

Zeitschrift: Eclogae Geologicae Helvetiae
Herausgeber: Schweizerische Geologische Gesellschaft
Band: 82 (1989)
Heft: 2

Artikel: Trace fossils from the Helminthoid Flysch (Upper Cretaceous-Paleocene) of the Ligurian Alps (Italy) : development of deep marine ichnoassociations in fan and basin plain environments
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DOI: <https://doi.org/10.5169/seals-166382>

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Trace fossils from the Helminthoid Flysch (Upper Cretaceous–Paleocene) of the Ligurian Alps (Italy): development of deep marine ichnoassociations in fan and basin plain environments

By LECH K. POWICHROWSKI¹⁾

ABSTRACT

A poorly preserved, but diverse ichnoassociation (22 ichnogenera) reflects mainly the activities of infaunal deposit feeders in the pelitic horizons, while sand/shale interfaces were left to less specialized scavengers or detritus feeders. At the tops of certain turbidites also occur endopelitic structures interpreted as farming burrows. Eight principal ichnoassemblages, distinguished by tiering or random juxtaposition of constituent trace fossils reflect different depositional regimes: 1. tiered assemblages in turbidites, 2. complex assemblages in oxic hemipelagic sediments, 3. mixed assemblages in turbid surge deposits. Intermittent gravity flow deposition versus gradual hemipelagic accumulation of sediment controlled the preservation or mixing of the original tiering. There is a distinct tendency to behavioural diversification towards the fan-influenced distal parts of the basin (fan fringe, turbiditic basin plain), particularly where there was an increased supply of redeposited lime mud. The high number of ichnocoenoses probably reflects the fluctuation of trophic conditions imposed by turbidites.

RÉSUMÉ

Le Flysch à Helminthoïdes des Alpes ligures, d'âge crétacé–paléocène, a fait objet d'une étude ichnologique qui a permis d'identifier 22 formes de traces fossiles au niveau générique. Les associations de traces reflètent principalement l'activité des animaux sédimentivores dans les niveaux pélagiques, et dans une moindre mesure, l'activité des détritivores et des « balayeurs » (scavengers) caractéristique des interfaces grès-pélite. Les parties supérieures de certains bancs turbiditiques calcaires portent des traces interprétées comme terriers de culture ou de piégeage des micro-organismes. Huit ichnoassociations, distinguées sur la base des schémas de répartition verticale des traces, se sont développées probablement en relation étroite avec les régimes sédimentaires prédominants:

1. dans les turbidites: associations en étages,
2. dans les dépôts hémipélagiques oxydés: associations condensées,
3. dans les dépôts de bouffées turbides: associations mixtes.

Le rapport entre la sédimentation intermittente des courants gravitationnels et l'accumulation hémipélagique a déterminé l'ampleur des phénomènes de condensation de structures biogènes, en permettant de conserver les traces de la stratification originelle des ichnocénoses dans le dépôt turbiditique. Les associations étudiées montrent une nette tendance à la diversification éthologique dans les zones du bassin qui ont été soumises à l'influence atténuée du cône sous-marin (frange de cône, plaine du bassin turbiditique). Cette diversification prend son ampleur surtout pendant les périodes de l'apport intense de la boue calcaire par les courants de turbidité. Le nombre élevé des associations de traces suggère que les fluctuations trophiques ont été imposées par les courants de turbidité.

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Introduction

Trace fossils are excellent facies indicators because they are in general strictly autochthonous and because their morphologies and internal structures reflect behavioural responses of the trace-makers to environmental conditions. The wide stratigraphic and geographic range of many ichnogenera makes it possible to compare ichnocoenoses distant in time and space (SEILACHER 1953, 1967, FREY & SEILACHER 1980). Our increasing knowledge about modern deep-sea ichnocoenoses (CHAMBERLAIN 1975, EKDALE & BERGER 1978, BERGER *et al.* 1979, WETZEL & WERNER 1981, WETZEL 1982 and 1984, EKDALE *et al.* 1984) and about the ecology of modern endobenthic communities (LEVINTON 1972, GRAY 1981 and many references therein) also allow an uniformitarian approach. Tiering is commonly preserved in the flysch facies (SEILACHER 1962, 1974, 1978) since bioturbation occurred intermittently between successive turbiditic events. Zoned bioturbation patterns observed in modern pelagic continental margin deposits (WERNER & WETZEL 1982, WETZEL 1982 and 1984) stem from the tiering of trace-makers, whose penetration depth into the substrate is controlled by environmental factors. It is the goal of the present study to use this actualistic evidence for a high-resolution paleoenvironmental reconstruction of ancient deep sea basins. The Helminthoid Flysch of the Ligurian Alps (Italy) of Cretaceous–Paleocene age, rich in ichnofossils, and representing the major turbiditic and hemipelagic facies associations, is well suited for such an approach.

Stratigraphy and sedimentology

The Helminthoid Flysch of the Ligurian Alps, which was dated by sparse foraminiferal faunas as being of Late Cretaceous–Paleocene age (LANTEAUME 1968), crops out in the Helminthoid Flysch thrust sheet. The outcrops occur in a roughly triangular area which extends about 50 km along the western Mediterranean shore (Fig. 1). The nappe, which is completely autochthonous, overthrusts the geological limit of external and internal Alpine units (LANTEAUME 1968). It consists of two structural slabs: the westerly Imperia unit and the easterly Alassio unit (FOUCAULT & POWICHROWSKI 1984). Only the former has been examined in detail in this study (Fig. 1). Its sedimentary record comprises two major sedimentary units (Fig. 2):

- San Bartolomeo Fm (SAGRI 1980, “*complexe de base*” of LANTEAUME 1968); Albian/Cenomanian–Lower Senonian? Dark manganese-rich shales, variegated at the top; the varicoloured shales are followed by a thin-bedded sandy-pelitic flysch.
- Helminthoid Flysch *s.str.*; Campanian–Maastrichtian/Paleocene. Thick-bedded sandstone and conglomerate flysch, which makes up the lower part of the succession (Bordighera Sandstone: SAGRI 1980), passes stratigraphically upwards and laterally into a thick limestone flysch (San Remo Fm: SAGRI 1980). The latter is made up mostly of medium- and thick-bedded sandy, calcareous and marly turbidites with greenish-gray shaly intercalations.

Stratigraphic details are given by LANTEAUME (1968) and POWICHROWSKI (1984). The sedimentology of the Bordighera Sandstone was examined by SAGRI (1980). The recent

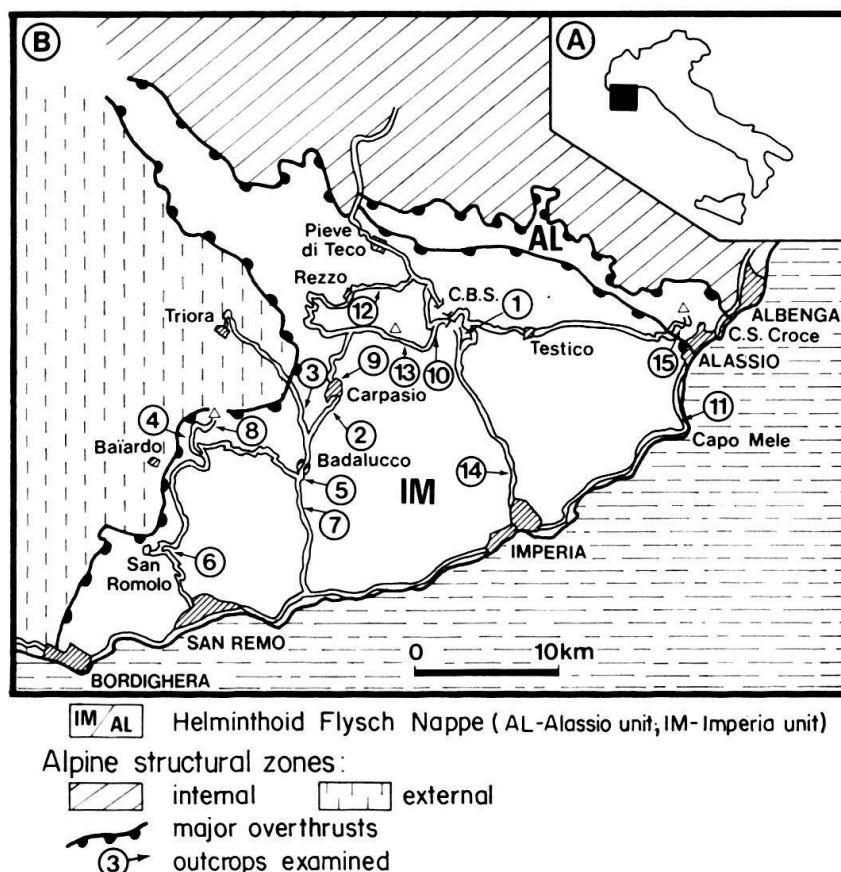
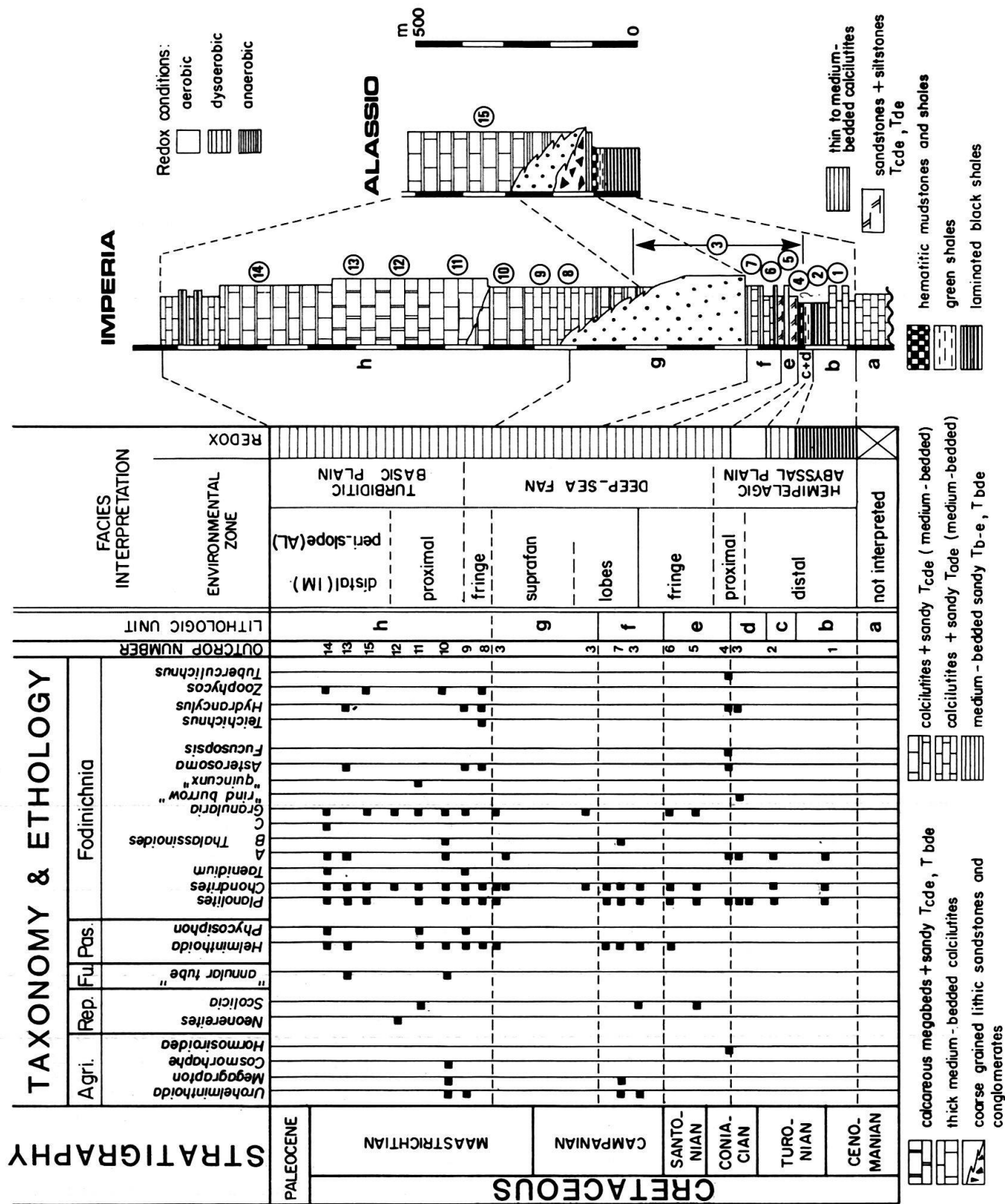


Fig. 1. Locality map of the Helminthoid Flysch in the Ligurian Alps. A: General situation: black rectangle = area of study. B: Schematic geological situation (for the stratigraphic position of the outcrops see Fig. 2). C.S.B. = Colle San Bartolomeo.

progress concerns the sedimentary models of the San Remo Formation (SAGRI 1984) and of the San Bartolomeo Formation ("complexe de base", POWICHIROWSKI 1984).

The entire stratigraphic succession is interpreted by the author as an ancient deep-sea fan – abyssal plain system, which developed at a continental margin during the Late Cretaceous. This margin probably bordered from the west an oceanic terrane called the "Ligurian paleo-ocean" which extended (with a width of a several hundreds of kilometers) between the European and Apulian continental blocks (LANTEAUME 1968, SAGRI 1980). Two hypotheses were proposed for the tectonic setting of this margin: the deposition of the flysch took place either in a slowly subducting deep-sea trench (SAGRI 1979, 1980, 1984) or in a "dormant" trench (*sensu*: HESSE & BUTT 1976) connected with transform movements (SAGRI 1979 *pro parte*, POWICHIROWSKI 1984). The paleoenvironmental interpretation of deposition on the basis of sedimentary facies and facies associations and of the shale mineralogy (POWICHIROWSKI 1984) is given in Figure 2.

The San Bartolomeo Formation is interpreted as a mixed hemipelagic and turbiditic series deposited on the abyssal plain. Sedimentation rate was probably low (thorough bioturbation of shales) and bottom water oxygenation appeared to evolve from anaerobic/dysaerobic to aerobic conditions (POWICHIROWSKI 1984). By means of shale mineralogy and the presence or absence of primary sedimentary structures in the shales three principal facies can be recognized (see MAYNARD 1981, SAVRDA *et al.* 1984):



- aerobic (haematite, no lamination, thoroughly mottled),
- disaerobic (authigenic Fe-Mn-Ca-Mg carbonates, some pyrite, faint or no laminations),
- anaerobic (pyrite abundant, fine laminations).

The hemipelagic plain shale deposits are overlain by turbidite sediments of fan-fringe facies in an oxygen-deficient basin. The overlying wedge-shaped body is composed of coarse sandstone and conglomerate gravity flow facies and represents deposits of a low efficiency deep-sea fan (SAGRI 1980).

The terrigenous deep-sea fan, built up at the base of slope since the Late Cretaceous, invaded the basin plain from Coniacian(?) until Campanian times. This trend was reversed during the Campanian to Early Maastrichtian by a retreat of the fan, blanketing the fan deposits by a thick set (up to 1000 m) of sandy and calcareous turbidites and thick marly "megaturbidites" in a basin plain environment below the carbonate compensation depth (SAGRI 1979).

This development of the deep-sea fan – basin plain system was most probably controlled by fluctuations in the rate of sediment supply from various, siliciclastic or calcareous, sources. Generally, sandy turbidity currents predominated, prior to and during the sedimentation of the Bordighera Sandstone. The bulk of the San Remo Formation was likely deposited from turbidity currents loaded with intrabasinal lime mud (see CARON et al. 1981).

Classification and description

The observed trace fossils were indexed separately for each bed in the outcrops shown on Figure 2. Each log included two types of information:

- stratonomy (lithology, type of discontinuity surface, sedimentary structures)
- ichnology (taxonomy, relative frequency, relationship to the substrate, vertical distribution within the bed).

Examples of more characteristic ichnofossils encountered are shown in Figure 3.

The principal ichnoassemblage patterns and their stratinomic frameworks as presented in Figure 4 were established on the bases of field data. An ethological/ecological classification (SEILACHER 1953, with later developments by SEILACHER 1967, 1974, 1977, 1986 in prep., and EKDALE 1985) was used here. The trace fossils were identified in the field with the aid of HÄNTZSCHEL's work (1962) at the ichnogeneric level. Bibliographic references for each ichnogenus identified are given systematically, and, if necessary, short description follows if there were noticeable differences with respect to ichnogeneric

Fig. 2. Lithostratigraphy, facies and trace fossil distribution in the Helminthoid Flysch. Two facies provinces are distinguished: Imperia (IM) and the Alassio zone (AL) corresponding to the two structural slabs in Figure 1B. Lithostratigraphy: *San Bartolomeo Fm* ("complexe de base"): a = Testico flysch, b = Manganiferous flysch, c = Green shales, d = Red shales, e = "Black flysch", f = Thin-bedded calcareous flysch; *Helminthoid Flysch* s.str.: g = Bordighera sandstone, h = San Remo Flysch (and its lateral equivalent in the Alassio unit: Ubaga Limestones). The outcrop numbers refer to Figure 1B. Bed thickness scale according to CAMPBELL (1967). Ethology: Agri = farming, Rep = crawling, Fug = escape, Pas = grazing, Fodinichnia = feeding burrows.

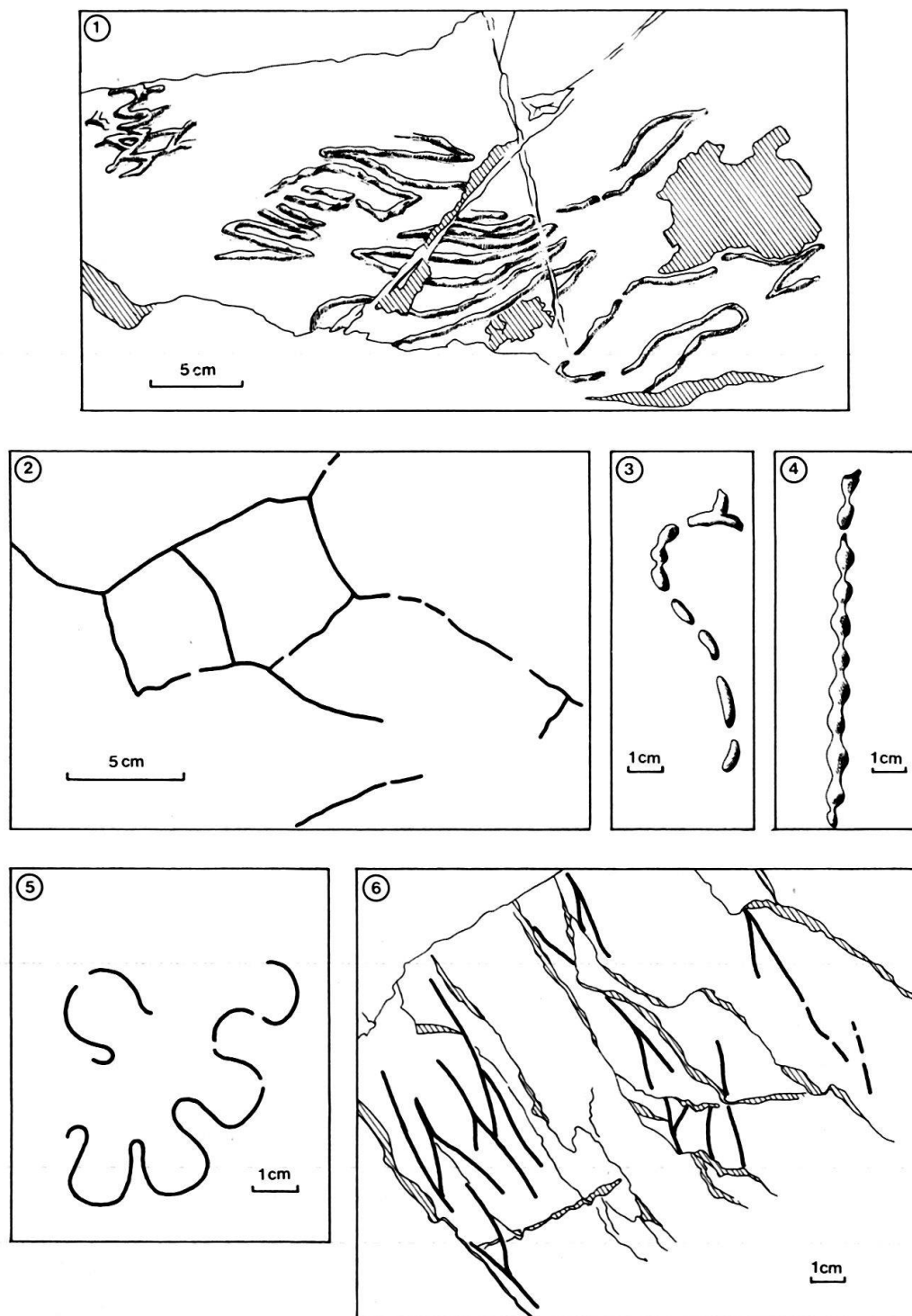


Fig. 3. Trace fossil examples from the Helminthoid Flysch (in parentheses: locality and outcrop number from Fig. 1 and 2).

1: *Urohelnthoida* hypichnial cast on the base of a silty turbidite. Fine-bedded calcareous flysch (below Glori, Argentina brook, 3). 2: *Megagraption* (endopelitic). San Remo Fm (Colle S. Bartolomeo, 10). 3: *Tuberculichnus* (hypichnial cast). Varicoloured shales (Colle Serro, 4). 4: *Hormosiroidea* (hypichnial cast). Varicoloured shales (Colle Serro, 4). 5: *Cosmorhaphie* (endopelitic). San Remo Fm (Colle S. Bartolomeo, 10). 6: *Urohelnthoida* (endopelitic) within the upper marly part of a thick calcareous turbidite. San Remo Fm (Carpasio, 9).

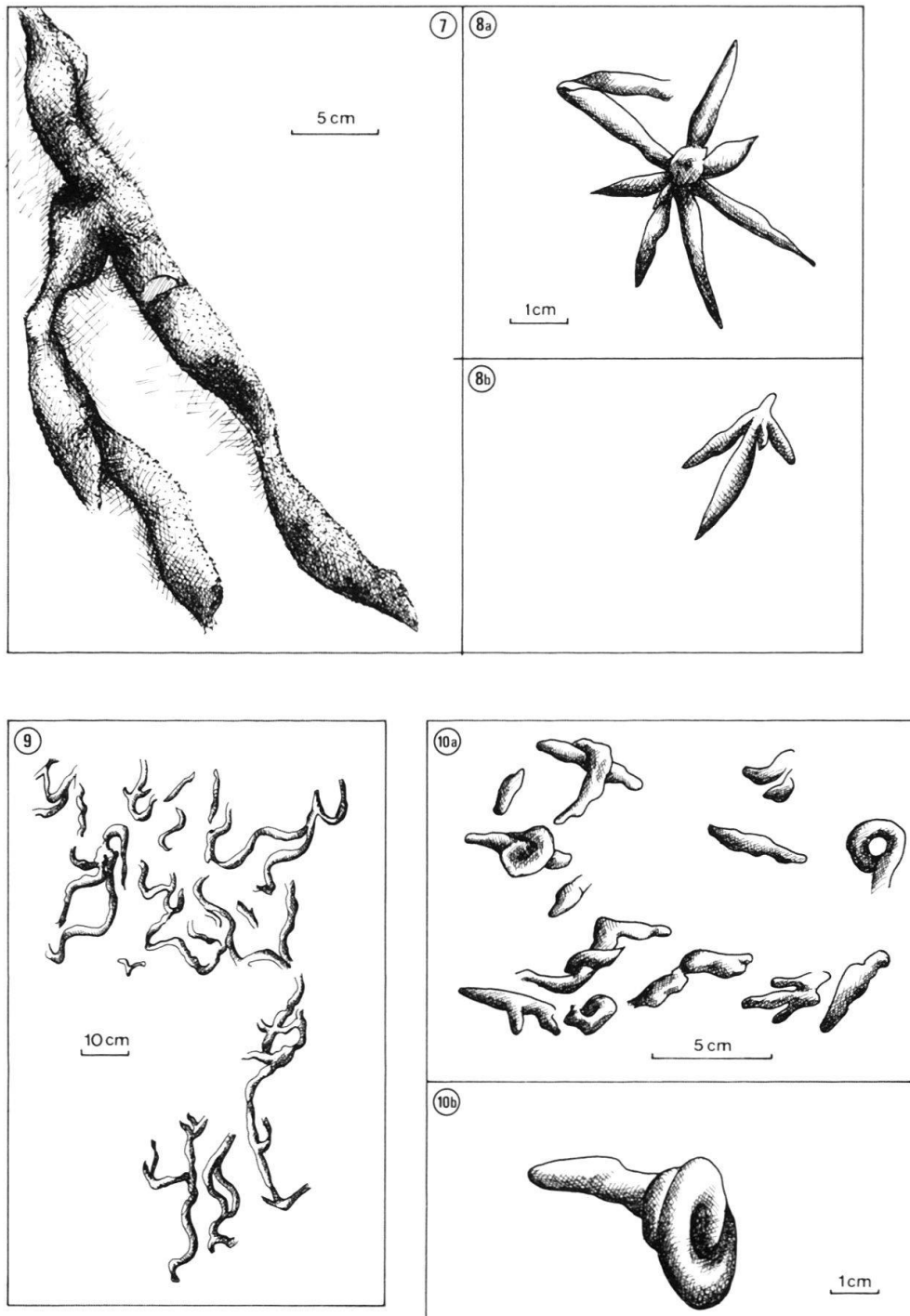


Fig. 3 (cont.)

7: *Thalassinoides* type A in hyporelief. Manganiferous Flysch (Pratti di Millio, 1). 8: *Granularia* hypichnial burrows (a, b). Fine-bedded calcareous flysch (below Glori, Argentina brook, 3). 9: *Thalassinoides* type B (sinuous maze in hyporelief). San Remo Fm (Colle S. Bartolomeo, 10). 10: *Thalassinoides* type C (with snail-like tapering offshoots; hypichnial). San Remo Fm (Frantoio d'Oneglia, 14).

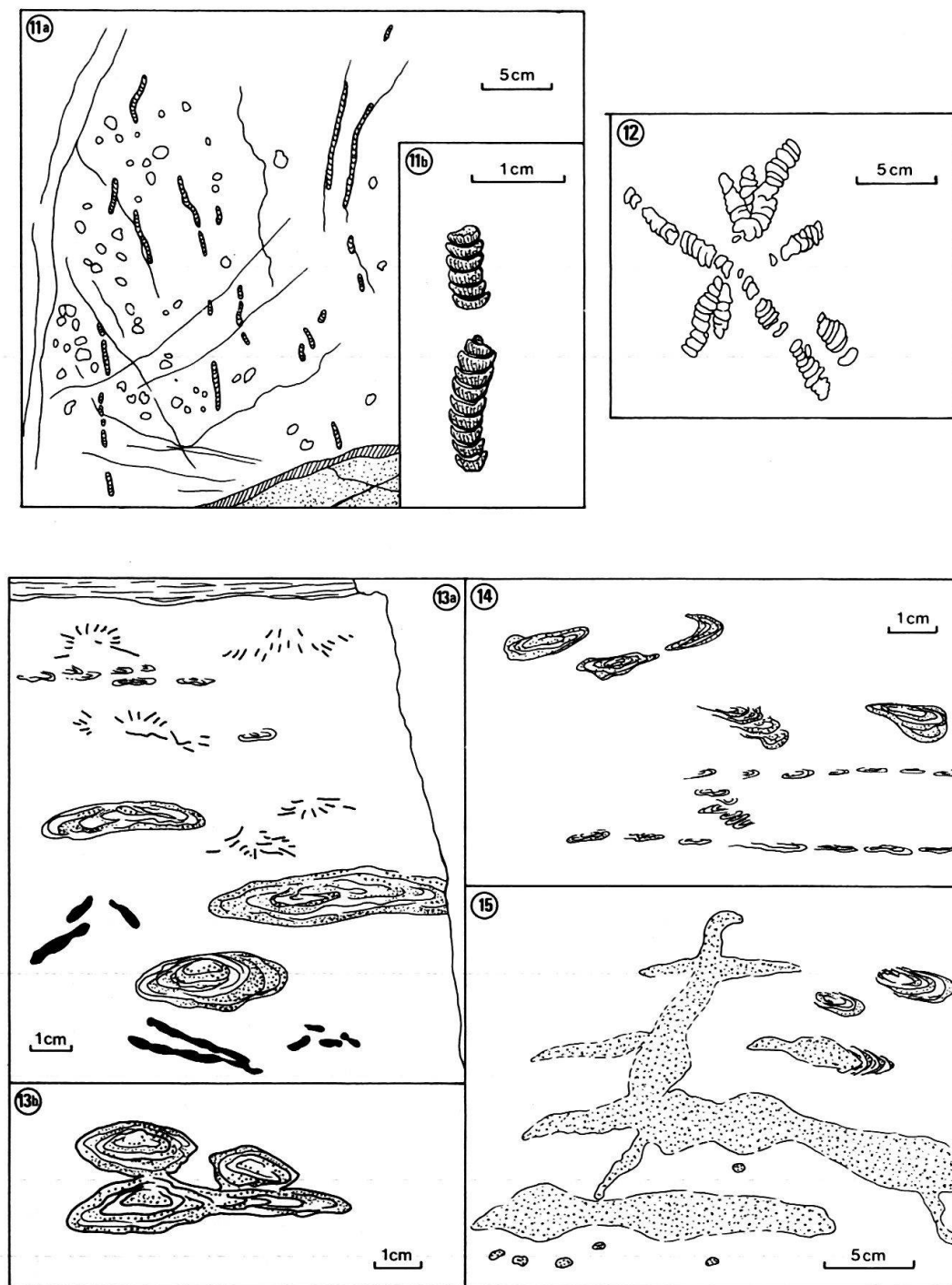


Fig. 3 (cont.)

11: "Annular tubes" with concave terminal backfill. Vertical section of a calcareous turbidite 55 cm thick. Bulges and pustules on the weathered limestone face are silty eddy-type biodeformational mottles. San Remo Fm (Colle S. Bartolomeo, 10). 12: *Taenidium* (endopelitic burrow; section parallel to bedding). San Remo Fm (Carpasio, 9). 13: Mixed *Chondrites*-*Asterosoma* assemblage in upper part of a thick calcareous bed (a); crowded *Asterosoma* branches in cross-section (b). Base of San Remo Fm (below Croce Praesto, 8). 14: *Asterosomids* and unidentified small spreiten in red mudstone (cross-section; drab-coloured silty parts dotted, red mudstone blank). Varicoloured shales (Colle Serro, 4). 15: *Asterosomid* (upper right) and *Thalassinoid* endichnial burrows in red mudstone with silt lenses. Varicoloured shales (below Glori, Argentina brook, 3).

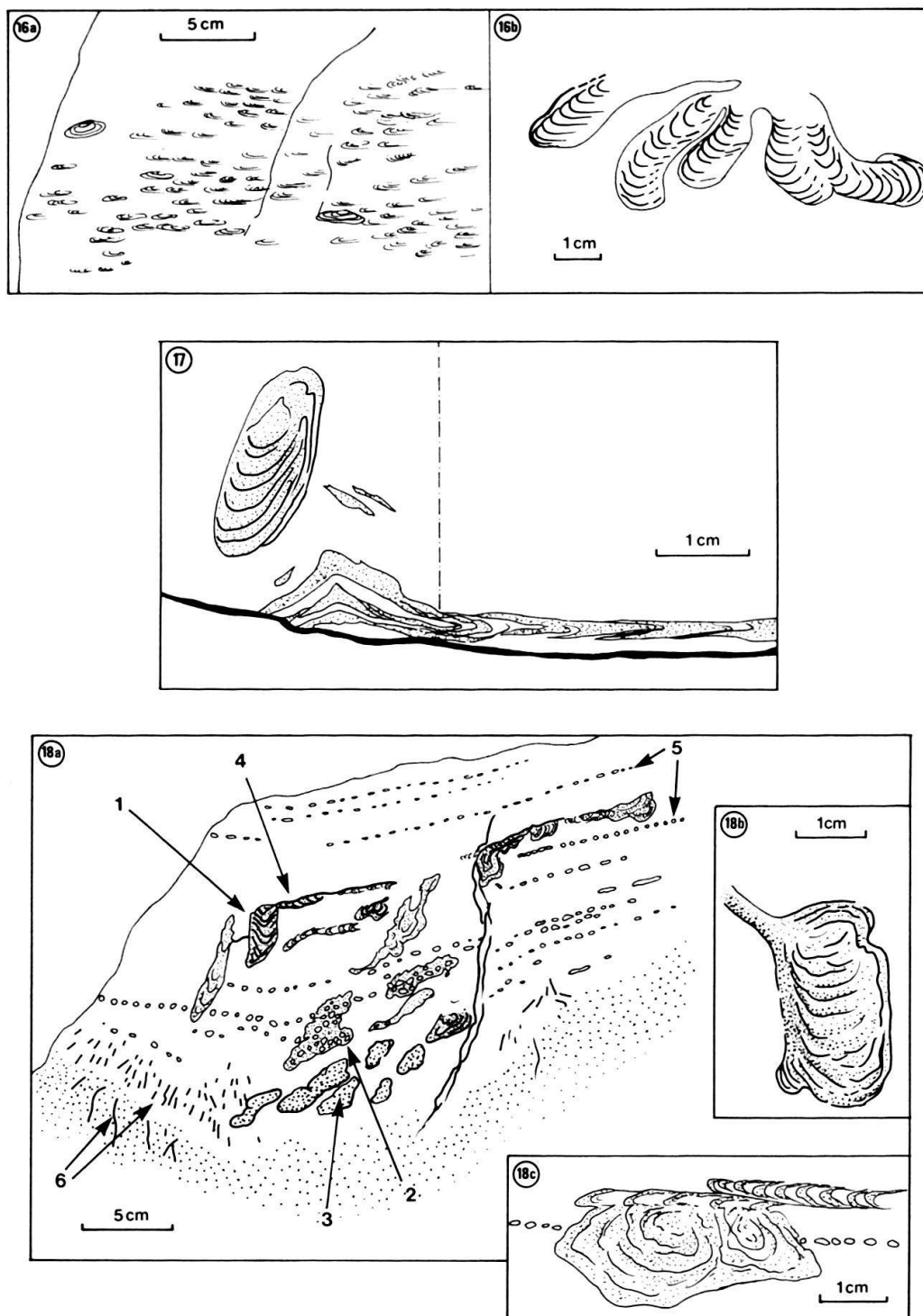


Fig. 3 (cont.)

16: *Hydracnylus* (endichnial leaf-like spreiten in vertical (a) and horizontal (b) cross-section). San Remo Fm (southern slopes of Mt Guardiabella, 13). 17: *Zoophycos* (single spreite lobe at the base of a medium-sized calcareous turbidite; vertical cross-section). Rounded U-filled burrow may represent an oblique section of a *Zoophycos* central shaft. Ubaga Limestone (Alassio unit, below Madonna della Guardia sanctuary, 15). 18: *Helminthoida* – *Chondrites* – *Asterosoma* – spreiten assemblage in the slumped pelitic interval of a medium sandy-calcareous bed (a). *Teichichnus* with U-backfill = 1, reworked by *Helminthoida* = 2, structureless = 3, *Zoophycos* = 4, *Chondrites* = 5, *Helminthoida* = 6. The same bed: *Teichichnus* with marginal U-tube (b); *Asterosoma* at the base of two juxtaposed *Zoophycos* lobes (c). San Remo Fm (below Croce Praesto, 8).

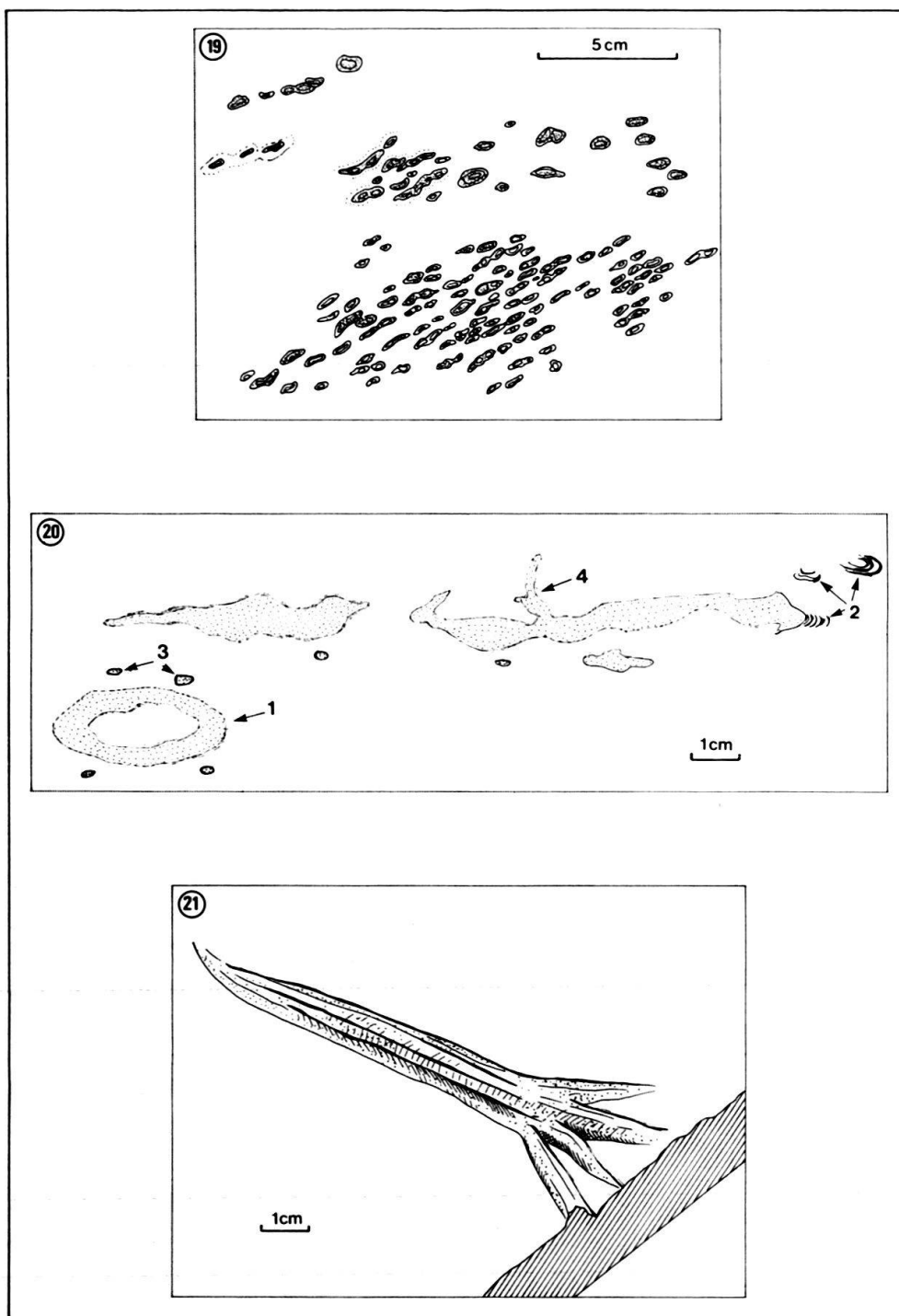


Fig. 3 (cont.)

19: "Quincunx galleries" (full relief endichnial burrows with silty terminal backfill; vertical cross-section through a thick calcareous turbidite bed). San Remo Fm (Capo Mele, No 1 National Road, 11). 20: Thalassinoid-Asterosomid assemblage in red mudstone (blank) with drab-coloured silty intercalations (dotted). ("Rind burrow" = 1, Asterosomid = 2, Planolites = 3, Thalassinoid = 4). Varicoloured shales (below Glori, Argentina brook, 3). 21: Fucusopsis in hyporelief (parallel ridges that run longitudinally are wrinkled). Varicoloured shales (Colle Serro, 4).

diagnoses. Sketches, photographs, and in some cases collected specimens served later as comparative material. The traces well-preserved enough to obtain good photographs in the field conditions were uncommon, and, consequently, the sketches appeared more suitable to taxonomic purposes.

To refine the taxonomic diagnosis I compared the material from the Helminthoid Flysch with specimens from the trace fossil collection of A. Seilacher at the University of Tübingen (FRG).

Preservation of biogenic structures in the Helminthoid Flysch

Due to strong tectonic deformations the preservation state of the biogenic structures is rather poor, especially in the turbidite soles. The turbidite strata with the richest ichnologic record are represented mostly by two calcareous lithologies:

- hard, nonporous, light-grey, yellow or rusty weathered biomicrite (40–60% CaCO_3) composed of nannofossils, sponge spicules, Radiolaria and rare pelagic Foraminifera,
- dark-grey, micritic mudstone (15–60% CaCO_3) composed of micritic grains, spicules, Radiolaria, phyllosilicates and quartz silt.

Although the organic markings are present on the bases of virtually all beds, in sets of irregular molds, bulges and pustules, the recognisable hypichnial traces are sparse. Comparatively, the endichnial traces appear to be well-preserved, probably thanks to diagenetic and alteration processes which enhanced the visibility of internal structures in the limestones (see KENNEDY 1975, BERGER, EKDALE and BRYANT 1979, EKDALE and BROMLEY 1983, EKDALE, MULLER and NOVAK 1984, SIMPSON 1987). The principal features highlighting the endichnial burrows are: pyritised infillings with limonite alteration stains, white reduction haloes (e.g. around Helminthoida burrows in the biomicrite, drab-coloured burrows in the red mudstone), slight contrast in sediment texture between the burrow and surrounding matrix (silt-sized burrow fill in Zoophycos, Teichichnus, Asterosoma, Thalassinoides).

The ichnologic record, largely predominated by various endichnial burrows, closely approaches the trace fossil record in the fine-grained sediments derived from calcareous plankton (EKDALE and BROMLEY 1984), or turbidite-like, calcareous, mud-dominated storm deposits (SIMPSON 1987). Noticeably, it shows lesser resemblance with that of siliciclastic deep-sea fan sequences, where the Endichnia are uncommon (SEILACHER 1962 and 1978, CRIMES 1977, KSIAŹKIEWICZ 1970 and 1977, CRIMES et al. 1981).

Systematic section

I. Agrichnia: farming/dwelling structures (EKDALE 1985).

These ichnofossils, which belong to the group of Graphoglyptids (SEILACHER 1977) occur here mostly as exichnia, and occasionally as moulds at the sandstone-shale interface. They are found at argillaceous tops of medium-bedded calcareous turbidites as tiny flat ribbons (0.5 to 1 mm wide) made up of brownish silty material, coarser than the surrounding pelite. Originally, these were probably mucus-lined void tunnels, filled passively later.

— Urohelminthoida SACCO 1880 (SEILACHER 1977, p. 307).

Two modes of preservation: hypichnial grooves (Fig. 3-1) and exichnial flattened tunnels (Fig. 3-6).

— Megagraption KSIĄŻKIEWICZ 1968 (SEILACHER 1977, Fig. 11e, p. 320, KSIĄŻKIEWICZ 1977, Fig. 44d, e, f, p. 184).

Loosely organised polygonal meshwork, solely endopelitic (Fig. 3-2).

— Hormosiroidea SCHÄFFER 1928 (SEILACHER 1977, Fig. 6n, p. 305).

Rosary-like smooth-walled hypichnial casts (Fig. 3-4).

— Cosmorhaphie FUCHS 1895 (SEILACHER 1977, p. 297).

Endopelitic ribbon-shaped meandering tunnels (Fig. 3-5).

II. Repichnia: crawling traces

— Scolicia DE QUATREFAGES 1849.

Backstuffed internal trails with an elliptical cross-section and bilobed symmetry, more or less winding. They were probably produced by irregular echinoids moving either within the muddy substrate (Taphrhelminthopsis) or along the lithologic interfaces within the deposit (Subphyllochorda). (CRIMES & SMITH 1983, Taphrhelminthopsis: KSIĄŻKIEWICZ 1970, Pl. 2c, d, f, p. 293 and Pl. 3f, p. 297; CRIMES 1977, Pl. 6a, b, p. 87; Subphyllochorda: KSIĄŻKIEWICZ 1970, Pl. 1f, p. 291).

— Neonereites SEILACHER 1960 (HÄNTZSCHEL 1962, p. W205, Fig. 126,3a, b, p. W203).

III. Fugichnia: escape structures

— “Annular tubes” (Skolithos? Planolites?).

Shafts of diameter ca. 5 mm, several centimeters or dozens of centimeters long, stuffed by concave silty meniscus laminae, pyritised with a limonitic alteration stain. Somewhat sinuous, they occur in several sub-parallel lines crossing the upper intervals of calcareous turbidite beds to a depth of 80 to 200 cm (Fig. 3-16). The tubes are thought to have been produced by a worm-like animal moving upward, perhaps to escape from a burial (similar forms found in the “Alberese” flysch by SCHOLLE 1971).

IV. Pascichnia: grazing structures made by vagile infaunal sediment feeders

— Helminthoida SCHAFHÄUTL 1851 (HÄNTZSCHEL 1962, p. W200).

— Phycosiphon FISCHER-OOSTER 1858 (HÄNTZSCHEL 1962, Fig. 129,6, p. W209–W210).

Endichnial burrow consisting of thread-sized strings that form loops arranged in antler-shaped systems. Occur intermingled with Helminthoida in upper part of calcareous pelites. No spreite-like structure is preserved between the arms of the loop, probably due to strong tectonisation, similar to forms collected from the Cretaceous “Alberese” flysch in the Northern Apennine (Seilacher’s collection).

V. Fodinichnia: made by infaunal, hemisessile sediment feeders

This is the most diverse group of traces in the examined flysch, thence several behavioural categories were distinguished here.

1. Disorganised feeding patterns produced by mobile vermiform animals:

— Planolites NICHOLSON 1873 (PEMBERTON, FREY, 1982, p. 864).

2. Chondritid arborescent burrows

They were probably made by hemi-sessile vermiform organism which probed the calcareous pelite and subsequently-backfilled the tunnels produced. This is suggestive of an animal having an U-shaped gut.

— Chondrites STERNBERG 1833 (KERN 1978).

— Taenidium HEER 1877: Fig. 3-17 (HÄNTZSCHEL 1962, Fig. 136,2, p. W217).

3. Thalassinoid burrows

This burrow type is characterised by a Y-shaped pattern of branching and by anastomosing tunnels (SEILACHER, pers. communication). The tunnels form frequently a random maze in, or about the interface sand-shale. Produced probably by decapod crustaceans that lined their burrows with faecal pellets.

— Granularia POMEL 1849.

Small (3–5 mm wide), twig-like tunnels branching frequently. The fill is usually coarser than the material of the overlying sandstone bed (Fig. 3-13a, b) (CRIMES et al. 1981, KSIĄŻKIEWICZ 1977, Fig. 10, p. 74 – under: Buthotrephis HALL 1847).

— Thalassinoides EHRENBURG 1944.

Form A: rough-walled rectilinear tunnels 1 to 2 cm wide which make up a random horizontal maze preserved as a hypichnial cast (Fig. 3-12) (FREY et al. 1978, Fig. 2G, p. 202 – under: Ophiomorpha LUNDGREN 1891).

Form B: similar to A but with neatly sinuous branches (Fig. 3-14) (KSIĄŻKIEWICZ 1977, Fig. 41c, d, Pl. 10d – under: Protopaleodictyon KSIĄŻKIEWICZ 1977; FREY et al. 1978, Fig. 2H, p. 202).

Form C: the maze composed of two tiers; the upper one consists of a horizontal maze of vermiform galleries which align roughly to the flute cast direction, the lower one is made of snail-shaped whorls that penetrate into the underlying shale (Fig. 3-15).

— “Rind burrow” (unidentified).

Cylindrical coarse-grained tunnels, elliptic in cross-section, that appear in highly bioturbated red mudstones. A drab-coloured silty sheath is wrapped around copper red muddy center, the cortical thickness being about 1 cm (Fig. 3-25). Similar traces have been reported from red muds in DSDP cores (CHAMBERLAIN 1975, p. 1083, Fig. 1, 2, 6, 8, Pl. I, CHAMBERLAIN 1978).

4. Asterosomid burrows

Radially backfilled bulbous structures produced by a worm-like animal inhabiting an U-tube. The organism backstuffed the tube by blowing up it's body, which eventually gave way to a fill of concentric wrinkled laminae (SEILACHER, pers. communication).

— *Fucusopsis* VASSOIEVITCH 1932 (Fig. 3-26)

(KSIĄŻKIEWICZ 1970, Fig. 1s, p. 284).

— ?*Asterosoma* VON OTTO 1854.

Large flattened bodies with concentric onion-shaped corrugated laminae of silt. The three-dimensional outline is not known, only numerous cross-sections in calcareous pelite or in red mudstone were observed (Fig. 3-18, 19, 20, 23, and 25).

5. Teichichnoid burrows

Vertically stacked structures with transversal backfill, produced supposedly by a deposit-feeder inhabiting an U-tube.

— *Teichichnus* SEILACHER 1955.

Arc-shaped protrusive spreite with marginal U-tube (Fig. 3-23b). Often reworked by Helminthoida or Chondrites burrows. (HÄNTZSCHEL 1962, p. W218).

6. Alectorurid burrows

Horizontally stacked spreite structures with complex systematic mining pattern (SEILACHER 1967).

— *Zoophycos* MASSALONGO 1855. (Fig. 3-22). (HÄNTZSCHEL 1962, p. W220).

— *Hydrancylus* FISCHER-OOSTER 1858. (Fig. 3-21). (HÄNTZSCHEL 1962, p. W200, Fig. 121,5, p. W196).

Certain types of burrows encountered in the Helminthoid Flysch fail to fit this behavioural classification, although they were interpreted as feeding structures on the basis of their vermicular outline.

— "Quincunx galleries" (not identified; Chondrites?).

Complex sets of burrows where individual tunnels, rice-shaped in cross-section display terminal backfill of very fine silty concentric laminae. Rows of contiguous tunnels are organized in sets of roughly rhombohedral outline which are slightly oblique (5 to 45 degrees) to the bedding. The mining pattern was likely to be systematic, the animal being able to guide its tunnel to avoid the parts already burrowed (Fig. 3-24).

— *Tuberculichnus* KSIĄŻKIEWICZ 1977 (Fig. 3-3)

(KSIĄŻKIEWICZ 1977, Fig. 27a, e, p. 140).

Trace fossil assemblages

The ichnologic examination of the Helminthoid Flysch deposits allows to distinguish eight standard ichnoassemblages according to their ichnofossil content and to their ichnofabric (*sensu* EKDALE & BROMLEY 1983). Relative to the modes of trace distribution two principal ichnofabric patterns were distinguished:

a) Tiered pattern, with different taxa occupying distinct levels within the bed. These levels, or tiers ("storeys" in WERNER & WETZEL 1982) may partially coalesce, but in general they can be easily recognized by the prevalence of a certain trace type in a given sediment slice.

b) Complex pattern, characterized by an intimate juxtaposition of different taxons throughout the bed.

In addition, mixed patterns of intermediate character were recognized, in which the complex ichnofabric is limited to certain lithologic intervals, while the overall tiering is still discernible.

Typology and description of ichnoassemblages

Trace fossil assemblages from this flysch can be subdivided into the following types (Fig. 4):

I. Helminthoida-Chondrites-Zoophycos tiered assemblage in medium- to thick-bedded calcareous turbidites.

The bed lithology displays a ternary pattern: fine-grained calcareous sandstone, graded or parallel-laminated, passing upwards into graded silty limestone, and capped by non-calcareous massive shale. The calcareous interval, the thickest of all three, comprises, from top to bottom, 3 to 4 distinctive tiers:

- grazing traces (Helminthoida), which may be present (Ia) or absent (Ib),
- small probing structures (Chondrites intricatus),
- big probing structures (Ch. furcatus),
- highly organised bulk mining structures (Zoophycos, "quincunx galleries", Hydrancylus).

It is noteworthy that the basal discontinuity lacks any identifiable trace.

This assemblage displays also a distinct vertical gradient in bioturbation density: traces concentrate in the topmost part of the calcareous interval and gradually disappear downwards depending on the taxon considered. This phenomenon is most striking with respect to Helminthoida trails: these burrows are very dense and coalescing near the top of the limestone (0 to 1 cm), but disappear below the 5 to 7 cm. A similar trend is found in Chondrites at a lower level (3 to 10 cm).

II. Graphoglytid-Helminthoida-Chondrites-Thalassinoid tiered assemblage.

Thin- to medium-bedded calcareous turbidites, which again show a ternary lithologic pattern: thin sandy, wavy- or ripple-laminated basal layer overlain by graded silty limestone which passes gradually upwards into fissile argillaceous biomicrite.

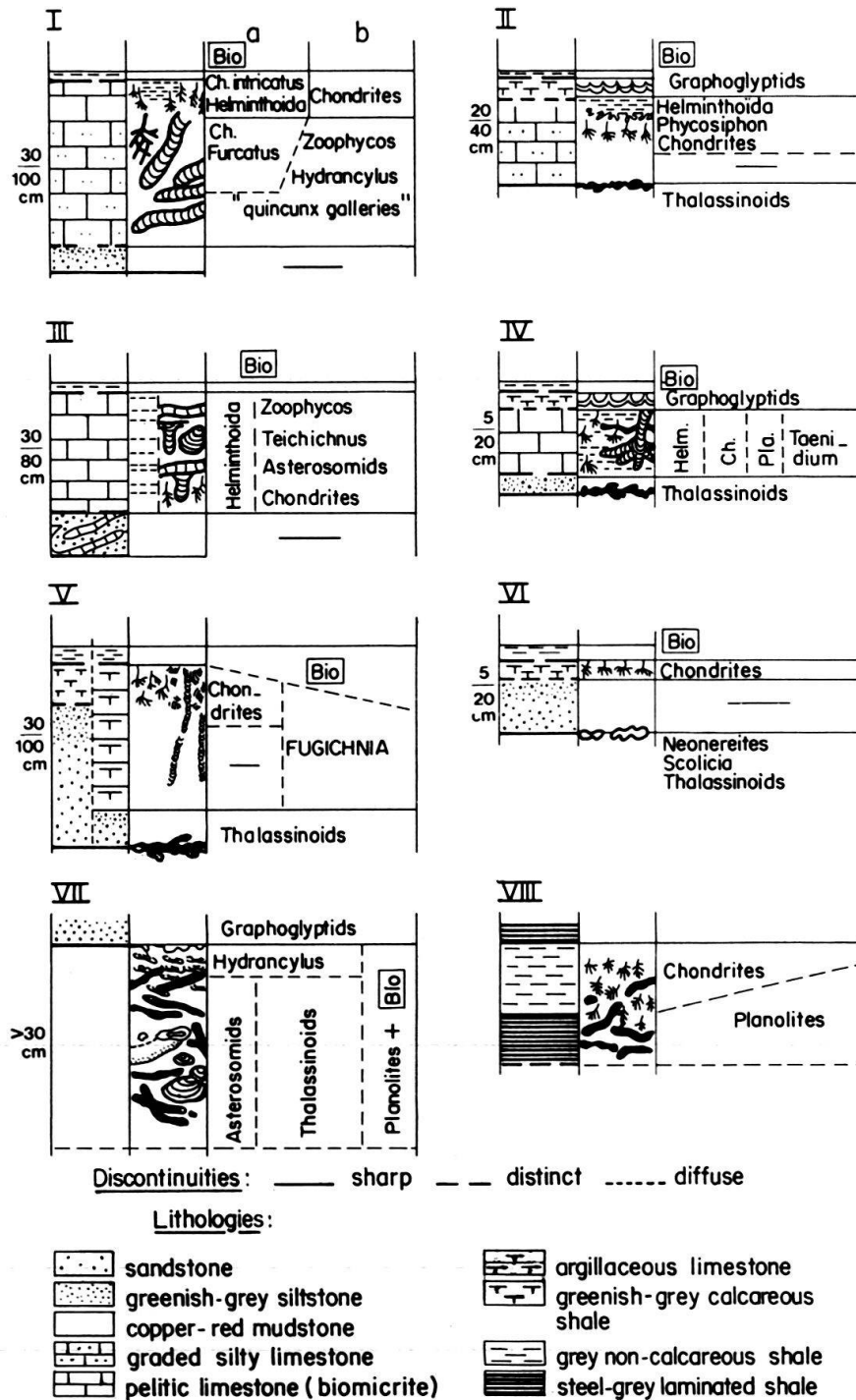


Fig. 4. Diagrammatic trace fossil assemblages from the examined outcrops of the Helminthoid Flysch. Columns in each show, from left to right: – lithology and sedimentary discontinuities – ichnofabric (arrangement of bioturbation structures), with schematic outlines of the ichnogenera present – taxonomic and morphologic names of traces. Type assemblages: I = tiered Helminthoida–Chondrites–Zoophycos assemblage (Ia = Helminthoida present, Ib = Helminthoida absent), II = tiered Graphoglyptid–Helminthoida–Chondrites–Thalassinoid assemblage, III = mixed Helminthoida–Chondrites–Asterosomid–spreiten assemblage, IV = mixed Helminthoida–Chondrites–Graphoglyptid assemblage, V = Chondrites–Fugichnia assemblage in thick siliciclastic (Va) and calcareous-marly (Vb) turbidites, VI = Chondrites–Scolicia–Thalassinoid assemblage, VII = complex Planolites–spreiten–Graphoglyptid assemblage, VIII = tiered Chondrites–Planolites assemblage. Ch = Chondrites, He = Helminthoida, Pla = Planolites, Bio = biodeformational structures and mottling.

Well developed storeys are present from the top to the bottom:

- farming structures (Graphoglyptids) in the argillaceous biomicrite,
- grazing traces (Helminthoida),
- probing structures (small Chondrites),
- large burrows (Thalassinoid) at the basal sandstone/shale boundary.

Zoophycos-like spreiten are notably absent from the calcareous interval. The density gradients of Helminthoida and Chondrites are similar as in the former assemblage (I). Levels deeper than 7–12 cm within the calcareous interval are devoid of traces.

III. Helminthoida-Chondrites-Asterosomid-Alectorurid mixed assemblage in medium-bedded pelitic calcareous turbidites.

The lithologic pattern is as follows: graded and/or evenly-laminated, fine-grained sandstone (sometimes extensively slumped) is overlain by calcareous pelite, which is silty and slightly graded in the lower part. Small slump folds with recumbent or inclined axial planes affect the sandy intervals. They may occur as trains in continuous layers, or be disrupted or float in shaly and calcareous matrix as isolated fold hinges. These deformation structures tend to disappear in the overlying calcareous interval, so that the limestone remains gently swollen or weakly bent. Bioturbation occurred prior to deformation of the calcareous interval, because spreite burrows and grazing trails are deformed. The calcareous interval shows the intimate cross-cutting of different traces: Helminthoida trails, which are scattered all over the bed (from 0 to 30 cm in depth), rework the Teichichnus spreiten, while the latter seemingly “rub out” some of the Chondrites structures. The Zoophycos lobes seem to be reworked sometimes by radial-backfill burrows (Fig. 3-18c; downward mixture of tiers).

IV. Helminthoida-Chondrites-Graphoglyptid mixed assemblage in thin-bedded pelitic calcareous turbidites.

The lithologic pattern resembles the foregoing assemblage (III), but the sandy term is reduced to a thin, wavy or ripple-laminated, film at the sole.

The ichnofabric is analogous to that observed in type III: traces are thoroughly mingled at all levels of the bed and, consequently, burrow density doesn't show any preferential trend. However, Thalassinoid burrows individualize the lower tier at the sandstone/shale interface.

V. Chondrites-Fugichnia tiered assemblage in medium- to thick-bedded siliciclastic (Va) and calcareous (Vb) turbidites.

Since the two distinguished lithologic types do not differ much with respect to the ichnologic record, they were lumped into one category. Their respective lithological sequences are as follows:

- a) lithic sandstone Ta-b, which passes upwards into very fine-grained calcareous sandstone Tc, and eventually into splintery argillaceous biomicrite,
- b) fine-grained calcareous sandstone Tb, sometimes intensely slumped, is topped by a thick interval of flaggy argillaceous limestone grading into splintery mudstone and shale.

Despite the scarcity of traces an indistinct tiering appears, from the top to the bottom:

- probing (Chondrites) and/or eddy-type biodeformational structures (see WERNER & WETZEL 1982) in the upper part (0 to 15 cm) of the calcareous horizon,
- escape structures (“annular tubes”) crossing the whole thickness of the calcareous interval (in b-type beds),
- Thalassinoids at the sole of both types of beds (less than 1 m thick).

VI. Chondrites-Scolicia-Thalassinoid tiered assemblage in thin-bedded sandy turbidites.

Lithologically, these beds represent “classical” siliciclastic turbidites with Bouma sequences Tbcde, Tbde and Tcde.

Bioturbation is two-tiered:

- probing burrows (small Chondrites) in the calcareous Td interval,
- Thalassinoid or crawling trails at the turbidite sole.

VII. Planolites-Asterosoma-Graphoglyptid complex assemblage in oxic mudstone.

The copper-red, non calcareous mudstone is homogeneous or mottled, occasionally more silty with cross-laminated lenses and thin diffuse laminae of drab-coloured siltstone.

The assemblage is rather monotypic with scattered Planolites burrows more or less abundant (VIIa). The ichnologic content shows higher diversity in the silty mudstones with occasional medium-bedded massive siliceous sandstone beds (20 to 50 cm thick). Diverse traces, such as Planolites, small spreite burrows (*Hydrancylus*), and feeding/dwelling structures (“rind burrows”, *Asterosoma*) appear juxtaposed to form a complex ichnofabric in this facies (VIIb). Nevertheless, a primary tiering can be perceived immediately below thicker sandstone beds:

- Graphoglypt burrow casts at the sole of the overlying sandstone bed,
- diverse burrows intermingled.

In this case the density of ichnofossils lacks any systematic gradient and seems not to be controlled by sedimentary events i.e. quick sandstone deposition.

VIII. Chondrites-Planolites tiered assemblage in anoxic shales and mudstones.

The assemblage occurs in banded steel-grey to olive-green non-calcareous shales (5 to 10 cm) intercalating with black pyritic laminated shales. It contains a low-diversity assemblage of ubiquitous traces (Planolites, Chondrites).

A disordered two-tiered pattern appears:

- abundant Chondrites plus Planolites in homogeneous olive shale,
- scattered Planolites in steel-grey laminated shale.

The density of traces is quite random in the bundles of banded shales, while in the surrounding black shales the traces seem to be absent.

Interpretations

Control of ichnofabric patterns by sedimentary regimes

The variety of burrow assemblages in the Helminthoid Flysch is probably related to different sedimentary processes operating in the basin, because ichnofabrics and particularly the trace density gradients within individual beds correlate fairly well with lithologies and sedimentary structures.

Noteworthy are variations in the vertical density gradient of burrows:

- a) a more or less distinct downward decrease in the turbiditic assemblages (I to VI),
- b) an apparently homogeneous vertical distribution of traces in the hemipelagic assemblages.

All turbiditic assemblages reviewed above show a direct relationship to the rhythmic deposition pattern, in that the traces never penetrate below the base of a given turbiditic bed, even if this bed is very thin. Therefore, bioturbation was periodic, triggered by the arrival of “fresh” unconsolidated sediment due to gravitational flows (see SEILACHER 1978). Turbidity currents operated extensively in the Helminthoid Flysch basin, destroying periodically the benthic life, eroding the benthos, or leading to its burial and smothering. The intermittent benthic re-colonisation resulted in tiered patterns (assemblages I, II, V and VI).

The mixed-type ichnofabric of assemblages III and IV is suggestive of repeated colonisation, however the depositional mode interpretation remains unclear: the upper bioturbation levels in assemblages III and IV should have been produced under steady-state conditions of relatively slow sedimentation, although the overall depositional mode was instantaneous, and related to gravity flows. Since the relative abundance of bioturbation can be expected to be inversely proportional to sedimentation rate (HOWARD 1975, RHOADS 1975), the density gradient of traces produced by the shallow diggers such as the Helminthoida-makers may be indicative of accretion rate. Ichnofabrics with a downward density drop (I and II) are indicative to a “classical” turbidity current model. Mixed-type ichnofabrics (III and IV) seems to result from the mode of bioturbation by gradational overlap (R. Goldring, pers. communication), which probably required gradational change in hydraulic conditions on the bottom or in mechanical properties of the substrate during the phases of extensive lime mud deposition and early burial.

A possible model for the deposition of the beds with assemblages III and IV is provided by the turbid surge mechanism (RAVENNE & BEGHIN 1983). It results from seeping out of a finite quantity of dense fluid, producing a voluminous turbulent cloud which settles very slowly. This process may be responsible for the deposition of calcareous pelites in a ponded deep basin below CCD.

The “dissipated” ichnofabric of the oxic mudstone and its independence of sandy sedimentation episodes suggest continuous bioturbation under steady-state conditions (R. Goldring: “successive tiering”). Thus, the resulting ichnoassemblage has an aspect of a “palimpsest”, in which the traces of different bioturbation episodes occur together in the same sediment slice. Similar patterns were encountered in hemipelagic calcareous deposits at modern continental margins (WERNER & WETZEL 1982) and in truly pelagic red muds (EKDALE et al. 1984).

The ichnofabric of assemblage VII (tiered but with random distribution of traces in burrowed intervals) appears to reflect "single colonization" style of bioturbation (R. Goldring), imposed by fluctuating redox conditions as it is characteristic for a stagnant basin conditions with short periods of improved aeration at the bottom (SEILACHER 1978, SAVRDA et al. 1984). Intermittance of endobenthic colonisation was probably caused by such fluctuations (from anaerobic to dysaerobic; see Fig. 2). The sedimentary regime was also likely to control the development of bioturbation tiers during the colonisation. Assemblages I and II are structured in 3 to 4 storeys, similar to the patterns found in sub-recent pelagic calcareous deposits at the continental margin off North-West Africa (WETZEL & WERNER 1981, WETZEL 1982). Assemblage VII of hemipelagic oxic shale intervals shows a certain stratification with 1 to 3 tiers. These data suggest a relationship between the level of oxygenation in the bottom water and the number of bioturbation storeys, analogous to the telescoping of tiers with increasing oxygen content of bottom waters that has been found in modern pelagic deposits (WETZEL 1982). Furthermore, lithologic differences (grain size, calcium carbonate content, organic carbon) probably played a role in the structuration of the assemblages. Differences in adaptative strategies, as well as exclusion of certain burrowers from particular substrate types (and possibly from a tier within the substrate), are likely to have operated. For instance, the presence of spreite-like permanent feeding structures in the calcareous assemblages probably reflects higher substrate stability, which is necessary to maintain the ventilation system of a sessile tube-dweller in an anoxic substrate (WETZEL & WERNER 1981). In addition, the spatial structures of ichnocoenoses in different subfacies (habitats) were probably controlled by properties of the substrate, such as grain size, mechanical strength and oxygen/hydrosulphide content.

Ichnoassociations in the fan-to-plain transition

Two sedimentary successions characterize the Helminthoid Flysch of the Ligurian Alps:

- a) a prograding suite from the San Bartolomeo Formation to the Bordighera Sandstone (Fig. 2a–g),
- b) a regrading succession within the San Remo Flysch (Fig. 2h).

These successions are thought to correspond to spatial shifts of environmental zones within the basin (POWICHROWSKI 1984):

- the former (a) indicates the transition from abyssal plain (anaerobic or aerobic) to deep-sea fan conditions; great amounts of the siliceous sand from the lateral sources were yielded into the basin (SAGRI 1980),
- the latter (b) reflects the transition from a deep-sea fan to a turbiditic basin plain; the axial supply of the lime mud prevailed during the retreat of the fan facies (SAGRI 1984, POWICHROWSKI 1984).

Since the depositional model of the Helminthoid flysch comprises few basal turbidite facies easy to distinguish (SAGRI 1980, 1984), it is possible to use a restricted set of outcrops to examine the relationship between facies and trace fossil distribution. The

outcrops where the trace fossils were analysed for the purpose of this study represent the main facies within the basin.

As it can be seen from Figure 2, the trace fossil distribution is closely linked with depositional environments throughout the basin, particularly if only the traces of presumably more environment-sensitive organisms (such as Graphoglyptids, meandering trails, or feeding spreiten-producers) are considered.

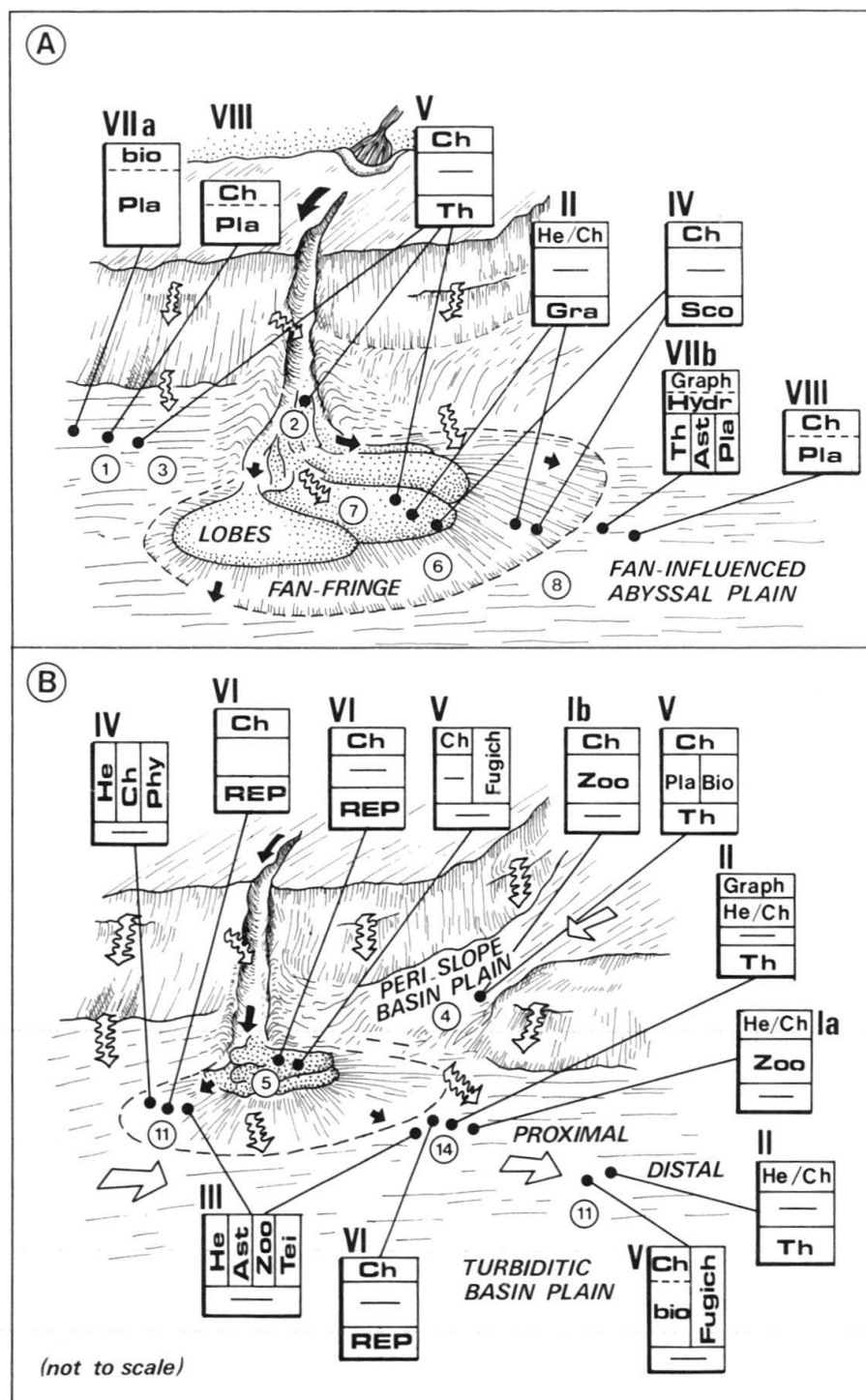
The link of the ichnoassemblage distribution with the prevailing sedimentary regime is shown diagrammatically in Figure 5. Fan progradation during periods of extensive terrigenous input favoured diverse burrowing activities in the outer fan zones (Fig. 5a):

- crawling feeding and subsurface grazing trails in the fan fringe,
- feeding and crawling traces, with a minor amount of grazing trails, in progradational lobes,
- infaunal spreiten, feeding/dwelling and occasional network structures in the fan-influenced hemipelagic abyssal plain.

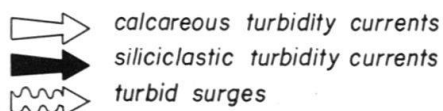
More distal zones of the abyssal plain were dominated by a monotypic *Planolites* association reflecting either aerobic or dysaerobic conditions.

The infaunal activity probably comprised modes of feeding other than sediment ingestion, such as micro-organism entrapment by hemi-sessile animals. Frequent arrivals of turbidity currents tended to eliminate spreiten-producers, while vagile sediment feeders or scavengers, such as *Scolicia*-makers (probably transported from the shelf or the slope to the deeper habitats) thrived the fan fringe. Analogous trends in trace fossil distribution were found in the other siliciclastic deep-sea fan sequences (CRIMES 1971, CRIMES et al. 1981).

An outburst of various digging activities marked the onset of fan retreat and the concomitant increase in the supply of remobilised lime muds (Fig. 5b). Draping of the fan fringe by calcareous sediments favoured the reappearance of a rich association of feeding and grazing traces quite often characterised by mixed ichnofabrics. Farther downslope, similar associations occurred, yet with well preserved tiering patterns. Complex foraging activities of diverse sessile or hemisessile pelite feeders and highly efficient mining programs prevailed, but mobile deposit feeders and grazers, and possibly animals using farming or trapping strategies were also present. The presence of shoal- and shelf-imported infauna (*Thalassinoid*-producers: large Crustaceans; *Scolicia*-type trails: Echinoids – CRIMES et al. 1981, CRIMES & SMITH 1983, EKDALE & BROMLEY 1984, WETZEL 1984) was linked with the turbidity flows. The presumably proximal parts of the basin plain (corresponding to the Alassio facies in Fig. 2) were inhabited by a deposit-feeding infauna that apparently lacked grazers. The abundance of opportunistic low-oxygen adapted species (*Chondrites*) indicates dysaerobic conditions probably caused by low-oxygen layer in the water column. The basin plain invaded by calcareous megaturbidites supported an association of low diversity, but exerting an extensive bioturbational effect on the sediment. In conclusion, the most diverse ichnoassociations, composed both of exogenous (shelf- or slope-derived) and endogenous animals, appeared in the outer fan and fan fringe zones during periods of extensive terrigenous supply, whereas more specialized deep-burrowing forms tended to spread onto the fan and basin plain in times of increased lime mud supply.



Types of sediment supply:



Evolution of behavioural diversity in the Helminthoid Flysch basin

With 22 ichnogenera recorded, the ethologic diversity in this flysch is remarkably high. The behavioural within-habitat diversity, i.e. the number of ichnotaxa in a specific habitat, corresponds roughly to the within-habitat species diversity (see SANDERS 1968), provided that the preservational bias did not affect much the original ratio of activity between deep and shallow diggers. Diversity trends based on endopelagic burrows, as in our example, should remain relatively unaffected by fossilization biases (MARTINSSON 1970, SEILACHER 1974). The ichnogenic diversity displays ranges from 1 to 3 taxa (channelized zone of suprafan, distal abyssal plain) up to 8–14 taxa (fan-influenced turbiditic basin plain), with the intermediate figures in other zones (Fig. 5). The tendency to behavioural diversification in the distal but fan-linked habitats becomes more obvious when ubiquitous facies-crossing taxa, such as *Planolites*, *Chondrites* or different *Thalassinoids*, are disregarded. Rich associations from the turbiditic basin plain notably contrast with monotypic *Planolites* associations from hemipelagic deposits on the abyssal plain in the same basin.

Observed compositional differences between ichnoassociations are thought to be related to the original infauna diversification rather than to ultimate “fossilization barriers”. For instance, spreite structures lack in calcareous turbidites of the San Bartolomeo Formation (Fig. 2e, f) but are present in basal parts of the San Remo Flysch (Fig. 2h); crawling trails are abundant in the “black flysch” (Fig. 2e), but disappear in the following fine-bedded calcareous flysch (Fig. 2f), although sedimentary patterns remained rather similar.

As to the trophic structure, the infaunal Helminthoid Flysch communities appear to be dominated by deposit feeders, analogous to what has been observed in muddy habitats of modern oceans, where sediment feeders make up more than 50 per cent of the infauna, regardless of basin depth (SANDERS & HESSLER 1969, LEVINTON 1972).

In analyzing the relationship between the inferred environmental time-stabilities and observed behavioural diversities in particular habitats, we note striking deviations from the presumed simple proportional relationship. The outbursts of various infaunal activities in the fan fringe and fan-influenced basin plain contrast with the scantiness and low diversity of the ichnologic record in otherwise stable environments, such as the abyssal plain. Similar trends occur in modern deep-sea deposits, where the *Planolites* association covers vast areas of abyssal bottoms, while the diversity of ichnocoenoses increases towards continental margins (BERGER et al. 1979, WETZEL & WERNER 1981, WETZEL 1982, 1984). This can be explained by the effects of destruction of upper tiers by the lower ones under steady and continuous pelagic sedimentation (WETZEL 1984).

Fig. 5. Model of distribution of ichnoassemblages vs sedimentary regimes in the Helminthoid Flysch basin (sedimentary model according to POWICHIROWSKI 1984). Two overall sedimentary regimes control the development of the ichnocoenosis: A: extensive lateral terrigenous supply by siliciclastic turbidity currents (San Bartolomeo Fm and Bordighera sandstone), B: high axial supply of lime mud by calcareous turbidity currents (San Remo Flysch). Ichnotaxa: He = Helminthoida, Ch = Chondrites, Graph = Graphoglyptids, Th = Thalassinoids (Gr = Granularia), Zoo = Zoophycos, Tei = Teichichnus, Ast = Asterosoma, Phy = Phycosiphon, Hydr = Hydrancylus, REP = crawling traces (Sco = Scolicia, Neo = Neonereites), bio = biodeformational structures. The Roman numbers correspond to the ichnoassemblages from the Figure 4; the circled Arab numbers refer to the ethologic diversity (number of ichnotaxa per environmental zone).

On the other hand, the high diversity of ichnocoenoses from the turbiditic basins might have resulted from an interplay between low growth rates of endobenthic populations and a particularly moderate level of environmental perturbation (turbidity currents), as to be expected if one applies Huston's model of biotic diversity (in: GRAY 1981, p. 58–66) to the ichnologic record. The rate of environmental perturbation, represented in the Helminthoid flysch basin mostly by the turbidity currents, was ascertained on the basis of the nannoplankton study (MANIVIT & PRUD'HOMME, in prep., FOUCAULT et al. 1987). The values of turbidity current frequency (in events/1000 yrs) and the recurrence time of turbidity currents for the main lithostratigraphic divisions may be estimated respectively to as:

- a) the San Bartolomeo Fm:
 - the Varicoloured Shale: 0 to 0.3 events/1000 yrs,
 - the Fine-bedded Flysch: 1 to 10 events/1000 yrs (recurrence time: 100 to 1000 yrs);
- b) the Bordighera Sandstone: 10 to 20 events/1000 yrs (50 to 100 yrs);
- c) the San Remo Fm: 0.3 to 1 events/1000 yrs (1000 to 3300 yrs).

These figures seem to correspond to the values supposed to be sufficient to maintain an exogenous burrowing fauna (Thalassinoids, Phycosiphon, Scolicia: WETZEL 1984). The ichnologic diversity seems to attain the maximum in the parts of the San Remo Flysch and the San Bartolomeo Formation which corresponded to the environmental zones of turbiditic/abyssal plain situated close to the fan fringe. Provided that the growth rates of the endobenthic communities were uniform, this trend in diversity can be explained by the variations of the turbidite current frequency due to the progradation or the retreat of the fan. The Huston's model is believed to explain short-termed changes in bioturbation patterns reflected by fluctuations of the trophic structure within a given community. However, when it is applied exclusively to surface-feeding behaviour, it shows no significant drop of diversity from the turbiditic to the pelagic substrate (HUGETT 1987). On the other hand, the time-stability hypothesis of SANDERS (1968) may be applied to long-term evolutionary trends in foraging behaviour, as suggested by SEILACHER (1974). This area is still open for more detailed studies based on more refined quantitative data.

Conclusions

Paleo-ichnologic studies in the Helminthoid Flysch of the Ligurian Alps made it possible to support the sedimentary model of a multi-phase transition from abyssal plain to fan and turbiditic basin plain by independent ecological evidence. The uniformitarian approach to ancient ichnocoenoses made it possible to infer a set of particular ecologic conditions that possibly controlled the foraging behaviour of the endobenthic community.

The ichnoassemblages, subdivided into eight principal types, display various ichnofabrics (i.e. spatial arrangements of trace fossils) in relation to lithology and sedimentary structures:

- tiered distributions in terrigenous and/or calcareous turbidites,
- complex ("palimpsest") patterns with random distributions of traces in oxic hemipelagic mudstones and shales,

- mixed patterns (overall zonated, but complex in certain intervals) in calcareous gravity flow deposits probably of turbid surge type.

The tiering of turbiditic assemblages is comparable to that reported from other Cretaceous–Paleocene flyschs (SEILACHER 1962, 1978). It is thought to reflect the original ecologic stratification of the ancient endobenthic community, which was preserved thanks to intermittent bioturbation phases between successive turbidity currents. The colonisation of a “virgin” calcareous bed probably took place sequentially with the arrival of endobenthic animals from peripheral slope and shoals that had remained unaffected by the turbidite deposition. Ecologic tiering in the assemblages and differential distributions of ichnoassociations within the basin were linked to the competitive interaction of foraging species in an environment, in which the availability of food was probably the main limiting factor. The zonal distribution of ichnoassemblages within the basin was controlled by prevailing sedimentary regimes. In particular, the increase of calcareous turbidite supply during the regrading phase of the fan appears to have resulted in a genuine enrichment of the ichnocoenosis with highly efficient feeding structures towards the border of the fan. On the other hand, diverse crawling and feeding associations (produced by burrowers imported from shallower environments) characterized the outer fan while it was prograding.

The tendency to behavioural diversification in the distal fan zones is responsible for the overall richness of the Helminthoid Flysch ichnocoenosis. It is tentatively explained, following Huston’s model of diversity (in: GRAY 1981), as an interaction between low turnover rates in deep-sea benthic populations and the moderate environmental perturbation typical for distal fan-influenced zones. Therefore, high local diversities of ichnocoenoses were probably due to a certain degree of environmental unpredictability, although overall trends in evolution of foraging behaviour should have resulted from the general ecologic stability typical for deep-sea basins.

Acknowledgments

Prof. A. Seilacher kindly reviewed the manuscript and made numerous suggestions which permitted to refine the taxonomical determinations. I would like to thank him, too, for the permission to access to the collection of ichnofossils at the Institute of Geology and Paleontology of the University of Tübingen during my visit in December 1985.

Prof. R. Goldring (Reading) and Dr. W. Winkler (Zürich), the reviewers, made numerous remarks concerning the ichnologic concepts applied in this paper, which helped much to improve its quality.

I am greatly indebted to Prof. J. Dercourt, Dr. A. Foucault and Prof. L. Leclaire (Paris) for their assistance during my investigations. Special thanks to Mrs. A. Cambreleng from the Laboratory of geology at the Muséum National d’Histoire Naturelle for preparing the drafts.

Financial support for this work was given from the Ministry of the Research and Industry (DGRST studentship number 81291) and from the IFREMER (Paris).

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