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From the river to the sea: Pramollo, a new ichnolagerstätte from the Carnic Alps (Carboniferous, Italy-Austria)

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SUMMARY - *From the river to the sea: Pramollo, a new ichnolagerstätte from the Carnic Alps (Carboniferous, Italy-Austria)* - Pramollo Pass and its surroundings have been celebrated since the 19th century for the outstanding palaeontological heritage preserved in the Permian-Carboniferous units, especially palaeoflora and palaeofauna. The exceptional ichnological record of the Pramollo area is – for the first time – described in this study. The ichnofauna is abundant, diverse, and exceptionally well-preserved. For these reasons, Pramollo can be erected as one of the major Palaeozoic ichnolagerstätten of the Alps. The most recurrent ichnogenera include *Parataenidium moniliformis, Dictyodora liebeana*, *Curvolithus simplex* (form 1 and 2), *Psammichnites* cf. *plummeri*, *Nereites jacksoni*, *Ancorichnus* isp., *Beaconites* isp. (form 1 and 2), *Cylindrichnus* isp., *Planolites* isp., *Helminthoidichnites*, *Skolithos* isp., *Zoophycos* isp., *Archaeonassa* isp., *Protopaleodictyon* isp., *Asterosoma* isp. (form 1 and 2) and the new ichnogenus *Pramollichnus pastae.* The trace fossil analysis has evidenced 9 recurrent ichnoassemblages, covering a wide environmental spectrum from estuarine to marine settings. Estuarine settings comprise the ichnoassemblages *Skolithos-Cylindrichnus* (estuarine point bars), *Psammichnites-Skolithos-Cylindrichnus* (lower estuarine deposits), *Zoophycos-Skolithos-Cylindrichnus* (storm-derived sand bodies), *Curvolithus*(large)-*Ancorichnus-Skolithos* (deltaic-influenced nearshore) and pyritised burrows (anoxic shallow environments). Marine environments are defined by the assemblages *Curvolithus* (small)-*Beaconites* (transition to offshore), *Zoophycos-Beaconites* (distal settings below wave influence), *Zoophycos* (lower offshore) assemblages. The *Dictyodora-Nereites* ichnoassemblage is interpreted as corresponding to deep marine settings associated to delta-front, organic-rich muds.

RIASSUNTO - *Dal fiume al mare: Pramollo, un nuovo ichnolagerstätte delle Alpi Carniche (Carbonifero, Italia-Austria)* - L'area di Passo Pramollo è celebre sin dal diciannovesimo secolo per il patrimonio paleontologico della successione permo-carbonifera. Infatti la paleoflora e la paleofauna sono state dettagliatamente studiate, mentre il record icnologico ha sinora ricevuto scarsa attenzione. Questo studio descrive – per la prima volta – il registro icnologico dell'area di Pramollo. L'icnofauna è abbondante, diversificata ed eccezionalmente ben preservata: per queste ragioni, Pramollo può essere considerato uno dei maggiori icnolagerstätten delle Alpi. Gli icnogeneri più comuni sono *Parataenidium moniliformis*, *Dictyodora liebeana, Curvolithus simplex* (forma 1 e 2), *Psammichnites* cf. *plummeri*, *Nereites jacksoni*, *Ancorichnus* isp., *Beaconites* isp. (forma 1 e 2), *Cylindrichnus* isp., *Planolites* isp., *Helminthoidichnites tenuis*, *Skolithos* isp., *Zoophycos* isp., *Archaeonassa* isp., *Protopaleodictyon* isp., *Asterosoma* isp. (forma 1 e 2) e il nuovo icnogenere *Pramollichnus pastae.* Lo studio dell'icnofauna rivela 9 icnoassociazioni ricorrenti, che corrispondono ad uno spettro paleoambientale compreso fra ambienti di estuario e marini. Gli ambienti di estuario sono caratterizzati dalle icnoassociazioni *Skolithos-Cylindrichnus* (*point bars*), *Psammichnites-Skolithos-Cylindrichnus* (zona di estuario inferiore), *Zoophycos-Skolithos-Cylindrichnus* (corpi sabbiosi legati ad eventi di tempesta), *Curvolithus* (grande)-*Ancorichnus-Skolithos* (*nearshore* con influenza fluviale) e tane piritizzate (ambienti anossici poco profondi). Gli ambienti marini sono definiti dalle icnoassociazioni *Curvolithus-Beaconites* (transizione all'*offshore*), *Zoophycos-Beaconites* (ambienti distali non influenzati dal moto ondoso), *Zoophycos* (*offshore*). L'icnoassociazione *Dictyodora-Nereites* corrisponde ad ambienti marini profondi associati a fanghi ricchi in materia organica.

Key words: Nassfeld, estuarine Ichnology, *Pramollichnus*, *Dictyodora*, *Zoophycos*
Parole chiave: Nassfeld, Icnologia di estuario, *Pramollichnus*, *Dictyodora*, *Zoophycos*

1. INTRODUCTION

1.1. Geological and geographical setting

Pramollo Pass and its surroundings are famous for the exceptional palaeontological heritage preserved in the Permian-Carboniferous stratigraphical succession. The attention to this site, known since the 19th century, has been almost exclusively given to the body-fossil record, represented either by palaeofloral or palaeofaunal assemblages.

Up to now the exceptional ichnological record of Pramollo Pass has not been studied. In fact, the Pramollo area houses an ichnolagerstätte. It is located on the Italian-Austrian borderland and pertains to the geographical domain

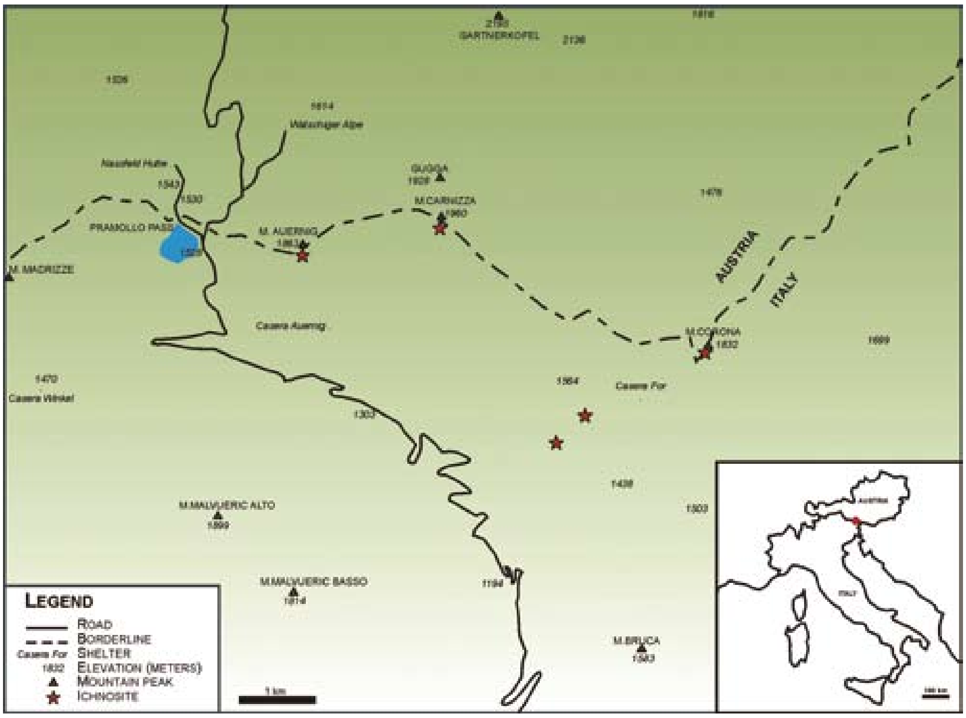

Fig. 1 - The Pramollo ichnolagerstätte: geographical setting with the main ichnosites.

Fig. 1 - L'ichnolagerstätte di Pramollo: inquadramento geografico e maggiori icnositi.

of the Carnic Alps (Fig. 1). The present preliminary research took also into account the nearby fossiliferous localities (Cason di Lanza, Italy; Straniger Alm, Austria).

The studied area exhibits mainly a Carboniferous to Permian stratigraphical succession attributed to the Pontebba Supergroup (upper Moscovian-Lower Permian; Venturini 2002), unconformably overlying the Variscan basement. In literature the Pontebba Supergroup is also called "Permocarbonifero Pontebbano" by the Italian authors (Selli 1963) or "Nassfelschichten" by Austrian ones (Heritsch 1934).

According to the nomenclature of stratigraphic units pointed out by Venturini (2002), the Pontebba Supergroup is constituted from bottom to top by the Bombaso Formation, the Pramollo Group (formerly "Auernig Group", i.e. Venturini 1990, 1991), the Rattendorf and Trogkofel Groups. This study considers in detail the ichnological record preserved within the Bombaso Formation and Pramollo Group.

The Bombaso Formation (upper Moscovian-Kasimovian; Venturini 2002) comprises conglomerates, pebbly mudstones, sandstones and shales. The palaeoenvironmental framework of the Bombaso Formation is attributed to alluvial fans and fan-deltas, but marine environments are also represented (Venturini 1990).

The petrographic analysis of the Bombaso Formation and the Pramollo Group reveals dramatic differences in terrigenous supply. The Pramollo Group exhibits high quartz content, while the Bombaso Formation is rich in radiolaritic, arenitic, volcanic and carbonatic clasts. Bombaso Formation-Pramollo Group transition is gradational; the lithic content decreases and concomitantly the amount of detrital quartz increases (Venturini 1990). The Pramollo Group is constituted by quartz-rich sandstones, conglomerates and shales (frequent in the Meledis, Corona and Carnizza Formations) with bioclastic limestone layers. The Pramollo Group is constituted by the Meledis (upper Moscovian-Kasimovian), Pizzul (Kasimovian-Gzhelian A-E), Corona (Gzhelian E), Auernig (Gzhelian E), Carnizza (Gzhelian E) Formations; the aforementioned chronological data are quoted from Venturini (2002). In some cases the Meledis and Pizzul Formations are eteropically substituted by the Bombaso Formation.

The palaeoenvironment corresponding to the Pramollo Group is generally interpreted as marginal marine: the palaeoenvironment range from fluvial-deltaic to shoreface and also includes open shelf conditions (maximum estimated depth: 40-60 m; Venturini 1991).

1.2. Palaeogeography and palaeoclimate

The deposition of the Pontebba Supergroup was significantly influenced by tectonics. According to Venturini (1983, 1990) synsedimentary faults delimited structural highs and troughs. The main troughs in which the Permian-Carboniferous sequence accumulated are respectively named as the Forni, Pramollo and Tarvisio basin (Venturini 1991). We refer to Venturini (1990, 1991) for a more detailed analysis of the Permian-Carboniferous tectonics. At present, the best exposed and preserved succession of the Pontebba Supergroup corresponds to the Pramollo basin, which is considered in the present study.

This paper focuses on the Bombaso Formation and the Pramollo Group. A palaeolatitude between 5°N and 10°S for the Carnic Alps during the Late Carboniferous was estimated by Manzoni *et al.* (1989) and Schönlaub (1992). Plant fossil assemblages representative of tropical-humid environments (Fritz & Boersma 1990) confirm the palaeoequatorial position stated by the aforementioned authors. The abundance of coal lenses in addition to the lack of arid-environment indicators imply a rainy, warm palaeoenvironment which frames properly in the above mentioned palaeoequatorial context (cf. Samankassou 2002).

1.3. *Previous ichnological studies*

The Pramollo Pass area and its surroundings have been very well-known since the 19th century for the richness of the palaeofauna (e.g. Metz 1936; Gauri 1965; Hahn & Hahn 1987; Hahn *et al.* 1989) and palaeoflora (e.g. Unger 1869; Schellwien 1892; Frech 1894; Reichardt 1937; Francavilla 1974; Fritz & Boersma 1986, 1990) included in the Permian-Carboniferous succession. In fact the palaeontological heritage of the Pramollo Group is constituted by a rich and diverse record, including corals, bryozoans, brachiopods, bivalves, cephalopods, crinoids, trilobites, arachnids, insects and an abundant well-preserved palaeoflora (cf. Venturini 2006).

While the body-fossil record is very well-documented, on the other hand the ichnological record of the Pramollo Pass area lacks of extensive research. For instance Selli (1963) cites "physiological traces" and "vermiculations" found in the Pontebba Supergroup, probably referring to trace fossils. Vai *et al.* (1979) also noted the presence of *Rhizocorallium*. Various authors refer to undetermined burrows and *Zoophycos* (Vai *et al.* 1979; Venturini *et al.* 1991) as a complement to stratigraphical analysis, but without a specific ichnological approach.

Barbiero *et al.* (1990) figured two slabs from the Auernig Formation bearing ichnofossils and proposed their identification (*Rusophycus*, a meandering trail identified as *Helmintoraphe* or *Cosmoraphe*, *Gyrochorte*, a bilobated trail identified as *Psammichnites* or *Scolicia* and an "unknown meandering trace"). Venturini (2006) illustrated and identifed some trace fossils, among which *Hylopus* cf. *hardingi*, *Zoophycos*, *?Helmintorhaphe* and "*Spiralilia elegans*".

The Karawanken Alps (Slovenia, Austria) are well-correlated with the units outcropping in the Pramollo area. Tessensohn (1968) showed a *Dictyodora* from the Karawanken Alps (the specimen is briefly discussed in Seilacher 2007). This specimen is referred to Carboniferous units, possibly correlative to the stratigraphical sequence of the Pramollo area. Tessensohn (1968) referred to other trace fossils from the Pontebba Supergroup in the Austrian sector. As regards the Slovenian Karawanken Alps, Novak (2007) briefly identified trace fossils from the Pramollo and Rattendorf Groups.

The above-mentioned studies do not present a specific ichnological approach, while the main works dealing with trace fossils of the Pontebba Supergroup concern limuloid tracks. In fact Conti *et al.* (1990, 1991) describes in detail some slabs with *Kouphichnium* from the surroundings of the study area.

2. TRACE FOSSILS OF THE ICHNOLAGERSTÄTTE

2.1. *Introduction*

The area rich in ichnofossils is geographically and geologically continuous and well-delimited. It corresponds to the central core of the Pramollo Basin which is comprised among Mt. Corona, Mt. Madrizze, Gartnerkofel and Mt. Bruca (Fig. 2). Several elements establish Pramollo as an ichnolagerstätte (trace fossil-lagerstätte of Mángano & Buatois 1995; ichnofossil-lagerstätte of Savrda 2007; Tab. 1). In fact the study area presents an extraordinary quality and quantity of ichnological information. The Pramollo ichnofauna provides outstanding materials for studying the taxonomy, ecology and taphonomy of several ichnotaxa. More in detail, the fine preservation of the traces defines Pramollo as a conservation-ichnolagerstätte (*sensu* Savrda 2007). This point is confirmed by the notable preservation of traces from shallow tiers. The ichnofauna is associated to an exceptional body-fossil record and to an outstanding sedimentary geology (Venturini 1990, 1991, 2006). These features and the abundance, diversity and preservation of trace fossils make Pramollo an ideal site to understand the Ichnology of fluvio-marine systems. The mentioned "ornamental features" (Tab. 1) nourish the importance of the ichnolagerstätte, which belongs to the major ichnological sites of the Alps.

Each ichnospecies is addressed with respect to its morphology, stratigraphical occurrence, proposed behavioural and palaeoenvironmental interpretation. Sedimentological features are briefly considered, as the sedimentary framework is used to complement the environmental analysis. The major sedimentary facies are summed up in the table 2. The reader is addressed to Venturini (1990, 1991) for a detailed sedimentological and stratigraphical analysis of the Pramollo Basin.

Ichnogenera are organized into morphological groups only for reader convenience; no genetic or interpretative purpose is intended. The morphological groups are based on Książkiewicz (1977) classification which the "meniscate" group has been added to.

2.2. *Meniscate structures*

Ancorichnus Heinberg, 1974

Diagnosis. Cylindrical, weakly sinuous, horizontal (or gently inclined) burrow characterized by a central meniscate fill and a structured mantle (after Keighley & Pickerill 1994).

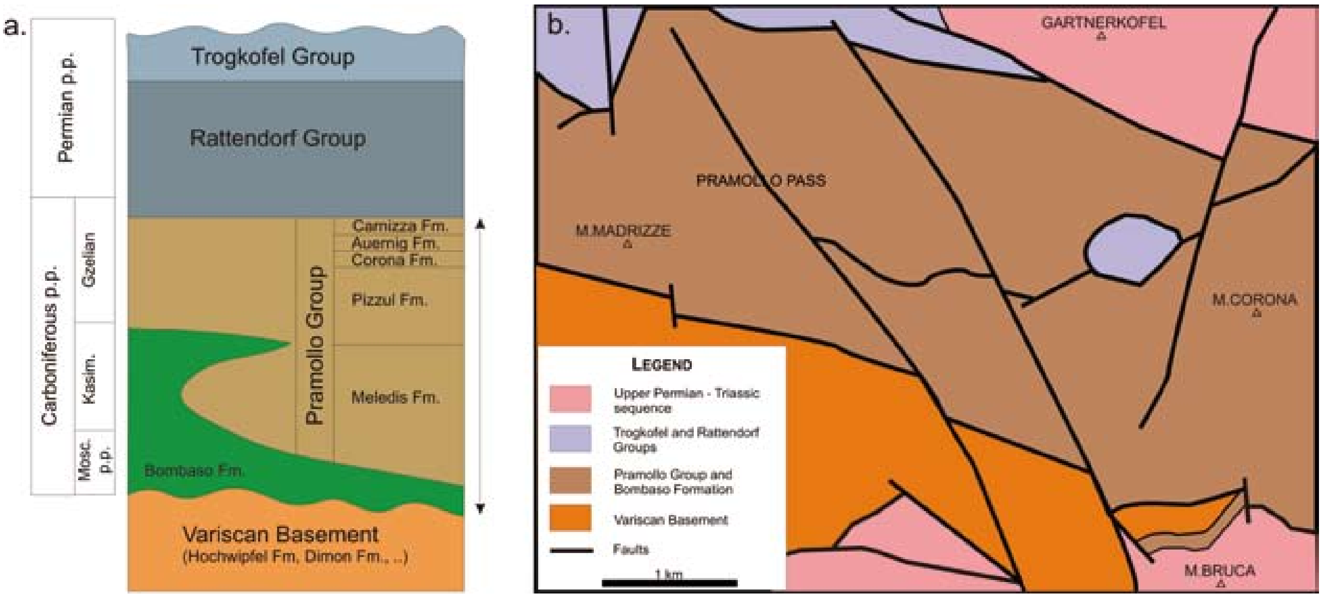

Fig. 2 - Stratigraphical scheme (a) and geological framework (b) of the Pramollo area (based on Venturini 2002). Arrows show the studied units.

Fig. 2 - Schema stratigrafico (a) e geologico (b) dell'area di Pramollo (basato su Venturini 2002). Le frecce mostrano le unità studiate.

Tab. 1 - Major features of the Pramollo Geosite.

Tab. 1 - Caratteristiche salienti del Geosito di Pramollo.

1. Ichnological features of the Pramollo Geosite		Comments
Geographical features	Spatial features	the area rich in ichnofossils is geographically and geologically continuous and well-delimited.
	Location of selected ichnosites	the whole area exhibits an important ichnological record; some sites (Fig. 1) are noteworthy for ichnodiversity and exposure: Mt. Auernig N46 33.494; E13 17.201 Mt. Carnizza N46 33.585; E13 17.926 Mt. Corona N46 33.127; E13 19.309 Section S of Casera For (1) N46 32.773; E13 18.520 Section S of Casera For (2) N46 32.971; E13 18.701
Crucial features	Abundant ichnofauna	the studied area is remarkably rich in trace fossils
	Diverse ichnofauna	Pramollo is characterized by a noteworthy ichnodiversity
	Well-preserved ichnofauna	the trace fossils from Pramollo usually exhibit detailed morphological features, as a consequence of the good status of preservation
	Exceptional palaeontological information	the Pramollo ichnofauna provides outstanding materials for studies on the taxonomy, ecology, taphonomy and environmental setting of several ichnotaxa
Ornamental features	Estuarine- to deep-marine setting	the ichnological record covers a wide environmental spectrum, ranging from estuarine to deep-marine conditions
	Interaction with the body-fossil record	the ichnological record is accompanied by an abundant paleofaunal and paleofloral heritage
	Geological heritage	the ichnofauna is associated to an impressive geological heritage in the fields of sedimentology, stratigraphy and basin analysis

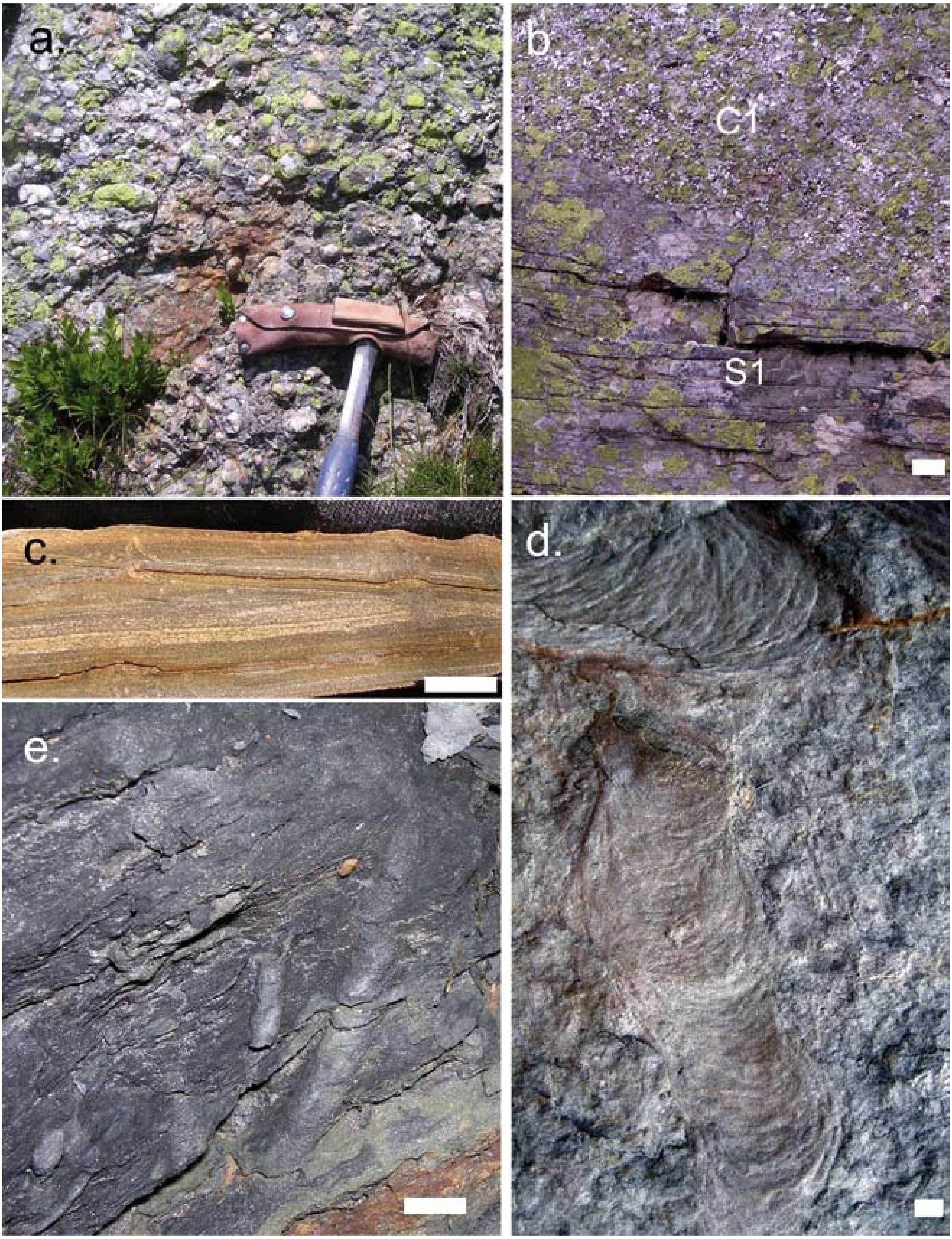

Fig. 3 - Sedimentary features of the studied area. a. Conglomeratic facies, hammer as scale (facies C1). b. Erosive contact between conglomerates (facies C1) and laminated sandstones (facies S1). Scale bar 10 cm. c. Laminated sandstone (facies S1), polished slab. Scale bar 1 cm. d. Micaceous sandstones with *Zoophycos* (facies S3). Scale bar 1 cm. e. Bioturbated sandstone rich in organic material (facies S4).
Fig. 3 - Caratteristiche sedimentarie dell'aera studiata. a. Facies conglomeratica, martello come scala (facies C1). b. Contatto erosivo tra un'unità conglomeratica (facies C1) e una arenitica (facies S1). Scala 10 cm. c. Arenaria laminata (facies C1). Scala 1 cm. d. Arenaria micacea con Zoophycos *(facies S3). Scala 1 cm. e. Arenaria bioturbata ricca in materiale organico (facies S4).*

Ancorichnus isp.

Description. Horizontal, unbranched, winding cylindrical full relief burrow having gentle annulations on the surface (Fig. 4). Weathered specimens may exhibit a meniscate core.
The traces appear clearly structured when examining polished slabs, with an outer layer (up to 0.3 mm) and an inner meniscate core. Spacing between successive menisci is about 0.4-0.6 cm. The outer layer is slightly darker than the rusty-coloured core, and sometimes it is associated with mica flakes.

Occurrence. Pramollo Group, facies S1 and S2. Well-preserved specimens are reported from the Corona Formation; *Ancorichnus* is also present in the Meledis, Pizzul and Auernig Formations.

Remarks. The presence of a mantle distinguishes *Ancorichnus* from morphologically similar ichnogenera such as *Beaconites*. According to Keighley & Pickerill (1994), a mantle is not an insulation against external environment and it does not represent an ease for the passage through the substrate as it happens for a wall. In fact mantle is the locomotory evidence of such passage.
The outer part of the studied specimens is more consistent with a mantle. In fact the annulations on the outer surface possibly correspond to locomotory behaviour and clear evidences of applied lining are lacking. Nevertheless, determining whe-

Tab. 2 - Schematic list of the most recurrent sedimentary facies occurring in the Pramollo ichnolagerstätte. Pramollo Group is characterized by a cyclical facies organization (Massari & Venturini 1990) which is expressed by pelitic and sandstone layers in alternation with thick conglomerate and limestone beds.

Tab. 2 - Lista schematica delle facies ricorrenti nell'ichnolagerstätte di Pramollo. Il Gruppo di Pramollo è caratterizzato da un'organizzazione ciclica di facies (Massari & Venturini 1990), espressa da livelli pelitici e arenitici alternati con spessi banchi conglomeratici o carbonatici.

	Facies code	Description
Sandstone facies	S1	fine- to medium-grained sandstones presenting planar, trough or cross-bedding. Light brown colour, vegetal and skeletal remains usually rare. This facies is organized in plurimetric bodies where bedding is centimetric to decimetric (Fig. 3C, 3B).
	S2	fine- to medium-grained sandstones in decimetric layers, usually interbedded in pelitic sequences. Bioclastic horizons are frequent (mainly brachiopods and crinoids), as well as planar- or hummocky- cross-lamination. Sedimentary evidences are probably indicative of storm-deposition (Fig. 19).
	S3	micaceous sandstones organized in thick (meter-scale), massive units. Rare vegetal fragments. Grey-brown to greenish colour; fine- to medium-grained (Fig. 3D).
	S4	dark-coloured, medium- to coarse-grained sandstones. Coal lenses and/or thin pelitic layers are frequently overlying the coarser lithotypes. Vegetal fragments abundant (Fig. 3E).
	S5	medium- to coarse-grained sandstones organized in metrical, massive layers. The sandstones are rusty-brown coloured, at times associated with thin bioclastic horizons.
Pelitic facies	P1	siltstones and sandy siltstones locally rich in marine body fossils (trilobites, brachiopods, gastropods) and pyrite. This facies occurs in thick (meter-scale) units where occasionally sandstone layers (corresponding to facies S2; thickness: 10-30 cm) are found.
	P2	siltstones, frequently rich in well-preserved plant remains; Massari & Venturini (1990) inferred alluvial-plain to deltaic settings for this facies.
	P3	dark, fissile shales, often presenting planar lamination; thin, coarser horizons (turbidites?) are occasionally interbedded. This facies occurs in thick units decimetrically bedded (Fig. 23).
Conglomeratic facies	C1	The most widespread conglomeratic facies consist of medium- to coarse grained conglomerates, often organized in plurimetric units with erosive base; channel bodies are frequently reported. Novak (2007) and Massari & Venturini (1990) refer these deposits to fluvial-deltaic and coastal depositional settings (Fig. 3A).
Limestone facies	L1	The most represented limestone facies is represented by algal wackestone-packstones; the commonest bioclasts include fusulinids, brachiopods, gastropods, echinoderms and bryozoans. Novak (2007) and Massari & Venturini (1990) refer similar facies to open marine settings.

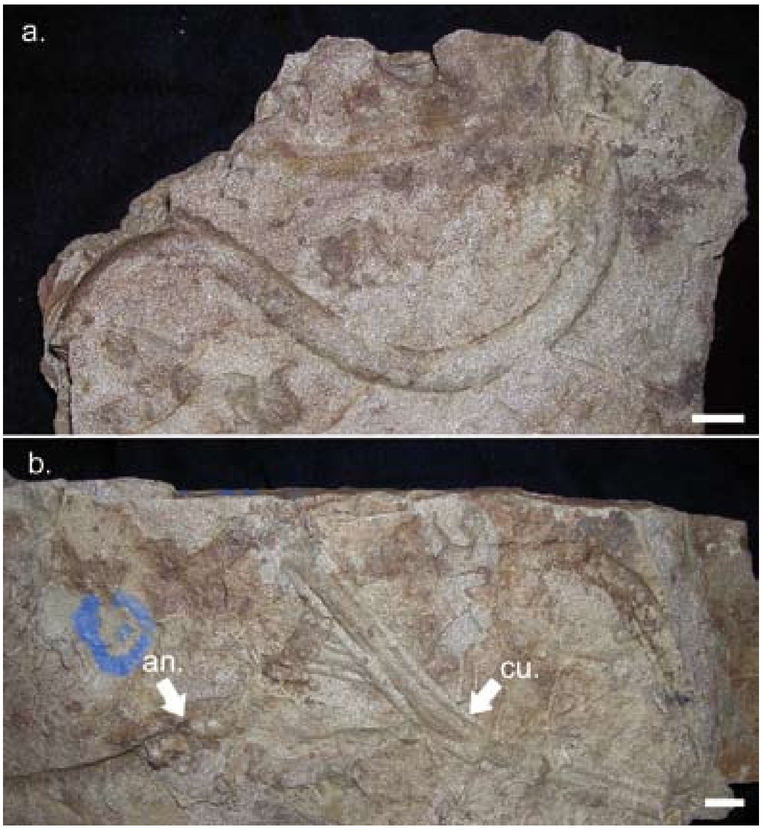

Fig. 4 - *Ancorichnus* from Monte Corona, type locality of the Corona Formation; scale bar 1 cm. a. Sole bed with *Ancorichnus.* The specimen shows gentle annulations; menisci are evident only in polished sections or in weathered specimens. b. *Ancorichnus* (an) and *Curvolithus* (cu) on the top of a bedding plane.
Fig. 4 - Ancorichnus *dal Monte Corona, località tipo della formazione omonima. Scala 1 cm. a. Esemplare di* Ancorichnus *che mostra delicate annulazioni superficiali; i menischi sono osservabili solo in sezione lucida o in campioni attaccati dagli agenti atmosferici. b.* Ancorichnus *(an) e* Curvolithus *(cu) su una superficie di strato.*

ther a structure is a mantle or a wall is problematic. Consequently further studies are required to confirm the taxonomic status of the here considered burrows.
Ancorichnus has been documented from inner shelf environments (Keighley & Pickerill 1994).

Beaconites Vialov, 1962

Diagnosis. Cylindrical, unbranched, walled meniscate burrow. Weakly to strongly arcuate meniscate packets enclosed by distinct, smooth and unornamented burrow lining. Straight or sinuous, horizontal or more rarely inclined or vertical burrow (after Keighley and Pickerill 1994).

Beaconites isp.

Description. Lined, horizontal or slightly oblique meniscated trace preserved as full-relief; true branching do not occur, but overcrossings are common (Fig. 5). Menisci present a micaceous, light-coloured fill, while the lining is markedly darker. Adjacent menisci are separated by thin arcuate segments of sediment, texturally analogous to the lining. Two forms are recognized:

1. Large forms are 1.2-1.7 cm wide; distance betwe en successive menisci is 0.3-0.7 cm.
2. Small forms are 0.5-1 cm wide; distance between successive dark menisci is 0.2-0.3 cm.

Normally large forms are not associated with small forms.

Occurrence. Beaconites is found within the Meledis, Pizzul and Auernig Formations. Possibly, it also occurs in the Bombaso Formation. Beaconites is mostly associated with dark-coloured, fine- to medium-grained sandstones (facies S3).

Remarks. The taxonomic status of various meniscate trace fossils is disputed by several authors, such as D'Alessandro & Bromley (1987), D'Alessandro *et al.* (1987), Keighley & Pickerill (1994), and Goldring & Pollard (1996); in this paper we follow Keighley & Pickerill (1994).
In their ichnotaxonomic discussion about meniscate traces Keighley & Pickerill (1994) distinguish *Taenidium* as "simple, unwalled, meniscate, backfilled structure" and *Beaconites* as "simple meniscate structure with a distinct but unornamented and unstructured wall".
Ancorichnus is identified as a trace with meniscate core and structured mantle. The studied specimens show clear affinities with *Beaconites*.
This ichnogenus has been reported from non-marine environments (lacustrine, fluvial), but it also occurs in intertidal and shelf environments (Keighley & Pickerill 1994).

Ichnogenus *Parataenidium* Buckman 2001

Diagnosis. Horizontal to sub-horizontal trace fossil, which is composed of short, commonly densely packed and imbricate protrusions running up from a common, smooth basal cylinder. In horizontal section, the topmost part of some specimens gives an impression of a meniscate filling (after Buckman 2001; Uchman & Gaździcki 2006).

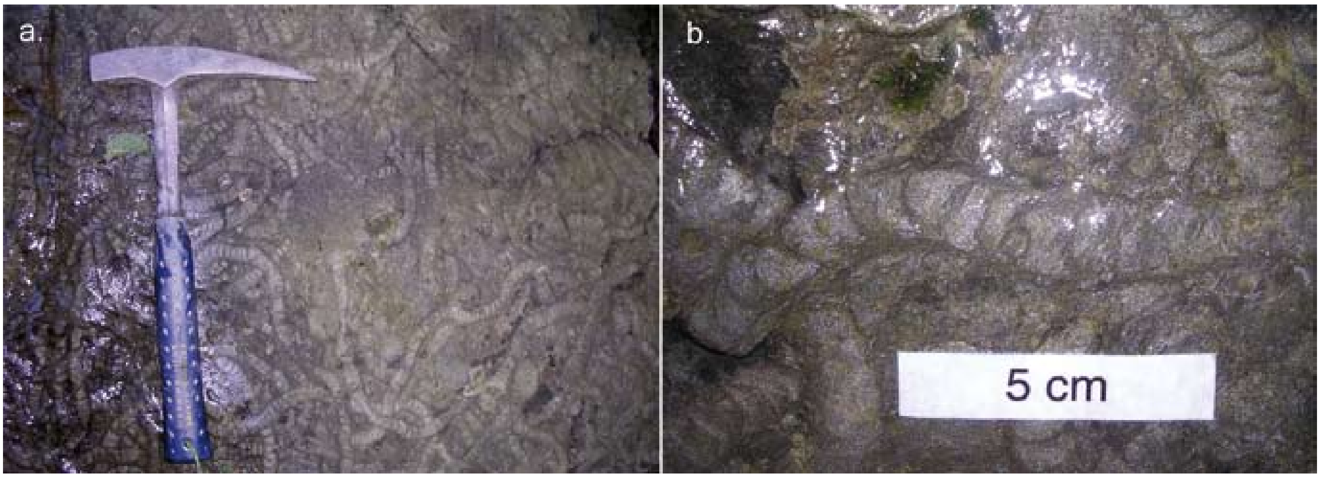

Fig. 5 - *Beaconites* from the Pramollo ichnolagerstätte. a Image of a bed intensely bioturbated by *Beaconites.* See hammer for scale. b Close-up of the bed mentioned in a.

Fig. 5 - Beaconites *dall'ichnolagerstätte di Pramollo. a. Strato intensamente bioturbato da Beaconites. Martello come scala. b. Particolare di a.*

Parataenidium moniliformis Buckman, 2001

Description. Unlined meniscate full-relief burrow presenting two levels: the upper one is constituted by bulbous, bullet-shaped, regularly arranged bulges (menisci); the lower one is almost smooth, seemingly lacking any evident structure (Fig. 6). When examining the structures in polished slabs, the burrow fill appears markedly darker than the host rock. The upper and the lower level do not exhibit textural differences. In some specimens, a very weak chromatic contrast between the two levels is inferred. True branching is absent, while crossovers and interpenetrations are found.

These structures are usually between 0.8 - 1.5 cm wide, while the distance between successive menisci ranges between 1.2 and 1.5 cm. Upper and lower level has similar vertical extent, ranging between 0.7-1 cm.

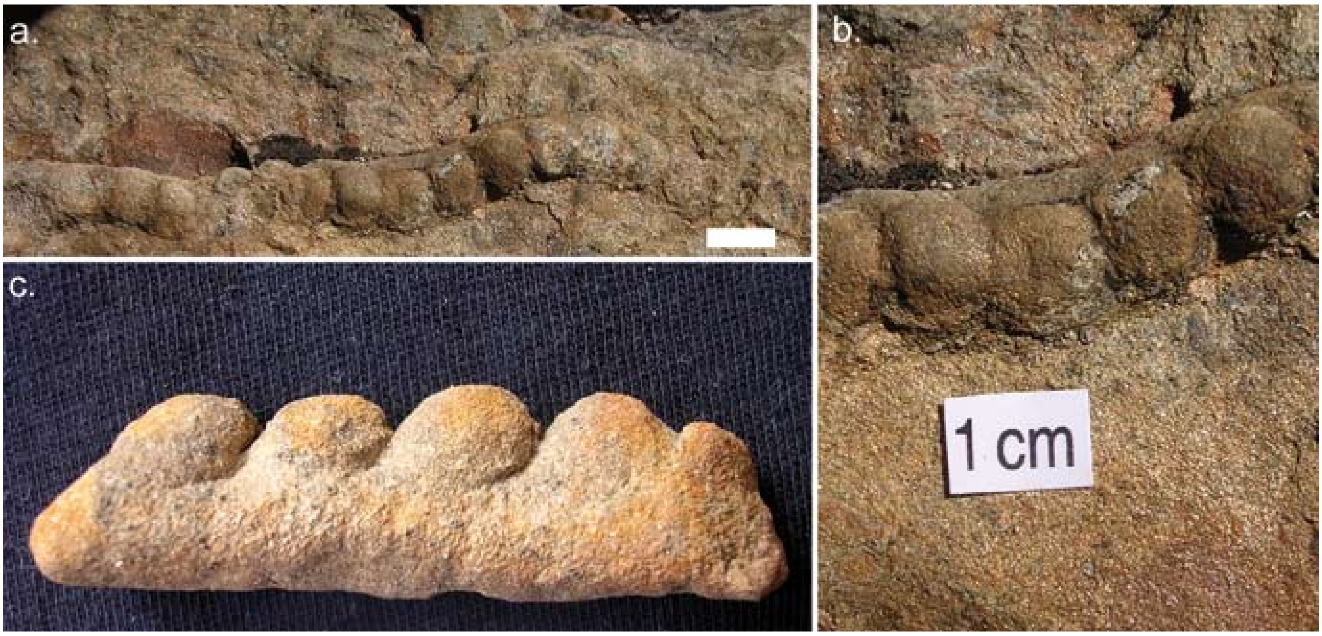

Fig. 6 - *Parataenidium moliniformis* from Monte Carnizza (Auernig Formation). Scale bar 1 cm. a. *Parataenidium moliniformis* seen from top view. b. Detail of the specimen shown in a, with the upper level (constituted by bulbous, bullet-shaped bulges) of the trace fossil. The lower level, represented by a string of structureless sediment, is partly visible. c. Lateral view of *Parataenidium*. The upper meniscate level is clearly distinguishable from the lower massive one.

Fig. 6 - Esemplari di Parataenidium moliniformis *provenienti dal Monte Carnizza (Formazione dell'Auernig). Scala 1 cm. a. Esemplare* di Parataenidium moliniformis *visto in piano. b. Dettaglio di a: si osserva chiaramente il livello superiore della struttura (costituito da protuberanze bulbose, a forma di proiettile), mentre quello inferiore è parzialmente visibile. c. Vista laterale di* Parataenidium. *Il livello superiore, meniscato, si distingue chiaramente da quello inferiore.*

Occurrence. Pramollo Group, facies S1. *Parataenidium* also occurs within facies S5 in oligospecific ichnoassociations. The best specimens of *Parataenidium* are coming from the Auernig Formation.

Remarks. Because in the most of the cases only the upper meniscate level is visible on the bedding plane, the discussed trace seemingly resembles a *Taenidium*-like structure (e.g. *Taenidium*, *Beaconites*). On the contrary, when it is possible to analyze the whole burrows (characterized by the diagnostic upper meniscate level and the lower structureless one) it seems convenient to include these traces in the ichnospecies *Parataenidium moniliformis* (see Buckman 2001).

The lack of textural differences between upper and lower level of the traces do not fully correspond to the description of Buckman (2001). He interpreted the lower level of the trace as being of locomotory origin, while the upper meniscate level is interpreted as produced by feeding.

The ichnogenus is usually reported in shallow-marine deposits (cf. Uchman & Gaździcki 2006); normally *Parataenidium moniliformis* occurs above fair-weather wave-base (Buckman 2001).

2.3. Simple structures

Ichnogenus *Cylindrichnus* Toots in Howard 1966

Diagnosis. Vertical to horizontal structure, constituted by a central core and an exterior wall concentrically laminated. Circular to elliptical in cross-section (Häntzschel 1975).

Cylindrichnus isp.

Description. Vertical or inclined unbranched burrows, circular or elliptical on bedding plane; lining concentrically laminated and surrounding a central core representing the burrow fill. The fill frequently differs from the host rock, but not necessarily the difference of texture is markedly manifest. The fill often consists of material chromatically contrasting with the host rock, or it is constituted by coarser material than the host rock.

In longitudinal sections, the burrows are generally cylindrical with a rounded lower side. In other cases they are amphora-shaped or they exhibit a gently arcuate shape, then the diameter decreases towards the lower part.

The burrow diameters on the bedding plane usually range between 0.3 and 0.8 cm, infrequently larger specimens may occur. It must be pointed out that the measured diameters indicate the width of random cross-sections, not necessarily the maximum diameters of the traces.

Occurrence. Pramollo Group, facies S1 and S2. The best specimens are found within the Auernig and Corona Formations.

Interpretation. The difficulty to distinguish the diagnostic concentrically laminated lining implies the potential confusion with the ichnogenus *Skolithos.* Vertical or steeply inclined forms of *Cylindrichnus* have been inferred to high-energy environments (Frey 1990), while horizontal forms have been proposed for low-energy environments (e.g. Rotnicka 2005).

Ichnogenus *Helminthoidichnites* Fitch, 1850

Diagnosis. Endichnial and hypichnial, horizontal, winding cylinder with occasional loops (after Uchman *et al.* 2005).

Helminthoidichnites tenuis Fitch, 1850

Description. Small, simple and unbranched, winding traces preserved as positive hyporeliefs (Fig.7). Trace width about 0.1-0.2 cm; maximum length (as measured on the bedding plane) does not exceed 1.5 cm. The structures are mainly horizontal and gently curved ("C"/"J"/"σ" shape) with very rare self-overcrossings. The specimens reported from the Pizzul Formation exhibit a fill darker than the host rock, while the burrow fill of the specimens from the Auernig and Corona Formations is weakly contrasting with the adjacent rock.

Occurrence. Helminthoidichnites occurs in facies S1, S3. This ichnospecies is common in the Corona, Auernig Formations and rare in the Bombaso, Pizzul Fomations.

Remarks. The morphology of *Helminthoidichnites* diverges from other ichnogenera:

1. *Helminthoidichnites* differs from *Gordia*, which typically presents self-overcrossings.
2. *Helminthopsis* is distinguished from *Helminthoidichnites* by its tendency to meander (Kim *et al.* 2002).
3. Typical *Planolites/Palaeophycus* are usually larger than *Helminthoidichnites*, although size is usually rejected as a valid ichnotaxobase (Bertling 2007). Probably *Helminthoidichnites* can be distinguished from *Planolites/Palaeophycus* by its proportions (i.e. curving/length ratio); however at present time there are no morphometric studies on the argument.

Helminthoidichnites is interpreted as a pascichnia produced in shallow tiers by vagile tracemakers. The producers are identified as nematomorphs or insect larvae (Buatois *et al.* 1997a). *Helminthoidichnites* has been reported either from deep marine settings (Buatois & Mángano 2003) or continental freshwater environments (Buatois & Mángano 2007). More in detail, *Helminthoidichnites* is a typical element of *Mermia* ichnofacies (Buatois *et al.* 1997a; MacEachern *et al.* 2007).

Ichnogenus *Planolites* Nicholson, 1873

Diagnosis. Unlined, rarely branched, straight to tortuous, smooth to irregularly walled and ornamented, horizontal to slightly inclined burrow, circular to elliptical in cross-section, with variable dimensions and configurations. Burrow fill essentially massive, differing from the host rock (after Fillion & Pickerill 1990).

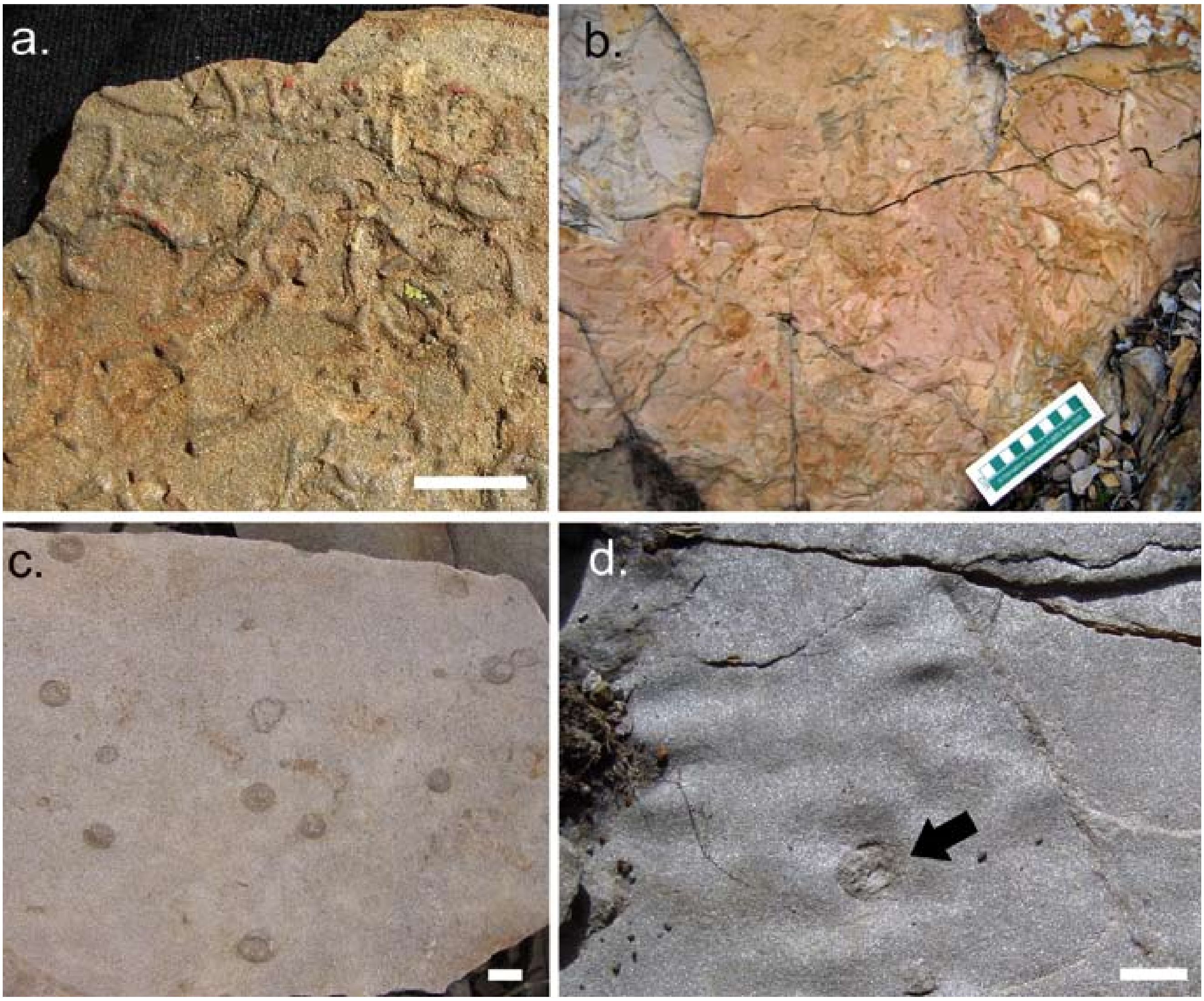

Fig. 7 - Simple structures. a. *Helminthoidichnites*, M. Carnizza (Auernig Fm.). Scale bar 1 cm. b. *Planolites*, M. Carnizza (Auernig Fm.). Scale bar 1 cm. c. Bedding plane with vertical structures (*Cylindrichnus* and *Skolithos*). Monte Corona. Scale bar 1 cm. d. Rippled bedding plane with *Skolithos* (arrowed), M. Carnizza (Auernig Fm.). Scale bar 1 cm.

Fig. 7 - Strutture semplici. a. Helminthoidichnites*, M. Carnizza (Formazione dell'Auernig). Scala 1 cm. b.* Planolites*, M. Carnizza (Auernig Fm.). Scala 1 cm. c. Piano di strato con strutture verticali (*Cylindrichnus *and* Skolithos*). Monte Corona. Scala 1 cm. d. Piano di strato con ripples e* Skolithos *(indicato da una freccia), M. Carnizza (Formazione dell'Auernig). Scala 1 cm.*

Planolites isp.

Description. Horizontal or gently inclined, unlined, unbranched structures, circular to elliptical in cross-section and constant in diameter along burrow axis. Burrow fill typically differs in texture from the host rock. Trace width generally comprised between 0.4 and 0.5 cm, while the maximum length measured ranges between 3 and 4 cm. Generally the burrow fill differs from the host rock by the paucity of mica flakes or by presenting a different granulometry. The examined specimens are generally straight, even though it is not infrequent to observe curved ones.

Occurrence. These burrows are found in all the stratigraphical units considered, especially associated with facies S1 and S2. Particularly good specimens come from the Pizzul, Meledis, Corona, and Auernig Formations. The small forms are more abundant in fine-grained sandstones, while the large ones seem to occur more frequently within medium-grained sandstones.

Remarks. Planolites has been interpreted as reflecting the activity of deposit-feeders. In marine environments the tracemaker is identified as a worm-like organism (cf. Pemberton & Frey 1982; Pemberton *et al.* 2001). In continental environments Planolites is also referred to arthropods (e.g., Buatois & Mángano 1993). Planolites is a typical example of environment-crossing ichnogenus.

Some specimens show a dark-coloured lining and a reddish, sandy fill. The mentioned features possibly correspond to the ichnogenus *Macaronichnus*, but it is difficult to consider if the rusty fill is the result of sediment processing by the tracemaker or it is a diagenetic product.

Ichnogenus *Skolithos* Haldeman 1840

Diagnosis. Simple, unbranched, lined or unlined, vertical or gently inclined burrow. The structure, cylindrical to sub-cylindrical, has typically a uniform diameter throughout its length (after Häntzschel 1975, Gregory *et al.* 2006).

Skolithos isp.

Descripton. Vertical or inclined unbranched burrows, circular on the bedding plane, plug-shaped or cylindrical with rounded lower base in longitudinal sections; a thin, dark lining could define the burrow boundaries. Frequently the burrow fill differs from host rock, being constituted by coarser material or represented by chromatically contrasting sediment (for instance lighter-coloured and more micaceous). The burrow fill is essentially structureless. The diameter of the burrow is usually between 0.1-0.8 cm, larger specimens are rare.

Occurrence. Pramollo Group, facies S1 and S2. The best specimens are found within the Auernig and Corona Formations.

Remarks. Skolithos is commonly ascribed to suspension-feeding organisms. It is usually considered an indicator of high energy, shallow marine and deltaic marine environments (e.g. Alpert 1974; Pemberton *et al.* 2001). In marine settings, *Skolithos* producers are ascribed to vermiform animals (polychaetes, sipunculan and phoronid worms) or eel-like fishes and sea-anenomes (Bromley 1996; Gregory *et al.* 2006). *Skolithos* is also reported from non-marine environments such as flood plain and fluvio-lacustrine settings; in these environments inferred tracemakers include cicadas, spiders, beetles, crickets, ants and termites (see Gillette *et al.* 2003; Gregory *et al.* 2006). Although *Skolithos* is traditionally ascribed to animal burrowing activity, Gregory *et al.* (2006) illustrated convincingly *Skolithos*-like structures produced by plants.

2.4. Spreiten structures

Ichnogenus *Zoophycos* Massalongo 1855

Diagnosis. Spreite structure comprising small, more or less U- or J- shaped, protrusive burrows of variable length and orientation, arranged in helicoids spirals with an overall circular, elliptical or lobate outline; a central vertical tunnel or marginal tube may be present (according to Rodríguez-Tovar & Uchman 2004 after Frey 1970; Häntzschel 1975; Wetzel & Werner 1981; Fillion & Pickerill 1984).

Zoophycos isp.

Description. Helically coiled spreite burrows, constituted by numerous structures revolving around a central axis (Figs. 8-9). The mentioned organization typically results in a circular outline shown by the whole structure. Such structures could reach considerable diameter (30-40 cm), even though smaller (15-25 cm diameter) specimens are more common.
Some specimens exhibit a clear vertical, three-dimensional development, while other forms are represented by flattened, sheet-like laminae. Lobes can be present in both forms, even though they are rarer in sheet-like specimens. It is not yet clear if the two aforementioned forms reflect only diagenetical processes (i.e. different compaction rates) or if they are linked with the behavior of the tracemakers.

Occurrence. Zoophycos is one of the most common traces of the whole Pramollo Group. *Zoophycos* is mainly reported within S2, S3 and P1 facies; it is also found in facies S1 and S5. The best specimens are found within the Meledis, Pizzul, Corona, Carnizza Formations.

Remarks. Zoophycos is one of the most celebrated ichnogenera, although it remains one of the most enigmatic ones, either for ichnotaxonomy (i.e. Olivero 2007) or palaeoethology (i.e. Bromley 1991; Olivero & Gaillard 2007). The "traditional" models for the palaeocology of *Zoophycos* are generally imputed to strip-mining actions led by deposit-feeders (e.g. Seilacher 1967; Wetzel & Werner 1981). Kotake (1989, 1991) proposes a model with the tracemaker ingesting detritus near the sea-floor, further depositing the feces into the burrow. Bromley (1991) proposed the *refuse dump model* (sediment is deposited as ballast; deposit-feeding behaviour), the *cache model* (the tracemaker revisited deposited fecal material) and the *gardening model* (gardening of microbial content thanks to the marginal tube, where present). Olivero & Gaillard (2007) have recently studied numerous specimens of *Zoophycos* (ranging from Devonian to Cretaceous) and proposed a sediment-feeding strategy (see also Neto de Carvalho & Rodrigues 2003): according to this hypothesis, the *Zoophycos* producer exploited nutrients stored inside the sediment.
As concerns the palaeoenvironmental significance of this ichnogenus, it is well-known that *Zoophycos* occupied different bathymetrical ranges during the Phanerozoic (Bottjer *et al.* 1988). The Palaeozoic occurrences of *Zoophycos* are registered in environments going from the nearshore to slope and deep basin. Buatois *et al.* (2005) reported *Zoophycos* as a common component of Carboniferous estuarine deposits. During the Mesozoic the distribution of *Zoophycos* registered a progressive deepening trend, with the progressive disappearance of the ichnogenus from shallower environments (e.g., Neto de Carvalho & Rodrigues 2003).
The distribution of *Zoophycos* across time shows its wide environmental range: the tracemaker tolerated several bathymetrical settings, being an element of *Cruziana, Zoophycos* and *Nereites* ichnofacies (Pemberton *et al.* 2001). Quiet-water, stressed environments (in particular those exhibiting anoxia) seem to be the preferential conditions under which *Zoophycos* tracemaker established (Pemberton *et al.* 2001).
With respect to the Pramollo occurrences, *Zoophycos* is mainly referred to marine settings below storm wave base. This is

Fig. 8 - *Zoophycos* from the stream SW of Casera For. a. *Zoophycos* is a common constituent of Pramollo ichnolagerstätte. b. *Zoophycos* is frequently associated to marine micaceous sandstones.
Fig. 8 - Zoophycos *dal ruscello a SW di Casera For. a.* Zoophycos *è un comune costituente dell'ichnolagerstätte di Pramollo. b.* Zoophycos *è frequentemente associato ad areniti micacee di ambiente marino.*

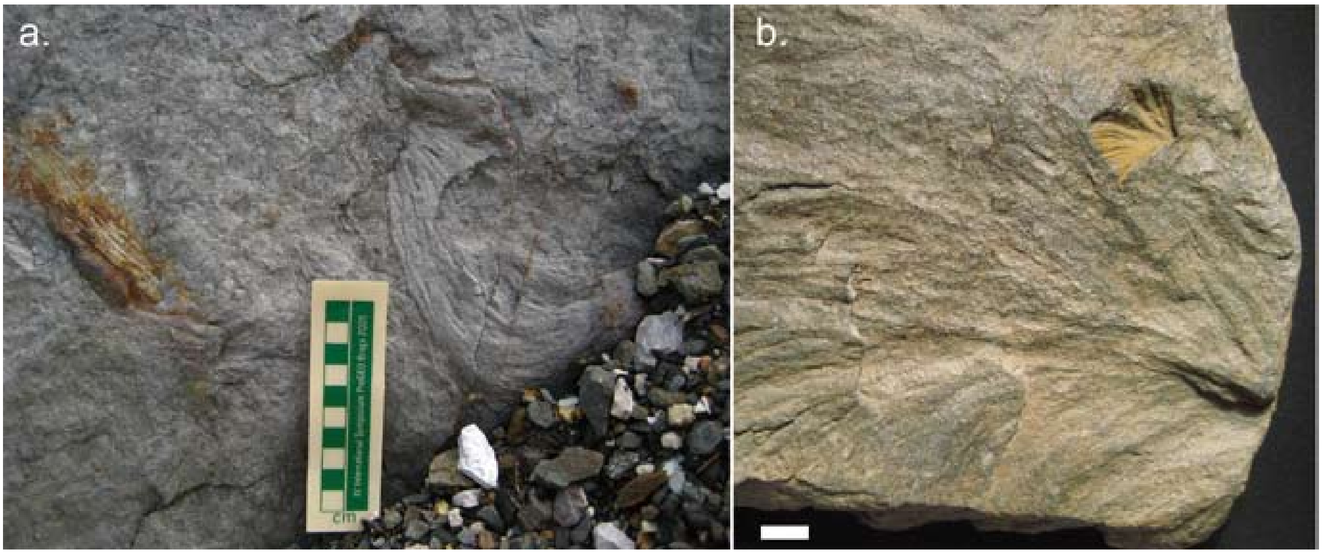

Fig. 9 - *Zoophycos* is frequently associated with organic debris, such as vegetal remains (a) or crinoid and brachiopod accumulations (b).
Fig. 9 - Zoophycos *è frequentemente associato con resti organici, come (a) frustoli vegetali o accumuli di crinoidi e brachiopodi (b).*

typically the case of *Zoophycos* occurring within fine-grained facies associated with abundant marine faunas (productids and crinoids, facies P1). Nevertheless, dense, oligospecific *Zoophycos* assemblages are locally found within storm-deposited sandstones associated with *Skolithos*, bioclastic horizons and hummocky lamination (facies S2).

Ichnogenus *Dictyodora* Weiss 1884

Diagnosis. Complex three-dimensional burrow, roughly conical, vertical to bedding; apex of cone upward; very thin spreite with exterior surface delicately striated. On bedding plane, the structures appear as a meandering (or roughly spiraling) "band", which corresponds to the intersection of the three-dimensional spreite with the bedding surface (after Häntzschel 1975; Benton 1982).

Dictyodora liebeana (Geinitz, 1867)

Description. Spreite burrow, coiling spirally meanwhile meandering; the coiling axis is vertical (Fig. 10). This arrangement results in a roughly conical three-dimensional struc-

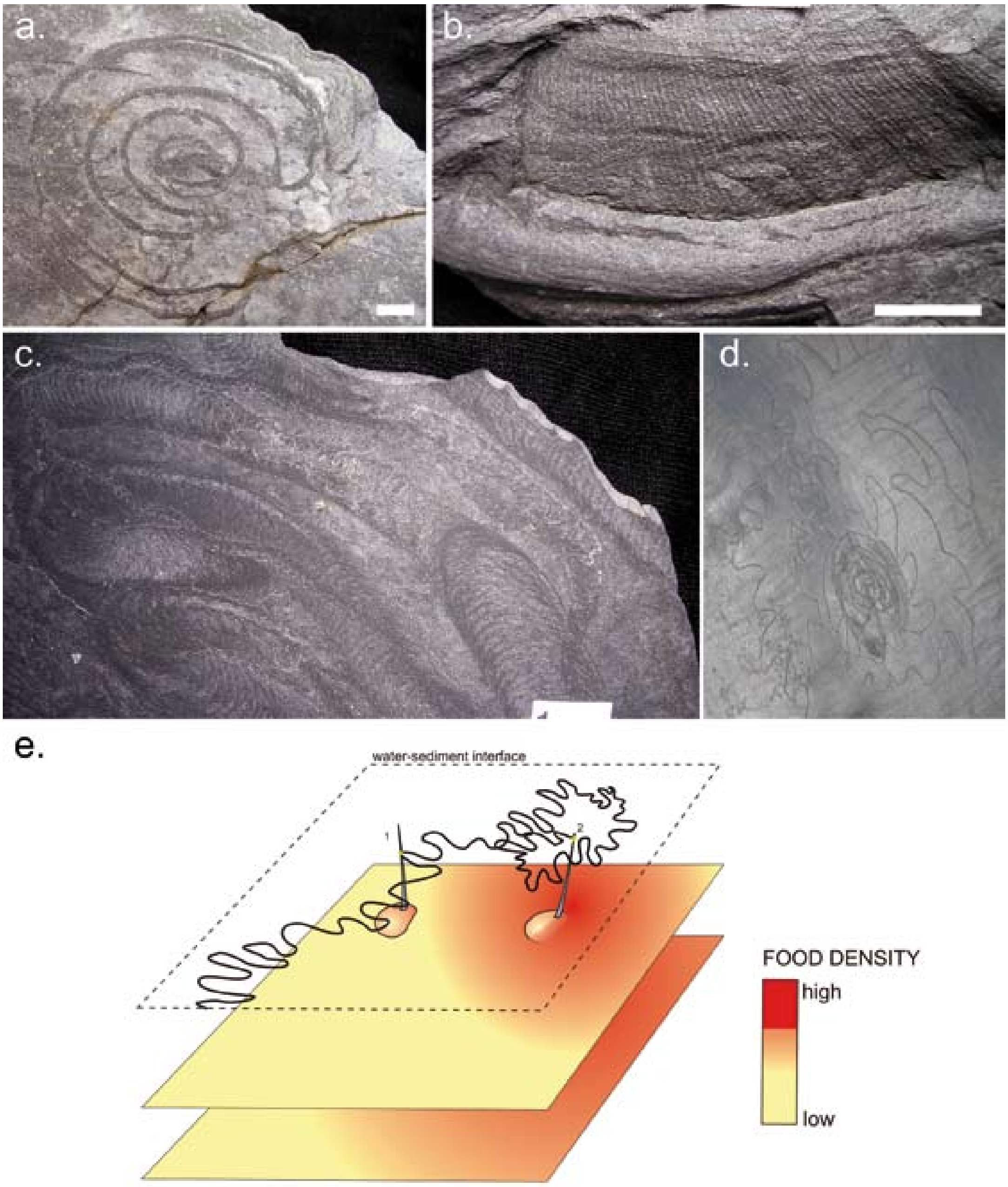

Fig. 10 - *Dictyodora* from the stream SW of Casera For. Scale bar 1 cm. a. On bedding planes *Dictyodora* appears as meandering or spiraling "bands" b. Lateral view of the spreite: it is possible to distinguish an upper, striated part and a lower string of bioturbated sediment c. Polished section of a *Dictyodora* specimen. Section parallel to bedding plane. d. This specimen is meandering while coiling spirally. e. Some specimens of *Dictyodora* show complex foraging strategies for exploiting patchy food resources. In these cases the trace is initially meandering, then it starts to coil (see text for more details). The proposed interpretation is: the tracemaker meanders straightforward (1) until it reaches a food-rich patch. Then the producer starts to coil to exploit the patch and, at the same time, it deepens the tier (2) to exploit the vertical gradient of food resources. The yellow circle indicates the intersection between the tracemaker's snorkel and the water-sediment interface.

Fig. 10 - Dictyodora *dal torrente a SW di Casera For. Scala 1 cm. a. Sui piani di stratificazione* Dictyodora *appare come "bande" meandreggianti o a spirale. b. Visione laterale del profilo: è possibile vedere un livello superiore (striato) e un livello inferiore di sedimento bioturbato. c. Sezione lucida di un esemplare di* Dictyodora*. d. Questo esemplare meandreggia mentre si avvolge a spirale. e. Alcuni esemplari di* Dictyodora *mostrano strategie complesse per sfruttare risorse di cibo distribuite irregolarmente. In questo caso la traccia è inizialmente meandreggiante, poi inizia ad avvolgersi (vedi testo). L'interpretazione proposta è: l'organismo produttore meandreggia (1) finché raggiunge un'area ricca di cibo. A questo punto l'organismo avvolge il suo andamento e, allo stesso tempo, approfondisce il tier (2) per sfruttare il gradiente verticale di nutrienti. Il cerchio giallo indica l'intersezione tra lo snorkel dell'organismo e l'interfaccia acqua sedimento.*

ture. The spreite, when visible, is constituted by two parts: an upper, striated part, and a lower one represented by a string of bioturbated sediment. On the bedding plane the structure results as a thin (1 mm or less) irregularly meandering or spiraling "band". On the bedding plane trace diameter reaches easily 15-20 cm; some exceptionally specimens reach more than 50 cm of diameter.

Occurrence. Dictyodora is found exclusively within dark shales, markedly fissile (facies P3). This facies is found almost exclusively in the south-eastern part of the ichnolagerstätte, where significant tectonic disturbance occurs in an intensely vegetated area. As a consequence, stratigraphic position is uncertain. The studied specimens possibly belong to the Bombaso Formation, although further studies are required to exclude correlation with the Variscan basement (i.e. Hochwipfel Formation). In fact the stratigraphic uncertainty is nourished by the chronostratigraphic value of *Dictyodora liebeana:* the ichospecies is considered a good trace fossil indicator of the Lower Carboniferous (Uchman 2003, 2007). According to this interpretation, the considered shales would be consistent to the Variscan Basement (i.e. the Hochwipfel Formation is Middle Visean-Bashkirian; the Bombaso Formation is markedly Upper Carboniferous).

Remarks. Similar specimens of *Dictyodora liebeana* are reported by Benton (1982) from the Lower Carboniferous of Thuringia and by Orr *et al.* (1996) from Menorca. These occurrences, as well as the Pramollo ones, are interpreted according to Seilacher (2007): the tracemaker explored deep tiers while being connected to the surface by a long snorkel-like tube.
Moreover, some specimens from Pramollo show a very interesting morphology: the structure is initially meandering (similarly to *Dictyodora scotica* M'Coy, 1851), then, at a certain point, the trace starts to coil and change tier.
This morphology is interpreted as a complex foraging strategy for taking advantage of patchy food resources. According to this interpretation, the strategy can be divided in two behavioral routines:

1. meandering: the tracemaker is exploring the sediment;
2. spiraling and meandering: after finding a food patch, the tracemaker is exploiting it systematically.
   Thanks to this strategy, the tracemaker optimized efficiently its energy for exploiting patchy food resources (Fig. 10e).

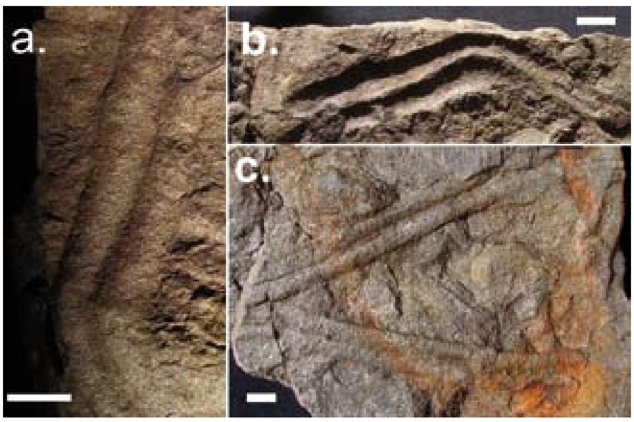

Fig. 11 - *Archaeonassa* have been produced by a vagile organism laterally displacing the sediment. Scale bar 1 cm. a. Convex epirelief, Monte Corona, Auernig Fm. b. Concave hyporelief preservation, Auernig Formation c. Convex epirelief, stream SW of Casera For.

Fig. 11 - Archeonassa *è stata prodotta da un organismo vagile, che ha spostato lateralmente il sedimento. Scala 1 cm. a. Epirilievo convesso, Monte Corona, Formazione dell'Auernig. b. Iporilievo concavo, Formazione dell'Auernig. c. Epirilievo convesso, ruscello a SW di Casera For.*

2.5. Winding structures

Ichnogenus *Archaeonassa* Fenton and Fenton 1937

Diagnosis. Simple, unbranched, straight, curved to meandering, horizontal trail represented by a regular furrow flanked by two narrow lateral ridges; furrow usually V-shaped in cross-section. Furrow rarely smooth, mostly crossed by rounded wrinkles (after Häntzschel 1975; Buckman 1994; Yochelson & Fedonkin 1997; Mángano *et al.* 2005).

Archaeonassa isp.

Description. Horizontal, straight or gently winding trail constituted by two symmetrical lobes separated by a central furrow. Usually preserved as positive epirelief. Negative relief preservation can occur (Fig. 11b). Width of the structures ranging between 0.6 and 1.6 cm.

Occurrence. Pramollo Group, facies S1 and S2. Particularly good specimens come from the Meledis, Pizzul, Corona and Auernig Formations.

Remarks. The ichnotaxonomic status of *Archaeonassa* is still debated (Buckman 1994; Yochelson & Fedonkin 1997). This trace fossil is usually interpreted as a pascichnia produced by invertebrates, among which arthropods and mollusks (see the discussion in Mángano *et al.* 2005).
The Pramollo specimens are partly consistent with the aforementioned hypothesis. In fact the bilobed morphology is interpreted as the product of the locomotion of an animal moving in proximity of the sediment/water interface. According to this hypothesis, the crests would be the result of the sediment lateral displacement produced by the moving organism. Possibly the Pramollo structures represent grazing behaviour, but they could be also produced by predaceous organisms moving in proximity to the sea-floor. *Archaeonassa* has been reported from Buatois & Mángano (2002) in floodplain deposits.

Ichnogenus *Curvolithus* Fritsch, 1908

Diagnosis. Unbranched, sub-horizontal (rarely oblique), straight to curved, ribbon-like or tongue-like structures; mostly endostratal. The trace is characterized by three rounded lo-

Fig. 12 - Morphology of *Curvolithus* from the Corona Formation. Scale bar 1 cm. a. This specimen exhibits the main features of *Curvolithus*: central ridge with two lateral strings. In the lower part of the picture it is possible to see a meniscate trace, possibly *Ancorichnus*. b. *Curvolithus* with chevron-shaped ornamentation on the central ridge. c. *Curvolithus* from Monte Corona; Corona Formation.

Fig. 12 - Curvolithus *dalla formazione di Corona. Scala 1 cm. a. Questo campione mostra le caratteristiche salienti di* Curvolithus*: una cresta mediana con due stringhe laterali. Nella parte bassa dell'immagine, una traccia meniscata, possibilmente* Ancorichnus*. b.* Curvolithus *con ornamentazione a chevron. c.* Curvolithus *dal Monte Corona, Formazione di Corona.*

Fig. 13 - Among the sites of the ichnolagerstätte, Monte Corona (Corona Formation) is the richest in *Curvolithus*. a. *Curvolithus* associated with numerous vertical structures (*Skolithos* and, possibly, *Arenicolites*). Scale bar 1 cm. b. *Curvolithus*; note the crest on the median ridge.

Fig. 13 - Il Monte Corona è particolarmente ricco di Curvolithus*. a.* Curvolithus *associato a numerose strutture verticali (*Skolithos *e, forse,* Arenicolites*). Scala 1 cm. b.* Curvolithus*, si noti la cresta mediana.*

bes on upper surface and up to four lobes on concave or convex lower surface. The central lobe on upper surface is wider than lateral ones and separated from them by shallow, angular furrows. Faint, narrow central furrow dividing central lobe in upper surface may be present (after Häntzschel 1975; Buatois *et al.* 1998).

Curvolithus simplex Buatois *et al.*, 1998

Description. Unbranched, winding sub-horizontal structures with a central lobe flanked on both sides by a lateral string (Figs 12-13). Central lobe is usually smooth but rarely it exhibits chevron-shaped ornamentation (Fig. 12b); a narrow median crest is frequently present. Usually preserved as positive relieves on the top of the beds; on the sole of the beds negative relief preservation may also occur. Usually horizontal, locally the traces may gently plunge into the beds.

On the basis of the width of the trace, two forms are distinguished:

1. Large form: Trace width ranging 1.4-1.8 cm. The lateral lobes are very thin compared to the central ridge: central ridge/lateral lobe ratio is between 3 and 4.
2. Small form: Trace width not exceeding 1.2 cm, more frequently ranging between 0.4 and 0.8 cm. The late-

ral lobes are wide: central ridge/lateral lobe ratio ranges between 0.6 and 2.5.

Occurrence. The best specimens are coming from the Corona Formation, in which either small or large forms occur. Small forms are present in dense assemblages especially within the Bombaso, Pizzul and Meledis Formations. *Curvolithus* is commonly found within facies S1 and S2.

Remarks. Curvolithus has been usually interpreted as a locomotion trace of endostratal invertebrate carnivores. Lockley *et al.* (1987) support this hypothesis by taking into account the absence of structures indicative of deposit-feeding. Inferred tracemackers include gastropods (Heinberg & Birkelund 1984), polychaetes, nemerteans, holothurians (Lockley *et al.* 1987) and flatworms (Seilacher 2007). According to Heinberg (1973), the *Curvolithus*-producer transported sediment from front to rear while digging into the sediment.

As reported by Buatois *et al.* (1998), *Curvolithus* commonly occurs within shallow-marine deposits, either of normal or slightly brackish salinity. It is frequently associated to delta or fan delta settings, especially related to slightly brackish water conditions. Lockley *et al.* (1987) proposed a subset of *Cruziana* ichnofacies – *Curvolithus* ichnofacies – corresponding to deltaic-influenced nearshore environments subject to rapid deposition exceeding physical reworking.

Ichnogenus *Psammichnites* Torell 1870

Diagnosis. Horizontal trace characterized by a narrow median ridge and small transverse ridges. The overall form is straight to curvaceous, in some cases looping. It is usually found on the top of bedding planes, but occasionally negative hyporelief preservation is found (after Häntzschel 1975; Mángano *et al.* 2002a).

Psammichnites cf. *plummeri* (Fenton and Fenton 1937)

Description. Horizontal, winding, looping or meandering traces having a thin median string. Arcuate- or chevron-shaped transverse ridges are doubtfully inferred (Fig. 14). True branching is not recognized, but crossovers or interpenetrations are found. Trace width about 1 cm. The considered structures are preserved on the top of the beds.

Occurrence. Pramollo group, facies S1. The best specimens are reported from the Auernig Formation.

Remarks. The behavioral pattern of *Psammichnites* is commonly referred to the feeding activity of an animal moving through the sediment and being connected to the sediment surface by a snorkel device (cf. Seilacher 1997; Mángano *et al.* 2002b). Rowland (2006) infers that the snorkel-device represented a sensory receptor of a predator. As regards palaeoenvironment, *Psammichnites* is often reported from marginal-marine environments (Mángano *et al.* 2002a, 2002b); during the Carboniferous *Psammichites* constitutes a common element of lower estuarine settings (Mángano *et al.* 2005).

2.6. Meandering structures

Ichnogenus *Nereites* MacLeay 1839

Diagnosis. Meandering trails, represented by a narrow median furrow flanked on both sides by morphologically va-

Fig. 14 - *Psammichnites*. a. *Psammichnites* from M. Carnizza, Auernig Formation. Scale bar 1 cm. b. *Psammichnites* (Ps) and *Pramollichnus* (Pr), M. Carnizza, Auernig Formation. Hammer as scale. c. *Psammichnites* and meniscate traces. Stream nearby Malga Auernig. Scale bar 1 cm.

Fig. 14 - Psammichnites. *a.* Psammichnites*, M. Carnizza, Formazione dell'Auring. Scala 1 cm. b.* Psammichnites *(Ps) e* Pramollichnus *(Pr), M. Carnizza. Martello come scala. c.* Psammichnites *e tracce meniscate. Torrente nei pressi di Malga Auernig. Scala 1 cm.*

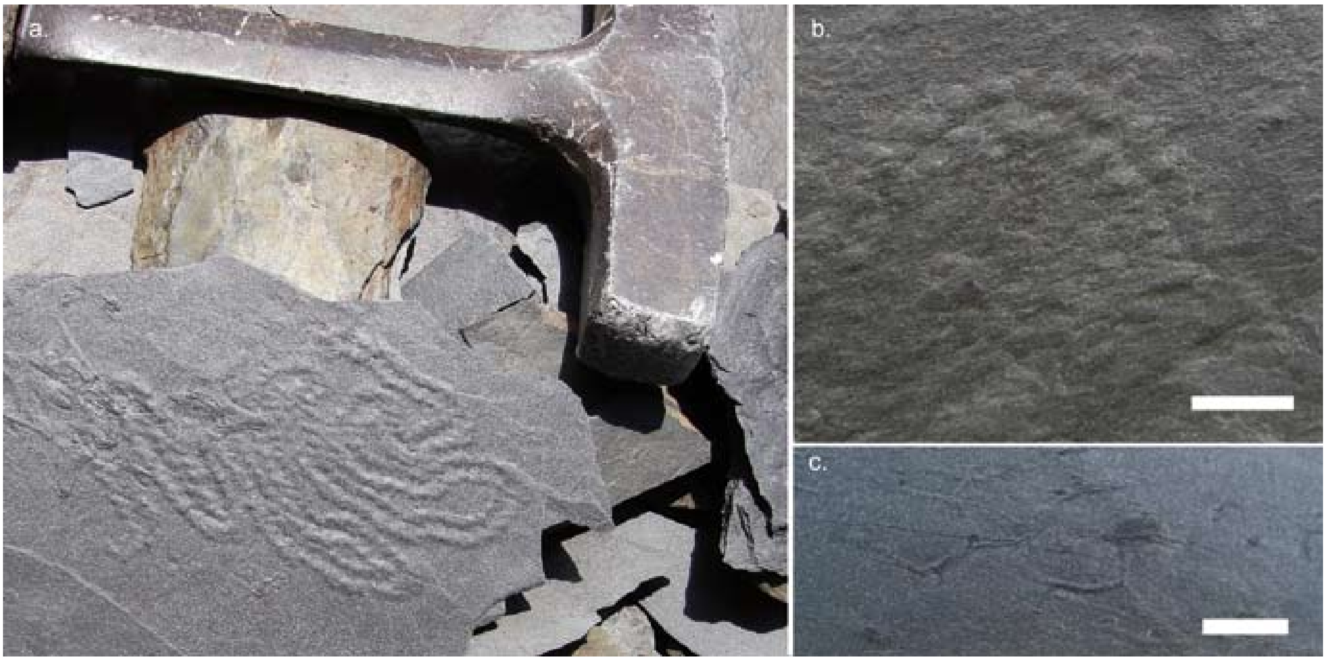

Fig. 15 - Trace fossils from the stream SW of Casera For. a. *Nereites*. Hammer as scale. b. *Nereites*. Scale bar 1 cm. c. *Protopalaeodictyon*. Scale bar 1 cm.
Fig. 15 - Tracce fossili dal torrente a sudovest di Casera For. a. Nereites*. Martello come scala. b.* Nereites*. Scala 1 cm. c.* Protopalaeodictyon*. Scala 1 cm.*

riable lobes (i.e. leaf-shaped, ovate, pinnate); meanders may be densely spaced (after Häntzschel 1975).

Nereites jacksoni Emmons, 1844

Description. Irregurarly meandering trail, constituted by a median furrow with closely-spaced lobes on both sides (Fig. 15). The lobes present rounded morphology and are organized in parallel (3-4 lobes/cm). Occasionally loopings have been found. The structure is narrow (0.4-0.7 cm wide).

Occurrence. Nereites is reported from dark, fissile shales (facies P3); it is usually found in dense assemblages within finer-grained laminae. Stratigraphic position is uncertain, possibly corresponding to the Bombaso Formation (see *Dictyodora* for details).

Remarks. The lobes are interpreted as the sediment reworked by the animal as supported by the texture of the lobes, which are darker and finer respect to the host rock. This feature is not appreciable in the figures, as the different texture is clearly visible only in weathered specimens. This particular is compatible with the traditional interpretation of the ichnogenus: the tracemaker removed sediment in front and backfilled the rejected material at both sides of the burrow (cf. Seilacher 2007). Neoichnological observations in deep sea-environments (Wetzel 2002; see also Wetzel & Uchman 2001) inferred chemotactic guidance for the *Nereites* producer, which possibly fed on microbes nearby the redox boundary layer.

Traditionally the producer of *Nereites* has been identified as vermiform animals (i.e. Seilacher 2007), but Martin & Rindsberg (2007) pointed out the possibility of an arthropod tracemaker.

According to Wetzel (2002), *Nereites* is linked with soft to soupy, oxygenated muddy sediments with a well-developed redox boundary near the sediment surface. These conditions are associated more commonly to deep environments than to shallow ones. In fact *Nereites* normally occurs in deep marine environments, but shelf occurrences are known (Seilacher 2007). Neoichnological observations reported *Nereites*-like structures from tidal-flat environments too (Martin & Rindsberg 2007).

2.7. Nets

Ichnogenus *Protopaleodictyon* Książkiewicz, 1970

Diagnosis. Uniramous and biramous graphoglyptid burrow composed by wide first order meanders and sine shaped second order undulations with distinct appendages, all at the same level (Seilacher 1977).

Protopaleodictyon submontanum (Azpeitia-Moros, 1933)

Description. Winding graphoglyptid burrow (see McCann & Pickerill 1988) forming irregularly polygonal nets. The structure is branching, usually in correspondence of the apical bends of meanders. Branches are mostly constant in diameter (less than 2 mm wide; see Fig. 15c).

Occurrence. Facies P3 (see *Dictyodora* for discussion on stratigraphic position).

Remarks. As concerns Pramollo, *Protopaleodictyon submontanum* is rarely found, usually associated with *Nereites jacksoni* and *Dictyodora liebeana.* According to McCann & Pickerill (1988) *Protopaleodictyon submontanum* typically occurs in deep-water flysch successions. The Pramollo occurrences are consistent with this hypothesis, as confirmed by the sedimentologic features (facies P3) associated with *Protopaleodictyon*. Shallow occurrences of *Protopaleodictyon submontanum* are reported from the Lower Cambrian (Crimes & Anderson 1985), long before of the Ordovician deep-sea radiation.

2.8. Other structures

Ichnogenus *Asterosoma* von Otto, 1854

Diagnosis. Radial arrangement of 3 to 9 horizontal bulbous burrows starting from an axial tube, simple or budding dichotomously or in a fan-like pattern. Bulbs with narrow tips might have or not concentric *spreite* and are connected by a tube positioned sub-central to eccentrically; ornamentation is absent or constituted by striae and longitudinal to sub-angular furrows (Häntzschel 1975; Schlirf 2000).

Asterosoma isp.

Description. Two forms of *Asterosoma* have been found:

1. Form 1 has several bulbs diverging dichotomously from a curvilinear main tunnel (bulbs are less than 2 cm wide). The burrow fill usually differs from the host rock by being more micaceous (see Fig. 16).
2. Form 2 is constituted by 9 bulbs extending from a central area.

Occurrence. Form 1 occurs exclusively in facies P3 (see *Dictyodora* for discussion on stratigraphic position). Form 2 has been found in loose sandstone slabs; therefore its stratigraphic position is uncertain (Meledis Fm.? Pizzul Fm.? Auernig Fm.?).

Fig.16 - *Asterosoma* (form 1). Bedding plane view. Scale bar 1 cm.

Fig. 16 - Asterosoma *(forma 1). Visuale perpendicolare al piano di strato. Scala 1 cm.*

Remarks. Form 1 shows morphological affinities with the asterosomid burrow described as "Tatzelwurm" by Seilacher (2007), while form 2 is partly compatible with *Asterosoma radiciforme.*

Ichnogenus *Pramollichnus* nov. igen.

Diagnosis. Crescent-shaped structure formed by curved, juxtaposed cylindrical burrows connecting two common apical points.

Derivatio Nominis. Trace from Pramollo, the type locality of this new ichnogenus.

Pramollichnus pastae nov. isp.

Diagnosis. The same as for the ichnogenus.

Derivatio Nominis. Pastae derives from the Latin *pasta* (*vermiculata*), which means "spaghetti". In fact the term *pastae* refers to the spaghetti-like burrows which constitute the trace.

Description. Set of spaghetti-like burrows that are linking two common apical points (in the holotype the distance between apical points is 34 mm). The burrows are juxtaposed and curved, therefore the structures exhibit a diagnostic crescent-shaped morphology (Fig. 17a,b). The spaghetti-like burrows are cylindrical and show a very regular diameter (3-6 mm wide). Burrow ornamentation is absent.

The trace fossils are usually preserved as endichnia or positive epirelieves; negative epirelieves occur in case of weathering of the burrow fill (Fig. 17c).

Holotype. PRAM-1 (Fig. 17a,b) is housed in the ichnological collection of Centro Cultural Raiano (Idanha-a-Nova, Portugal).

Occurrence. Pramollichnus occurs within fine- to medium-grained sandstones (facies S1).

Remarks. Pramollichnus has been figured by Barbiero *et al.* (1990), although no interpretation is given apart from "unknown meandering trace". Venturini (2006) cites *Pramollichnus* as "Spiralilia elegans", which is a *nomen nudum* because the author does not provide any description.

The morphology of *Pramollichnus* diverges from other described ichnogenera:

1. *Rhizocorallium* Zenker, 1836 markedly differs from *Pramollichnus* for being U-shaped (while *Pramollichnius* is crescent-shaped) and for having an actual *spreite* (not present in *Pramollichnus*). Moreover, *Rhizocorallium* is usually elongated respect one axis, while *Pramollichnus* is not.
2. *Arenituba* Chamberlain, 1971 (formerly *Micatuba*, see Stanley & Pickerill, 1995) is not consistent with *Pramollichnus*, for radiating from a central gallery (*Pramollichnus* presents two apical points), for being irregularly arranged (*Pramollichnus* exhibit a set of regularly organized burrows) and for the outline (*Pramollichnus* is crescent-shaped).

Pramollichnus exhibits a systematical arrangement of burrows which effectively covers the two-dimensional space. Consequently, it is convenient to hypothesize that the trace-maker exploited systematically the substrate for food. Basically, the tracemaker followed its previous burrow by thigmotaxy; the apical points probably corresponded to vertical shafts connecting the structure to the sea-floor (Fig. 17d). *Pramollichnus* is associated to estuarine-related ichnogenera (see chapter 3). Moreover, *Pramollichnus* is usually accompanied with simple structures such as *Skolithos* and *Cylindrichnus*.

The unconventional co-occurrence of efficient, systematical strategies (corresponding to *Pramollichnus*) and simple ones (*Skolithos*, *Cylindrichnus*) is probably related to the disposability of resources. Minter *et al.* (2006) (after Valentine 1971) assume that predictable levels of resources favour specialized and efficient populations. This postulation fits well in deep-sea environments, where graphoglyptids are consistent with low but predictable resources. Furthermore, the mentioned model well-predicts certain tidal-flat assemblages, where specialized strategies coexist with unspecialized ones. In fact, as Minter *et al.* (2006) point out, resources are often abundant and predictable within tidal environments (the tidal rhythms are very regular).

However, this model do not fit with the estuarine occurrence of *Pramollichnus:* if tidal influence is modest, fluvial-influenced settings are far from being predictable. In fact such settings commonly present unpredictable fluctuations in sedimentation, food supply and salinity. These features are confirmed by the patchy distribution of traces associated to *Pramollichnus.* Consequently, it seems more convenient to postulate an alternative hypothesis for the case of Pramollo. Patchy food resources can explain efficient, sy-

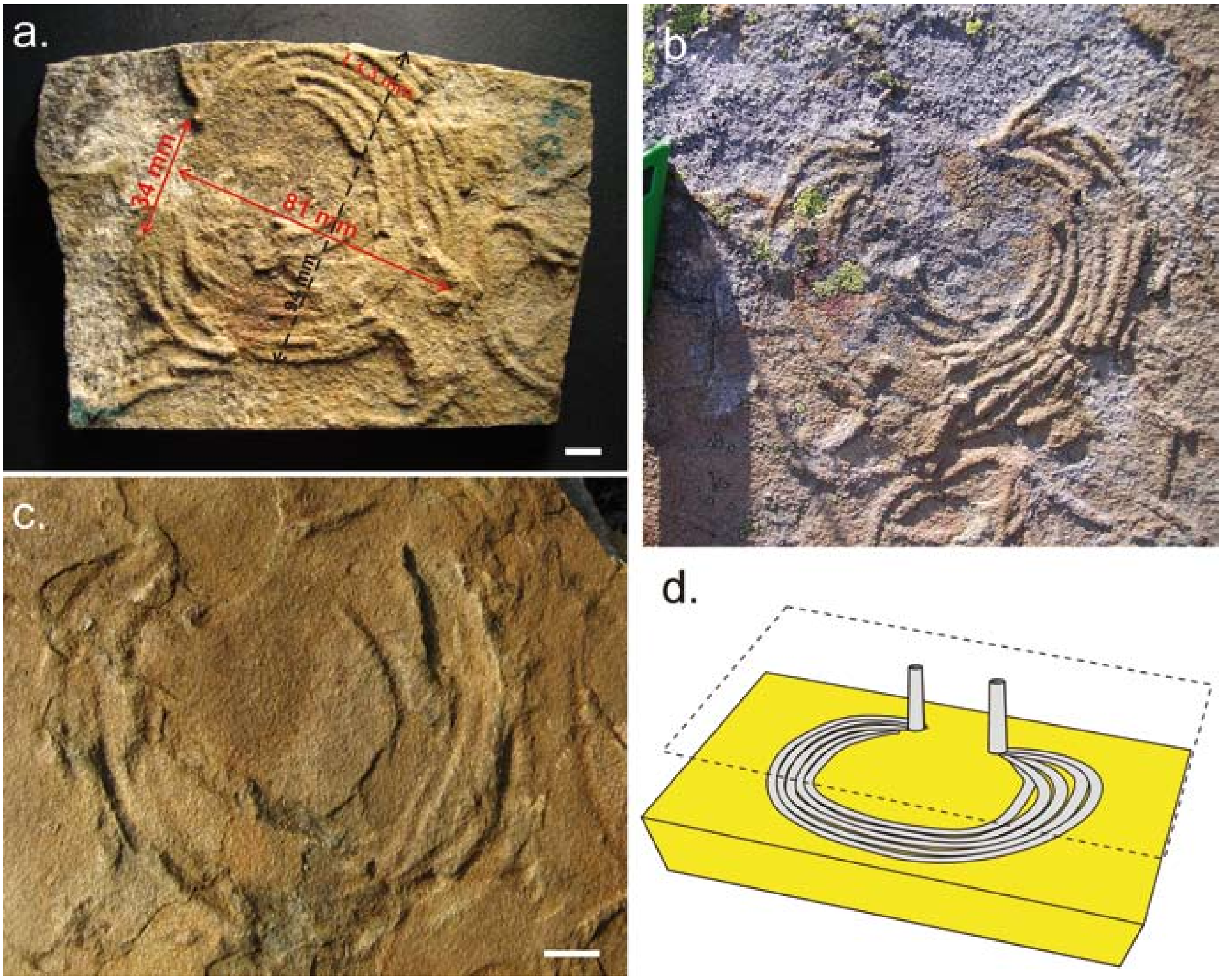

Fig. 17 - The new ichnogenus *Pramollichus.* a. Holotype of *Pramollichnus* with measurements. Scale bar 1 cm. b. Holotype of *Pramollichnus*, field photograph. c. Weathered specimen of *Pramollichnus*, showing concave epirelief preservation. d. Interpretation of *Pramollichnus*. Dotted plane represents the sediment-water interface.

Fig. 17 - Il nuovo icnogenere Pramollichnus*. a. Olotipo, con misure. Scala 1 cm. b. Olotipo, foto sul campo. c.* Pramollichnus *preservato come epirilievo concavo. d. Interpretazione di* Pramollichnus.

stematical strategies such as *Pramollichnus.* In fact complex movement pathways may indicate finite patch of resources (see the foraging simulations of Koy & Plotnick 2007). The "patchy food" hypothesis is confirmed by the meandering pattern of many traces associated with *Pramollichnus* (i.e. *Psammichnites*, meniscate traces). This scenario may be integrated by the role of competition and predator pressure (Brown 2000): the risk of predation and the presence of competitors are good reasons to forage more efficiently.

Moreover, this scenario also includes simple strategies (*Cylindrichnus* and *Skolithos*). In fact the marked stressing factors of estuarine settings (fluctuations in sedimentation, food supply and salinity) open a door for opportunistic strategies too. This assumption is supported by the fact that the producers of *Cylindrichnus* and *Skolithos* (most probably suspension-feeders) were not competing for resources with the *Pramollichnus*-maker (deposit-feeder).

In conclusion, the described occurrence of *Pramollichnus* is related with lower estuary settings, probably characterized by environmental stressors and patchy food resources.

3. DISCUSSION: ICHNOASSEMBLAGES AND ENVIRONMENTAL SETTING OF THE PRAMOLLO BASIN

3.1. *Introduction*

The Pramollo Group and the Bombaso Formation are characterized by recurring ichnoassemblages and sedimentary facies (Fig.18). Ichnoassemblages are here divided in two main groups.

1. *Estuarine assemblages*. A considerable number of ichnoassemblages is characterized by abundant and moderately large estuarine-related ichnogenera, impoverished marine ichnoassemblages, a low to moderate degree of bioturbation (as indicated by distin-

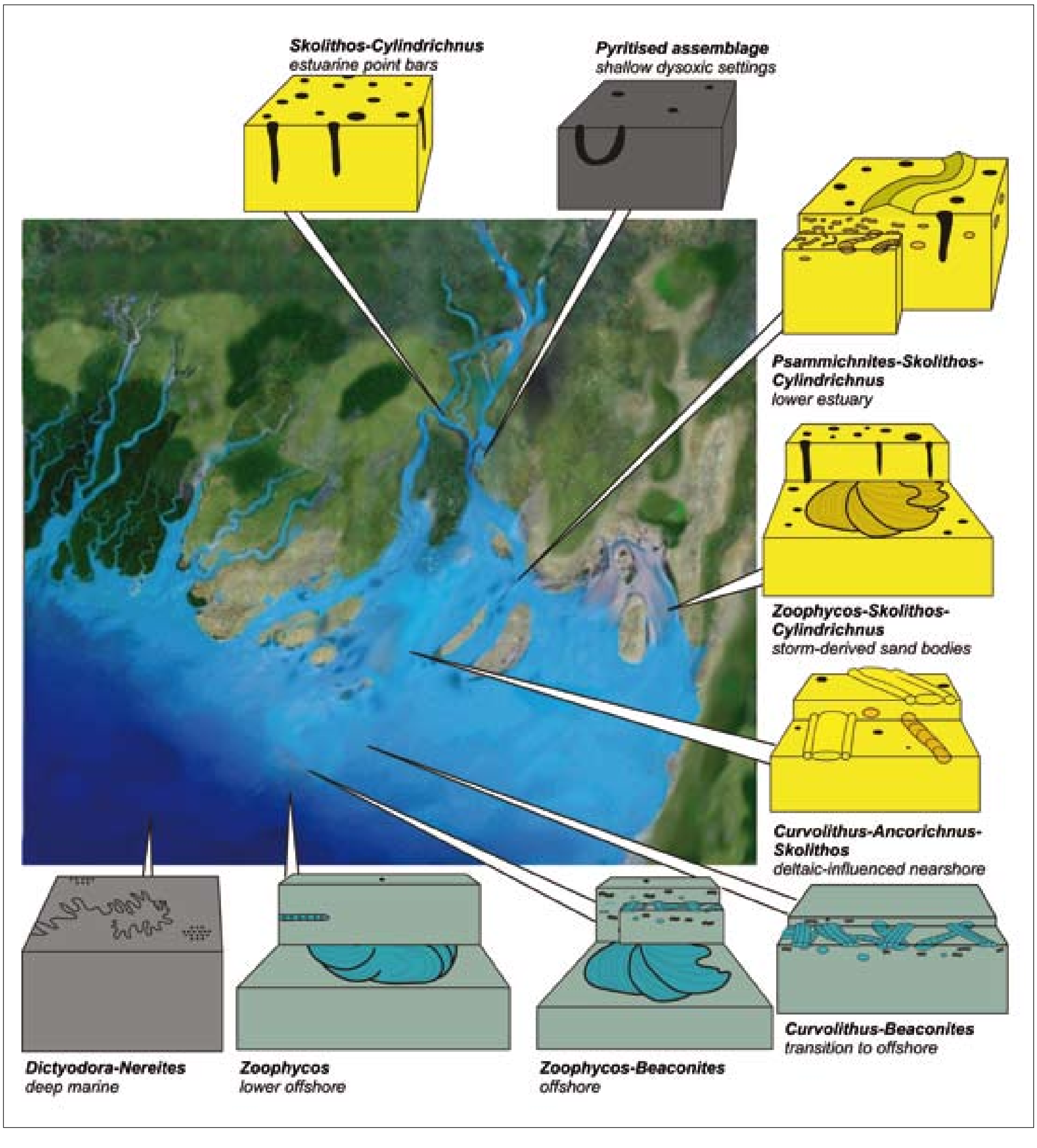

Fig. 18 - Ichnoassemblages and environmental reconstitution of the Pramolo ichnolagerstätte.

Fig. 18 - Icnoassociazioni e ricostruzione ambientale dell'ichnolagerstätte di Pramollo.

ct primary lamination), varying intensity of bioturbation, vertical and horizontal traces typical of *Skolithos* and *Cruziana* ichnofacies. The commonest lithofacies include planar, trough or cross-bedded sandstones (facies S1; see Tab. 2) and dark siltstones rich in vegetal remains (facies P2). These elements are consistent with the main features of brackish faunas and ichnofaunas (i.e. Remane & Schlieper 1971; Buatois *et al.* 1997b; Pemberton 1998; Gingras *et al.* 1999; Pemberton *et al.* 2001; Taylor *et al.* 2003; Mángano & Buatois 2004).

2. *Marine assemblages*. Several ichnoassemblages present horizontal traces and/or 3D-spreite structures common of distal *Cruziana* ichnofacies. Estuarine-related ichnogenera are absent or present a small size, degree of bioturbation is constant and generally intense. Lithofacies are dominated by fine-grained sandstones (facies S3), dark siltstones with stenohaline body fossils (facies P1), shales (facies P3). According to these features, the corresponding environmental setting is more marine than estuarine-influenced.

3.2. *Estuarine assemblages*

Skolithos-Cylindrichnus assemblage

The presence of *Cylindrichnus* and *Skolithos* is typical of this assemblage; *Helminthoidichnites* constitutes an accessory element. The degree of bioturbation is generally low, rarely moderate; Ichnofabric Index 2-3 is inferred for the most of the occurrences of this assemblage. This assemblage is commonly associated to medium grained sandstones with cross-bedding and hummocky stratification (facies S1).

The mentioned sedimentary features and the widespread occurrence of suspension-feeding strategies probably reflect moderate-/high-energy levels capable to raise considerable suspended material, even though excessive turbidity negatively affects suspension-feeders (cf. Bann & Fielding 2004). The main characteristics of this assemblage are simple forms, low diversity, low degree of bioturbation, locally prolific trace densities and absence of complex burrow systems.

They point to a stressed community and/or opportunistic colonization in shallow settings. All these features are consistent with a number of environmental conditions, although in the Pramollo Group they mainly point to estuarine, brackish water settings. In fact the *Skolithos-Cylindrichnus* assemblage is markedly characterized by varying intensity of bioturbation and patchy distribution of traces, which are elements common of brackish water ichnofaunas (Buatois *et al.* 2005). Moreover, the assemblage laterally passes to *Psammichnites-Skolithos-Cylindrichnus* assemblage, which presents clear evidences of estuarine conditions. Sedimentary structures (trough cross-bedding, planar lamination) are also consistent with this environmental interpretation.

Several stress factors characterize estuarine environments, such as considerable fluctuations in salinity, hydrodynamic energy and sedimentation rates. They are often responsible for low-diversity assemblages dominated by vertical burrows. Buatois *et al.* (2005) cite *Cylindrichnus* and *Skolithos* as common constituents of Palaeozoic estuarine settings. Pemberton *et al.* (2001) quotes a *Skolithos-Cylindrichnus* assemblage as a typical expression of brackish channel environment, characterizing estuarine point bar deposits. Consequently, it is convenient to interpret the *Skolithos-Cylindrichnus* assemblage as an estuarine, brackish water association.

Psammichnites-Skolithos-Cylindrichnus assemblage

Meniscate traces, vertical and simple horizontal structures are characteristic of this assemblage. The commonest ichnogenera include *Planolites*, *Cylindrichnus*, *Skolithos*, *Psammichnites*, *Helminthoidichnites*, *Archaeonassa*, *Parataenidium*, *Pramollichnus*. *Taenidium?* and *Beaconites?* occur frequently. This assemblage presents a high lateral variability. The traces are distributed in patches, laterally passing to non-bioturbated sandstones or to *Skolithos-Cylindrichnus* assemblage.

The major ichnogenera constituting the ichnoassemblage have been reported from shallow environments, marine or freshwater-influenced (e.g. Keighley & Pickerill 1994; Buckman 2001; Pemberton *et al.* 2001; Buatois *et al.* 2005). Several elements are indicative of a freshwater-influenced environment for the ichnoassemblage from Pramollo:

1. Patchy distribution of traces can reflect stressful conditions that result from fluctuating environmental parameters (Buatois *et al.* 2005). This element, the low- to moderate degree of bioturbation and the varying intensity of bioturbation point to stressed communities from brackish water settings (i.e Buatois *et al.* 1997b; Pemberton 1998; Gingras *et al.* 1999; Pemberton *et al.* 2001; Taylor *et al.* 2003; Mángano & Buatois 2004).
2. *Psammichnites* is a common constituent of lower estuarine deposits during the Carboniferous (Buatois *et al.* 2005; Buatois & Mángano 2007);
3. *Cylindrichnus* and *Skolithos* are frequently reported from estuarine, brackish water deposits (Pemberton *et al.* 2001; Buatois *et al.* 2005);
4. Meniscate traces are abundantly described from freshwater-influenced settings (e.g. Buatois & Mángano 2007).

At light of these elements and the prevailing sedimentary features (facies S1), it seems convenient to refer this assemblage to estuarine settings. This hypothesis is confirmed by Buatois *et al.* (2005): associated *Psammichnites*, *Skolithos* and *Cylindrichnus* are typical representatives of lower estuarine settings during the Carboniferous. Moreover, the association of efficient behavioural programs (*Pramollichnus)* with inefficient ones (*Skolithos, Cylindrichnus*) has been interpreted as the effect of patchy food resources in a stressful environment; see *Pramollichnus* for more details.

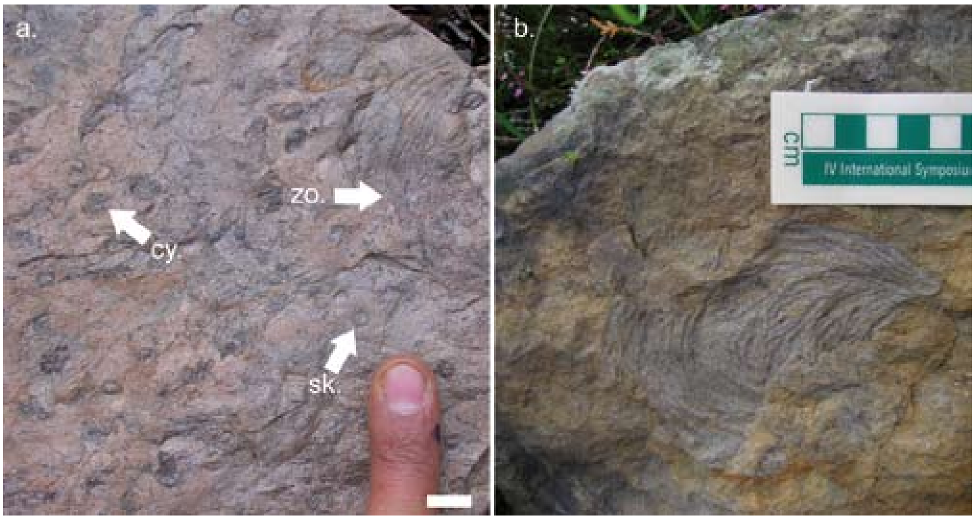

Fig. 19 - Features of *Zoophycos-Skolithos-Cylindrichnus* assemblage. a. Typical occurrence of the assemblage found nearby Monte Corona. *Zoophycos* (Zo), *Skolithos* (Sk), *Cylindrichnus* (Cy). Scale bar 1 cm. b. *Zoophycos* in coarse-grained sandstone. Monte Carnizza, Auernig Formation.

Fig. 19 - Icnoassociazione Zoophycos-Skolithos-Cylindrichnus*. a.* Zoophycos *(Zo),* Skolithos *(Sk),* Cylindrichnus *(Cy). Scala 1 cm. B.* Zoophycos *in arenarie grossolane. Monte Carnizza, formazione dell'Auering.*

Zoophycos-Skolithos-Cylindrichnus assemblage

This assemblage (Fig. 19) is characterized by *Zoophycos* associated to vertical traces (*Skolithos*, *Cylindrichnus*). It is related to sandstones with hummocky-cross-lamination and storm-horizons (facies S2) which are indicating sediments deposited during high-energy events. *Cylindrichnus* and *Skolithos* are in line with this interpretation, as they are usual indicators of high energy, shallow marine and deltaic environments (e.g. Alpert 1974; Pemberton *et al.* 2001; Frey 1990). *Zoophycos* apparently does not fit well in this scenario. In fact *Zoophycos* is usually associated to fine sediments deposited in quiet settings, at times being related to dysoxic conditions (Olivero & Gaillard 2007). Nevertheless, it is demonstrated that complex foraging strategies may also occur in shallow environments when resources are predictable (Minter *et al.* 2006) or patchy (Koy & Plotnick 2007). The sedimentary framework of the *Zoophycos-Skolithos-Cylindrichnus* assemblage indicates storm-deposition which is more consistent with patchy resources rather than predictable ones. *Zoophycos-Skolithos-Cylindrichnus* assemblage would represent sand bodies rapidly emplaced in shallow settings and colonized by tracemakers adapted to stressful conditions. This environmental interpretation is confirmed by the widespread occurrence of *Zoophycos* in estuarine deposits from the Carboniferous (Martino 1989; Buatois *et al.* 2005; Mángano & Buatois 2007).

Curvolithus (large)-Ancorichnus-Skolithos assemblage

This assemblage (Fig. 20) is particularly rich in horizontal traces such as *Curvolithus* (large forms), *Ancorichnus* and *Archaeonassa*. Vertical traces (*Skolithos* and *Cylindrichnus*) are also well- represented. Intensity of bioturbation is variable, usually moderate (Ichnofabric Index 3-4).

The assemblage is characterized by a mixed association of horizontal and vertical burrows. Horizontal traces are attributable to mobile deposit-feeders and predators, while ver-

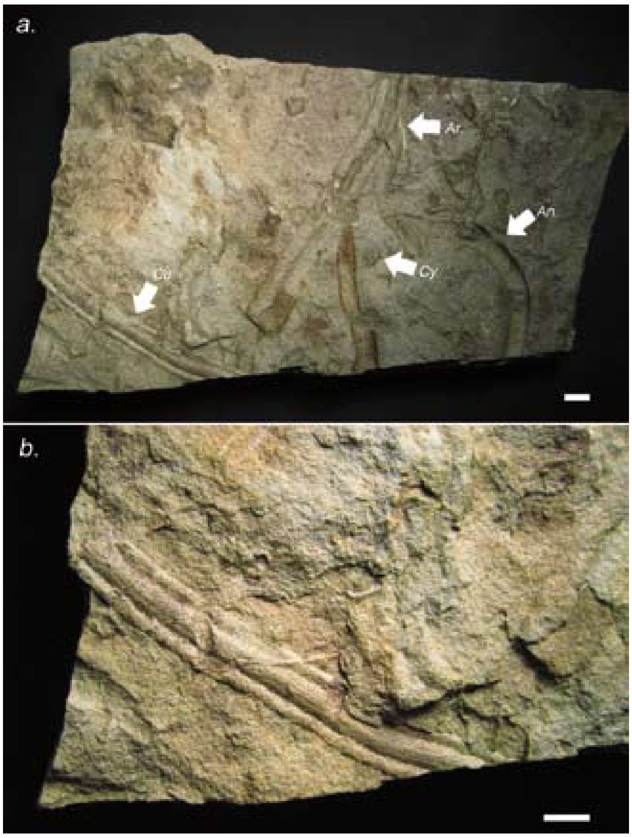

Fig. 20 - *Curvolithus-Ancorichnus-Skolithos* assemblage. Scale bar 1 cm. a. This slab presents the typical features of the *Curvolithus-Ancorichnus-Skolithos* assemblage: *Curvolithus* (Cu), *Ancorichus* (An), *Cylindrichnus* (Cy), *Archaeonassa* (Ar). b. Detail of the *Curvolithus* represented in a.

Fig. 20 - Associazione Curvolithus-Ancorichnus-Skolithos*. Scala 1 cm. a. Questa lastra presenta le tipiche caratteristiche dell'associazione* Curvolithus-Ancorichnus-Skolithos*:* Curvolithus *(Cu),* Ancorichus *(An),* Cylindrichnus *(Cy),* Archaeonassa *(Ar). b. Dettaglio dell'esemplare di* Curvolithus *raffigurato in a.*

tical traces may point to suspension-feeding strategies. With respect to these elements, it is convenient to group this assemblage into the proximal *Cruziana* ichnofacies. The presence of deposit- and suspension-feeding reflects the availability of both suspended and deposited material: the assemblage corresponds to a moderately agitated environment. This interpretation is supported by the associated sedimentary structures (cross-lamination, bioclastic horizons) and by the abundant occurrence of *Curvolithus*, which is probably reflecting a deltaic-influenced, nearshore setting (see Lockley *et al.* 1987; Buatois *et al.* 1998).

Pyritised assemblage

This assemblage is characterized by unlined, horizontal or inclined burrows with pyrite-enriched fills. The pyritised fill is not easily distinguishable from the host rock and the spatial features of the traces are not easily understandable. Consequently the general form of these burrows (linked by common preservational features) is only ambiguously inferred. Probably this preservational style regards diverse ichnotaxa (*Skolithos? Arenicolites? Planolites?*). The assemblage is found within dark-coloured sandstones frequently associated with coal lenses (facies S4).

Although the ichnotaxonomic position is ambiguous, the preservational style is linked with precise environmental conditions. In fact abundance of organic matter and pyritisation are significant of reducing, dysoxic setting.

3.3. Marine assemblages

Curvolithus (small) - *Beaconites* assemblage

The most characterizing elements of this assemblage are *Curvolithus* (small form) and *Beaconites.* Accessory components include *Archaeonassa*, *Helminthoidichnites tenuis* and *Planolites*. Vertical traces are scarce. The intensity of bioturbation is often significant (bedding plane bioturbation index: 4-5; ichnofabric index: 2-4). The assemblage is typified by the abundance of horizontal traces produced by mobile organisms and rare vertical traces. These elements correspond to the *Cruziana* ichnofacies. The extreme paucity of vertical traces possibly reflects the scarceness of suspended organic material. Consequently it is possible to infer a marine environment with moderate/low hydrodynamics, while the consistent and uniform bioturbation is probably mirroring uniform salinity.

The scarceness of vertical structures and the small size of *Curvolithus* are coherent with a distal position respect to the *Curvolithus* (large) - *Ancorichnus-Skolithos* assemblage. *Curvolithus-Beaconites* assemblage probably represents a transition between deltaic-influenced nearshore settings (*Curvolithus-Ancorichnus-Skolithos* assemblage) and lower offshore environments (*Zoophycos-Beaconites* assemblage, described below).

Zoophycos-Beaconites assemblage

This assemblage includes *Zoophycos* and *Beaconites. Helminthoidichnites tenuis* and *Curvolithus* (small forms) are accessory elements. *Zoophycos-Beaconites* assemblage presents common sedimentary and ichnological features with the above-described *Curvolithus-Beaconites* assemblage (Fig 21). Consequently, the here considered assemblage is referred to marine settings typified by uniform salinity and moderate/low hydrodynamic energy. However, *Zoophycos-Beaconites* assemblage possibly reflects a slightly deeper environment than *Curvolithus-Beaconites* assemblage. The abundance of *Zoophycos* together with the relative scarceness of *Curvolithus* is possibly related with quie-

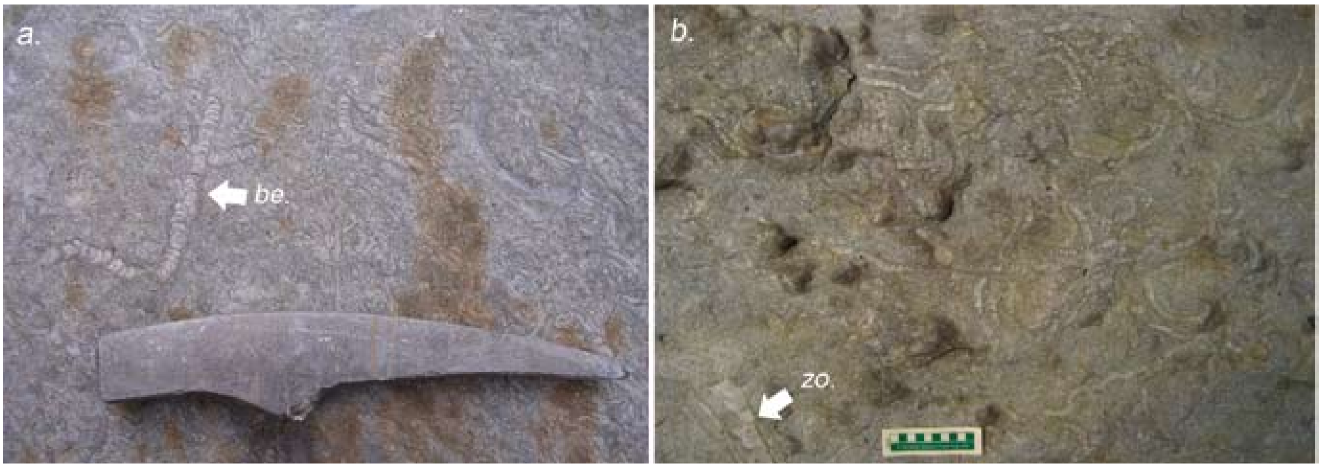

Fig. 21 - When analyzing stratigraphical sections, *Zoophycos-Beaconites* assemblage often passes vertically to *Curvolithus-Beaconites* assemblage. a. Distinct examples of *Beaconites* (be) and pervasive bioturbation by *Curvolithus*. b. *Zoophycos-Beaconites* assemblage with a distinct *Zoophycos* lamina (zo).

Fig. 21 - L'associazione Zoophycos-Beaconites *ha spesso termini transizionali con l'associazione* Curvolithus-Beaconites*. a. Esemplari di Beaconites (be) e intensa bioturbazione per mezzo di* Curvolithus *b. Associazione* Zoophycos-Beaconites *con una lamina di* Zoophycos *(zo).*

Fig. 22 - *Zoophycos-Beaconites* assemblage. a. Typical aspect of *Zoophycos-Beaconites* assemblage. Hammer as scale. b. Detail of a.
Fig. 22 - Associazione Zoophycos-Beaconites*. a. Aspetto tipico dell'associazione* Zoophycos-Beaconites*. Martello come scala. b. Dettaglio di a.*

ter, more distal settings than *Curvolithus* (small) - *Beaconites* assemblage.

Zoophycos assemblage

Zoophycos assemblage (Fig. 22) occurs within micaceous sandstones (facies S3) and siltstones with marine body fossils (facies P1). This assemblage is characterized by the predominant occurrence of *Zoophycos* accompanied by mottling (facies S3) or associated to rare *Planolites* and doubtful specimens of *Chondrites* (facies P1). The traces constituting the assemblage are known for occupying a vast bathymetrical range. In fact *Zoophycos* has been registered from the nearshore to deep basin, while *Planolites* and *Chondrites* are typical facies-crossing ichnogenera (Seilacher 2007). Consequently, we took into account sedimentary facies to better define the palaeoenviroment.

1. *Facies P1.* Fine grain-size and marine body fossils point to a quiet, fully marine environment. Low-oxygen conditions are confidently assigned to facies P1 because of the association with *Chondrites* and for the sedimentary features (dark siltstones with abundant pyrite) (see Pemberton *et al.* 2001). These elements and the dominance of *Zoophycos* indicate dysoxic settings below the wave-base. These conditions are common to quiet-water, lower offshore-shelf environments.
2. *Facies S3.* The diffuse mottling demonstrate that bioturbation had enough time to disrupt shallow tiers, preserving only deeper ones (*Zoophycos*). Lack of vertical structures can be related to mottling or, most probably, it reflects the absence of suspension feeders. These elements induce to consider quiet, fully-marine settings below the wave base; the assemblage is correspondent to the *Zoophycos* ichnofacies. With respect to these elements, it is convenient to refer this assemblage to lower offshore-shelf environments.

In conclusion, *Zoophycos* assemblage indicate offshore to shelf settings; its occurrence within facies P1 is related with dysoxic conditions.

Dictyodora-Nereites assemblage

The diagnostic components of this assemblage are *Dictyodora* and *Nereites*, whereas *Protopalaeodictyon* is an accessory component (Fig. 23). The major constituents of this ichnoassemblage are regarded as typical traces of deep-marine environments (Wetzel 2002; Wetzel & Uchman 2001; Benton 1982; Orr *et al.* 1996; Seilacher 2007). Sedimentary features such as turbidites and the predominance of fine sediments support this hypothesis. However, the presence of vegetal remains implies a not too far continental area, although there are no obvious evidences of a delta-front setting. The *Dictyodora-Nereites* assemblage is interpreted as a deep-marine, mainly disaerobic suite, where specialists exploited food resources leaving complex geometrical patterns.

4. CONCLUSIONS

Pramollo ichnolagerstätte

Pramollo has been renowned as an outstanding site for paleoflora, paleofauna and sedimentary geology since the 19th century, but, until now, it received only little attention with respect to its abundant, diversified and well-preserved ichnofauna. Pramollo exhibits an extraordinary quality and quantity of ichnological information. For these reasons it can be

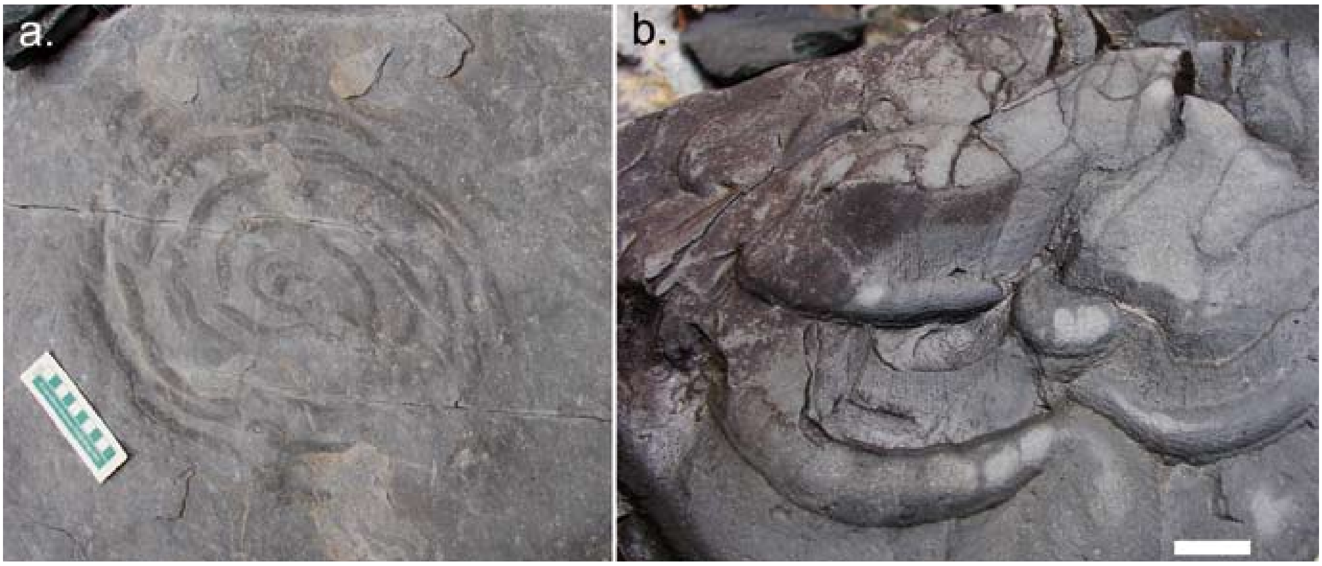

Fig. 23 - *Dictyodora-Nereites* assemblage. a. Pramollo ichnolagerstätte bears enormous *Dictyodora*: the figured specimen measures about 50 cm of diameter. b. *Dictyodora* is represented by an upper, striated part and a lower bioturbated string; some specimens (like the figured one) present delicate striations in the lower bioturbated string.
Fig. 23 - Associazione di Dictyodora-Nereites*. a. L'ichnolagerstätte del Pramollo presenta* Dictyodora *di dimensioni notevoli: l'esemplare in figura ha 50 cm di diametro. B.* Dictyodora *è rappresentata da una parte superiore striata e una stringa inferiore bioturbata. Alcuni esemplari (come quello in figura) presentano delicate strie nella stringa inferiore.*

erected as an ichnolagerstätte and, more precisely, it can be defined as a conservation-ichnolagerstätte (Savrda 2007) for the fine preservation of the ichnofossils.

Ichnofauna

The commonest ichnogenera of the Pramollo ichnolagerstätte are *Parataenidium moniliformis*, *Dictyodora liebeana*, *Curvolithus simplex* (form 1 and 2), *Psammichnites* cf. *plummeri*, *Nereites jacksoni*, *Ancorichnus* isp., *Beaconites* isp. (form 1 and 2), *Cylindrichnus* isp., *Planolites* isp., *Helminthoidichnites tenuis*, *Skolithos* isp., *Zoophycos* isp., *Archaeonassa* isp., *Protopaleodictyon* isp., *Asterosoma* isp. (form 1 and 2) and the new ichnogenus *Pramollichnus pastae.*

Pramollichnus pastae

The new ichnogenus *Pramollichnus pastae* is a crescent-shaped trace constituted by curved, juxtaposed burrows connecting two apical points. *Pramollichnus* is interpreted as the result of systematic exploitation of the substrate. The trace occurs in lower estuary deposits, associated with meandering/winding traces (*Psammichintes,* meniscate traces) and vertical structures (*Skolithos, Cylindrichnus*). The behaviour is interpreted to reflect the exploitation of patchy resources in a stressful environment.

Ichnoassemblage analysis

Nine recurrent ichnoassemblages have been distinguished in the Pramollo ichnolagerstätte. A group of ichnoassemblages is consistent with estuarine conditions and presents features significant of brackish ichnofaunas (i.e. Remane & Schlieper 1971; Pemberton 1998; Mángano & Buatois 2004): abundant and moderately large estuarine-related ichnogenera, impoverished marine ichnoassemblages, a low to moderate degree of bioturbation, patchy bioturbation, vertical and horizontal traces typical of *Skolithos* and *Cruziana* ichnofacies.

A second group of ichnoassemblages shows marine features: estuarine-related ichnogenera are absent or they present a small size, degree of bioturbation is constant and usually intense. Marine ichnoassemblages are dominated by small or horizontal traces and/or 3D-spreite structures common of *Nereites*, *Zoophycos* or distal *Cruziana* ichnofacies.

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