

# PART W SUPPLEMENT 1

## TRACE FOSSILS AND PROBLEMATICA

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### CONTENTS

	PAGE
INTRODUCTION .....	W2
Acknowledgments .....	W2
Glossary of terms .....	W2
Geological occurrence and significance of trace fossils for stratigraphy and tectonics .....	W3
General remarks .....	W3
Stratigraphic use .....	W9
Use in structural geology .....	W9
Position of traces in the sediment, their fossilization and preservation .....	W11
Exogenic traces .....	W11
Endogenic traces .....	W12
Historical review .....	W14
Classification .....	W16
Morphological-descriptive classification .....	W16
Preservational aspects .....	W18
Ethological aspects .....	W20
Taxonomic-stratinomic-morphologic classification proposed by Vyalov .....	W23
NOMENCLATURE OF TRACE FOSSILS .....	W24
Significance of trace fossils for sedimentology .....	W27
Significance of trace fossils for paleoenvironmental investigations .....	W32
TRACE FOSSILS .....	W35
BORINGS .....	W122
Generic names of Recent boring organisms used for fossil borings .....	W136
COPROLITES .....	W139
TRACE FOSSILS OR MEDUSAE INCERTAE SEDIS .....	W144
BODY FOSSILS .....	W149
MICROPROBLEMATICA .....	W153
PSEUDOFOSSILS .....	W168
UNRECOGNIZED AND UNRECOGNIZABLE "GENERA" .....	W180
GENERA OF RECENT LEBENSSPUREN .....	W189
INVALID NAMES .....	W190
REFERENCES .....	W191
ADDENDUM (MICROPROBLEMATICA) .....	W258
INDEX .....	W259

## INTRODUCTION

When the manuscript of the first edition of Part W of the *Treatise* (1962) was completed, it was the first of a very few such general compilations to be published. Since its appearance, not only have numerous new trace fossils been described and new ichnogenera named, but also, the results of many new investigations in general ichnology have been published. The significance of trace fossils for sedimentology, facies interpretation, and paleontology is becoming more and more recognized, and this branch of paleontology arouses worldwide interest. Thus, it has become necessary to revise and expand the entire edition.

It is the primary purpose of this revision not only to give complete descriptions of the increasing number of important ichnogenera but also to increase the number and improve the quality of the illustrations selected from new literature.

This introduction, which was likewise revised and expanded, cannot be an extensive treatment of general ichnology. Instead, one may refer to a complete discussion of this general subject given recently by FREY (1971). Presently, an exhaustive book on ichnology is in preparation under the editorship of FREY (1974, in press) with the collaboration of many paleontologists. The materials in this edition of the *Treatise* have been divided into many sections, each with an expanded introduction. Within each section, the generic names are listed in alphabetical order as in the first edition.

A criticism of the 1962 edition was that unidentified trace fossils were not included. This has been practically impossible to correct as such descriptions are generally incomplete and are hidden and scattered in the world literature.

In the present volume, an attempt has been made to take into consideration all the trace fossil literature of the world published until about the beginning of 1973. As a result, the bibliography of the earlier

edition has been extensively enlarged. Because of the extraordinarily scattered trace fossil literature, this reference list was necessary, especially since the last detailed list in *Fossilium Catalogus* (HÄNTZSCHEL, 1965) had only limited distribution.

## ACKNOWLEDGMENTS

Numerous paleontologists, in all parts of the world, have assisted me in the preparation of this second edition of my contribution to the *Treatise*, Part W. Their kind assistance has made available to me specimens, literature, illustrations, and other information. It is not possible to name individually these people, and my thanks to them are expressed collectively. I would also like to thank Professor CURT TEICHERT for granting all my requests in regard to the illustrations and the increased number of references. Similar thanks go to the *Treatise* editorial staff at the University of Kansas for the very careful preparation of manuscripts and numerous illustrations for printing.

## GLOSSARY OF TERMS

- ichnocoenosis, ichnocoenose** (DAVITASHVILI, 1945; again proposed independently by LESSERTISSEUR, 1955, p. 10). Association of trace fossils, corresponding to biocoenosis; ichnocoenosis used by DAVITASHVILI only for Recent assemblages of traces; a fossil association regarded by him as an oryctocoenosis EFREMOV (see RADWAŃSKI & RONIEWICZ, 1970).
- ichnofossil** (SEILACHER, 1956a, p. 158) (German, Spuren-Fossil, KREJCI-GRAF, 1932, p. 21). Trace fossil.
- Ichnolites** (HITCHCOCK, 1841, p. 476). Name proposed for a "class" including all sorts of tracks, divided into "orders" (depending on number of feet of animal that made the tracks): Polypodichnites, Tetrapodichnites, Dipodichnites.
- ichnolithology** (HITCHCOCK, 1841, p. 770). "History of fossil footmarks"; same as ichnology, term not widely adopted.
- ichnology** (BUCKLAND, about 1830). Entire field of lebensspuren (all tracks, trails, burrows, and borings); in fossil state, paleoichnology or palichnology; Recent, neoichnology.
- lebensspur** (ABEL, 1912, p. 65) [Synonymous Ger-

man terms: *biogene Spur*, *organogene Spur* (KREJCI-GRAF, 1932); French, *trace physiologique* (D'ORBIGNY, 1849); *vestige fossile de vie* (VAN STRAELEN, 1938); *trace de vie* (ROGER, 1962); *trace d'activité animale* (LESSERTISSEUR, 1955); Italian, *impronte fisiologiche* (DESIO, 1940); Spanish, *huella problematica* (MACSOTAY, 1967); Russian, sled, bioglyph (VASSOEVICH, 1953); *International Code of Zoological Nomenclature* (1964) refers to "work of an animal". Used for fossil and Recent tracks, trails, burrows, and borings; fossil *Lebensspur* = trace fossil, ichnofossil (German, *Spuren-Fossil* KREJCI-GRAF, 1932); ABEL (1912) did not define term, but using it in a wide sense he (ABEL, 1912, 1935) included under this heading not only tracks, trails, burrows, borings, coprolites, but also death agony, pathological phenomena, symbiosis, parasitism, gastroliths, etc. Shortest definition (preferred here) was given by HAAS (1954, p. 379): "Lebensspuren are structures in the sediment left by living organisms"; in my opinion the words "or in hard substrates" should be added behind "in the sediment," thus including borings. New definition given by OSGOOD (1970, p. 282): "Evidence of the activity of an organism in or on the sediment, produced by some voluntary action of that organism." FREY (1971, p. 94) included coprolites, fecal castings, and similar features and excluded biostratification structures as stromatolites, byssal mats, biogenic graded bedding, and related phenomena. SIMPSON (1957, p. 477) restricted the term trace fossil to activity of an animal moving on or in the sediment at time of its accumulation, which excludes borings in shells or in consolidated sediment. There is still some discussion on the best definition of this term. (Also for discussion, see MARTINSSON, 1970, p. 323-324.)

**nucleocavia** (RICHTER & RICHTER, 1930, p. 168). General name (not generic) for small, winding canals, which generally occur in form of furrows on surfaces of originating steinkerns; producers are probably worms, small arthropods, or other animal groups. (See also RICHTER, 1931, p. 308.)

**spreite**. German noun, often literally translated as "spread," meaning structures spread between limbs of a U-tube comparable to web of duck's foot and representing a transverse zone of disturbed sediment appearing as series of concentric arcs between limbs of U-tube, and generally parallel to base of tube; produced by shifting tube transversely through sediment. Protrusive and retrusive spreiten are to be distinguished, indicating deepening or elevation of bottom of tube respectively, according to erosion or accumulation of sediment. *Spreite* plus U-tube = spreite burrow (German, *Spreitenbau*); observed as early as in Lower Cambrian sand-

stones, fossil spreite burrows may be horizontal, oblique, or perpendicular to bedding, blade-like or spiral-shaped. Recent spreite burrows are very difficult to observe in unconsolidated sediment, but are known in various environments, and are made by animals of very different systematic position (SEILACHER, 1967b, p. 414, fig. 1).

**track, trackway**. Impression left in sediment by feet of animals; term sometimes used for isolated impressions left by individual feet, but also used for the "trackway," or assemblages of tracks reflecting directional locomotion.

**trace fossil**. Fossil lebensspur.

**trails**. More or less continuous grooves left by (mostly creeping) animals as they move over bottom and have part of their bodies in contact with substrate or sediment surface. PACKARD (1900), CASTER (1938), NIELSEN (1949), and OSGOOD (1970, p. 351) used "track" for "the whole record of walk" of an arthropod (see also CASTER, 1938, p. 5, footnote 2).

**vestigiofossil** (R. C. MOORE, written commun., 1956). Unpublished suggestion to replace term "ichnofossil" because of its bilinguistic derivation from both Latin and Greek.

For terms on arthropod (especially trilobite) tracks, see OSGOOD (1970, p. 351), for terms on U-tubes with and without spreite, see OSGOOD (1970, p. 314), and for further terms and their definitions see the following chapters: Introduction, Nomenclature, Position of Traces in the Sediment, and, particularly, Classification.

Until recently, the majority of the world's literature on trace fossils had been published in either German or French. Because of this, Table 1 has been included to facilitate the translation of foreign terms into English. In addition, the Russian language is well represented by a book by VYALOV (1966), which describes many different types of trace fossils.

## GEOLOGICAL OCCURRENCE AND SIGNIFICANCE OF TRACE FOSSILS FOR STRATIGRAPHY AND TECTONICS

### GENERAL REMARKS

Trace fossils occur in marine, lacustrine, and continental sedimentary rocks of all

TABLE 1.—*Equivalent Terms in English, German, and French\** (after Frey, 1973, append. 1, mod.).

(List of German terms prepared by H.-E. Reineck and G. Hertweck; list of French terms prepared by J. Lessertisseur)

ENGLISH	GERMAN	FRENCH
active fill	aktive Verfüllung	remplissage actif
back fill	Versatzbauten; Versatzgefüge	terrier ( <i>or</i> galerie) remblayé
biodeformational structure	Verformungswühlgefüge	structure de biodéformation
bioerosion structure	Bioerosion	structure de bioérosion
biogenic sedimentary structure	biogenes Sedimentgefüge	structure sédimentaire biogène
biogenic structure	biogenes Gefüge	structure biogène
biostratification structure	biogenes Schichtgefüge	structure de biostratification
bioturbate texture	Verwühlung	texture bioturbée
bioturbation	Verwühlung; Bioturbation	bioturbation
bioturbation structure	Wühlgefüge; Bioturbationsgefüge	structure de bioturbation
body fossil	Körperfossil	corps fossile; fossile corporel
boundary relief	Grenzrelief	relief limite
burrow	Gang	terrier
burrow cast	Gangverfüllung	moulage (du terrier)
burrow lining	Gangwandung	paroi (du terrier)
burrow mottle	durch Gänge erzeugte Flecken	amas ( <i>or</i> agglomérat) de terriers
burrow system	Gangsystem	terrier composé
cleavage relief	Spaltrelief	relief sur clivage (sur délit)
configuration	Konfiguration	configuration
crawling trace	Kriechspur	trace de locomotion ( <i>or</i> de reptation, <i>in a restricted sense</i> )
dwelling burrow	Wohngang	terrier d'habitation
dwelling structure	Wohnbau	structure d'habitation ( <i>or</i> , logement)
dwelling tube	Wohnröhre	tube d'habitation
epirelief	Epirelief	épirelief
escape structure	Fluchtspur	structure d'évitement
ethology	Verhaltensforschung; Ethologie	éthologie
feeding structure	Fresspur	structure de nutrition
full relief	Vollrelief	plein relief
grazing trace	Weidespur	trace de pacage
groove	Furche	sillon
hyporelief	Hyporelief	hyporelief
ichnocoenose	Ichnocoenose	ichnocénose
ichnofauna	Ichnofauna	ichnofaune
ichnoflora	Ichnoflora	ichnoflore
ichnology	Ichnologie; Spurenkunde	ichnologie
lebensspur; spoor	Lebensspur	trace d'activité; trace de vie
neoichnology	Neo-Ichnologie	néoichnologie
palichnology	Palichnologie	palichnologie
passive fill	passive Verfüllung	remplissage passif
resting trace	Ruhspur	trace de station
ridge	Kamm; Grat; Rücken	bourrelet
semirelief	Halbrelief	demirelief
shaft	Schacht	tube; tuyau
spreite	Spreite	traverse
stuffed burrows	Stopfbauten; Stopfgefüge; Stopftunnel	
trace; spoor	Spur	trace
trace fossil; ichnofossil	Spurenfossil; Ichnofossil	trace fossile; fossile de trace; ichnofossile
track	Trittsiegel; ( <i>in a strict sense</i> , Fusspur)	empreinte
trackway	Fährte	piste; ( <i>at depth</i> , galerie)
trail	Kriechspur	" " " " ( <i>de reptation</i> )
toponymy	Toponomie	toponomie
tunnel	waagerechter Gang	tunnel

\* Not all of these terms have exact counterparts in English, German, and French, but an attempt was made to approximate a common meaning as closely as possible. Several ichnological terms derived directly from classical words, such as *pascichnion* and *endichnion*, are cognates in all three languages, and are not listed here.

geologic systems from the Precambrian to the Recent (Fig. 1). Trace fossils are most abundant and best preserved in clastic rocks with alternating sandy and shaly beds.

Trace fossils found in the Late Precambrian are particularly significant for the investigation of the development of life before the Cambrian, especially that of metazoans. Also important is the comparison of lebensspuren in Late Precambrian sediments with those of undoubted Early Cambrian age. Such investigations have been made by SEILACHER (1956a) and GLAESSNER (1969) in the United States and Australia and have proven that trace fossils are scarce in Late Precambrian rocks when compared with their occurrences in lowest Cambrian rocks. In the Ediacara fauna of South Australia, there are perhaps six different ichnofossils produced by soft-bodied organisms creating grazing trails and ingesting sediment (GLAESSNER, 1971, p. 1337). GLAESSNER (1969, p. 381) has assigned one of these trace fossils to *Margaritichnus* BANDEL [= *Cylindrichnus* BANDEL], and the others remain unknown.

In general, the oldest lebensspuren are somewhat uncertain finds in the Grand Canyon Series (Hakatai Shale) and the Belt Series of the United States. These occurrences are both about 1,000 m.y. old, but whether or not they are genuine trace fossils must be verified. A trace fossil that is certainly of Late Precambrian age is *Bunyerichnus* GLAESSNER, 1969, which was discovered in South Australia (Brachina Formation, Wilpena Group) (see Fig. 30,3). *Bunyerichnus* is a crawling trail, 2 to 3 cm. wide, produced by a bilaterally symmetrical animal undoubtedly related to primitive mollusks. Precambrian lebensspuren cannot always be definitely identified when a distinction between body fossils and inorganic pseudofossils is difficult. This is shown by old and new discoveries of such fossils in the Precambrian from Canada, most recently discussed by HOFMANN (1971).

In several Paleozoic rocks, trace fossils

are so characteristic and numerous that they have furnished the names of stratigraphic units, e.g., the *Skolithos* Sandstone, Fucooid Sandstone, and *Diplocraterion* Sandstone of the Lower Cambrian in Sweden, the *Phycodes* beds of the Lower Ordovician in Germany, the "Grès à *Harlamia*" in the Paleozoic of North Africa, and others (see Fig. 37,2; 59,2; 64,2). In these types of sediments, contemporaneous body fossils are usually absent, but the trace fossils inform us of the existence of large numbers of bottom-dwelling animals. SEILACHER (1970) has pointed out that trace fossils can be considered to be a useful aid in the age determination and the stratigraphic correlation of such "unfossiliferous" sediments.

Trace fossils found in flysch facies are numerous and morphologically diverse. These synorogenic geosynclinal sediments have worldwide distribution and are generally deposited during orogenic times of the earth's history. Petrographically, flysch deposits are characterized by rhythmic alternations of coarser clastic sediments intercalated with pelitic sediments. Such rocks are especially favorable for the preservation of trace fossils. Since body fossils are rare in flysch deposits, the only paleontological evidence in these sediments are the ichnocoenoses, composed of traces of sediment ingestion, *Fressbauten*, and predominantly grazing trails, *Weidespuren* (see p. W32).

Also, many marine epicontinental sediments of all geological ages are rich in lebensspuren. However, these trace fossil associations are of different composition and show less diversity than those in flysch facies.

In sediments not entirely marine in origin, for example, the Lower Triassic Buntsandstein, which was deposited under essentially continental conditions, trace fossils are also present. However, in contrast to the ichnocoenoses of marine environments, the number of different types of nonmarine trace fossils is considerably less.

Sediments without lebensspuren are rare. There are also sediments in which some

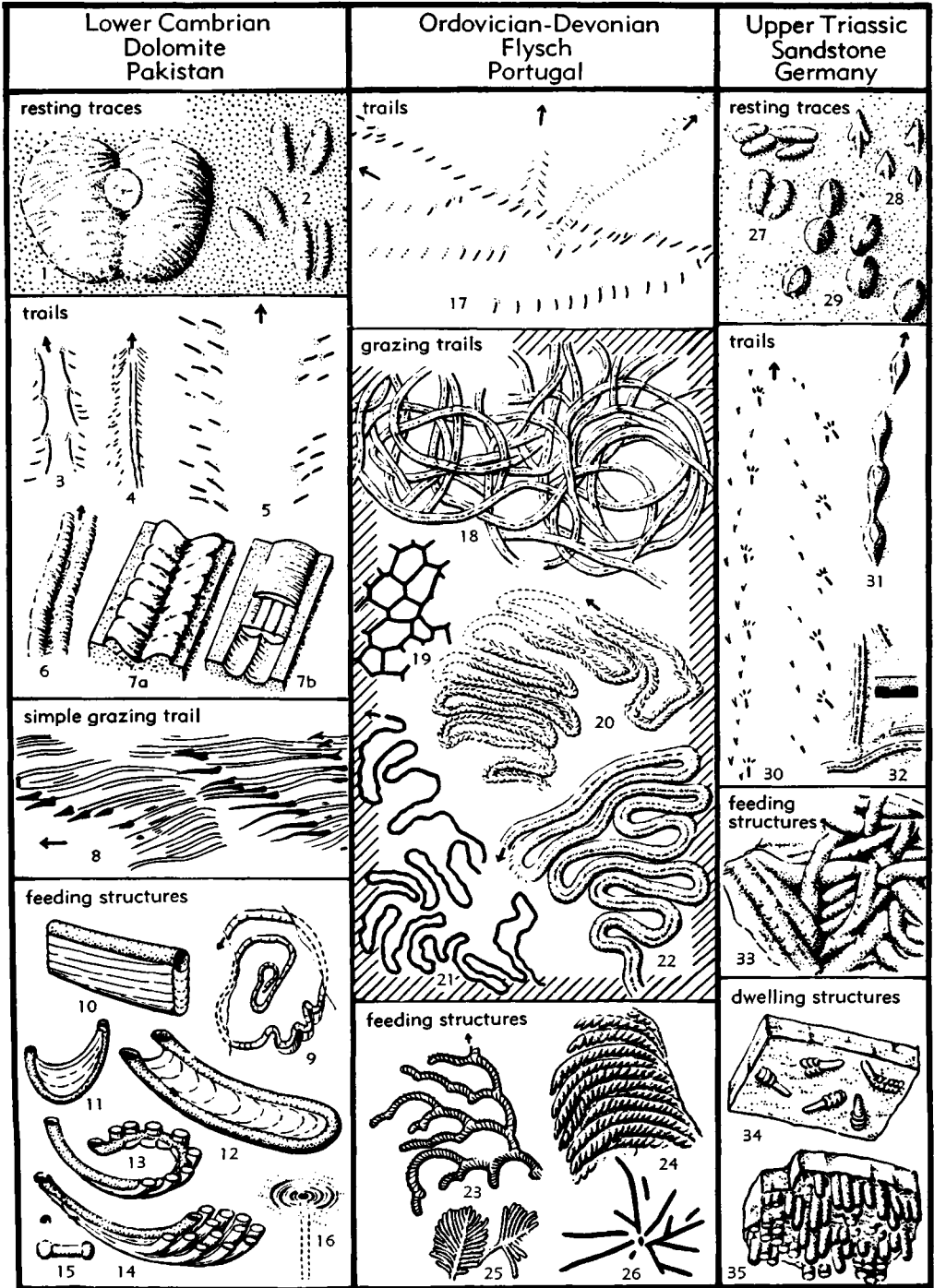


FIG. 1. Examples of different trace fossil assemblages (modified from Seilacher, 1955). (For explanation see p. W8.)

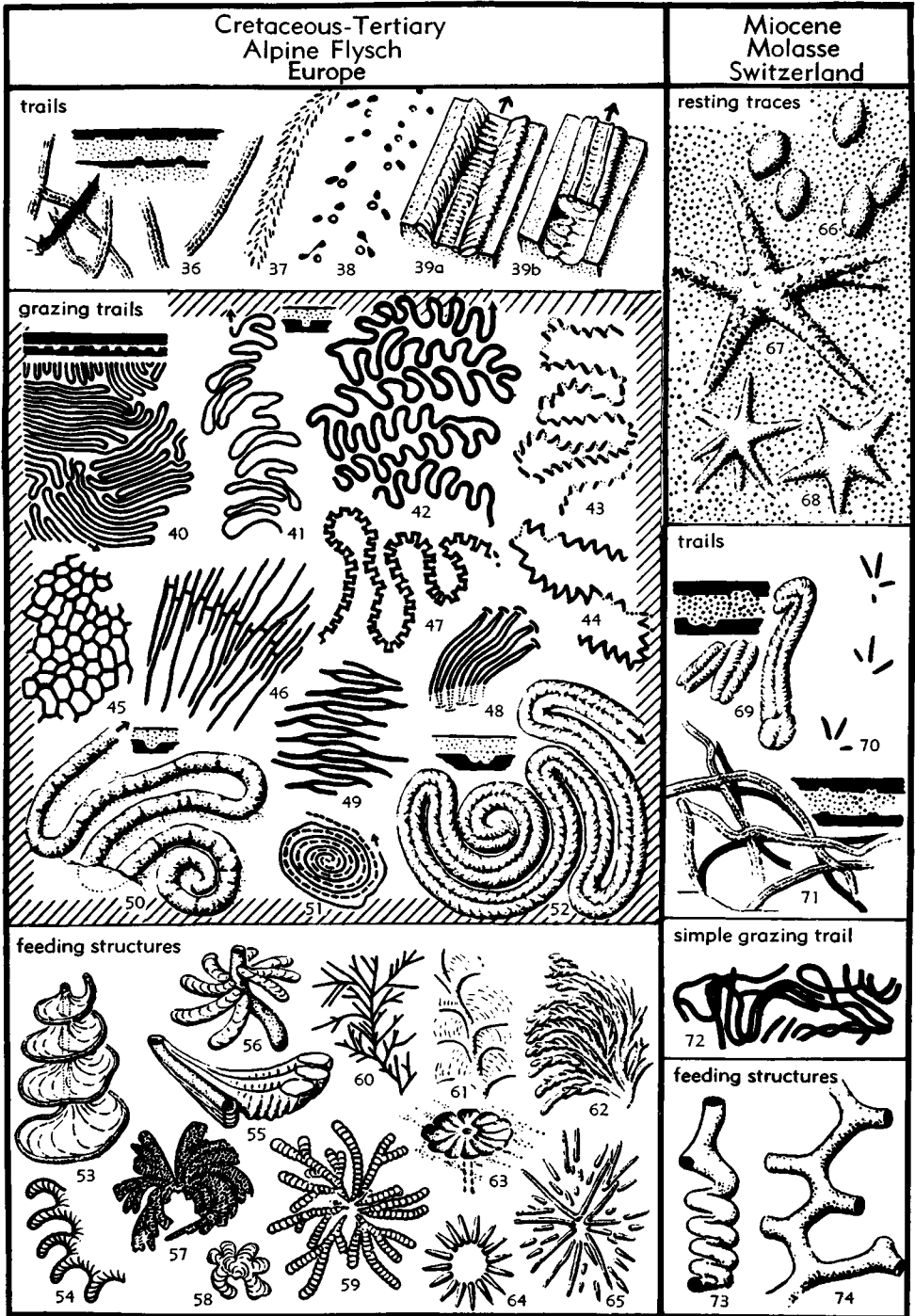


FIG. 1. (Continued from facing page; for explanation see p. W8.)

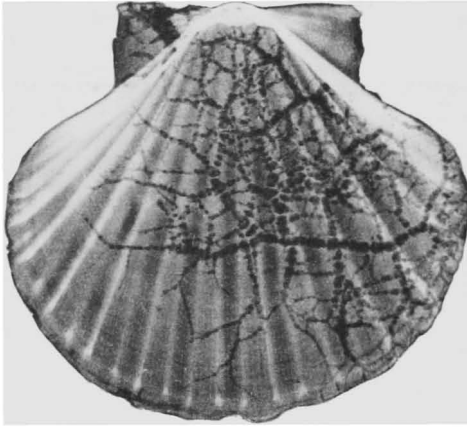


FIG. 2. Radiograph of *Pecten maximus* with camerate boring of *Cliona vastifica* (Bromley, 1970,

exogenic traces are preserved, whereas endogenic burrows are absent, due to ecologically unfavorable substrates. An example of such sediments is the Solnhofen Limestone (ABEL, 1927).

Homogeneous sediments may appear completely devoid of lebensspuren, but this is often only due to the fact that the lebensspuren are not visible to the unaided eye. HAMBLIN (1962, 1965) was the first to recognize distinct burrows in homogeneous sediments by the use of X-ray photography. X-radiography has also revealed elaborate boring networks in shell material (Fig. 2).

p. 75, in: *Trace Fossils*, edited by T. P. Crimes & J. C. Harper, Geol. Jour. Spec. Issue 3, Seel House Press, Liverpool).

FIG. 1. (Continued from page W6, 7.)

- |   |  |
|---|--|
| 1.2. <i>Rusophycus</i> , $\times 0.3$ , $\times 0.75$ .           | 40. <i>Helminthoida</i> , $\times 0.5$ .                     |
| 3.4. <i>Protichnites</i> , $\times 0.75$ .                        | 41. "Helminthoida," $\times 0.25$ .                          |
| 5. <i>Diplichnites</i> , $\times 0.75$ .                          | 42. <i>Cosmorhapha</i> , $\times 0.16$ .                     |
| 6. <i>Crossopodia</i> , $\times 0.75$ .                           | 43. <i>Helicolithus</i> , $\times 0.75$ .                    |
| 7a,b. <i>Scolicia</i> .   | 44. <i>Belorhapha</i> , $\times 0.75$ .                      |
| 8. <i>Dimorphichnus</i> , $\times 0.3$ .                          | 45. <i>Paleodictyon</i> , $\times 0.5$ .                     |
| 9. <i>Dictyodora</i> , $\times 0.3$ .                             | 46. <i>Desmograpton</i> , $\times 0.5$ .                     |
| 10. <i>Teichichnus</i> , $\times 0.3$ .                           | 47. <i>Paleomeandron</i> , $\times 0.75$ .                   |
| 11. <i>Corophioides</i> , $\times 0.3$ .                          | 48. "Unnamed form," $\times 0.3$ .                           |
| 12. <i>Rhizocorallium</i> , $\times 0.3$ .                        | 49. <i>Helminthoida</i> , $\times 0.25$ .                    |
| 13,14. <i>Phycodes</i> , $\times 0.7$ , $\times 0.3$ .            | 50. <i>Spirophycus</i> , $\times 0.3$ .                      |
| 15. <i>Bifungites</i> , $\times 0.75$ .                           | 51. <i>Spirorhapha</i> , $\times 0.3$ .                      |
| 16. <i>Laevicyclus</i> , $\times 1.3$ .                           | 52. <i>Taphrhelminthopsis</i> , $\times 0.16$ .              |
| 17. "Trilobite trails," $\times 0.3$ .                            | 53. <i>Zoophycos</i> , $\times 0.25$ .                       |
| 18. "Irregularly circular bilobate trails," $\times 0.5$ .        | 54. <i>Phycosiphon</i> , $\times 0.75$ .                     |
| 19. <i>Paleodictyon</i> , $\times 0.3$ .                          | 55. <i>Pennatulites</i> , $\times 0.1$ .                     |
| 20. <i>Nereites</i> , $\times 0.3$ .                              | 56. "Gyrophyllites," $\times 1$ .                            |
| 21. ? <i>Nereites</i> , $\times 0.3$ .                            | 57. "Chondrites," $\times 0.25$ .                            |
| 22. <i>Crossopodia</i> , $\times 0.3$ .                           | 58. <i>Hydrancylus</i> , $\times 0.5$ .                      |
| 23. <i>Phycosiphon</i> , $\times 0.75$ .                          | 59. <i>Taenidium</i> , $\times 0.2$ .                        |
| 24. <i>Lophoctenium</i> , $\times 0.5$ .                          | 60. <i>Chondrites</i> , $\times 0.3$ .                       |
| 25. "Undescribed trail similar to <i>Oldhamia</i> ," $\times 1$ . | 61. "Unnamed form," $\times 0.3$ .                           |
| 26. <i>Chondrites</i> , $\times 0.5$ .                            | 62. <i>Lophoctenium</i> , $\times 0.5$ .                     |
| 27. <i>Rusophycus</i> , $\times 0.75$ .                           | 63. <i>Gyrophyllites</i> , $\times 0.3$ .                    |
| 28. <i>Sagittichnus</i> , $\times 1.5$ .                          | 64. <i>Lorenzina</i> , $\times 0.3$ .                        |
| 29. <i>Lockeia</i> , $\times 0.75$ .                              | 65. "Unnamed star-shaped feeding structure," $\times 0.16$ . |
| 30. <i>Kouphichnium</i> , $\times 0.3$ .                          | 66. <i>Lockeia</i> , $\times 0.75$ .                         |
| 31. "Unnamed bivalve trail," $\times 0.3$ .                       | 67,68. <i>Asteriacites</i> , $\times 0.25$ , $\times 0.75$ . |
| 32. "Bilobate worm trail."  | 69. " <i>Isopodichnus</i> ," $\times 0.16$ .                 |
| 33. "Unilobate feeding structures," $\times 0.3$ .                | 70. "Bird tracks," $\times 0.25$ .                           |
| 34. <i>Biformites</i> , $\times 0.5$ .                            | 71. <i>Gyrochorte</i> , $\times 0.5$ .                       |
| 35. <i>Cylindricum</i> , $\times 0.5$ .                           | 72. <i>Helminthoida</i> , $\times 0.5$ .                     |
| 36. <i>Gyrochorte</i> , $\times 0.5$ .                            | 73. <i>Gyrolithes</i> , $\times 0.16$ .                      |
| 37. "Undetermined articulated trail," $\times 0.2$ .              | 74. " <i>Spongites</i> ," $\times 0.05$ .                    |
| 38. "Large tetrapod striding trail," $\times 0.05$ .              |  |
| 39a,b. <i>Scolicia</i> , $\times 0.3$ .                           |  |



### STRATIGRAPHIC USE

Lebensspuren usually have little importance in stratigraphy. In restricted areas, however, they may attain the rank of index fossils. A burrow, *Arenicolites franconicus* TRUSHEIM, 1934, from the Muschelkalk of southern Germany may serve as an example: this fossil occurs abundantly in a layer only 3 to 4 cm. thick and may be followed for a horizontal distance of 26 km. (see Fig. 24,2). Another example is a track-bearing horizon in the Eocene Green River Formation of Utah, which is traceable laterally for about 40 km. (MOUSSA, 1968, p. 1434). It consists of three beds containing bird and mammal tracks associated with invertebrate trails some of which are of very regular wave-like shape.

A long time-range is one of the characteristics of most biogenic structures, the vast majority of which remain unchanged throughout geologic time. This is true for nondescript, smooth, furrowlike crawling trails and cylindrical burrows, as well as for more distinctive U-shaped burrows with spreite and even for the honeycomb-like networks named *Paleodictyon* by MENEGHINI (in MURCHISON, 1850), which are known from Silurian to Tertiary.

In some cases, ichnospecies of widely distributed and "long-lived" ichnogenera have been proven to be useful guide fossils for age determinations. Species of the ichnogenus *Cruziana* D'ORBIGNY have been proven to be useful guide fossils for lower Paleozoic rocks in Wales (*Cruziana simplicata* for Upper Cambrian, *C. furcifera* for Lower Ordovician). In homogeneous rocks of uncertain age in which body fossils are absent, the generally abundant trace fossils may be used for stratigraphic correlation (CRIMES, 1968, 1969, 1970; SEILACHER, 1960, 1970). CRIMES distinguished between Cambrian and Ordovician rocks by determining the differences in morphological characteristics between certain mo-

tion trails (*Laufspuren*) and grazing trails (*Weidespuren*) of trilobites. SEILACHER (1970) established an elaborate stratigraphic succession for *Cruziana* in lower Paleozoic rocks (Fig. 3). Some other trace fossils have also proven themselves to be useful for age determination, such as *Oldhamia* for the Cambrian and *Phycodes circinnatum* for the Ordovician. Another example is the beaded coprolite *Tomaculum* GROOM, which so far has been found only in Ordovician strata of England, France, Germany, and Czechoslovakia.

### USE IN STRUCTURAL GEOLOGY

In structurally complicated areas where inverted beds may be expected to occur, burrows and trails may be useful for distinguishing top and bottom of strata as has been rather extensively discussed by SHROCK (1948, p. 175-188) and more recently by FREY (1971). Especially well suited for this purpose are U-shaped burrows, which are invariably built either horizontally or with the curved part toward the bottom. Burrows of the *Skolithos* type are usually excavated vertical to the bedding in undisturbed beds. If they are inclined strongly in one direction in disturbed beds they may serve to determine direction and amount of the tectonic movement. Burrows or borings of pelecypods that are enlarged and rounded at the bottom may be used as reliable top and bottom criteria by their shape.

By observing vertical and horizontal burrows that originally had tunnels with circular cross sections and now are elliptical, the amount of lateral and vertical compression may be quantitatively determined. PLESSMANN (1966) has measured the vertical diagenetic "contraction" and the lateral compressional forces on sediments in the flat Upper Cretaceous deposits at the northern margin of the Harz Mountains in Germany and in the flysch deposits of Sanremo in the Maritime Alps of Italy.

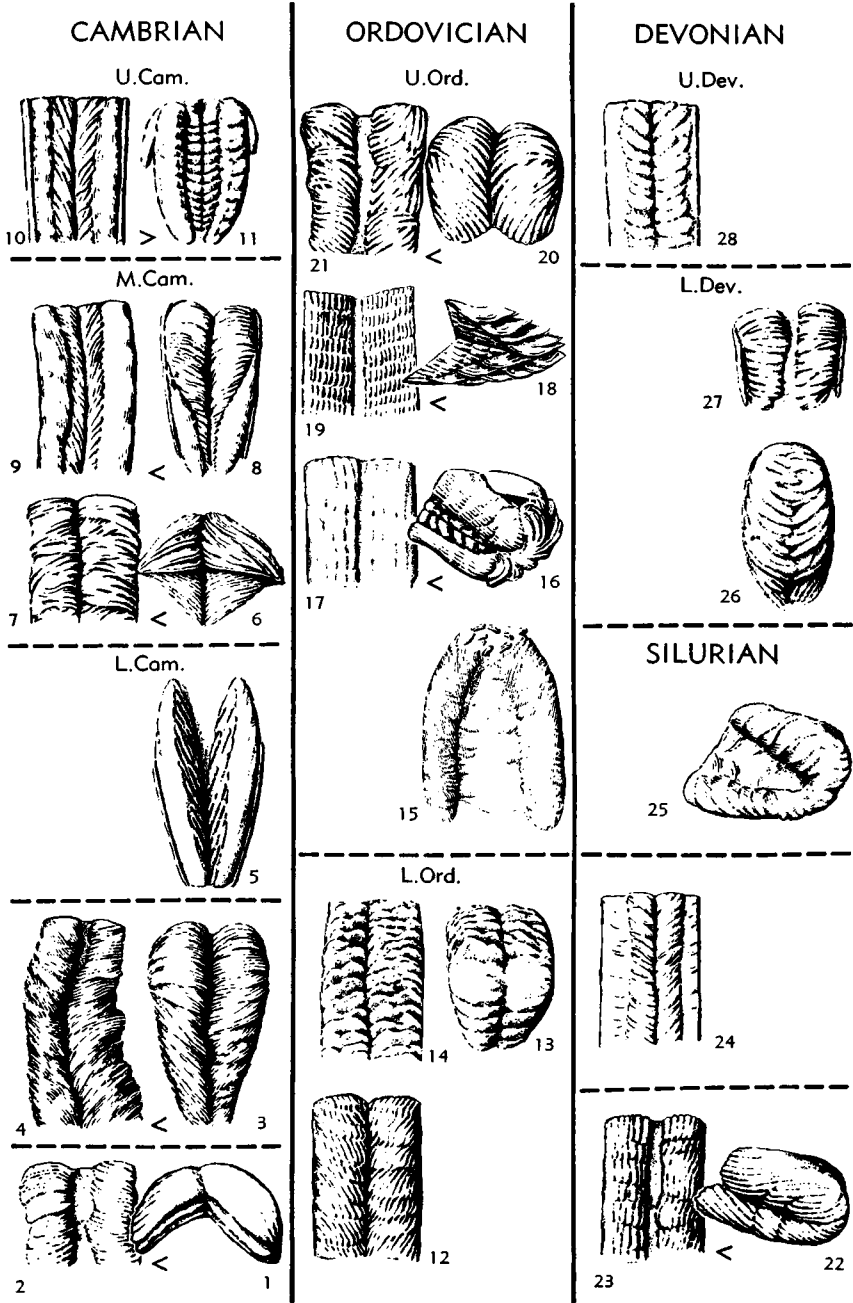


FIG. 3. *Cruziana* stratigraphy of Paleozoic sandstone of Europe, North Africa, and Southwest Asia (after Seilacher, 1970, p. 458, in: *Trace Fossils*, edited by T. P. Crimes & J. C. Harper, Geol. Jour. Spec. Issue 3, Seel House Press, Liverpool). < and > signs indicate whether the furrow (left) or the resting track expression (right) is more common. Forms not separated by dashed line may occur in the same unit.

**POSITION OF TRACES IN THE  
SEDIMENT, THEIR  
FOSSILIZATION AND  
PRESERVATION  
EXOGENIC TRACES**

The most remarkable forms of traces observable in Recent sediments are lebensspuren made on the surface of sediments. They originate on the sediment surface at the bottom of flowing or stationary water at all depths or subaerially on the land (HERSEY, 1967; HEEZEN & HOLLISTER, 1971). Such lebensspuren are called surface, or surficial, trails, which is the same as exogene epirelief of SEILACHER (1953a) (Fig. 4). They belong to the group of semi-, or demi-reliefs.

It has often been noted that surficial trails produced in marine environments, especially in shallow water with tidal currents, have only a very small chance of preservation. Such trails can be destroyed by currents or wave action, especially on tidal flats. There is, however, a chance of preservation under certain favorable conditions, such as 1) rapid drying-up of the sea bottom during ebb tide especially near the shore, 2) cementation of the sediment by mucus, or 3) by infilling of the trail by wind-blown sand or by rapidly accumulating sediment. Preservation of trace fossils may also be expected to be more common in quiet, current-free, deep water. Here grain size and consistency of the sediment play an important role. In Recent clayey sediments of some coherency, trails are distinctly preserved under water. Preservation

of such features as small ripples and micro-ripples, and especially very thin, linearly striated groove casts and similar marks frequently found on bedding planes show that not all such features are easily destroyed. In pelitic freshwater sediments, as, for example, in the Lower Permian of Germany, delicate arthropod tracks have been preserved on the bedding planes of claystone. Such trails also have been discovered in Pleistocene varves in Germany and in Upper Paleozoic varves in Natal (SAVAGE, 1971), and surface trails have been preserved in ancient terrestrial sandstones. An example of this would be vertebrate tracks in the eolian Permian Coconino Sandstone of Arizona (United States), described by MCKEE (1947). MCKEE also performed experiments with several types of lizards moving on Recent sand dunes and determined that preservation of tracks was likely to occur as the sand surface, moistened by dew or mist, was consolidated and attached to dry eolian sand that covered it.

Ethologically considered, surface trails are either movement traces (running or crawling traces, more seldom swimming trails), resting traces, or sediment-ingesting trails.

When surface trails are normally epichnial grooves (MARTINSSON, 1965) or concave epireliefs (SEILACHER, 1964a), they can later become epichnial ridges or convex epireliefs, respectively. These "relief-tracks" may be formed from vertebrate trails (WASMUND, 1936) when the footprints are more resistant to the wind than the surrounding sediment. They have been

FIG. 3. (Continued from facing page.)

- |   |   |
|---|---|
| 1,2. <i>C. cantabrica</i> , Spain.              | 16,17. <i>C. almadenensis</i> , Spain.    |
| 3,4. <i>C. fasciculata</i> , Spain.             | 18,19. <i>C. flammosa</i> , South Jordan. |
| 5. <i>C. carinata</i> , Spain.                  | 20,21. <i>C. petraea</i> , South Jordan.  |
| 6,7. <i>C. barbata</i> , Spain.                 | 22,23. <i>C. acacensis</i> , Libya.       |
| 8,9. <i>C. arizonensis</i> , USA (Mont.-Ariz.). | 24. <i>C. quadrata</i> , Libya.           |
| 10. <i>C. semiplicata</i> , North Wales.        | 25. <i>C. pedroana</i> , Spain.           |
| 11. <i>C. polonica</i> , Poland.                | 26. <i>C. uniloba</i> , Algeria.          |
| 12. <i>C. rugosa</i> , Northern Iraq.           | 27. <i>C. rhenana</i> , Germany.          |
| 13,14. <i>C. imbricata</i> , Portugal.          | 28. <i>C. lobosa</i> , Libya.             |
| 15. <i>C. lineata</i> , South Jordan.           |   |

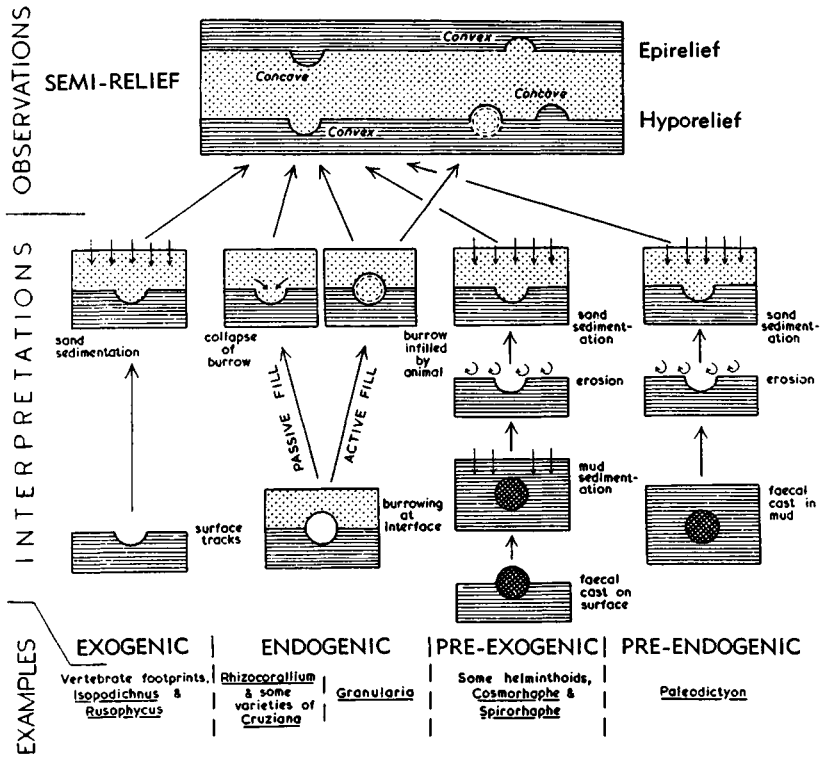


Fig. 4. Diagrammatic representation of different types of trace fossil preservation (after Webby, 1969a).

observed in snow as well as in terrestrial and marine sediments (TEICHERT, 1934; LINKE, 1954; SCHÄFER, 1951).

**ENDOGENIC TRACES**

Lebensspuren originating within sediment layers are designated as endostratal or endogenic. They are produced by animals that either move constantly in the sediment or live more or less permanently in structures within the sediment. There is also a transition between endostratal and surface trails. It is not always discernible whether a crawling surface trail has originated on an exposed sandy layer or whether the sedimentary surface was covered by a layer of sediment and endostratal lebensspuren were produced by the mixing and digging of an animal at the sediment interface in the sand beneath. If clay is overlain by sand, a distinct endo-

stratal resting trace is produced in the clay, and an indistinct concave form is produced in the sandstone. Running arthropods, especially limulids and trilobites, leave behind in the sediment surface trackways of different appearance, varying according to which part of the animal's extremities were impressed to different depths on the sediment surface (undertracks, GOLDRING & SEILACHER, 1971, p. 424; cleavage relief type, OSGOOD, 1970, p. 292) (Fig. 5; FREY, 1973a, fig. 5). Another transitional form between surficial and endostratal trails are tunnel trails (*Tunnelfährten*).

Very many trace fossils occur at sedimentary interfaces where sand is underlain by mud. They are then found on the underside of the sandstone beds and generally are well preserved. They have been described as convex hyporeliefs (SEILACHER, 1964a) or hypichnia (MARTINSSON, 1965).

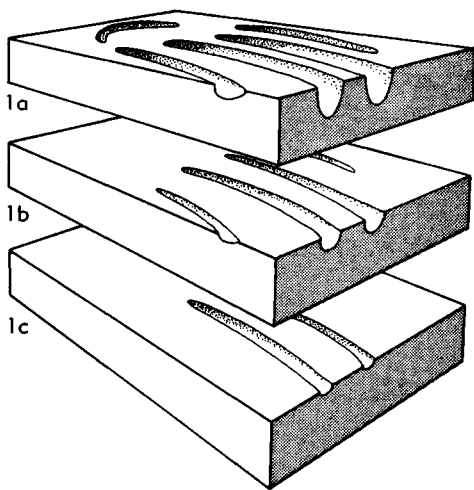


FIG. 5. Differential preservation of a hypothetical arthropod track (after Osgood, 1970; mod.). Each block is 1 mm. thick.—1a. Concave epirelief at depositional interface; quadrifid track with an arcuate posterior fringe.—1b. Cleavage relief 1 mm. below depositional interface; arcuate fringe not preserved.—1c. Cleavage relief 2 mm. below depositional interface; only two imprints preserved.

SEILACHER especially called attention to this kind of trace fossil, and employed the German word *Innenspuren*.

All trace fossils on lithologic bedding planes are semi- (demi-) reliefs. It is possible to distinguish between "cleavage reliefs" in a uniform sediment and "boundary reliefs" between petrographically different layers, especially between sandstone and shale (SEILACHER, 1953a, p. 438). However, in practice, this distinction may be difficult to make.

Clearly delineated burrows within one stratum that were originally formed as hollows (endogene full reliefs) have been named *endichnia* by MARTINSSON (1965) (=fossitextura figurativa, SCHÄFER, 1956a; 1972). Such burrows can be actively or passively filled. Burrowing textures (*Wühlgefüge*) are bioturbate shapes without sharp outlines, which may be filled in from above. MARTINSSON has named these structures *exichnia* (=fossitextura deformativa, SCHÄFER, 1956a).

There are still more complex endogenic

burrows, especially in flysch sediments, which have been described as pre-exogene or pre-endogene. Their origin is shown in Fig. 4 (see also p. W20).

Endostratal lebensspuren also include dwelling burrows in the sediment having very different morphological features, such as vertical shafts, J- or U-shaped tubes with or without spreite, Y- or W-shaped tunnels, irregular and complicated tunnel systems that may be arranged horizontally, vertically, or in netlike forms, or a combination of all three.

The walls of such Recent burrows are usually compacted by mucus and many animals press infiltrating sand grains against the walls, which are thereby strengthened. Burrows constructed in this manner have a good chance of being preserved as fossils. This is seen in the tidal flats of the North Sea where the upper end of *Arenicola* U-tubes may be solidified and thus escape being washed away. The tubes may protrude several centimeters above the sediment surface (HÄNTZSCHEL, 1938). In Recent lime muds from Florida and the Bahamas, SHINN (1968) has observed unoccupied decapod burrows that were still open. Covered by sediment, such burrows could possibly remain open for centuries. That such burrows can become indurated relatively rapidly is shown by the sedimentation of the U-shaped *Spreitenbauten* (*Rhizocorallium*) in the Lower Jurassic of southern Germany (SCHLOZ, 1968).

In Recent sediments, complex forms of endostratal burrows (*Innenspuren*) are more difficult to observe than in the fossil record. Especially fine structures of back-fill origin (*Versatzbauten*) or *Spreitenbauten*, for example, in the sandy mud flats of the North Sea, are difficult to recognize. Thus, little is known about Recent spreiten structures, although they are common as fossils. Diagenetic processes greatly enhance the preservation and recognition of trace fossils in the sediment (SEILACHER, 1957). In order to study and observe endo-

stratal burrows in Recent sediments, special methods must be used (HERTWECK & REINECK, 1966).

## HISTORICAL REVIEW

No complete history of paleoichnological investigations has been written. WINKLER'S "*Histoire de l'ichnologie*" (1886) represents only a chronologically arranged, annotated bibliography covering paleoichnological publications (mainly on vertebrate tracks) for the period 1828 to 1886. The following section briefly describes only a few stages of the rather discontinuous development of this branch of paleontology.

OSGOOD (1970, p. 286-291) has published a comprehensive survey of the historical development of ichnology, to which reference may be made. He divided the history of ichnology into three parts: 1) the "age of the fucoids" and 2) the "period of reaction," followed by 3) rapid advances in paleoichnology and neoichnology since the 1920's and continuing to the present time. The development of ichnology is important for paleontology and sedimentology, because it is a "development of ethological and paleoecological approaches."

In the early years of paleontology, many fossils, especially cylindrical and U-shaped burrows, now identified as lebensspuren, were considered to be remains of marine algae. This is apparent in names such as *Fucoides*, *Algacites*, *Chondrites*, and the many generic names having the ending *-phycus*. Ramification of the burrows was considered the most conclusive evidence for their interpretation as plants. In publications of these "algae," Recent Thallophyta were commonly figured in order to show the identity or relationship of the fossil forms with them. Occasionally, even the drawings of the fossils were modified so as to make them look more like algae.

According to OSGOOD, the "age of the fucoids" began in 1828, the year that *Fucoides* BRONGNIART, 1822, was divided into "sectiones," and it ended in 1881. Nevertheless, in the nineteenth century,

many "*Fucoiden*" were described as marine algae. Most were labeled *incertae sedis*, although a few paleontologists recognized and named traces produced by invertebrates. One of these paleontologists was E. HITCHCOCK (1792-1864), geologist, astronomer, minister, and pedagogue. He named the first ichnogenus with the characteristic ending *-ichnus*, i.e., *Cochlichnus* HITCHCOCK, 1858, an invertebrate meander trail. In the same year, JARDINE established many genera with the same ending. Most of these were vertebrate tracks. The oldest established names for invertebrate trace fossils are *Harpagopus* HITCHCOCK, 1848, and *Herpystozeum* HITCHCOCK, 1848. HITCHCOCK was the first to publish a detailed description of a trace fossil assemblage consisting of numerous trails from Triassic sandstone of the Connecticut Valley (HITCHCOCK, 1858, 1865).

DAWSON (1864, p. 367) recognized that the traces named *Rusophycus* HALL, 1853, especially *R. grenvillensis* BILLINGS, were produced by trilobites as resting impressions, or as cavities made for shelter. He suggested, therefore, that the name *Rusophycus* should be changed to the more descriptive name *Rusichnites*.

Astonishingly, some ethological or general genetic interpretations of certain trace fossils have remained valid for nearly a century. NICHOLSON (1873, p. 288-289) regarded *Skolithos*-structures as true burrows of habitation, whereas he explained horizontal burrows as wandering tunnels excavated by worms in search for food. NICHOLSON also declared that forms combined by him under the name *Planolites* were "not the actual burrows themselves but the burrows filled up with sand or mud which the worm has passed through its alimentary canal." His interpretations were repeated, independently, decades later by subsequent authors. These early contributions must be recognized again, today.

Often, in the "age of the fucoids," forms such as *Nereites* MACLEAY (1839) were not considered to be trace fossils but body fossils. *Nereites* was claimed to be a *Nereis*-

type worm. Other grazing trails, such as *Helminthoida*, puzzled paleontologists, but it, too, was explained as being of plant origin. Some of the best examples of botanical interpretation of many trace fossils are found in the important, voluminous monograph, "*Flora fossilis Helvetiae*" (HEER, 1877), in which numerous flysch lebensspuren are described in great detail as plants.

The next forty years, from 1881 to about 1921, is OSGOOD's second period in the development of ichnology, the "period of reaction." This period should be expanded to begin with the publication of the classic works by the Swedish paleobotanist NATHORST (1873, 1881a,b). On the basis of systematic neoichnological observations and experiments on traces of marine animals, he pointed out the striking similarity of many "fucoids" and problematica to the tracks and trails of marine invertebrates. This evidence, together with the information that animal trails may ramify, permitted NATHORST to challenge the doctrine of plant origin for these fossils. The years between 1881 and 1885 were characterized by the violent controversy between NATHORST and his opponents DELGADO, LEBESCONTE, and DE SAPORTA, who tenaciously defended the botanical origin of these doubtful fossils. These arguments also dealt with the origin of the genera *Cruziana* and *Rusophycus*, which are today recognized as definite trilobite lebensspuren, at least in the majority of Paleozoic sediments. However, specimens of *Cruziana* and *Rusophycus* have been recognized in Triassic sediments in East Greenland and questionably attributed to notostracans or conchostracans (BROMLEY & ASGAARD, 1972). Since the recounting of this embittered controversy would take up too much space and because it has only historical significance, the reader is referred to OSGOOD (1970, p. 287-288) for a more detailed account.

Independently of NATHORST and without knowledge of his publications, J. F. JAMES (1857-97) in the United States published

numerous and often overlooked works protesting the plant interpretation of most fucoids of the Cincinnati. He explained their origin as animal trails, marks, or body fossils, and cautioned against many hasty publications and the assignment of names to poorly preserved and uncertain "fucoids." Attention must be called to his warning, which was long ignored but is still valid: "When every turn made by a worm or shell, and every print left by the claw of a Crustacean is described as a new addition to science, it is time to call halt and eliminate some of the old before making any more new species."

Only gradually did NATHORST's interpretation of many fossil "algae" as lebensspuren become accepted. Even today several "genera" of lebensspuren (e.g., *Chondrites*, *Fucoides*) are sometimes interpreted as algae. Canadian and Indian papers from 1938 and 1949 refer typical trace fossils to algae. FUCINI (1936, 1938), in extensive publications, described Problematica from the Cretaceous "Verrucano" of Toscana, Italy, mainly inorganic markings, as plant fossils.

Even in the beginning of this century many forms of lebensspuren were not recognized as trace fossils, including all grazing trails in Cretaceous or Tertiary flysch sediments in Europe called hieroglyphs or graphoglyphs. A number of these especially peculiar forms such as the ichnogenera *Paleodictyon*, *Urohelminthoida* [= *Hercorhapse*], and *Spirorhapse* were assumed by FUCHS (1895) to be spawn, presumably of gastropods. Similar interpretations are still being discussed for similar forms (e.g., *Spirodesmos*).

After several decades of stagnation following the turn of the century, substantial progress was made in lebensspuren studies by ABEL and his pupils, and especially in the course of "actuopaleontologic" investigations in marine biology of the North Sea tidal flats by RUDOLF RICHTER. His studies included 1) a survey of Recent and fossil worm trails and burrows, 2) an elucidation of general questions of palichnology, and

utilization of lebensspuren for paleogeographic interpretation, and 3) an interpretation of many problematica, as well as an analysis of numerous arthropod trails and Recent and fossil U-shaped burrows. Until World War II, the efforts and results of RICHTER and his collaborators at the marine-geologic Forschungsanstalt "Senckenberg" in Wilhelmshaven (HÄNTZSCHEL, SCHÄFER, SCHWARZ, TRUSHEIM) were focused in the same general direction.

Since the end of World War II, paleontologists and geologists, especially those from Europe and North America, have developed a tremendous interest in neoichnology and even more in paleoichnology. This interest was stimulated by the intensive investigations concerning the nature and origin of depositional basins, and the inorganic and biogenic textures of Recent and fossil sediments. It has been shown by trace fossil investigations that there are types of ichnocoenoses with characteristic elements having worldwide distribution independent of sediment age. Single lebensspuren, and especially ichnocoenoses, are good facies indicators, and they give reference to paleoenvironments. Trace fossils are usually not rare in rocks containing them, but are the most common fossils. Trace fossils and trace fossil associations are of great value for sedimentology and paleontology owing to their facies range. This significance of trace fossils is becoming more and more recognized in paleoecology because they furnish direct evidence of autochthonous life in the sediment, and thanatocoenoses do not exist. Many types of trace fossils remain unchanged and can be recognized during very long periods of time in the stratigraphic record. Such forms, therefore, permit the evaluation of ichnofacies.

### CLASSIFICATION

The possible diversity of lebensspuren made by an individual animal, dependent on its activity (crawling, eating, running, burrowing, swimming), and the depen-

dence of traces on fortuitous preservational properties of the sediment, make it impossible to clarify lebensspuren in a manner corresponding to a zoological pattern.

Classifications, or at least categorizing, of similar forms into groups have been attempted from many different viewpoints based on either: 1) the shape (morphological arrangement) of the trace fossil, 2) the kind of preservation and occurrence in the sediment, specifically the position of the boundary between calcareous and arenaceous sediments (stratinomic or toponomic arrangement), 3) ethological interpretations, or 4) a combination of the taxonomic, morphologic, and stratinomic bases (VYALOV, 1968b). In addition, an attempt has been made to arrange lebensspuren by taxonomic rank of the producer of the trace. HITCHCOCK (1844, p. 318) proposed a "new order including all sorts of footless trails made by worms, molluscs, and fishes," to be called Apodichnites. Lebensspuren produced by animals with more than four feet were called Polypodichnites (HITCHCOCK, 1841, p. 476). SALTER (1857, p. 204) named long, sinuous surface trails or filled-up burrows of marine worms without impressions of lateral appendages *Helminthites* (= *Helmintholites* MURCHISON, 1867, p. 514). Possibly a classification of trails produced by vertebrates will become feasible when footprints prove to be assignable with certainty to a particular taxonomic group of vertebrates.

### MORPHOLOGICAL-DESCRIPTIVE CLASSIFICATION

In the early stages of paleontological research, most trace fossils were interpreted as marine algae, and were arranged exclusively according to morphological characters. The shape of the "thallus" was regarded as a determining factor and fucoid species were distinguished according to the angle of divergence of branches. FUCHS (1895), accepting such structures to be trace fossils, tried to arrange them into family-like groups, determined mainly by morphological criteria.



Many excellent, well-preserved examples of trace fossils can be seen in the Cretaceous-Tertiary flysch of southern Europe. FUCHS described the following different types:

- 1) GRAPHOGLYPHEN (FUCHS, 1895, p. 394; =*Hieroglyphen s.s.*, FUCHS, 1895, p. 394). Trace fossils appearing as reliefs on lower surface of beds (mostly sandstones) and resembling ornaments, or letters (e.g., *Paleodictyon*, *Paleomeandron*, explained by FUCHS, however, as strings of spawn of gastropods).
- 2) VERMIGLYPHEN (FUCHS, 1895, p. 390). Collective name for threadlike, straight, or variously winding reliefs on undersurface of sandstone beds in flysch and similar sediments; mostly unbranched; width usually only a few millimeters.
- 3) RHABDOGLYPHEN (FUCHS, 1895, p. 391). General and informal name for nearly straight bulges, mostly on undersurface of sandstone beds of flysch and similar sediments; greatest diameter several centimeters.

RUDOLF RICHTER presented good examples of a possible simple classification by 1) the distinction of U-shaped burrows with or without spreite (Rhizocorallidae, Arenicolitidae; see RICHTER, 1926, p. 211), and 2) the division of worm trails according to "basic architectural forms" (*bauliche Grund-Formen*) on a mechanical and biological basis (RICHTER, 1927a). Similarly, RICHTER (1941) arranged trails from the Hunsrück Shale morphologically into the following groups:

- 1) *Ichnia taeniata*. Regularly developed, bandlike grooves and tunnels, not filled by sediment.
- 2) *Ichnia catenaria*. Strings of pearl-like trails.
- 3) *Ichnia spicea*. Spike-shaped trails.
- 4) *Ichnia disserta*. Arthropod trails of separated rows of footprints.

However, this classification has not been generally adopted and has enjoyed very little use in the literature.

KREJCI-GRAF (1932) proposed a very

comprehensive classification based on the life activities of the animals. He established three division units: 1) traces of rest, 2) traces of motion, and 3) traces of "existence," and defined these units with extremely detailed subdivisions. However, the number of minor categories makes the application of this elaborate classification difficult.

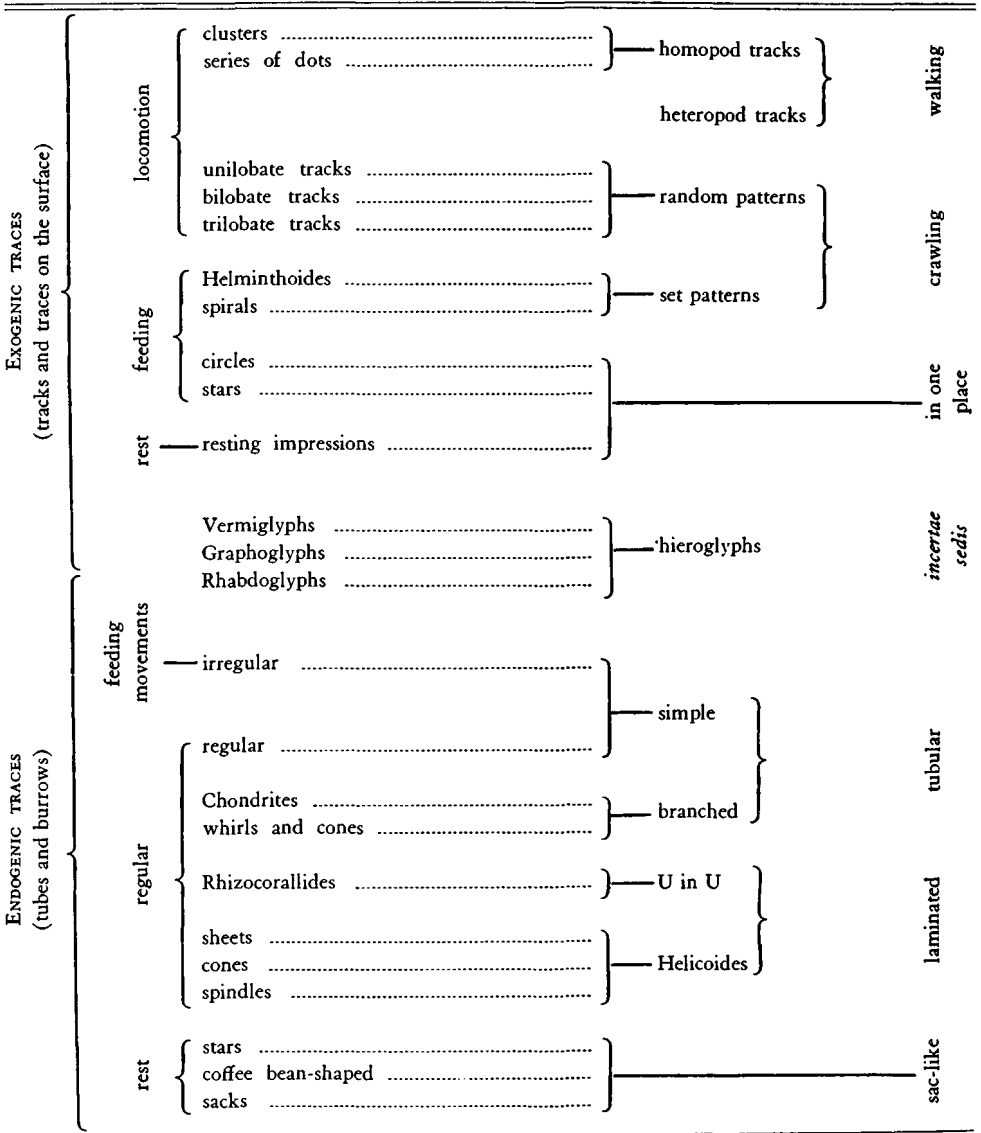
LESSERTISSEUR (1955) suggested a classification based mainly on morphological criteria which distinguishes 1) *traces exogènes* (simple bilobate and trilobate crawling trails, meanders, spirals, starlike trails, etc.) and 2) *traces endogènes* (burrows and tunnels of various forms, fucoids, resting trails, U-shaped burrows with or without spreite, and screw-shaped burrows) (Table 2).

VASOEVICH (1953, p. 41) devised a classification that is strictly morphological in content and may be called "Fucoids in a wider sense." Accordingly, lebensspuren have been categorized as to whether they are two-dimensional or three-dimensional. These two major divisions are further subdivided on the basis of similarities of morphology such as meanders, braids, screw shapes, spiral shapes, U- or J-structures, presence or absence of branches, and other characters.

EWING & DAVIS (1967, p. 265-267) developed a very detailed morphological classification of Recent trails and dwelling structures found in the deep sea, arranged in geometric groups. Because the producers of lebensspuren almost always remain unknown, these authors adopted a strictly morphological classification. They distinguished between ridges and sets of ridges, lumps and sets of lumps, grooves and sets of grooves, depressions and sets of depressions and one or more grooves together, and sculptured strips. However, because transitional forms exist and there are problems of definition of the forms, nomenclatural problems arise.

HOROWITZ designed a new descriptive classification of lebensspuren which has been reproduced by FREY (1971, p. 96)

TABLE 2.—*Lessertisseur's (1955) Proposed Classification for Traces of Activity of Invertebrates* (translated from Lessertisseur, 1955).



(Fig. 6). This classification is similar to LESSERTISSEUR's in using two main groups, i.e., intrastratal and bedding-surface structures, which then are further subdivided.

**PRESERVATIONAL ASPECTS**

Most trace fossils are preserved at the

interface between clay and coarser-grained clastic sediments. For example, in flysch sediments, trace fossils are found on the underside of the coarse-grained clastic beds.

Therefore, it has also been possible to establish classifications based on the position of the trace fossil relative to the sediment

- I. Intrastratal Structures
  - A. Shape
    - 1. Unbranched
      - a. Straight
      - b. Curved
        - (1) U-shaped
        - (2) J-shaped
        - (3) Other
      - c. Lined
      - d. Flaring Sides
      - e. Crenulate Walls
    - 2. Branched
      - a. Regular
      - b. Irregular
  - B. Filling
    - 1. Patterned
    - 2. Homogeneous
  - C. Size
  - D. Orientation (with respect to bedding)
    - 1. Horizontal
    - 2. Vertical
    - 3. Inclined
    - 4. Random
- II. Bedding-Surface Structures
  - A. Shape
    - 1. Round or Ovate
    - 2. Star-Shaped
    - 3. Digitate
      - a. Number of Digits
    - 4. Ridges and Furrows (systematic or unsystematic pattern)
      - a. Single
        - (1) Straight
        - (2) Smooth Curves
        - (3) Sharp Ridges
        - (4) Branched
      - b. Multiple
        - (1) Branched
        - (2) Unbranched
  - B. Internal Pattern
  - C. Size
  - D. Orientation

FIG. 6. Descriptive classification of lebensspuren proposed by HOROWITZ (Horowitz in Frey, 1971).

interface. MARTINSSON (1965, p. 202-203) created a "stratinomic classification" or, as it has also been called, a "topographic classification." Recently, MARTINSSON (1970) has given another detailed discussion of his trace fossil classification, which he renamed the "Toponomy of Trace Fossils" (Fig. 7). It is a purely descriptive terminology including no ethological interpretation of the trace or trace producer. Only the position

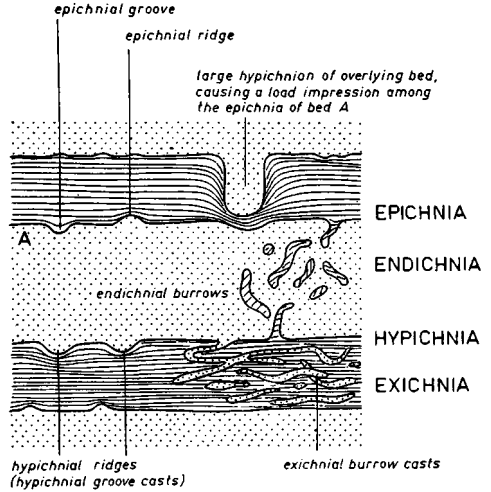


FIG. 7. Diagrammatic representation of toponomic terminology suggested by MARTINSSON (1970) and shown in cross section (Martinsson, 1970, p. 327, in: *Trace Fossils*, edited by T. P. Crimes & J. C. Harper, Geol. Jour. Spec. Issue 3, Seel House Press, Liverpool). [Stippled areas are siltstones and ruled areas, shales. For descriptive terms at right refer to bed A.]

of the trace fossil in the sediment is important and is identified by the following four "toponomic" terms.

- 1) EPICHNIA. Traces on upper surfaces of the main casting medium.
- 2) ENDICHNIA. Traces inside sediment within the casting medium (in German, *Innenspuren*).
- 3) HYPICHNIA. Traces in firm primary contact with the lower surface of the clastic bed (sole trails).
- 4) EXICHNIA. Mostly burrows in calcareous sediments but consisting of coarser materials introduced from a coarser bed.

These four terms have the advantage that they can be used either as adjectives (epichnial) or as nouns (epichnion). They may also be combined with simple morphological terms such as ridge, groove, furrow, burrow, or cast (e.g., epichnial ridge).

In the strictest sense, such a descriptive "system" is actually not a classification of lebensspuren, as any descriptive system

must be supplemented with an ethological analysis and interpretation of trace fossils in general.

In this connection the classification developed by SEILACHER (1964a, p. 254-255; 1964c, p. 297) must be mentioned, which takes into consideration both the type of preservation and the origin of the trace fossils (but not in an ethological sense). In an expansion of his earlier somewhat schematic, stratynomic terms (SEILACHER, 1953a, p. 437), in his 1964 publications he has further refined previous classification.

- 1) FULL RELIEFS (Ger., *Vollformen*). Preservation of the entire structure ("fills" comparable to internal molds, "cavities" = open burrows).
- 2) SEMIRELIEFS (Ger., *Halbformen*; French, *demireliefs*). Sculptures on sand/clay interfaces; two kinds are to be distinguished, a) epireliefs, grooves or ridges on the top surface of a psammitic sediment, and b) hyporeliefs, on the undersurface of psammitic beds (ridges or grooves).

These forms can be produced in different ways, and additional observations are necessary. Thus, endogenic burrows may be exposed on the surface if the overlying sediments are eroded away, after which another layer of sediment may be deposited on the erosional surface, filling the excavated burrow. This burrow will then be preserved as "pseudoexogenic." Therefore, it must be determined if a burrow underwent active or passive filling. WEBBY (1969a, p. 90) felt that the term pseudoexogenic was unsatisfactory, and proposed that forms such as *Paleodictyon* are best named "preendogenic." Ichnogenera *Cosmorhapse* and *Spirorhapse*, originally surface fecal casts that have been eroded and later filled with sand, are described as "preexogenic" (Fig. 4).

Lebensspuren from flysch sediments that are generally interpreted as turbidites have been differentiated as either predepositional or postdepositional, based upon their chronologic relation to turbidity currents

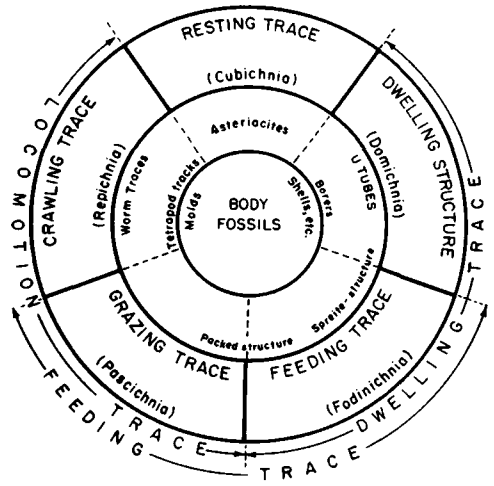


FIG. 8. Ethologic classification of trace fossils proposed by SEILACHER (1953) (from Osgood, 1970).

(KSIĄŻKIEWICZ, 1954, p. 446). A classification of the numerous trace fossils from Polish flysch deposits was made by KSIĄŻKIEWICZ (1970, p. 315-317) according to whether they were predepositional or postdepositional in origin. A discussion of his criteria for division and classification has been included because some forms are impossible to place in either group. SEILACHER (1962, p. 230) discussed a similar arrangement for sole trails in flysch deposits of northern Spain where similar turbidite sequences have been observed. Some sole trails were obviously of endogenic origin, and after weak compaction, were exposed on a bedding plane, eroded and later filled by sediment. Such trails were called "pre-endogene" by WEBBY (1969a) (see Fig. 4). A comparison of the lists given by KSIĄŻKIEWICZ (1970) and by SEILACHER (1962) of ichnogenera which they regarded as predepositional and postdepositional shows some agreement, but also some uncertainties of such a classification.

#### ETHOLOGICAL ASPECTS

A classification according to ethological principles proposed by SEILACHER (1953a, p. 432-434) (Fig. 8), is based on the fact that different groups of animals with simi-

lar life habits or behavioral patterns produce traces with similar basic characters, even though the animals themselves have quite different body shapes. Working out these common basic characters, SEILACHER distinguished five ethological groups: dwelling structures (domichnia), feeding structures (fodinichnia), grazing traces (pascichnia), resting traces (cubichnia) (=Ger., *Ruhespuren*, RICHTER, 1926, p. 223; repose imprints, KUENEN, 1957, p. 232), and crawling traces (repichnia) (=Herpichnites GÜMBEL, 1897, general term, not used as "genus"). For each of these groups typical features may be characterized as follows:

- 1) DOMICHNIA. Simple or U-shaped burrows or burrow systems with horizontal and vertical components, or dwelling tubes; perpendicular or oblique to the surface. More or less permanent domiciles for most sessile suspension-feeding animals.
- 2) FODINICHNIA. Various shaped burrows (with or without spreite) and burrow systems, at various angles to the bedding. More or less temporarily by used sessile sediment-eaters simultaneously as domicile, "mine," or hunting-ground.
- 3) PASCICHNIA. Highly winding bands or furrows, not crossing each other, with intense utilization of the surface available for grazing or feeding, commonly resulting in surface ornamentation such as meanders or letterlike patterns ("parqueting").
- 4) CUBICHNIA. Isolated, mostly shallow depressions of troughlike relief, outlines corresponding roughly to the shapes of their producers. Commonly arranged parallel to each other as a result of like orientation (rheotactic rectification) toward currents, vertical and horizontal repetition possible.
- 5) REPICHNIA. Furrows, trackways, trails, and shallow crawling tunnels of variable direction, linear or sinuous, ramified or unramified, smooth or sculptured.

SEILACHER's system has the advantage of grouping ethologically similar assemblages of lebensspuren. Questions as to identity of their producers may be disregarded here, for these can only rarely be answered unequivocally on the basis of morphological criteria. The characterization of groups is, also, independent of time; for example, the assemblage termed cubichnia is equally valid for extinct arthropods of the Paleozoic (e.g., trilobites), as for Recent arthropods that have a corresponding mode of life. BERGSTRÖM (1972) has observed that the bend in the anterior cephalic margin of the trilobite *Cryptolithus* appears to have the same function in plowing as the limulid prosoma.

Due to its easy application, this system has proved useful for fossil and Recent lebensspuren. In the literature dealing with trace fossil associations, ichnogenera are assigned to one or the other of these groups. The ethological classification makes it possible to compare different ichnocoenoses which are characterized by giving percentage contribution by each group ("trace fossil-spectra"). In this manner, SEILACHER was able to distinguish several ichnofacies (e.g., *Nereites* facies and *Cruziana* facies) characterized by pascichnia in which cubichnia predominate. (For a complete discussion, see p. W32-W33.)

Trace fossils reflect the behavioral patterns of their producers. Therefore, in SEILACHER's ethological classification, it is not possible to assign each trace fossil to a particular group. An example is the vertical dwelling tube (*Wohnröhre*) of a polychaete worm that produces star-shaped grazing trails (*Weidespuren*) in the sediment surface surrounding the opening of the burrow, because such structures can be described as a combination of domichnia and pascichnia (HÄNTZSCHEL, 1970, p. 262). FREY (1971, p. 99) has considered trace fossils produced by two behavioral patterns in giving the name "combined feeding-dwelling burrows" to burrows produced by sediment-ingesting organisms that also double as domiciles for those animals.

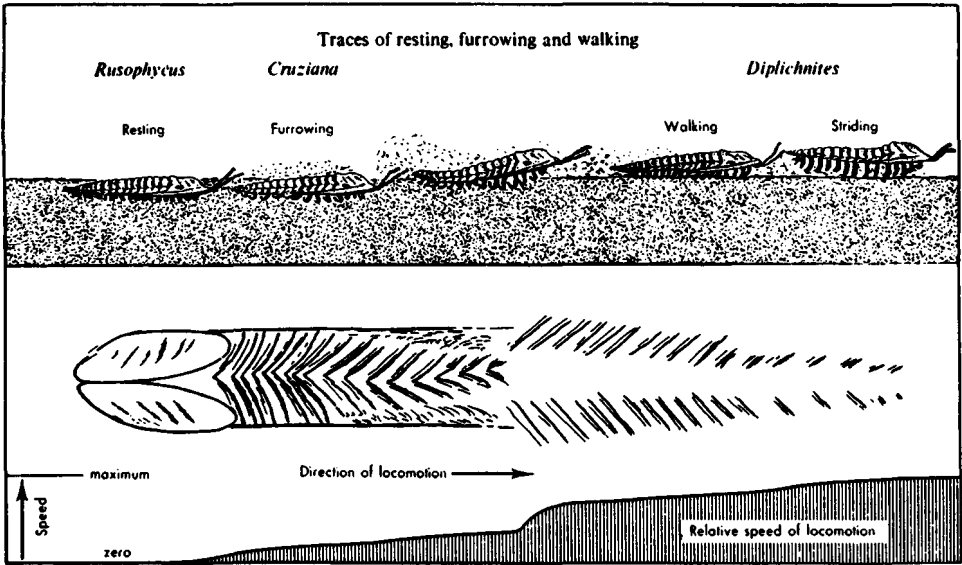


FIG. 9. Transitional relationships of trilobite traces (Crimes, 1970b).

Another example is the transition from resting impressions (*Ruhe Spuren*) to motion trails (*Bewegungsspuren*) of trilobites observed by CRIMES (1970c, pl. 5, fig. e) (Fig. 9). Nomenclatural problems arise when the two forms have received names, because they are also found singly (e.g., the motion trail *Cruziana* and the resting impression *Rusophycus*), both made by trilobites. One could, of course, consider these names to be synonyms and use only the older one (*Cruziana*) as was done by SEILACHER (1970).

SEILACHER (1953a, p. 434-435) supplemented his classification, especially for Recent lebensspuren, by including swimming trails, hatching structures, and functional structures mostly for the seizure of food (i.e., nets, traps, and others).

MÜLLER (1962, p. 25-28; 1963, p. 167) expanded SEILACHER's classification (see Fig. 10 [from OSGOOD, 1970, p. 290, fig. 3] for a complete English translation) and distinguished four main groups: Quietichnia (resting traces), Cibichnia (feeding structures), Movichnia (movement traces),

and Bioreactions (disease, parasitism, etc.), and four subgroups: Mordichnia (biting and gnawing traces), Cursichnia (running traces), Natichnia (swimming traces), and Volichnia (flying traces).

However, by the use of this expanded

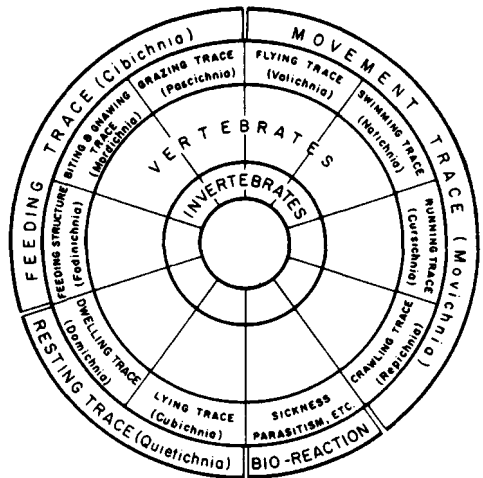


FIG. 10. MÜLLER's (1962) ethologic classification of lebensspuren as an expansion of SEILACHER's (1953) classification (from Osgood, 1970).

system, the application of the German terms can be misunderstood, and it also appears that this system is not entirely correct, as dwelling traces (*domichnia* SEILACHER) are included as a subgroup of *quietichnia* MÜLLER (= *Ruhespuren* MÜLLER, 1962; *non Ruhespuren* RICHTER, 1926, *nec* SEILACHER, 1953). By strict definition, bioreactions are not trace fossils. Swimming traces have so far been described from the Culm of Western Germany (FIEGE, 1951) and the Dwyka Group of South Africa (ANDERSON, 1972), but flying trails are, as yet, known only in the Recent and are difficult to identify as such. Therefore, I recommend that in the future, SEILACHER's (1953a) classification be adopted with his original definitions.

#### TAXONOMIC-STRATINOMIC-MORPHOLOGIC CLASSIFICATION PROPOSED BY VYALOV

VYALOV (1968b, p. 125; 1972) named all *lebensspuren* *zoichnia* or *vivichnia*. Since his classification differentiated between *vertebratichnia* and *invertebratichnia*, it was the first to classify trace fossils according to their producers (e.g., *piscichnia*, *amphibipecta*, etc.). *Lebensspuren* produced by invertebrates were divided into two main groups, *bioendoglyphia* and *bioexoglyphia*, which respectively correspond to endogenic and exogenic structures. VYALOV named traces produced by the appendages of organisms *podichnacea*, and all others, *apodichnacea*. These terms, respectively, correspond to the terms tracks and trails. *Lebensspuren* produced within a substrate have been named either 1) *foroglyphia*, produced in solid substrates such as hardgrounds and shells, or 2) *fossiglyphia*, produced in unconsolidated sediments. VYALOV (1968b, p. 126-127) introduced numerous additional morphological subgroups with so many new names that it is impractical to quote them all here. The names of these groups have endings analogous to those used for higher taxonomic units of the

VIVICHNIA
Invertebratichnia
Bioendoglyphia (traces within the sediment)
Foroglyphia (borings in hard substrate)
Lithoforida (in stones and rocks)
Coproforida (in organic substrate)
Conchoforoidea (in shells)
Arboforoidea (in wood)
Fossiglyphia (burrows in unconsolidated sediment)
Endotubida (tubular)
Rectotubae (straight; <i>Skolithos</i> , <i>Tigillites</i> )
Arcotubae (U-shaped; <i>Arenicolites</i> )
Spirotubae (spiral; <i>Gyrolithes</i> , <i>Xenohelix</i> )
Chondritae ( <i>chondrites</i> ; <i>Chondrites</i> )
Crustolithida (branched, unordered; <i>Ophiomorpha</i> , <i>Radomorpha</i> )
Helicoidida (helical; <i>Zoophycos</i> )
Cryptoptida (subsuperficial; <i>Scolicia</i> )

FIG. 11. A portion of VYALOV's (1968b, 1972) classification of trace fossils (after Vyalov, 1968b).

zoological system (i.e., -a and -ae) and are easy to recognize. In 1972 VYALOV summarized and slightly modified his earlier views and presented them in tabular form (Fig. 11).

In this system, it could happen that ethologically and morphologically heterogeneous ichnogenera are placed in the same group. For example VYALOV (1968b, p. 127, table 3) placed the sinusoidal crawling trace *Cochlichnus*, the cylindrical and horizontal burrow *Palaeophycus*, and the meandering, grazing trail, *Cosmorhappe*, all in the subgroup *Vermiglyphidae*, a subdivision of the *Unipartoidae*. I maintain

that a classification that unites so many different forms in one and the same group

is of little use. Even VYALOV described his classification as “artificial and conditional.”

## NOMENCLATURE OF TRACE FOSSILS

Since about 1850 it has become customary to use binary nomenclature for trace fossils in the same way that it has been used for body fossils. With trace fossils, however, the terms “genera” and “species” have a meaning different from that which is applicable to body fossils. As may be understood from the history of palichnology, too many finely differentiated genera and species have been established for trace fossils, because they originally were believed to be fossil plants, in particular, marine algae. This is especially true for the host of fucoids, as evidenced by the description of the history of the “genus” *Fucoïdes* by JAMES (1884).

The numerous, isolated descriptions scattered throughout world literature in paleobotanical, paleozoological, faunistic, stratigraphical, regional geological, and strictly palichnological papers have led to an excessive number of described genera and species. Because of the worldwide distribution and considerable vertical ranges of numerous trace fossils, the “new” forms were often published without knowledge or consideration of earlier literature.

Binary nomenclature has not been accepted universally for lebensspuren. Many authors have declined to give even descriptive informal names to trace fossils, which is an understandable and justifiable procedure, especially with poorly preserved forms. However, experience shows that these unnamed forms usually escape notice in later literature. I agree with OSGOOD (1970, p. 295), who asserts that “a form must be named if it is not to be ‘lost’ in the literature.”

FAUL’s (1951) suggestion of a designation by formulas may perhaps be suitable for vertebrate tracks, but it is not applicable to trails of invertebrates.

Repeatedly, the early term *Ichnium* was used as a blanket designation for undifferentiated trails. This was done in connection with species names, especially for Lower Permian vertebrate trails described from Germany (publications by PABST from 1896 to 1908) and later for invertebrate trails from the Lower Permian of Germany (SCHMIDTGEN, 1927, 1928). Some authors preferred HITCHCOCK’s general term *Ichnites* for “all footmarks.” This served as 1) a collective name, or 2) a special description when accompanied by a specific name describing single trails produced by vertebrates or invertebrates. A few paleontologists have generally opposed the use of names for trace fossils. NATHORST (1883a, p. 34, 287) observed that in view of the great similarity of trails produced by totally different animals, names for fossil forms were nearly worthless.

However, to make possible international discussion about individual forms or components of ichnocoenoses, trace fossils must be formally named. Supposedly new names of ichnogenera and ichnospecies should be based only on well-preserved material with well-defined morphological characteristics. Names should not be given to poorly preserved material or obscure forms. As long ago as 1894, JAMES drew attention to the many useless names which did not represent scientific progress, but were only a burden in the literature.

JARDINE (1853) proposed that the ending *-ichnus* be added to the generic names of vertebrate trails from Scotland so that it would be possible to distinguish names of trace fossils from body fossils by their characteristic endings. Soon after this, invertebrate trails were named in the same manner (i.e., *Cochlichnus* HITCHCOCK, 1858). More recently, SEILACHER (1953a, p. 446)



and HÄNTZSCHEL (1962, p. W182) have recommended the application of the *-ichnus* ending for new ichnogenera, and this procedure is, at present, often employed.

When describing new ichnogenera or ichnospecies, it is suggested that the abbreviations *nov. ichnogen.* or *nov. ichnosp.* should follow the proposed names, not *nov. gen.* or *nov. sp.*

A survey of ichnogenera shows that quite frequently the name of the animal that produced the trail or structure is incorporated in the name of the ichnogenus. Some examples are *Arenicolites* SALTER and *Annelidichnus* KUHN. Just as often, trace fossils were named because of morphological characteristics (e.g., *Asterichnites* BROWN & VOKES, *Cylindricum* LINCK, and *Monocraterion* TORELL), or because they were originally thought to be of plant origin (e.g., names having the ending *-phycus* and such names as *Fucoides* BRONGNIART and *Hormosiroidea* SCHAFFER). Only occasionally is the age of the trace fossil indicated by its name (i.e., *Archaeichnium* GLAESSNER and *Permichnium* GUTHÖRL) or the locality where it is found (*Steigerwaldichnium* KUHN).

It is unavoidable that trace fossils, which were formerly assumed to be bodily preserved plants or animals and were named accordingly, now carry inconsistent names that have to be retained (e.g., *Fucoides*, for feeding burrows of marine animals).

The question as to whether a previously unknown trace fossil should be named as a new ichnogenus or should be established as a new ichnospecies of an existing "related" ichnogenus, is very difficult to answer. Such judgments are more or less subjective and depend entirely on the personal opinions of the investigator who establishes the new name. The same is true in considerations of questions of synonymy and the establishment of validity of names. When trace fossils are described according to the International Code, as has been common practice, the establishment or designation of a type species is necessary, but

the great variability of forms makes it very difficult to select an ichnospecies that adequately represents all morphological variations of an ichnogenus. For this reason alone, a large number of monotypic ichnogenera have been established, and the number of trace fossil names is disarmingly large.

In view of these difficulties, it is understandable why MARTINSSON (1965, p. 204; 1970, p. 324) suggested that for trace fossils the practice of formalizing generic descriptions and designating type species should be abandoned. He proposed replacing ichnogeneric and ichnospecific names "by adopting terms which designate ecological types rather than taxa, such as *cruziana*, *dimorphichnia*, and *halopoans*" (MARTINSSON, 1965, p. 204). Undoubtedly, a loose and unconstrained terminology has merit since these names would not be printed in italics and thus could be distinguished from generic names given to body fossils. Therefore, no diagnosis of new forms would be required. On the other hand, without clear and concise definitions of such terms as "a *cruziana*" or "a *halopoa*," they would be impossible to use in practice.

There are two opposing definitions of the meaning of names of trace fossils, which can be considered either 1) for the trace fossil itself, as the "work of an animal" (Code, Art. 16,a), or 2) for the producer of the trace fossil. These different points of view have been discussed quite recently, and it is still possible to speak of "two apparently irreconcilable schools" (OSGOOD, 1970, p. 296-297). SEILACHER (1956b, p. 158) stated, "*Ichnofossilien werden nicht in Stellvertretung ihres Urhebers benannt*" [Trace fossils are not to be named as substitutes for their producers] and considered trace fossils to be features independent of their producers. I am of a similar opinion, and believe that a name should describe only the trace fossil and not its producer. It must, however, be taken into consideration that when only

behavioral patterns and biogenic sedimentary structures are named, one can only guess as to the identity of the animal that produced a particular trace fossil, particularly if the producer is an invertebrate.

For trace fossils in hard substrates, such as borings, BROMLEY (1970) has emphatically insisted that only the names of the trace and not that of the animal producer of the trace should be valid. Names such as *Cliona* or *Polydora* should not be applied to borings because they apply to the producer of the structure. The name of a boring should suggest no more than that it is a hole in a shell or some other hard substrate. An example of the alternative interpretation of trace fossil names is the description of the genus *Ixalichnus* CALLISON (1970), which by the ending *-ichnus* is clearly established as a trace fossil. However, CALLISON (1970) assigned *Ixalichnus* as a new genus to the subphylum Trilobitomorpha, phylum Arthropoda, adding that *Ixalichnus* "spent much of his time swimming. . ."

The trace fossil and its producer are rarely found together. This situation has been observed for trilobite lebensspuren when a typical resting impression is found associated with its producer *in situ* (OSGOOD, 1970, p. 296, pl. 57, fig. 1 and pl. 58, fig. 4,5). In a few rare cases, the producer is found at the end of its running or crawling trail and in this manner, a definite producer can clearly be demonstrated (e.g., limulid trails from the Upper Jurassic Solnhofen Limestone) (Fig. 12).

Since the *Code* is inconsistent and contradictory in regard to the naming of ichnotaxa, the nomenclature of trace fossils is in a state bordering on chaos. As regards names established before 1931, Article 12 of the *Code* prescribes that, in order to be available, such a name must be accompanied by a "description, definition, or indication." Article 16 defines "what constitutes an indication" and includes as one of the definitions "the description of the work of an animal, even if not accompanied



FIG. 12. A *Limulus* preserved at the end of its trail (Abel, 1935).

by a description of the animal itself." It is thus perfectly clear that names given to trace fossils before 1931 are available under the *Code* and have to be treated on an equal footing with all other zoological names. This is further clarified by Article 24 (b) (iii) which states that the Law of Priority applies "when, before 1931, a name was founded on the work of an animal before one is founded on the animal itself."

However, for names published after 1930 a different set of rules applies. The critical rule is that stated in Article 13 (a) (i) which requires that such a name must be "accompanied by a statement that purports to give characters differentiating the taxon." This requirement is, of course, impossible to fulfill in the case of trace fossils of which the producer is generally not known. Hence, names for trace fossils established after 1930 are not available under the *Code*.

In order to clarify this situation, HÄNTZSCHEL & KRAUS (1972) submitted an application to the I.C.Z.N. which has been published in Volume 29 of the *Bulletin of*

**Zoological Nomenclature.** In this application, the authors asked the Commission to issue a Recommendation (Appendix E of the *Code*) that all names of lebensspuren should be treated in the same way as prescribed for categories of names presently governed by the *Code*. They also recommended that names of ichnogenera should not be italicized, but for purpose of conformity with general *Treatise* style, such names are printed in italics here. With this exception, the trace fossil names in the present volume are dealt with in conformity with recommendations made by HÄNTZSCHEL & KRAUS (1972). (See also Editorial Preface, p. vii.)

[As might be expected, the HÄNTZSCHEL & KRAUS proposal has received critical review from scientists in many countries (FREY, 1972; MARTINSSON, 1972; TEICHERT, 1972; VOIGT, 1973; LEMCHE, 1973; YOCHELSON, 1973). All are unanimous in their desire that the problem of the availability of trace fossil names be faced now and settled once and for all, but not everyone has agreed on how this should be accomplished.

FREY, MARTINSSON, TEICHERT, and YOCHELSON agreed basically with the proposal supporting availability of all names for trace fossils and emphasized the need for these names to continue in italic print. YOCHELSON (p. 71) in addition suggested a logical solution for all this confusion: "by removing the post-1930 restriction, the rules will be allowed to operate for the 'indications' of animals. A minimum of problems results from such a course of action."

LEMCHE (p. 70) on the other hand believed that there was excellent justification for the freeing of all post-1930 trace fossil names from the rules of the *Code*, adding that if anybody can propose a better system "than that proposed by the present applicants, he should hasten to do so." Perhaps SARJEANT & KENNEDY (1973) have already answered LEMCHE's plea with their "Proposal of a code for the nomenclature of trace fossils" which would exempt the names of trace fossils from the rules of both the Zoological and Botanical Codes. However, as the title suggests, this is only a proposal, or more properly, a "draft and not a finished product" which "may at least stimulate thought and discussion" (SARJEANT & KENNEDY, 1973, p. 465). It has no legal standing, especially if the HÄNTZSCHEL & KRAUS proposal is accepted.—CURT TEICHERT, W. G. HAKES.]

## SIGNIFICANCE OF TRACE FOSSILS FOR SEDIMENTOLOGY

Inorganic sedimentary structures produced by physical processes can be altered or destroyed by burrowing, crawling, agitating, and ingesting the sediment by infaunal elements (Fig. 13). These biological processes produce sedimentary structures that have been described as bioturbation or biogenic sedimentary structures.

Vagile sediment ingestors and the more or less stationary dwelling structures of animals in the sediment interact with the sedimentation processes in their environ-

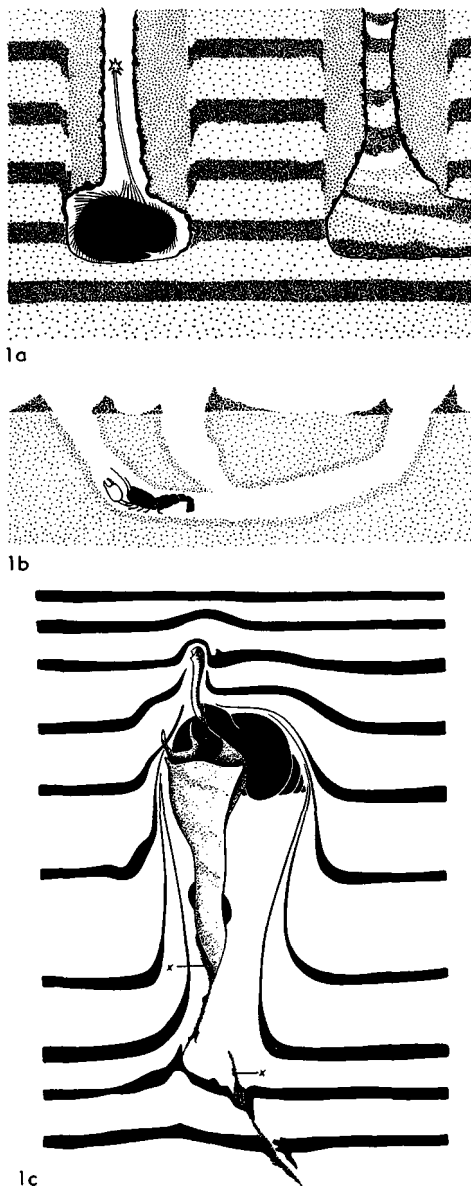


FIG. 13. Some examples of sedimentary structures associated with biogenic activity (Schäfer, 1956). —1a. Left: *Echinocardium* at the bottom of its burrow; right: after sea urchin leaves its burrow, cavity is later filled by inorganic sedimentation. —1b. Cross section of *Callianassa* burrow. Sediment is piled at openings of burrow by the crab. —1c. Deformation of sand layers produced by the upward movement of the gastropod *Buccinum* in the sediment (x = sand mixed with mucus).

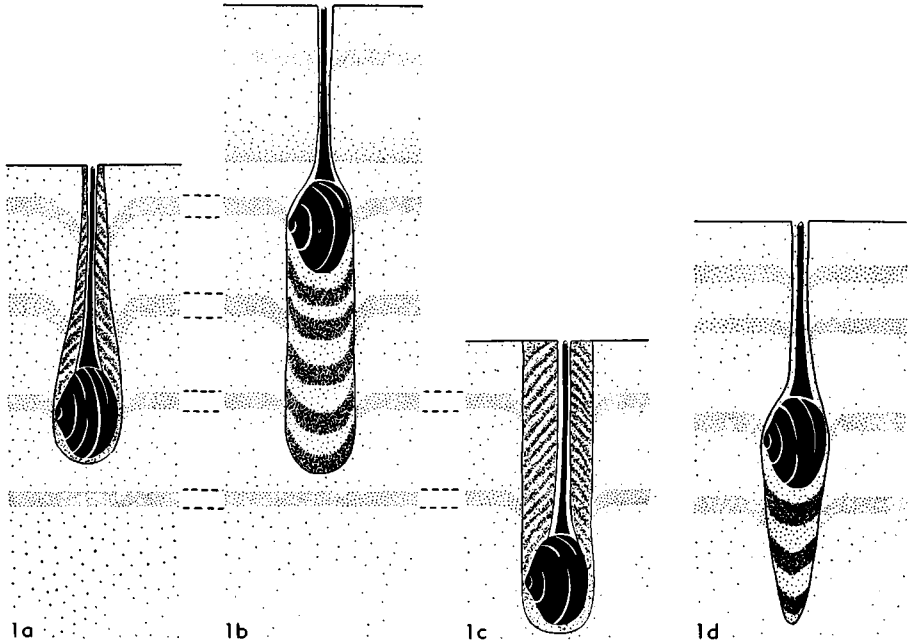


FIG. 14. Relationships of burrowing structures of unisiphonal pelecypods to rates of sedimentation (Reineck, 1958a).—*1a*. No sedimentation: a conical burrow forms above a growing pelecypod.—*1b*. Rapid sedimentation: as the animal moves upward through the sediment, a burrow is formed below equal to the animal's width.—*1c*. Erosion: animal migrates downward in sediment producing a burrow above it equal to its width.—*1d*. Very slow sedimentation: a growing pelecypod follows the accumulation of sediment upward creating a conical burrow beneath it.

ment. Rapid or slow sedimentation, non-deposition, or the removal and change of sedimentary processes can often be determined by studying trace fossils.

The paleoichnology of marine sediments must be based on detailed knowledge of the relationships of Recent benthonic communities to the sediment. SCHÄFER (1956; 1972) and REINECK (1958a,b; 1972) have studied the influence of different benthonic organisms on the bedding of Recent sediments by observations on the tidal flats of the North Sea and in aquariums. However, little is as yet known about occurrences of lebensspuren in the neritic, bathyal, and abyssal zones of the ocean (HERSEY, 1967; HEEZEN & HOLLISTER, 1971; PEQUEGNAT *et al.*, 1972).

Benthonic organisms live at specific depths in the sediment (Fig. 14). When

excessive amounts of sediment accumulate above an animal, it will create an escape structure or tunnel, primarily by digging upward, in order to raise its position in the sediment. This upward motion within the sediment produces a displacement or bending of the sedimentary layers above and below the animal's escape burrow (Fig. 13,1c; Fig. 15,4). The very vagile *Sipunculus* produces upward warping of the sedimentary layers during the production of escape tunnels (Fig. 15,3). In comparison, downward arching of sedimentary layers has been observed mostly in the escape tunnels of polychaetes (Fig. 15,2), some bivalves (Fig. 14,1b), and the sea anemone, *Cerianthus* (Fig. 15,1). Similar sedimentary deformation is produced by the burrowing of many polychaetes, echinoderms, and brachyurans, and such bioturbate sedi-

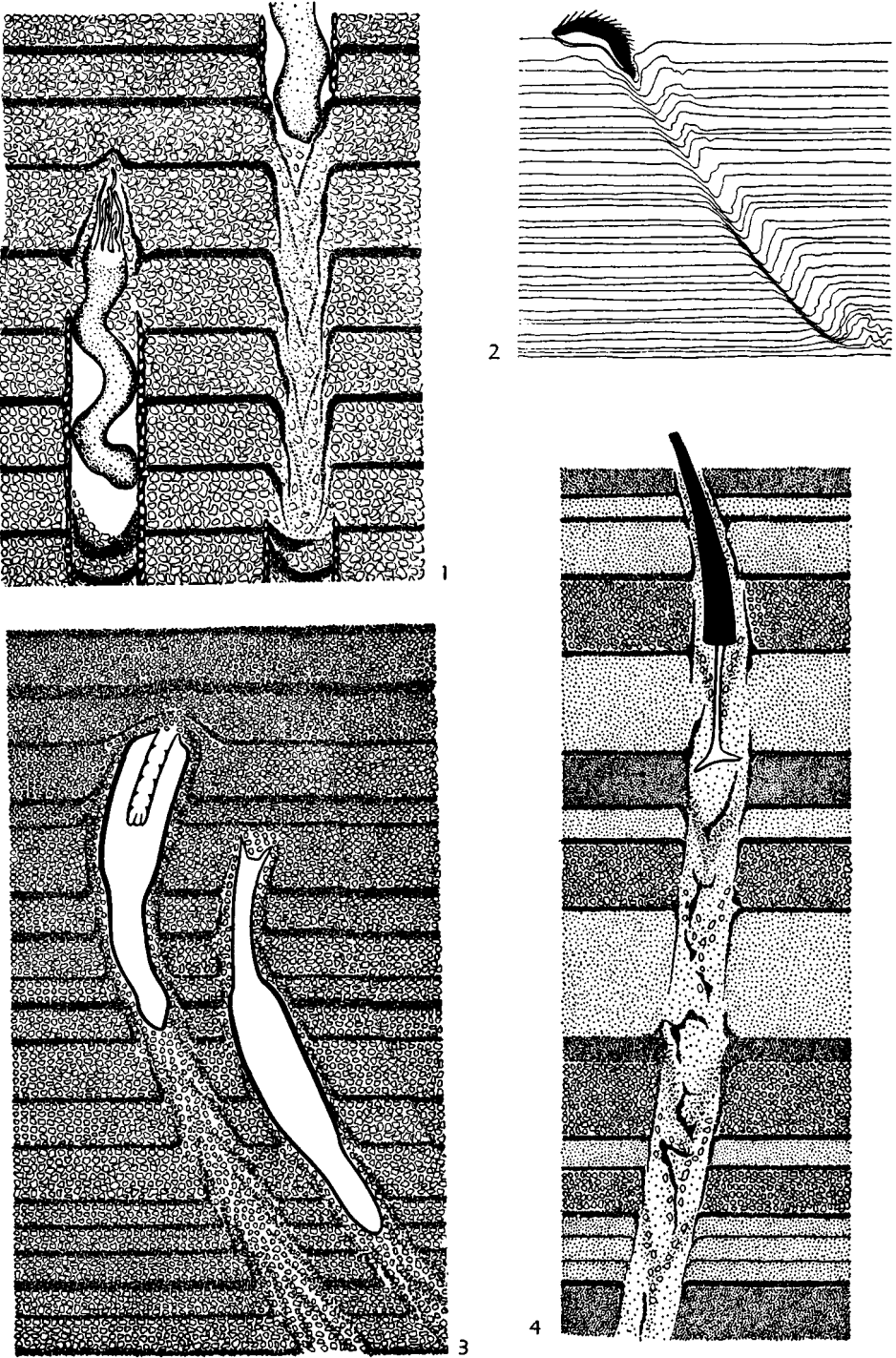


FIG. 15. Examples of escape structures (from Schäfer, 1972).—1. Sea anemone, *Cerianthus*, covered by sediment, evacuates its burrow and moves upward in the sediment (schem.).—2. As large polychaete, *Aphrodite aculeata*, moves upward, beds sag downward behind it (schem.).—3. *Sipunculus* moves upward in the sediment, and beds are pulled upward with the animal,  $\times 0.3$ .—4. Turbate trail of scaphopod moving upward in the sediment (schem.).

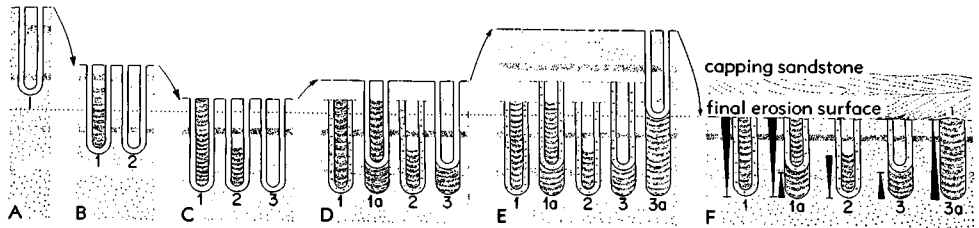


FIG. 16. Movement pattern of *Diplocraterion yoyo* (Goldring, 1964). In the Upper Devonian Baggy Beds, England, this trace occurs in various types shown in (F), where all have been truncated to a common erosion surface. Repeated phases of erosion and sedimentation led to the development of the various types. Stage (A), development of burrow (1): with degradation of surface, this tube migrates downward, and at intervals, new tubes (2 and 3) are constructed (B and C). Sedimentation follows (D and E) but some of the tubes are abandoned. Stage (F): all tubes are abandoned and erosion reduces them to a common base.

mentary structures occur around burrowed tubes in Cambrian sandstone and quartzite beds in Europe. However, it appears that such "escape structures" have been recorded only rarely in the literature (FREY, 1973b). Perhaps they have been overlooked.

Erosion can cause infaunal elements to migrate downward through horizontal sedimentary layers in order to reach their required living depth. This is especially true of pelecypods, which also produce similar biogenic structures (Fig. 14, 1c).

An excellent example of the reaction of sediment-dwellers to sedimentation processes is seen in the Upper Devonian *Diplocraterion* tubes in England studied by GOLDRING (1962) (Fig. 16). Different types of U-shaped tubes, normal protrusive, retrusive, and abandoned, with spreite structures, give an indication of the reaction of the infauna to repeated changes from deposition to erosion. For these occurrences, the appropriate species name *Diplocraterion yoyo* was coined. In the Aptian of England, MIDDLEMISS (1962) concluded that poorly preserved burrows are commonly found in highly turbated beds deposited during periods of slow sedimentation, whereas better preserved burrows indicate rapid sedimentation. In Jurassic sandstones, resting impressions such as *Asteriacites* have been observed to exhibit vertical repetition of impressions within the sediment. These oc-

currences are undoubtedly the result of the upward escape of the animal through the sediment in response to considerable sediment influx (SEILACHER, 1953b) (Fig. 17).

Areas of slow deposition or nondeposition provide favorable substrates for the settlement in the sediment of burrowing organisms and filter-feeders. For the most part, presence of numerous excavated burrows (*Wühlspuren*) indicates stable substrates or slow sedimentation rates.

Occasionally, during temporary nondeposition of sediment the surface of fine-grained sediments may be converted into hardgrounds. Such occurrences are typical for the Upper Cretaceous of western Europe where domiciles (*Wohnbauten*) of crustaceans and echinoderms are found in such rocks in many places. The abutment of such burrows against an obstacle such as a shell, or detour of a tunnel around an obstacle, indicate that the burrow was excavated before the sediment was lithified (RASMUSSEN, 1971).

Many seemingly homogeneous sediments have completely lost their original bedding as a result of intense bioturbation (MOORE & SCRUTON, 1957, p. 2743). However, complete obliteration of bedding features is rare and occurs only if an abundant infauna was present, sedimentation was slow or absent, and if the infaunal animals had enough time to rework the sediment.

These examples show the importance of

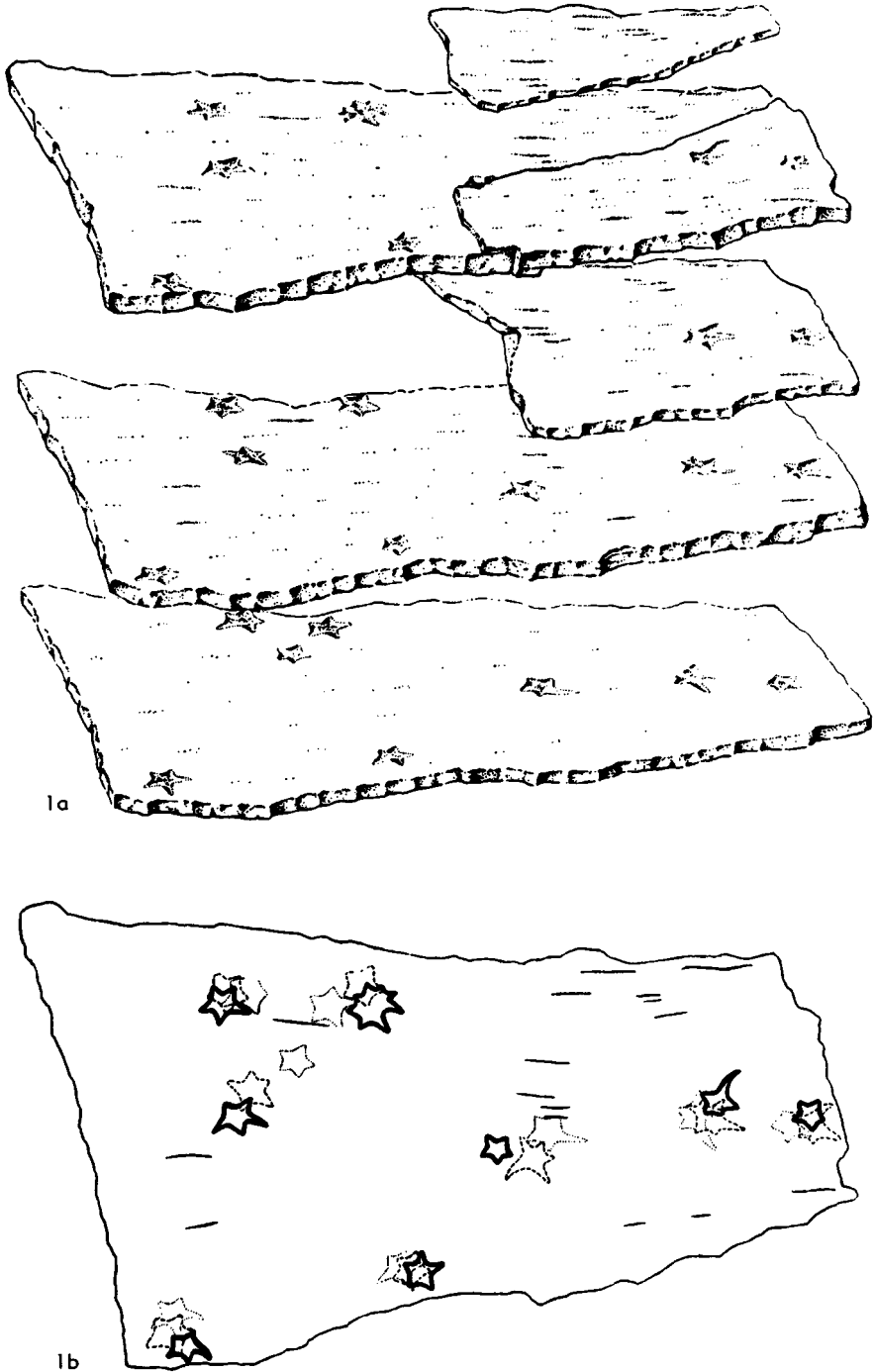


FIG. 17. Starfish impressions, *Asteriacites lumbricalis*, Lower Triassic, southern Tirol (Seilacher, 1953).  
 —1a. Expanded view of bedding planes showing upward migration of starfish as a result of rapid sediment influx.—1b. Composite overview of 1a, solid outlines indicate impressions stratigraphically above dotted outlines.

endogenic traces and burrows for the clarification of sedimentological problems and for interpretation of the depositional history of many sediments. Further investigations on interrelationships between Recent in-fauna and sediments in different biotypes are necessary to provide a sounder basis for paleoichnological research.

### SIGNIFICANCE OF TRACE FOSSILS FOR PALEOENVIRONMENTAL INVESTIGATIONS

For the most part, the paleoenvironment of marine sediments can be interpreted by investigating lithology, primary sedimentary structures, and faunal elements. In recent years, trace fossils and associations of trace fossils, because of their autochthonous nature, have been shown to be particularly useful in paleogeographic investigations. With very few exceptions trace fossils are preserved *in situ*. They cannot be displaced, and, in contrast to many body fossil assemblages, they form no thanatocoenoses. *Lebensspuren* provide certain evidence of life on and within the sediment. In addition, many trace fossils are good facies indicators.

Through worldwide comparison of ichnocoenoses in marine sediments of different ages, SEILACHER (numerous publications since 1954) has shown that characteristic trace fossil assemblages occur in many places in sediments of different ages. Each such assemblage belongs to a particular marine environment and is composed of specific associations of trace fossils, constituting an ichnofacies. The environment is characterized by the composition and texture of the sediment, and by oceanographic factors such as water depth, salinity, water circulation, and many others.

The contrasts between different ichnofacies are best recognized in the "ichnospectra," which give a quantitative picture of the individual trace fossil associations according to their ethologic classification. As a rough generalization, the differences between trace fossil assemblages in shallow

and deep water can be characterized as follows: In shallow water, vertical tubes, burrowing structures, dwelling burrows, and resting impressions predominate. In deep water, complicated spreitenbauten and many, varied, grazing trails of sediment-ingesters develop. SEILACHER (1954, 1955, 1959) was first to call attention to different ichnocoenoses and their time-independent facies relationships associated with flysch and molasse deposits. The trace fossils associated with geosynclinal flysch sediments contain assemblages of different grazing trails, whereas epicontinental and paralic molasse deposits are characterized by various resting impressions. Both of these examples have been found in Paleozoic, Mesozoic and Cenozoic rocks. The ichnocoenoses in predominantly fluviatile and continental deposits, with only periodic marine inundations, again show a different composition. Here, all ethologic associations are represented, with the exception of grazing trails. These associations have low diversity, but are generally rich in individuals. The ichnocoenoses of the Buntsandstein ("Bunter," Lower Triassic) and the Keuper Sandstone (Upper Triassic) of central Europe are examples.

More recent investigations of ichnocoenoses of different ages and from different geographic areas have shown the necessity to establish additional types of trace fossil assemblages. In some cases, small, local "subassociations" of trace fossils have been established. Every ichnocoenosis corresponds to a defined relatively narrow, facies range. There are no restrictions to certain sediment types and they are named after trace fossils characteristic for them. SEILACHER (1967b) distinguished the following ichnofacies and compared them with their particular environments at different bathymetric levels (Fig. 18):

- 1) *Scoyenia* facies: nonmarine; commonly redbeds.
- 2) *Skolithos* facies: littoral; rapid sedimentation and frequent transportation.
- 3) *Glossifungites* facies: littoral; ero-



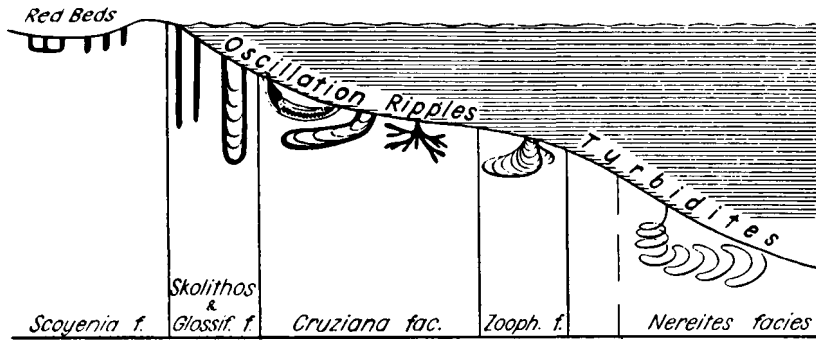


FIG. 18. Bathymetric zonation of trace fossil assemblages [*f* = facies] (Seilacher, 1967b).

sional surfaces, restricted to single bedding planes (erosion surfaces).

- 4) *Cruziana* facies (formerly: resting-impression facies): deeper shallow water, below the true littoral zone.
- 5) *Zoophycos* facies: transitional to bathyal zone.
- 6) *Nereites* facies (formerly: grazing-trail facies): bathyal to abyssal; pelagic sediments and turbidites.

CHAMBERLAIN (1971c) established a *Chondrites* assemblage in the Upper Paleozoic of Oklahoma (United States) which is a bathymetric zone transitional between the *Nereites* and *Zoophycos* associations.

Almost certainly, marine trace fossil assemblages are not solely depth-dependent. SEILACHER and, more recently, OSGOOD (1970, p. 403) and FREY (1971, p. 110-111) have pointed out that in addition to oceanographic conditions, factors such as nutrient supply may influence the composition of biologic ichnocoenoses, independent of bathymetry. Future investigations probably will introduce additional subassociations of trace fossils, or the boundaries between ichnofacies will be less distinct. OSGOOD (1970, p. 403) believes that, for example, a coexistence of pascichnia and cubichnia "at some intermediate depth" is possible and that a sharp distinction between the *Cruziana* facies and *Nereites* facies cannot be made. He also doubted that the *Zoophycos* facies was anything but a transitional facies, because it seems that

in the United States *Zoophycos* occurs in both deep and shallow water sedimentary deposits. [See OSGOOD & SZMUC (1972) for a more detailed discussion.] FREY & MAYOU (1971) have studied the distribution of Recent decapod burrows from Holocene barrier island beaches along the Georgia coast, and according to these authors, burrow orientation and morphology reflects distance from shore (Fig. 19).

On the other hand, similarities exist between Recent lebensspuren produced at great depths and trace fossils that were probably produced in a similar environment. Thus, spiral lebensspuren have been observed in the abyssal zone of the present seas which are similar to many grazing trails found in flysch deposits (BOURNE & HEEZEN, 1965; EWING & DAVIS in HERSEY, 1967; HEEZEN & HOLLISTER, 1971). Also, very large star-shaped lebensspuren have been found on the deep sea bottom which resemble similar forms found in Polish and Spanish flysch sediments. SEILACHER (1967b) compared the cross section of horizontal spreite structures found in Recent deep sea muds to *Zoophycos*, which is found in many flysch deposits.

As might have been expected, regional geological investigations have shown that as the depositional environment changes with time, trace fossil assemblages vary in vertical succession through the rock sequence. They reflect accurately the geological development, especially in geosynclinal

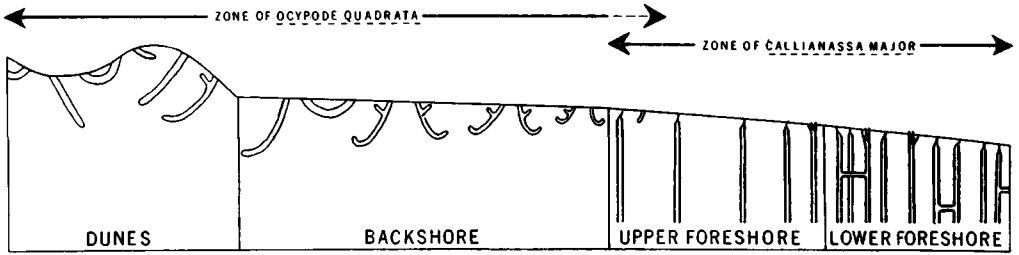


FIG. 19. Zonation of decapod burrows in Holocene barrier island beaches, Georgia. Diagram stresses form and configuration, rather than size and relative abundance, of ghost crab burrows (Frey & Mayou, 1971).

areas. Successive stages are also reflected in the lithology of the sediments and their primary structures. Such investigations make it possible to check paleogeographic conclusions drawn from observation of changes in the ichnocoenoses (see SEILACHER, 1963; SEILACHER & MEISCHNER, 1965; CHAMBERLAIN, 1971a,c).

Regional comparisons of trace fossil as-

semblages are also possible in the horizontal dimension. If lithologies change from one to another, the trace fossil assemblages associated with them are also different. It is therefore possible by combined ichnologic and sedimentologic studies to reconstruct the paleogeographic development of large areas.

In some instances, the occurrence of just

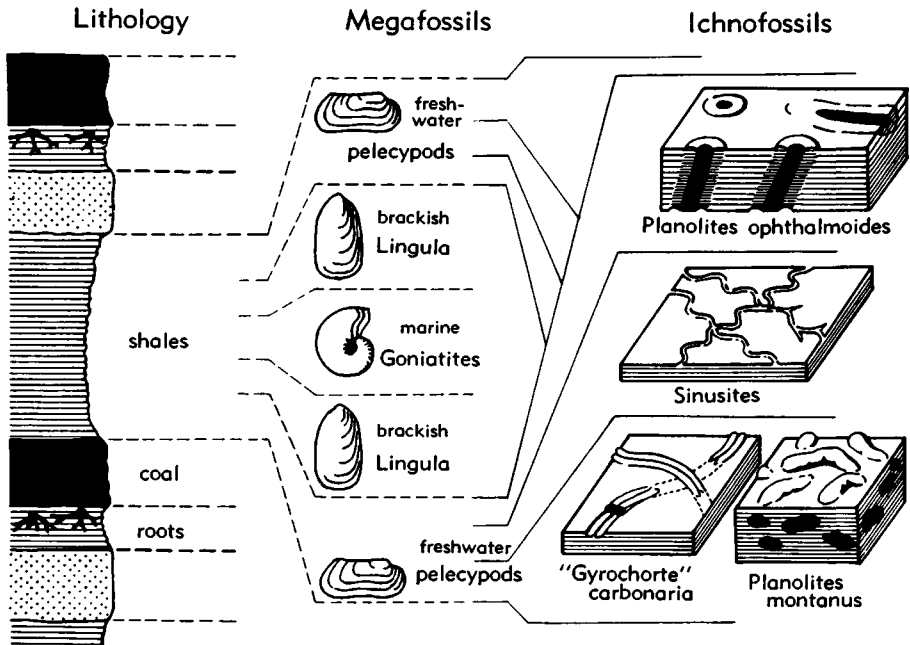


FIG. 20. Within lithologic cyclothems in paralic deposits of Carboniferous age in the Ruhr Basin, as shown above, more members can be recognized with the help of trace fossils. For this purpose it makes no difference that these trace fossils belong to rather insignificant types which in other formations may occur in dissimilar types of facies (Seilacher, 1964c).

a few trace fossils is sufficient to make possible deductions regarding the depositional environment of the sediment. RUDOLF RICHTER (1931) demonstrated that the occurrence of *Chondrites* in the Hunsrück Shale of Germany indicates that the original sediment did possess an infauna and was not an H<sub>2</sub>S-rich sapropel as had been believed previously. In a genuine euxinic environment, lebensspuren would be entirely absent.

Trace fossils can also help to determine certain characteristics of the depositional environments of sediments, especially in the marine realm. By studying trace fossils, lithologies, and body fossils in paralic Upper Carboniferous cyclothems of western Germany, SEILACHER (1963, 1964c, p. 307) (Fig. 20) has been able to distinguish

whether a sediment was deposited in fresh-water, brackish water, or under marine conditions. Some conclusions as to the strength and direction of currents can be drawn from the study of trace fossils. A few examples are: 1) deviation and obliteration of trilobite running trails, especially by lateral currents across the trails, 2) current orientation of resting impressions parallel to the direction of flow (rheotactic orientation, mostly against current direction), 3) existence of different kinds and varying abundances of lebensspuren in areas with strong, as contrasted with weak currents, and 4) orientation against the current (presumably tidal currents) of some dwelling structures in the Jurassic of England (FARROW, 1966).

## TRACE FOSSILS

The definition of the concept "trace fossil" in the Introduction indicates the kind of fossils discussed in this section. As the result of the very numerous trace fossil investigations undertaken since the first edition of this chapter (HÄNTZSCHEL, 1962), the number of ichnogenera has increased considerably. Unfortunately, many forms lacking definite characters have been given names when only simple morphological descriptions were needed. In some cases, descriptions as well as illustrations were insufficient. Some of the original "generic" diagnoses were changed by some authors, mostly expanded, so that forms that diverged considerably from the early definitions were listed under the old names. Also, many transitional forms between well-defined and well-known ichnogenera have been recognized. This was to be expected and it demonstrates the difficulties of identification and nomenclature of trace fossils. It is not easy to find a compromise between a narrow and a broad definition of trace fossil generic concept. Frequently also, au-

thors have changed their ideas about the definition of an ichnogenus, thus creating synonyms.

I have tried to list all ichnogenera published before the end of 1971. Since good, clear illustrations are very important in the description of trace fossils, the illustrations have been improved and their number has been increased as far as possible. In many recent ichnological publications, ichnocoenoses have been classified according to the well-known "ecological" system of SEILACHER discussed above. However, in this volume, for reasons given in the first edition, the arrangement of ichnogenera in alphabetical sequence of names has been preserved. Descriptions of especially widespread and important ichnogenera are given in greater detail, and following them, expanded statements concerning former and present interpretations. Complete references to old and new literature about ichnogenera are found in the reference list.

In a review of the *Treatise Part W* of