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Ecology of the Devonian charophyte algae from the Holy Cross Mts

ABSTRACT: Mass occurrence of the charophyte algae in the Devonian of the Holy Cross Mts was for the first time recorded. Charophyte species *Karpinskya oscolensis* has been found in the Middle to Upper Devonian boundary beds of the Gałęzice syncline. The associated echinoderm-spiculitic microfacies, distributional pattern and taphonomic data point to the autochthonous nature of the fossil assemblage. The very diversified biota of the charophyte-bearing level are to be interpreted as a relict of a unique community of the charophyte meadows related to generally open marine habitat. The non-actualistic, open marine character of the genus *Karpinskya* is emphasized.

INTRODUCTION

Among primitive, Silurian to Early Carboniferous charophyte algae the most typical are the Trochiliscaceae, differing from Recent forms in first order by the dextral coiling of the enveloping cells. They are known chiefly from the Devonian of the Soviet Union and North America, and they have also been found in Poland (Nehring 1971, Baliński 1973).

The present paper contains the results of investigations of a newly discovered mass occurrence of the Trochiliscaceae in the Devonian of the Holy Cross Mts (Text-fig. 1). The Trochiliscaceae, as opposed to general non-marine extant charophytes, are frequently associated with marine sediments and biota (*e.g.* Peck 1934, and others), and the described occurrence also belongs to this type. Conclusions from a detailed ecologic analysis are a basis for the discussion on paleoenvironmental significance of primitive charophytes (Racki 1981).

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tentaculitids, J. Malec, M. Sc. the ostracodes, and Dr. E. Głuchowski the crinoids, which is here gratefully acknowledged. Thanks are also due to L. Łuszczewska, M. Sc. and S. Skompski, M. Sc. for taking the most photos, and Mrs. L. Wawro for drawing figures.

GEOLOGIC SETTING, MATERIAL AND METHODS OF STUDY

The investigated gyrogonites (calcified parts of the female reproductive organ of charophytes) were found in the small rural quarry located on a hill south of Posłowice (in the northern limb of the Gałęzice syncline; *cf.* Text-figs 1—2) in the western part of the Holy Cross Mts. Organodetrital and coral limestones containing *Alveolitella*, *Alveolites* and *Crassialveolites* (see also Filonowicz 1973), exposed here, belong to the lowermost part of a thick sequence of stromatoporoid-coral limestones termed the Sitkówka Beds by Kaźmierczak (1971). They are traditionally (*see* Kaźmierczak 1971 for review) considered to be mainly of Upper Givetian age (= Stringocephalus Stage). However, a recent study of conodonts (Racki 1980) shows, that they span the Middle to Upper Devonian boundary.

The studied collection (up to 1000 specimens of gyrogonites) has been obtained by washing the more weathered and marly intercalations. Most of the gyrogonites are therefore compacted and weathered, and casts of oosphere are quite common (Text-fig. 3*h*). In addition, slightly etched surfaces of gyrogonite-bearing rock and thin sections were studied. An ecologic interpretation of the charophyte level was made after the microfacies investigations, and insoluble residuum were studied in quantitative terms (*see* Racki & Baliński 1981 for methods). Also preliminary geochemical characteristics of carbonate fraction were estimated for the calculation of Jaffrezo & Renard (1979) indexes for salinity [Sr + Na + + Kx4 + Mg/10] and for continental influences [Fe + Mnx2]. Elements K and Na were determined on *FLAPHO-4* flame photometer, and Mg, Sr, Fe and Mn were analyzed using *Pye-Unicam SP-1900* atomic absorption spectrophotometer in an air-acetylene flame.

PALEONTOLOGIC CHARACTERISTICS

Systematics of the Trochiliscaceae is a matter of considerable disagreement (*see* e.g. Peck & Morales 1966, Conkin & *al.* 1974, Sajdakovsky & Schaikin 1976, Wang Zhen & Lu Hui-nan 1980). The authors accept the concept of Croft (1952), who distinguished two morphological groups (= genera of Grambast 1962) within this family differing in their development of a polar ring-like structure. The proper recognition of

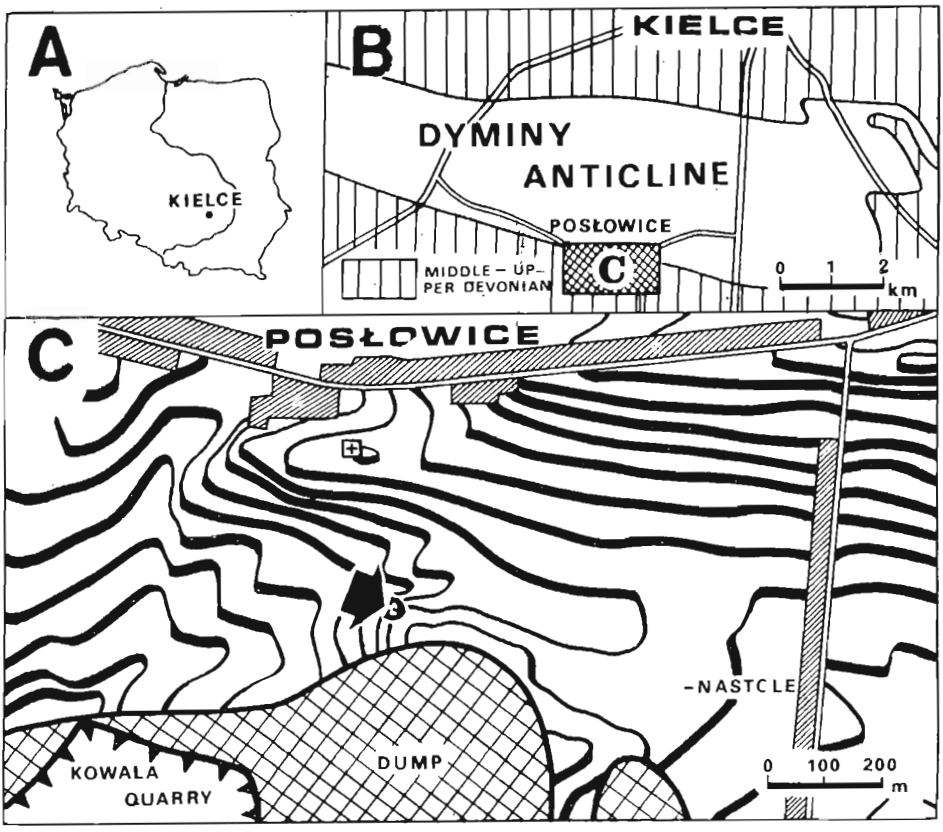


Fig. 1. Location of the charophyte-bearing deposits (*arrowed*) in Poland (**A**), Kielce region in the Holy Cross Mts (**B**), and in Posłowice area (**C**)

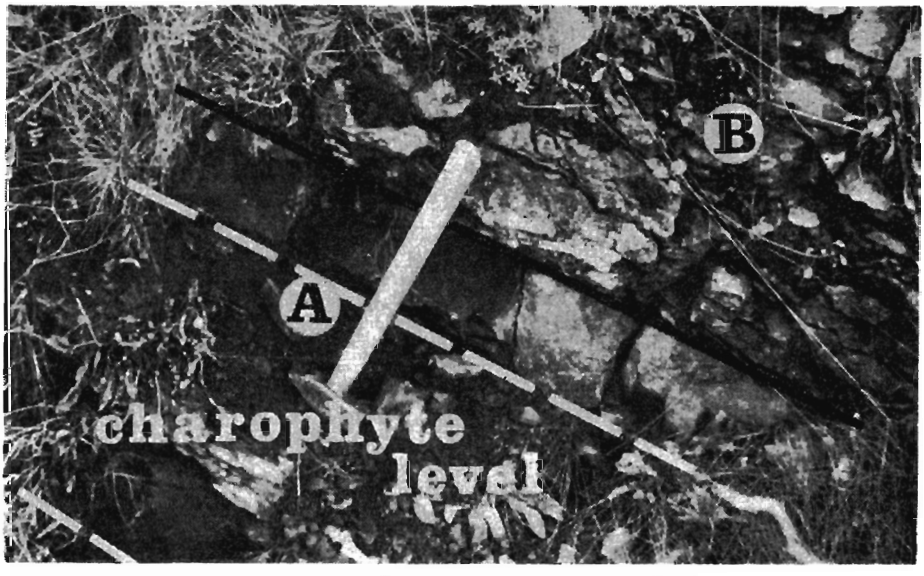
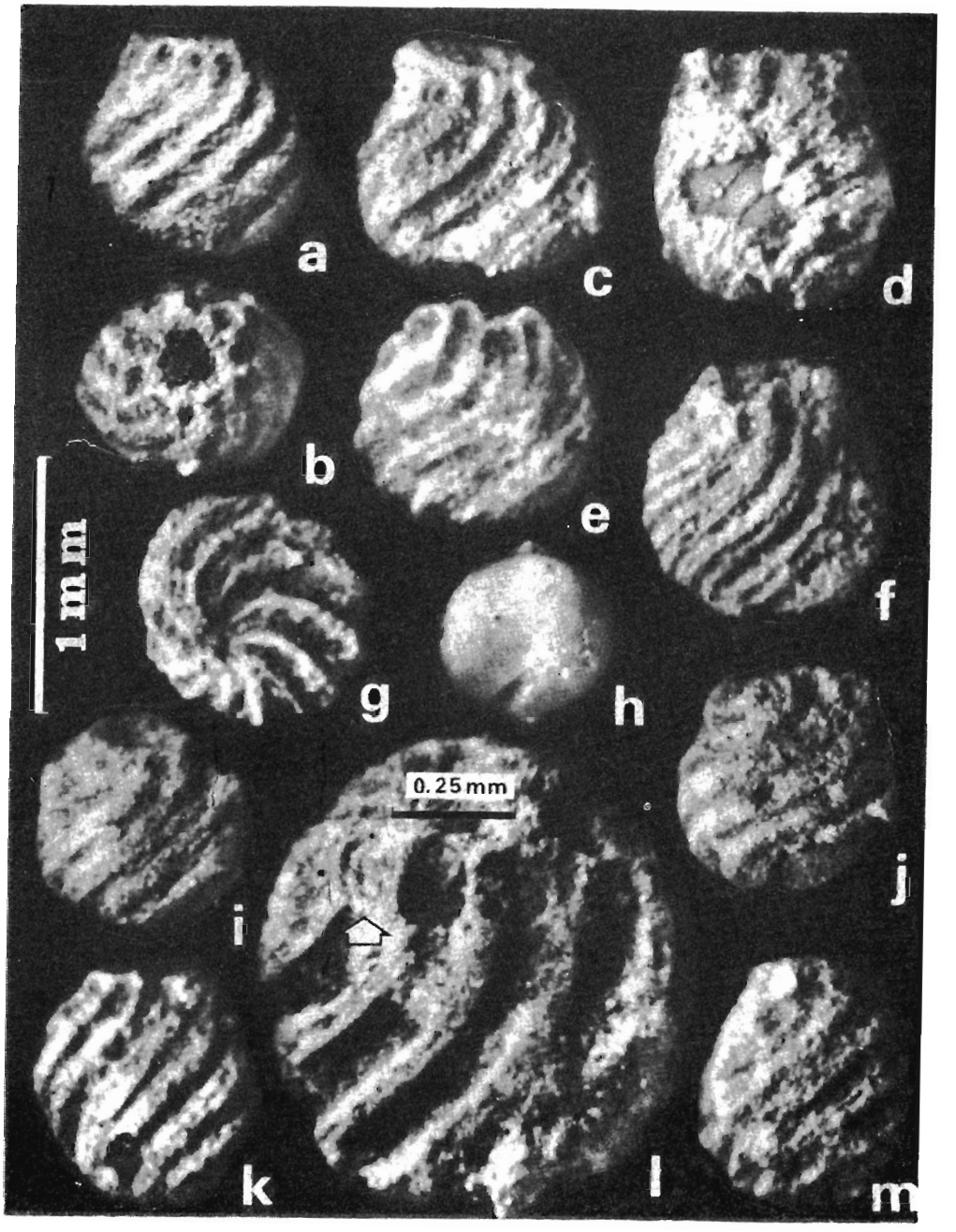


Fig. 2. Exposure of the charophyte-bearing deposits at Posłowice; **A-B** — lithologic sets distinguished in the sequence (*see* Text-fig. 5)



Gyrogonites *Karpinskya oscolensis* (Samoilova)

a, b — side and apical views of undistorted specimen; c-f, i-m — side views of gyrogonites; g — basal view of gyrogonite; h — cast of oosphere. Note prolate shape of gyrogonites (*e.g.* non-compacted specimen in Fig. 3*m*), different development and preservation of coronula cells (*e.g.* coronula unit — arrowed, and pits after them in Fig. 3*i*; *see also* Peck 1934, Pl. 11, Fig. 5), as well as variability of spiral cells due to various degree of their calcification

this structure may be difficult due to the mode of calcification and/or preservation (*see* Peck 1934, Kesling & Boneham 1966, Peck & Morales 1966, Rice 1970, Conkin & *al.* 1974) and therefore the concept of the genus *Moellerina* and associated species is unclear (*compare* Peck & Morales 1966 with Conkin & *al.* 1974, *and* Conkin & Conkin 1977).

The traditional (*after* Peck 1934) orientation of gyrogonites is confirmed by the presence of a plate (Pl. 1, Fig. 5a-b) first recognized in the coronulate Trochiliscaceae, which identifies its basal pole (Malsov 1963).

Genus *KARPINSKYA* (Croft, 1952) Grambast, 1962

Karpinksya oscolensis (Samoilova, 1961)

(Text-fig. 3 and Pl. 1)

Synonymy: **1961. *Trochiliscus (Karpinskya) oscolensis* n. sp.; Samoilova, p. 206, Figs 1—3.**

Remarks. The state of preservation of the material sometimes makes it difficult to recognize details of the apical structure. However, the studied gyrogonites obviously belong to the coronulate genus *Karpinskya*. The following features point to their identity with *K. oscolensis*: (*1*) large size (*see* Table 1), (*2*) spheroidal-ellipsoidal shape (in Horn's terminology; *vide* Peck & Morales 1966), and (*3*) high equatorial angle. There are only small differences in the diameter of the basal opening. The studied gyrogonites display some variability in the character of the spiral cells and coronula, but similar differentiation most probably occurs in the Russian species. This identification is also supported by the biogeographic data, because *K. oscolensis* was described from the Upper Givetian of the Kursk area (Central Devonian Field) in the Soviet Union.

Table 1

Measurements (in *mm*) of *Karpinskya oscolensis* (Samoilova)

	Height of gyrogonite with coronula	Width of gyrogonite	Height of coronula	Width of coronula	Diameter of apical opening	Diameter of basal opening	Number of spiral cells
Range	0.82-1.20	0.77-1.15	0.12-0.24	0.36-0.67	0.14-0.31	0.05-0.12	9-10
Average	1.00	0.94	0.22	0.50	0.22	0.10	10
Number of measurements	71	74	33	43	32	22	16

Nevertheless, interspecific limits of the 3 known species of *Karpinskya* are not very clear. Some of the largest specimens (*e.g.* Text-fig 3*d, f*) are similar to *K. laticostata* (Peck, 1934) from the Lower Carboniferous of the USA (*cf.* Peck & Morales 1966, Conkin & *al.* 1974), but differ in having their prolate shape, as well as generally weaker calcification of the spiral cells. The studied material is distinguished from the American Devonian species *K. bilineata* (Peck, 1934) by its generally larger size (*see also* Peck & Morales 1966, Conkin & Conkin 1977). In all the other aspects *K. oscolensis* and *K. bilineata* seem to be quite similar and may be conspecific (see diagnosis of *K. bilineata* in Conkin & *al.* 1974).

ECOLOGIC SETTING OF THE CHAROPHYTE LEVEL

COMPOSITION OF THE ASSEMBLAGE

Members of the following groups were stated (approximately in order of biovolume) in the assemblage of the charophyte-bearing level at Posłowice (asterisked are the dominant taxa within the given taxonomic group):

Tabulata: *Cladopora* sp.*, *Thamnopora* sp. (identified by Dr. A. Nowiński);
Charophyta: *Karpinskya oscolensis* (Samoilova);
Echinoidea: *Kongielechinus magnituberculatus* Jesionek-Szymańska *, 2 other unidentified genera (spines, coronal plates, Aristotle lantern elements, tooths; identified by Dr. W. Jesionek-Szymańska);
Brachiopoda: *Crurithyris "inflata"* (Schnur) *, *Productella* sp.;
Gastropoda: *Tropidodiscus* sp.*, *Halopea* sp., *Euomphalus* sp., *?Platyceras* sp. (identified by Dr. L. Karczewski);
Spongiae: monaxone spicules;
Tentaculitida: *Dicricoconus mesodevonicus* Lyashenko (identified by Dr. B. Hajłasz);
Ostracoda: *Microcheilinella* cf. *fecunda* (Přibyl & Snajdr) *, *Aparchites* cf. *crumena* (Kummerow), *Bairdia* sp., *Bairdiocypris* sp., *?Hollinella* sp., *?Svislinella* sp. (identified by J. Malec, M. Sc.);
Crinoidea: *Stenocrinus degradus* Dubatolova *, *Anthinocrinus kulagaiensis* Dubatolova, *Exaesiodiscus minutus* (Moore & Jeffords), *?Hexacrinites* sp., *Mediocrinus* sp. (identified by Dr. E. Głuchowski);
Ophiuroidea: arm plates;
Pisces: Acanthoda (tooths, scales), Crossopterygi (ornamented scales);
Bryozoa: Cryptostomata;
Holothurioidea: *Eucaudina* sp.

In thin sections the following fossils were also recorded: algae (chiefly *Girvanella*), tubular foraminifera and some microproblematics, and in residuum: conodonts (narrow-platformed polygnathids, *Ozarkodina brevis*, icriodids, compounds forms), scolecodonts and lingulids.

This assemblage is unique in the stromatoporoid-coral sequences of the Sitkówka Beds in containing both a high diversity fauna and predominance of open-marine faunal groups (*e.g.* echinoderms, sponges, tentaculitids). Presence of the orthoceratid nautiloids, scutellid trilobites, some brachiopods (atrypids, *Schizophoria*; for others see Filonowicz 1973) and tetracorals (*Disphyllum, Dębnikella*; identified by T. Wrzołek, M. Sc.) at Posłowice section is notable in this context.

TAPHONOMIC DATA

The investigated fossil assemblage includes remains which vary widely in their size and geometric form, but the more abundant forms are small and strongly elongated. Fossil orientation (Text-fig. 4) sometimes

points to current action and this is consistent with frequency of single valves of brachiopods and ostracodes (Text-figs 4—5 and Pl. 2). On the other hand, it is evident that many of the mechanical distortions can be

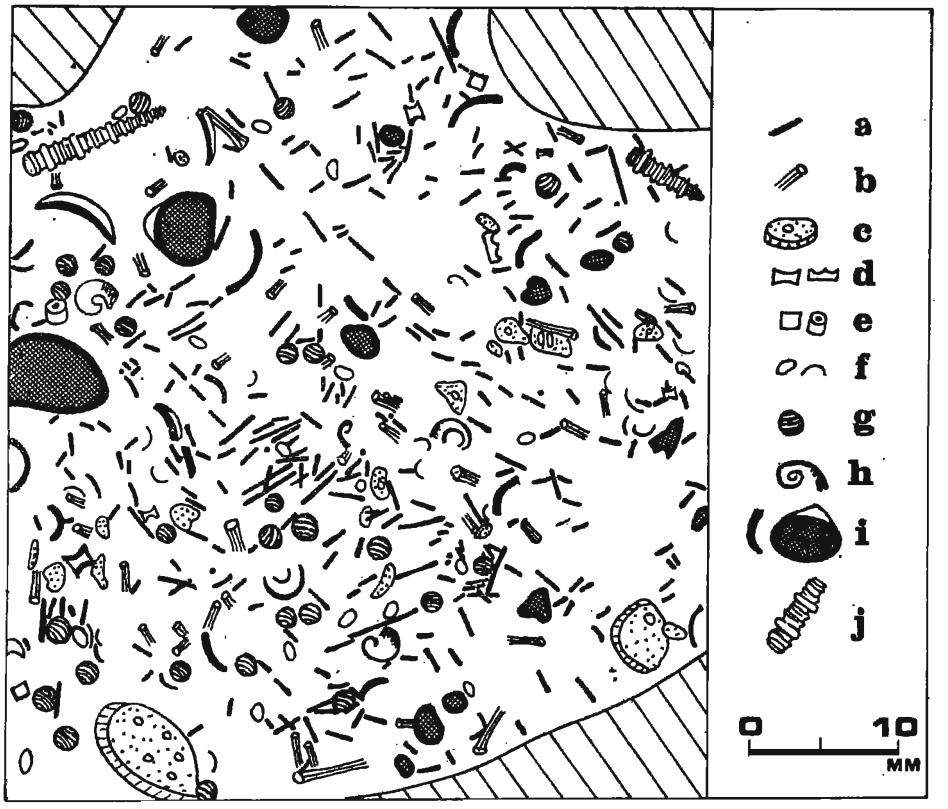


Fig. 4. Fragment of etched surface of the gyrogonite-bearing limestone from Posłowice; note slightly directional arrangement of spicules and echinoid spines
a spicules, *b* echinoid spines, *c* echinoid plates, *d* ophiuroid plates, *e* crinoid columnals, *f* ostracodes, *g* gyrogonites, *h* gastropods, *i* brachiopods, *j* tentaculitids

attributed to compaction (*see* Pl. 1, Fig. 8; and Pl. 2). As a whole the fossil assemblage is rather well preserved. Fragile skeletal remains (*e.g.* microornamentation of brachiopod valves) are quite common. Also gyrogonite ridges are occasionally present with sharp crests (*cf.* Text-fig. 3 and Pl. 1). Their weaker preservation is probably related chiefly to the degree of weathering and/or diagenetic effects of compaction (*see* Hacquaert 1932).

MICROFACIES DATA

The charophytes are almost exclusively found in a thin (about 50 cm) level of dark, bituminous limestone associated with irregular shale par-

tings (Text-figs 2 and 5). This level forms the most important part of the sequence of calcarenites and calcisiltites containing a poor coral fauna. Microfacially they represent packed, echinoderm-spiculitic biomicrites and biopelmicrites, frequently with a clotted structure of neomorphised micritic matrix (Pl. 2). The charophyte-bearing level is distinguished by a better developed nodular structure. This kind of limestones is usually interpreted as deposits of a low to moderate energy environment with quick bioclastic sedimentation and early submarine cementation. As indicated by the ostracode articulation, charophyte-bearing level can be marked by a slight lowering of energy level (*see* Text.--fig. 5).

GEOCHEMICAL DATA

There is no distinct trend in changes of geochemical indexes in the Posłowice section (Text-fig. 5). But amphiporoid-microproblematics limestones, both at this locality (below and above of the measured section)

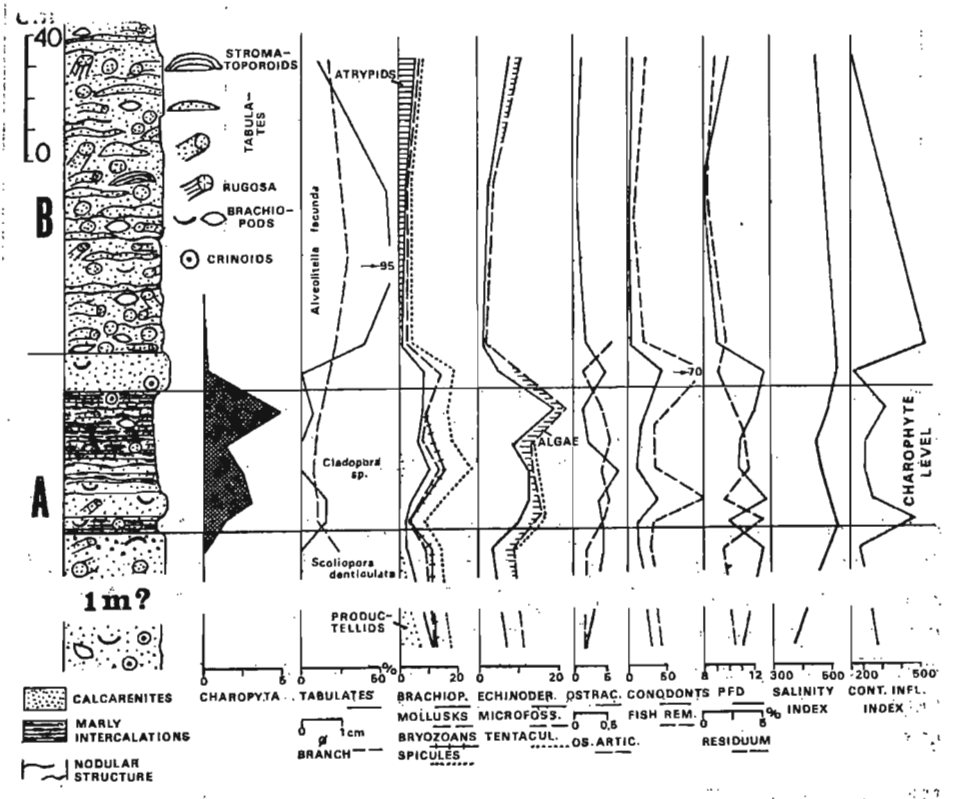


Fig. 5. Results of microfacial, residuum and geochemical investigations of the Posłowice section

Frequencies of macrofaunal remains were estimated for area 100 mm², and spicules and microfaunal fraquencies for 1.44 mm² (average from 5 measurments); *OS. ARTIC.* — ostracode articulation, *PFD* — petrographic fossil diversity.

as at the other sites in the Holy Cross Mts, as well as crinoid and brachiopod limestones of Chęciny (*see* Racki & Baliński 1981) have distinctly lower salinity indexes in comparison to charophyte-bearing ones (170—290 and 230—330 respectively).

SPATIAL DISTRIBUTION

Locality of Posłowice is the first known Devonian site with abundant charophytes in the Holy Cross Mts. It must be noted however, that their time and facies equivalents (lower part of platy limestones of Filonowicz 1973) are very poorly exposed in the central part of the Holy Cross Mts. Singular gyrogonites of the Trochiliscaceae were reported by Baliński (1973) from the stromatoporoid-coral limestones at Jurkowice-Budy in the eastern part of the Holy Cross Mts.

ENVIRONMENTAL INTERPRETATION OF THE CHAROPHYTE LEVEL

The presented data on taphonomy, petrology and spatial distribution suggest that large scale postmortem transport of any element of the analyzed assemblage is unlikely. At the time of the Middle to Upper Devonian boundary the nearest land environment (as possible source of freshwater fossils) was certainly outside the Holy Cross region (*see* Pajchlowa 1970, Baliński 1973).

At present, there is no evidence for the existence of nearby emerged areas, *e.g.* an island suggested by Sobolev (1909). All known sediments of this age are pure carbonates with many organic build-ups (Kaźmierczak 1971). Also in the investigated section residuum and geochemical data (Text-fig. 5) point to low and almost unvariable continental supply.

Bituminosity of charophyte-bearing limestones, and their probably limited distribution indicate rather their relation to local gross development of algal meadows (*cf.* Poyarkov 1966, Samoilova & Prinada 1966) in the offshore part of a vast carbonate shelf. It seems that most of the studied epifauna-dominated assemblage is autochthonous and directly or indirectly associated with algal growth (*see* e.g. Johnson 1964). In fact, an abundance of small gastropods with moderately streamed shells suggests simple trophic relationships (*cf.* Peel 1978, Linsley 1979). The extraordinary high abundances (in stromatoporoid-coral facies) of such groups as echinoids, tentaculitids, ostracodes, and fishes, which might had found suitable life conditions in presence of large accumulations of plant matter, may be coincidental, but could equally represent a "life assemblage". There are similarities to others late Paleozoic plant dominated marine biota, *e.g.* of the phylloid algal organic build-ups (*see* Toomey 1976 for review).

Abundance of diminutive fauna and strong domination of particular taxonomic group by single species indicates a probably high environmental stress, in spite of high assemblage diversity reflecting a richness of available ecologic niches offered by the phytal community.

Higher juvenile mortality of ambocoellid brachiopods, possible decrease of size of crinoid columnals and presence exclusively in the charophyte-bearing level of thin-branched tabulate species (*see* Text-fig. 5) suggest a deterioration of their life conditions. These adverse ecologic changes are also supposed by shifts in frequencies of organic components, especially by a higher frequency of ambocelliid brachiopods (characteristically a pioneer assemblage of restricted lagoons; *see* Jux & Strauch 1965), absence of other open-marine faunal group occurring in the Posłowice section, lowering of conodont frequency and decrease in petrographic fossil diversity. It is therefore concluded that charophytes are connected with some worsening of a biotope for the marine biota.

Consequently, it seems probable that this fossil assemblage of the charophyte-bearing level at Posłowice represents, in large part, a relict of a unique community of charophyte meadows or rather several directly adjacent and strictly ecologic unified biocoenoses. Habitats of these biota are related to the waters with at most slightly brackish or fluctuating salinity (*see* geochemical index in Text-fig. 5) in semiprotected sheltered part of intershoal area, surrounded among others by thickets of tabulate corals. In a sense components of *Karpinskya oscolensis* assemblage represent the most euryhaline forms of generally open-marine groups.

Consequently, *Karpinskya oscolensis* was presumably a charophyte species adapted to generally open marine, offshore conditions. This conclusion agrees well with data on ecology of this species in several regions of the Soviet Union (*see* Samoilova & Prinada 1966, Samoilova 1967), as well as of the American species of the genus (*see* Peck & Morales 1966). Therefore, the genus *Karpinskya* is the best documented representative of non-actualistic, open marine ecologic group of the early charophytes (Racki 1981).

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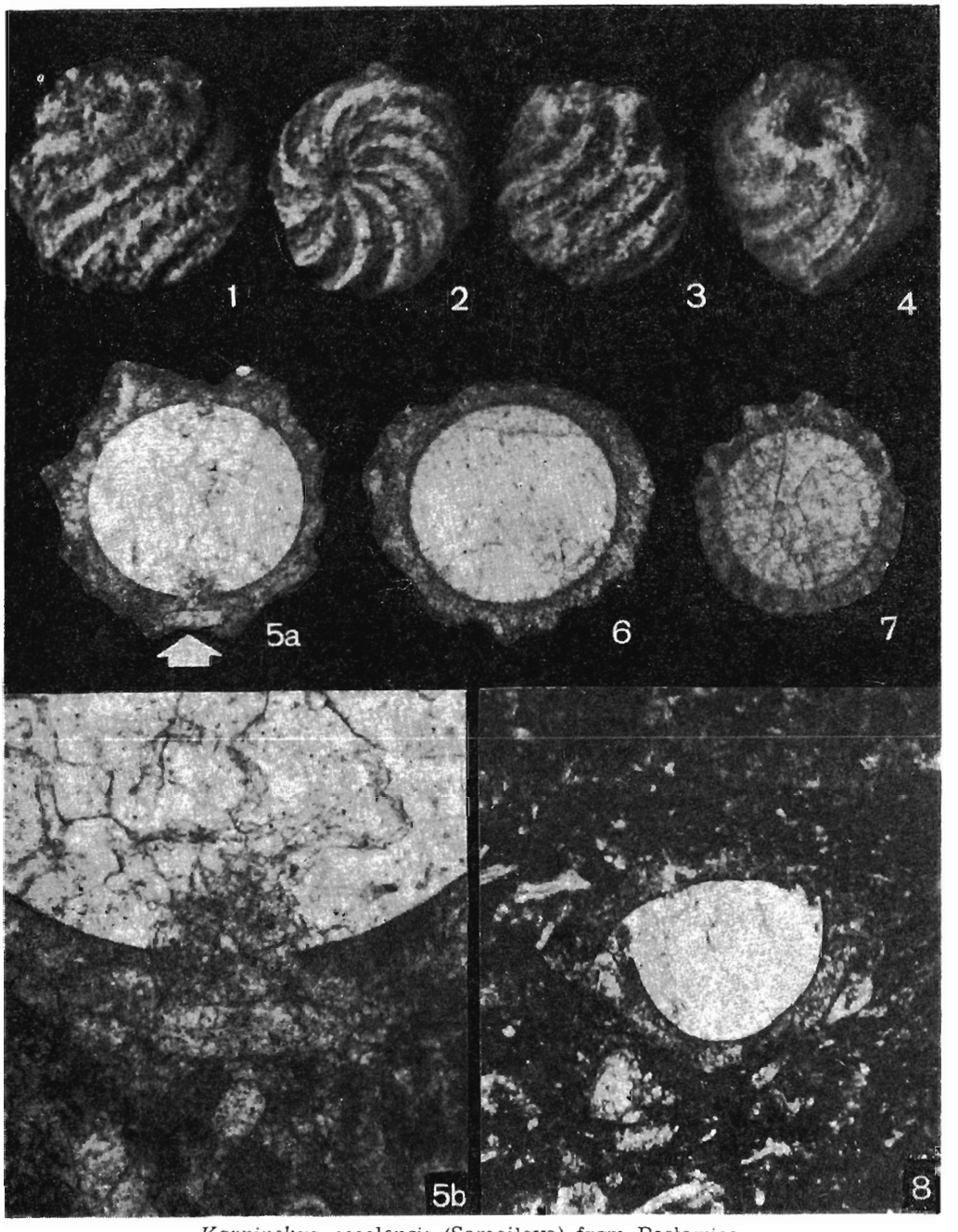
G. RACKI i M. RACKA

EKOLOGIA RAMIENIC (CHAROPHYTA) Z DEWONU GÓR ŚWIĘTOKRZYSKICH

(Streszczenie)

W wapieniach stromatoporoidowo-koralowcowych (pogranicze dewonu środkowego i górnego) odsłaniających się w Posłowicach (synklina gałęzicka) stwierdzono (*patrz* fig. 1—5, tabela 1 oraz pl. 1—2) masowe występowanie glonów z gromady ramienic (Charophyta), oznaczonych jako *Karpinskya oscolensis* (Samoilova). Mikrofacja szkarłupniowo-spikulowa, przypuszczalnie lokalny zasięg geograficzny, oraz dane tafonomiczne wskazują na autochtoniczny charakter bardzo urozamiconego zespołu skamieniałości z poziomu zawierającego badane ramienice. Zespół ten zinterpretowano jako relikt unikalnej biocenozy łąk glonowych rozwiniętych w pełnomorskim środowisku o co najwyżej nieznacznie brakicznym lub zmiennym zasoleniu. Nieaktualistyczny charakter wymagań ekologicznych rodzaju *Karpinskya* wynika także z danych pochodzących z innych obszarów (*patrz* Racki 1981).

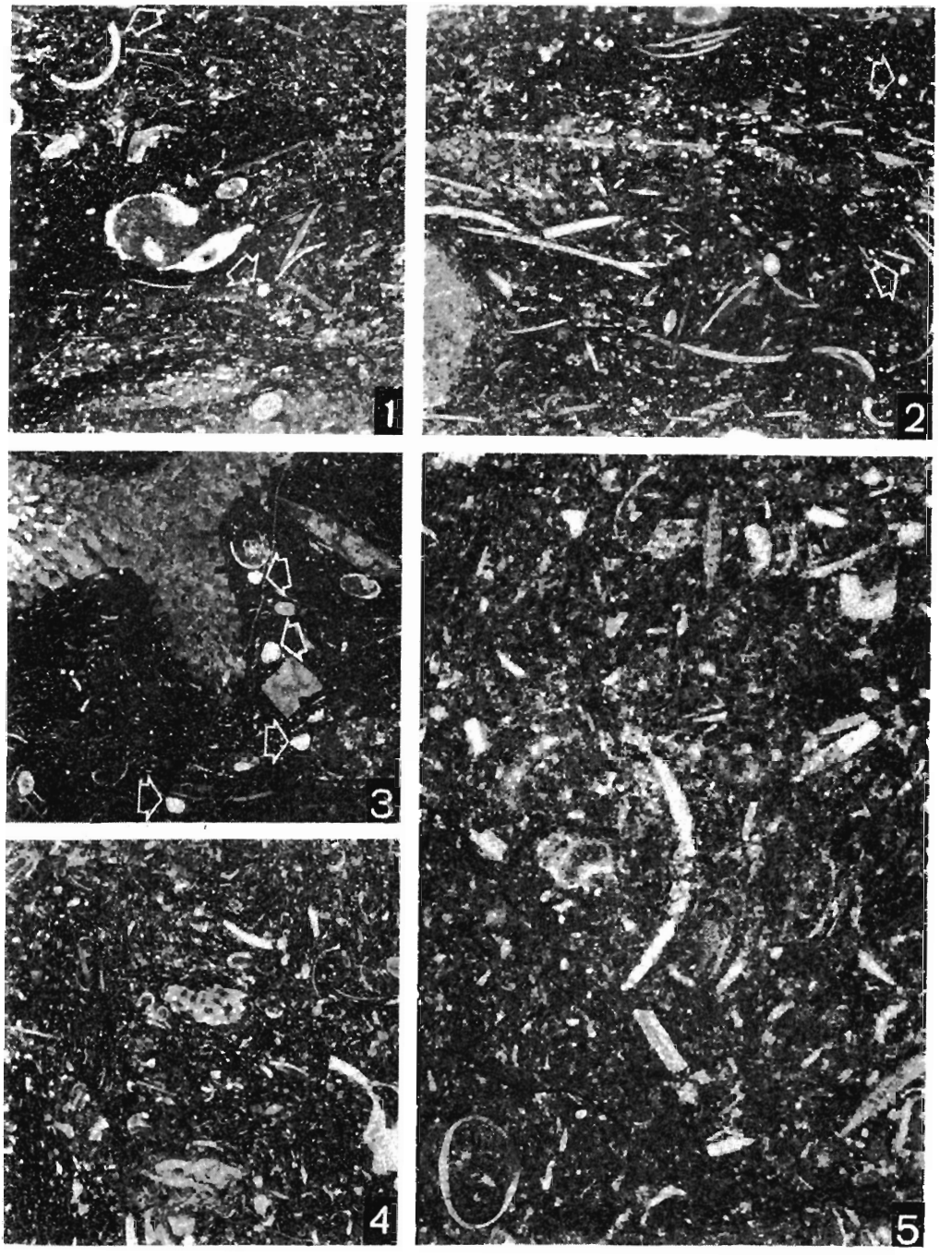


Karpinskya oscolensis (Samoilova) from Posłowice

1, 3 — side, **2** — basal, and **4** — oblique views of gyrogonites; **5a-5b** — approximately longitudinal, and **6-7** — oblique sections of gyrogonites; **8** — detail of charophyte microfacies with compactional structure

Note different preservation and calcification of gyrogonites, and the presence of the basal plate (arrowed in Fig. 5*a*, and magnified in Fig. 5*b*)

Figs 1—4 taken × 30, Figs 5*a* and 6—8 taken × 35, Fig. 5*b* taken × 100



Charophyte-bearing microfacies from Postowice

Gyrogonites (*arrowed*) of variable frequency within the numerous remains of echinoderms, sponge spicules, brachiopods, ostracodes, and gastropods; note the lighter parts of the deposit displaying cementation structure (Figs 1—2); Figs 1—4 taken × 5, Fig. 5 taken × 15