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Triassic brittlestar beds of Poland: a case of *Aspiduriella ludeni* (v.HAGENOW, 1846) and *Arenorbis squamosus* (E. PICARD, 1858)

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ABSTRACT:

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Exemplified by a new occurrence site of mass-aggregated *Aspiduriella ludeni* (v.HAGENOW, 1846) from the Lower Muschelkalk (lowest Anisian) sequence of the Holy Cross Mountains, Central Poland, discussed are life conditions of ophiuroids in that region of the Muschelkalk Basin (Middle Triassic) in Central Europe. Postulated is their fast deposition (burial) by the rip-current transport of alive, possibly torpid, and/or newly dead specimens captured by stormy agitation from their shallow subtidal and/or intertidal habitats. The palaeogeographical setting of the Holy Cross region is compared to that of the Silesia region in southern Poland, highly influenced till the early-Middle Triassic by oceanic waters of the Tethyan Realm. Shortly reviewed and/or discussed are the formerly known ophiuroid occurrences in Silesia, to be supplemented by a mass-aggregated case of *Arenorbis squamosus* (E. PICARD, 1858). Commented are also other ophiuroid aggregations reported from the Muschelkalk Basin, and whose occurrence is considered in terms of their environmental conditions controlled both by physical (fluctuation of water parameters, and its dynamics) and biotic (low predation stress) agents. A biogeographical significance of the genus *Aspiduriella* during Triassic is outlined, to suggest its Muschelkalk-refugee provenance in the late Middle and Late Triassic of the Tethyan Realm.

Key words: Ophiuroids, *Aspiduriella*, *Aspidura*, Eco-taphonomy, Brittlestar beds, Palaeobiogeography, Middle Triassic, Muschelkalk, Poland.

INTRODUCTION

The ophiuroids are very outstanding elements of the Muschelkalk (Middle Triassic) sequence of Central Europe, where they occur relatively often, either as associates of diverse faunal assemblages, or to form their own monospecific aggregations lacking any other faunistic elements (*brittlestar beds* of ARONSON 1989, 1992b). Similar assemblages appear locally also within the Triassic sequences of the Tethys Ocean. On the other way, the Triassic ophiuroids, due to their more or less ideal state of preservation, are so spectacular that even single specimens have more than once been subjected to separate publications (see e.g., ENTSCHEVA 1960, BACHMAYER & KOLLMANN 1968, HESS 1972).

Subjected to this report are mass-aggregated Muschelkalk ophiuroids of the genus referred, since over more than a century, to *Aspidura* AGASSIZ, 1835. The studied ophiuroids were collected from the Lower Muschelkalk sequence in the Holy Cross Mountains, Central Poland (see Text-fig. 1), the region of an extremely poor record of ophiuroids. Worthy of attention is thus not only their new occurrence site in the region, but also their representation by a species unknown as yet from Poland. Moreover, a mass-occurrence of the recognized species has not hitherto been reported from any part of the Muschelkalk Basin in Central Europe, and from any Triassic sequences of the Tethyan Realm as well.

In the Holy Cross Muschelkalk, any echinoderm remains other than trivial crinoid columnals are very rare. Such ones are the ophiuroids, of which the remains of *Aspidura* sp. were once reported by SENKOWICZOWA (1961, p. 79), with no precise location, from a site nearby the studied locality. Moreover, in the whole region, isolated arm-vertebrae were noted as common in various biocalcarenites of Lower Muschelkalk (RADWAŃSKI 1968, p. 59; GŁAZEK & RADWAŃSKI 1968, p. 94 and Pl. 4, Fig. 1).

LOCATION OF THE OPHIUROIDS STUDIED

The studied mass-aggregated ophiuroids come from the Lower Muschelkalk sequence, the so-called *Łukowa Beds* of local lithostratigraphical subdivision (SENKOWICZOWA 1959, 1961), exposed at Polichno near Chęciny, along the slopes of Grabówka Hill (see SENKOWICZOWA 1959, Fig. 4) that forms a ridge bounding northerly the village. The small rural excavations are typified herein by a common occurrence of peculiar burrows ascribed by KAŹMIERCZAK & PSZCZÓŁKOWSKI (1969) to the activity of enteropneustans. The exposed succession has formerly been presented by KAŹMIERCZAK & PSZCZÓŁKOWSKI (1969, Fig. 2*B*) and TRAMMER (1971, Fig. 2; and 1975, Pl. 4, Figs 1-3). It represents a lower part of the *Łukowa Beds* that is contained within the Lower Anisian, while the uppermost part of these Beds reaches the Lower Pelsonian (TRAMMER 1972*b*, 1975, 1980).

The ophiuroids were found in a limestone slab lying loose in the scree (dump) of that temporary excavation. This slab, 8 by 8 cm in size, bears almost all ophiuroid remains mass-aggregated at its surface, and only few are scattered through the slab interior. Compared with ophiuroid settings within the section exposed, where scanty ophiuroid remains are preserved on the top surface of particular beds, the collected ophiuroid aggregation (see Plate 1) is thought to represent that very surface, over which 17 almost complete skeletons are associated with a maze of fragmented arms. Of the fully preserved specimens, 8 are oriented with their mouth down, and 9 with mouth upwards (see Text-fig. 2), what is commented hereafter.

The nature of the maze of fragmented arms of the studied ophiuroids remains unclear: it may result either from a post-mortem damage of skeletons by hydrodynamic agents, or from arm autotomy caused by environmental stress (cf. LAWRENCE & VASQUEZ 1996, p. 434; for asteroids see LAWRENCE 1992). In the Triassic ophiuroids the process of autotomy has already been recognized by MÜLLER (1969, 1976; see also STOLL 1980). It was certainly functioning in a way similar to that in present-day crinoids in which it was postulated as an anti-predatory adaptation (OJI & OKAMOTO 1994). Moreover, a preservational artifact involved by weathering must also be taken into account.

Environmental conditions of the Lower Muschelkalk succession at Polichno, as apparent from a uniformitarian evidence of the enteropneustans, have precisely been interpreted by KAŹMIERCZAK & PSZCZÓŁKOWSKI (1969) as lower intertidal to shallow subtidal, temporarily influenced by storm agitation and erosion. Such very environmental conditions of the *Łukowa Beds* have also been recognized from their floral and burrow content (GAŹDZICKI & KOWALSKI 1974, and TRAMMER 1974, respectively).

SYSTEMATIC ACCOUNT

An obvious fact is, that most of the Triassic ophiuroids are of a very unclear, if not dubious, taxonomic status at the genus level, especially when their relationship to the modern genera is attempted to recognize (see ECK 1872, 1879; HESS 1965, *and* 1970, pp. 1063-1064; BROGLIO LORIGA & CAVICCHI 1969). Unfortunately for the genus *Aspidura* AGASSIZ, 1835, this situation also concerns its own name, as recently evidenced by BOLETTE (1998; see also HAGDORN 1999), who recognized a younger-homonym nature of this name opposing *Aspidura* WAGLER, 1830, introduced earlier for a Sri Lankan (Ceylonese) snake. Consequently with the ICZN rules and the priority law, the Agassizian genus had to be renamed for *Aspiduriella* BOLETTE, 1998, as coined up by BOLETTE, to retain an original Agassizian sound in the name of Triassic ophiuroids.

The higher taxonomic hierarchy of the genus *Aspiduriella* BOLETTE, 1998, as given below, is that to follow SPENCER & WRIGHT (1966).

Ophiuroidea GRAY, 1840
Order Ophiurida J. MÜLLER &TROSCHEL, 1840
Family Ophiuridae LYMAN, 1865
Subfamily Ophiurinae LYMAN, 1865
Genus *Aspiduriella* BOLETTE, 1998
(pro *Aspidura* L. AGASSIZ, 1835; see BOLETTE 1998, p. 401)

TYPE SPECIES: *Asterites scutellatus* Blumenbach, 1804; *SD* Hess (1965, p. 155).

REMAKS: The species content of the genus *Aspiduriella* Bolette, 1998, has long been discussed and variably treated through authors and years. The successive revisions, by Fritz Kutscher (1940), Hess (1965, 1970), Broglio Loriga & Cavicchi (1969), and finally by Bolette (1998), allowed to retain within the genus *Aspiduriella* seven species alone, as follows:

A. scutellata (Blumenbach, 1804), being the type,
A. camuna (Rossi Ronchetti, 1965),
A. dorae (Lepsius, 1878),
A. italica (Crema, 1896),
A. ludeni (v.Hagenow, 1846),
A. montserratensis (Calzada & Gutiérrez, 1988),
A. streichani (M. Kutscher, 1987).

Of these species, only *A. scutellata* and *A. ludeni* are known from more than one locality (and more than one believable record). Moreover, only these two species (*A. scutellata*, *A. ludeni*) plus *A. streichani* are typical of the Muschelkalk Realm, whereas the others are reported exclusively from the Tethyan Realm of the Alps (Lepsius 1878, Crema 1896, Rossi Ronchetti 1965; see also Broglio Loriga & Cavicchi 1969), Bulgaria (Entscheva 1960), and Spain (Calzada & Gutiérrez 1988).

The other Muschelkalk species, often classified within the genus *Aspidura* formerly, such as *Aspidura squamosa* of E. Picard (1858) and *Aspidura similis* of Eck (1865), have been transferred to other genera. Their modern status is established to represent:

Ophiomusium(?) *simile* (Eck, 1865), as suggested by Schmidt (1928, p. 130) and revealed by Hess (1965),
Arenorbis squamosus (E. Picard, 1858), as revealed by Hess (1970),

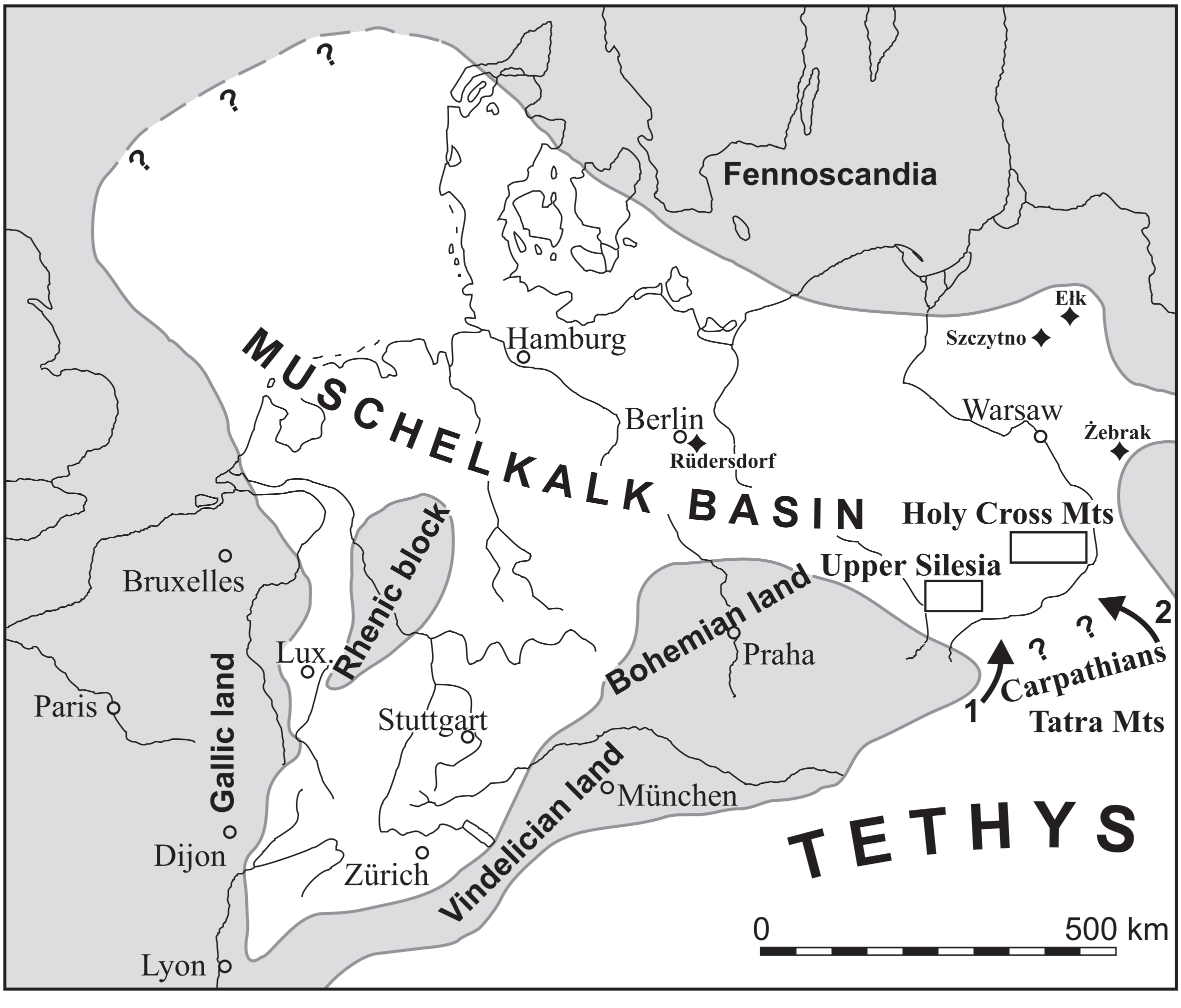


Fig. 1. Palaeogeographical sketch of the Muschelkalk Basin in Central Europe at Early Anisian (Lower Muschelkalk) time; *adopted from* Trammer (1980, Fig. 1; *cf. also* Schwarz 1975, Fig. 1); Tethys-to-Muschelkalk seaways (*after* Hagdorn 1991): **1** – Silesia-Moravian Gate, **2** – East Carpathian Gate

and under such very names these two species are referenced hereafter, to review their occurrence in the Polish part of the Muschelkalk Basin, precisely in the Silesia region.

Aspiduriella ludeni (v. HAGENOW, 1846)

1846. *Aspidura Ludeni*; F. v.HAGENOW, p. 21, pl. 1, figs 1*a*-1*d*.
1928. *Aspidura Ludeni* v.HAGENOW; M. SCHMIDT, p. 130, text-fig. 251.
1940. *Aspidura ludeni* v.HAGENOW; F. KUTSCHER, p. 12, pl. 1, figs 1, 4.
non 1960. *Aspidura ludeni* HAGENOV; M. ENTSCHEVA, p. 235, pl. 1, Fig. 1*a* [?*Aspiduriella scutellata*].
1965. *Aspidura Ludeni* v.HAGENOW, 1846; H. HESS, p. 154.
1969. *Aspidura ludeni* v.HAGENOW; A.H. MÜLLER, p. 390, pl. 1, figs 1-2 (*non* pls 2-4 [*Aspiduriella scutellata*]).
non 1980. *Aspidura Ludeni*?; A. STOLL, text-figs 1-2 [*Aspidura streichani* of M. KUTSCHER (1987)].
1998. *Aspiduriella ludeni* (HAGENOW, 1846); D.P. BOLETTE, p. 401.

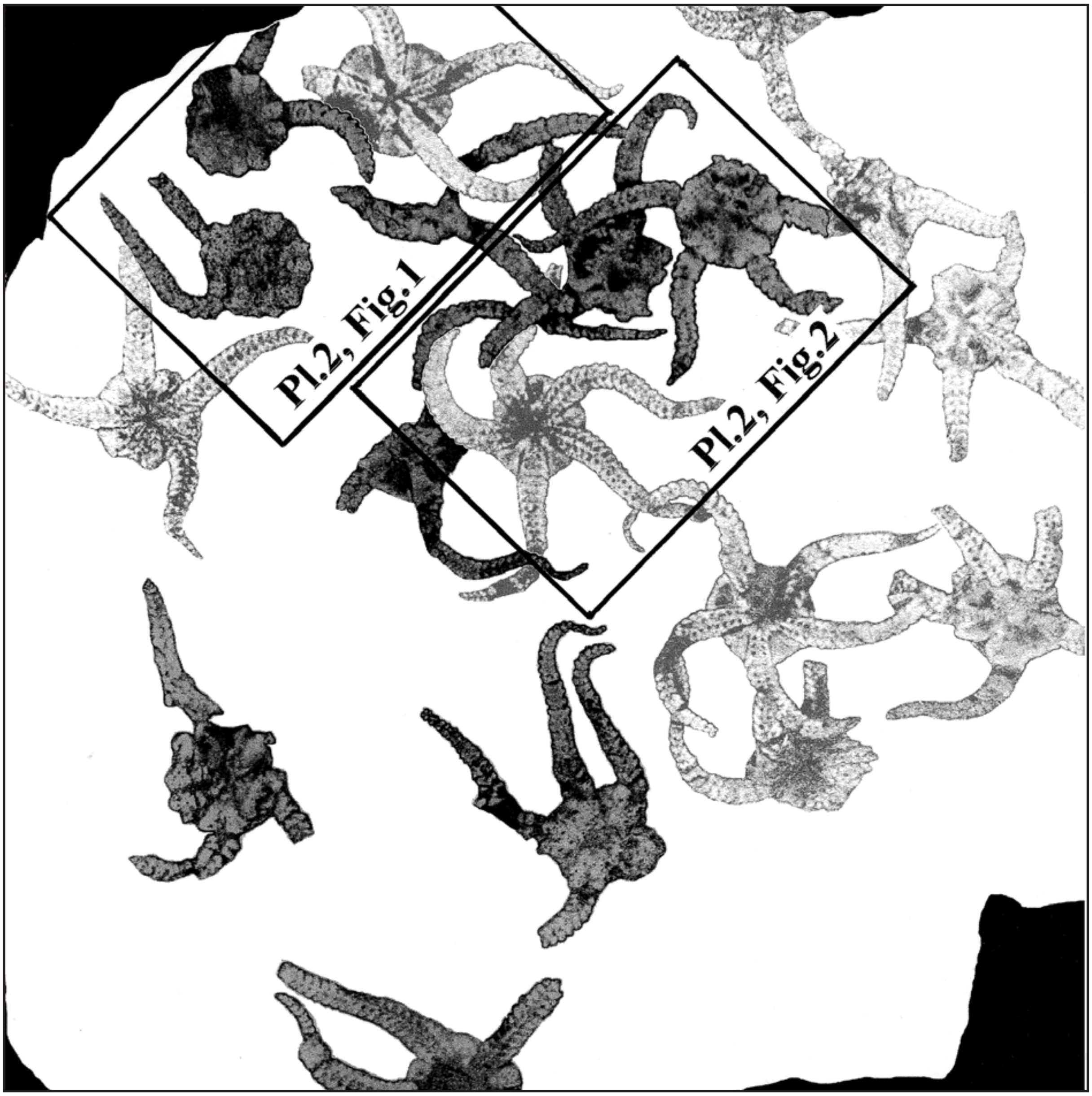
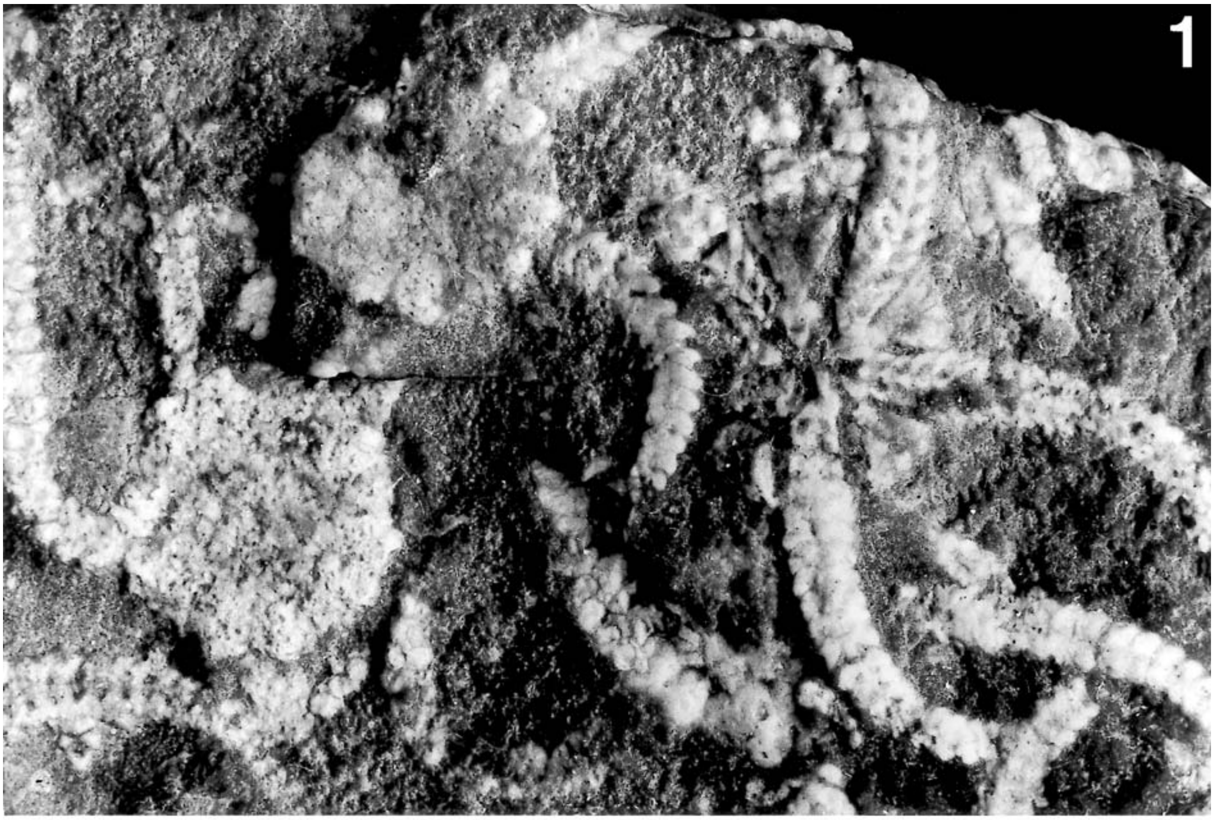
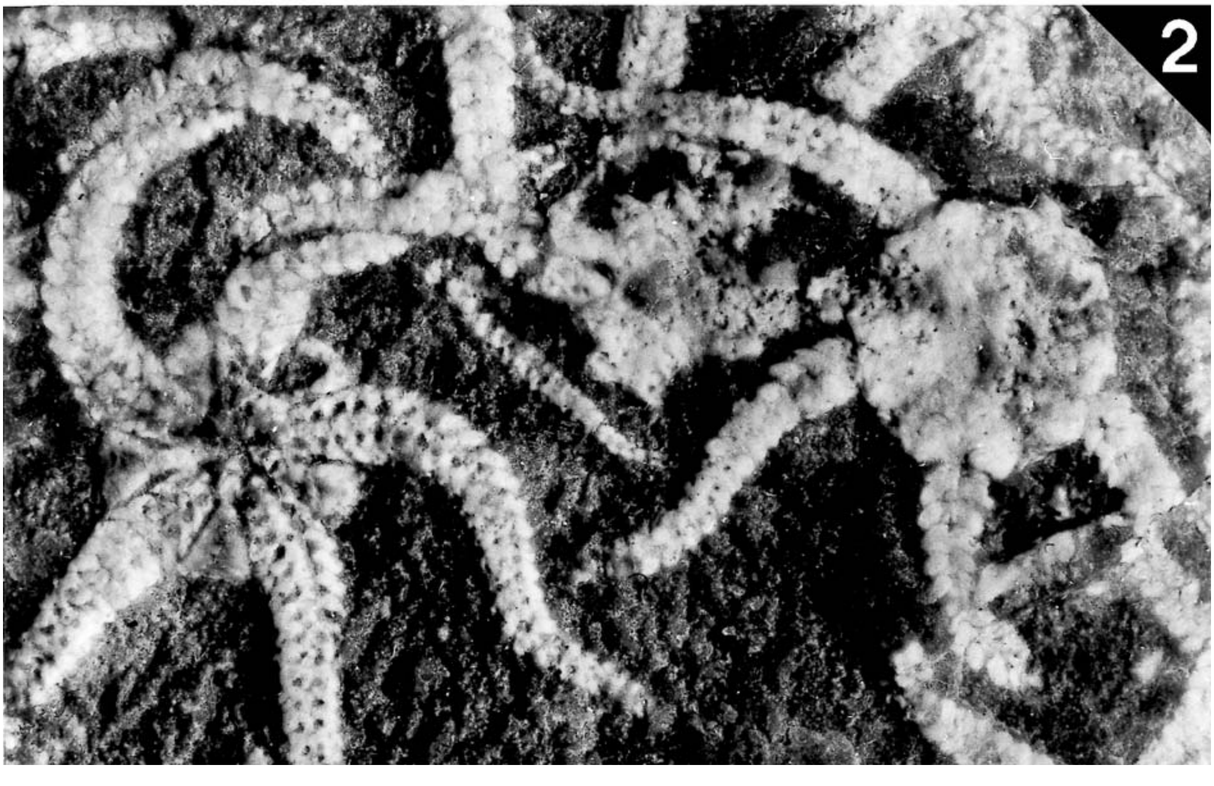


Fig. 2. Scan-sketch of the attitude of complete skeletons of *Aspiduriella ludeni* (v.HAGENOW, 1846) presented in Plate 1, to distinguish specimens lying mouth-down (*shaded*) and those mouth-up (*lightened*); rectangled are parts magnified in Pl. 2, Figs 1-2

Aspiduriella ludeni (v.HAGENOW, 1846)

General view of the limestone slab with mass-aggregated skeletons and fragmented arms (for attitude of complete specimens *see* Text-fig. 2); × 2; Lower Muschelkalk; Polichno near Chęciny, Holy Cross Mountains, Central Poland





Aspiduriella ludeni (v.HAGENOW, 1846)

1-**2** – Close-up views of parts (indicated in Text-fig. 2) of the limestone slab with mass-aggregated specimens (*see* Plate 1), to show their skeletons more or less abraded (? due to weathering in the exposure), regardless of their orientation mouth-down or mouth-up; × 5

REMARKS: The species is relatively large-sized for the genus, reaching 7.5-8.2 mm in disk diameter for the studied specimens (see Plate 1), and about 8 mm for the holotype (see v.HAGENOW 1846, Pl. 1, Fig. 1*a*).

The species has long been known from specimens having only their dorsal side exposed (v.HAGENOW 1846, SCHMIDT 1928), and it was F. KUTSCHER (1940) followed by MÜLLER (1969) who reported and illustrated the ventral side. Little is to be added to these former recognitions as morphological details of the disk and arms in the specimens studied are hardly discernible (see Plate 2), having been more or less abraded, most likely due to weathering in the exposure.

The species is herein first reported from the Polish part of the Muschelkalk Basin (Holy Cross Mountains, Silesia). In the German part, it is known from the Lower Muschelkalk solely (F. KUTSCHER 1940, HESS 1965), with the holotype coming from the vicinity of Jena (v.HAGENOW 1846), and numerous specimens from other localities, Rüdersdorf near Berlin including (see F. KUTSCHER 1940). Moreover, the studied material is the first to demonstrate a mass occurrence of this species. An interpretation of this state of burial and preservation is presented hereafter.

To the studied species the closest is similarly-sized *Aspiduriella streichani* (M. KUTSCHER, 1987) from the Lower Muschelkalk of Rüdersdorf near Berlin (see Text-fig. 1) where it occurs not rarely (see M. KUTSCHER 1987, p. 703), having been earlier ascribed to *A. ludeni*, albeit with a question mark, by STOLL (1980).

INTEGRATED ECO-TAPHONOMY

The studied ophiuroid aggregation of *Aspiduriella ludeni* (v.HAGENOW, 1846) demonstrates a case of "Fossillagerstätte" *sensu* SEILACHER & *al*. (1985). To recognize environmental conditions under which it was formed, three points should be considered: (*i*) Life habit and habitat of the studied ophiuroids, (*ii*) Their death agent and burial that prevented disintegration of skeletons, (*iii*) Depositional agent that produced finally the studied "Fossillagerstätte".

Life habit and habitat

The studied ophiuroid assemblage is polyindividual and monospecific, and thus may be inferred to correspond to the gregarious mode of life in monospecific communities. Regardless to subsequent transport (see below), the population density of the studied *Aspiduriella ludeni* (v.HAGENOW, 1846), as counted from the collected slab (8 by 8 cm in size, with at least 17 specimens), estimates to about 2,000 specimens per one square metre. This number compares well to that of some present-day and/or fossil ophiuroid communities (see SCHÄFER 1962, ARONSON & HARMS 1985, ARONSON 1992b, BLAKE & ARONSON 1998, ARONSON & BLAKE 2001).

Under present-day circumstances, the ophiuroids are known to live fully exposed in protected areas (coastal saltwater lakes including, see ARONSON & HARMS 1985). but in open-shore areas they tend to live cryptically, or amidst the other biota to which they may become commensals (see HENDLER 1984, ARONSON & HARMS 1985). When exposed, they suffer a high predation stress by carnivorous fish, crabs, lobsters, sea stars, and other ophiuroids (see VASSEROT 1966; HENDLER 1984; ARONSON & HARMS 1985; ARONSON 1987, 1989, 1991, 1992b; LAWRENCE 1992; LAWRENCE & VASQUEZ 1996; ARONSON & BLAKE 2001) as well as by stomatopods (see HENDLER & *al*. 1995, p. 95). A relative ubiquity of the ophiuroid-aggregated beds (*starfish beds* of GOLDRING & STEPHENSON 1972, ARONSON 1987; or *brittlestar beds* of ARONSON 1989, 1992b) in the Triassic sequences of Europe is therefore thought to have resulted from an extensive development of the ophiuroids in areas where, and at time when predatory fish, crabs, and others have not yet evolved. This conclusion concurs well with that expressed by ARONSON (1987, 1989, 1991, 1992b) in his study of ophiuroid arm damages by predation upon Palaeozoic *versus* Early-Jurassic-to-Recent specimens.

Consequently, the Triassic ophiuroids, the studied species *Aspiduriella ludeni* (v.HAGENOW, 1846) including, are thought to have lived preferably in their own, monospecific communities lacking any predators, and having been more or less opportunistic in habitats they occupied. Some species could associate to *crinoid meadows*, as noted from Silesia and the Tatra Mts (LANGENHAN 1903; KLINGHARDT 1930, p. 716; ASSMANN 1937, p. 21; LEFELD 1958, pp. 60, 64 and 70; GŁAZEK & RADWAŃSKI 1968, p. 94; HAGDORN 1996, p. 24), to concur with the present-day cases (see IRIMURA & KUBODERA 1998). At time of low, or none, predatory pressure such habitats, those of the *Łukowa Beds* particularly, could be installed both over the open seafloor shallows, as well as in protected areas along the shore. Extensive shallows with unstable extent of the shoreline could then favour development not only of widespread plains of the tidalflat type (like at Rüdersdorf, see STOLL 1980), but also of saltwater lakes/lagoons (like the modern case, see ARONSON & HARMS 1985) or sabkhas similar to those recognized by KWIATKOWSKI (1991) from the uppermost Lower Triassic (Röth) of Silesia.

Demise of the community

A death agent for a community of the studied *Aspiduriella ludeni* (v.HAGENOW, 1846) should be recognized in fluctuations of the biotope conditions. Within the shallows of the Lower Muschelkalk basin, and/or near to its shorezone where the *Łukowa Beds* originated, such fluctuations might have been caused both by the physical stress (cf. MÜLLER 1969; SCHWARZ 1975; DŻUŁYŃSKI & KUBICZ 1975; STOLL 1980; ARONSON 1991, 1992a,b) and biogenic agents (?bacterial, or algal bloom; cf. ARZUL & *al*. 1995). Fluctuation of salinity (to either oligo-, or hyper-) and temperature (primarily overwarming), regardless to its action either together, or separately, were certainly the most dramatic. An overwarming, fatal by itself, involves an increase of evaporation (thus, of salinity) combined with oxygen deficiency, and thus a hypoxic event. Of other agents, temporary exposition to air at an extreme sealevel drop (? ebbs) may also be taken into account as lethal to the ophiuroids. An overwarming and/or exposition to air are thought to have acted similarly as they do with the present-day echinoids (see HENDLER 1977; SMITH 1984, p. 15; HENDLER & *al*. 1995, e.g. pp. 204 and 228).

Anyway, a haphazard orientation (either mouth-down, or mouth-up) of ophiuroid skeletons in the studied assemblage of *Aspiduriella ludeni* (v.HAGENOW, 1846) containing a maze of fragmented arms (compare Plate 1 and Text-fig. 2) indicates that this assemblage does not represent a community buried *in vivo* and *in situ*. Of the aforementioned causes of arm fragmentation, the autotomy, if regarded to be an anti-predatory adaptation as it is in modern crinoids (see OJI & OKAMOTO 1994), should rather be excluded since the predation pressure was then very low or none. Regardless to whom the fragmented arms belonged (specimens mechanically injured in their environment, or those weathered in the exposure), their preservation in a very good state, together with the complete skeletons, indicates a rapid burial of the whole ophiuroid remains studied. Such a burial is postulated since the ophiuroid skeletons, after death of their owners, disarticulate very fast within days, or even hours, as noted under present-day circumstances (see SCHÄFER 1962; GOLDRING & STEPHENSON 1972; MÜLLER 1976; HENDLER & *al*. 1995, p. 95), and concluded for other Triassic occurrences (F. KUTSCHER 1940, p. 5).

The disintegration rate in ophiuroids is comparable to that of other echinoderms, the echinoids particularly, in which it was observed both under natural conditions and in laboratory tanks, as well as argued from taphonomic evidence (see ASLIN 1968; SMITH 1984, pp. 15-21; RADWAŃSKA 1999, pp. 299 and 352-355; RADWAŃSKI & WYSOCKA 2001, pp. 301-302). The completely preserved skeletons are therefore regarded to have belonged to specimens buried immediately after death, or when still alive. The latter possibility becomes more realistic if we assume a rapid agent that acted upon live specimens and could simultaneously cause death of some, or all specimens that could not escape from the smothering sediment (cf. SCHÄFER 1962).

The depositional agent

Of the depositional agents, many have been attempted to explain the origin of particular occurrence sites of the ophiuroids of various age, or of other Muschelkalk fauna, and they ranged from storms producing tempestites, tsunamis, to turbidity currents (F. KUTSCHER 1940, MÜLLER 1969, GOLDRING & STEPHENSON 1972, DŻUŁYŃSKI & KUBICZ 1975, STOLL 1980, MEYER 1984, SEILACHER 1988). As reasonably argued for the Muschelkalk sequence of Silesia by DŻUŁYŃSKI & KUBICZ (1975), all these agents take an action at depths greater than might be ascribed to that sequence. Quite the same may be said about the basin depths of the Holy Cross region studied. To comply with the data of former students (KAŹMIERCZAK & PSZCZÓŁKOWSKI 1969, GAŹDZICKI & KOWALSKI 1974, TRAMMER 1975), it is herein suggested that the only agents that could effectively act at the extremely shallow depths in that region when the *Łukowa Beds* formed were rip currents, the erosional and depositional significance of which has recently been discussed by GRUSZCZYŃSKI & *al*. (1993, *and* full references therein). These currents, that originate at extremely shallow depths, the beach zone including, but at a storm-induced high water-stand, can scour and sweep away all physical and biotic material, and transport it seaward beyond the breaker line to the zone where sediment could been accumulated. The rip current scenario allows to assume that the induced water motion has captured the ophiuroids from their habitats, and transported them away with very little or no sediment. The captured ophiuroids may have been either still alive, or just killed by the induced stress, and deposited haphazardly, either mouth-down, or mouth-up. The specimens oriented mouth-up are supposedly those transported as dead, and deposited with their heavier, disk-bearing part downwardly. The mouth-down specimens could be these deposited still alive and able to overturn to the life position if settled upside-down. Interestingly, such bimodal orientation of ophiuroid skeletons is typical of the most of their Triassic mass-aggregated occurrences.

A comparative database

The mass aggregation of Triassic ophiuroids that form *brittlestar beds* has called attention of some former authors, primarily of F. KUTSCHER (1940, pp. 4-5; older references therein), who suggested their preservation by a rapid (catastrophic) burial of live communities in nearshore habitats. The former authors (since POHLIG 1878, p. 261) have also noticed that in such *brittlestar beds* some specimens are mouth-up, while others are oriented in life position, that is mouth-down. The ratio of these two groups varies, but tends quite often to be equal, as evidenced by the studied aggregation (see Text-fig. 2) – 8 specimens mouth-down, and 9 mouth-up, and ascertained from the referenced examples:

In the classical, QUENSTEDT's aggregation (see ZITTEL 1903, Fig. 352; re-figured by SPENCER & WRIGHT 1966, Fig. 81/5a) of *Aspiduriella scutelleta* from the Upper Muschelkalk of Germany – 5 specimens mouth-down, and 6 mouth-up;

HAGDORN's slab with *Arenorbis squamosus* from the Upper Muschelkalk of Germany (see HAGDORN 1985, p. 84) – 5 specimens mouth-down, and 3 mouth-up;

MÜLLER's report of aggregated *Arenorbis squamosus*, also from the Upper Muschelkalk of Germany (see MÜLLER 1976, p. 1401) – 7 specimens mouth-down, and 9 mouth-up;

A slab with *Aspiduriella camuna* of ROSSI RONCHETTI (1965, p. 55) – 6 specimens mouth-down, and 3 mouth-up;

A Rhaetian slab with *Praeaplocoma hessi* of BROGLIO LORIGA & CAVICCHI (1969, Plate 2) – 11 specimens mouth-down, and 5 mouth-up.

To note, all the above counts concern isolated, relatively small-sized slabs collected, and may thus be biased in regard to the complete brittlestar bed analysed. However, in the comparable case of a large slab with the rich assemblage of 144 specimens from the Lower Callovian of La Voulte-sur-Rhône, France, reported by DIETL & MUNDLOS (1972, p. 452), the ratio is almost ideally equal of 71 specimens oriented mouth-down to those 73 oriented mouth-up. The same is also apparent from a dense population reported by MEYER (1984, p. 657) from the Oxfordian of Schofgraben, Switzerland, where 42% of specimens are mouth-down, against 58% being inverted.

A conclusion from the above data is, that these Triassic occurrences (and some Jurassic as well) did not result from an *in situ* rapid (catastrophic) burial of live communities, but they are aggregations formed by hydrodynamic agents which carried the ophiuroids out of their habitats.

In aggregations formed supposedly by a longer transport, or long-termed accumulation, the discussed ratio is variable. In the Rhaetian material of the Tethyan Realm, for instance, where the ophiuroids *Ophiolepis bertrandi* are settled on coquina-like lags of bivalve or brachiopod shells, it is 2 mouth-up to 2 mouth-down in a block from the Maritime Alps (see LANQUINE 1917, p. 88 and Pl. 1, Figs 1-6), or 9 mouth-up but only one mouth-down in a slab from the Tatra Mountains (see GŁAZEK 1962, p. 219).

All the reviewed brittlestar beds of the Muschelkalk, and some of the Tethyan Realm, display significant analogies to that of *Aspiduriella ludeni* (v.HAGENOW, 1846) studied. It may therefore be assumed that they correspond to very similar mode of life of particular species, their habitats, and environmental conditions responsible for their death, transport, and burial. None of the Muschelkalk ophiuroid mass-occurrences are reported from typical tempestite or turbidity beds. If the sediment covering a brittlestar bed is known, it is noted as very thin, fine-grained. This allows to postulate that the depositional agent was not the cause of death, but all the specimens have already become torpid due to stress events preceding the stormy agitation and induction of rip currents. To note, the storms themselves even with over 9 metres swells are recognized as doing a very low or none damage to ophiuroid communities of the Caribbean back-reef and lagoonal shallows (ARONSON 1991, 1992a; ARONSON & BLAKE 2001).

PALAEOGEOGRAPHICAL SETTING OF OPHIUROID SITES IN POLAND

The Middle Triassic Muschelkalk Basin in Central Europe has long been interpreted as epicontinental, having been connected to, but more or less distinctly separated from, the Tethys Ocean widespreading over the parent territories of the Alpine and Carpathian arch (see Text-fig. 1). It has also been long considered that the Lower Muschelkalk fauna, locally ubiquitous but dominated by monospecific assemblages of bivalves and one terebratulid species, has strongly been influenced by abnormal biotope conditions (cf. DŻUŁYŃSKI & KUBICZ 1975), of still unknown origin (? oligo- or hypersalinity, ? chemical influx from the bordering landmasses, ? water stagnation and its deoxygenation, or overwarming). Under such environmental conditions, any appearance of the open-marine elements within the Muschelkalk assemblages provokes a discussion, particularly of the migration routes.

At Early Anisian time, when the studied ophiuroid-bearing *Łukowa Beds* of the Holy Cross region in

Central Poland were formed (see TRAMMER 1980, Fig. 2), the seaway connections are assumed to have been opened through southernmost Poland (see Text-fig. 1, *adopted from* TRAMMER 1980, Fig. 1). At that time the strong Alpine influences in the whole Muschelkalk Basin were present primarily just in southern Poland, in the Silesia region, whose many faunal assemblages bear a significant number of the Tethyan migrants (see ECK 1865; ASSMANN 1915, 1937; SCHMIDT 1928; TRAMMER 1973, 1980), that have certainly entered through the Silesia-Moravian Gate (marked *1* in Text-fig. 1).

In the Lower Muschelkalk sequence of the Holy Cross Mountains the oceanic Tethyan influence has long been known, having been documented by the otherwise very rare cephalopods (one pleuronautilid and ammonites; see ŁUNIEWSKI 1923, SAMSONOWICZ 1929, SENKOWICZOWA 1962, TRAMMER 1972a) as well as by the more frequent conodonts (see TRAMMER 1971, 1972b, 1973, 1975), and the locally occurring *Aciculella bacillum* PIA, 1927 – a green alga of the dasycladacean family (see GAŹDZICKI & KOWALSKI 1974).

An intriguing occurrence, in the slightly higher Lower Muschelkalk, of the large foraminifer *Glomospira densa* (PANTIĆ, 1965) of Tethyan-Asiatic provenance in the Holy Cross region earlier (Pelsonian) than in the Alpine Realm (Illyrian) resulted in the conclusion (GŁAZEK, TRAMMER & ZAWIDZKA 1973; cf. also TRAMMER 1973, 1980) that another seaway connection had existed eastwards the Holy Cross region: this is the East Carpathian Gate (suggested earlier by SENKOWICZOWA 1962) that is herein assumed to have functioned (marked *2* in Text-fig. 1) at the time the *Łukowa Beds* have been formed.

As concerns the possible migration routes, it is noteworthy that the studied ophiuroid genus *Aspiduriella* is present in the Holy Cross region in the Lower Muschelkalk, *i.e.* the Lower Anisian (Hydaspian *in* LEFELD 1958, TRAMMER 1973; Bithynian *in* HAGDORN 1991), thus at a time more or less coeval to that of the Recoaro section in the Venetian Alps (CREMA 1896), but generally much earlier than noted in other localities of the Tethyan Realm (Ladinian – ENTSCHEVA 1960, CALZADA & GUTIÉRREZ 1988; mid-Carnian – ROSSI RONCHETTI 1965).

When the faunal assemblages of the Holy Cross and Silesia regions are compared, it is evident that these of the Lower Muschelkalk of the Holy Cross region display a much lower frequency and diversity than those of the Silesia region situated near to, or just passing into, the Tethyan Ocean in southernmost Poland, that is the territories of the present-day Tatra Mountains in the Carpathians. An evident faunal impoverishment may thus be regarded as resultant from the setting of the Holy Cross region in the marginal part of the Middle Triassic epicontinental (Muschelkalk) basin, and its being placed farther off the oceanic, open-marine influences (see Text-fig. 1).

The Silesia region had much wider connections to the Tethys, that acted till low-Middle Muschelkalk time (*Diplopora* Dolomites; cf. SENKOWICZOWA 1962, *and* correlations by TRAMMER 1980, Fig. 1). At Lower Muschelkalk time, they are documented by ubiquitous fauna of various type (corals, brachiopods, echinoids, ammonites), known from several comprehensive monographs (ECK 1865, ROEMER 1870, LANGENHAN 1903, SCHMIDT 1928, ASSMANN 1937). Complementary to the latter are numerous newer accounts, published in the last half-century, especially those on:

corals (see review by MORYCOWA 1988),
crinoids (LEFELD 1958, HAGDORN & GŁUCHOWSKI 1993,
 HAGDORN 1996),
ammonites (see review by KAIM & NIEDŹWIEDZKI 1999).

Of the brachiopods, noteworthy are the inarticulates of the Tethyan genus *Discinisca* DALL, 1871, whose species have long been reported (see ECK 1865; LANGENHAN 1903; ASSMANN 1914, 1915, 1937; SCHMIDT 1928, pp. 137-138; and further references in RADWAŃSKI & SUMMESBERGER 2001, p. 118). Associated to the above reviewed groups are the ophiuroids, whose revised taxonomy, and the occurrence mode are treated separately hereafter, to compare with those of the Holy Cross region.

Contrary to the above settings, the Tethyan influences in Poland have completely ceased in the Upper Muschelkalk which then became connected with the German Muschelkalk faunal province exclusively (TRAMMER 1972b, 1973).

The Late Triassic ophiuroids and other echinoderms in Poland are therefore known solely from the Tethyan Realm of the Tatra Mountains, where they occur both in the shallow-marine high-tatric, and the deeper-marine sub-tatric sequence. In the first, they are represented by isolated arm-vertebrae freed in calcareous ooze of biocalcarenites, or entrapped as nuclei of ooids (see RADWAŃSKI 1968, pp. 58-59, 133-134 and Pl. 9, Figs 1-6; Pl. 10, Fig. 2). In the second, significant are well preserved, complete skeletons (see GŁAZEK 1962; GŁAZEK & RADWAŃSKI 1968, Pl. 1, Fig. 1; GAŹDZICKI 1974, Pl. 15, Figs 4-8 and Pl. 21, Fig. 1) of *Ophiolepis bertrandi* LANQUINE, 1917, the Alpine species (cf. LANQUINE 1917) whose generic assessment has been queried by HESS (1965, p. 159), and still remains unsolved. Evidently of the Tethyan provenance in the Rhaetian sequences (see RADWAŃSKI & SUMMESBERGER 2001) are inarticulate brachiopods *Discinisca* known from few occurrences in the subtatric sequence of the Tatra Mountains and from one locality of the Carpathians in Slovakia (see GOETEL 1917, RADWAŃSKI & SUMMESBERGER 2001, pp. 117 and 120).

OPHIUROIDS OF THE SILESIA REGION

In the Muschelkalk sequence of Silesia, whose fame of the Triassic ophiuroids has long flourished allover the world (ECK 1865; LANGENHAN 1903; SCHMIDT 1928; KLINGHARDT 1930, 1933; ASSMANN 1937; F. KUTSCHER 1940), the present state of their recognized occurrence concerns evidently the two species, *Ophiomusium*(?) *simile* (ECK, 1865) and *Arenorbis squamosus* (E. PICARD, 1858), and doubtedly the two other, *Ophioderma hauchecorni* (ECK, 1872) and *Aspiduriella scutellata* (BLUMENBACH, 1804).

***Ophiomusium*(?) *simile* (ECK, 1865)**

This tiny-sized species (disk diameter *ca*. 2 mm), "*Aspidura similis*" of ECK (1865, Pl. 1, Fig. 5*a*-5c), whose separateness had been objected by POHLIG (1878) but defended by ECK (1879), has long been regarded as a rarity noted from one locality (Chorzów) in Silesia (ASSMANN 1914, 1937; SCHMIDT 1928; F. KUTSCHER 1940). It was thus regarded as endemic to this region (F. KUTSCHER 1940, p. 14), having been confined to the lowest Muschelkalk. Noteworthy is its association with the crinoid *Dadocrinus gracilis* (v.BUCH, 1845), to which it was claimed to have been a symbiont (ASSMANN 1937, p. 21).

Quite recently, BOCZAROWSKI & SALAMON (2000 *internal circular*) have reported its mass occurrence (about 400 complete skeletons) in another locality (Wojkowice), but they did not inform about the nature of the find (specimens isolated, or aggregated?).

***Arenorbis squamosus* (E. PICARD, 1858)**

This species, "*Aspidura squamosa*" of E. PICARD (1858, p. 431), commonly known in Germany and Poland, has long subjected to an extensive debate on its generic assessment and the associated (? closely related) two species established by E. PICARD (1858), and his son, Karl PICARD (1886), who assigned these three species to the genus *Acroura*, albeit with a question mark. It was already ECK (1872, p. 85) who classified the species *squamosa* within the genus *Ophioderma*. Such generic assignment has been shared by some subsequent authors (SCHÖNDORF 1914; KÖNIG 1920; KLINGHARDT 1930, 1933; ASSMANN 1937; F. KUTSCHER 1940; PIOTROWSKI 1986), but neglected by others (*e.g.* SCHMIDT 1928, HESS 1965, MÜLLER 1976). A further study by HESS (1970) resulted in a creation of the new genus *Arenorbis* HESS, 1970, with *Aspidura squamosa* of E. PICARD (1858) as the type of that genus which remains monotypic.

The species *Arenorbis squamosus* (E. PICARD, 1858) is known from many localities in Germany and the Silesia region in Poland, having been noted as common (F. KUTSCHER 1940). It ranges Lower through Upper Muschelkalk (SCHÖNDORF 1914, F. KUTSCHER 1940, M. KUTSCHER 2000), the Keuper *sensu* E. PICARD (1858) including (=euryhaline Warburg Formation of Upper Muschelkalk; H. HAGDORN, *pers. comm.*; cf. also ECK 1879, p. 47). The species seems to be most likely eurytopic, to survive hyperhaline conditions of the Middle Muschelkalk in Poland (see PIOTROWSKI 1986).

In Silesia, the first record of *Arenorbis squamosus* (E. PICARD, 1858) was ascribed, by ASSMANN (1937, p. 20), to ECK (1865, p. 50) who noted the presence of two specimens of "*Acroura* sp." (locality Chorzów). [F. KUTSCHER (1940, p. 11) did not accept this assignment, and suggested another interpretation]. An extensive collecting by Paul ASSMANN, first announced by himself (ASSMANN 1914, p. 284) and by SCHÖNDORF (1914, p. 215), gave about two hundred specimens from one locality (Roitza/Rojca near/at Beuthen/Bytom; see also KLINGHARDT 1930, 1933; F. KUTSCHER 1940, p. 5; HESS 1970), although lacking a note on their mode of occurrence (isolated, or aggregated; see ASSMANN 1937, p. 20). An evident aggregation was reported by PIOTROWSKI & LISZKOWSKI (1981 *internal circular*) who have found two slabs replete with ophiuroids amounting the figure of 120 (locality Będzin, Lower Muschelkalk) or 130 specimens (locality Wojkowice Kościelne; Middle Muschelkalk, *Diplopora* Dolomites). The latter slab was partly illustrated by PIOTROWSKI (1986, p. 107 and Pl. 39, Figs 1-2). The present repository of that slab is unknown (Dr. A. BOCZAROWSKI, *pers. comm.*), but its photo, once taken at the Institute of Geology, University of Warsaw, has safely survived to be included into this paper (Plate 3; its interpretation *in* Text-fig. 3).

The slab (see Plate 3) contains over 150 more or less complete skeletons associated with a maze of fragmented arms. Of the complete skeletons, noteworthy is a high frequency of juveniles and semi-adult specimens, which supposedly represent all ontogenetic classes of the species. The attitude of specimens cannot be recognized precisely as some are damaged, and their venter, or ventral side, seem to be visible due to abrasion of the disk oriented upwards. [Moreover, the

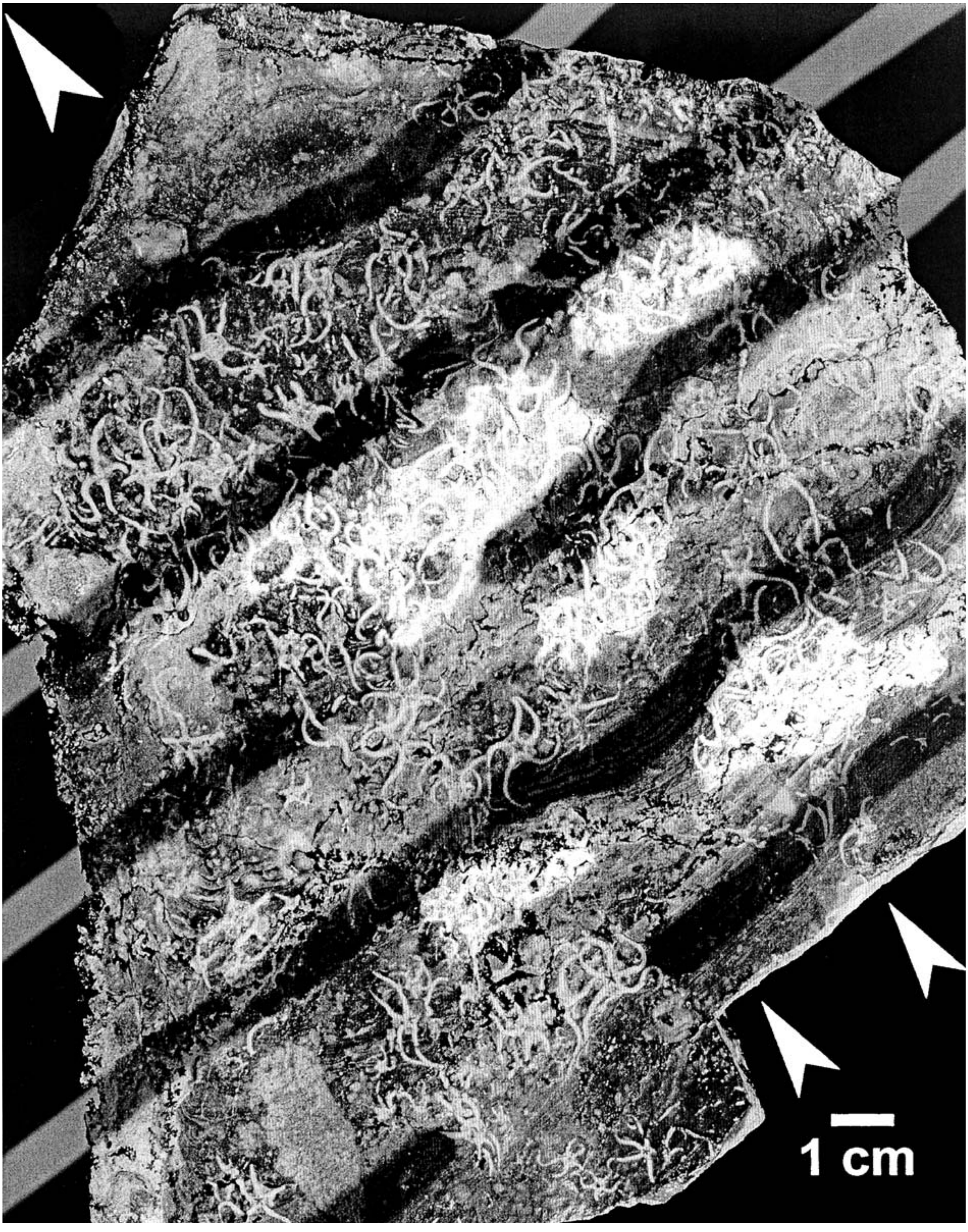
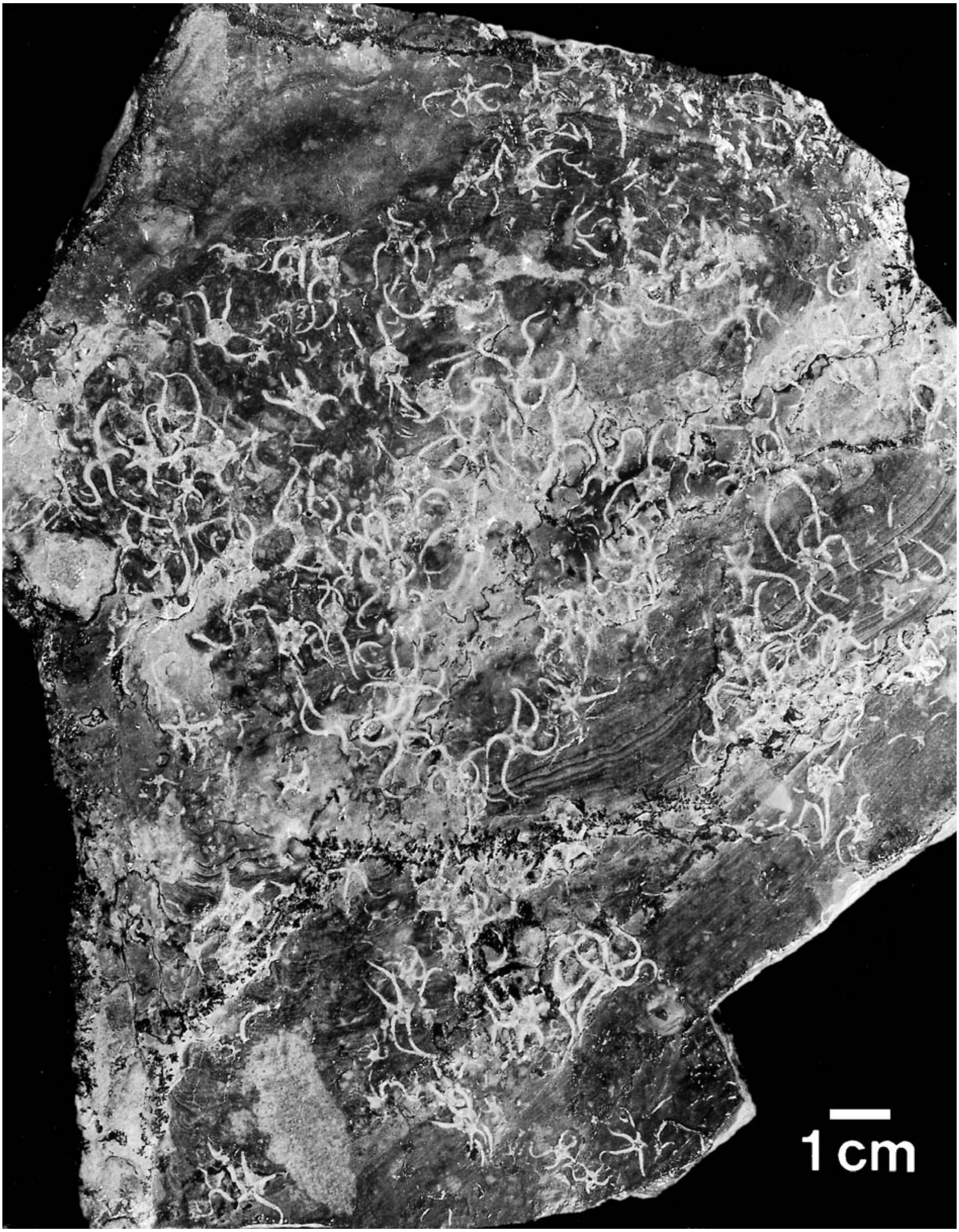


Fig. 3. Scan-sketch of the limestone slab containing mass-aggregated *Arenorbis squamosus* (E. PICARD, 1858) presented in Plate 3, to elucidate its supposed origin



Arenorbis squamosus (E. PICARD, 1858)

General view of the limestone slab (actual size), a part of which was presented by PIOTROWSKI (1986, Pl. 39, Fig. 1); The slab was then reported as collected by J. LISZKOWSKI, and kept at the Institute of Geology, Faculty of Earth Sciences, Silesian University at Sosnowiec (IG UŚ); locality was reported as the Middle Muschelkalk (*Diplopora* Dolomite) of Wojkowice Kościelne, Upper Silesia, southern Poland; photo through a water film; taken by S.K. ZIELIŃSKA (1979)

total image is slightly diffused as the photo was taken through a thin film of water; when the slab was dry, the ophiuroids vanished from sight almost totally!].

An interpretation of the complex taphonomic structure of the ophiuroid assemblage preserved in this slab, and its dependence upon sedimentary structures of the slab, is presented in the form of a scan-sketch (Text-fig. 3). This ophiuroid assemblage is hypothesized to have been formed by transport of still alive (? torpid) and/or newly dead specimens over a bottom sculptured by current ripplemarks, the crests of which (*hatched*) display scrolls of lamination on their stoss-sides. If so, it is easy to recognize that the hank-like maze of entangled ophiuroid material (? corpses, and fragmented arms) is distributed in patches (*whitened*) within the troughs along leeside of the crests; the apparent current direction is indicated by arrows. Many of the complete specimens, especially those outside the hank-like patches, have their arms outstretched along this very direction indicated as of the current (*arrowed*). These are interpreted as the current-oriented arms of specimens either tethered, or of corpses, rather than those of live specimens vigorously moving forward (suggested by KLINGHARDT 1930, Figs 1-2, *and* 1933; DIETL & MUNDLOS 1972, Fig. 11). The slab presented by DIETL & MUNDLOS (1972, Fig. 2) is herein regarded to have formed in a way identical to that studied, to bear the ophiuroids combed by a current.

To conclude from that interpretation (see Text-fig. 3), the studied assemblage of *Arenorbis squamosus* (E. PICARD, 1858) represents typically a *thanatocoenosis* that comprises all ontogenetic classes transported from their original habitat(s) (=*hypoautochthonous assemblage* of ARONSON 1992*b*) and killed prior to, or during, their transport and deposition.

Another aggregation of this species, from the locality then reported as Roitza (*vel* Roitzka)/Rojca near/at Beuthen/Bytom has never been illustrated but discussed repeatedly (ASSMANN 1914; SCHÖNDORF 1914; KLINGHARDT 1930, 1933), and commented still by F. KUTSCHER (1940, p. 5) and recently by ARONSON (1989, p. 22, Table 2; *and* 1992b, p. 6, Table 2).

Ophioderma hauchecorni (ECK, 1872)

This distinctly large-sized species (disk diameter 22 mm!), whose separateness had been objected by POHLIG (1878), but positively reconsidered by ECK (1879), and whose generic assignment is still doubtful (see SCHMIDT 1928, pp. 131-132; HESS 1965, p. 159), was vaguely established by ECK (1872) upon two fragmentary specimens [the holotype (ECK 1872, Pl. 1, Fig. 2) is a combined picture of these two specimens] from the Lower Muschelkalk of Rüdersdorf near Berlin. It was reported from a coeval sequence in Silesia (locality Scharley/Szarlej) by ASSMANN (1914, p. 297; *and* 1937, p. 20), but it has not been taken into account by F. KUTSCHER (1940, pp. 14-15).

The species name is herein kept in its original spelling of ECK (1872; see also ZITTEL *in* ECK 1879, pp. 36-37; HESS 1965, p. 159), accordingly with the ICZN rules, instead of that with the character 'e' introduced by ECK himself (1879) and followed by some authors (SCHMIDT 1928, F. KUTSCHER 1940).

Aspiduriella scutellata (BLUMENBACH, 1804)

This species, the type of the genus *Aspiduriella* BOLETTE, 1998, with which the species "*Aspidura loricata* GOLDFUSS, 1833" is synonymized (see POHLIG 1878; SCHMIDT 1928, p. 130; F. KUTSCHER 1940, p. 13; HESS 1965, p. 155; not accepted by SPENCER & WRIGHT 1966, p. *U*95), ranging Lower to Upper Muschelkalk, has credibly been reported from Silesia (one specimen, locality Chorzów) only by ECK (1865, p. 49; see also ASSMANN 1937, p. 21; F. KUTSCHER 1940, pp. 10 and 14). The species seems to be typical of the Upper Muschelkalk, according to most of the newer reports (see SCHMIDT 1928; MÜLLER 1969, 1976; SEILACHER 1988; CALZADA & GUTIÉRREZ 1988; HAGDORN 1985, 1999).

This species is the only of the Muschelkalk forms that has been reported from the Tethyan Realm of the Venetian Alps, and noted as common by ZEUSCHNER (1844, p. 56, as "*Ophiura scutellata*"; see also ECK 1879, pp. 48-50; and F. KUTSCHER 1940, p. 13).

FINAL REMARKS

A general conclusion of inter- to shallow subtidal environmental conditions under which the studied ophiuroids in the Lower Muschelkalk (*Łukowa Beds*) of the Holy Cross region lived, and were buried, is amazingly concordant with that offered by KAŹMIERCZAK & PSZCZÓŁKOWSKI (1969) upon their studies of enteropneustan burrows. It can not be however recognized which agent was decisive for the death of an ophiuroid community that produced the studied brittlestar bed of the genus *Aspiduriella*. Both an overwarming and a salinity drop (? or, a rise) may be taken into account. Salinity fluctuations, caused either by terrestrial outwash or evaporation, would in any way indicate, together with the overwarming conditions, the vanishing seaway connection of the Holy Cross area to the Tethys Ocean at Lower Muschelkalk time.

Consequently, the genus *Aspiduriella* ranging in the Alpine Realm up to the Upper Triassic (mid-Carnian; see ROSSI RONCHETTI 1965, cf. also BROGLIO LORIGA & CAVICCHI 1969), is thought to have really been a refugee from the Muschelkalk Basin at Middle Muschelkalk time when this lost connection to the Tethys, and became hypersaline, thus eliminating ophiuroids from the animal spectrum. At Upper Muschelkalk time, to the German part of the Muschelkalk Basin the genus *Aspiduriella* re-entered from the Tethys through a new seaway, the Burgundy Gate throughout the Vindelician Land, not opened yet at Lower Muschelkalk time (see Text-fig. 1; cf. also SCHWARZ 1975, TRAMMER 1980, HAGDORN 1991).

The suggested inter- to shallow subtidal environment of the studied Lower Muschelkalk succession, precisely of the *Łukowa Beds*, is well suited within the Holy Cross area whose setting was marginal to the extent of the Middle Triassic marine basin of Central Europe (see Text-fig. 1). Within this basin in Poland, open marine conditions have however spread, temporarily at least, as far as the site documented by the Żebrak borehole near Warsaw, some 200 kms northeast of the Holy Cross area (see Text-fig. 1). The Lower Muschelkalk sequence in this borehole (depth 1005 m) still contains a terebratulid coquina with abundant holothurian sclerites and some ophiuroid remains/ossicles (SENKOWICZOWA 1972). The occurrence range of ophiuroids at Early Muschelkalk time was thus temporarily well extended, competing with fluctuating environmental conditions (water depth, temperature, salinity) that prevailed along the margins of the Middle Triassic (Muschelkalk) epicontinental sea in Poland. Further to the north, the Lower Muschelkalk sequence continues as far as the vicinity of Szczytno (borehole Olszyny) and the city of Ełk (see Text-fig. 1) where marl-sandy and/or dolomitic deposits still contain "typical Muschelkalk" bivalves, and lobsters (cf. KÖNIG 1920), as recognized by SZYPERKO-ŚLIWCZYŃSKA (1967, 1976). A high frequency of the inarticulate brachiopod *Lingula* in the whole Muschelkalk sequence of that region, reported by SZYPERKO-ŚLIWCZYŃSKA (1967), indicates environmental conditions so extreme shallow or, marginally marine, as documented for this brachiopod genus in present-day and other post-Palaeozoic occurrences (see EMIG & *al.* 1978, PLAZIAT & *al.* 1978, LEE & CAMPBELL 1987).

An overview of the reported mass-aggregated ophiuroid occurrences in the Muschelkalk Basin and the Tethyan Triassic sequence shows that presumably none of them represent an *in situ*, that is an autochthonous burial suggested by ARONSON (1989 and 1992b, p. 6, Table 2). All of them are evidently more less allochthonous, and as such they may speak of the monospecific structure of the communities, but do not inform about the life habit and behavior of particular species. Little, or almost nothing, has also been known about the ontogeny of particular species, although two reports on the preservation of juveniles have recently been given by HAGDORN (1985, 1999), in both cases of *Aspiduriella scutellata* (BLUMENBACH, 1804) from the Upper Muschelkalk of Germany. From the mode of occurrence of numerous babies nearby several adults, HAGDORN (1999) discusses a baby-sitting behavior of this species, competing with that of some present-day species (see BYRNE 1991, HENDLER & *al.* 1999, HENDLER 2000). These new discoveries are of a good hope that the biology of at least some Muschelkalk ophiuroids is to be seen in the coming future.

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