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Middle Devonian sea-anemone burrows, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., from the Holy Cross Mountains

ABSTRACT: The new ichnotaxa, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., are established for the casts of burrows attributable to the life activity of sea-anemones, and occurring within the finegrained clastic deposits of late Middle Devonian (presumably Upper Givetian) age in the Holy Cross Mountains, Central Poland. The sedimentary structures featuring the ichnotope and a comparative study of the life requirements of the present-day burrowing sea-anemones indicate a shallow sublittoral environment in which these coelenterates have gregariously lived. An ichnological analysis shows that the newly established ichnotaxa should be included into the *Bergaueria* group of the sea-anemone burrows. The taphonomical conditions under which the swarmy populated biotopes of the sea-anemones were suddenly buried had resulted from the deposition of sandy material from storm-agitated waters (*i.e.*, formation of tempestites). It is also suggested that other gregariously occurring sea-anemone burrows display a similar thanatocoenotic character.

NTRODUCTION

The Variscan sequence of the Holy Cross Mountains in Central Poland is widely known from its content of diverse Cambrian ichnofossils preserved in finegrained clastic deposits (*see* ORŁOWSKI, RADWAŃSKI & RONIEWICZ 1970; SEILACHER 1970; CRIMES 1970). The other members of this sequence, due to their development in shaly or carbonate facies, are rather poor from ichnological point of view. An exception has, however, been offered by the so-called Świętomarz Beds (SOBOLEV 1909), a finegrained clastic series of which is developed in the northern part of the Holy Cross Mts, and which is generally regarded as of late Midddle Devonian age (GÜRICH 1896, SOBOLEV 1909, CZARNOCKI 1950, PAJCHLOWA 1957, MIZERSKI 1981, KŁOSSOWSKI 1985). Within these Beds, in their stratotypic section exposed between the villages Świętomarz and Śniadka, east of Bodzentyn in the north-central part of the Holy Cross Mts (*see* Text-fig. 1*A*), a rich material of the formerly unknown trace fossils has recently been found. It consists primarily of the bulb-shaped casts of burrows, sculptured by more or less concentric wrinkles, and densely spaced on the undersides of sandstone layers. The peculiar features of these burrows allow to recognize them as representing the new taxa, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., and to ascribe them to the life activity of sea anemones.

REGIONAL SETTING OF THE DEPOSITS

The Middle Devonian deposits yielding the investigated trace fossils, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., are exposed in the famous Świętomarz — Śniadka section, continuing along a deeply incised ravine of the Psarka stream (*see* Text-fig. 1 and Pl. 1, Figs 1—2) which follows the Świętomarz fault and traverses the Bodzentyn syncline (*see* Text-fig. 1 *A-B*). The section between the villages Świętomarz and Śniadka runs through the Middle Devonian sequence which is composed of marly dolomites and limestones at its base, and of finegrained clastics (shales, siltstones, thin-bedded sandstones) in its higher part (*see* Text-fig. 1*C*).

The Middle Devonian deposits of the section have long been investigated both with regard to their faunal content (GÜRICH 1896; SOBOLEV 1909; BEDNAR-

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Fig. 1. Location of the deposits yielding the trace fossils *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. in the Holy Cross Mountains, Central Poland

A — General map of the central part of the Holy Cross Mountains, to show location of the Świętomarz — Śniadka section in the northern limb of the Łysogóry unit (= southern limb of the Bodzentyn syncline); adopted from the map by SAMSONOWICZ (1952)

C — Cambrian, S — Ordovician and Silurian, D_1 — Lower Devonian, D_{23} — Middle and Upper Devonian, C_1 — Lower Carboniferous, δ — Variscan dykes (diabases and lamprophyries), P_2 — Upper Permian (Zechstein), T — Triassic, J_{23} — Middle and Upper Jurassic, MM — Middle Miocene (Badenian).

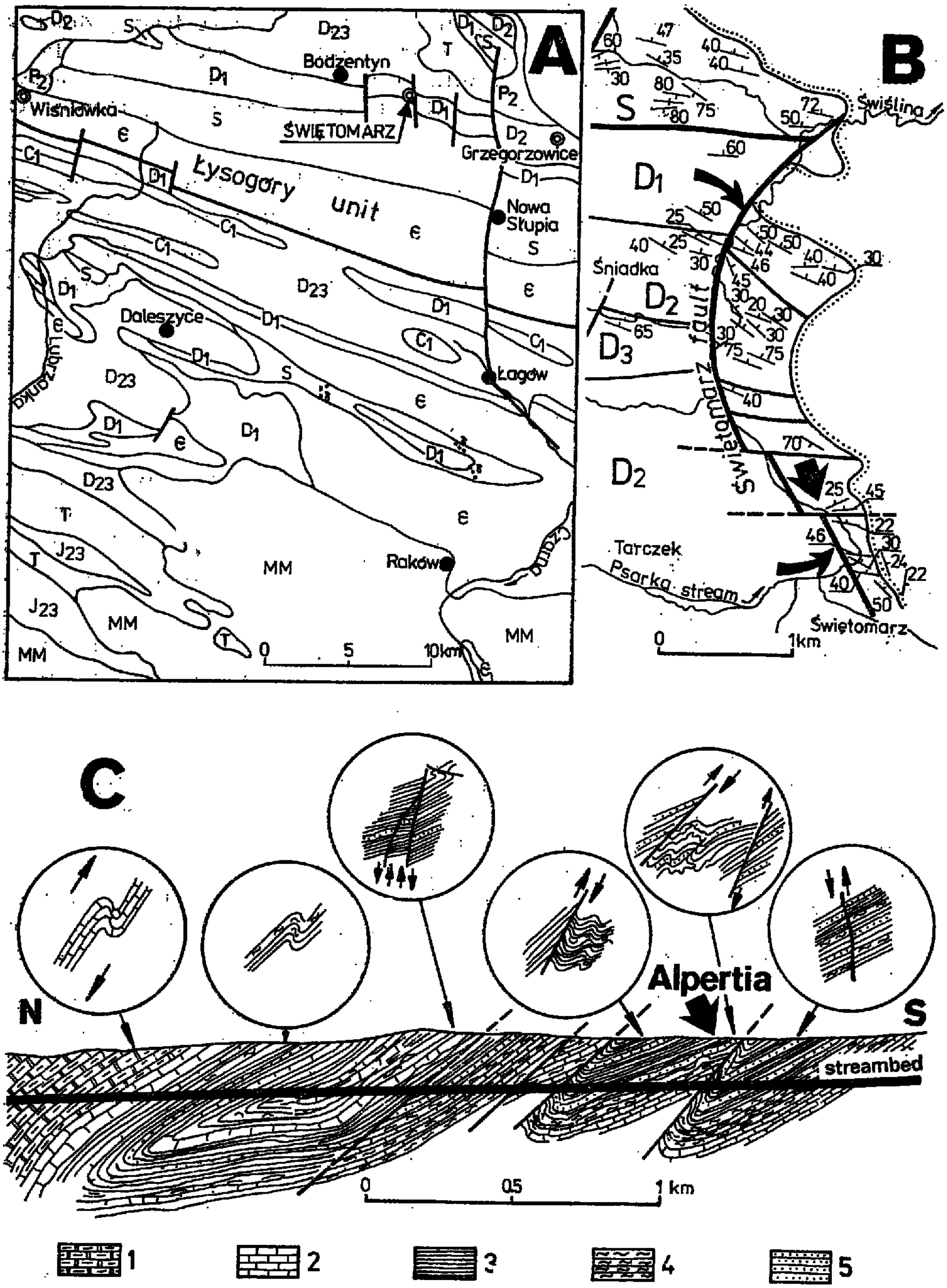
B — Tectonic sketch of the Świętomarz — Śniadka section through the Bodzentyn syncline, exposed along the Psarka stream: *curved arrows* denote the frame of the section presented in Text-fig. 1*C*, *heavy arrow* indicates the occurrence site of *Alpertia sanctacrucensis* ichnogen. et ichnosp. n.; the sketch taken from MIZERSKI (1981, Fig. 2; Devonian deposits are divided into: D_1 — Lower Devonian, D_2 — Middle Devonian, D_3 — Upper Devonian)

C — Świętomarz — Śniadka section exposed along the Psarka stream (framed as in Text-fig. 1*B*), to show location of the occurrence site of *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. (indicated by a heavy line is the streambed of Psarka; *compare* Pl. 1, Figs 1—2); the section taken from MIZERSKI (1981, Fig. 7)

LITHOLOGY: *1* marly dolomites, *2* limestones, *3* shales, *4* siltstones, *5* sandstones

CZYK 1955; BIERNAT 1966; KŁOSSOWSKI 1976, 1985) and tectonic structure (CZARNOCKI 1950; KŁOSSOWSKI 1976, 1985; MIZERSKI 1981).

The tectonic structure of the Bodzentyn syncline, regarded formerly as featured by secondary folds (GÜRICH 1896; SOBOLEV 1909, CZARNOCKI 1950, BEDNARCZYK 1955), has recently been recognized (KŁOSSOWSKI 1976, 1985; MIZER-



SKI 1981) to represent a single synclinal form, but transected by a few longitudinal faults, due to which the sedimentary sequence is repeated several times (*see* Text-fig. 1C). The Bodzentyn syncline itself is overturned southerly, but all the strata of its southern limb display normal attitude, and thus a northward dipping. The tectonic disturbances expressed by minor deformations, some of which represent small-sized overturnings, are confined either to local faults or to some competent layers (*see* MIZERSKI 1981; *and* Text-fig. 1 C).

A part of the sequence which yields the investigated trace fossils, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., is situated near to a local fault (*see* Pl. 1, Figs 1-2), but it has obviously a normal attitude which is evidenced by the appearance of such sedimentary structures as current ripplemarks on the topsides of particular layers (*see* Pl. 2, Figs 1-2).

The stratigraphic age of the discussed part of the Middle Devonian sequence is not precisely recognized yet. Generally, it is attributed to the Upper Givetian (CZARNOCKI 1950, BEDNARCZYK 1955, PAJCHLOWA 1957) or to a part of the Givetian, supposedly not the youngest (KŁOSSOWSKI 1976, 1985).

THE ICHNOTOPE

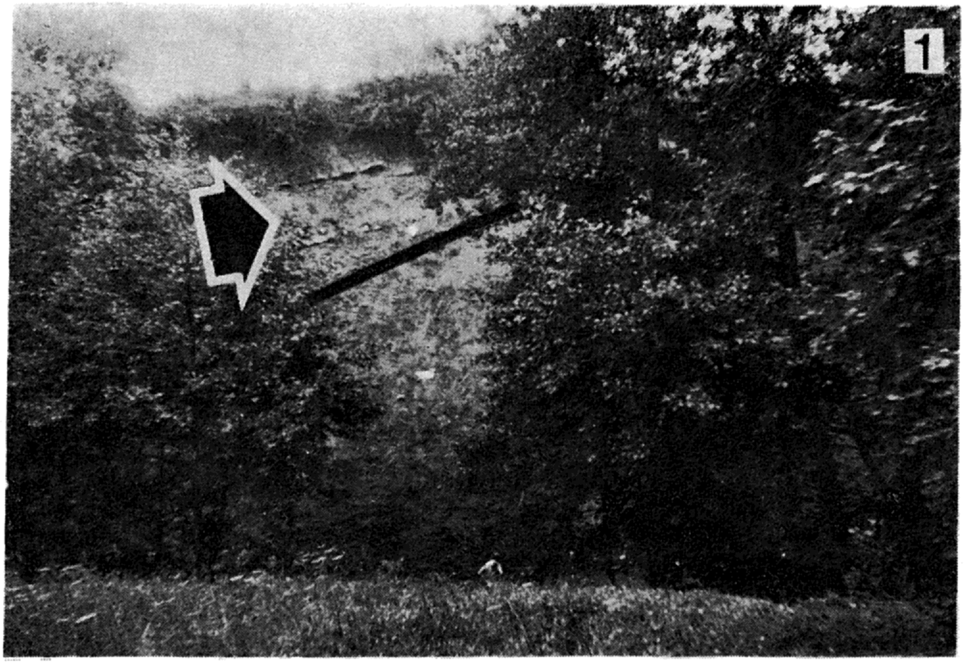
A set of the Middle Devonian deposits (Świętomarz Beds) which yield the investigated trace fossils, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., consists of the dominating olive-gray, locally reddish or even cherry-violet shales which are alternated with thin, and sometimes lenticular sandstone layers (*see* Pl. 1, Figs 1—2). The latter vary in thickness from a few millimeters to over a dozen centimeters. The thicker layers are usually featured at their topsides by diverse ripplemarks, the most common of which are either transformed (*see* Pl. 2, Fig. 1) or undisturbed current ripples (*see* Pl. 2, Fig. 2).

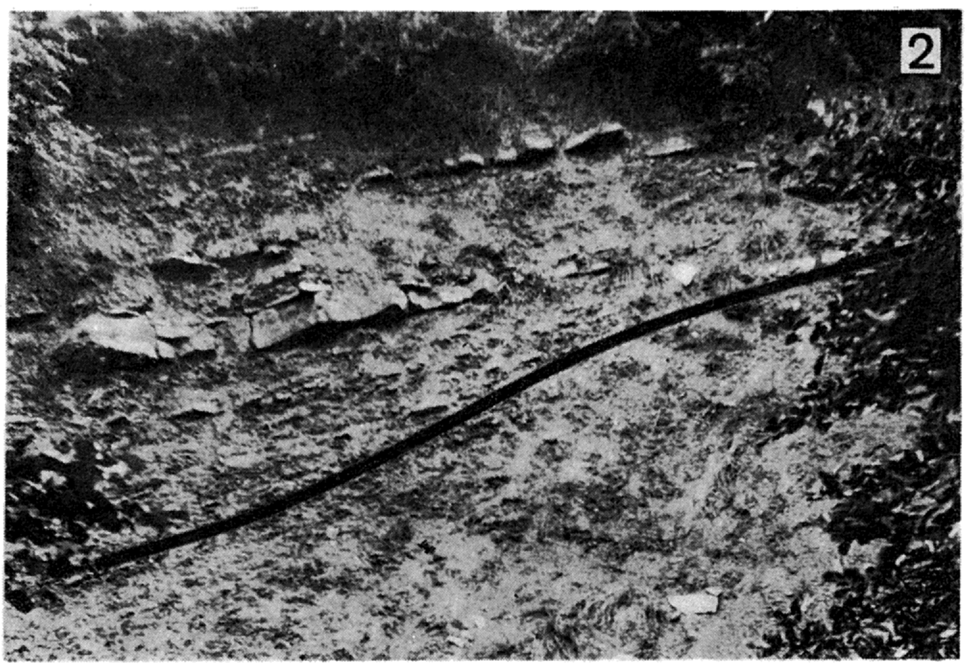
The clastic material of the sandstone layers is of a mature type, being composed of quartz grains and small admixture of clay minerals (those responsible for reddish coloration are possibly of a laterite origin; *cf.* CZARNOCKI 1950) and muscovite flakes, and locally of carbonized plant detritus.

The layers topped by ripplemarks display the current-ripple bedding as their internal structure. The underside of these layers are, as a rule, smooth, but sometimes sculptured by fine scratches that presumably reflect the current lineation.

The trace fossils *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. occur patchily, but usually gregariously on the undersides of some sandstone layers (*see* Pl. 3, Fig. 2 and Pls 4—5) of peculiar internal structure. The better preserved specimens, with well pronounced morphological details, are usually these which occur at the base of thinner layers (*see* Pls 4—5). The thicker sandstone layers usually bear the discovered trace fossils poorly preserved (*see* Pl. 3, Fig. 3).

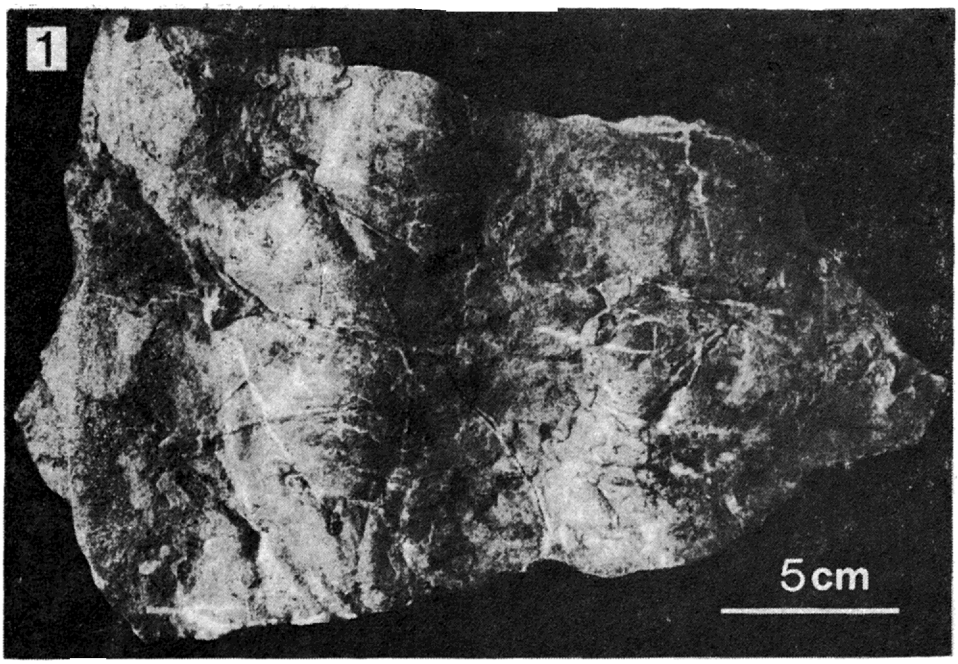
All the layers furnished with the investigated trace foossils, *Alpertia sanctacrucensis* ichngen. et ichnosp. n., are homogenous (structureless),

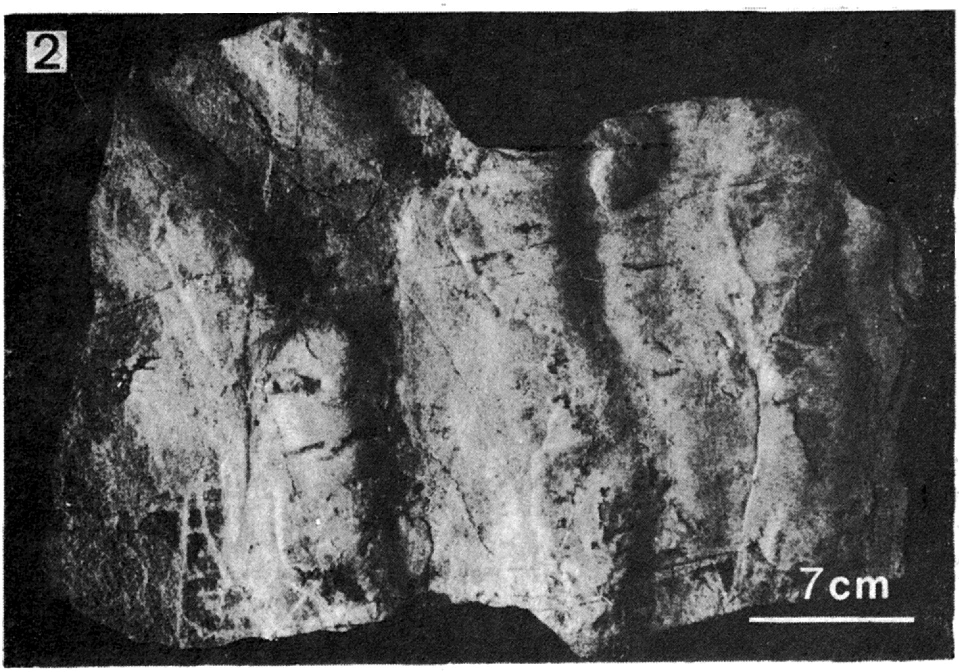




1 — General view of the Middle Devonian sequence exposed along the eastern bank of the Psarka stream: arrowed is the set of layers, above a local fault, presented in Fig. 2

2 — Close-up view, to show the set of layers yielding the trace fossils *Alpertia sanctacrucensis* ichnogen. et ichnosp. n.





1 — Transformed current ripples at the topside of a sandstone layer

2 — Undisturbed current ripples at the topside of another sandstone layer devoid of any internal structures, with their topsides more or less plain, covered by muscovite flakes. Some of these topsides display effects of scouring, in places evidenced by the presence of small-sized claystone intraclasts (*e. g.* in the layer, the underside of which is presented in Pl. 5).

THE ASSOCIATED TRACE FOSSILS

The ichnotope containing the investigated trace fosssils, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., was sparsely inhabited by other trace-makers, the life activity of which resulted in the formation of such ichnotaxa as *Cruziana* sp., *Diplocraterion* sp., and *Planolites* sp.

The most important of these trace fossils are those determined as *Cruziana* sp. All these trackways are rather small-sized and short (the largest is 3 cm long and 1.7 cm wide), featured by two series of more or less continuous ridges of variable thickness and oriented almost transversally to the median groove; the both series of ridges approach the margins of the trackway bluntly, and thus no marginal ridge is developed. Taking into account the commonly accepted trilobite provenance of these trace fossils (*see* CRIMES 1970; SEILACHER 1970; ORŁOWSKI, RADWAŃSKI & RONIEWICZ 1970), the collected specimens (*see* Pl. 3, Figs 1—2) may be interpreted in terms of the life activity of Middle Devonian trilobites.

The largest of the specimens (Pl. 3, Fig. 1) represents a short trackway which is terminated by two series of acutely angled scratches (down in the photo *in* Pl. 3, Fig. 1) which certainly correspond to the moment when the trilobite suddenly took off the bottom and started to swim in the water (direction indicated by an arrow *in* Pl. 3, Fig. 1; *cf.* CRIMES 1970, Fig. 6).

The second of the illustrated specimens (Pl. 3, Fig. 2) presents two smaller trackways, superposing each other, and the younger of which (marked *b* in Pl. 3, Fig. 2) is comparable to the preceding one (Pl. 3, Fig. 1). The older trackway (marked *a* in Pl. 3, Fig. 2) is shallower and represents a fragment of the longer, but superficial furrow left by another trilobite.

The investigated trilobite trackways are the best comparable with some forms referred to as *Cruziana* sp., but not determined ichnospecifically, and reported from younger Paleozoic deposits of the United States. Such very similar forms were noted, for instance, from the Lower Famennian of Utah (GUTSCHICK & RODRIGUEZ 1977, p. 203 and Pl. 1g) and from the Upper Pennsylvanian of Kansas (HAKES 1976, pp. 24—25 and Pl. 5, Fig. 1).

The other of the associatedd trace fossils are of much lesser value. Single forms of *Diplocraterion* sp., preserved as lower parts of the *U*-shaped loop, are morphologically undistinguishable from those occurring in the Upper Cambrian of the Holy Cross Mts (*see* RADWAŃSKI &

RONIEWICZ 1963, Pl. 9, Fig. 1 and Pl. 10, Fig. 1). More common forms of *Planolites* sp. fall well within the variability range of this widely distributed ichnogenus (*see* PEMBERTON & FREY 1982); they appear either singly, when associated with gregarious *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. (*see* Pl. 5) or densely packed when the sea-anemone burrows are less frequent (*see* Pl. 4). All these forms of *Planolites* are morphologically close to *P. beverleyensis* (BILLINGS), especially to some of those illustratedd by PEMBERTON & FREY (1982, Pl. 3, Figs 1 and 7—8).

DESCRIPTION OF THE SEA-ANEMONE BURROWS

The investigated trace fossils display a set of features (general shape, dimensions, gregarious occurrence) which allow to attribute them to the burrowing activity of sea anemones. The sculpture of the burrows differs them, however, from any other trace fossils attributable either to sea anemones or to other groups of coelenterates. Consequently, the investigated trace fossils are regarded as new in the ichnological taxonomy, and thus the new taxa are introduced both at the ichnogeneric and ichnospecific level.

Ichnogenus *Alpertia*, ichnogen. n.

DIAGNOSIS: Bulb-shaped casts of burows, of a diameter ranging from 1.0 up to 2.0-2.5 cm, sculptured by discontinous wrinkles arranged more or less concentrically; typically, they tend to occur gregariously.

DERIVATION OF THE NAME: In honor of Dr. Stephen P. ALPERT, University of California, who pronouncedly contributed to the knowledge of Paleozoic sea-anemone burrows.

Ichnospecies *Alpertia sanctacrucensis* ichnosp. n.
(Pl. 3, Fig. 3 and Plates 4—5)

HOLOTYPE: The burrow arrowed in Pl. 5 (one of the largest and best preserved of the collected specimens).

PARATYPES: The gregariously occurring specimens presented in Pls 4—5.

TYPE LOCALITY: Świętomarz — Śniadka section (exposure indicated by an arrow in Text-fig. 1B—C, near the village of Świętomarz); north-central part of the Holy Cross Mountains, Central Poland.

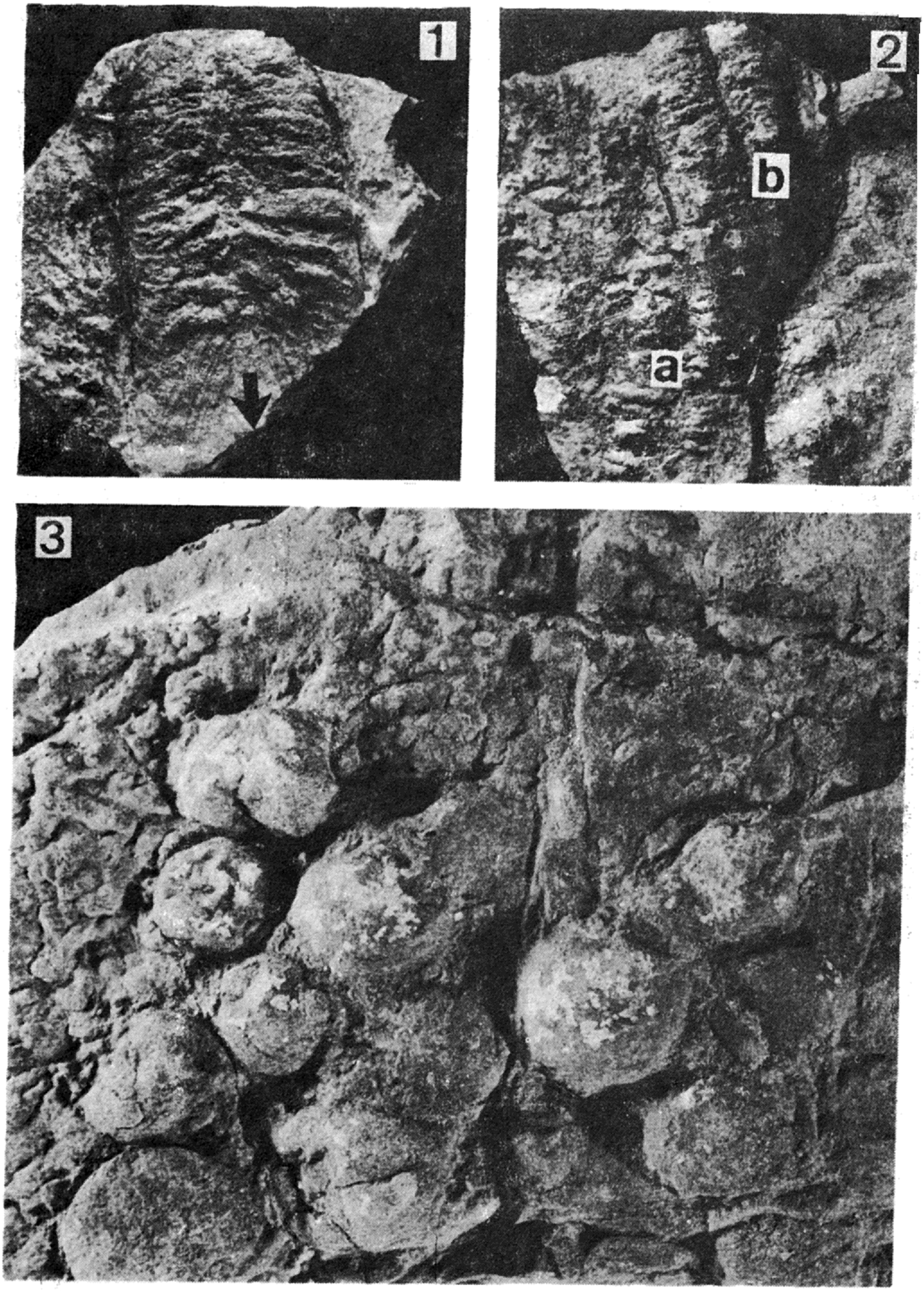
TYPE HORIZON: Middle Devonian (Givetian).

DERIVATION OF THE NAME: Latin *sanctacrucensis*, after the Holy Cross region.

DIAGNOSIS: The same as for the genus.

MATERIAL: Gregarious casts of burrows on the undersides of sandstone layers. In some groups the burrows are distributed relatively scarcely (*see* Pl. 3, Fig. 3). In the most striking occurrences the burrows are closely spaced and they tightly cover the layer undersides (*see* Pls 4—5); the frequency then averages almost 40 in a dcm² for smaller forms (Pl. 4), and attains about 20 in a dcm² for larger forms (Pl. 5). The given numbers correspond, respectively, to the value of 4000 or 2000 specimens per one square meter.

DIMENSIONS: The smaller specimens (*see* Pl. 4) range between 11 and 15 mm, and the larger ones (*see* Pl. 5) average 15—25 mm in their diameter. The diameter of the specimen designated as the holotype (*arrowed* in Pl. 5) is 26.5 mm.



1-2 — Fragments of trackways *Cruziana* sp., attributable to the life activity of trilobites (explanation in the text); both magn. ×2

3 — Poorly preserved trace fossils, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., devoid of morphological details; associated are numerous forms of *Planolites* sp.; nat. size

Gregarious occurrence of smaller forms of *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., slightly compacted diagenetically; nat. size

DESCRIPTION: All the investigated specimens occur either in smaller groups (Pl. 3, Fig. 3) or gregariously, in swarmy aggregates (Pls 4-5), always on the undersides of sandstone layers. All of them are therefore casts of the burrows produced in a deposit not preserved in the investigated slabs of sandstones, and which is recognizable as a clayey shale when studying the field section (*see* Pl. 1, Figs 1-2).

The specimes are generally of a bulb-like shape, and are almost totally covered by short wrinkles, arranged more or less concentrically; the central part of the specimens is usually almost smooth, featured by broader, less regular and less frequent wrinkles which sometimes disappear.

REMARKS: The specimens devoid of wrinkles and thus acquiring an almost plain surface, become similar to the "bald" forms of the ichnogenus *Bergaueria* PRANTL, 1945. Such badly preserved specimens, rare in gregariously spaced aggregates (*see* Pls 4-5), are typical of smaller groups (*see* Pl. 3, Fig. 3) which are confined to thicker sandstone layers.

ECOLOGICAL ACCOUNT: All the investigated specimens, due to their general bulb-like shape are attributed to the life activity of sea-anemones, precisely to the stubby forms comparable to the present-day genus *Cereus* burrowing in sandy substrates (*see* LESSERTISSEUR 1955). The mode of burowing ot the inferred sea anemones is thought to have been similar to that presented by CHAMBERLAIN (1971, Fig. 4). The more or less concentric wrinkles on the surface of the investigated specimens are interpreted as casts of more or less concentric musculature of the sea anemones, the traces of which (grooves) have been marked on the burrow wall when the animal was contracting and expanding its body (*see* Text-fig. 2). The successive series of grooves originated supposedly during the final stage of the burrowing and the extreme contraction of the body to stabilize well the animal in the sediment. This clayey sediment was consolidated to an extent sufficient for protection of the grooves against collapsing and diffusion.

The inferred sea anemones (*see* Text-fig. 2) were supposedly producing the burrows more or less elongated (*A-B* in Text-fig. 2), and shaping them by an expansion of the body column (*scapus*). The lowest, more spherical part of the body (*physa*) was broadly attached (?sucked) to the burrow bottom, to anchorage the animal securely in the sediment; this part of the body did not groove the burrow, the bottom of which thus remained smooth. Under normal hydrodynamic conditions, the animals were certainly stretching up their tentacles well above the sediment/water interface (*A* in Text-fig. 2).

TAPHONOMICAL ACCOUNT: The preservation of all studied burrows in a very similar shape, corresponding to the extreme contraction of the sea-anemone bodies, suggests a coeval burial of all animals living in densely populated biotopes. The investigated specimens are thus interpreted as the lower parts of the burrows, the upper parts of which have completely been removed prior to the burial (*C* in Text-fig. 2). The lower parts of the burrows, with the buried alive animals (*D* in Text-fig. 2), were subsequently filled with the liquified sandy sediment after the decay of the sea-anemone bodies (*E* in Text-fig. 2). Diagenetic processes in the sandy sediment (*F* in Text-fig. 2) are responsible for a more (*see* Pl. 4) or less advanced compaction (*see* Pl. 5) of the freshly originated casts of the burrows, due to which the wrinkles became more pronounced, and locally for the formation of synaeresis cracks (marked *sc* in Pl. 5).

The mode of preservation of morphological features in *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. is obviously dependent on the thickness of sandstone layers to which undersides they are associated. The best preserved specimens (Pls 4-5) are confined to relatively thinner sandstone layers, whereas poorly preserved

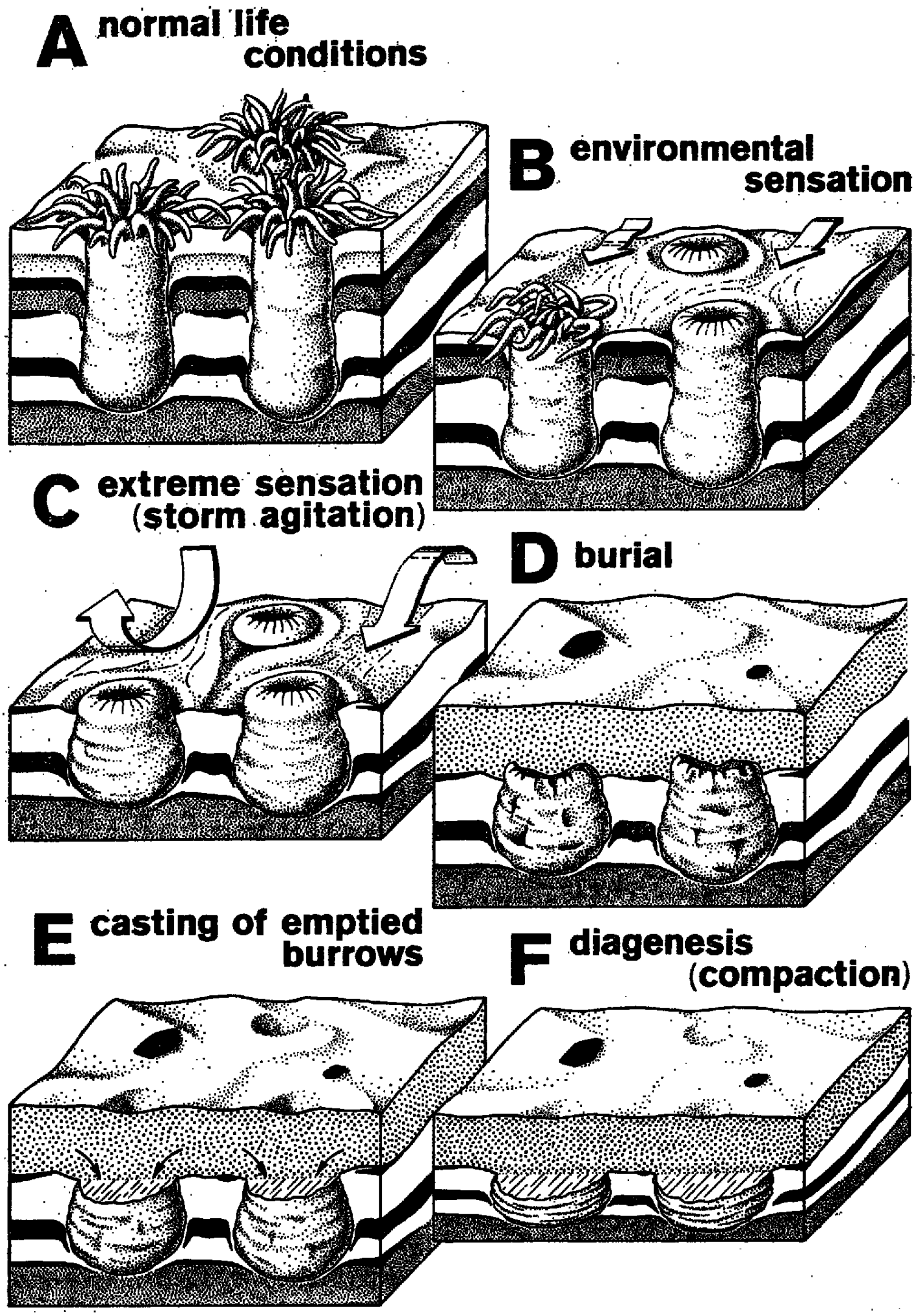
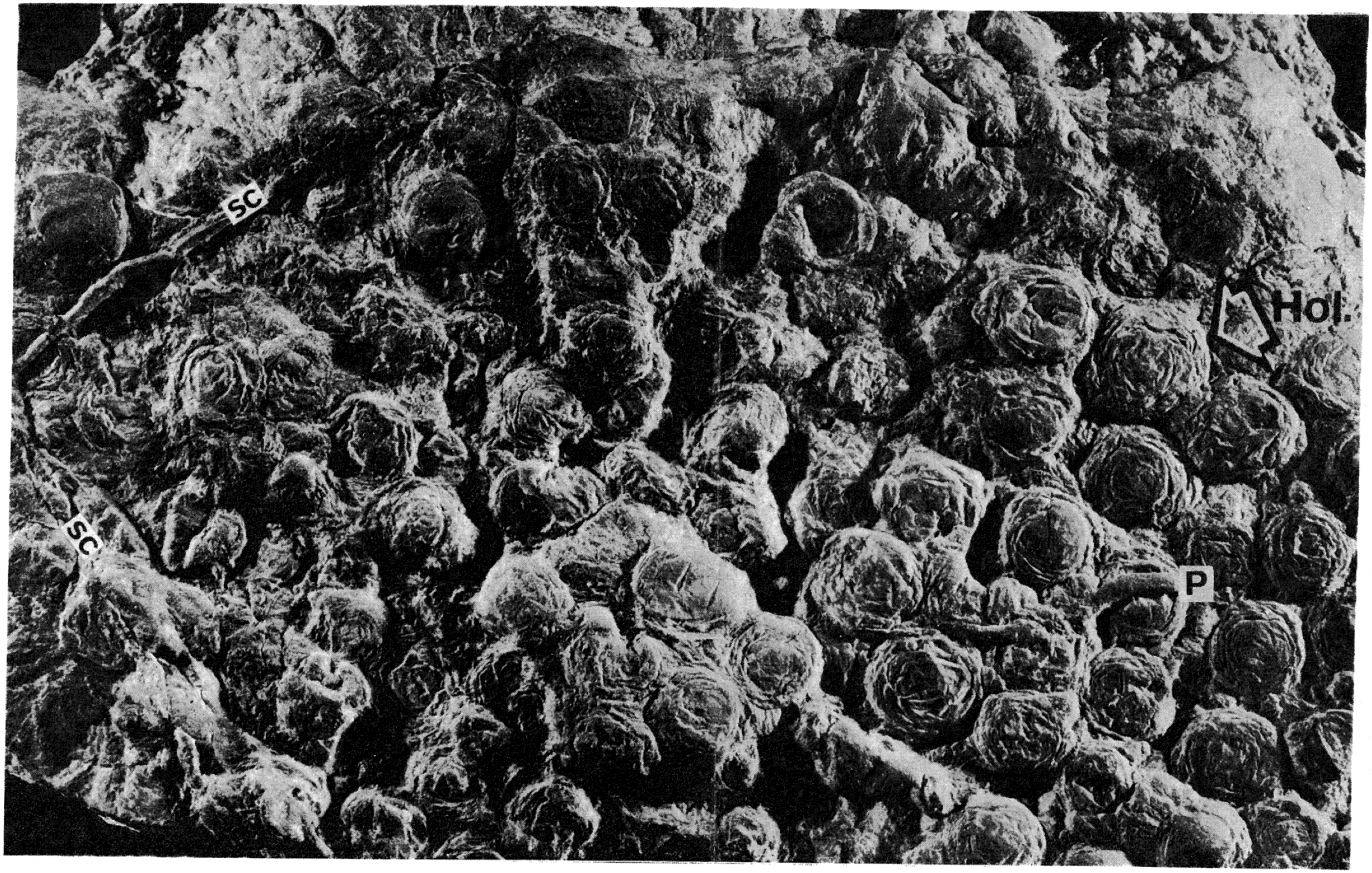


Fig. 2. Environmental and taphonomical history of the burrowing sea-anemones from the Middle Devonian (Givetian) Świętomarz Beds in the Holy Cross Mountains, and resulting in the formation of the trace fossils *Alpertia sanctacrucensis* ichnogen. et ichnosp. n.; detailed explanation in the text

NOTE: The clayey bottom is schematically marked by alternating black and white stripes, to indicate the corresponding portions of the sediment

***Alpertia sanctacrucensis* ichnogen. et ichnosp. n.**



Gregarious occurrence of normal-sized, well preserved forms (arrowed is the holotype), with a single form of *Planolites* sp. (marked as *P*); indicated are also synaeresis cracks (marked as *sc*); nat. size ones (Pl. 3, Fig. 3) are those confined to relatively thicker layers. This relation may be interpreted in terms of the differentiated load of the sediment overlying the sea-anemone burrows. The greater load is thus suggested to have been responsible for obliteration of morphological details of the burrows produced in a weakly consolidated clay deposit on the sea bottom. Such heavily overloaded burrows, if produced in weakly consolidated sediments then acquire the features close to those typical of the otherwise separate ichnogenus, *Bergaueria*.

Regardless the above differences, all the groupped (Pl. 3, Fig. 3) or gregarious occurrences (Pls 4-5) of *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. in the exposed section (*cf.* Pl. 1, Figs 1-2) concern the sandstone layers which display the homogenous nature (structureless), and thus any features above the burrows are not observable when these layers are sectioned (*F* in Text-fig. 2).

COMPARISON WITH OTHER SEA-ANEMONE BURROWS

The burrows attributable to various sea anemones are considerably often recorded from diverse ancient deposits. Some of them bear good analogies to the modern forms, the others rather fall into a general category of the biogenic structures. The latter group contains primarily the traces of the escape from the sediments, which are usually recognizable when the sequence of deposits is sectioned.

The escape traces produced by sea anemones reared in aquarium were first studied by SHINN (1968), who showed how these animals keep pace with an "artificial" sedimentation: a specimen of *Phyllactis conguilegia* (DUCHASSAING & MICHELOTTI) withdrew overnight through a portion of sediment leaving cone-in-cone structures in laminated sand (*see* SHINN 1968, Pl. 112, Figs 1—2). To this species, commonly living in agitated waters of the Bahama Banks, SHINN (1968) compared the escape traces found in the Pleistocene sediments of that region. The forms of similar internal structure, and thus produced by sea anemones of the same life strategy have also been reported to occur frequently in some finegrained, laminated sands of the Vejle Fjord Formation (Hagenør — Børup sequence) of Miocene age in Denmark (RADWAŃSKI, FRIIS & LARSEN 1975, pp. 233—235 and Fig. 7). The others were subsequently noted in the Pleistocene of North Carolina, United States (CURRAN & FREY 1977).

Other biogenic structures attributable to sea anemones, and recognizable in sectioned deposits, were reported from the Middle Triassic (Muschelkalk) of Poland (TRAMMER 1974), and the Lower Jurassic of England (HALLAM 1960); the latter acquired a formal ichnological nomenclature, as *Kulindrichnus langi* HALLAM (*see* HALLAM 1960; HÄNTZSCHEL 1962, 1975). Comparable to *Kulindrichnuus* are also the burrows described as *Conichnus conicus* MÄNNIL and *Amphorichnus papillatus* MÄNNIL, and commonly occurring in the Ordovician limestones of Estonia, Soviet Union (MÄNNIL 1966; *see also* HÄNTZSCHEL 1975). In all these burrows no traces of upward migration of the animal were reported.

The oldest forms which display traces of upward migration are those of *Conostichnus broaheadi* LESQUEREUX, the trace fossils commonly reported from the Mississippian — Pennsylvanian (Carboniferous) deposits of the United States (*see* PFEFFERKORN 1971; CHAMBERLAIN 1971; ALPERT 1973; HAKES 1976; GUTSCHICK & RODRIGUEZ 1977), and interpreted by CHAMBERLAIN (1971) as produced by burrowing sea anemones, probably the halcampoids. Because in all older Paleozoic burrows which are attributed to the life activity of sea anemones (*Bergaueria, Conichnus, Amphorichnus)* there are no traces of escape, it is to remind an impressive suggestion given by ALPERT (1973, p. 921) that "the ability for burrowing sea anemones to migrate upward in the sediment, to keep pace with relatively rapid sedimentation, evolved sometime between the Ordovician and Pennsylvanian periods". This suggestion is thought to be adequate, but when taking into account the herein introduced *Alpertia,* the spantime needed for such evolution must be reduced to "between the Middle Devonian and Pennsylvanian". On the other hand, some sea anemones have evidently not acquired this ability during their phylogeny, as appears from the sporadical occurrences of *Bergaueria* in the Upper Carboniferous of Kansas (HAKES 1976) and Upper Jurassic of England (FÜRSICH 1974, 1975), and of *Conichnus* (synonymyzed with *Amphorichnus* by FREY & HOWARD 1981) in the Upper Cretaceous of the Western Interior, United States (FREY & HOWARD 1981).

The old Paleozoic burrows attributable to the sea anemones, devoid of any internal structures, and preserved as hyporeliefs on the layer undersides, belong to the well-defined ichnogenus *Bergaueria* PRANTL, and are commonly noted from the Cambrian through Ordovician of Europe and North America (*see* PRANTL 1945; HOWELL & HUTCHINSON 1958; HÄNTZSCHEL 1958, 1962, 1975; RADWAŃSKI & RONIEWICZ 1963; ARAI & McGUGAN 1968, 1969; ORŁOWSKI, RADWAŃSKI & RONIEWICZ 1970, p. 352; ALPERT 1973, 1975, 1976; CRIMES & *al.* 1977, with other references). The Lower Cambrian unique ichnogenus *Dolopichnus* ALPERT & MOORE, preserved as hyporeliefs continuing into a structure passing throughout the overlying deposits is interpreted as burrows of sea anemones which preyed upon trilobites (ALPERT & MOORE 1975, ALPERT 1976, BIRKENMAJER 1977).

In regard with the above review, it is noteworthy that the gregarious occurrence of the sea-anemone burrows, so typical of the investigated forms *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. has also been stated for some *Bergaueria,* as reported by HOWELL & HUTCHINSON (1958, Pls 1—2; remarked as "a reef-like mass"), RADWAŃSKI & RONIEWICZ (1963, Pl. 9, Fig. 3), and ARAI & McGUGAN (1968, Pl. 36, Fig.

12; remarked as "colony"), as well as for some *Conichnus* as reported by MÄNNIL (1966; frequency of 300—400 specimens per sq. m).

All these mass occurrences concern the Lower or Middle Paleozoic forms when the ability of the sea anemones to escape from the deposited sediment has not yet been realized. It certainly means that in the cases of violent sedimentation and sudden burial all the gregariously living specimens had to die. The sudden death of the whole community inhabiting the ichnotope produces thus a thanatocoenose (*cf.* RADWAŃSKI & RONIEWICZ 1970). Consequently, all these densely spaced burrows are thought to have corresponded to the thanatocoenoses of the sea anemones living gregariously in swarms.

ENVIRONMENTAL ACCOUNT

The environmental conditions under which the Middle Devonian (Givetian) strata containing the trace foossils *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., have been deposited are considered both upon the physical and biotic criteria.

The physical conditions are recognizable from the record of sedimentary structures and from the inferred mode of formation and preservation of biogenic structures. The presence of the current ripplemarks on the topside of some layers, and of the current ripple-bedding in the interiors of these layers indicates the activity of currents induced supposedly by waving. The latter is inferred primarily from the recognition of the homogenous nature of the other sandstone layers, especially those provided with casts of the sea-anemone burrows *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. on their undersides. All these structureless layers are interpreted as tempestites, the material of which was deposited from storm-agitated waters which had earlier stirred up the more or less local material. The scouring of the finegrained sediments and deposition of claystone intraclasts upon the tempestite layers indicate the final stages of storm action and/or of storm-induced currents. The sandy material was thus moved either by storm events or by bottom currents, and transported onto the finer-grained areas of the seafloor. The scouring of the latter evidences that all these agents were acting not deeper than the wave base.

An association of the sea-anemone burrows with the homogenous (structureless) sandstone layers, to which they all are confined, simply means that the storms and storm-originated deposition were responsible for a sudden burial and thus for coeval death of all the sea anemones living in a biotope, *i.e.*, for the formation of a thanatocoenose. The repetitions of storm events have obviously led to the formation of successive thanatocoenoses.

The biotic conditions are recognizable by the presence of gregarious sea-anemones themselves, the Recent occurrences of which are limited to extreme shallow marine biotopes, ranging from shallow sublittoral to intertidal (*see* LESSERTISSEUR 1955; SCHÄFER 1956, 1962; SHINN 1968; FREY 1970; HERTWECK 1972; RADWAŃSKI, FRIIS & LARSEN 1975; CURRAN & FREY 1977). To shallow marine environments, enplaced above the wave base, attributed are also the biotopes of trilobites which furrowed the bottom when foraging for food (*see* RADWAŃSKI & RONIEWICZ 1963; ORŁOWSKI, RADWAŃSKI & RONIEWICZ 1970, 1971; CRIMES 1970; SEILACHER 1970).

The qualitative content of the investigated ichnocoenose from the Middle Devonian (Givetian) strata, represented by casts of the sea-anemone burrows, trilobite-attributable *Cruziana* sp., and polychaete-attributable *Diplocraterion* sp., is well comparable to that of the classical Upper Cambrian locality Wielka Wiśniówka in the same region (for location *see* Text-fig. 1*A*). At Wielka Wiśniówka, an extremely rich ichnocoenose contains primarily diverse resting and furrowing traces of trilobites, associated with other trilobite traces (*see* RADWAŃSKI & RONIEWICZ 1960, 1963, 1972; ORŁOWSKI, RADWAŃSKI & RONIEWICZ 1970, 1971), sea-anemone burrows *Bergaueria perata* PRANTL and polychaete-attributable *Diplocraterion* sp. (*see* RADWAŃSKI & RONIEWICZ 1963), as well as unique trace fossils *Aglaspidichnus sanctacrucensis* RADWAŃSKI & RONIEWICZ attributable to the aglaspid xiphosurans (*see* RADWAŃSKI & RONIEWICZ 1967). This ichnocoenose is scattered through the deposits featured commonly by divers ripplemarks and other sedimentary structures which all are indicative of a shallow sublittoral environment (*see* RADWAŃSKI & RONIEWICZ 1960, 1963).

Consequently, when both physical and biotic criteria are taken into account, the deposition of the Middle Devonian (Givetian) strata yielding *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. is ascribed to a shallow sublittoral environment, and the same is also suggested for both the under- and overlying shaly parts of the Świętomarz Beds (*see* Text-fig. 1*C* and Pl. 1, Figs 1—2).

PALEOGEOGRAPHIC IMPLICATION

The recognition of shallow sublittoral conditions for the investigated member of the Świętomarz Beds, yielding the newly established taxa of trace fossils, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n., agrees well with a general environmental pattern of the late Middle and early Upper Devonian in the Holy Cross area. This recognition conicides with some older interpretations (CZARNOCKI 1950, PAJCHLOWA 1957), according to which the sedimentary area of the whole Świętomarz Beds was regarded generally as shallow marine. Similar environmental conditions are also thought to have occurred herein throughout a longer spantime during deposition of the Middle/Upper Devonian succession.

In the Świętomarz — Śniadka section the overlying member, the Śniadka Beds (*"Śniadka Formation"* of KŁOSSOWSKI, 1985), is developed as shales or marly shales intercalated with marly limestones containing abundant shallow marine benthic fauna (coelenterates, brachiopods, trilobites, gastropods and bivalves, crinoids) indicative of good photic and trophic conditions. Within the neighboring, classical section exposed at Grzegorzowice (for location *see* Text-fig. 1*A*), the member overlying the Świętomarz Beds is that of the Pokrzywianka Limestones (CZARNOCKI 1950, PAJCHLOWA 1957) which should be consequently regarded as a time-equivalent of the Śniadka Beds (*see* a blank item *in*: KŁOSSOWSKI 1985, Fig. 1). The Pokrzywianka Limestones make up lenticular ("reefoidal") bodies within the topmost part of the Świętomarz Beds in the eastern part of the Bodzentyn syncline (CZARNOCKI 1950; *cf. also* Text-fig. 1*A*).

The regional shoaling of the Middle Devonian sea and an increase in supplies of terrestrial clastic and laterite materials during the deposition of the Świętomarz Beds were regarded by CZARNOCKI (1950) as a result of an epeiric uplift confined to the northern part of the Holy Cross basin ("Pokrzywianka phase" of the Variscan movements *in* CZARNOCKI, 1950). The "reefoidal" nature of the Pokrzywianka Limestones, developed somewhen at the Middle/Upper Devonian boundary (*see* CZARNOCKI 1950, PAJCHLOWA 1957) may counterpart the foundation of the biohermal limestones (the so-called Kadzielnia Limestones) of early Frasnian age in the southern part of the Holy Cross basin (*see* SZULCZEWSKI 1971; SZULCZEWSKI & RACKI 1981).

The clastic material during deposition of the investigated Świętomarz Beds was supplied from the north, as correcty indicated by KŁOSSOWSKI (1985), and confined to the northern part of the Holy Cross basin. The sedimentation of coeval stromatoporoid-coral limestones in the more distant offshore areas of the southern Holy Cross region (the so-called Sitkówka Beds underlying the Kadzielnia Limestones; *see* SZULCZEWSKI & RACKI 1981) was only locally influenced by the delivery of fine materials from the adjacent continent (supposed laterite wastes giving reddish coloration to some limestone units; *see* CZARNOCKI 1950).

The Middle/Upper Devonian carbonate platform of the Holy Cross basin was thus distant to the shore situated northwardly, and separated from it by the shallow sublittoral areas of clastic sedimentation of the Świętomarz Beds. This statement contradicts some older, but commonly referenced opinions, or solely a belief, that the sedimentary area of the Świętomarz Beds was deeper ("geosynclinal") than the carbonate platform of the southern Holy Cross region.

FINAL REMARKS

The gregarious occurrences of the burrows attributable to the life activity of sea anemones represent rather unique fossil records of a few juxtaposing events, controlled both by biotic and physical conditions. The first is an establishment of biotopes swarmy populated by sea anemones; the second is their rapid burial which caused sudden death of all members of these biotopes; the third is a contrast in lithology between the bottom sediment in which the sea anemones have burrowed, and the sediment violently settled upon the biotopes. All these events could get into action only in an area the environmental conditions of which had favored both the life requirements of the sea anemones, and the hydrodynamic agents (waving, currents) responsible for sudden supplies of lithologically contrasted sediments. Such biotic and physical conditions may obviously be realized only in extreme shallow marine environments, as just exemplified by the Middle Devonian Świętomarz Beds in the Holy Cross Mountains, and as to be suggested for other gregarious occurrences of the sea-anemone burrows reported from older Paleozoic deposits allover the world (HOWELL & HUTCHINSON 1958, MÄNNIL 1966, ARAI & McGUGAN 1968).

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HIEROGLIFY ORGANICZNE *Alpertia sanctacrucensis* **ichnogen. et ichnosp. n., ORAZ ŚRODOWISKO ICH POWSTAWANIA W OBRĘBIE WARSTW ŚWIĘTOMARSKICH W GÓRACH ŚWIĘTOKRZYSKICH**

(Streszczenie)

Przedmiotem pracy jest opis i analiza środowiskowa śladów organicznych występujących masowo w niewielkim odcinku warstw świętomarskich (żywet, przypuszczalnie górny) odsłaniających się w klasycznym profilu Świętomarz — Śniadka koło Bodzentyna w północnej części Gór Świętokrzyskich (*patrz* fig. 1 oraz pl. 1, fig. 1—2). Ślady te, stanowiące nowe taksony ichnologiczne, *Alpertia sanctacrucensis* ichnogen. et ichnosp. n. (*patrz* pl. 3, fig. 3 oraz pl. 4—5), są odlewami dolnych partii nor utworzonych przez ukwiały. Spośród form towarzyszących zwracają uwagę drobne okazy *Cruziana* sp. (*patrz* pl. 3, fig. 1—2), będące odlewami śladów rozgrzebywania osadu przez trylobity. Masowe nagromadzenie śladów ukwiałów w obrębie warstw o charakterze burzowym wskazuje na pogrzebanie tych zwierząt w czasie ich życia (*patrz* fig. 2), co nadaje badanej ichnocenozie charakter tanatocenotyczny. Obecność utworów burzowych, stowarzyszonych z rozmaitymi strukturami prądowymi (m.in. zmarszczkami, *patrz* pl. 2, fig. 1—2) wskazuje na płytko-sublitoralne środowisko powstawania osadów badanego ichnotopu, które reprezentują epizod ekstremalnie płytkomorski w czasie sedymentacji warstw świętomarskich.
