* with low height/width ratio and bioglyphs, which constitute an additional evidence for insect tracemakers (Rindsberg and Kopaska-Merkel, 2005).

While the above mentioned burrow styles are simplified by conic curves, many U-shaped traces deviate significantly from these ideal forms:

– Echiurid- and amphipod-style: Long, straight segments characterize the U-burrows of many marine tracemakers. For instance, echiurid worms build U-burrows with two curved shafts connected by a straight horizontal segment (Anker et al., 2005). In other cases, straight segments characterize the vertical shafts of the U-burrows (Frey et al., 1989). This is the case of amphipod U-burrows, presenting two straight, vertical segments (Weissberger et al., 2009). In both burrow styles, height/width ratio is not strictly depending by the mean curvature of the burrow.

– Polychaete-style 2 (wiggled). Another possibility to deviate from the ideal shape of a conic curve is to frequently make slight changes in curvature. For instance, burrows of the polychaete *Nereis* are U-shaped at a global scale, but at a local scale they display a multitude of wiggles (Davey, 1994). It might be tempting to explain these irregularities as small-scaled inefficiencies in the behavioural program. To the contrary, these wiggles are the signature of the extreme behavioural efficiency of many tracemakers, which burrow by crack propagation. This burrowing dynamics, thoroughly described in Dorgan et al. (2005), consists of extending fractures with an alternating ‘anchor’ system.

Within homogeneous materials, a crack will propagate perpendicular to the direction in which the force is exerted, whereas heterogeneous sediments present small-scale variations in material properties (Dorgan et al., 2006). Consequently, wiggles are the small-scaled weaknesses followed by burrowers during crack propagation.

The studied *Arenicolites* have a low height/width ratio (0.2–0.3) and do not present straight segments or wiggles. Consequently, they fall in the second group (‘mayfly-style U-burrows’) and therefore are here interpreted as insect burrows. According to morphological similarities with modern burrows (see Wallace and Merritt, 1980), the studied specimens could be the burrows of nymphs of mayflies or dragonflies, behaving as filter-feeders or predators respectively.

Occurrence: Cala Viola Sandstone Fm.; facies S4.

Diplocraterion isp.

Description. Vertical, spreite-bearing U-shaped burrows. Vertical limbs are concentrically laminated in transverse section. Full relief preservation. Limb separation: 1–2 cm.

Remarks. Based on the general morphology and the presence of a spreite, the studied structures are confidently assigned to the ichnogenus *Diplocraterion* (Cornish, 1986; Oloriz and Rodriguez-Tovar, 2000). Ichnospecific identification is difficult because of the absence of vertical sections.

The spreiten of *Diplocraterion* derives from the vertical shift of a U-tube, usually interpreted as the response to events of sedimentation or erosion (Cornish, 1986). *Diplocraterion* is a characteristic component of shallow-marine, high energy environments (Rodríguez-Tovar and Uchman, 2004), but it is also reported from freshwater environments (Zonneveld et al., 2012).

Occurrence: Cala Viola Sandstone, facies S4.

4.3. Helical structures

Helical burrow S – small

Description. helical, lined burrow with a terminal clavate chamber (Fig. 10A). Oval cross-section; lining irregularly laminated. Penetration depth: 15–20 cm; helical angle of incline (Meyer, 1999): 30°–40°; chamber width: 4–5 cm; chamber length: 7–8 cm.

Remarks. Keeping with Meyer (1999), an extra effort is needed to dig a helical burrow versus a simpler, straight one. Given the great effort expended for burrow construction, a permanent or semi-permanent occupation of the burrow is hypothesized. For the same reason, the extra effort should be explained with a functional advantage. At this regard, Neto de Carvalho and Baucon (2010) distinguished five recurrent functions of fossil and recent helical burrows, implemented in Table 3.

Table 3 show a wide range of morphologies, tracemakers, environments and functions, which are often mutually non-exclusive. This complex scenario is solved by functional analysis of the studied Permian specimens. In fact, the presence of a chamber indicates that the burrow served as a domicile, while its position implies that favourable conditions existed at depth. In light of these considerations, the studied structures are likely to be climate refuges.

This hypothesis is supported by the close morphological similarity with modern temperature-damping burrows (Table 3). In particular, the arid zone scorpion (*Urodacus yaschenkoi*) constructs a helical burrow which permits to survive to the extreme temperatures of the interior of Australia (Koch, 1978; Shorthouse and Marples, 1980). The terminal chamber of the scorpion burrow is cool and damp (20–25 °C, >80% humidity), while the above-ground environment is hot and dry during daytime, cold during the night (0–60 °C, <10% relative humidity; Calver and Lymbery, 2009).

Other arthropods are known to build helical burrows as a response to arid conditions (i.e. millipedes; Hembree, 2009), but the morphology of the studied structures is more consistent with a scorpion (i.e. *Urodacus yaschenkoi*: Koch, 1978; *Hadrurus arizonensis*: Hembree et al., 2012). Indeed, the studied burrow shares salient features with modern scorpion burrows:

1. burrow architecture: burrows of many scorpions from arid zones are helical (Koch, 1978; Shorthouse and Marples, 1980; Polis, 1990; Hembree et al., 2012).

2. helical angle of incline: the helical angle of incline of scorpion burrows ranges between 20 and 40° (Polis, 1990).

3. terminal chamber: scorpion burrows often present a terminal chamber, which is positioned directly under or away from the direction of the burrow opening (Polis, 1990; Hasiotis and Bourke, 2006).

4. burrow depth: the majority of scorpion burrows are 15 to 50 cm deep, although deeper

burrows are known (Polis, 1990).

5. laminated lining: such lining may be the result of compaction, which is commonly part of the burrowing cycle of scorpions (Polis, 1990).

6. oval cross-section: oval entryways are diagnostic of scorpion burrows and allow to distinguish them from other arthropod burrows (Polis, 1990). It is not known if burrow openings are preserved in the studied Permian structures, but the cross-section is oval and therefore conforms to a scorpionid body plan. This observation is confirmed by Hasiotis and Bourke (2006), who reported scorpion burrows with spiral, flattened tunnels.

For these reasons, the studied burrow is interpreted as a scorpion burrow with climate damping function. The climate refuge hypothesis is supported by the sedimentological attributes of the host sediment, consisting of thick (>5 m), red paleosols with caliches and rhizolites.

Occurrence: Cala del Vino Fm., Facies P1

Helical burrow L - large

Description: helical burrows with a terminal bulb-shaped chamber made of 3–5 enlarged lumps. Coiling loose and irregular. Burrow section generally circular, although enlargements are frequent (Fig. 10B). Penetration depth: 50 cm, helical angle of incline (Meyer, 1999): 21°–50°; chamber width: 13–15 cm; chamber length: 13 cm.

Interpretation: The presence of a terminal chamber, united to the extra effort needed to build a helical burrow (Meyer, 1999), points to a domichnial function. General morphology resembles the vertebrate burrow described by Storm et al. (2010), although the Nurra specimen is smaller and helical. However, few specimens have been found, therefore further research is needed to clarify the author and ethology of this burrow.

Occurrence: Cala del Vino Fm.; facies S2.

4.3. Branched structures

Camborygma type XL – very large

Description: mainly vertical, Y-branching burrow systems consisting of straight to curved segments (Fig. 11A). Burrow section circular, approximately constant at the scale of the entire burrow but with numerous centimetric bumps (knobs, pustulations, transverse ridges). Wall texture characteristically knobby, with frequent millimetric features such as hair-like ridges and clusters of parallel scratch marks (Fig. 11A, B). Mudchips locally abundant. The upper part of the burrow ('chimney') commonly presents tightly packed pellets, which are spherical, oblate or tear-shaped ('sediment balls'; Fig. 11C). Penetration depth: 1–2 metres; burrow width: 10–25 cm.

Remarks: Surface features and burrow architecture correspond to the ichnogenus *Camborygma,* comprising branched and unbranched ornamented burrows with knobby textures (Hasiotis and Mitchell, 1993). More in detail, the specimens are similar to the branched ichnospecies *Camborygma eumekenomos* (i.e. Hasiotis and Honey, 2000: fig. 7), but further studies are required for an ichnospecific identification. At the present state of research, *Camborygma* has always been attributed to crayfishes which burrowed down to reach the water table (Hasiotis and Mitchell, 1993; Hasiotis and Honey, 2000).

Functional analysis of the studied *Camborygma* confirms the aforementioned interpretation. In fact, large, branched burrow systems may be produced by vertebrates and invertebrates alike. However, the predominantly vertical orientation is functionally more suitable to invertebrate tracemakers (Miller et al., 2001; Hasiotis, 2002). Bioglyphs exclude anellids and other worm-like tracemakers because scratch marks require a skeletonized body for being produced. Hence, an arthropod tracemaker is likely. This hypothesis is supported by the presence of mudchip lining, common in modern and fossil crayfish burrows but absent in vertebrate ones (Miller et al., 2001).

Among arthropods, spiders, insects and various decapods build chimneys around their burrow entrances (Griffis and Suchanek, 1991; Eiseman et al., 2010). Burrow size restrict the studied traces to decapods, as well as their architecture. Indeed, the presence of Y-branching, lined walls and surface marks is typical of decapod crustaceans (Bedatou et al., 2008).

Decapod crustaceans are also suggested by bioglyph morphology. In fact, bioglyphs are the expression of the external body parts, therefore transverse ridges, pustulations and parallel scratches imply that the tracemaker had at least three types of specialized appendages. This aspect is strongly reminescent of decapods and, in particular, of crayfishes. In fact, Hasiotis and Mitchell (1993) demonstrated that fossil and modern crayfishes produce transverse ridges, pustulations and parallel scratches with chelae, walking legs and telson, respectively.

Pelleted walls are apparently a weak evidence for tracemaker identity, as crabs, crayfishes and thalassinidean shrimps are able to build pelleted walls. However, thalassinidean shrimps cover the entire burrow system with pellets, while crayfishes and crabs build pelleted chimneys (de Gibert et al., 2006; Muñiz et al., 2010). For this reason, the studied structures are similar to crab and crayfish burrows.

Finally, the studied *Camborygma* are referred to crayfishes, because parallel scratches – here interpreted as telson imprints – are not compatible with the small curled telson of crabs. This aspect is in line with the history of Brachyura, as the first fossil crab date back to early Jurassic (Klaus et al., 2011). The mentioned evidences are confirmed by the striking resemblance with modern and fossil crayfish burrows (Hasiotis and Mitchell, 1993; Miller et al., 2001).

A closer look to the structures provides information on burrowing mechanics of Permian crayfishes (Fig. 12A). Large bumps on the wall are evidences of digging and maintenance of the burrow, while the exceeding material was probably the source for chimney-building. This behaviour is largely documented in modern crayfishes, which use their appendages to dig sediment and manipulate it into a pellet; each pellet is carried to the surface and piled on the existing chimney (Shufeldt, 1897; Thomas and Taylor, 2007; Wells, 2009). With the words of Thomas and Taylor (2007) , “the crawfish moves through the burrow looking like a fullback carrying a football”.

Although indirectly, pellet deformation provides evidence of such behaviour, which implies multiple phases of chimney-building. Spherical pellets are found in the upper part of chimneys, while flattened ones in the lower one (Fig. 12B). Hence, the lower pellets were deformed under the weight of the upper ones, implying that pellets were used as bricks and progressively placed on top of the existing chimney. The function of crayfish chimneys is not completely clear; researchers suggest that modern chimneys serve to control evaporation, deter predators or simply to store the exceeding material of the excavation (Wells, 2009).

Despite being surficial structures without lateral constraints, chimneys have a remarkable preservation potential. Indeed, modern crayfish chimneys are considerably resistant to erosion after desiccation, so that they constitute an obstacle to farm machinery (Butler, 1995, 2002).

Occurrence: Cala del Vino Fm.; facies S2, P1.

Camborygma type L – large

Description: vertical, gently curved burrows with circular cross-section and knobby lining. Small-scale bumps (knobs, transverse ridges) are frequently found. Helical or chicane-shaped sections are common, while horizontal branches may be present (Fig. 11D). The penetration depth is frequently exceeding 40 cm. Burrow diameter: 3–5 cm.

Remarks: The helical and the chicane-shaped sections are not explicitly described in the diagnosis of the ichnogenus, but they are not contrasting with the broad morphospace of *Camborygma* (Hasiotis and Honey, 2000). The structures show strong affinities with the ichnospecies *Camborygma litonomos*, consisting of a simple vertical or U-shaped shaft with bioglyphs and knobby texture (Hasiotis and Honey, 2000).

A crayfish origin is suggested not only by literature data on the ichnogenus, traditionally attributed to fossorial crayfishes (Hasiotis and Honey, 2000). In fact, this morphotype shares the same bioprint with *Camborygma* type XL, although smaller dimensions suggest smaller tracemakers.

The great effort for building helical sections (Meyer, 1999) points to a permanent or semi-permanent domichnial function of the burrow. Although certain marine decapods build helical branched traces (i.e. Dworschak and Rodrigues, 1997), modern crayfish burrows are the closest modern analogue of the studied structures. In particular, *Fallicambarus fodiens* build a single vertical shaft often descending in an irregular spiral (Hobbs, 2001). Similarly, vertical crayfish burrows with helical segments are reported by Hasiotis and Bourke (2006, fig. 5A, B).

According to these evidences, the studied burrow is interpreted as the domicile of a crayfish, burrowing at depth to reach the water table.

Occurrence: Cala del Vino Fm.; facies S2, P1.

Ophiomorpha nodosa

Description: lined, unbranched or Y-branching burrows with pelleted outer surface and smooth interior (Fig. 13). Tunnels horizontal or oblique. Pellets are spherical, equidimensional and regularly distributed; oblate pellets are rarer. Detached pellets are commonly found within the sediment. Burrows cylindrical, with very constant diameter. Burrow width: 0.5–2 cm; Pellet diameter: 1 mm.

Remarks: The studied structures present the diagnostic features of *Ophiomorpha,* a vertical or horizontal burrow system with pelletoidal lining (Häntzschel, 1975). In light of the lining morphology, the burrows are attributed to the ichnospecies *Ophiomorpha nodosa,* which is characterized by dense, regularly distributed pellets (Uchman, 1995). Keeping with Bottjer et al. (1988), *Ophiomorpha* first apperared during Permian in nearshore environments, while it colonized deeper settings during the Mesozoic (i.e. *O. rudis:* Uchman, 2009; *O. annulata*: Tchoumatchenco and Uchman, 2001*)*. Only two unambiguous nonmarine occurrences are known, dating back to Cretaceous and Eocene (Loope and Dingus, 1999). In contrast, robust *Ophiomorpha nodosa* are typical components of the *Skolithos* and *Cruziana* ichnofacies, which are often associated to shallow-marine environments (Pemberton et al., 2001; Buatois and Màngano, 2011). Either in the fossil or modern record, thalassinid shrimps are recognized as the producers of *Ophiomorpha* (Chamberlain and Baer, 1973; Frey et al., 1978; Bromley, 1996; Miller and Curran, 2001; Pemberton et al., 2001; de Gibert et al., 2006). The only exception are the crayfish-related *Ophiomorpha* described by Loope and Dingus (1999), but the specimens are helical, knobby and with spreite.

The most prominent feature of the studied *Ophiomorpha* is certainly its constructional lining. In this context, it is possible to specify the general principles which govern lining structure:

Lining = chemical binding + building blocks + physical actions.

Chemical binding lays at the core of the aforementioned ‘lining equation’, but its low preservation potential negate its paleontological application. With the exception of fecal pellets (i.e. Seilacher, 2007: p.56), building blocks are rarely specific of a given tracemaker. However, the physical actions which operated on them are a direct function of animal behaviour and physiology. At this regard, the studied *Ophiomorpha* evidence sediment manipulation, because the pellets are non-fecal, rounded, equidimensional and regularly packed. While other physical actions (i.e. particle selection, secretion;) are proper of both limbed and limbless tracemakers, sediment manipulation is a prerogative of limbed ones. Consequently, an arthropod tracemaker is likely for the studied *Ophiomorpha.*

Keeping with Buatois and Mangano (2011), such kind of constructional lining is a common adaptation for facing high-energy environments and shifting substrates.

Y-branching and lined walls are among the typical features of decapod burrows (de Gibert et al., 2006; Muñiz et al., 2010). In particular, the studied traces fully coincide with the bioprint of thalassinidean shrimps. Indeed, pellet-lined burrows are exclusively produced by thalassinidean shrimps, while crayfishes and crabs build pelleted chimneys only (de Gibert et al., 2006; Muñiz et al., 2010). In addition, fossil and modern crayfish burrows are characteristically knobby and bumpy (Hasiotis and Mitchell, 1993). At the contrary, the burrow diameter of the studied specimens is constant, lacking of small-scale variations in the height of the burrow surface. Hence, the tracemaker completely filled the lumen of the burrow, suggesting a body plan with equal width and height. These features are consistent with the behaviour and anatomy of thalassinidean shrimps; for instance, *Callichirus major,* the modern author of *Ophiomorpha*, fits tightly its burrow diameter with its elongated, sub cylindrical body (Bromley, 1996: p. 87–88).

The above-mentioned interpretation matches with literature data on the ichnospecies *Ophiomorpha nodosa,* which has always been attributed to thalassinid shrimps, either in the fossil or in the modern record (e.g., Chamberlain and Baer, 1973; Frey et al., 1978; Miller and Curran, 2001; de Gibert et al., 2006).

Occurrence: Cala del Vino Fm.; facies S2, S3.

Rhizohaloes

Description: gray or green mottles, frequently branching and tapering downwards. Rarer lateral sprouts. Trace course mostly vertical, rare horizontal segments. Frequent small-scale changes in direction and irregular diameter provide a jagged or wrinkled appearance to the structures. Rare specimens are differentially weathered and provide a three-dimensional picture of the structures. A wide range of sizes characterize the structures: structure height 5–200 cm; diameter: 1–25 cm.

Remarks: Irregular diameter and tapering are diagnostic features of root traces (rhizolites; Klappa, 1980). In particular, their morphology coincides with rhizohaloes, as defined by Kraus and Hasiotis (2006). Trace morphology is explained by plant behaviour (i.e. search for nutrients and moisture) and root morphology (i.e. tapering), while colour is explained by a mixture of behavioural and taxonomic effects. In fact, in line with Kraus and Hasiotis (2006), the gray mottles are iron-depleted areas which result from fluctuating soil moisture and root decay. Keeping with Kraus and Hasiotis (2006), the presence of rhizohaloes within red paleosols (facies P1) is indicative of moderately well-drained paleosols.

Occurrence: Cala Viola Sandstone, Cala del Vino Fm., Porto Ferro Fm. Facies P1.

Rhizocretion-like

Description: roughly oblate structures (Fig. 4A) arising from several constituting elements:

1. yellow-brown, brown or purple matrix consisting of medium-grained sandstone. Texture is usually massive, but occasionally faint cylindrical structures are recognized. Matrix is volumetrically predominant with respect to the other constituting elements.
2. Cylindrical unlined structures, lighter than the surrounding matrix. Width: 1 mm.
3. Cylindrical unlined burrows with purple massive fill. Width: 1.5 cm.
4. Horizontal burrows with bioglyphs. Width: 3–5 cm.
5. Branched knobby burrows, horizontal or vertical. Width: 7–25 cm.

Bioturbation intensity and cementation are higher than the surrounding sediment. Structures are discrete and patchily distributed. Width of the entire structure: 100–300 cm.

Remarks: The structure comprise discrete burrows with differing sizes and architectures, therefore it represents a composite trace fossil (Buatois and Mángano, 2011). In particular, knobby traces and burrows with bioglyphs correspond to the crustacean ichnotaxa *Camborygma* and *Spongeliomorpha,* respectively. Smaller unlined structures are likely to represent animal burrows or rhizoliths. The massive aspect of the matrix possibly derives from biogenic homogenization, while cementation may be related to the minerals which commonly accumulate around roots (Cramer and Hawkins, 2009). At this regard, the studied structures share major textural and morphological features with the manganesiferous rhizocretions described by Kraus and Hasiotis (2006). Similar intricate, clustered root systems are also described by Genise et al. (2010) (‘rhizolith balls’), but their walled architecture is not recognized in the here studied specimens.

Root systems offer a convenient explanation for the concurrent presence of animal burrows (i.e. *Camborygma*) and for the patchy distribution of the structures. In fact, the high bioturbation index suggests the existence of a discrete resource that attracted crustaceans and other organisms. At this regard, tree roots are a major source of nutrients and protection in modern fluvial environments. More in detail, many species of crayfishes preferentially burrow among roots (Wells, 2009; Noro and Buckup, 2010). In conclusion, these structures are interpreted as composite plant-animal traces, although further observations are needed to confirm rhizoturbation.

Occurrence: Cala del Vino Fm.; facies S2.

Spongeliomorpha

Description: branched, cylindrical burrows with transverse, parallel and oblique bioglyphs. Burrow width: 3–5 cm (Fig. 14B).

Remarks: Burrow architecture and bioglyphs are reminescent of the striated ichnogenus *Spongeliomorpha* (Häntzschel, 1975). In light of its architecture and ornamentation, *Spongeliomorpha* is interpreted as the work of decapod crustaceans within firm substrates (de Gibert and Ekdale, 2010). Consequently, *Spongeliomorpha* may represent the work of the *Ophiomorpha* or *Camborygma* producers within dewatered substrates. Robust occurrences of *Spongeliomorpha* are known from shallow-marine and fluvial deposits (Tchoumatchenco and Uchman, 2001; de Gibert and Ekdale, 2010; Buatois and Mángano, 2011). In particular, *Spongeliomorpha* is a characteristic component of the post-dessiccation suite of the *Scoyenia* ichnofacies (Buatois and Mángano, 2011).

Occurrences: Cala del Vino Fm.; facies S2, S3.

4.4. Other traces: isolated and fragmentary structures

A number of isolated and fragmentary specimens have been found within the Cala del Vino Formation (facies S and P). The present section documents these occurrences, which represent definite ichnotaxa but require further findings for a comprehensive taxonomic and palaeoethologic interpretation.

Large, curved burrow segments with large knobs are found within the *Camborygma*-bearing levels. Possibly, they represent another morphotype of *Camborygma* but the available exposures are too limited to define the architecture of the specimens. A sinuous, branched system (width: 5 cm) with chambers have been found in the same horizons (Fig. 14C). Its morphology is reminding of the ichnogenus *Sinusichnus,* typically related to decapod crustaceans (Seilacher, 2007; Buatois et al., 2009). A weathered vertebrate footprint is reported from an isolated slab; further studies and occurrences are needed to define its ichnotaxonomic affinity. Finally, the Cala del Vino Formation bears abundant small rhizolites (diameter: 0.5–4 mm), displaying sandy or cemented fill. Further studies are required to define recurring morphotypes and their behavioural/ecological significance.

5. **Ichnonetwork analysis**

5.1. From stratigraphical data to ichnonetworks

Many natural, social and technological systems are described by web-like structures, capturing the connections among the units they are made of (Réka and Barbási, 2002; Palla et al., 2005). For instance, food webs consist of species connected by trophic interactions; social networks are made by people connected by relations; the World Wide Web is formed by webpages connected by hyperlinks (Wassermann and Faust, 1994; Réka and Barbási, 2002). Network theory proved to be an efficient tool in analyzing these systems by mapping units as nodes and connections as links. In fact, this emerging discipline provides tools for identifying critically important nodes in networks, finding groups and comparing the topology of different networks (Bhadra et al., 2009).

Ichnlogical systems can be conceived as networks, and therefore they can be analyzed by network theory. In fact, according to Baucon and Felletti (2013), ichnological systems are behavioural networks (ichnonetworks) consisting of mutually interconnected elements.

More specifically, an ichnonetwork maps which ichnotaxa is associated to each other, and the strength of each association relationship. Until now, only neoichnological data has been analyzed with ichnonetwork analysis (Baucon and Felletti, 2013), although a standard stratigraphical log (Fig. 15) holds sufficient information for deriving an ichnological network. In fact, the idea is to represent ichnotaxa as nodes, and connect with a line (edge) those ichnotaxa that co-occur in the same bed.

The strength of each association relationship is given by the Jaccard index, which measures the probability of co-occurrence of ichnotaxa pairs (Hammer and Harper, 2006):

$$J_{A,B} = \text{number of beds with ichnotaxa A and B / number of beds with ichnotaxa A or B}$$

In practical terms, it is convenient to store the presence/absence data into a spreadsheet, from which to derive an adjacency matrix (Fig. 16). As each entry of the matrix corresponds to the Jaccard index of a given pair of ichnotaxa, the adjacency matrix can be used to draw the ichnonetwork. These operations can be performed by a number of freeware and open-source softwares, among which PAST and Gephi; the resulting network maps ichnotaxa (nodes), association relationships (edges) and their intensity (edge weight; Fig. 16).

Topological attributes of ichnonetworks emerge from the palaeoenvironmental properties which control ichnoassociation composition and, consequently, ichnonetwork analysis allows to understand palaeoenvironmental features from ichnological data. In this regard, network science provides quantitative measures to describe (a) nodes properties and (b) network architecture (Wassermann and Faust, 1994; Bhadra et al., 2009; Perreault, 2010).

5.2. Nodes properties

The most immediate network measure is the degree of a node, which is the number of links that are incident with it (Wassermann and Faust, 1994). In ichnological terms, node degree represents the number of ichnotaxa co-occurring with a given one (Fig. 17A). Consequently, nodes with zero degree (isolated nodes) correspond to ichnotaxa which occur exclusively in monoichnospecific assemblages. For this reason, isolated nodes are likely to represent stressed ecosystems.

In the studied ichnonetwork, the isolated nodes are *Arenicolites, Skolithos* and *Palaeophycus,* which are completely disconnected from the rest of the network. Intriguingly, these ichnotaxa pertain to the Triassic units of the studied succession. In contrast, the highest degrees are associated to the Permian Cala del Vino Formation, as manifested by *Treptichnus, Camborygma, Ophiomorpha* and *Taenidium.* The periphery of the network is occupied by rhizohaloes and *Helminthoidichnites,* which have fewer connections with the rest of the network.

Node degree ignores any indirect links a node may have (Scott, 2000), therefore it mirrors local structure. However, the relationship between two indirectly connected (non-adjacent) nodes might depend on the other nodes in the network, especially the nodes lying on the paths between the two (Wassermann and Faust, 1994). Consequently, it is important to consider the extent to which a given node lies between the others, that is node betweenness (Scott, 2000).

This property measures how often a node is present in the set of all shortest paths (Steuer and Zamora López, 2008), and therefore describes how an ichnotaxon is embedded within the whole system. Accordingly, high-betweenness nodes are 'intermediaries' between different structural units of the ichnonetwork, and therefore they may correspond to environment-crossing ichnotaxa ('bridge ichnotaxa' *sensu* Baucon and Felletti, 2013). This interpretation is appropriate for *Camborygma,* because it lies between hydrophilic nodes (e.g. *Ophiomorpha*) and hygro- to terraphilic ones (i.e. rhizolites; Fig. 17B). This observation is supported by the environmental distribution of modern and fossil *Camborygma,* ranging from river channels to distal floodplains (Butler, 2002; Hasiotis et al., 2007). Nevertheless, the high betweenness of *Camborygma* is also explained by its considerable penetration depth, which allows to overprint previously emplaced ichnosuites, regardless of their environmental affinity.

An analogue phenomenon is reflected by *Treptichnus,* although at a smaller scale. In fact, despite of the co-occurrence with *Ophiomorpha* and *Camborygma,* cross-cutting relationships and preservation style suggest that *Treptichnus* colonized the substrate diachronously with respect to decapod traces. Consequently, the high betweeness of *Treptichnus* may evidence the overlapping of different ichnosuites in response to variations in water saturation, which is a common phenomenon in fluvial environments (Buatois and Mángano, 2011).

Besides betweenness, it is interesting to understand if the traces associated with a given node are also associated to each other. This question is answered by the clustering coefficient of a node, which quantifies how densely its adjacent nodes are connected to each other. It is calculated as the number of links between the neighbours of a given node divided by the maximum number of links between them (Bhadra et al., 2009). In the studied network, rhizohaloes, *Taenidium* and *Ophiomorpha* display the highest clustering coefficients, implying that each of these traces are embedded in a group of co-occurring ones.

5.3. *Network architecture*

The architecture of real-world networks is rarely regular, commonly presenting grouping patterns of nodes. These groups, termed communities, are subsets of nodes that are densely connected to each other but sparsely connected to other dense groups (Radicchi et al., 2004; Fortunato, 2010). Hence, communities correspond to ichnoassociations, which are groups of recurrently associated ichnotaxa.

Intuitively, the studied network is constituted by a central, densely connected group of nodes (*G* in Fig. 18) and three isolated satellites (*Arenicolites, Palaeophycus, Skolithos*). This intuitive observation is confirmed by topological analysis, as *G* is the giant connected component, i.e. the largest group of nodes which are connected to one another through a continuous chain of connections (Scott, 2000).Within a component, all nodes are mutually reachable, but no path is directed outside from the component itself (Scott, 2000; Fig. 18A). The same architecture is revealed by the Infomap algorithm, one of the most accurate community-finding methods (Coscia et al., 2011). This approach, which has already been successfully employed in ichnology (Baucon and Felletti, 2013), is based on a combination of information-theoretic techniques and random walks (Coscia et al., 2011).

In light of these observations, *Arenicolites, Palaeophycus* and *Skolithos* represent monoichnospecific ichnoassociations. Being isolated from other nodes, these ichnotaxa indicate stressful environmental conditions, which are unsuitable to other ichnotaxa. On the other hand, the significance of the central group *G* is more elusive, although it can be confidently assigned to the continental *Scoyenia* ichnofacies for the presence of meniscate traces (*Taenidium*), vertical domiciliary burrows (*Camborygma*) and plant traces (rhizolites). In line with Buatois and Mángano, (2011), the *Scoyenia* ichnofacies typically covers a wide variety of fluvial subenvironments. In this regard, a finer structure is underlying the organizational level of connected components. In fact, the central group *C1* includes two nodes with high betweeness (*Treptichnus, Camborygma;* Fig. 17B), which are therefore lying between different structural areas of the network. Hence, these intermediary nodes suggest that the central group *G* is hierarchically organized, being constituted by smaller modules. This aspect is confirmed by analysis of cliques, which are groups of nodes that are all connected to each other, and such that no other nodes exist connected to all of them (Boccaletti et al., 2006). The clique concept is more restrictive than the idea of connected component, as it implies not only node reachability, but complete interconnection between nodes (Fig. 18B). Consequently, a clique qualifies as a community since it is has the greatest possible edge density (Yan and Gregory, 2009). Given the small size of the Nurra ichnonetwork, the recommendation of Wassermann and Faust (1994) are relaxed by considering also dyads in clique-finding. Accordingly, the central group *G* consists of three cliques (Fig. 18C):

- *G1: Helminthoidichnites-Treptichnus*
- *G2: Taenidium-Treptichnus-Camborygma-Ophiomorpha*
- *G3: Camborygma*-Rhizohaloes-*Treptichnus*

In addition with the monoichnospecific occurrences of *Arenicolites, Skolithos* and *Palaeophycus,* these network communities represent the major ichnoassociations of the studied system. Because ichnoassociations represent groups of recurring behaviours, they reflect specific sets of environmental conditions, which will be discussed in the following section 6.

6. **Discussion**

6.1. Evolution of the ichnonetwork in time: the Permian/Triassic contrast

Permian and Triassic ichnofaunas are very different, both in composition and structure. In fact, ichnonetwork analysis demonstrates a striking difference between the Permian and the Triassic ichnofaunas, the latter of which is dominated by simpler, unbranched, horizontal or vertical structures (i.e. *Arenicolites, Skolithos, Helminthoidichnites*; Fig. 17). In parallel, isolated nodes are typical of Triassic units, while the ichnotaxa of the Cala del Vino Formation are densely interwoven. These evidences are highlighted by producing time-specific subnetworks, accounting for a structured Permian ecosystem and an Early Triassic scenario dominated by monoichnospecific assemblages (Fig. 19).

Such ecological restructuring suggests an underlying environmental change accounting for the progressive simplification of ichnonetwork structure. In this regard, the disappearance of *Camborygma* from the Triassic units provides direct evidence for a dramatic change in the hydrologic regime. In fact, *Camborygma* requires the permanent presence of the water table, even if seasonally fluctuating and moderately deep (Hasiotis and Mitchell, 1993: fig. 19). Consequently, absence of *Camborygma* in the Triassic units indicates little seasonal precipitation (Dry climate *sensu* Hasiotis et al., 2007), while its common presence in the Cala del Vino Formation documents seasonal precipitation and a balanced precipitation/evapotranspiration ratio (Wet-Dry climate *sensu* Hasiotis et al., 2007). Such climatic change is confirmed by the declining presence of rhizolites in the Triassic units, indicating that flora experienced a drought stress. The Porticciolo Conglomerate manifests the driest conditions, being characterized by absence of rhizolites and very low bioturbation index. This phenomenon is not a preservational artefact, because the Porticciolo Conglomerate comprises both conglomerates and sandstones (facies C1 and S1, Table 1).

Sedimentologic evidences support the mentioned interpretation, as indicators of dry conditions are commonly found in the Cala Viola Formation (i.e. dominant red paleosoils, wind-worn clasts, caliches) and Porticciolo Conglomerate (wind-worn clasts). In the Cala Viola Formation, the sparse distribution of vegetation-induced sedimentary structures (centroclinal cross-strata, creeping-stem moulds) are expression of discontinuous plant cover. In contrast, the sedimentary record of the Cala del Vino Formation (green-red carbonate palaeosols, caliches) account for an alternately wet and dry to relatively mild semi-arid climatic conditions. This interpretation is supported by the presence of large caseid pelycosaurs (cf. *Cotylorhynchus*), which required considerable amounts of vegetation (Ronchiet al., 2011).

Although the studied dataset is local, the corresponding drying trend is the expression of global phenomena. In fact, the acme of the ecological restructuring corresponds to the Porticciolo Conglomerate (Fig. 19), which marks an hyper-arid period occurring in many other parts of Europe in the late Induan-early Olenekian (Durand et al., 1989; Durand, 2006, 2008; Cassinis et al., 2007) or in the late Smithian according to other authors (Bourquin et al., 2007, 2011). This event is framed in the warming trend occurring at the Permian-Triassic boundary and persisting in Early Triassic times (Preto et al., 2010). In fact, palaeontological data (Early Triassic coal gap; Retallack, 1997), geochemical proxies (oxygen isotopes; Sun et al., 2012) and climatic models (Kidder and Worsley, 2004) account for a marked warming affecting both marine and continental realms across the Permian-Triassic boundary. In this context, the Nurra ichnonetwork pictures how the freshwater ecosystem answered to the global phenomena occurring at the Permian-Triassic boundary (Figs. 18, 19):

1. deep stationary infauna (e.g. crayfishes) was negatively affected by a change in the hydrologic regime. This evidence reflects global rather than local phenomena, as coeval changes in fluvial style are reported from Spain, Australia, South Africa and Brazil (Arche and Lopez-Gomez, 2005).
2. Primary producers suffered from drought stress, as evidenced by the decreasing abundance of rhizolites. Such phenomenon may have occurred at a global scale, as palaeontological data record a floral change above the Permian-Triassic boundary (Sun et al., 2012). Furthermore, Arche and Lopez-Gomez (2005) proposed that a decline in plant cover caused the aforementioned change in fluvial style.
3. Habitats fragmented, as evidenced by dominance of isolated nodes in Triassic subichnonetworks.

Climate warming provide a parsimonious explanation for these evidences, collectively converged in restructuring of freshwater ecosystems. Although not conclusive *per se*, these results support the crucial role of climate warming in driving the end-Permian crisis and its prolonged recovery time (see Hallam and Wignall, 1997; Preto et al., 2010; Sun et al., 2012). In fact, the biological realm is severely influenced by direct effects (i.e. lethal hot temperatures; Sun et al., 2012) and indirect phenomena (i.e. marine anoxia; Hallam and Wignall, 1997) linked to extreme warming. In turn, the cause of Permian-Triassic warming is generally ascribed to greenhouse gases, among which volcanic CO_2, CH_4 from gas hydrates and/or CO_2 from contact metamorphism (Preto et al., 2010)

6.2. *Ichnoassociations and environments*

Topological analysis revealed six structural areas (network communities; section 5.3) in the studied ichnonetwork. Because communities are groups of nodes which play similar roles within the network (Fortunato, 2010), a fundamental question then arises of what is the significance of the detected grouping patterns.

Being sets of interconnected nodes, network communities represent ichnoassociations, the structure of which was modelled by environmental conditions. In light of these observations, environmental interpretation is provided for each ichnoassociation, which has been named after the dominant ichnotaxon:

1. Rhizohaloes ichnoassociation: Ichnonetwork analysis reveals a set of nodes comprising rhizolites, *Camborygma* and *Treptichnus* (Fig. 18C). Network analysis show that rhizohaloes are the most representative ichnotaxon of this ichnoassociation. In fact, high clustering index (Fig. 18C) shows that rhizolites lie at the core of their ichnoassociation, while their low betweenness (Fig. 18B, C) demonstrates that this ichnotaxon is not an environmental generalist. In fact, rhizolites are a tendentially terraphilic component of continental ichnofaunas, inhabiting the vadose zone (Hasiotis, 2007). This observation is supported by the environmental range of modern roots, which is restricted not only by draught, but also by excessive soil moisture. In fact, water-saturated conditions led to oxygen deficiency in the soil and therefore affect negatively root respiration (Nagarajan and Nagarajan, 2010).

In contrast to rhizolites, *Camborygma* and *Treptichnus* are the highest-betweeness nodes of the network, implying that they are shared with other subenvironments and/or ichnosuites. Field observations show that they are accessory components of the here discussed ichnoassociation, at times being substituted by helical burrows type L. The climate damping function of helical burrows indicate drier, well-drained soils, especially if *Camborygma* is absent from the ichnoassociation. In fact, the presence of *Camborygma* implies a permanent, relatively shallow water-table.

In conclusion, the Rhizohaloes ichnoassociation represents vegetated substrates under vadose, unsaturated conditions. This interpretation is confirmed by sedimentological features, as this ichnoassociation is reported from palaeosols. The presence/absence of *Camborygma* and helical burrows is dependent on the hydrologic regime, with *Camborygma* associated to shallower water tables (1-5 m; Hasiotis, 2007).

2. *Taenidium/Ophiomorpha* ichnoassociation: In the Nurra ichnonetwork, *Taenidium, Treptichnus, Camborygma* and *Ophiomorpha* constitute a densely connected set of nodes, which can be further

partitioned into subgroups. In fact, edge weights are not uniformly distributed within these nodes, as it would be expected from a completely homogeneous environment (Fig. 18). In fact, this ichnoassociation represents the overlapping of two ichnosuites, each of which is in equilibrium with a defined set of environmental properties:

- *Ophiomorpha* ichnosuite. *Ophiomorpha* plays an important role in the ichnonetwork, because its low betweenness is the signature of environmental specificity, corresponding to lotic conditions. In fact, the diagnostic constructional lining of *Ophiomorpha* is an adaptation for facing high-energy hydrodynamics. This observation implies permanently submersed conditions with running water, environmentally contrasting with the traces produced by insects and other small arthropods (i.e. *Taenidium, Treptichnus*).

  Such lotic conditions are tolerated by the *Camborygma* producers, although deep specimens indicate the presence of groundwater at depth (Hasiotis and Mitchell, 1993). Consequently, this ichnosuite covers an environmental gradient ranging from active fluvial channels, with *Ophiomorpha* and shallow *Camborygma*, to periaquatic subenvironments, with deep specimens of *Camborygma.* The latter condition is correspondent to the *Camborygma* ichnocoenose of Hasiotis (2007), denoting a shallow phreatic zone within seasonal, imperfectly drained substrates.

  This interpretation is confirmed by the studied ichnonetwork, which documents a relatively weak link between *Ophiomorpha* and *Camborygma,* therefore indicating a partial habitat overlapping. In particular, *Camborygma* tolerated a wider set of hydrologic conditions, being intermediary between terraphilic (rhizohaloes) and hydrophilic (*Ophiomorpha*) components. Finally, field observations suggest that *Spongeliomorpha and Sinusichnus*-like traces pertain to the same ichnosuite, being commonly found with *Camborygma.*

- *Taenidium* ichnosuite. A relatively conspicuous number of traces co-occur with *Taenidium*, which therefore display one of the highest degrees of the ichnonetwork (Fig. 18A, C). Nevertheless, *Taenidium* is characterized by low betweeness and high clustering coefficient, indicating a remarkable environmental specificity. According to Morrissey and Braddy (2004) and Buatois and Mángano (2007) ichnofabrics dominated by meniscate traces (i.e. *Taenidium, Beaconites*) record colonization of subaerially exposed sediment in response to desiccation. These environmental conditions are typical of abandoned fluvial channels, which are the typical sedimentary environment of *Taenidium* (Buatois and Mángano, 2004, 2011). This interpretation explains the common overprinting of the *Taenidium* ichnosuite with the *Ophiomorpha* ichnosuite, representing the active and inactive phase of the channel, respectively.

In other cases, the *Taenidium* ichnosuite is not accompanied by the *Ophiomorpha* ichnosuite, indicating non-equilibrium with channel conditions. Copious horizontal burrows, diagnostic of this ichnosuite, show that the sediment constituted a resource for the insect tracemakers of *Taenidium* and *Treptichnus*. In this case, the *Taenidium* ichnosuite corresponds to overbank (i.e. crevasse splays) settings, which are favourable subenvironments for insect tracemakers. In fact, modern insects colonize floodplain substrates short after their inundation, because river flooding brings nutrients and favour microalgal blooms on the surface of soft-sediments (Baucon, pers. obs.). This interpretation fits with the flood pulse concept, according to which river floods are not biologically catastrophic events, but they are responsible for existence, productivity and interactions of the major biota in river-floodplain systems (Junk et al., 1989).

3. *Helminthoidichnites* ichnoassociation: *Helminthoidichnites* occurs in nearly monoichnospecific assemblages within the intraformational conglomerates of the Cala Viola Sandstone, rarely accompanied by *Treptichnus.* Low diversity and low bioturbation intensity account for a stressed environment, where endobenthic biomass was low. This interpretation is supported by sedimentological evidences, as this ichnoassociation is reported from small channelized bodies.

4., 5., 6. Monoichnospecific ichnoassociations (*Palaeophycus*, *Skolithos*, *Arenicolites*): These ichnoassociations have no links with other nodes of the ichnonetwork, therefore they demonstrate environmental incompatibility with other ichnotaxa. Whereas these monoichnospecific associations collectively indicate stressful conditions, each of them has specific environmental declinations. *Palaeophycus* ichnoassociation is accompanied by low bioturbation intensity, therefore corresponding to an extremely harsh endobenthic environment. In this regard, lining may be an adaptation to shifting substrates.

In contrast, *Skolithos* and, especially, *Arenicolites* ichnoassociation show high bioturbation intensities, accounting for gregarious behaviour. In light of the environmental interpretation of individual ichnotaxa, *Skolithos* ichnoassociation corresponds to dry overbank settings, while *Arenicolites* ichnoassociation shows the opportunistic colonization of aquatic environments.

These ichnoassociations are framed in a topological context with distinct features, the first of which is their time-specificity (section 6.1). Secondly, the studied ichnonetwork shows a marked hierarchical organization of ichnoassociations, with smaller modules contained in bigger ones. In particular, the ichnoassociations of the Cala Viola Formation are nested within the larger group *C1*. This mirrors the structure of the environment, consisting of a wide environmental context made by subenvironments. These subenvironments represented a gradual continuum, as evidenced by significant overlapping between the components of the rhizolites and the *Taenidium/Ophiomorpha* ichnoassociation.

At the present state of the research, these results cannot be compared with the Porto Ferro and Pedru Siligu formations, as the outcrop quality and extension is significantly lower. Qualitatively, the studied ichnofauna is comparable with the coeval succession of Southeastern France, fully correlable with the Nurra basin (Durand et al., 1989; Durand, 2008; Linol et al., 2009).

6.3. *Decapod shrimp evolution*

After elucidating the palaeoenvironmental scenario, the next step is to define the macroevolutionary significance of the decapod traces of Nurra. With this aim in mind, a time-environment database of the major occurrences of *Ophiomorpha* and *Camborygma* has been compiled after previous studies (Chamberlain and Baer, 1973; Bottjer et al., 1988; Hasiotis and Mitchell, 1993; Hasiotis and Honey, 2000; Tchoumatchenco and Uchman, 2001; Hasiotis, 2004).

The corresponding chart (Fig. 23) shows that *Camborygma* has colonized continental settings since its first appearance, while *Ophiomorpha* displays a deepening trend, which has already been noted by Bottjer et al. (1988).

The comparison between *Ophiomorpha* and *Camborygma* shows that their environmental ranges are well-separated in relatively recent units, but they tend to converge towards upper Palaeozoic. In this context, the Nurra occurrences correspond to the moment of convergence. In fact, the *Ophiomorpha* from Nurra are the missing link between the nearshore *Ophiomorpha* of Triassic times and the fluvial *Camborygma* from Permian. The Cedar Mesa *Ophiomorpha* (Permian; Chamberlain and Baer, 1973) is an outlier, but successive works (i.e. Loope, 1984) suggests that its depositional environment was continental rather than marine.

The significance of the environmental convergence of *Ophiomorpha* and *Camborygma* is explained by referring traces to their producers: *Ophiomorpha* to ghost shrimps ('thalassinideans'; Decapoda: Axiidea, Gebiidea) and *Camborygma* to crayfishes ('astacids'; Decapoda: Astacoidea, Parastacoidea). In fact, ghost shrimps and crayfishes are phylogenetically related (Porter et al., 2005; Tsang et al., 2008), therefore they derive from the same population. In light of this consideration, convergence of environmental ranges reflects the fact that the ancestral population was constituted by individuals living in the same geographical area.

This hypothesis is confirmed by confronting the time-environment diagram with the divergence times of major thalassinid and astacid lineages, based on molecular phylogenetic methods applied by Porter et al. (2005) (Fig. 23). The Nurra occurrences are almost coeval to the appearance of crayfishes, which diverged 278 mya from lobsters (Porter et al. 2005). This suggests that the studied ichnosite records the activity of basal crayfishes and thalassinideans.

Consequently, the most parsimonious explanation of the purported scenario is that astacid/thalassinid diversification happened in fluvial environments between Carboniferous and early Permian, while ghost shrimps has invaded marine environments at the Permian/Triassic boundary. Further Palaeozoic occurrences of *Camborygma* and *Ophiomorpha* are required to confirm this hypothesis.

7. **Conclusions**

This paper explored the ichnological heritage of the Permian-Triassic succession of Nurra, applying for the first time ichnonetwork analysis on the fossil record. This novel approach revealed to be a powerful tool for describing and analysing fossil ichnological systems, being able to discern critically important ichnotaxa, ichnoassociations and their environmental significance. Furthermore, ichnonetwork analysis shown that ghost shrimps and crayfishes – producers of *Camborygma* and *Ophiomorpha*, respectively – colonized freshwater environments during the middle Permian, suggesting that their diversification occurred in continental settings. Nevertheless, the pre-Triassic decapod record is very sparse, requiring further research to test this hypothesis. Consequently, several important directions for further work are identified. The first is to integrate the trace fossil record with the body fossil record and phylogenetic data, in order to better delineate trends and patterns. The second is to map the Permian-Triassic occurrences of decapod trace fossils in order to establish accurately the paleobiogeographic trends of this important stage of crustacean evolution. The third is to establish the role of global environmental changes in driving evolution of decapods, which had a rapid radiation after the end-Permian crisis (Schram and Dixon, 2004). Additionally, results from this study show that ghost shrimps shifted their environmental range across the Permian-Triassic boundary.

In this context, ichnonetwork analysis documented the ecological changes across the Permian/Triassic boundary, manifested in the simplification of network topology. Ichnonetwork restructuring is coherently explained by drought stress, supporting the role of climate warming in driving the end-Permian crisis and its aftermath. Intriguingly, modern fluvial ecosystems are experiencing comparable changes in response to the climate change, resulting in the radical restructuring of the dynamics and architecture of trophic networks (Perkins and Reiss, 2010 and references therein). Although scale and causes of modern global warming are under heated debate, these observations warn us on the extreme fragility of freshwater environments with respect to climate. Consequently, this study encourages further research on the climatic controls on ichnonetwork structure, both in fossil and modern environments.

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Figures

Fig. 1. Geological setting of Nurra.

Fig. 2. Stratigraphical and palaeontological setting of the studied succession.

Fig. 3. *Skolithos* from the Cala Viola formation. (A) Straight, vertical *Skolithos.* (B) *Skolithos* tend to occur in monoichnospecific assemblages. Dashed lines evidence the straight, cylindrical morphology of the here studied *Skolithos*; arrow points to a passively filled specimen.

Fig. 4. *Taenidium barretti,* medium-sized morphotype. (A) *Taenidium barretti* from Cala del Vino Fm. Arrow indicates the magnified area in B. (B) Particular of A, showing arcuate, tightly-packed menisci (traced). (C) *Planolites*-like preservation of *Taenidium*. Cala Viola Fm.

Fig. 5. *Taenidium barretti,* large morphotype. (A) Bedding plane with numerous specimens of *Taenidium barretti.* Menisci are very faint and observable only at close inspection. (B) Close-up highlighting arcuate menisci. Thick scale = 1 mm.

Fig. 6. *Treptichnus*. (A) Upper bedding surface with numerous specimens of *Treptichnus.* Arrows indicates angular turns; the specimen pointed by the lower arrow is magnified in B. Thick scale = 1 mm. (B) The studied *Treptichnus* are characterized by angular turns (t) and straight segments with arch-like annulations (s). (C) Arrow points to a set of inclined arches, which indicate a pushing phase during burrowing.

Fig. 7. Burrowing cycle of *Treptichnus*. (A) Tracemaker in its burrow; tracemaker morphology based on modern mud-loving beetles. (B) Push-up-phase and stop phase (C) Start of the tunneling phase

Fig. 8. *Arenicolites.* (A) Bedding plane with numerous *Arenicolites*. (B) Hyporelief preservation of *Arenicolites.* (C) Geometrical experiment showing the relationship between curvature and height/width ratio in *Arenicolites*.

Fig. 9. Tracemaker, behaviour and environment of modern U-burrows, grouped in morphological classes. Vertical axis in logarithmic scale. Height and width calculated as the dimensions of a rectangle excribing the burrow; larger funnels not considered. Height/width ratio calculated from

previous literature (Myers, 1979; Hughes et al., 1996; Dawson and Evans, 1996; Atkinson et al., 1997; Charbonneau et al., 1997; Atkinson and Froglia, 2000; Coelho et al., 2000; Gingras et al., 2001, 2010; Curran and Martin, 2003; Anker et al., 2005; Pearson and Gingras, 2006; Garrison et al., 2007; Pischedda et al., 2008; Hembree, 2009; Weissberger et al., 2009; Herringshaw et al., 2010; Hembree et al., 2012).

Fig. 10. Helical burrows. (A) Helical burrow with terminal chamber, small morphotype. Morphological, neoichnological and functional attributes are consistent with a scorpion burrow. (B) Helical burrow, large morphotype.

Fig. 11. *Camborygma*. (A) Large, branched *Camborygma* (type XL). (B) *Camborygma* with manifest knobby texture. (C) *Camborygma* characteristically include pelleted chimneys. D – Outcrop with numerous *Camborygma* L presenting helical and chicane-shaped sections. Hammer for scale.

Fig. 12. *Camborygma.* (A) Behaviours (bold) and ichnological signatures (italics) in the studied *Camborygma.* B - Pelletted chimney with lower, flattened pellets (f) and upper, spherical ones (s); part of the unpelletted burrow system is visible (u).

Fig. 13. *Ophiomorpha.* (A) *Ophiomorpha* with clear Y-branching, smooth interior, pelleted lining. Arrow refers to the area magnified in B. (B) Particular of the pelleted lining of the specimen A. Scale in mm. (C) Overview of a bedding plane bioturbated by numerous *Ophiomorpha.*

Fig. 14. Other traces. (A) Rhizocretion. Hammer for scale. (B) *Spongeliomorpha.* Bedding plane view. (C) Sinuous trace, similar to *Sinusichnus.* Bedding plane view.

Fig. 15. Cala Viola stratigraphic section. See Fig. 2 for legend of ichnotaxon symbols.

Fig. 16. Network analysis workflow with free and open source software: LibreOffice (https://www.libreoffice.org/), PAST (http://folk.uio.no/ohammer/past/), Gephi.(https://gephi.org/). In the ichnonetwork, edge thickness measures the strength of the association relationship. *Camborygma*, He: *Helminthoidichnites*, Op: *Ophiomorpha*, Pa: *Palaeophycus*, Rh: rhizolites, Sk: *Skolithos*, Ta: *Taenidium*, Tr: *Treptichnus*.

Fig. 17. Network statistics. (A) Degree. (B) Betweenness. (C) Comparison between degree, betweeness

and clustering coeffcient. See Fig. 16 for abbreviations.

Fig. 18. Grouping patterns. (A) Toy network showing the concept of connected component. Two components are present. (B) Toy network showing the concept of clique. Two cliques and two components are present. (C) Grouping patterns in the studied ichnonetwork. See Fig. 16 for abbreviations.

Fig. 19. Time-specific subnetworks, derived from the main ichnonetwork. See Fig. 16 for abbreviations.

Fig. 20. Palaeoenvironmental reconstruction of the Cala del Vino Fm., based on ichnonetwork analysis.

Fig. 21. Palaeoenvironmental reconstruction of the Porticciolo Conglomerate., based on ichnonetwork analysis.

Fig. 22. Palaeoenvironmental reconstruction of the Cala Viola Fm., based on ichnonetwork analysis.

Fig. 23. Decapod evolution in time. (A) Database of major occurrences of *Ophiomorpha* and *Camborygma,* derived from previous studies. (Chamberlain and Baer, 1973; Bottjer et al., 1988; Hasiotis and Mitchell, 1993; Hasiotis and Honey, 2000; Tchoumatchenco and Uchman, 2001; Hasiotis, 2004). (B) Divergence times of astacid and thalassinid lineages. Based on Porter et al. (2005).

Facies code	**Name**	**Description**
C1	Extraformational conglomerate	Conglomerate or breccia made of pebble-sized clasts; occasional sandy matrix
C2	Intraformational conglomerate	Sand-supported conglomerate made of clay chips
S1	Well-sorted sandstone	Well-sorted through-bedded sandstones organized in metrical bedsets. Occasionaly abundant ventifacts.
S2	Medium sandstone	Massive or trough bedded medium sandstones, often occurring in thick (1-5 m) layers
S3	Fine sandstone	Medium to fine sandstone with parallel lamination or small-scale ripples, organized in thin (< 1 m) layers
P1	Pelite	Red, green or purple pelite with minor sandy fraction.
V1	Volcanoclastic	

Table 1. Facies of the Nurra sedimentary succession.

	Ingestion-and-excretion backfilling	Excavation backfilling
Predominant process	Digestion of the sediment	Manipulation with limbs
Texture of the backfill	Different to the host rock	Equal to the host rock
Predominant tracemakers	Worm-like organisms	Arthropods

Table 2. Major features of ingestion-and-excretion backfilling and excavation backfilling.

Burrow function (besides domichnial)	Branches	Terminal Chamber	Tracemakers	Ichnotaxon	Environment	Reference
1. Deposit feeding burrow	yes	no	*Jaxea nocturna* (Decapoda)		Marine	Pervesler and Hohenegger, (2006)
			Axianassa australis (Decapoda)	Incipient *Gyrolithes*	Marine	Dworschak and Rodrigues (1997)
2. Gardening and drift catching burrow	yes	no	*Jaxea nocturna* (Decapoda)		Marine	Pervesler and Hohenegger (2006)
	no	no		*Gyrolithes**	Marine	Seilacher (2007)
3. Climate refuge	no	clavate	*Urodacus yaschenkoi* (Scorpionida)		Terrestrial	Calver and Lymbery (2009)
	no	clavate	*Hadrurus arizonensis* (Scorpionida)		Terrestrial	Hembree et al. (2012)
	no	straight	*Palaeocastor**	*Daimonhelix**	Terrestrial	Meyer (1999)
4. Anti-predator burrow	no	straight	*Palaeocastor**	*Daimonhelix**	Terrestrial	Meyer (1999)
5. Mate attraction	no	yes	*Ocypode saratan*		Semi-terrestrial	Hughes (1973)
	no	banana-shaped	Brachyuran crab*	*Macanopsis*	Marine	Carvalho and Baucon (2010b)
6. Spiral staircase	no	no	Rodents*, therapsids*	*Daimonhelix**	Terrestrial	Seilacher (2007)
7. Space optimization to avoid neighbouring burrows	no	straight	*Paleocastor**	*Daimonhelix**	Terrestrial	Meyer (1999)
	no	clavate	*Urodacus yaschenkoi* (Scorpionida)		Terrestrial	Shorthouse and Marples (1980)

Table 3. Form and function of modern and fossil (*) helical burrows.

Chemical binding	+	**Building blocks**	+	**Physical action**	=	**Wall**		**Reference**
						Fossil example	Modern example	
Mucus, silk or chitin		Unselected sediment particles				*Palaeophycus*	*Chaetopterus* burrow	Bromley, 1996
		Selected sediment particles		Particle selection		*Diopatrichnus*	*Diopatra* burrow	Bromley, 1996
		Fecal pellets		Defecation		Some *Rhizocorallium*	Earthworm chimney	Seilacher, 2007; Darwin, 1881
		Sediment pellets		Manipulation		*Ophiomorpha*	*Callichirus major*	This study; Bromley, 1996

Table 4. General principles governing lining structure. Active or passive incorporation of building blocks within the binding medium is implicitly contemplated in ‘physical action’.

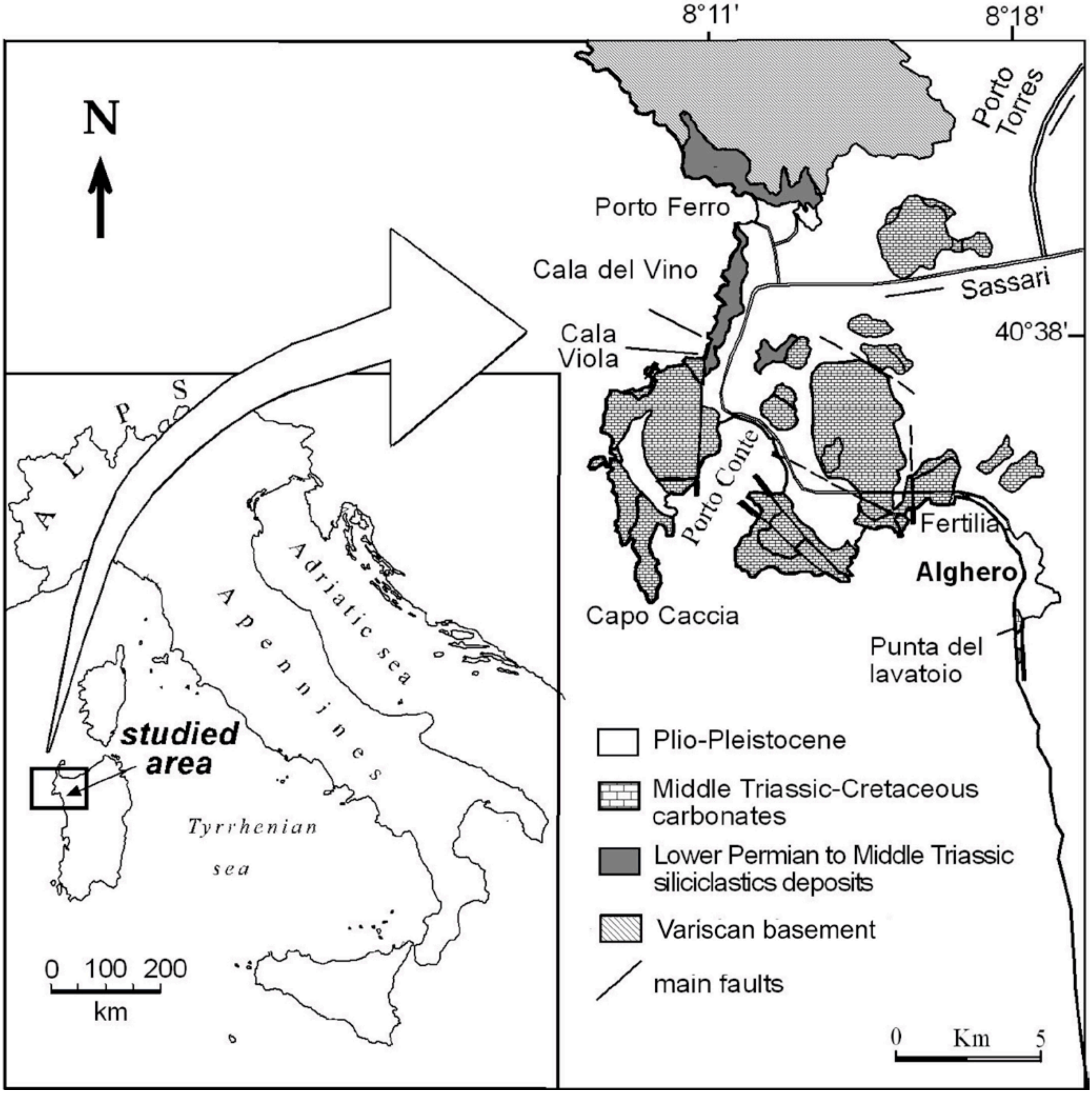

N
8°11'
8°18'
40°38'
Porto Torres
Porto Ferro
Cala del Vino
Cala Viola
Sassari
Porto Conte
Fertilia
Alghero
Capo Caccia
Punta del lavatoio
Plio-Pleistocene
Middle Triassic-Cretaceous carbonates
Lower Permian to Middle Triassic siliciclastics deposits
Variscan basement
main faults
0 Km 5
A L P S
Adriatic sea
Apennines
studied area
Tyrrhenian sea
0 100 200
km

Fig. 1.

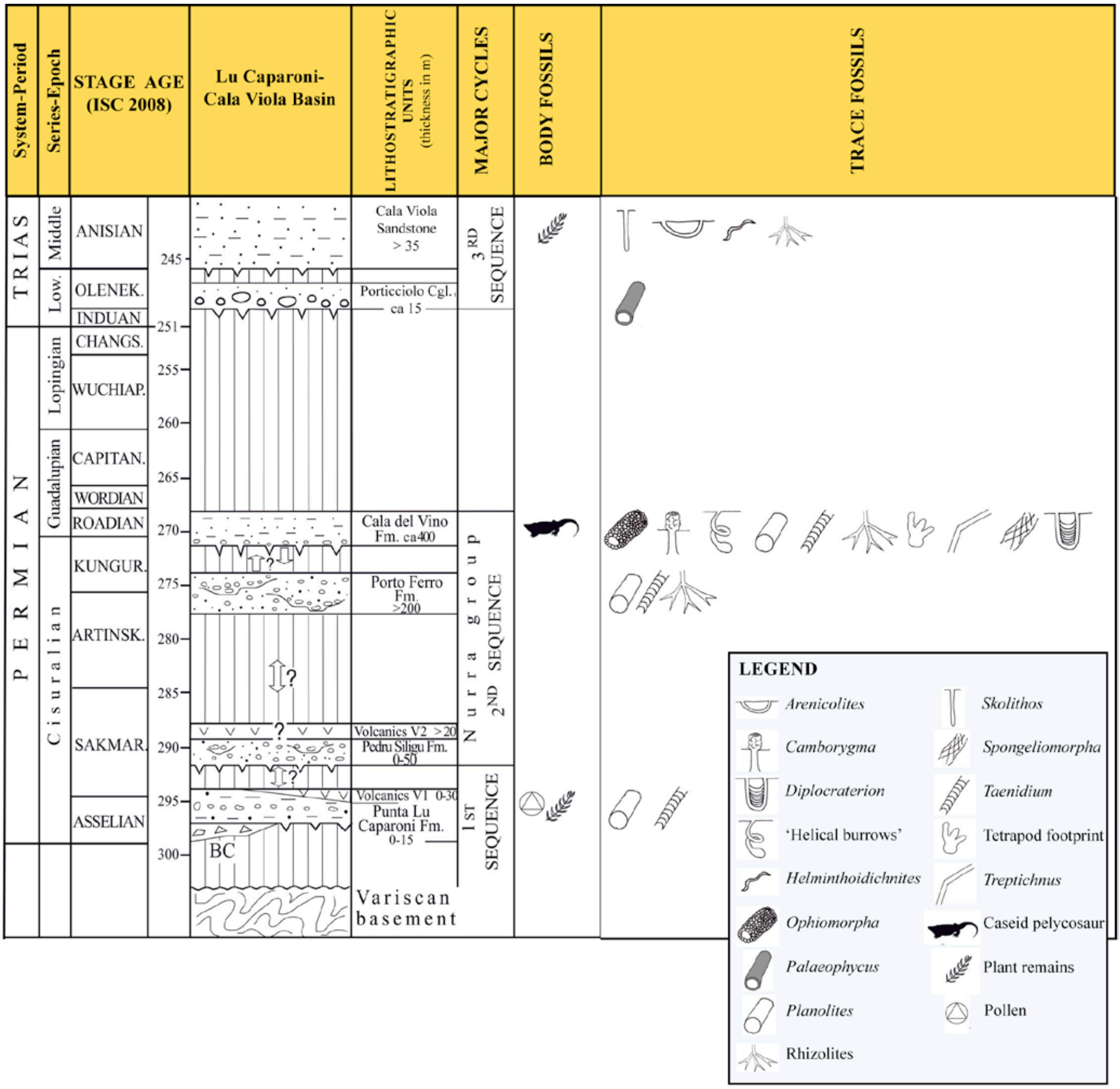

System-Period
Series-Epoch
STAGE AGE (ISC 2008)
Lu Caparoni-Cala Viola Basin
LITHOSTRATIGRAPHIC UNITS (thickness in m)
MAJOR CYCLES
BODY FOSSILS
TRACE FOSSILS
TRIAS
PERMIAN
Middle
Low.
Lopingian
Guadalupian
Cisuralian
ANISIAN
OLENEK.
INDUAN
CHANGS.
WUCHIAP.
CAPITAN.
WORDIAN
ROADIAN
KUNGUR.
ARTINSK.
SAKMAR.
ASSELIAN
245
251
255
260
265
270
275
280
285
290
295
300
?
BC
Cala Viola Sandstone > 35
Porticciolo Cgl. ca 15
Cala del Vino Fm. ca400
Porto Ferro Fm. >200
Volcanics V2 >20
Pedru Siligu Fm. 0-50
Volcanics V1 0-30
Punta Lu Caparoni Fm. 0-15
Variscan basement
3RD SEQUENCE
Nurra group
2ND SEQUENCE
1ST SEQUENCE
LEGEND
Arenicolites
Skolithos
Camborygma
Spongeliomorpha
Diplocraterion
Taenidium
'Helical burrows'
Tetrapod footprint
Helminthoidichnites
Treptichnus
Ophiomorpha
Caseid pelycosaur
Palaeophycus
Plant remains
Planolites
Pollen
Rhizolites

Fig. 2.

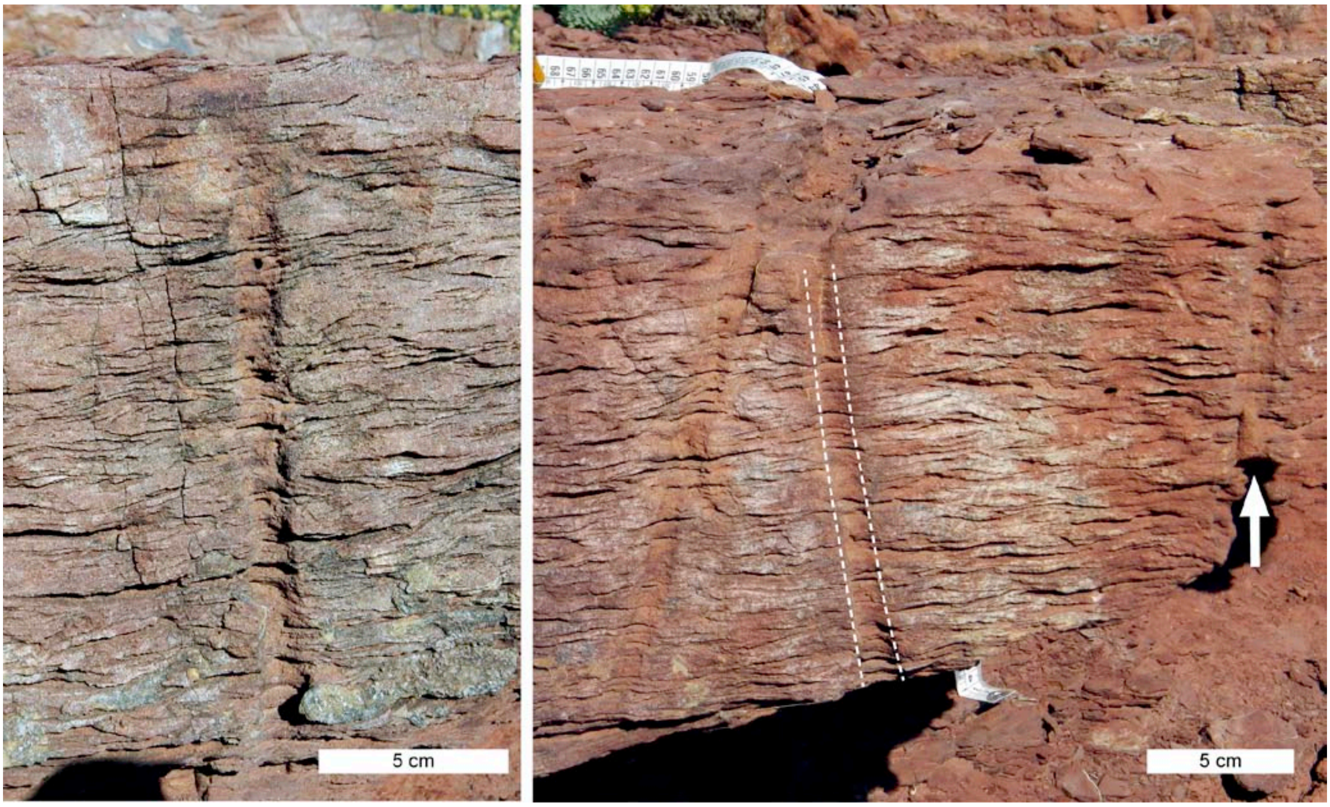


Fig. 3.

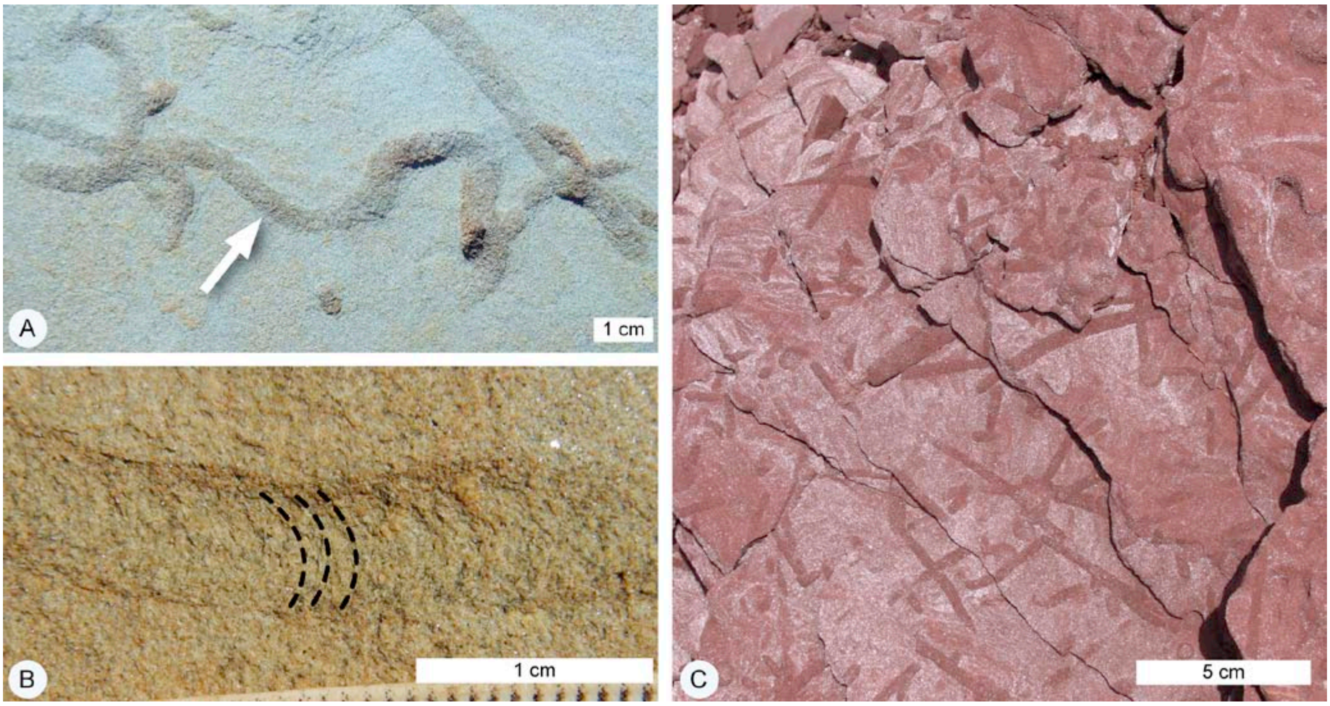


Fig. 4.

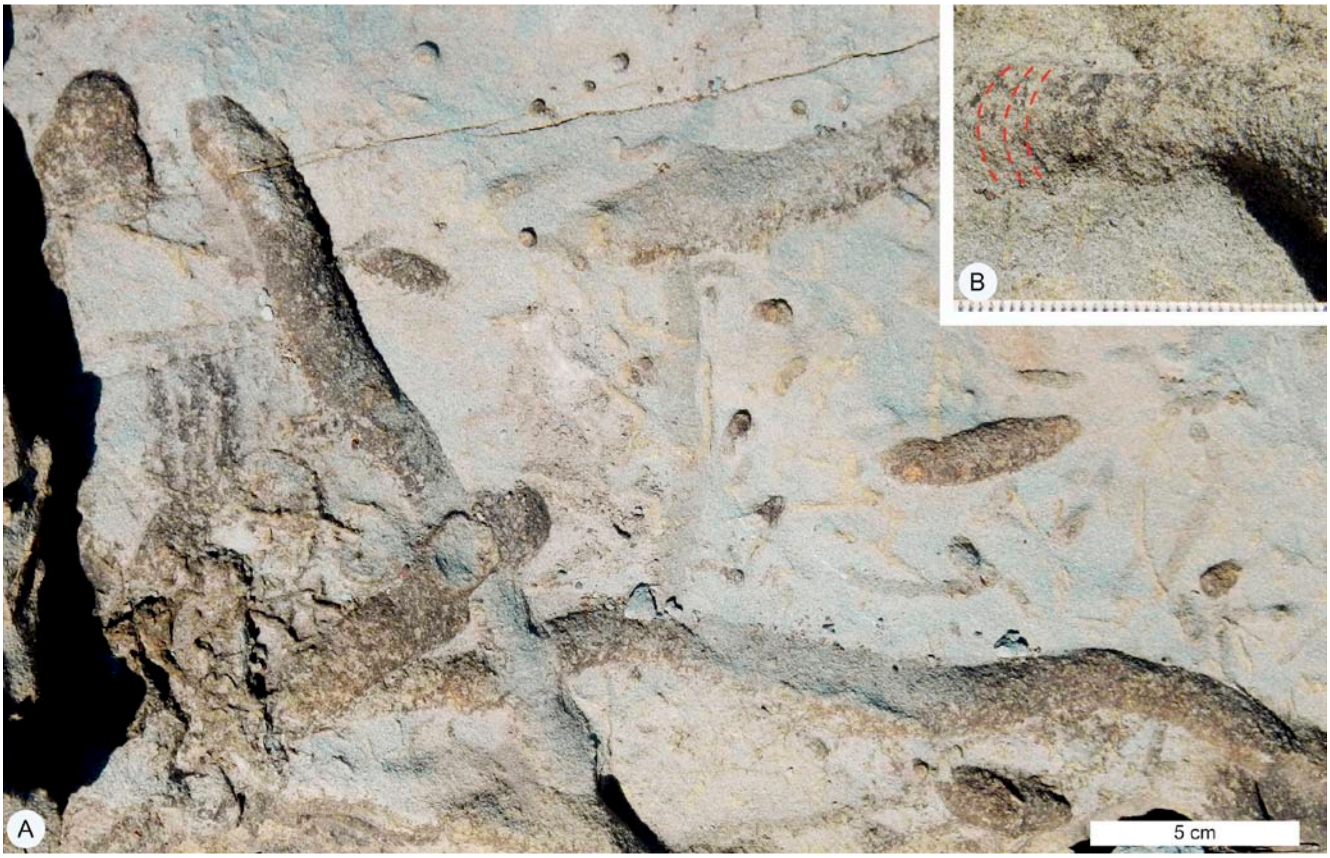


Fig. 5.

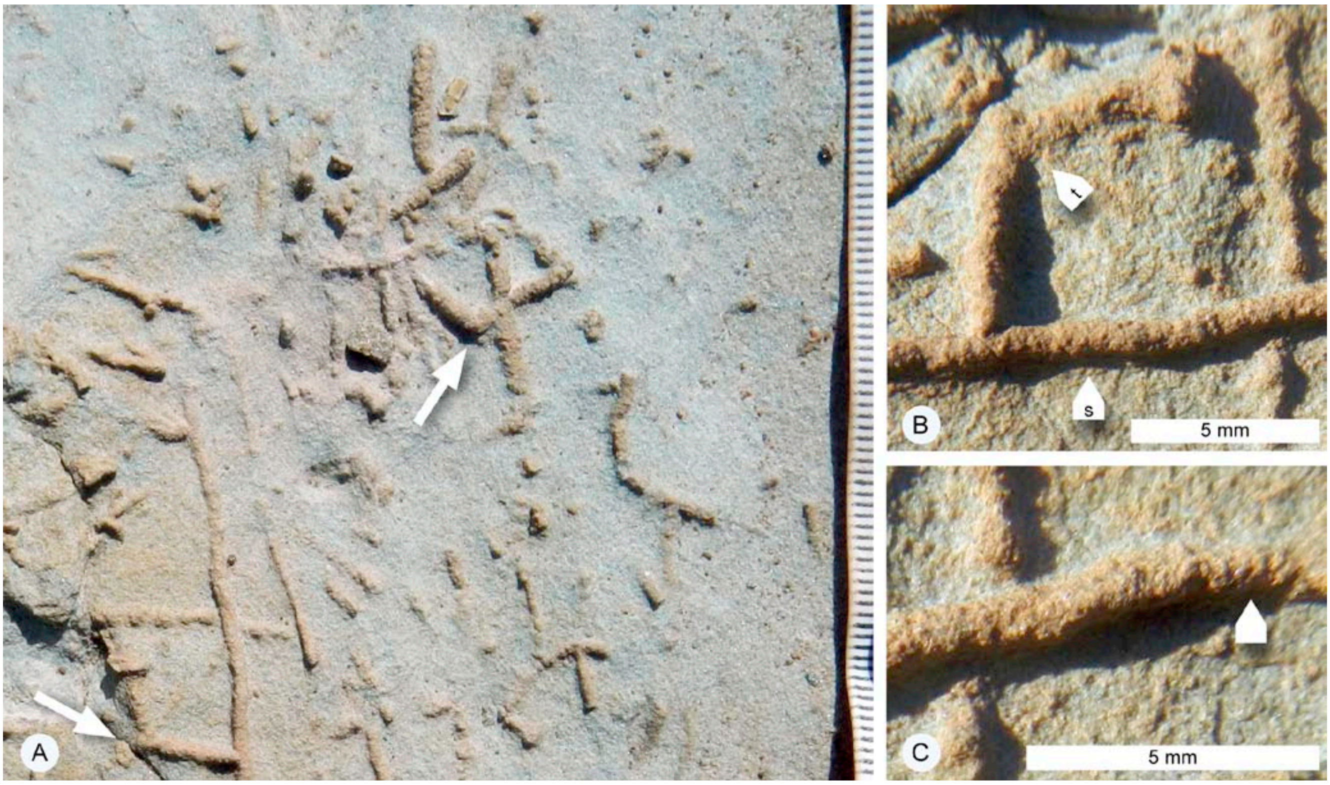


Fig. 6.

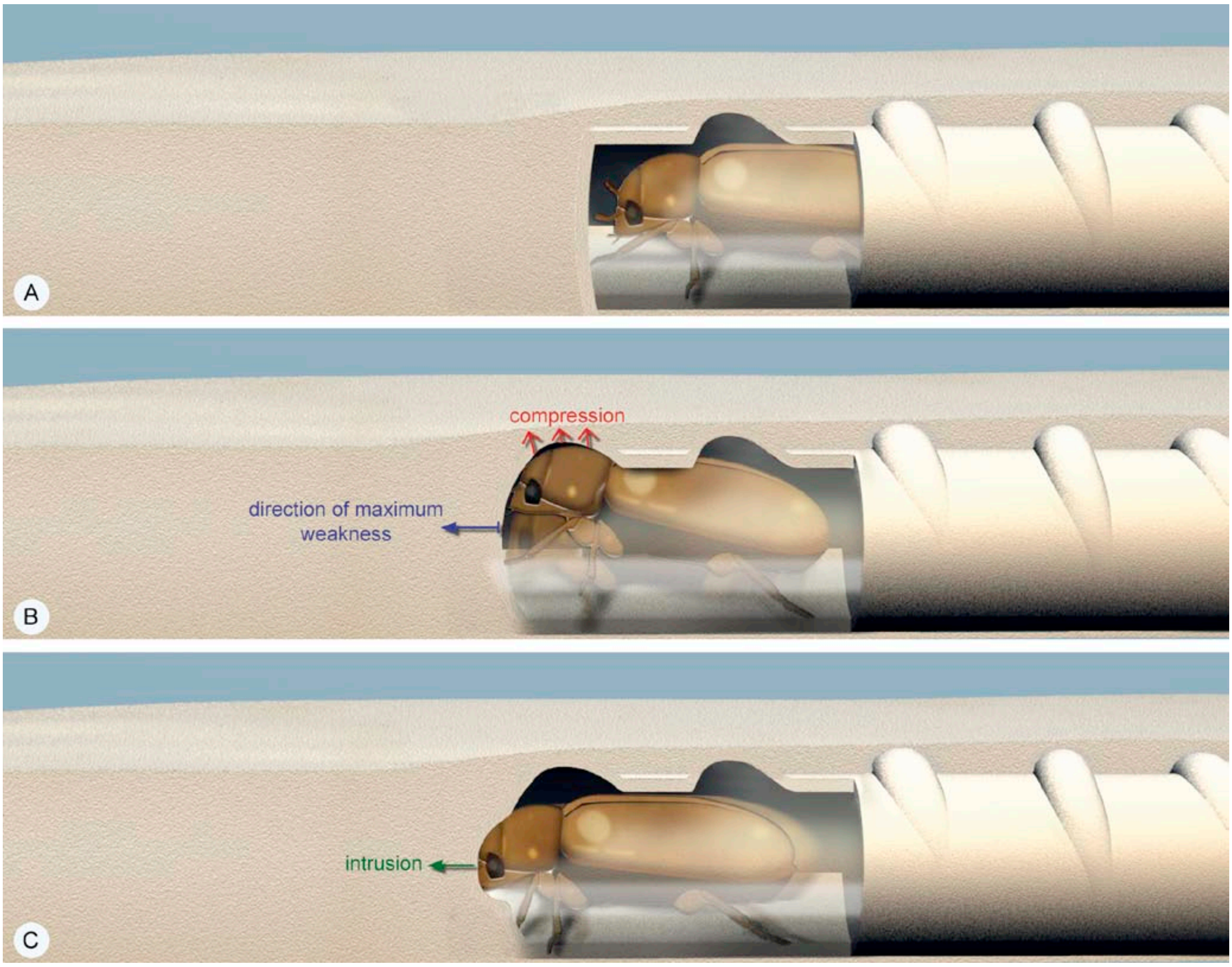


Fig. 7.

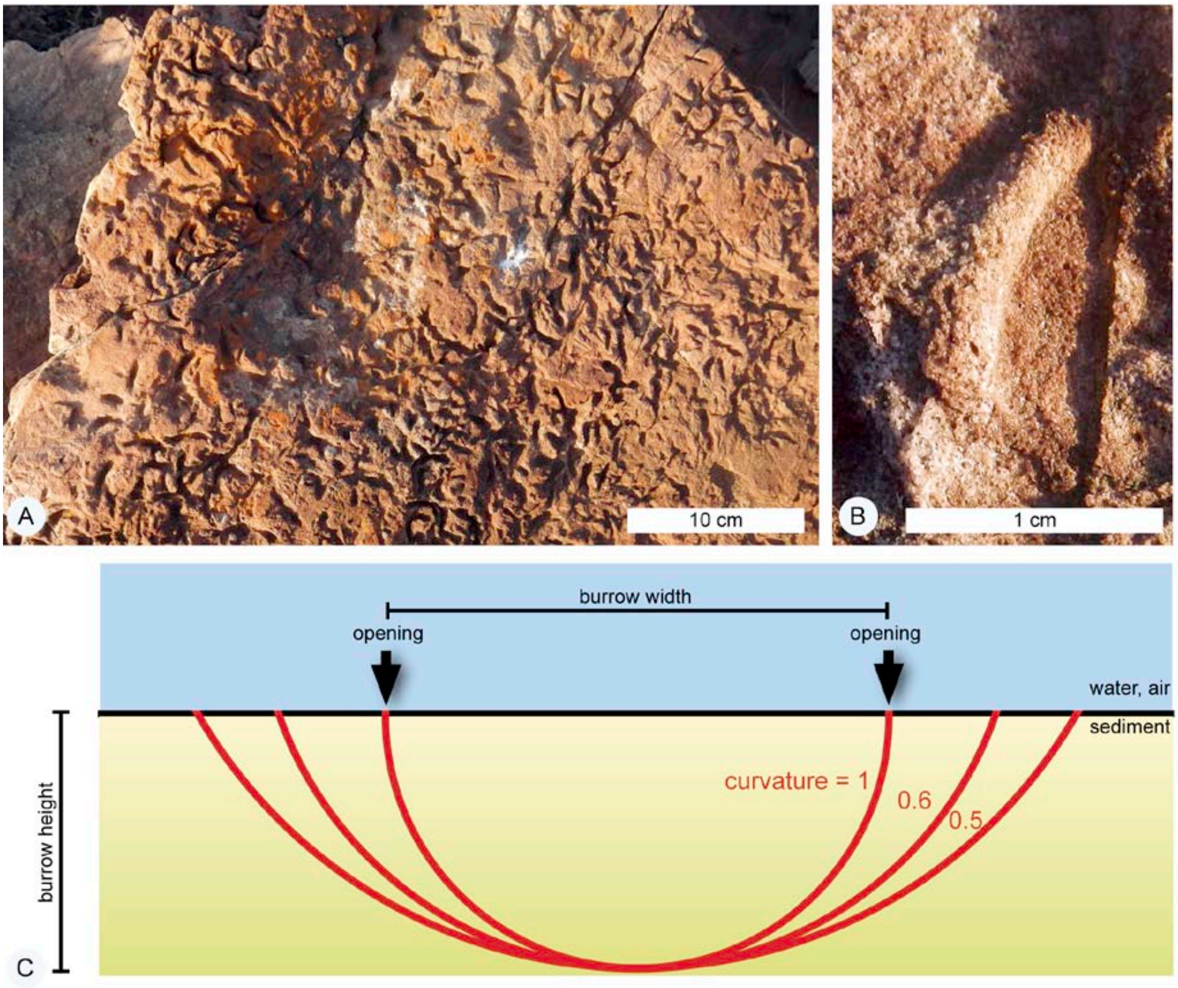

A
10 cm
B
1 cm
burrow width
opening
opening
water, air
sediment
curvature = 1
0.6
0.5
burrow height
C

Fig. 8.

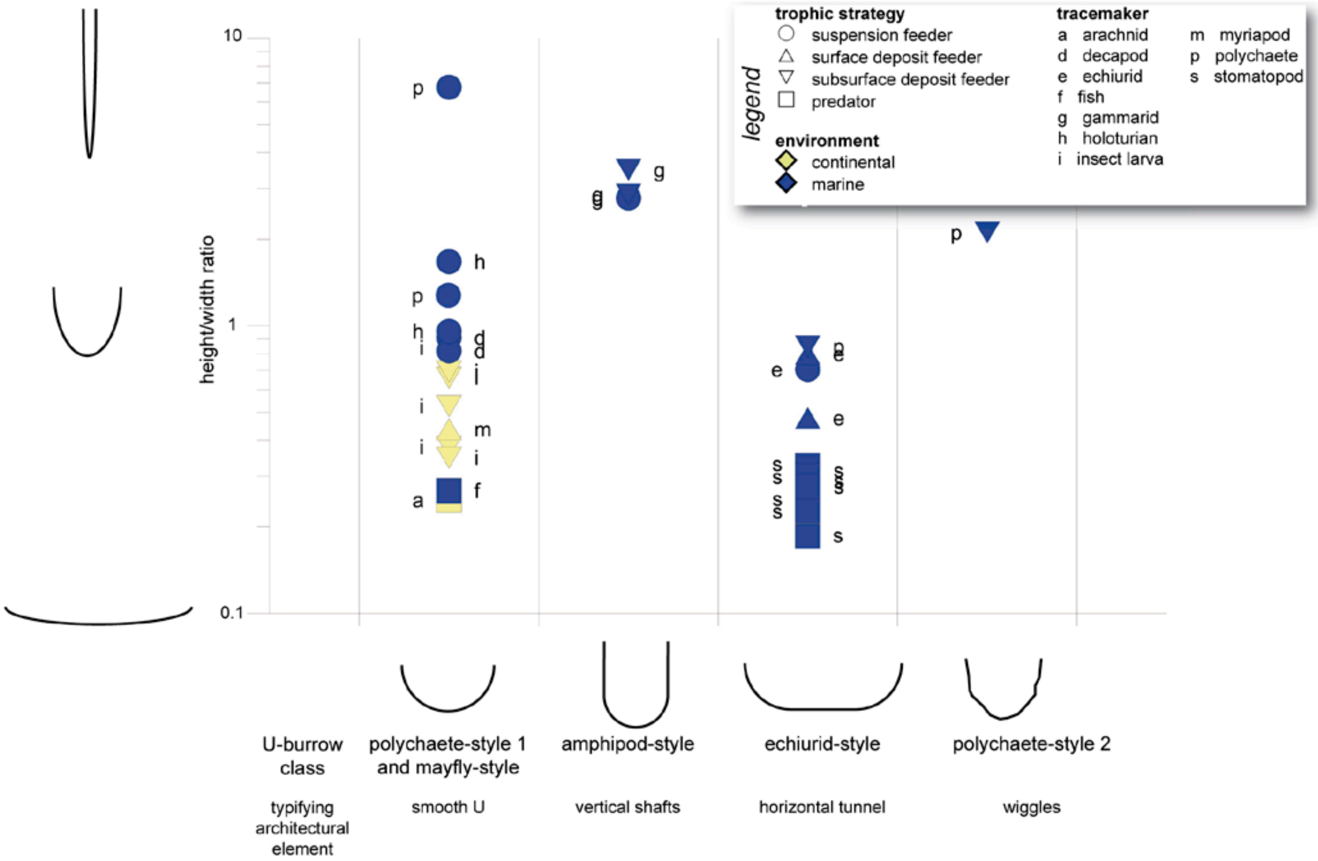

10
1
0.1
height/width ratio
legend
trophic strategy
○ suspension feeder
△ surface deposit feeder
▽ subsurface deposit feeder
☐ predator
environment
◆ continental
◆ marine
tracemaker
a arachnid
d decapod
e echiurid
f fish
g gammarid
h holoturian
i insect larva
m myriapod
p polychaete
s stomatopod
U-burrow class
polychaete-style 1 and mayfly-style
amphipod-style
echiurid-style
polychaete-style 2
typifying architectural element
smooth U
vertical shafts
horizontal tunnel
wiggles

Fig. 9.

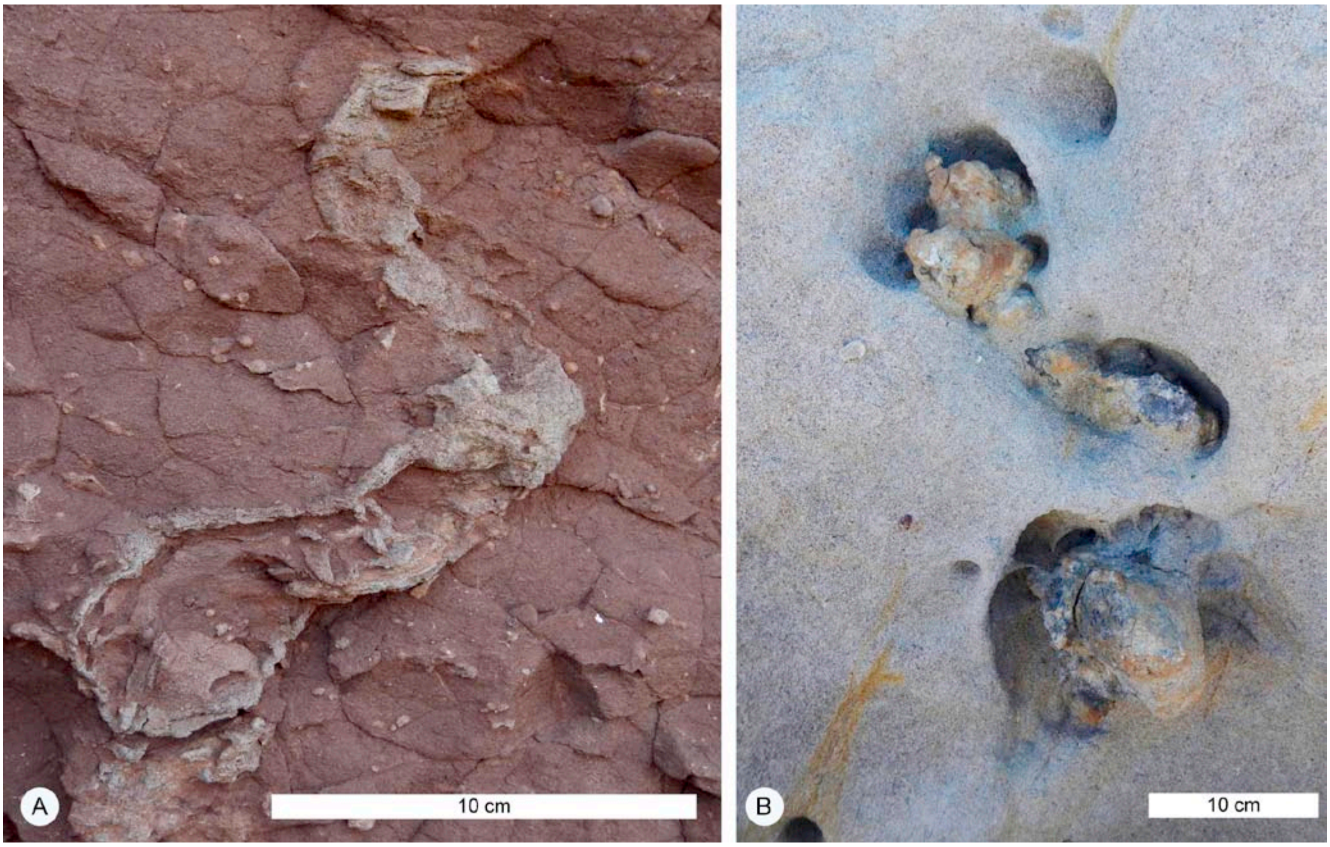


Fig. 10.

Fig. 11.

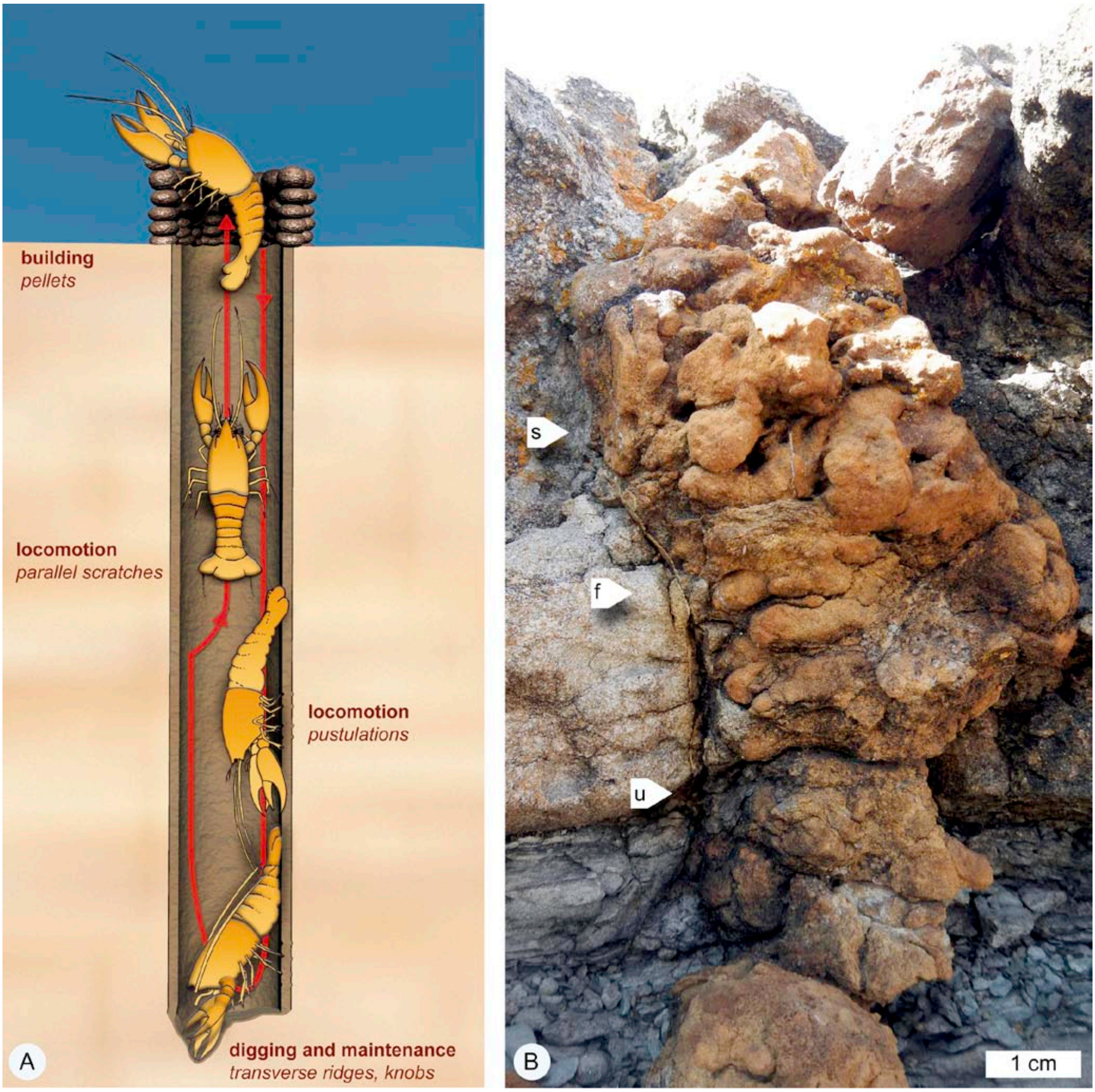

building
pellets
locomotion
parallel scratches
locomotion
pustulations
digging and maintenance
transverse ridges, knobs
A
s
f
u
B
1 cm

Fig. 12.

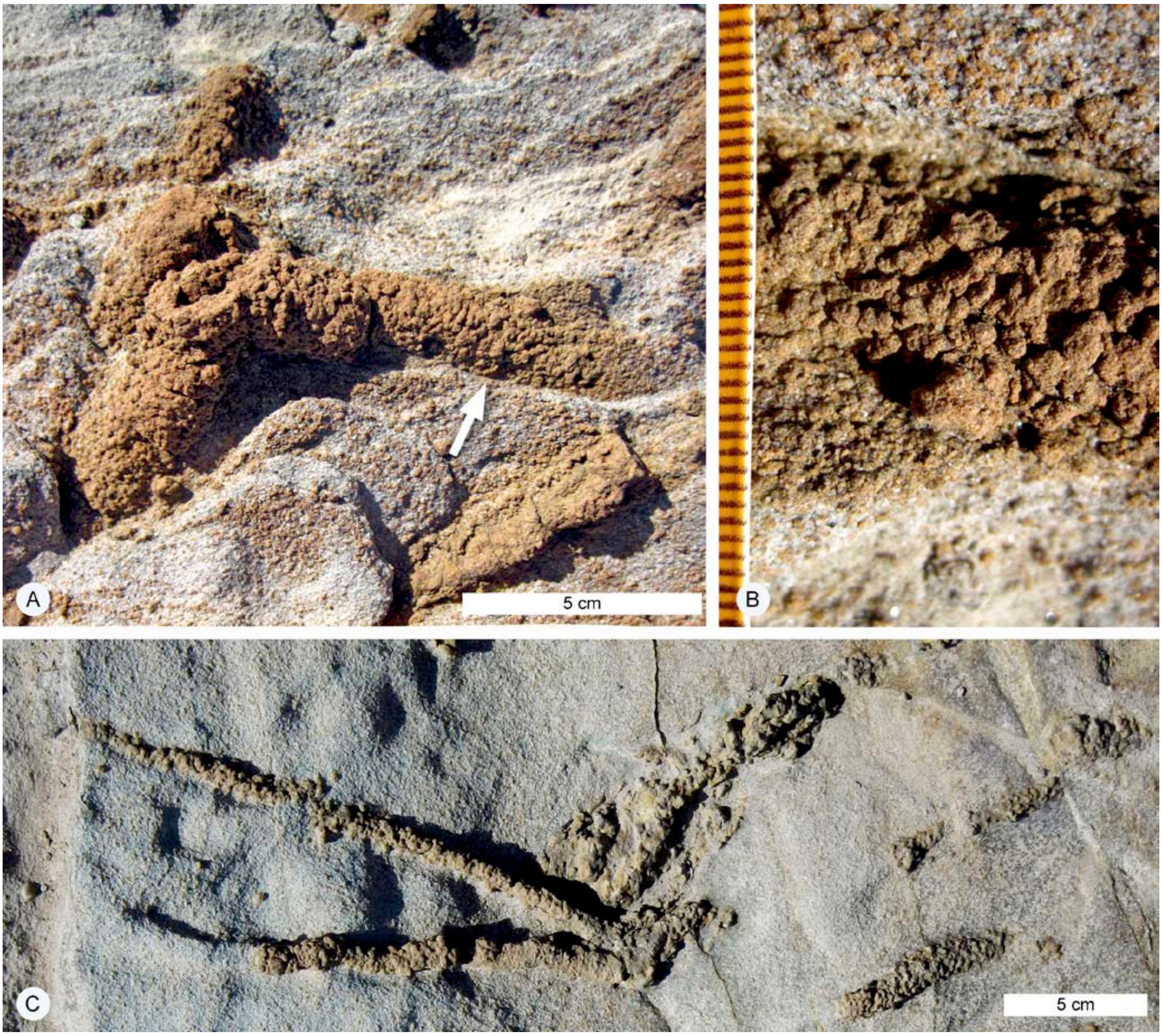


Fig. 13.

Fig. 14.

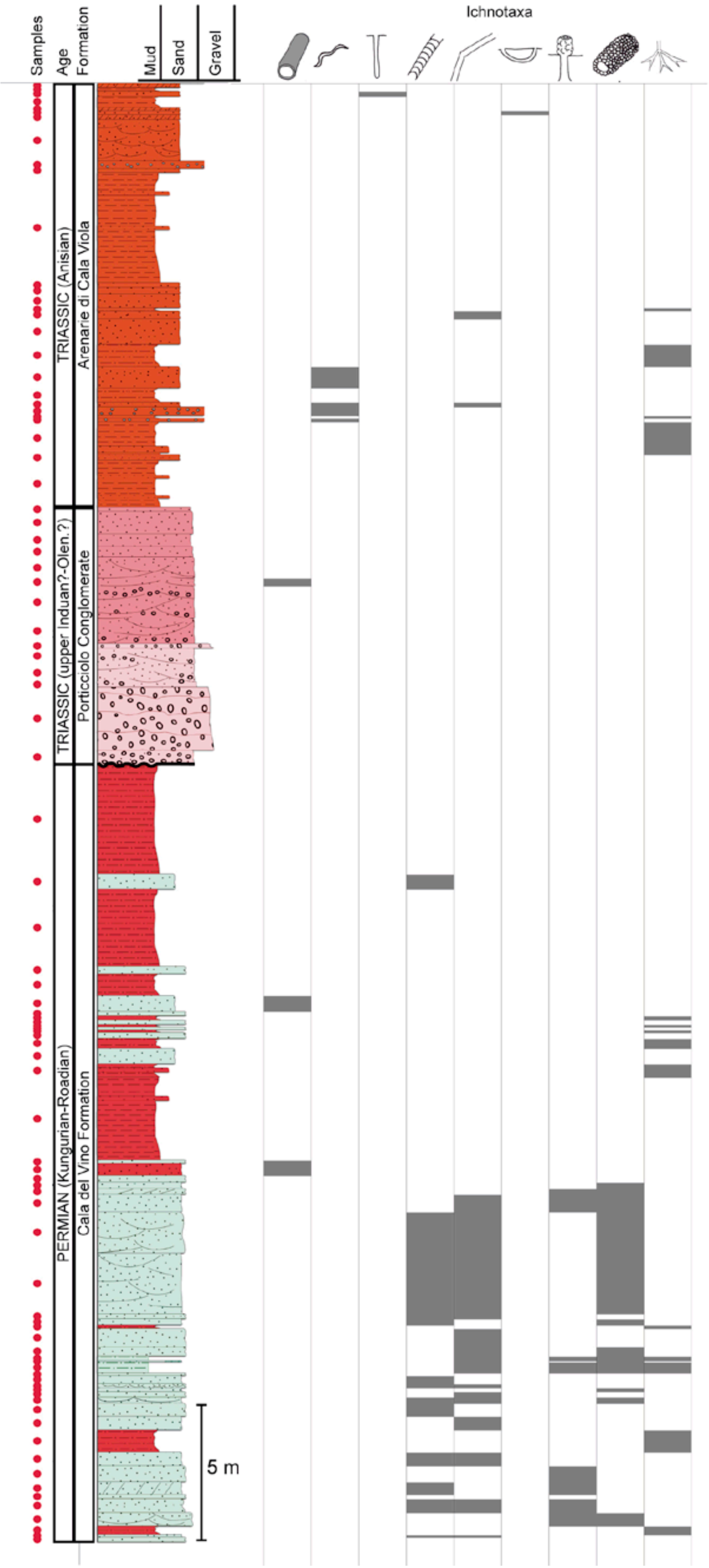
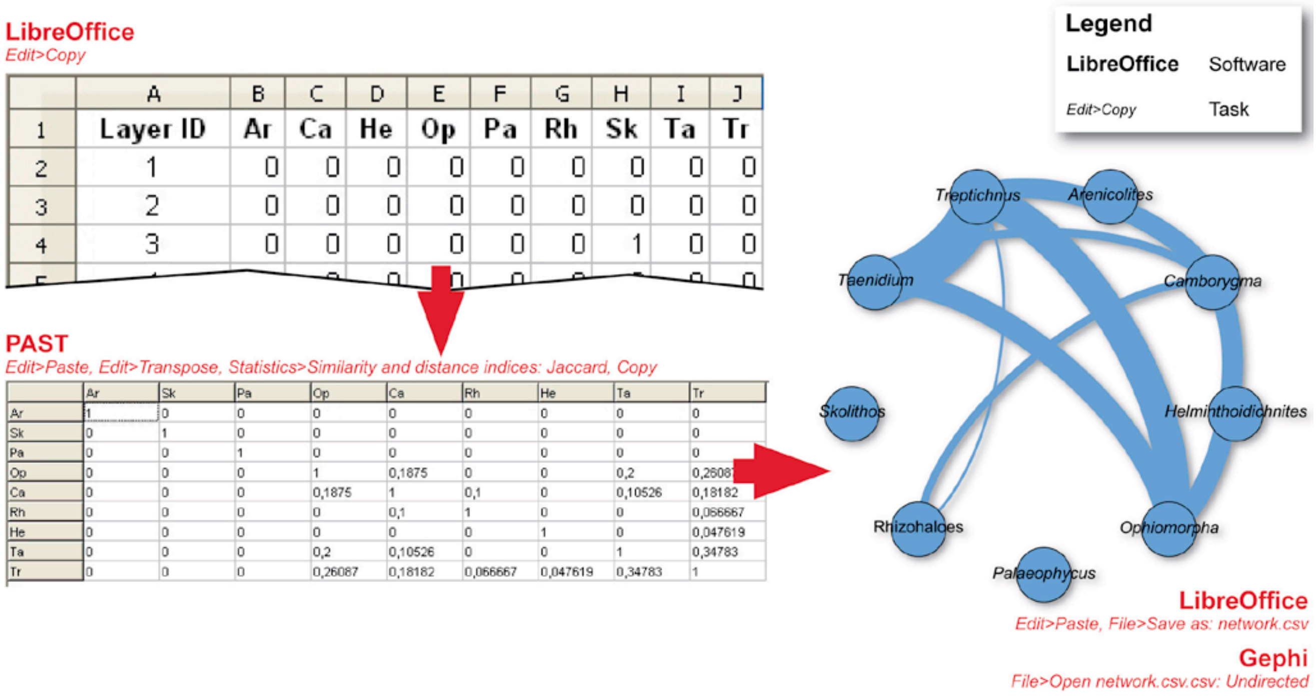

Samples
Age
Formation
Mud
Sand
Gravel
Ichnotaxa
TRIASSIC (Anisian)
Arenarie di Cala Viola
TRIASSIC (upper Induan?-Olen.?)
Porticciolo Conglomerate
PERMIAN (Kungurian-Roadian)
Cala del Vino Formation
5 m

Fig. 15.



LibreOffice
Edit>Copy

	A	B	C	D	E	F	G	H	I	J
1	Layer ID	Ar	Ca	He	Op	Pa	Rh	Sk	Ta	Tr
2	1	0	0	0	0	0	0	0	0	0
3	2	0	0	0	0	0	0	0	0	0
4	3	0	0	0	0	0	0	1	0	0

PAST
Edit>Paste, Edit>Transpose, Statistics>Similarity and distance indices: Jaccard, Copy

	Ar	Sk	Pa	Op	Ca	Rh	He	Ta	Tr
Ar	1	0	0	0	0	0	0	0	0
Sk	0	1	0	0	0	0	0	0	0
Pa	0	0	1	0	0	0	0	0	0
Op	0	0	0	1	0,1875	0	0	0,2	0,2608
Ca	0	0	0	0,1875	1	0,1	0	0,10526	0,18182
Rh	0	0	0	0	0,1	1	0	0	0,066667
He	0	0	0	0	0	0	1	0	0,047619
Ta	0	0	0	0,2	0,10526	0	0	1	0,34783
Tr	0	0	0	0,26087	0,18182	0,066667	0,047619	0,34783	1

LibreOffice
Edit>Paste, File>Save as: network.csv

Gephi
File>Open network.csv.csv: Undirected

Fig. 16.

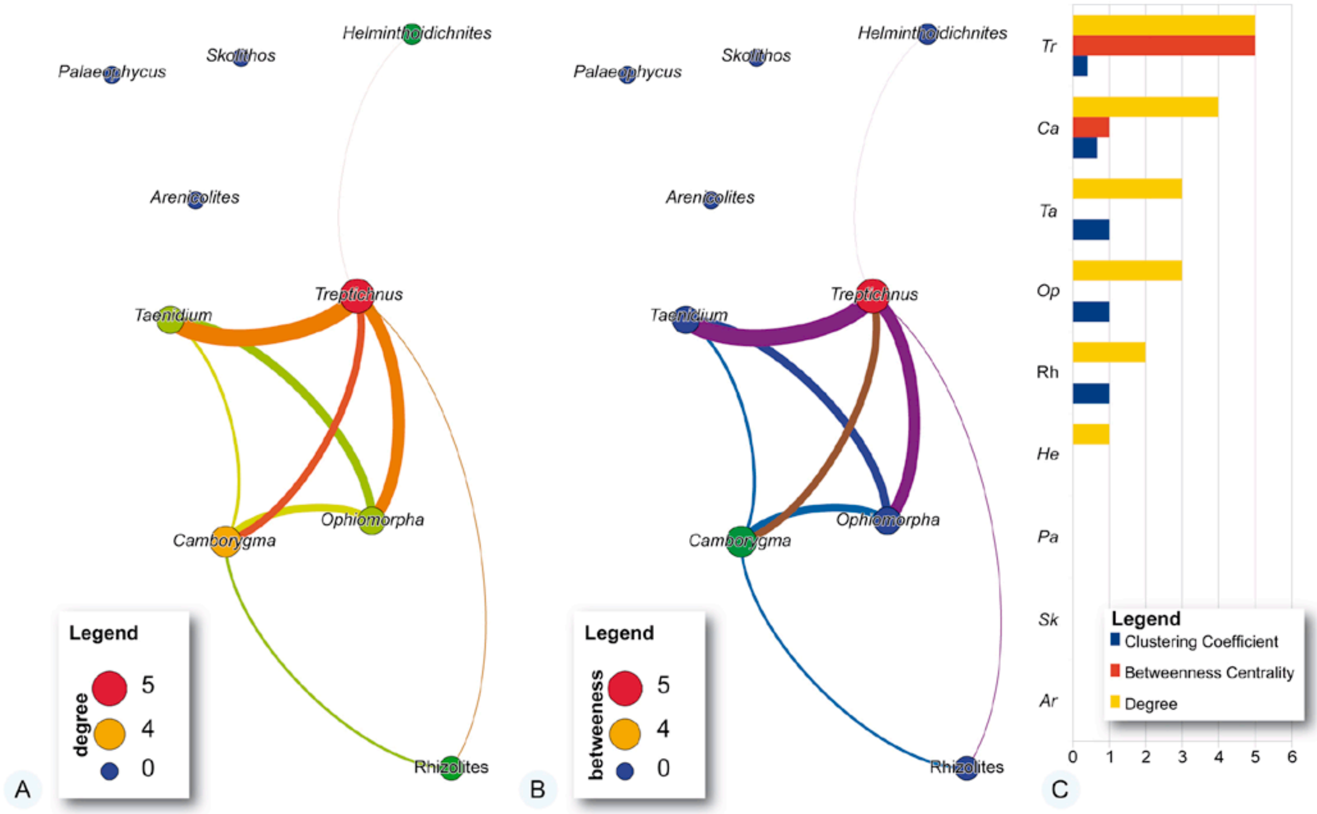

Helminthoidichnites
Skolithos
Palaeophycus
Arenicolites
Treptichnus
Taenidium
Ophiomorpha
Camborygma
Rhizolites
Legend
degree
5
4
0
A
Helminthoidichnites
Skolithos
Palaeophycus
Arenicolites
Treptichnus
Taenidium
Ophiomorpha
Camborygma
Rhizolites
Legend
betweeness
5
4
0
B
Tr
Ca
Ta
Op
Rh
He
Pa
Sk
Ar
Legend
Clustering Coefficient
Betweenness Centrality
Degree
0
1
2
3
4
5
6
C

Fig. 17.

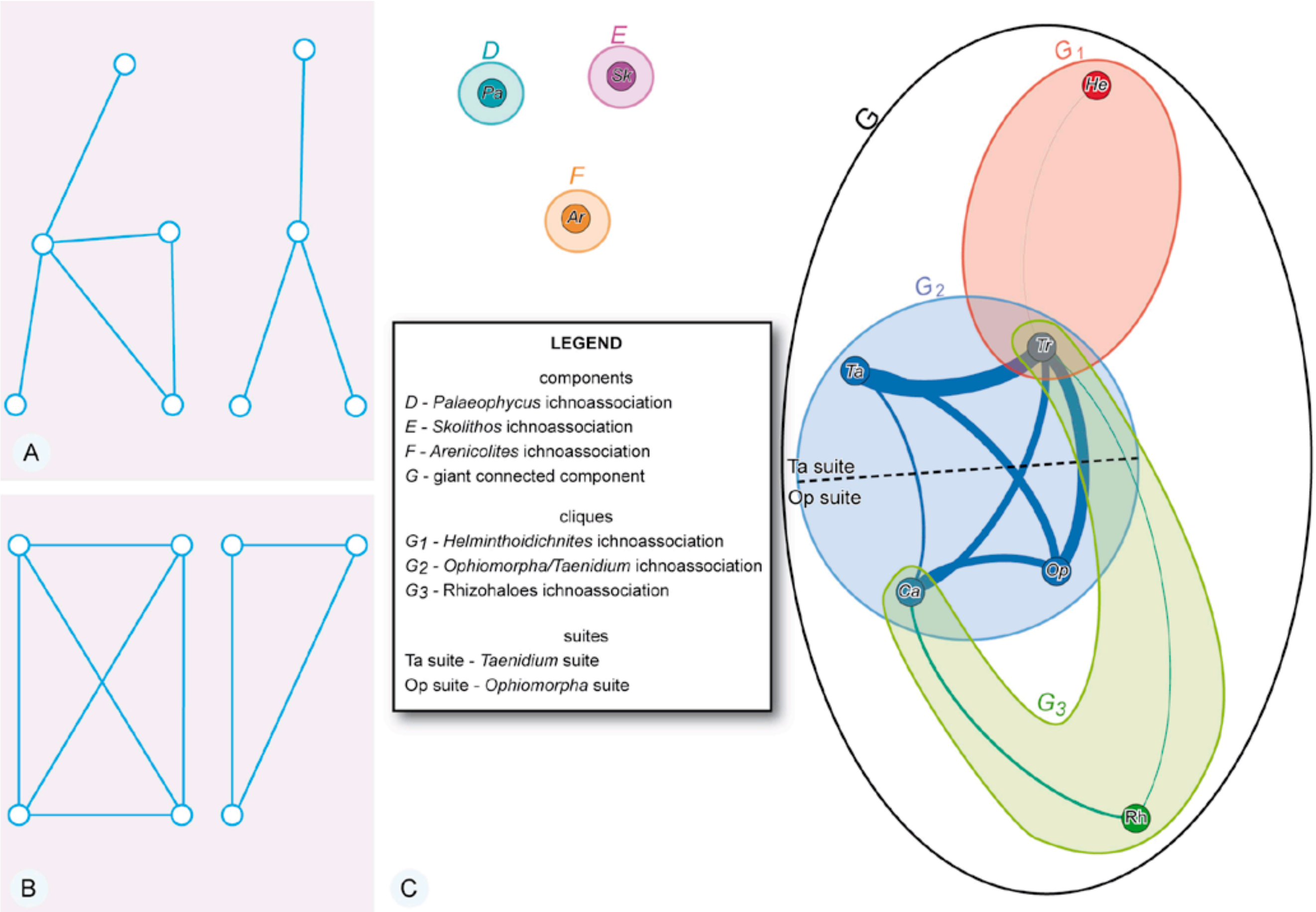

A
B
C
D
Pa
E
Sk
F
Ar
G
G1
He
G2
Tr
Ta
Op
Ca
G3
Rh
Ta suite
Op suite
LEGEND
components
D - Palaeophycus ichnoassociation
E - Skolithos ichnoassociation
F - Arenicolites ichnoassociation
G - giant connected component
cliques
G1 - Helminthoidichnites ichnoassociation
G2 - Ophiomorpha/Taenidium ichnoassociation
G3 - Rhizohaloes ichnoassociation
suites
Ta suite - Taenidium suite
Op suite - Ophiomorpha suite

Fig. 18.

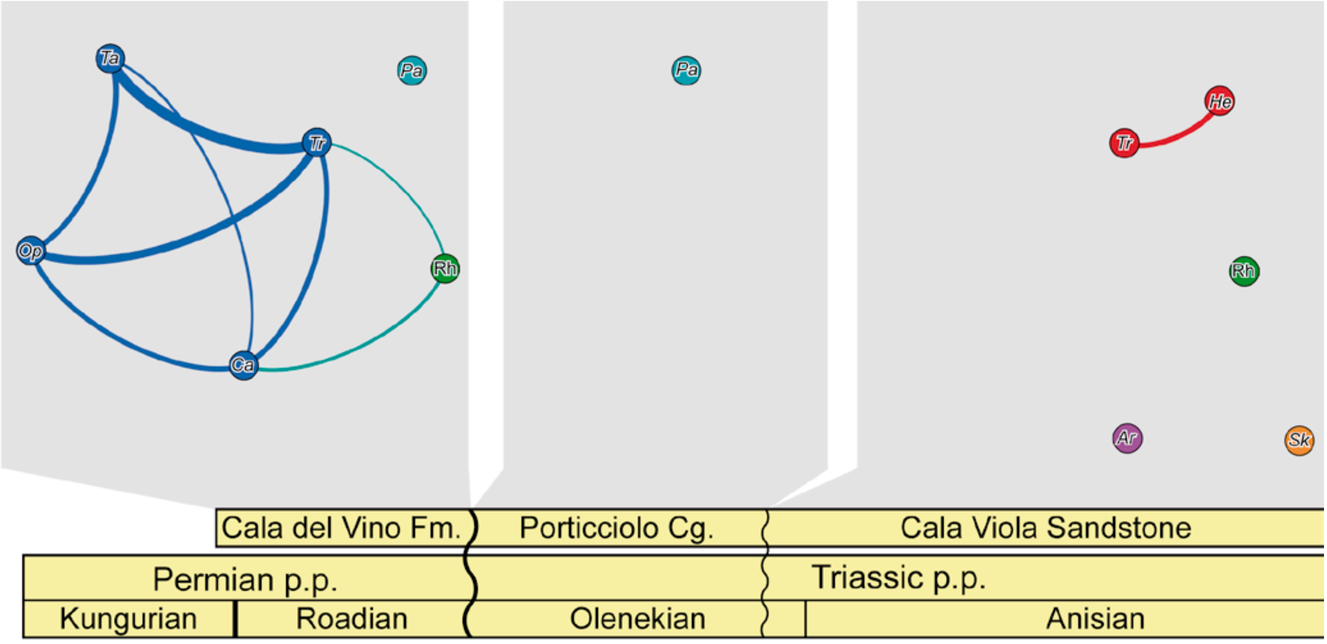

Ta
Pa
Tr
Op
Rh
Ca
Pa
He
Tr
Rh
Ar
Sk
Cala del Vino Fm.
Porticciolo Cg.
Cala Viola Sandstone
Permian p.p.
Triassic p.p.
Kungurian
Roadian
Olenekian
Anisian

Fig. 19.

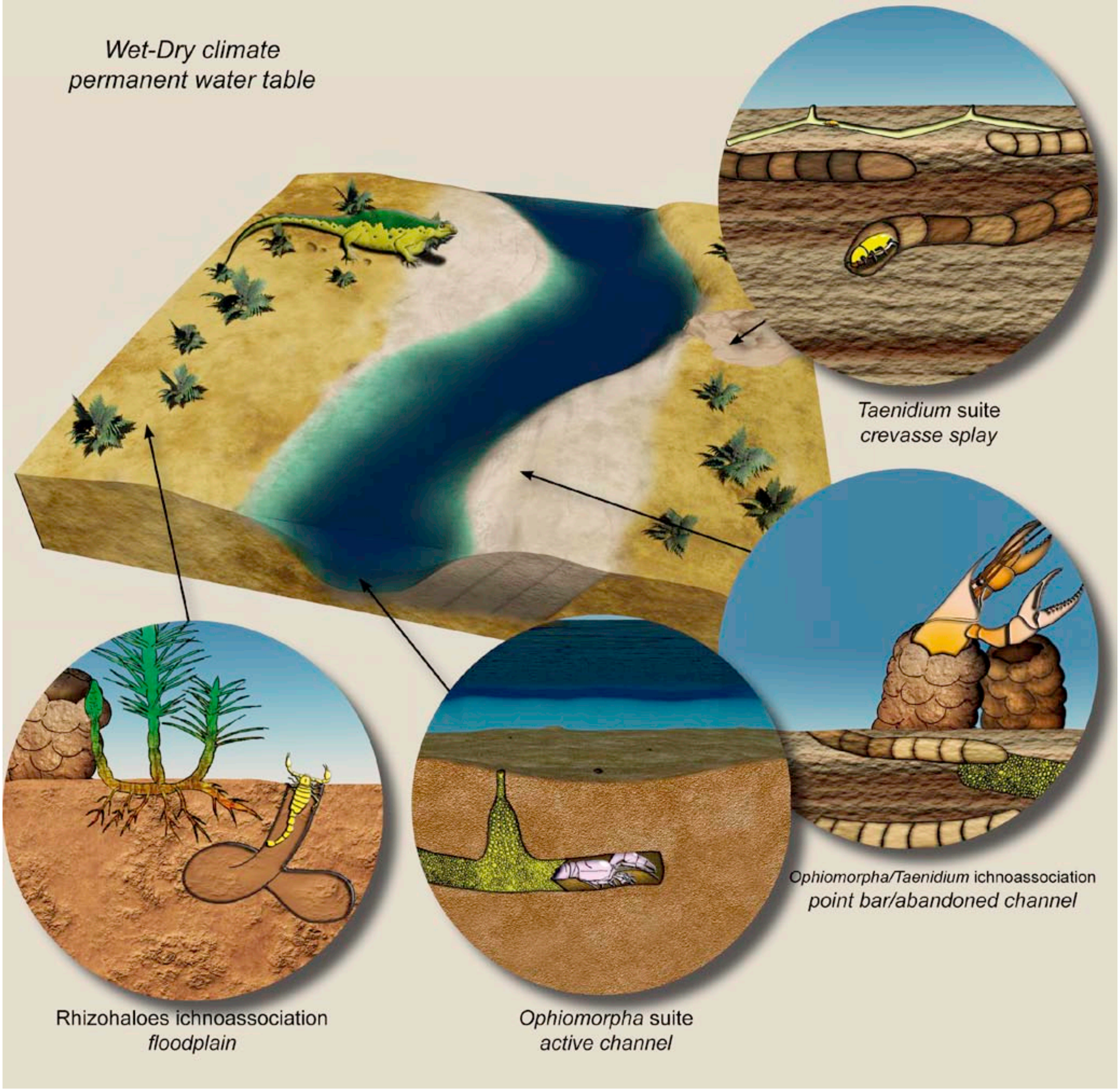

Wet-Dry climate
permanent water table
Taenidium suite
crevasse splay
Ophiomorpha/Taenidium ichnoassociation
point bar/abandoned channel
Rhizohaloes ichnoassociation
floodplain
Ophiomorpha suite
active channel

Fig. 20.

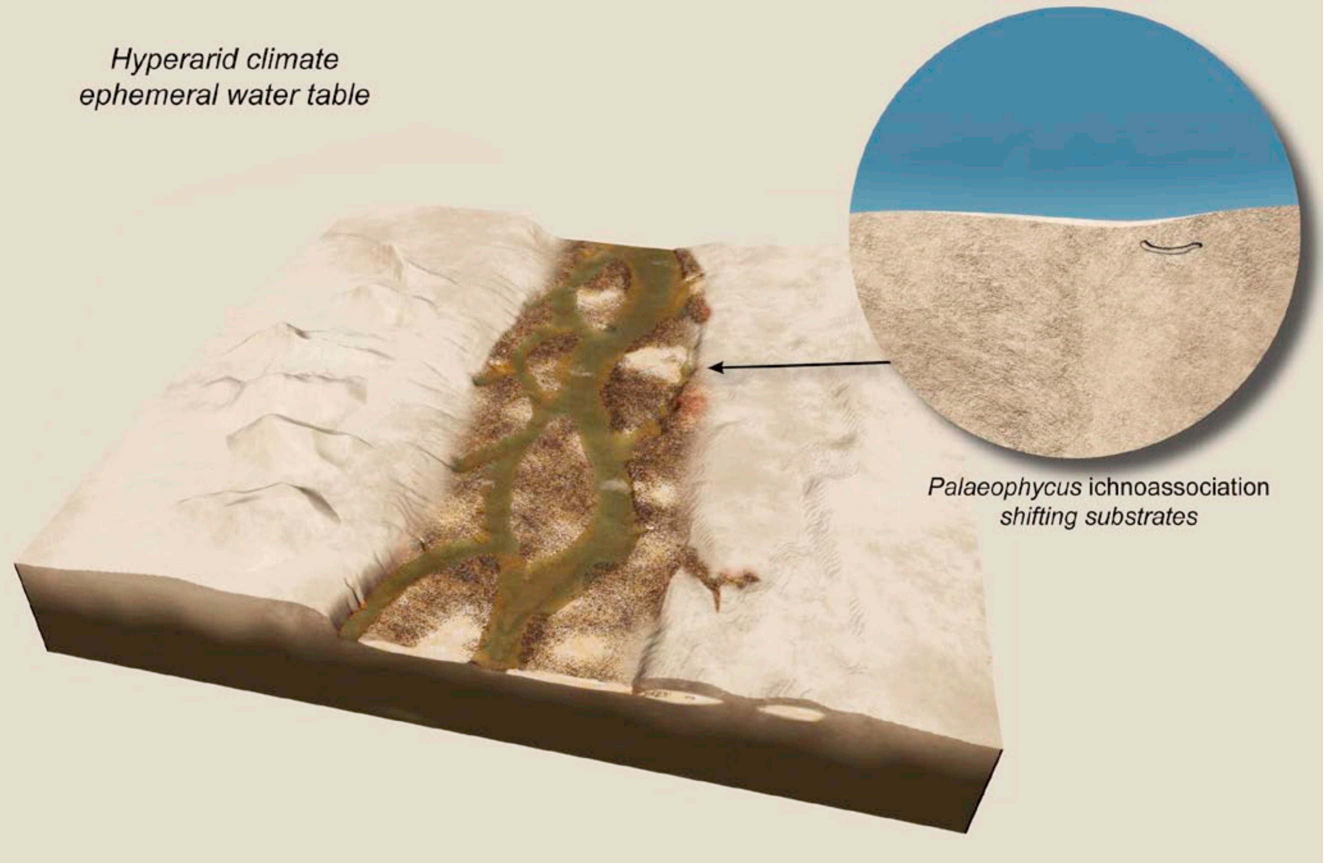

Hyperarid climate
ephemeral water table
Palaeophycus ichnoassociation
shifting substrates

Fig. 21.

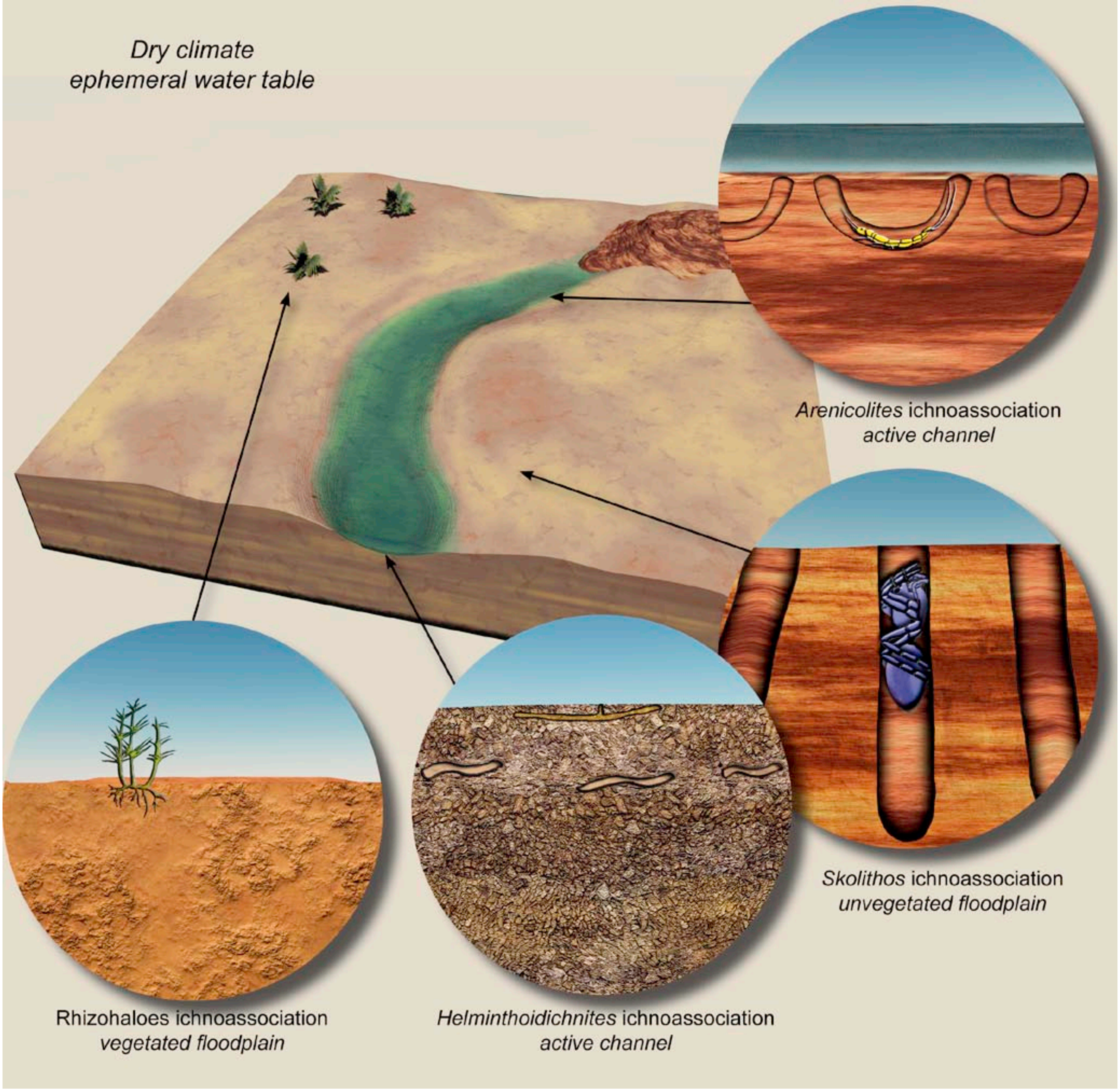

Dry climate
ephemeral water table
Arenicolites ichnoassociation
active channel
Skolithos ichnoassociation
unvegetated floodplain
Rhizohaloes ichnoassociation
vegetated floodplain
Helminthoidichnites ichnoassociation
active channel

Fig. 22.

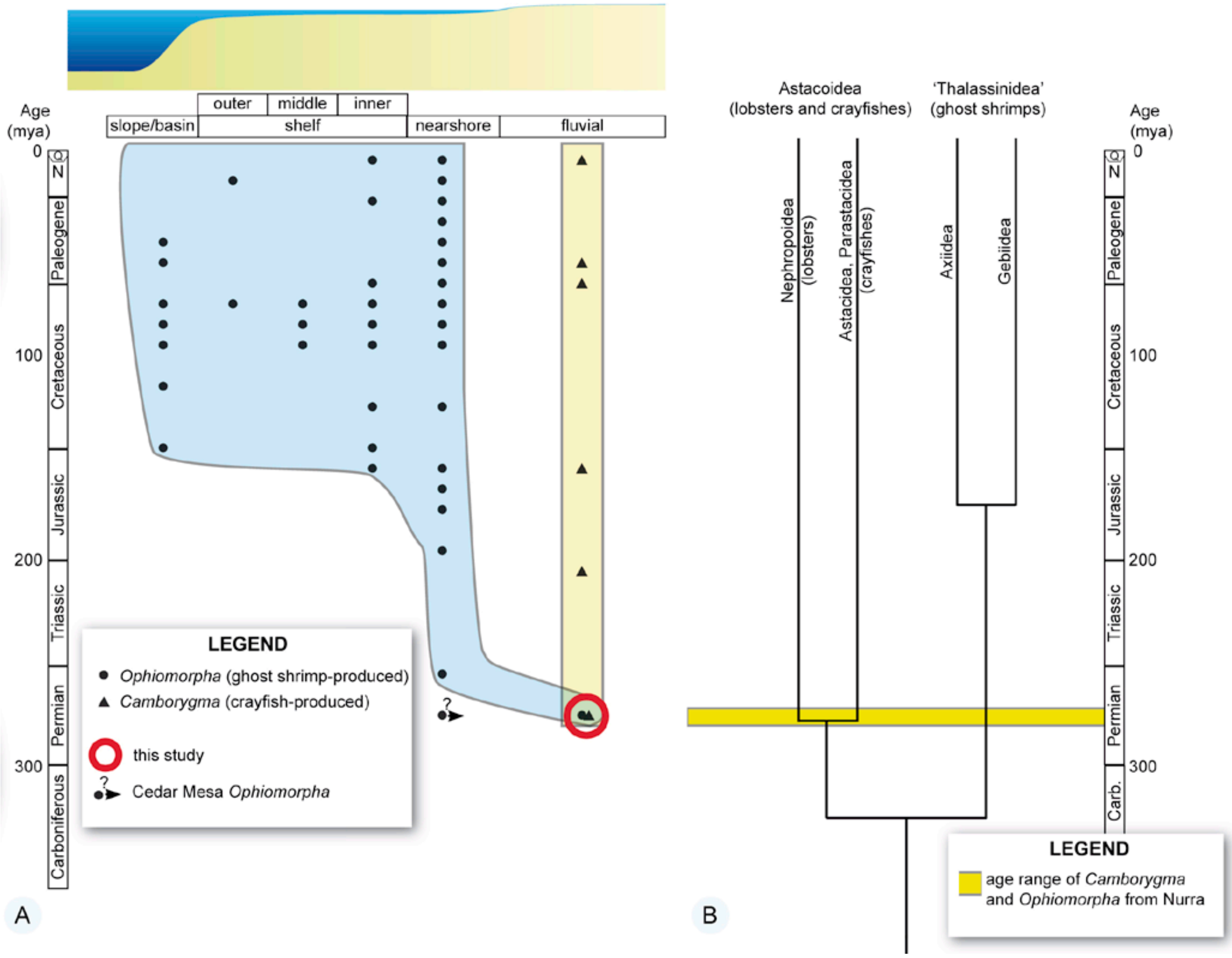

Age (mya)
0
100
200
300
Q
N
Paleogene
Cretaceous
Jurassic
Triassic
Permian
Carboniferous
outer
middle
inner
slope/basin
shelf
nearshore
fluvial
LEGEND
● Ophiomorpha (ghost shrimp-produced)
▲ Camborygma (crayfish-produced)
this study
Cedar Mesa Ophiomorpha
A
Astacoidea (lobsters and crayfishes)
'Thalassinidea' (ghost shrimps)
Nephropoidea (lobsters)
Astacidea, Parastacidea (crayfishes)
Axiidea
Gebiidea
Carb.
LEGEND
age range of Camborygma and Ophiomorpha from Nurra
B

Fig. 23.

Chapter 4

4.4 Multifractals and capacity dimension as measures of disturbance patch dynamics in *Daedalus* ichnofabrics

From: Neto de Carvalho, C., Baucon, A., 2013. Multifractals and capacity dimension as measures of disturbance patch dynamics in *Daedalus* ichnofabrics. In: Pardo-Igúzquiza, E.; Guardiola-Albert, C.; Heredia, J.; Moreno-Merino, L.; Durán, J.J.; Vargas-Guzmán, J.A. (Eds.). Mathematics of Planet Earth. Proceedings of the 15th Annual Conference of the International Association for Mathematical Geosciences. Lecture Notes in Earth System Sciences Springer, Berlin

Full paper in Appendix E

Multifractals and Capacity Dimension as measures of disturbance patch dynamics in *Daedalus* ichnofabrics

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Abstract. An ichnofabric includes all structure and textural changes of the sediment resulting from bioturbation (and bioerosion) at all scales. Abundance and distribution of burrows reflects the non-linear sorting effects of physical and biological parameters, resulting in a disturbance regime which generates patchiness. To analyze the patch dynamics of trace fossils as a result of environmental disturbance, this study quantifies bioturbation rates and spatial and temporal variation based on fractal geometry. Multifractal spectrum is used as a measure of spatial ichnofabric heterogeneities. The magnitude of the *Daedalus* ichnofabric fluctuations for the two stratigraphic sequences sampled shows that sandflat substrate colonization by the *Daedalus halli* worm producer after each storm event was opportunistic, mostly multigenerational, with an exclusive and significant occupation of emptied ecospace, for the purpose of meiofauna harvesting in clean sands.

Keywords: *Daedalus halli*; Ichnofabric analysis; fractal dimension; multifractals; opportunistic harvesting.

1 Introduction

Behavior is the set of strategically and flexible responses of any phenotype for purposes of protection and transmission of its genetic legacy. This programmed responses allow the homeostatic development necessary to an organism exert some control over its ecosystem, which is intrinsically unpredictable. The fossilized remains of biological activity or ichnofossils are, in this context, the preserved solutions for the chaotic and aperiodic ecological constraints that define the evolution of behavior. The resulted programs were developed and modified by genetic pre-adaptations and by ecological parameters originally prevailing, that may have been preserved or even changed in the geological record by diagenesis imprint and tectonics. Ichnology, the discipline of paleontology focused on organism-substrate interaction dynamics (description, classification and interpretation), is a fundamental link between the evolutionary biological mechanisms and geological processes. In fact, ichnofossils represent the functional morphology and behavior of organism producers as well as the physical-chemical properties of the substrate where they were generated [1]. As ichnofossils are fossilized snapshots of behavioral and physiological functions, they translate organism producers condition to specific ecological situations. An ichnofabric includes all sediment structure and textural changes resulting from bioturbation and bioerosion at all scales [2]. Methods have been developed to improve quantification of past and present biological sedimentary reworking. Quantifying bioturbation has been a very useful tool for supporting evolutionary theories of ecological radiation, among many other applications (see for example [3]). Descriptive or semi-quantitative methods were developed for analysis of ecospace used by benthic communities in shifting substrate environments based on bioturbation percentual indices, e.g. [3], [4], [5], [6]. Our research is based in new methods for quantifying bioturbation and ichnofabrics, based on fractal geometry, which permits, at the same time, to recognize with precision the ways in which benthic communities organize and explore their ecological niches and the ecological succession with the temporal evolution of environmental parameters. As application, we used fossil domiciliary/feeding behavior patterns classified as *Daedalus halli*, occasionally very abundant in siliciclastics deposited in sandflat subtidal marine bottoms almost 480 million years ago that are commonly present in the Floian-age Armorican Quartzite Formation from Portugal. For this study we quantified dense ichnofabrics of *Daedalus* in the sections of Serra de Barreiras Brancas [7], and Angueira valley, near Serapicos. *Daedalus* ichnofossils are burrows of a still unknown worm-shaped producer that reworked sands in the three spatial directions by the coiled, protrusive or retrusive displacement of a vertical-to-oblique J-tube [8], [9], intersecting bedding planes normal or at high-angle, and reaching 50 cm deep.

2 Fractal and Multifractal Estimation of Bioturbation Spatial and Temporal Heterogeneities

One of the primary goals in the use of fractals is that statistically descriptive methods were developed in order to better describe natural forms. In this way, the measure of fractal dimension of certain ichnofossils is of particularly interest in more quantitative approaches to ichnotaxonomy [10], [11], [12]. Meanders, spirals or branches in feeding biogenic structures are ways of food processing and foraging that increase extraordinarily the explored area in a restricted volume, as well as collecting information from environmental stimuli. Fractal dimension in the ichnological context determines the probability of sediment to be covered by the producer' behavioral activity. Capacity fractal dimension estimation is particularly useful in the study of ichnofossils with complex patterns, which occur in sedimentary bedding planes. For fractal determination it is used the Box Counting theorem as described in [10], [11]. We used the free software FRACTALYSE 2.4.1 to estimate capacity dimension of monochrome sketches (.bmp) of *Daedalus halli*. Those images are covered with a grid of side *a*, the software counting the minimal number of squares *N(a)* which includes bioturbation. Counting should be repeated M times for different *a* sizes (M>2 orders of magnitude). The absolute value of slope of the regression line adjusted to Richardson plot of *logN(a)* versus *loga* corresponds to Fractal Dimension by the relation

$$logN(a) \propto \log(const) + Dlog(^1/_a) \qquad \textbf{(1)}$$

Standard deviation of error describes the adjustment quality of regression line. Approaching to 0, *logN(a)* and *log(1/a)* both reach a very high value when compared with *log(const)*. In the limit when *a* tends to 0, it is obtained the exact definition of Hausdorff or Capacity Dimension

$$D_0 = \lim_{n \to 0} \frac{\log N(a)}{\log \left({}^{1}/_{a} \right)} \qquad \textbf{(2)}$$

Multifractal describes several processes with fractal signatures (fractals or pseudofractals) when characterized at multiple levels of information. Multifractal spectra can be used as a measure of spatial or sequential ichnofabric heterogeneities. It is based on the box counting method thus enabling quantitative analysis of ecospace occupation strategies translated for behavioral forms preserved on the bedding planes. The heterogeneity measure is given by a probability distribution which can be estimated, according to [13], as

$$P_v(a) = \frac{N_v(a)}{N} \qquad \textbf{(3)}$$

where is the number of identified bioturbations within the *v*-square grid and *N* is the total number of *Daedalus* in the digitalized image. This probability *v* fits in the equation that quantifies density distribution in [14],

$$D(q) = \log_{n \to 0} \frac{1}{q-1} \frac{\log \sum_{v=1}^{N(a)} [P_v(a)]}{\log a} \qquad \textbf{(4)}$$

where *v* identifies the square of side *a* and registers the relative weight of *v*-square as expression of the total density. Generalized fractal dimensions spectra, *D(q)*, quantify non-uniformity in ichnofossil distribution density, which is dependent of *q* momentum[13] .

3 Discussion: Evaluating Community Strategies in Space and Time for the *Daedalus* Producer

Multifractal *D(q)* anisotropies along the 40m^2 bedding plane at Martim Preto shows spatial heterogeneity (1,61±0.07≤*D(q)*≤1,89±0.14). A non-uniform distribution of ichnofossils may be consequence of intraspecific low competition for resources, which actually does not promote the regular distribution of organisms. Otherwise, discrimination of a faint clustering by multifractal analysis could be a sign of stable and favorable environmental conditions during *Daedalus* fabrication by producers' population. This patchy distribution pattern opens the possibility for a model of meiofauna harvesting to explain *Daedalus halli* architecture based on the subtidal pump mechanism of interstitial water exchange by wave action.

Recurrence of tempestitic phenomena and its persistent effects in ecological succession can be evaluated from fractal data obtained in the Serapicos stratigraphic section. We measured bed-by-bed fractal frequence of *Daedalus* for 36 bedding planes. About 75,5% of observed layers are bioturbated, with a Capacity Dimension mean value of $D_0 = 1.62 \pm 0.15$. Data shows that subtidal substrate settlement after each tempestitic event by *Daedalus* producers was intense, mostly multigenerational, with an exclusive and significant occupation of the emptied ecospace.

The presence of only one preserved behavioral strategy, the substrate depth affected by these structures, the high density of burrows and passive patchiness rates are characteristics of r-selected populations. Such large-scale and frequent disturbance events as storms, extreme on a gradient of disturbance intensities, were responsible for some of the earliest opportunistic behaviors in the fossil record. *Daedalus* was among the most resilient of them in the Early Paleozoic.

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