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TRACE FOSSILS IN THE "FLYSCH DEL GRIVÒ" (YPRESIAN) IN THE JULIAN PRE-ALPS, NE ITALY: PRELIMINARY OBSERVATIONS*

TRACCE FOSSILI NEL "FLYSCH DEL GRIVÒ" (YPRESIANO) NELLE PREALPI GIULIE, ITALIA NORD-ORIENTALE: OSSERVAZIONI PRELIMINARI*

Abstract - Twenty four ichnogenera were identified in the two best sections of the Ypresian (Upper Paleocene-Lower Eocene) "Flysch del Grivò" in the Julian pre-Alps. This unit contains a lot of megabeds. A great number of graphoglyptids and other predepositional forms as well as sedimentary features indicate well aerated bottoms. Quick colonization of vast areas of uninhabited sea floor is indicated by occurrence of trace fossils on top of the megabeds as well as by the presence of graphoglyptids on the soles of overlying thin turbiditic beds. Trace fossils are tiered in thin- and medium bedded turbidites and on top of the megabeds.

Key words: Trace fossils, Flysch, Ypresian, Julian pre-Alps, NE Italy.

Riassunto breve - *Ventiquattro ichnogeneri sono stati identificati nelle due successioni più significative del "Flysch del Grivò" (Ypresiano) affiorante nelle Prealpi Giulie. L'elevato numero di grafoglittidi e di altre forme predeposizionali così come le caratteristiche sedimentologiche stanno ad indicare un fondo ben ossigenato. La rapida colonizzazione di vaste aree dei depositi del fondo marino, in precedenza non popolate, è dimostrata dal rinvenimento di tracce fossili nei livelli sommitali dei megabanchi e dalla presenza di controimpronte di grafoglittidi nei sottili strati torbiditici soprastanti il megabanco. Le tracce fossili sono organizzate verticalmente (tiering) soprattutto dove la sequenza è caratterizzata da predominanti strati torbiditici fini e medio-fini e al top dei megabanchi.*

Parole chiave: *Tracce fossili, Flysch, Ypresiano, Prealpi Giulie, Italia nord-orientale.*

Introduction

Trace fossils provide important data about palaeoenvironmental parameters, especially

on oxygenation, food supply, rate of sedimentation, turbulence, and palaeodepth (FREY, 1975; CRIMES & HARPER, 1970, 1977; EKDALE et al., 1984; BROMLEY, 1990, and others). Considered here is the Ypresian "Flysch del Grivò" on the Italian part of the Julian pre-Alps (Fig. 1) which displays abundant trace fossil assemblages. The assemblages contain 30 ichnogenera which belong to almost all morphological groups. An occurrence of spectacular megabeds, interbedded with thin packages of "normal" flysch deposits, is the main feature of the "Flysch del Grivo". Thus, we have an opportunity to observe the influence of deposition of the megabeds on benthic life registered in trace fossils.

This paper provides preliminary data on taxonomic composition and palaeoecology of trace fossils in the two best sections of the "Flysch del Grivò", namely in the Vernasso quarry and in the Montina-Mt. Noas section (section A and section B respectively in Fig. 1). Data on sedimentology and general geology of these sections were provided by the first co-author (GT) while the ichnological work was done by the second co-author (AU). The illustrated specimens are housed in the Institute of Geological Sciences of the Jagiellonian University in Krakow and can be found under the abbreviation TFJA.

Geological setting

The Julian Basin (or the Slovenian Basin) was a narrow, elongated basin limited by a carbonate platform (Friuli Platform) along its southern border. From the Maastrichtian up to the Early Eocene the basin, located in the Julian pre-Alps and Tolmin Mountains, was characterized by a mixed carbonate/siliciclastic depositional system. Within the stratigraphic framework of the Julian Basin, carbonate megabeds are particularly frequent during the Thanetian-Ypresian. These megabreccia deposits are related to strong tectonic activity that occurred along the margin of the Friuli Platform (TUNIS & VENTURINI, 1992). The thick sequence with the most important carbonate megabeds was subdivided into two informal stratigraphic units, called " Flysch di Masarolis" (PIRINI et al., 1986) and "Flysch del Grivò" (TUNIS & VENTURINI,1987b) respectively.

The "Flysch del Grivò" (Upper Paleocene p.p.-Lower Eocene p.p.) crops out in the Southern Julian pre-Alps (region of the Torre Valleys and Natisone Valleys) and continues through western Slovenia (Goriška Brda) to the Banjšice plateau region (Anhovo). TUNIS & VENTURINI (1987b) mark the beginning of the "Flysch del Grivò" sequence with a giant complex megabed, called "Mt. Ioanaz Megabed". The "Flysch del Grivò" sequence reaches a maximum thickness of 1450 m and is characterized by several spectacular megabeds. The megabeds roughly make up half of the entire thickness of the sequence. The megabeds gradually thin and become less frequent in the upper part of the section. Between the
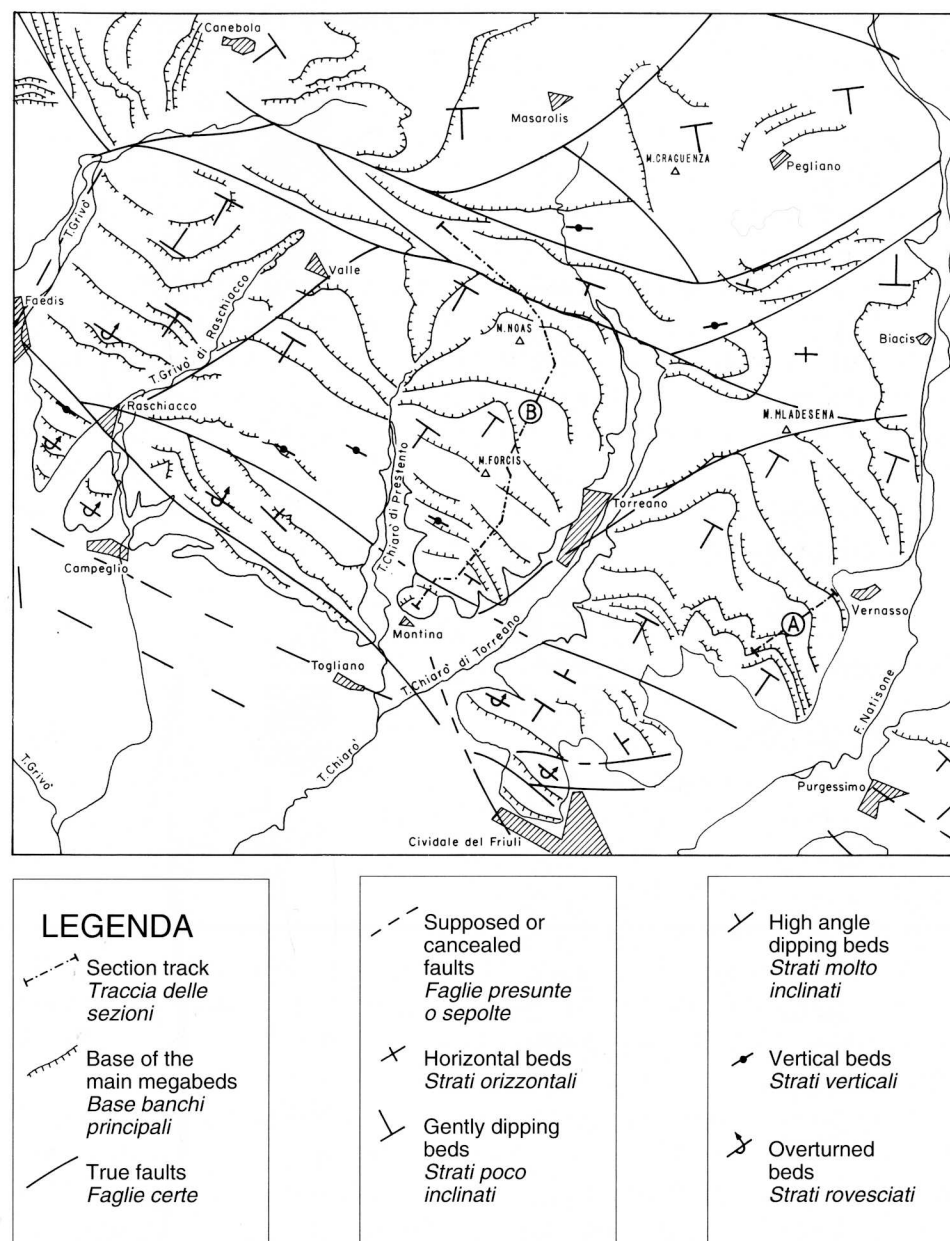
LEGENDA

Section track
Traccia delle sezioni

Base of the main megabeds
Base banchi principali

True faults
Faglie certe

Supposed or cancealed faults
Faglie presunte o sepolte

Horizontal beds
Strati orizzontali

Gently dipping beds
Strati poco inclinati

High angle dipping beds
Strati molto inclinati

Vertical beds
Strati verticali

Overturned beds
Strati rovesciati

Fig. 1 - Location map showing extension of the main megabeds of the "Flysch del Grivò" in the study area. Examined sections A and B of Figs. 2 and 3 respectively.
- *Ubicazione dell'area esaminata con i principali megabanchi del "Flysch del Grivò". Le sezioni A e B vengono rappresentate nelle Figg. 2 e 3.*
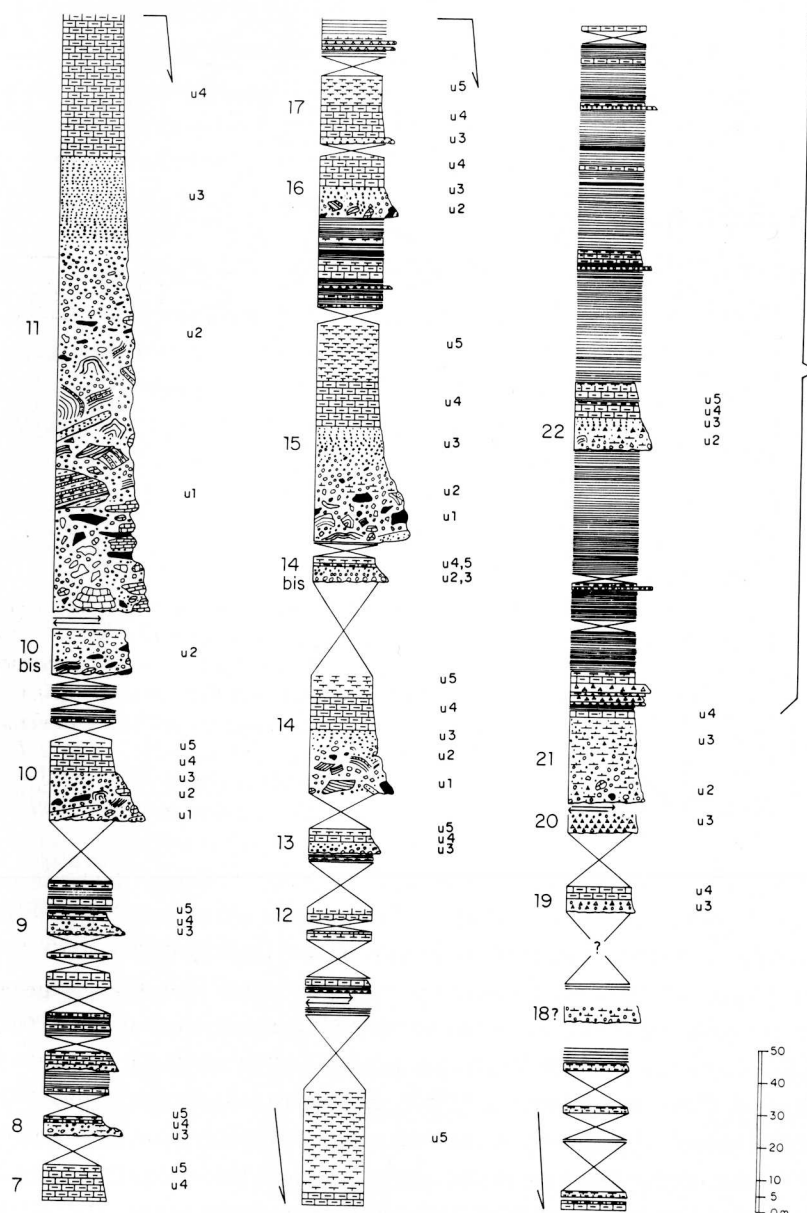
REANT - M.NOAS - FORCIS - MONTINA SECTION

Fig. 2 - Reant-Mt. Noas-Forcis-Montina section. Numbers symbolize individual megabeds; Unit 1, 2, etc. represent internal units of the megabeds.
- *Sezione Reant-M.Noas-Forcis-Montina. I numeri stanno ad indicare i megabanchi principali; U1, U2, ecc. rappresentano le unità interne dei megabanchi.*
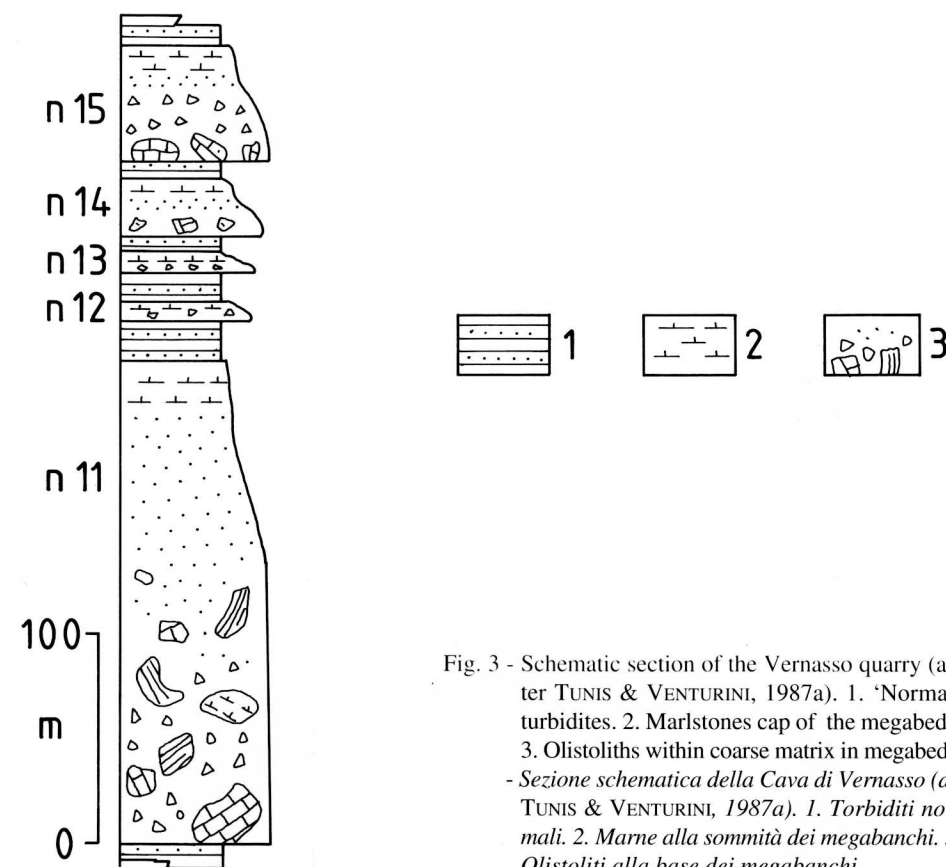
Fig. 3 - Schematic section of the Vernasso quarry (after TUNIS & VENTURINI, 1987a). 1. 'Normal' turbidites. 2. Marlstones cap of the megabeds. 3. Olistoliths within coarse matrix in megabeds.
- *Sezione schematica della Cava di Vernasso (da TUNIS & VENTURINI, 1987a). 1. Torbiditi normali. 2. Marne alla sommità dei megabanchi. 3. Olistoliti alla base dei megabanchi.*

megabeds, siliciclastic turbidites, carbonate turbidites, hybrid (mixed) sandstones, massive calcarenites and debrites can be observed. Siliciclastic distal turbidites and proximal calciturbidites predominate in the lower and middle part of the "Flysch del Grivò" sequence. Siliciclastic, mainly proximal turbidites prevail in the upper part of the sequence. The proximal features of these turbidites may be related to the south-south-eastward prograding of deltaic complexes (TUNIS & VENTURINI, 1992). The "Flysch del Grivò" is overlain by the Flysch di Cormons of Lower to Middle Eocene age. As for the stratigraphy of the "Flysch del Grivò", about fourty sections have been recently measured in Friuli and Western Slovenia: description of the examined sections and of the lateral variations of the megabeds can be found in TUNIS & VENTURINI (1992). Herein the examination of the trace fossils is restricted to two sections measured in the western to central part of the Natisone Valleys (Figs. 1, 2, 3,4).

Tabl. I

G - graphoglyptids

Predepositional forms			Postdepositional forms	
Bergaueria isp.		x	*Sabularia simplex*	x
Laevicyclus isp.		x	*Planolites* isp.	x
Lockeia isp.		x	*P. punctatus*	x
Chondrorhaphe bifada	G	x	*Chondrites* isp.	x
Helminthopsis isp.		x	*Ophiomorpha* isp.	x
Tuberculichnus isp.		x	*Thalassinoides* isp.	x
Spirophycus bicornis		x	*Zoophycos* isp.	x
S. involutissimus		x	*Z.insignis*	x
Cosmorhaphe tremens	G	x	*Phycosiphon incertum*	x
C. ?sinuosa	G	x	*Spirorhaphe* isp.	x
C. lobata	G	x	*Tubulichnium incertum*	x
Spirocosmorhaphe helicoidea	G		*Subphyllochorda* isp.	x
Helicolithus tortuosus	G	x	*Scolicia prisca*	x
Cochlichnus isp.				
?Gordia isp.		x		
Helminthorhaphe crassa	G			
Paleomeandron biserialis	G	x		
Urohelminthoida appendiculata	G			
Protopaleodictyon submontanum	G	x		
P.incompositum	G			
Megagrapton isp.	G	x		
Paleodictyon minimum	G			
P. latum	G	x		
P. strozzi	G			
P. majus	G	x		
18 ichnogenera, 26 ichnotaxa			11 ichnogenera, 13 ichnotaxa	

Trace fossils

Preservation of the trace fossils is highly variable, but, full- and semireliefs occurring on the surface of the beds are dominant. Predepositional as well as post-depositional forms (see KERN, 1980 for references) are represented (tabl. I). The classification of trace fossils by KSIĄŻKIEWICZ (1970, 1977) has been applied. Moreover, the taxonomic divisions by SEILACHER (1977) have been applied to most graphoglyptids. According to the classification of KSIĄŻKIEWICZ (1977), ten morphological groups are distinguished; these are: 1. Circular and elliptical, 2. Simple, 3. Branched, 4. Rosetted, 5. Spreiten, 6. Winding, 7. Spiral, 8. Meandering, 9. Winding and meandering with branches, and 10. Networks.

Systematic description

Circular and elliptical structures

Bergaueria PRANTL 1945
Diagnosis: Hemispherical or cylindrical convex hyporeliefs at the base of which there may be small, central, regular dimples or depressions further surrounded by a few tubercles or ledges; burrow-fill essentially massive (after PEMBERTON et al., 1988).

Bergaueria isp.
(not figured)
Description: Smooth hemispherical convex hyporeliefs up to 2 cm wide and up to 1 cm high with irregular non-distinct depression at the top, passively filled.
Remarks: Similar specimens were assiociated by KSIĄŻKIEWICZ (1977) with *Bergaueria prantli*. *Bergaueria* occurs in shallow-water deposits (NARBONNE, 1984; CRIMES & ANDERSON, 1985) and in flysch deposits (PRANTL, 1945; KSIĄŻKIEWICZ , 1977). It is probably a cubichnial or domichnial form produced by suspension feeders (FÜRSICH, 1975). These were probably coelenterates, chiefly sea anemones (PRANTL, 1945; ALPERT, 1973; PEMBERTON et al., 1988) similar to living *Cerianthus* or *Edwardsia* (PEMBERTON et al., 1988). Sea anemones are very widely distributed ranging from estuaries to abyssal plains (e.g., CARNEY, 1981). *Bergaueria* has been identified from the late Precambrian (e.g., CRIMES, 1987) to the Palaeogene (KSIĄŻKIEWICZ , 1977).

Laevicyclus QUENSTEDT 1879
Diagnosis: Approximately cylindrical bodies standing at right angles to the bedding plane; diameter variable in some specimens; perforated by central canal, visible on bedding planes as regular concentric circles with a diameter of several cm (after HÄNTZSCHEL, 1975).

Laevicyclus isp.
(Fig. 5A)
Description: Hypichnial elliptical convex ring, 18-20 mm in diameter, with central knob. The ring is about 2 mm thick and commonly discontinuous.

Fig. 4 - The megabeds 11 and 12 and overlying and underlying packages of flysch in the Vernasso quarry.
- *I megabanchi n.11 e n.12 con i pacchi di torbiditi sopra e sottostanti osservabili nella Cava di Vernasso.*

Remarks: *Laevicyclys* occurs in deep-water flysch deposits (D'ALESSANDRO, 1980, 1981; PIEŃKOWSKI & WESTWALEWICZ-MOGILSKA, 1986; UCHMAN, 1990a, LESZCZYŃSKI & SEILACHER, 1991, and others) as well as in shallow-water deposits (FREY & HOWARD, 1970; KENNEDY, 1970; NARBONNE, 1984). *?Laevicyclus* has been described from the Permian continental red beds in Germany (BOY, 1976). *Leavicyclus* is compared to the feeding trace of sedentary annelide *Scolecolepis squamata* which creates a circular trace, but only in calm waters (SEILACHER, 1953a, b). As calm hydrodynamic conditions on the bottom colonized by the *Laevicyclus* producer were not calm, the origin of this ichnogenus is unclear (cf. KEMPER, 1968, p. 79-80; FREY, 1970). There are opinions that this form could be produced by gas expulsion from the sediment (SCHMIDT 1934 in HÄNTZSCHEL, 1975; BOYD, 1975). Nevertheless, the here described forms are not the result of casting of a crater-like topography, which could have been made by gas, but by casting of delicate regular concave rings with a small central and vertical canal of organic origin.

     Laevicyclus has been identified from the Precambrian (CRIMES, 1987) to the Miocene (D'ALESSANDRO, 1980).

Lockeia JAMES 1879

Diagnosis: Small oblong horizontal bodies, rounded or pointed at both ends, which resemble the end of an almond projecting above the surface. Preservation as convex hyporelief or concave epirelief. Surface normally smooth, although a longitudinal crest may be present. Vertical section may reveal an overlying shaft of disturbed bedding conforming to the measurement of the specimen (after OSGOOD, 1970).

Lockeia isp.
(not figured)

Description: Convex hyporelief, elongate, consisting of smooth oval structure, about 30 mm long, about 15 mm wide, up to 5 mm high.

Remarks: Passive infilling shows that *Lockeia* is a predepositional form. *Lockeia* is a synonym of *Pelecypodichnus* SEILACHER (MAPPLES & WEST, 1988). The specimen illustrated by CRIMES (1977, Pl. 3d) from the Eocene flysch of northern Spain as *Pelecypodichnus* has been described as *Naviculichnium marginatum* by KSIĄŻKIEWICZ (1977).

     This form is regarded as a cubichnial trace of pelecypods (SEILACHER, 1953b), typical of deltaic deposits *sensu lato* (cf. CRIMES et al., 1981). *Lockeia* occurs in deposits of diverse environments from shallow-water, brackish (e.g., PIEŃKOWSKI, 1985), continental (BROMLEY & ASGAARD, 1979), to flysch deposits (CRIMES et al., 1981; UCHMAN, 1991a). It has been identified from the Ordovician (HÄNTZSCHEL, 1975) to the Pliocene (RINDSBERG, 1977).

Fig. 5 - Trace fossils in the Vernasso quarry. A. *Laevicyclus* isp., sole of turbidite sandstone. B. *Sabularia simplex* and *Cosmorhaphe* isp. (C), sole of turbidite sandstone. C. *Tuberculichnus* isp. D. *Thalassinoides* isp., sole of turbidite sandstone. E. *Tuberculichnus* isp. (the bigger and smaller form) sole of turbidite sandstone. F. *Zoophycos* isp., top of turbidite sandstone. Lense cap is 55 mm in diameter and the match 44 mm long and 2 mm thick.

- *Tracce fossili osservate nella Cava di Vernasso. A.* Laevicyclus *isp., controimpronta alla base della porzione arenitica delle torbiditi. B.* Sabularia simplex *e* Cosmorhaphe *isp. (C), controimpronte. C.* Tuberculichnus *isp. D.* Thalassinoides *isp., controimpronta, E.* Tuberculichnus *isp. (forma grande e piccola), controimpronta, F.* Zoophycos *isp. al top della porzione arenitica delle torbiditi. Il tappo dell'obiettivo ha un diametro di 55 mm e il fiammifero è lungo 44 mm e spesso 2 mm.*
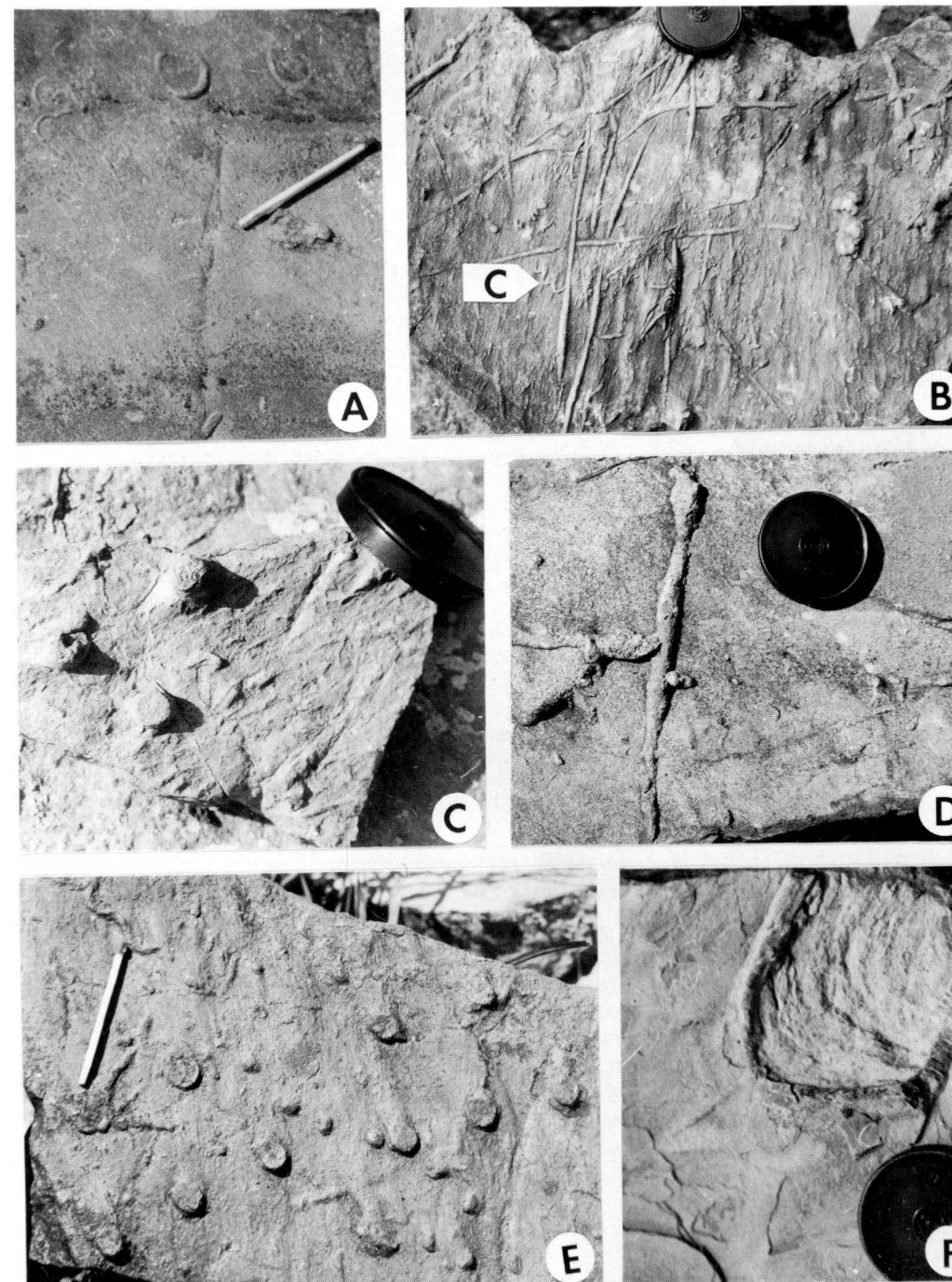
Simple structures

Sabularia KSIĄŻKIEWICZ 1977

Amended diagnosis: Mainly horizontal smooth full relief, straight or feebly curved, only rarely ramified (modified after KSIĄŻKIEWICK, 1977).

Sabularia simplex KSIĄŻKIEWICZ 1977
(Figs. 5B, 6D-E)

Diagnosis: Hypichnial, more rarely endichnial, epichnial or exichnial, string-sized cylindrical full relief, long, more or less straight, with smooth surface (after KSIĄŻKIEWICZ, 1977).

Description: Smooth straight or slightly curved, horizontal or slightly oblique, presumably hypichnial but also endichnial and rarely exichnial cylindrical burrows, 3-4 mm in diameter. They are preserved as full reliefs, rarely as convex semireliefs when hypichnial. The burrows are usually branched with swellings at the point of branching. Occasionally, the branches are very short forming dead ends. The tubes are 5-8 mm in diameter.

Remarks: This ichnotaxon is usually described as *Granularia* (e.g., SEILACHER, 1964; LESZCZYŃSKI, 1991). However, *Granularia* has distinct pellets covering its wall (HÄNTZSCHEL, 1975). *Sabularia* lacks any pellets. The type material of *Granularia* should be reinvestigated to clear this nomenclatorial problem. *Sabularia simplex* cross-cuts all other forms. It was produced probably by extremely deep burrowers. SEILACHER (1964) reported it from a sole of 5 m thick turbidite bed. The dead-ends are probably remains of incompletely filled tunnels linking the horizontal burrow system. Thus, *Sabularia* forms a box-work maze similar to *Ophiomorpha-Thalassinoides* (cf. FREY et al., 1978). These similarities show that *Sabularia* was produced probably by crustaceans (cf. SEILACHER, 1977). *Sabularia simplex* has been identified from the Valanginian to the Oligocene (KSIĄŻKIEWICZ, 1977).

Planolites NICHOLSON 1873

Diagnosis: Unlined, rarely lined, rarely branched, straight to tortuosus, smooth to irregularly walled or annulated burrows, circular to elliptical in cross-section, of variable dimensions and configurations: infilling essentially structureless, differing in lithology from host rock (after PEMBERTON & FREY (1982) and FILLION & PICKERILL (1984)).

Fig. 6 - Trace fossils in the Vernasso quarry. A. *Zoophycos* isp. (Z), *Chondrites* isp. (CH), cross section of the top of the megabed 12, polished slab of marlstone. B. *Chondrorhaphe bifada*, sole of turbidite sandstone. C. *Helminthorhaphe crassa*, sole of turbidite sandstone. D. *Cochlichnus* isp. (C) and *Sabularia simplex* (S), sole of turbidite sandstone. E. *Paleodictyon minimum* (P) and *Sabularia simplex* (S), sole of turbidite sandstone. F. *Cosmorhaphe ?sinuosa*, sole of turbidite sandstone. Lense cap is 55 mm in diameter and the match 44 mm long and 2 mm thick. Scale bar on B and D is 2 cm long.

- *Tracce fossili nella Cava di Vernasso. A. Zoophycos isp. (Z), Chondrites isp., sezione trasversale al top del megabed n.12, superficie esposta di marna. B. Chondrorhaphe bifada, controimpronta alla base della porzione arenitica delle torbiditi. C. Helminthorhaphe crassa, controimpronta. D. Cochlichnus isp. e Sabularia simplex, controimpronte. E. Paleodictyon minimum (P) and Sabularia simplex (S), controimpronte. F. Cosmorhaphe ? sinuosa, controimpronta. Il tappo dell'obiettivo ha un diametro di 55 mm e il fiammifero è lungo 45 mm e spesso 2. La scala di riferimento su B e D è lunga 2 cm.*
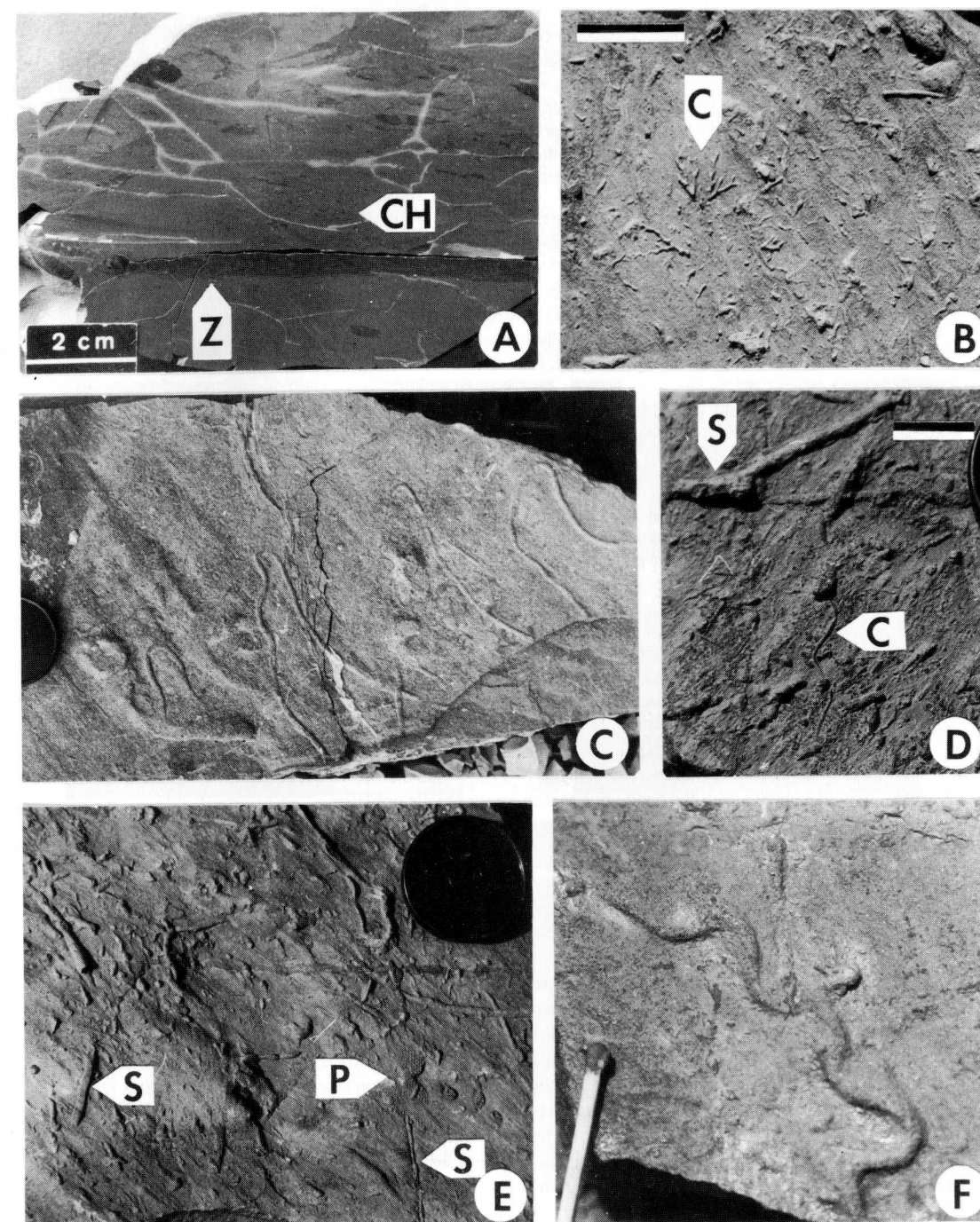
Planolites punctatus RONIEWICZ et PIEŃKOWSKI 1977
(not figured)

Diagnosis: Isolated, usually ovate and irregularly ornamented knobs or short ridges (after RONIEWICZ et PIEŃKOWSKI, 1977).

Description: Oval, convex hypo- and rarely, epireliefs, 3-8 mm in diameter, forming various knobs.

Remarks: This ichnospecies was included in *Planolites montanus* by PEMBERTON & FREY (1982), but *P. punctatus* stands out in a vertical development of burrows in comparison to *Planolites montanus* (PIEŃKOWSKI & WESTWALEWICZ-MOGILSKA, 1986). However, in our material it is difficult to distinguish these two taxa.

Planolites isp.
(Fig. 7B)

Description: Cylindrical, horizontal to oblique, unlined burrows, circular to elliptical in cross-section, 2-3 mm in diameter. Their infilling differs from the host rock by lighter colour.

Remarks: *Planolites* is an eurybathic, extremely facies-crossing form referred to polyphyletic vermiform deposit-feeders producing active backfilling (cf. PEMBERTON & FREY, 1982; FILLION & PICKERILL, 1990 with references).

Planolites has been identified from the Precambrian to the Recent (HÄNTZSCHEL, 1975).

Branched structures

Chondrites VON STERNBERG 1833

Diagnosis: Regularly branching tunnel systems consisting in a small number of mastershafts open to the surface which ramify at depth to form a dendritic network (after OSGOOD, 1970; FÜRSICH, 1974a).

Chondrites isp.
(Fig. 6A)

Description: A system of tree-like branched, downward penetrating, markedly flattened tunnels, 1-2 mm in diameter. In cross section, *Chondrites* appears as patches of small, 1-2 mm in diameter, circular or elliptical spots (Fig. 6A) (cf. WERNER & WETZEL, 1981, and others).

Remarks: *Chondrites* is a feeding system of uncertain tracemakers related to infaunal deposit feeders (e.g., OSGOOD, 1970). According to KOTAKE (1991b), this ichnotaxon was produced by surface ingestors, packing their faecal pellets inside burrows. According to FU (1990) and SEILACHER (1990), tracemakers of *Chondrites* may live under anaerobic conditions as a chemosymbiotic organism.

Chondrites has been identified from the Tommotian (CRIMES, 1987) to the Holocene (e.g., WERNER & WETZEL, 1981).

Fig. 7 - Trace fossils in the Vernasso quarry. A. *Taphrhelminthopsis* isp., sole of turbidite sandstone. B. *Paleomeandron biserialis* (P) and *Planolites* isp. (P), sole of turbidite sandstone. C. *Spirophycus involutissimus*, sole of turbidite sandstone. D. *Urohelminthoida appendiculata* (U) and *Paleodictyon latum* (P), sole of turbidite sandstone. E. *Spirorhaphe* isp., top of turbidite sandstone. F. *Spirocosmorhaphe helicoidea*, sole of turbidite sandstone. Lense cap is 55 mm in diameter and the match 44 mm long and 2 mm thick. Scale bar on B is 2 cm long.
- *Tracce fossili nella Cava di Vernasso. A.Taphrhelminthopsis isp., controimpronta alla base della porzione arenitica delle torbiditi. B. Paleomeandron biserialis (P) and Planolites isp. (P), controimpronte. C. Spirorhaphe involutissimus, controimpronta. D. Urohelminthoidea appendiculata (U) and Paleodictyon latum (P), controimpronte. E. Spirorhaphe isp. al top di un'arenaria torbiditica. F. Spirocosmorhaphe helicoidea, controimpronta. Tappo dell' obiettivo di 55 mm di diametro, fiammifero lungo 44 mm e spesso 2 mm. La scala di riferimento su B è lunga 2 cm.*
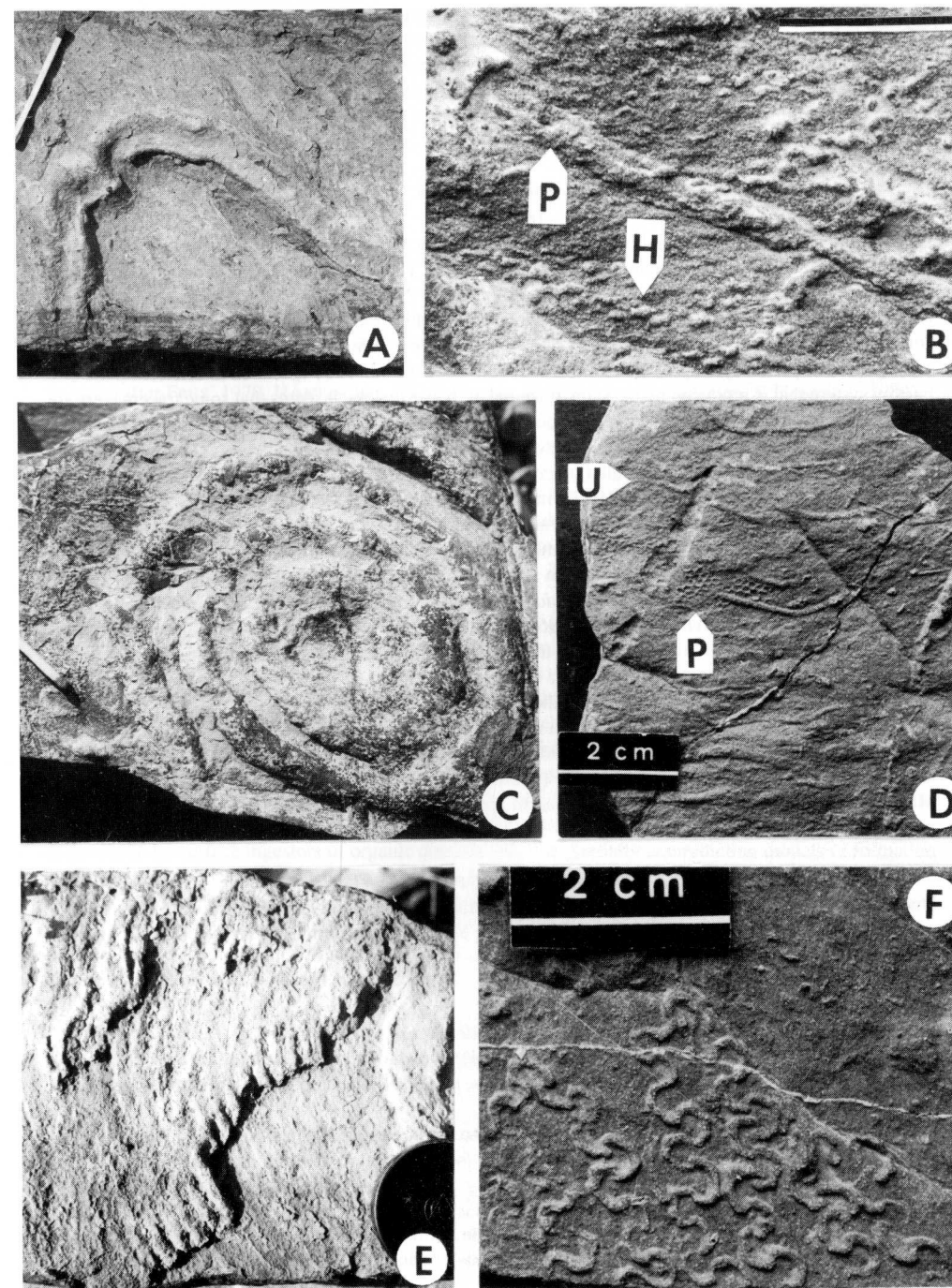
Ophiomorpha LUNDGREN 1891

Diagnosis: Simple to complex burrow systems distinctly lined with agglutinated pelletoidal sediment. Burrow: Lining more or less smooth interiorly: densely to sparsely mammelated or nodose exteriorly. Individual pellets or pelletal masses may be discoid, ovoid, mastoid, bilobate or irregular in shape. Characteristic of the lining may vary within a single specimen (after FREY et al., 1978).

Ophiomorpha isp.
(not figured)

Description: System of endichnial or exichnial, chiefly vertical but also oblique and horizontal cylindrical burrows which are partially covered by pelletoidal knobs. The burrows are 0.8-1.5 cm in diameter. The horizontal burrows are commonly flattened by compaction.

Remarks: Some parts of the burrows lack the knobs and, in this case if horizontal, they resemble *Thalassinoides* (cf. KERN & WARME, 1974). *Ophiomorpha, Thalassinoides, Spongeliomorpha* and *Gyrolithes* are regarded as partial synonyms (FÜRSICH, 1972; BROMLEY & FREY, 1974) related to different parts of a burrow system that is produced by the same tracemaker. Nevertheless, it seems that some tracemakers are able to produce only one type of burrow assigned to one of these ichnotaxa. Thus, separate use of these ichnotaxonomic names is more descriptive and less ambiguous. Full intergradation between *Ophiomorpha* and *Thalassinoides* is observed in the studied outcrops.

Sabularia rudis (KSIĄŻKIEWICZ, 1977), including the holotype, strongly resembles *Ophiomorpha* (UCHMAN, 1991a) and may be regarded as a synonym of the latter. *Granularia* (POMEL, 1849; HÄNTZSCHEL, 1975) differs from *Ophiomorpha* in smaller dimensions, and is regarded as a small "flysch version" of *Spongeliomorpha* (SEILACHER, 1977) which in turn is related to *Ophiomorpha* (FREY et al., 1978).

In the Mesozoic-Cenozoic erathems, *Ophiomorpha* was produced mainly by shrimps compared to today's *Callianassa major* (WEIMAR & HOYT, 1964; FREY et al., 1978). Moreover, other animals, mainly arthropods are able to produce structures related to *Ophiomorpha* (FREY et al., 1978). *Callianassa* is mainly a suspension feeder (PRYOR, 1975; BROMLEY, 1990).

Ophiomorpha occurs predominantly in shallow-water near-shore deposits (WEIMAR & HOYT, 1964; FREY et al., 1978), but has also been reported from deep-sea deposits (KERN & WARME, 1974; CRIMES, 1977; CRIMES et al., 1981; UCHMAN, 1988, 1989, 1990a, b, 1991a) since the Mesozoic (BOTTJER et al., 1987). This ichnogenus occur also in terrestrial deposits (GRADZIŃSKI, 1969 p. 222; STEWARD, 1978; BOWN, 1982; MERRILL, 1984). The forms related to *Callianassa* are known since the Triassic (HÄNTZSCHEL, 1975).

Thalassinoides EHRENBERG 1944

Diagnosis: Three-dimensional burrow systems consisting predominantly of smooth-walled, essentially cylindrical components of variable diameter; branches Y- to T-shaped, enlarged at the points of bifurcation (after HOWARD & FREY, 1984).

Thalassinoides isp.
(Fig. 5D)

Description: Horizontal or oblique cylindrical burrows, having Y-shaped branches, 05-3.0 cm in diameter.

Remarks: In our sections, transition of *Thalassinoides* to *Ophiomorpha* isp. is observed, and its origin, as well as the remarks about its environment, are similar (see description of *Ophiomorpha*).

Chondrorhaphe SEILACHER 1977

Diagnosis: Radial graphoglyptids displaying dichotomous ribs and knoblike marks at most bifurcations (after LESZCZYŃSKI & SEILACHER, 1991).

Chondrorhaphe bifada SEILACHER 1977
(Fig. 6B)

Diagnosis: Same as for ichnogenus.

Description: Root-like branched hypichnial convex semirelief, about 2 mm in diameter. Our specimen has poorly exemplified tubercles.

Remarks: This rarely described form (SEILACHER, 1977; LESZCZYŃSKI & SEILACHER, 1991) was included in graphoglyptids (SEILACHER, 1977).

Spreiten structures

Zoophycos MASSALONGO 1855

Diagnosis: Variable shaped spreiten structures comprised of numerous small protrusive more or less U- or J-shaped burrows of variable length and orientation. Spreite tubular or arranged in helicoid spirals giving an overall outline of circular, elliptical or lobate shape; a central vertical tunnel or marginal tube may be present (after FREY, 1970, HÄNTZSCHEL, 1975, WETZEL & WERNER, 1981; FILLION & PICKERILL, 1984).

Zoophycos insignis SQUINABOL 1890
(not figured)

Diagnosis: *Zoophycos* displaying elongate tongue-like lobes (based on KSIĄŻKIEWICZ's (1977) description).

Description: Tongue-like lobes with spreite structure stretched between narrow marginal tubes. Occasionally, small elliptical pellets are preserved along the spreite laminae.

Remarks: *Z. insignis* may be related to the trumpet-like *Zoophycos* according to WETZEL & WERNER (1981).

Zoophycos isp.
(Figs. 5F, 6A)

Description: A) Planar spreite structure, observed on bedding plane, showing comparatively wide marginal canal (Fig. 5F). B) Horizontal, vertically repeating spreite structure, observed in cross-section, 6 mm thick. A well preserved marginal canal terminates on one side of the structure (Fig. 6A).

Remarks: *Zoophycos* is produced by deposit-feeding, unknown organisms. Their producers are most likely found among sipunculoids (WETZEL & WERNER, 1981), polychaete annelids, arthropods (EKDALE & LEWIS, 1991), and enteropneust hemichordates (KOTAKE, 1992). According to KOTAKE (1989, 1991a), *Zoophycos* is produced by surface ingestors of organic detritus. Diverse, partially contradicting models of formation of *Zoophycos* have been presented (see EKDALE & LEWIS, 1991; BROMLEY, 1991). It has been proposed that this ichnotaxon occurs in shallow-water deposits in the Palaeozoic, and in deep-sea and rarely in shallow-water deposits after the Palaeozoic (BOTTJER et al., 1987; EKDALE & LEWIS, 1991).

Zoophycos has been identified from the Precambrian (CRIMES 1987) to the Recent (e.g. EKDALE & BERGER 1978; WETZEL & WERNER, 1981; WETZEL 1983a, b).

Phycosiphon FISCHER-OOSTER 1858

Diagnosis: Small U-shaped loops which may be connected to form antler-like pattern. Parallel or oblique to bedding (after MARINTSCH & FINKS, 1982).

Phycosiphon incertum FISCHER-OOSTER 1858
(not figured)

Diagnosis: Same as for ichnogenus.

Description: *Phycosiphon* occurs on parting surfaces as small, strongly flattened burrows, about 1 mm wide, forming loops. The burrow fill is darker than the host sediment.

Remarks: *Anconichnus horizontalis* (KERN, 1978) is a more recent synonym of *Phycosiphon incertum* (R.G. BROMLEY, pers. comm.).

We do not observe spreite between loops which might be preserved (HÄNTZSCHEL, 1975; WETZEL, 1983a). Some authors (e.g., EKDALE & MASON, 1988; CHAMBERLAIN & CLARK, 1989) doubt that *Phycosiphon* contains spreite at all.

Phycosiphon is produced by unknown deposit feeders, and is common in poorly oxygenated sediments (e.g., EKDALE & MASON, 1988).

It has been identified from the Ordovician (HÄNTZSCHEL, 1975) to the Recent (RINDSBERG, 1987).

Winding structures

Helminthopsis HEER 1877

Diagnosis: Unbranched, irregularly winding or meandering, horizontal burrows or trails that do not touch or cross themselves. Only one order of meandering may be present. Burrow fill massive (after FILLION & PICKERILL, 1990).

Helminthopsis isp.
(not figured)

Description: Smooth loosely meandering convex hypichnial string-like semirelief, 2-4 mm in diameter.
Remarks: *Helminthopsis* is an eurybathic form, common in flysch deposits, produced probably by polychaetes or priapulids (FILLION & PICKERILL, 1990). It occurs from Cambrian (CRIMES, 1987) to the Recent (WETZEL, 1983a, b).

Scolicia DE QUATREFAGES 1849

Diagnosis: Tripartite, meandering trail or burrow, broadly U-shaped in cross-section, preserved as concave epirelief and locally full relief with floor and lateral walls. The floor is convex and narrow, or flat and larger, and shows transverse almost biserial laminae. The lateral walls show distinct, curved laminae and are separated from the floor by two grooves or two discrete, typically smooth, sediment strings (after SMITH & CRIMES, 1983; PLAZIAT & MAHMOUDI, 1988; FILLION & PICKERILL, 1990).

Scolicia isp.
(not figured)

Description: Three-lobed slightly meandering epichnial furrow, 2.5-3.0 mm wide, showing convex, narrow floor which forms a ridge-like structure with perpendicular ribs. The walls of the furrow are covered by assymetric riblets.
Remarks: *Scolicia* is a very rare form in the "Flysch del Grivò". Poorly preserved specimens resemble *S. prisca* (KSIĄŻKIEWICZ, 1977).

Since the Cretaceous, *Scolicia* is produced largely by echinoids (BROMLEY & ASGAARD, 1975; SMITH & CRIMES, 1983, and others). Relation of this ichnogenus to other echinoid burrows is still not clear (see FILLION & PICKERILL, 1990, for review).

Scolicia is a facies-crossing form which has been identified from the Early Cambrian (CRIMES & ANDERSON, 1985) to the Holocene (HEEZEN & HOLLISTER, 1971).

Subphyllochorda GOTZINGER ET BECKER 1931

Diagnosis: Feeding burrow preserved as a positive hyporelief. Meandering trilobate trace. Two prominent, smooth strings usually separeate three convex zones with transverse lamination. Lateral and axial zones show backfill structure. In longitudinal horizon sections, the curved laminae are uniserial, except near the top and base where they become biserialis, more or less alternating, comparable to *Laminites* (after PLAZIAT & MAHMOUDI, 1988).

Subphyllochorda isp.
(not figured)

Description: Slightly meandering convex trilobate full relief, 2.5 cm wide, with two parallel narrow strings along the central part of the burrow.
Remarks: This is an echinoid burrow (SMITH & CRIMES, 1983),which occurs mainly in flysch deposits (KSIĄŻKIEWICZ, 1977). It has been identified from the Albian to the Quaternary (SMITH & CRIMES, 1983).

Taphrhelminthopsis SACCO 1888

Diagnosis: Feeding or locomotion burrow preserved as positive hyporelief. Meandering bilobate trace frequently in coiling spirals or meanders. A more or less deep groove separates the prominent zones with transverse backfill lamination (after PLAZIAT & MAHMOUDI, 1988).

Taphrhelminthopsis isp.
(Fig. 7A)

Description: Slightly meandering hypichnial bilobate smooth predepositional trace, 2.8 cm wide, 3-4 mm high.
Remarks: This is an echinoid burrow (SMITH & CRIMES, 1983,; PLAZIAT & MAHMOUDI, 1988). Some authors (HANISH, 1972; SMITH & CRIMES, 1983) suppose that *Taphrhelminthopsis* is a cast of washed-out *Subphyllochorda* burrows.

This ichnogenus occurs from the Cambrian (CRIMES & ANDERSON, 1985) to the Recent (PLAZIAT & MAHMOUDI, 1988).

Tuberculichnus KSIĄŻKIEWICZ 1977

Diagnosis: Hypichnial full- or semireliefs composed of knobs and tubercles arranged in freely winding rows (modified after KSIĄŻKIEWICZ 1977).

Tuberculichnus isp.
(Fig. 5C, E)

Description: A group of hypichnial oval tubercles, 4-10 mm in diameter, 3-5 mm high. The tubercles taper gently to their ends. They are passively filled by this hypichnial sediment as in the host rock.
Remarks: Some regular *Tuberculichnus,* especially *T. meandrinus* (KSIĄŻKIEWICZ, 1977), resemble *Hormosiroidea* (see SEILACHER, 1977; CRIMES & ANDERSON, 1985). The origin of this form is enigmatic. Clusters of funnel-like pits have been photographed on the deep-sea floor (HERSEY, 1967, p.38, Figs. 1-19. a-c). *Tuberculichnus* may be a cast of such pits.

Tubulichnium KSIĄŻKIEWICZ 1977

Diagnosis: Unfilled subhorizontal and horizontal tubes with lined walls (after KSIĄŻKIEWICZ, 1977).

Tubulichnium incertum KSIĄŻKIEWICZ 1977
(not figured)

Diagnosis: Endichnial (sub-epichnial) horizontal and subhorizontal long empty tubes, irregularly winding, with the wall lined with argillaceous substance (modified after KSIĄŻKIEWICZ, 1977).
Description: Endichnial (sub-epichnial), strongly flattened unfilled tube, 88 mm wide, covered by small densely packed muddy pellets which are about 1 mm in diameter.
Remarks: This form is probably produced by arthropods (cf. KSIĄŻKIEWICZ, 1977; UCHMAN, 1991). It occurs from the Turonian through the Middle Eocene (KSIĄŻKIEWICZ, 1977) up to the Upper Eocene (UCHMAN, 1990).

Spiral structures

Spirorhape FUCHS 1895

Diagnosis: Spirally coiled graphoglyptid meanders, supposedly multi-floored (after SEILACHER, 1977).

Spirorhaphe isp.
(Fig. 7E)

Description: Rope-sized fullrelief at the top of sandstone bed, fragment of a large spiral structure. The string is about 10 mm in diameter, the radius of the spiral is about 25 cm long. The spiral string is tightly packed.
Remarks: The preservation indicates postdepositional origin. Therefore, in this case, ascribing it to graphoglyptids *sensu* SEILACHER (1977) is problematical.

Spirophycus HÄNTZSCHEL 1962

Diagnosis: Hypichnial, rope-sized trace, curved like a crosier at one end (after KSIĄŻKIEWICZ, 1977, modified).

Spirophycus bicornis HEER 1876
(not figured)

Diagnosis: Hypichnial, smooth, rope-sized hyporelief, curved in a crosier-like spiral (after KSIĄŻKIEWICZ, 1977, modified).
Description: Convex hypichnial smooth semirelief, about 1 cm thick, displaying termination in shape of a spiral coil. The spiral consists of 1-2 whorls.
Remarks: *Spirophycus* is a locomotion or feeding burrow produced probably by polychaetes or acorn worms (KSIĄŻKIEWICZ, 1977).

*Spirophycus involutissimus* SACCO 1888
(Fig. 7C)

Diagnosis: Spiral which is composed of strings (6-8 mm in diameter) which are on the whole thinner than in *S. bicornis*. The spiral is rather low, and there are usually three rings (based on KSIĄŻKIEWICZ's (1977) description).
Description: Hypichnial post-depositional spiral composed of three rings, 6-8 mm thick.
Remarks: This form is typical of flysch deposits and has been identified from the Senonian to the Upper Eocene (KSIĄŻKIEWICZ, 1977).

Fig. 8 - Trace fossils in the Vernasso quarry. A. *Cosmorhaphe lobata*, sole of turbidite sandstone. B. *Helicolithus tortuosus,* sole of turbidite sandstone. C. *Urohelminthoida appendiculata*, sole of turbidite sandstone. D. *Paleodictyon latum* (P) and *Cosmorhaphe sinuosa* (C), sole of turbidite sandstone. E. *Cosmorhaphe tremens* (C) and *Paleodictyon latum* (P), sole of turbidite sandstone. F. *Protopaleodictyon submontanum*, sole of turbidite sandstone. Lense cap is 55 mm in diameter and the match 44 mm long and 2 mm thick.
- *Tracce fossili nella Cava di Vernasso:* A. Cosmorhaphe lobata, *controimpronta alla base di areniti torbiditiche.* B. Helicolithus tortuosus, *controimpronta.* C. Urohelminthoida appendiculata, *controimpronta.* D. Paleodictyon latum *(P) e* Cosmorhaphe sinuosa *(C), controimpronte.* E. Cosmorhaphe tremens *(C) and* Paleodictyon latum *(P), controimpronte.* F. Protopaleodictyon submontanum, *controimpronta. Il tappo dell'obiettivo ha un diametro di 55 mm e il fiammifero è lungo 44 mm e spesso 2 mm.*
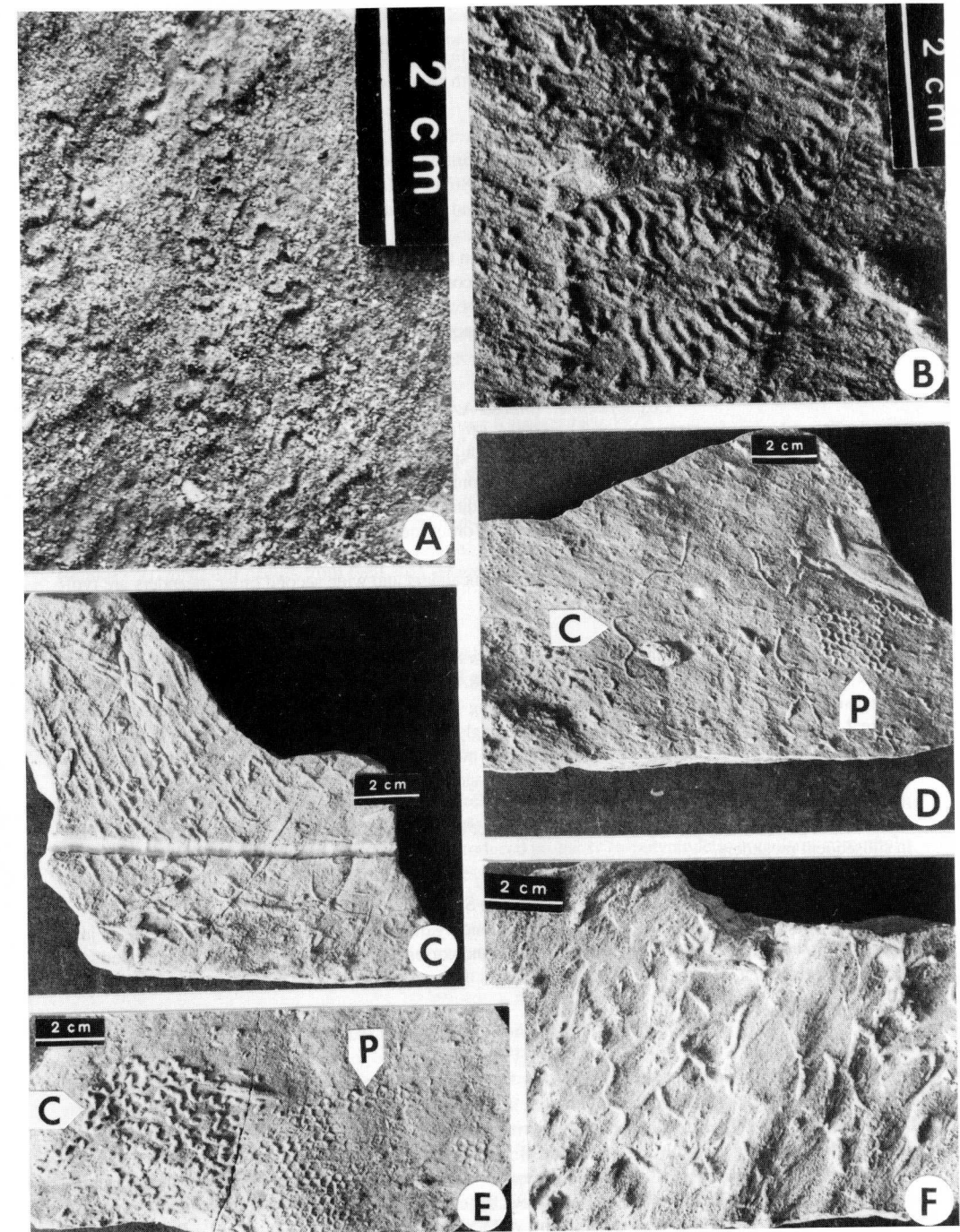
Meandering structures

Cosmorhaphe FUCHS 1895

Diagnosis: Unbranched graphoglyptid burrows with two orders of meanders or undulations (after SEILACHER, 1977).

Cosmorhaphe tremens SEILACHER 1977
(Fig. 8E)

Diagnosis: First order meanders densely guided; second order undulations small, irregular, and with very low amplitude (after SEILACHER, 1977).
Description: Hypichnial convex semirelief 1.8-2.0 mm thick, having irregular slightly undulated first order meanders, 2-5 mm high and 4-5 mm wide. The second order meanders are tightly spaced and curved, 1-6 mm wide, 40-60 mm long.
Remarks: *C. tremens* is hitherto known only from the Upper Cretaceous flysch (?) deposits of Northern Spain (SEILACHER, 1977).

Cosmorhaphe ?sinuosa AZPEITIA-MOROS 1933
(Figs. 6F, 8D)

Diagnosis of *C. sinuosa*: First order meanders widely spaced; second order undulations with greater wavelength than amplitude. Occasional shortcuts may connect successive turns (SEILACHER, 1977).
Description: Hypichnial convex fullrelief, 0.5 mm in diameter, having irregular first order meanders which are 3.0-4.0 mm high and 1.5-2.2 mm long. Second order meanders are wide. Assessment of their hight is difficult due to the lack of complete specimen.
Remarks: Characteristic geometry of the first order meanders and wide second order meanders are typical of *C. sinuosa* (cf. SEILACHER, 1977).

Cosmorhaphe lobata SEILACHER 1977
(Fig. 8A)

Diagnosis: First order meanders fairly dense, containing 15-20 turns of regular second order meanders, which are 2-3 times higher than wide and interlock strongly (after SEILACHER, 1977).
Description: Hypichnial convex semirelief, about 0.5 mm in diameter, forming irregular first order meanders. Each meander is 6-7 mm high and 2.0-3.5 mm wide. The second order meanders are 40-60 mm high and 0.5-1.5 mm wide.
Remarks: Typical *C. lobata* has a considerably greater height-width ratio in the first order meanders than in subsequent meanders.

Spirocosmorhaphe SEILACHER 1989

Diagnosis: Non-branched graphoglyptids, whose secondary meanders appear interrupted with ends in juxtaposition; interruptions appear in regular positions and correspond to loops in plane outside eroded surface (after SEILACHER, 1989).

Spirocosmorhaphe helicoidea SEILACHER 1977
(Fig. 7E)

Diagnosis: First order meanders irregular: turns of the fairly large and high second order undulations flattened by introduction of third helicoidal looping in the vertical plane (after SEILACHER, 1977).
Description: This is a hypichnial meandering convex semirelief, 1.0-1.5 mm wide. The first and second order meanders are irregular with characteristic S-like interruptions occupying alternating position.
Remarks: This rare graphoglyptid is hitherto known from the Upper Cretaceous-Eocene Tasna flysch in Austria (SEILACHER, 1977) and from the Cretaceous flysch of Alaska (MCCANN & PICKERILL, 1988; see discussion by SEILACHER (1989) and by PICKERILL & MCCANN, 1989).

Gordia EMMONS 1844

Diagnosis: Smooth, unbranched horizontal trails or burrows of uniform diameter throughout their length, winding but not meandering, with marked tendency to level crossing. Burrow-fill massive (after FILLION & PICKERILL, 1990).

?*Gordia* isp.
(not figured)

Description: Hypichnial winding thread-like predepositional convex burrow, about 1 mm in diameter, showing rare level crossings.
Remarks: *Gordia* is a facies crossing form, occurring from the Late Precambrian to the Recent (HÄNTZSCHEL, 1975).

Helicolithus AZPEITIA-MOROS 1933

Diagnosis: Graphoglyptid burrows with widely spaced first order meanders; small second order undulations form a regular helicoidal spiral, which changes screw direction at every turn of the first order meanders (SEILACHER, 1977).

Helicolithus tortuosus KSIĄŻKIEWICZ 1977
(Fig. 8B)

Diagnosis: Helicoidal undulation regular, without visible appendages (after SEILACHER, 1977).
Description: Convex hyporelief consisting of congruent, parallel and subparallel slightly sinuous riblets, 3-5 mm long, occasionally joined by short perpendicular elements which are 2 mm long. Each element is 1.0 mm thick.
Remarks: *H. tortuosus* occurs from the Late Cretaceous (SEILACHER, 1977) to Miocene (D'ALESSANDRO, 1980) in flysch deposits.

Cochlichnus HITCHOCK 1858

Diagnosis: Regularly meandering, horizontal trails and burrows resembling sine curves (after HÄNTZSCHEL, 1975).

Cochlichnus isp.
(Fig. 6D)

Description: Hypichnial thread-like convex semireliefs, 0.5-2.0 mm wide, slightly meandering, having only first order meanders. The meanders are very low.
Remarks: *Cochlichnus* is a facies-crossing form, produced probably by polyphyletic organisms commonly referred to annelids (HAKES, 1976) or to nematodes (MOUSSA, 1970).

Helminthorhape SEILACHER 1977

Diagnosis: Non-branching graphoglyptid burrows with only one order of smooth and very high meanders that are guided in a *Helminthoida*-like fashion (after SEILACHER, 1977).

Helminthorhaphe crassa SCHAFHÄUTL 1851
(Fig. 6C)

Diagnosis: Meanders widely spaced, relative to the burrow diameter, but rather irregular and poorly guided (after SEILACHER, 1977).
Description: Convex hyporeliefs, 2 mm in diameter, forming wide meanders.
Remarks: CRIMES & CROSSLEY (1991) questioned separation of *Helminthoida* and *Helminthorhaphe* (SEILACHER, 1977). KSIĄŻKIEWICZ (1977) mentioned a specimen with the morphology of *H. crassa* (present in his collection) which is preserved as full relief. In this case, its relation to graphoglyptids seems to be ambiguous.

Paleomeandron PERUZZI 1881

Diagnosis: Biramous graphoglyptid burrows, in which first order meanders are widely spaced and lobose, while second order undulations are small and regularly rectangular, without horizontal appendages (after SEILACHER, 1977).

Paleomeandron biserialis SEILACHER 1977
(Fig. 7B)

Diagnosis: Second order undulations with longitudinal pronounced elements , that appear as two series of longitudinal bars in alternating positions (after SEILACHER, 1977).
Description: The burrow is 0.5 mm thick, first order meanders are 1.8-2.0 mm high, and second order meanders are up to 40 mm high. The burrows pass into two series of longitudinal alternating bars, 2.0 mm long, 0.5 mm wide.
Remarks: Only two specimens of this species are hitherto known from Palaeocene flysch (?) deposits in Venezuela (SEILACHER, 1977, Fig. 8i, holotype) and from the Eocene Zumaya flysch in Spain (last. cit., Fig. 7b). *Paleomendron* is a typical predepositional example of graphoglyptids (SEILACHER, 1977), however some Carpathian forms seem to be postdepositional (KSIĄŻKIEWICZ, 1977, KERN, 1980). *Paleomeandron* has been identified from the Late Cretaceous to the Early Tertiary (HÄNTZSCHEL, 1975), winding and meandering with branches.

Urohelminthoida SACCO 1888

Diagnosis: Tightly meandering graphoglyptid meanders, in which the turning points are angular and drawn out into lateral appendages (after SEILACHER, 1977).

Urohelminthoida appendiculata HEER 1877
(Figs. 7D, 8C)

Diagnosis: The meanders are tight (distance 2-3 tunnel diameters) and very wide, their course becoming convex and slightly irregular by guidance along previous turns; appendages short (after SEILACHER, 1977).
Description: Convex hyporelief consisting of zigzag-like meanders. The turning points of the meanders have short outward appendages.
Remarks: This is a typical graphoglyptid (SEILACHER, 1977). Existence of postdepositional *Urohelminthoida* (KSIĄŻKIEWICZ, 1977) was not confirmed by KERN (1980).

Protopaleodictyon KSIĄŻKIEWICZ 1970

Diagnosis: More or less regular hypichnial meanders with one or two appendages usually branching from the apex of the meanders (after KSIĄŻKIEWICZ, 1977).

Protopaleodictyon submontanum AZPEITIA-MOROS 1933
(not figured)

Diagnosis: Hypichnial, thread-size burrows, irregularly winding and meandering, branching at various points, but mostly at the apical bends of the meanders. Occasionally this branching leads to formation of irregular networks which consist of meshes varying in size (after KSIĄŻKIEWICZ, 1977, modified).
Description: Convex hypichnial semireliefs, 1.8-2.0 mm in diameter, irregularly winding and meandering, branching at various points and forming pseudo-network. The pseudo-network consist of irregular meshes which reach up to 3.5 cm in diameter.
Remarks: Some specimens showing well expressed pseudo-network resemble *Megagrapton*.

Protopaleodictyon incompositum KSIĄŻKIEWICZ 1970
(Fig. 8F)

Diagnosis: Hypichnial string-sized burrow, forming composite meanders with short appendages branching at the apical bends of the second order meander. When the sole of the bed is densely covered an incomplete network may be formed (modified after KSIĄŻKIEWICZ, 1977).

Description: Hypichnial convex semirelief forming irregular first order meanders with short irregular appendages.
Remarks: KSIĄŻKIEWICZ (1977) indicated that *Protopaleodictyon submontanum* is a "full burrow". There is no evidence of a post-depositional origin of this form in his collection including the holotype (cf. KERN, 1980).

Networks

Megagrapton KSIĄŻKIEWICZ 1968

Diagnosis: Irregular second order meanders of low amplitude, branching and anastomosing to form meshes of irregular size and shape.

Megagrapton isp.
(not figured)

Description: Hypichnial convex semireliefs, 1.5 mm thick, arranged in irregular net, 3-5 cm in diameter.
Remarks: Seilacher (1977) included *Protopaleodictyon submontanum* in *Megagrapton irregulare*. However, the former form has smaller irregular meshes which do not display sharp angles. Right angles in net are typical of *Megagrapton* (cf. KSIĄŻKIEWICZ, 1977). Nevertheless, delineation between these two ichnotaxa is difficult.

Paleodictyon MENEGHINI 1850
Glenodictyum VAN DER MARCK 1863

Diagnosis: Uniform, hexagonal meshes without regular vertical outlets; complete systems are also hexagonal in outline (after SEILACHER, 1977).

Paleodictyon minimum SACCO 1888
(Fig. 6E)

Diagnosis: Small *Paleodictyon* with regular hexagonal net, 1.0-1.5 mm in size and 0.3-0.5 mm in string diameter (after KSIĄŻKIEWICZ, 1977).
Description: This is a net composed of regular hexagonal meshes of similar size as in the diagnosis.
Remarks: A very rare form found in the examined sections.

Paleodictyon latum VIALOV et GOLEV 1965
(Fig. 8D)

Diagnosis: Small *Paleodictyon* with regular hexagonal net, 1.0-3.0 mm in size and 0.5-1.0 mm in string diameter (after KSIĄŻKIEWICZ, 1977).
Description: This is a net composed of regular hexagonal meshes, 2.8-3.0 mm in diameter, with riblets 0.7-1.0 mm thick.
Remarks: Some of specimens display transition to *P. intermedium* (KSIĄŻKIEWICZ, 1970, 1977).
    Two different classifications of paleodictyonids are in use: one based on morphometric parameters (KSIĄŻKIEWICZ, 1977) and the second by SEILACHER (1977), based on the evolution of the network. However, the second is related to biological criteria, on the other hand the first is more descriptive.
    According to RÖDER (1971) and SEILACHER (1977), *Paleodictyon* is formed by unknown organisms which feed on cultivated or trapped microorganisms in its burrow system. Today's burrow systems of *Paleodictyon* have been photographed on deep-sea bottoms (EKDALE, 1980, MILLER, 1991); however, their tracemaker has not yet been identified.
    Paleodictyon is a typical graphoglyptid known from deep-sea flysch. Palaeozoic forms, however, occur also in shallow-water deposits (e.g., ARCHER & MAPLES, 1984).

Paleodictyon strozzi MENEGHINI 1851
(Fig. 7D)

Diagnosis: Small *Paleodictyon* with regular hexagonal net, 2.5-5.5 mm in size and 0.3-1.0 mm in string diameter (after KSIĄŻKIEWICZ, 1977).

Description: This is a net composed of slightly irregular hexagonal meshes, 3.0-4.0 mm in diameter with riblets 0.8-1.0 mm thick.

Remarks: This is a very widespread form of *Paleodictyon*.

Paleodictyon majus MENEGHINI 1879
(not figured)

Diagnosis: *Paleodictyon* whose meshes reach 9 mm in size and whose riblets measure 1.0-1-5 mm in diameter (after KSIĄŻKIEWICZ, 1977).

Description: This is a relatively large regular hexagonal net composed of meshes about 9 mm in diameter with riblets 1.2 mm thick.

Remarks: In some specimens, it is difficult to distinguish between *P. majus* and *P. carpathicum* (cf. KSIĄŻKIEWICZ, 1977).

Discussion

According to the classical concept of the recurring ichnofacies (cf. SEILACHER, 1967; EKDALE et al., 1984; FREY et al, 1990), the considered trace fossil assemblage resembles the Nereites ichnofacies. Nevertheless, the purity of the Nereites ichnofacies is disturbed by the occurrence of taxa belonging to the Cruziana ichnofacies, i.e., *Thalassinoides, Ophiomorpha, Lockeia*. These taxa seem to be common in Cenozoic well-aerated flysch deposits, not only in high energy proximal turbiditic facies (e.g., CRIMES et al., 1981), but also in distal facies (UCHMAN, 1988, 1989, 1991a).

The trace fossil assemblage is very diverse. Post-depositional forms (tabl. I) are dominated by abundant *Sabularia* and *Planolites*. Other post-depositional forms such as *Phycosiphon, Chondrites, Zoophycos*, and *Thalassinoides*, are relatively rare. Predepositional forms, including 16 ichnotaxa of graphoglyptids, are very common. The concept of r- and K-selected strategies of colonizations of the sea floor may be applied to trace fossils (EKDALE, 1985; VOSSLER & PEMBERTON, 1988). Roughly, the producers of post-depositional forms may represent a r-selected opportunistic strategy in colonizing the sea floor, while the predepositional forms a K-selected equilibrium strategy (UCHMAN, 1991c, 1992). The ratio of the post-depositional forms to the predepositional ones is relatively high (tabl. I). Thus, the abundant occurrence of K-selected forms indicates relatively stable ecological conditions on the sea floor. The occurrence of numerous graphoglyptids has probably been promoted by moderate shortage of food (cf. SEILACHER, 1977; MILLER, 1989, 1991). Such a situation is typical of well oxygenated flysch deposits indicated by the light colour of shales (UCHMAN, 1991c, 1992).

Laevicyclus isp.
?Lockeia isp.
Bergaueria isp.
Sabularia simplex
Planolites punctatus
Planolites isp.
Thalassinoides isp.
Ophiomorpha isp.
Chondrites isp.
Chondrorhaphe bifada
Zoophycos insignis
Zoophycos isp.
Phycosiphon incertum
Helminthopsis isp.
Tubulichnium incertum
Tuberculichnus isp.
Spirorhaphe isp.
Spirophycus bicornis
?Gordia isp.
Cosmorhaphe ?sinuosa
Cosmorhaphe lobata
Cosmorhaphe tremens
Helicolithus tortuosus
Cochlichnus isp.
Helminthorhaphe crassa
Paleomeandron biserialis
Urohelminthoida appediculata
Protopaleodictyon incompositum
Protopaleodictyon submontanum
Megagrapton isp.
Paleodictyon majus
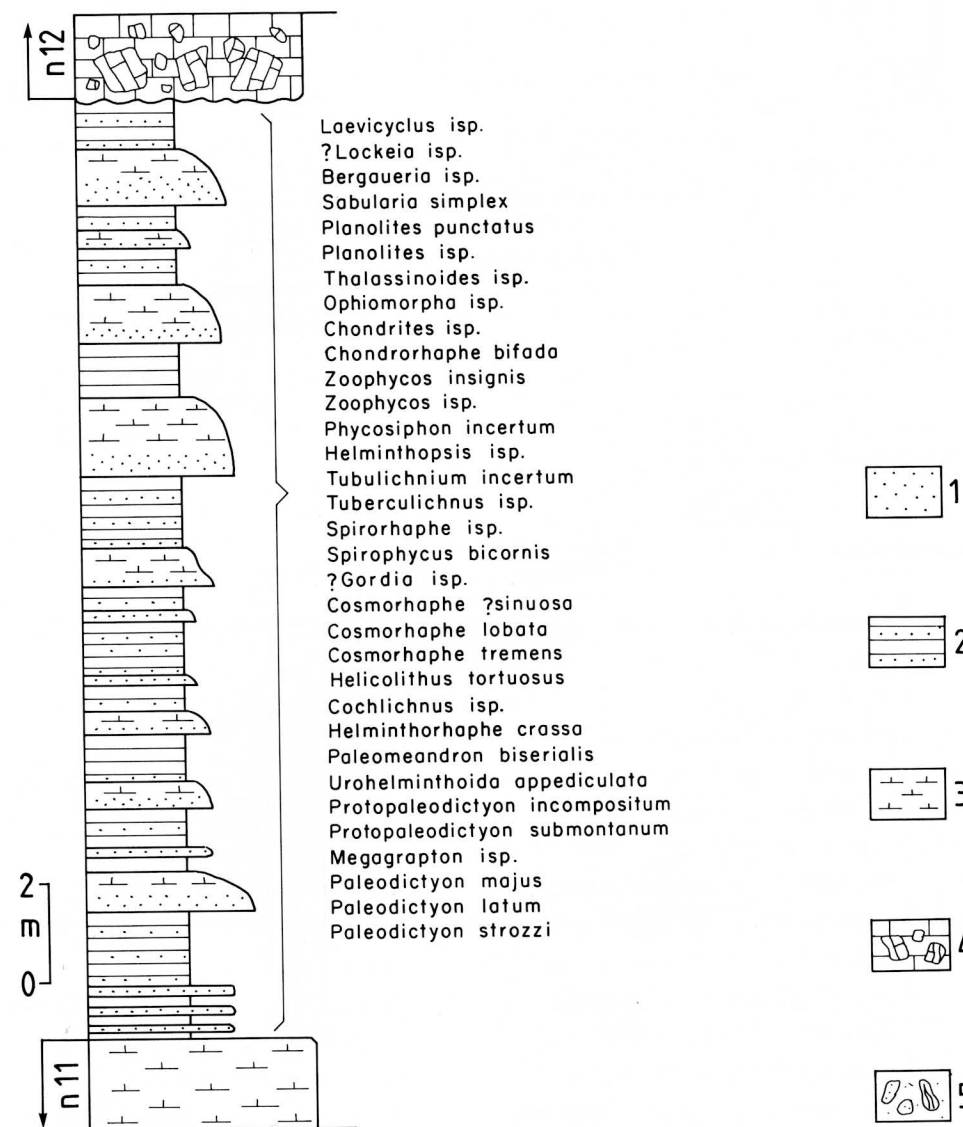Paleodictyon latum
Paleodictyon strozzi

Fig. 9 - Package of turbiditic deposits between the megabeds 11 and 12 and its trace fossils. 1. Sandstone of thick beds. 2. Thin- and medium bedded flysch deposits. 3. Marlstones. 4. Olistoliths of platform limestones within coarse-grained matrix. 5. Rip-up of thin- and medium thick turbidites within coarse grained matrix.

- Il pacco di torbiditi compreso tra i megabanchi n. 11 e n. 12 e relative tracce fossili osservate. 1. Arenarie in strati molto potenti. 2. Depositi torbiditici medio-sottili. 3. Marne. 4. Olistoliti di calcari di piattaforma alla base dei megabanchi. 5. Rip-up di torbiditi medio-sottili presenti nella parte basale del megabanco.
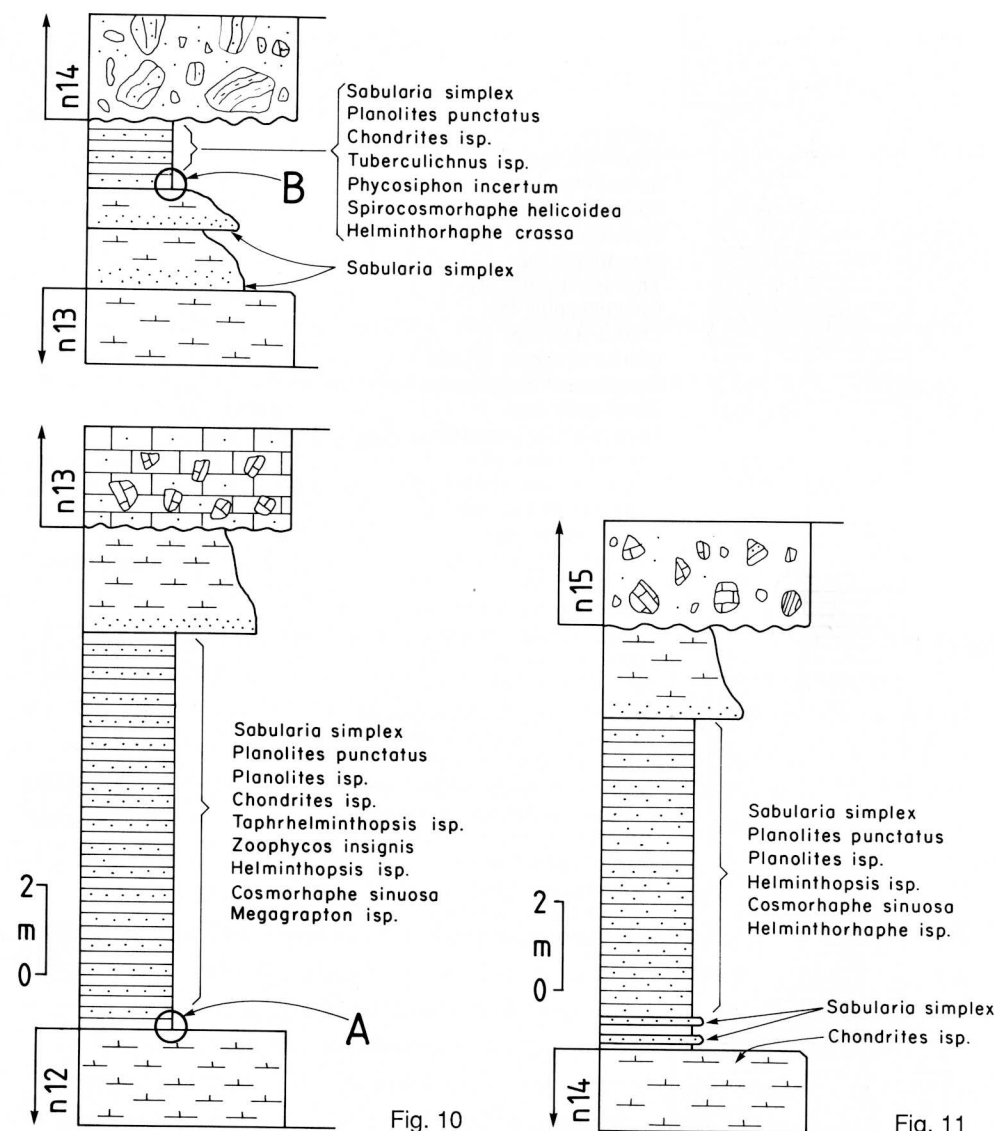
Fig. 10 - The packages of turbiditic deposits between the megabeds 12 and 13 and between 13 and 14 and their trace fossils. Signature as in Fig. 9.
- *Il pacco di torbiditi compreso tra i megabanchi n. 12 e n. 13 e tra n. 13 e n. 14 e relative tracce fossili osservate. Simboli come in Fig. 9.*

Fig. 11 - The package of turbiditic deposits between the megabeds 14 and 15 and its trace fossils. Signature as in Fig. 9.
- *Il pacco di torbiditi compreso tra i megabanchi n. 14 e n. 15 e relative tracce fossili osservate. Simboli come in Fig. 9.*
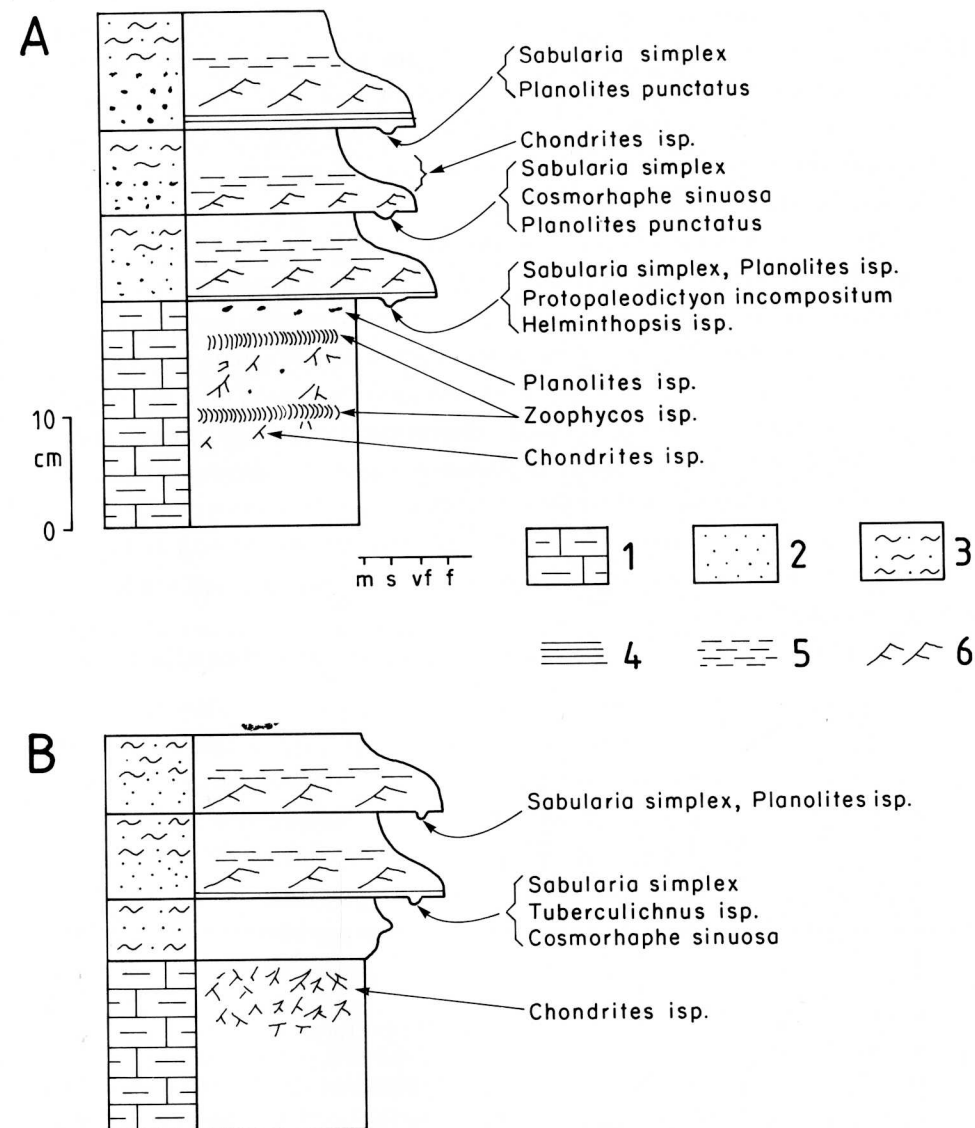
Fig. 12 - Distribution of trace fossils at the top of the megabed 12 (A) and 13 (B) and in the overlying turbiditic beds. 1. Marlstones. 2. Sandstones. 3. Mudstones. 4. Horizontal lamination Tb. 5. Horizontal lamination Td. 6. Cross lamination Tc. The grain size scale: m = mud, s = silt, vf = very fine sand, f = fine sand.
- *Distribuzione delle tracce fossili al top dei megabanchi n. 12(A) e n. 13(B) e negli strati torbiditici soprastanti. 1. Marne. 2. Arenarie. 3. Peliti. 4. Laminazione piano parallela Tb. 5. Laminazione piano parallela Td. 6. Laminazione incrociata Tc. Scala delle frazioni granulometriche: m = mud, s = silt, vf = sabbia finissima, f = sabbia fine.*

Normally, food particles reach the deep sea floor by plankton blooms twice a year, for short periods. The efficient manner of the feeding of graphoglyptid producers (microbe gardening or trapping) is well adapted to nutrient poor stable environments (cf. SEILACHER, 1977; MILLER, 1989, 1991). Moreover, in such biotopes, their complicated and delicate burrow systems are not damaged by producers of opportunistic taxa, which normally bioturbate more fertile sediments totally.

Deposition of turbidite beds leads to destruction of benthic life on relatively large areas. In case of thin layers of the newly deposited sediment, producers of some opportunistic taxa, such as *Thalassinoides, Sabularia simplex*, might survive and possibly were able to quickly recolonize the sediment. The limit of the depth of penetration of certain tracemakers varies (KSIĄŻKIEWICZ, 1977; LESZCZYŃSKI, 1991). Probably, burrowers were able to escape through thicker layers of suddenly deposited sediment than their average penetration depth. Of course, these abilities are also limited. Deposition of a layer a few decimetres thick, seems to have led to extermination of about 90% of the burrowers. Deposition of megabeds have killed them totally. Common occurrence of megabeds in the studied sections (Fig. 3) gives us an opportunity to observe trace fossils on top of the megabeds and in a few turbidite layers above the megabeds.

Fig. 12 shows that colonization of a new empty substrate, registered in trace fossil
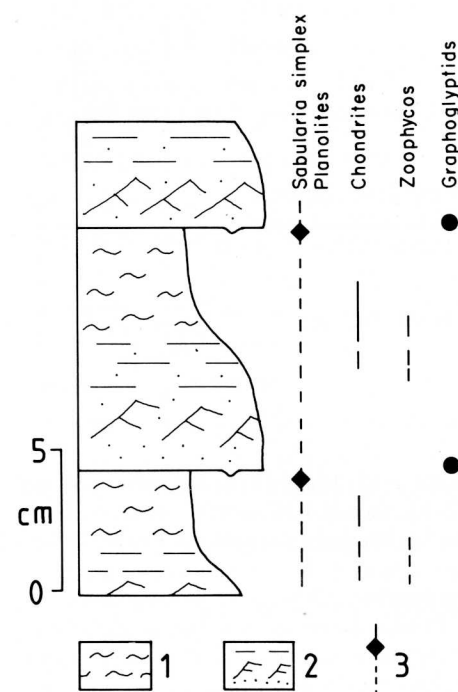
Fig. 13 - Tiering pattern of the most common trace fossils in hypothetical turbidite beds in the "Flysch del Grivo". 1. Mudstones. 2. Horizontally and cross laminated sandstones. 3. Thickness of range lines proportional to the relative frequence of forms.
- *Tiering pattern delle tracce fossili più comuni nel-l' ambito degli strati torbiditici del "Flysch del Grivò". 1. Marne. 2. arenarie con laminazione piano parallela ed incrociata. 3. Lo spessore delle linee di riferimento è proporzionale alla frequenza relativa delle forme.*

records on the top of megabeds and on the sole of the first overlying turbiditic bed, was very quick. This view may be confirmed by the common occurrence of graphoglyptids in the relatively thin packages of normal turbidites between the megabeds (Figs. 9-11), which shows that they easily recolonized a new substrate. Graphoglyptids are present on the sole of the first turbidite bed (Fig. 12A) which is 4 cm thick. In case, the first bed was thicker (130 cm, see Fig. 10), only opportunistic *Sabularia simplex* was present. The lack of other forms is possibly connected with erosion which usually proceeds deposition of thick turbidite beds. Erosion might remove sediment which acts as a host for the great variety of producers of predepositional forms. Moreover, the beds could be too thick to be colonized at their sole by a greater number of various shallower burrowers producing post-depositional forms.

Animals producing trace fossils live at different levels (tiers) in the sediment (cf. SEILACHER, 1964; WETZEL, 1983b, 1991; BROMLEY & EKDALE, 1986; WETZEL & AIGNER, 1986; LESZCZYŃSKI, 1991; UCHMAN, 1991b). In flysch deposits, tiering patterns are diversified and controlled by changing palaeoenvironmental parameters (UCHMAN, 1990a, 1991b). In the "Flysch del Grivò", the tiering pattern was reconstructed for the most common forms on the basis of the relation of trace fossils to bed surfaces, and by toponomic data (Fig. 12).

We repeatedly observed that post-depositional *Sabularia* and *Planolites* occur abundantly on soles of up to 2.5 m thick turbidite beds. Thus, we may suppose that those forms were produced by rapidly burrowing r-selected opportunists which occupied the deepest tier. Small *Chondrites* and *Zoophycos* appear within the shelly part and in the uppermost sandy part of some turbidites. Post-depositional hyporeliefs of graphoglyptids as well as *Spirorhaphe* and *Taphrhelminthopsis* were produced as shallow burrows in muddy sediment. These forms are preserved as a result of delicate scouring by bottom currents and casting of excavated biogenic tunnels and grooves (cf. SEILACHER, 1964).

Trace fossils are also tiered on top of the megabeds (Fig. 12A). *Chondrites* occurs up to 15 cm below the top. Probably, the depth of the burrowing of this form does not exceed twenty centimetres. Shallower burrows are represented by *Zoophycos* (up to 10 cm) and by graphoglyptids preserved on the sole of the overlying turbidite beds. The depth of their burrows probably does not exceed 1 cm. The time between deposition of megabeds and the first overlying turbidite was enough for full colonization by r-selected opportunists (*Chondrites, Planolites, Zoophycos*) and by equilibrium K-selected graphoglyptids (*Protopaleodictyon*), as well as for developing of tiering. How do animals do it ? We may speculate that possible planktonic larvae of many tracemakers are well adapted to this role.

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