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A new atrypid brachiopod, *Desquamatia macroumbonata* sp. n., from the Middle to Upper Devonian boundary beds of the Holy Cross Mts

ABSTRACT: The atrypid brachiopod *Desquamatia macroumbonata* sp. n. from the Middle to Upper Devonian boundary beds of the Holy Cross Mts, Central Poland, is described and analyzed from ecologic and stratigraphic viewpoint. This new, large-beaked and small-sized species belongs to pedunculate forms adopted to regimes of higher, at least periodically, hydrodynamic activity which strongly influenced the brachiopod association of the stromatoporoid shoal. The species has acquired a narrow stratigraphic range and it is thus recognized as a key for the biostratigraphic division of the stromatoporoid-coral sequence of the Holy Cross Devonian.

INTRODUCTION

The atrypid brachiopods constitute the most common shelly fossils in the stromatoporoid-coral limestones representing the Middle to Upper Devonian boundary beds (Sitkówka Beds of KAŹMIERCZAK 1971) of the south-western part of the Holy Cross Mts, Central Poland. The brachiopods from these beds are insufficiently known up till now and only one species belonging to the world-wide distributed genus *Desquamatia* has recently been monographed (RACKI & BALIŃSKI 1981).

The report is a part of the Ph. D. thesis (RACKI 1982) which has been done in the Institute of Paleobiology of the Polish Academy of Sciences, under the supervision of Professor G. BIERNAT.

The investigated paleontologic collection is housed at the Silesian University at Sosnowiec, Department of Earth Sciences, and kept under the cataloque numbers *GIUS* 4-194 *Jz*, 4-195 *Zl*, 4-196 *SG*.

MATERIAL

Almost 350 specimens of *Desquamatia macroumbonata* sp. n. were collected in the northern part of the Jaźwica Quarry near Bolechowice in the Holy Cross Mts (Text-figs 1 and 3*A*). Most specimens were gathered from the waste of the strongly weathered parts of massive limestones. In times of exploitation the karstified limestiones were left by the quarrymen, and now they are

forming a rocky bolt that divides northeren and southern parts of the quarry (Text-fig. 3*A—B*). Numerous juvenile specimens have been obtained by washing of the weathered limestone parts.

Compact limestones from the nearby Zelejowa Hill (western quarry) and Sowie Hill near Miedzianka (eastern quarry — *see* Text-fig. 1) yielded only a small part of the considered collection.

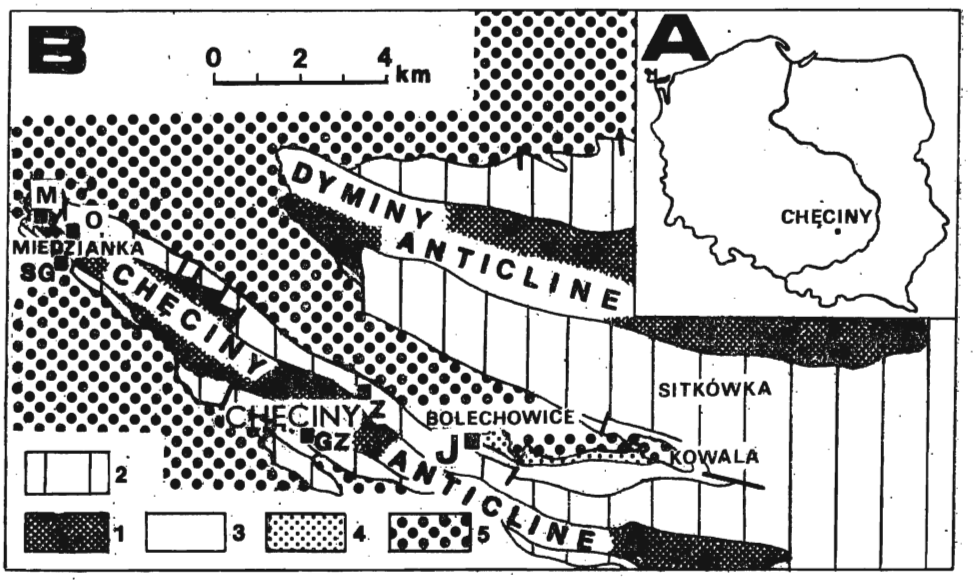


Fig. 1. Location of outcrops discussed in the text, in Poland (A), and in the south-western part of the Holy Cross Mts (B); *after* Szulczewski (1971, Text. 1; *simplified*)

1 Cambrian, Ordovician and Silurian; *2* Lower and Middle Devonian; *3* Upper Devonian; *4* Lower Carboniferous; *5* post-Variscan cover

J — Jaźwica Quarry; **Z** — western Zelejowa Quarry; **O** — Ołowianka Quarry; **SG** — eastern Sowie Hill Quarry; **M** — Miedzianka Hill; **GZ** — western quarry in the Zamkowa Hill

STRATIGRAPHIC AND REGIONAL SETTING

New species of *Desquamatia* occurs in the higher (but not topmost) part of the stromatoporoid-coral sequence in all localities. Everywhere it strongly dominated the brachiopod fauna from the thick (up to 50 m) sets of gray, massive to poorly-bedded stromatoporoid limestones (set *H* of the Jaźwica section in Text-fig. 2; *see also* RACKI 1981).

Basic problem of stage attribution and lithostratigraphic division of the stromatoporoid-coral limestones is still an open question (*see* RACKI 1980, SZULCZEWSKI 1981). In this paper the Givetian/Frasnian boundary is placed at boundary between sets *G* and *H* of the Jaźwica section (Text-fig. 2). Occurrence of the Kadzielnia Limestone (*see* SZULCZEWSKI & RACKI 1981) of early Frasnian age in sets directly overlying the boundary (set *J* of RACKI 1981) is significant in this context.

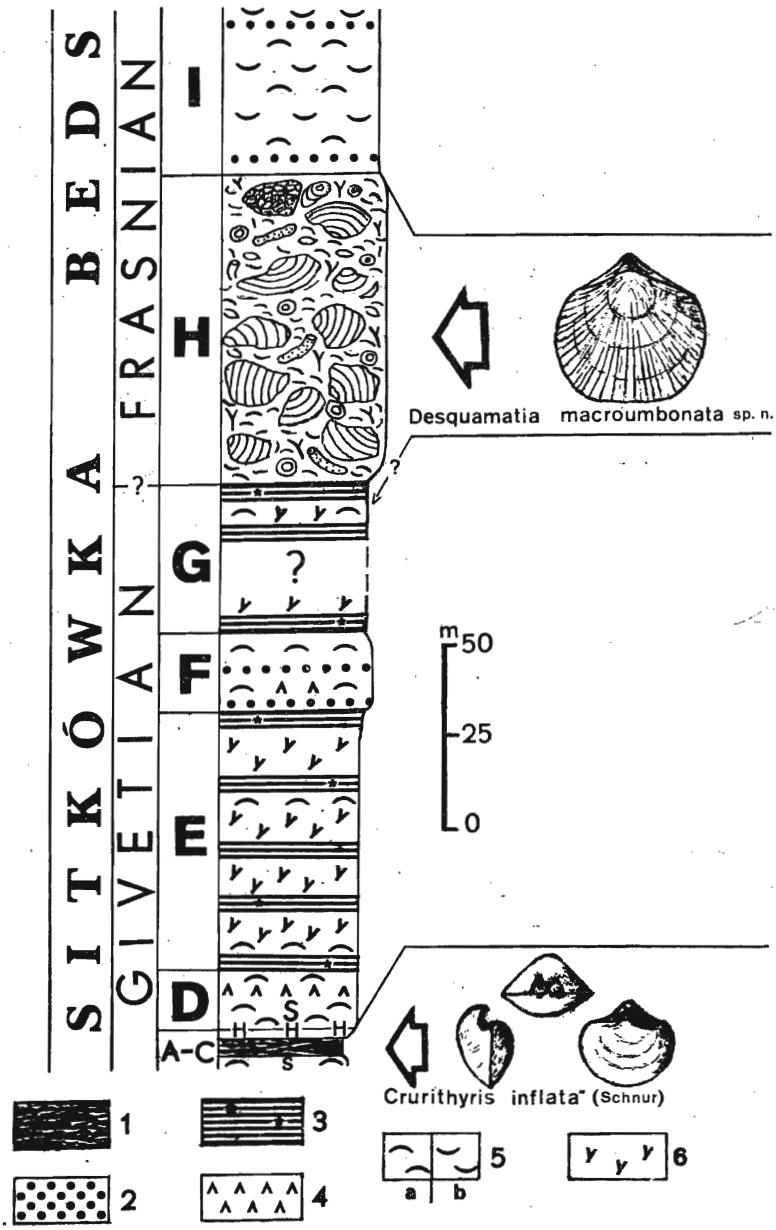


Fig. 2. Section of the Jaźwica Quarry near Bolechowice (*see also* Racki 1981); arrowed are sets containing abundant brachiopods

A-I — lithologic sets; 1 micritic limestones with marly intercalations and shelly fauna; 2 calcarenites with crinoids and/or brachiopods; 3 cryptoalgal laminites with fenestrae; 4 coral ilmestones (H — *Hexagonaria*); 5 limestones with rock-forming massive stromatoporoids (*a* biostromes, *b* biorudites) and *Stachyodes* (S); 6 amphiporoid limestones

REMARKS ON THE GENUS *DESQUAMATIA*

Biconvex shell, large ortocline beak and tubular-lamellar rib structure point that the new species belongs to the nominative subgenus of *Desquamatia* as defined by COOPER (1967b, 1973, 1978). Author's observations on the ecologic constrains of the *Desquamatia* taxonomy suggest some inadequacy of the present subdivision of the genus. As discussed below, such diagnostic features of the subgenus *Desquamatia* as biconvexity, strongly enlarged interarea and very prominent beak, and weakly folded anterior comissure (*e.g.*, in the type species *Desquamatia khavae* ALEKSEEVA) can be explained exclusively by a pedunculate mode of life in higher-energy environments.

More strict recognition of the habit and habitat relationships for particular species and/or species-groups (*see* e.g. study of ecophenotypic patterns of HURST 1978 and HURST & WATKINS 1978) is a first step towards more reliable — in biologic terms — taxonomy by selection of the characters which least, and best not, vary with environment (*see* JONES 1974). Consequently, in the present paper the genus *Desquamatia* is undivided into subgenera.

SYTEMATIC DESCRIPTION

Genus *Desquamatia* ALEKSEEVA, 1960
Desquamatia macroumbonata sp. n.
(Text-figs 4—7 and Pls 1—2)

HOLOTYPE: The specimen *GIUS 4-194 Jz-D|27*, illustrated in Pl. 1, Fig. 1a—1f.
TYPE HORIZON: Lowermost part (set *H* in Text-fig. 2) of the Upper Sitkówka Beds, lowermost Frasnian.
TYPE LOCALITY: Jaźwica Quarry, south of Bolechowice (Text-fig. 3), southern limb of the Gałęzice syncline in the Holy Cross Mts, Central Poland.
DERIVATION OF THE NAME: Latin *macroumbonata* — after possessing a large, protruding beak.

DIAGNOSIS: Small, finely-ribbed, circularly outlined and biconvex to weakly ventribiconvex *Desquamatia* with a very large, orthocline beak and feebly developed anterior fold, chiefly as medial depression in dorsal valve,; characterized by thin shell wall and internal structures, and large lateral cavities.

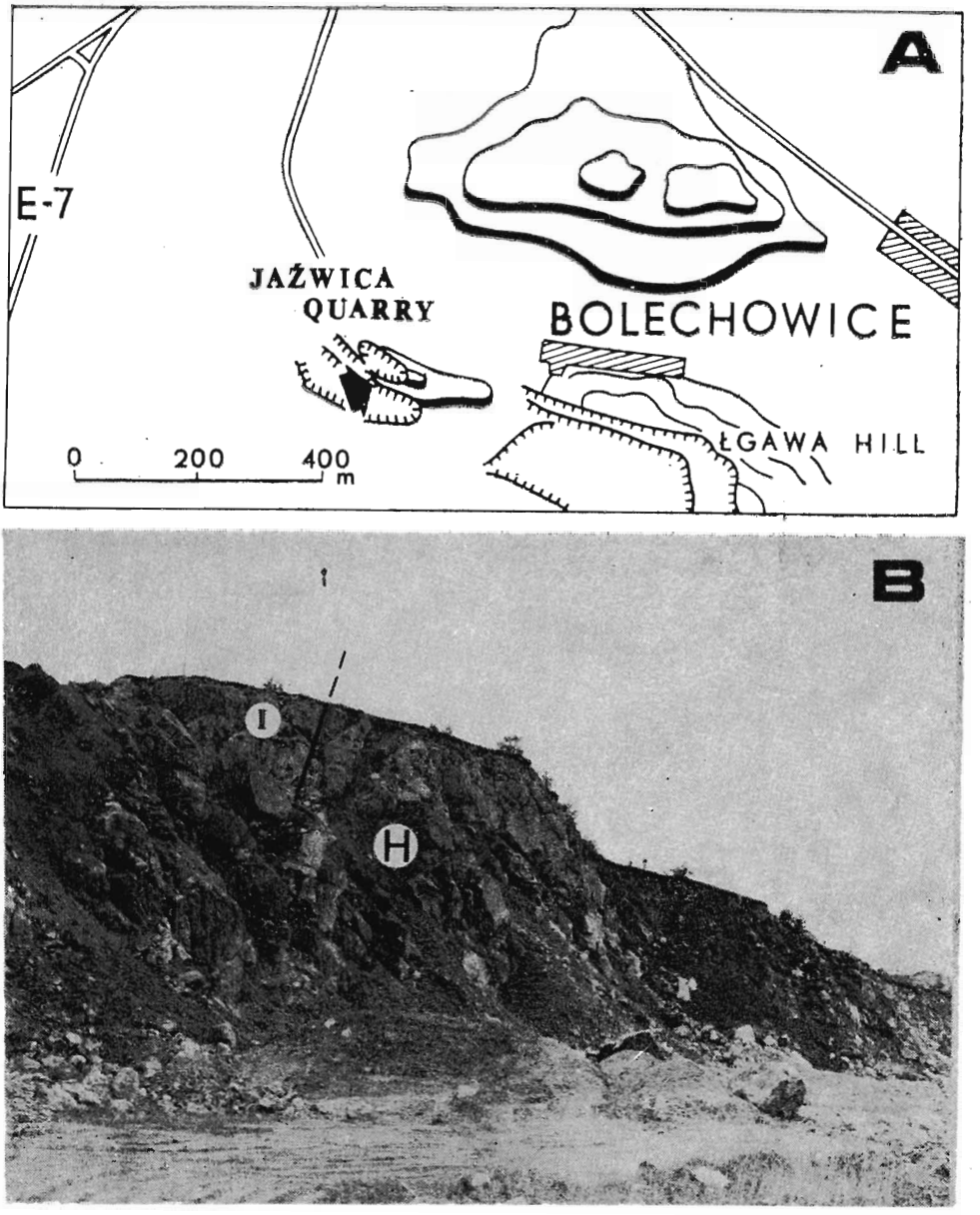
MATERIAL: 60 complete and 85 almost complete shells, and over 230 shell fragments, mostly weathered, sometimes par'ly deformed, exfoliated and recrystallized.

DESCRIPTION: Small-sized (up to 18 mm), non-globose, biconvex to slightly ventribiconvex, subcircular (length typically exceeding width) shells with distinctly curved cardinal margin; anterior commissure rectimarginate to weakly sulcate, frequently with shallow median depression in the dorsal valve (Pl. 1, Fig. 1c and Pl. 2, Fig. 5c).

Shell ornamented with fine, but coarsening distally costae bifurcating (and intercalating in dorsal valve) chiefly in the posterior part, and with closely spaced (1—2 mm), marginally crowded and slightly deflected, rather faint growth lamellae; only incipient frills are evidenced; microlines very delicate, up to 12 per milimeter.

Ventral valve bears a large beak protruding up to 2 mm above the dorsal apex, chiefly orthoclinal interarea with well-exposed deltidial plates (Text-fig. 4*B* and Pl. 1, Figs 1f, 8) and faint horizontal crenulation; submesothyridid pedicle opening is circular to ovoid in outline and (0.9—1.2 mm in diameter) has a distinct foraminal rim.

Shell wall is thin and muscle scars are only feebly impressed. Ventral valve has interiorly rather thin, long dental plates (*see* Pl. 1, Fig. 6), prominent, usually open lateral cavities and strong bilobate teeth; deltidial plates become hollow and split distally (*see* Text-fig. 5). Dorsal valve with not very thick hinge plates, showing a well-developed inner socket ridge and a distinct middle socket ridge; crural bases are thin, weakly knob-like and extended latero-ventrally; spiralia have up to 8—10 whorls (*see* Pl. 1, Fig. 7).



A — Location sketch map of the Jaźwica Quarry and the Łgawa Hill Quarry near Bolechowice; arrowed is the fragment of outcrop illustrated in Text-fig. 3*B*

B — Northern part of the Jaźwica Quarry, with a rocky bolt formed by *Desquamatia macroumbonata*-bearing stromatoporoid limestones in foreground and the overlying strata in background; *H-I* — lithologic sets (*see* Text-fig. 2)

VARIABILITY AND GROWTH: The smallest specimens, 1.2 mm in size (*see* Text-fig. 4*A*) are planar, elongated and ventribiconvex, with prominent, apsacline interarea, open delthyrium and strong median furrow in dorsal valve. On the other end, there are only singular specimens displaying gerontic characters, *i.e.* strongly deflected anterior commissure in dorsal direction, dorsibiconvexity and anacline beak incurvature (*see* Pl. 1, Fig. 3). Globose forms are virtually absent.

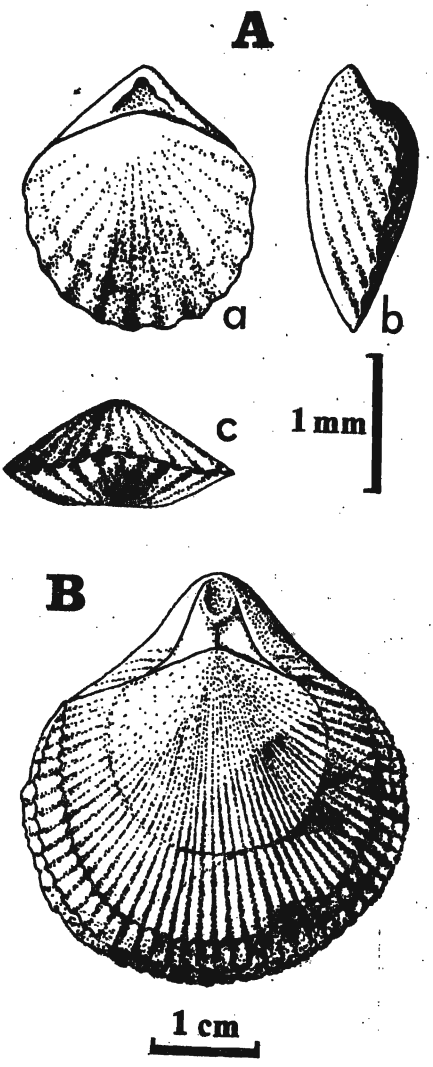


Fig. 4. *Desquamatia macroumbonata* sp. n.
A — Juvenile specimen in dorsal (*a*), lateral (*b*) and anterior (*c*) views
B — Small, immature specimen in dorsal view

There is much variation in mature shell shape and ornamentation, and the width index [width/ /length ratio] changes from 0.82 to 1.10 (Text-fig. 7). Some variability occurs also in the development of the anterior fold, convexities of valves and beak incurvature. A few specimens display an asymmetry (Pl. 2, Fig. 5).

REMARKS: Very prominent beak in comparison to small size is the most unique feature of the species. Similarly such large-beaked species, as the type species *Desquamatia khavae* ALEKSEEVA from the Eifelian of the Ural Mts (*see* ALEKSEEVA 1962, p. 60, Pl. 3, Fig. 6, Pl. 11, Fig. 2; JOHNSON & BOUCOT 1968, Pl. 160, Figs 11—15), as well as *Desquamatia hormophora* (CRICKMAY), *Desquamatia* (?) *matinobensis* (McCOMMON), and „*Atrypa*" *dignata* FENTON & FENTON from

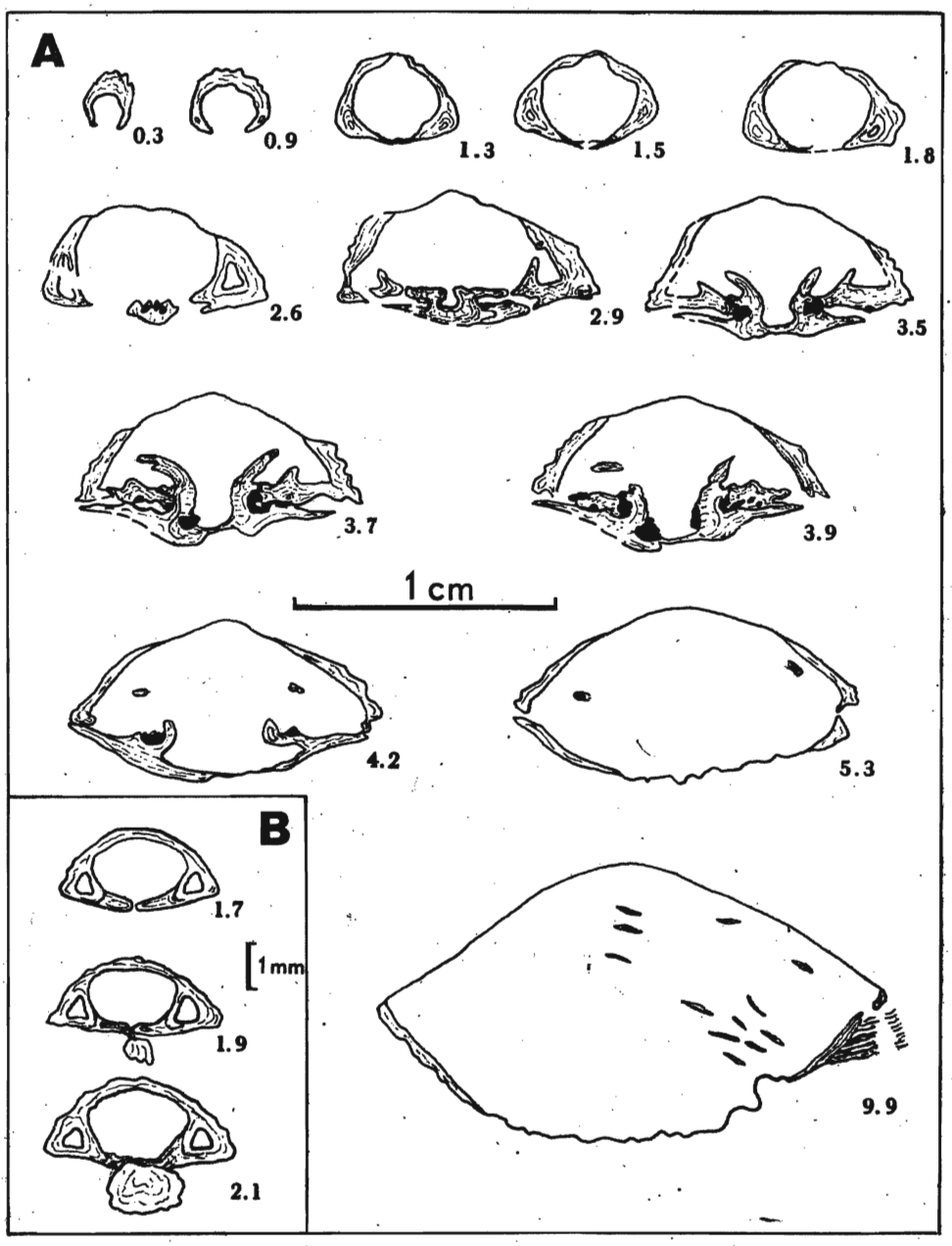
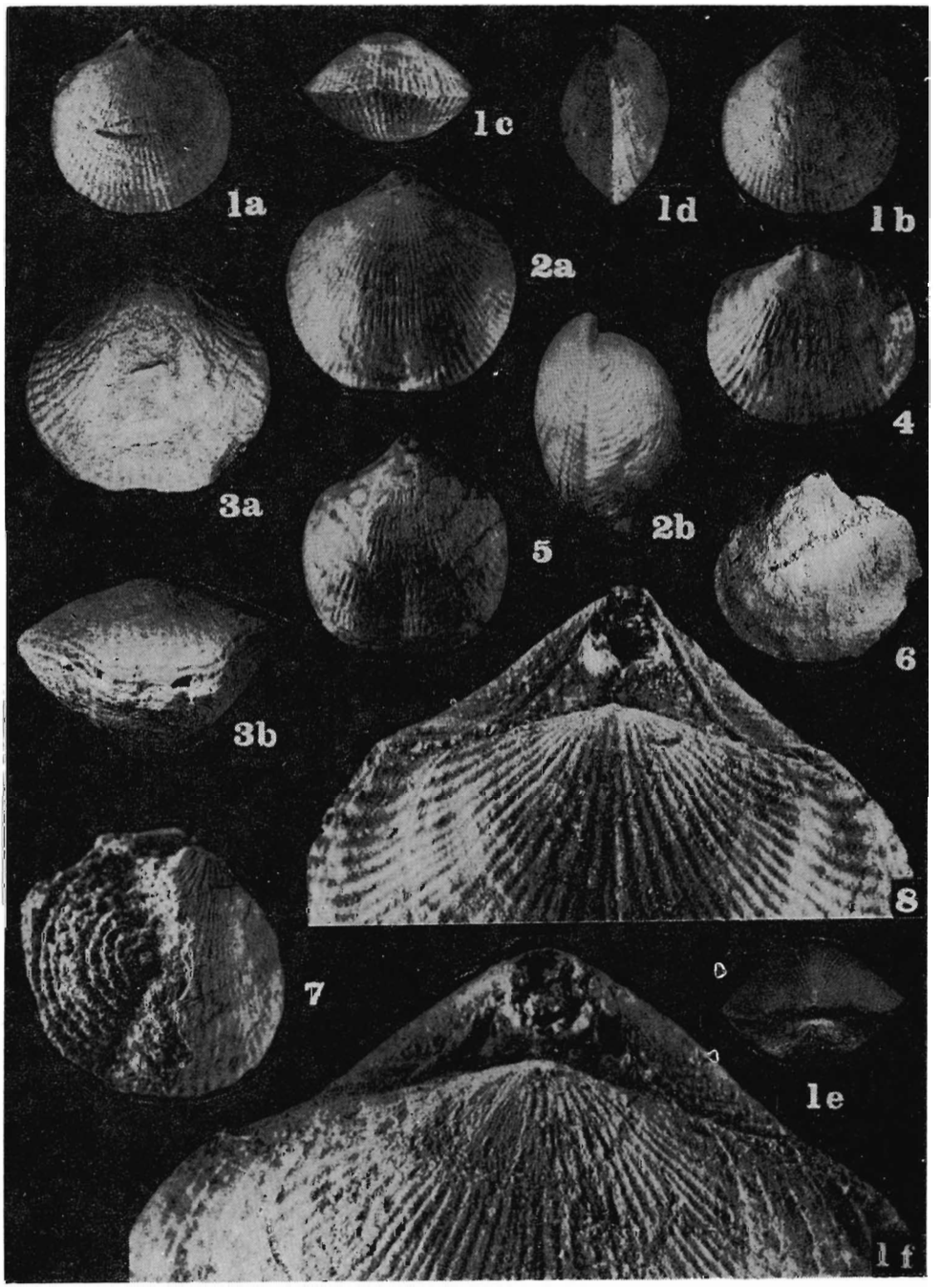
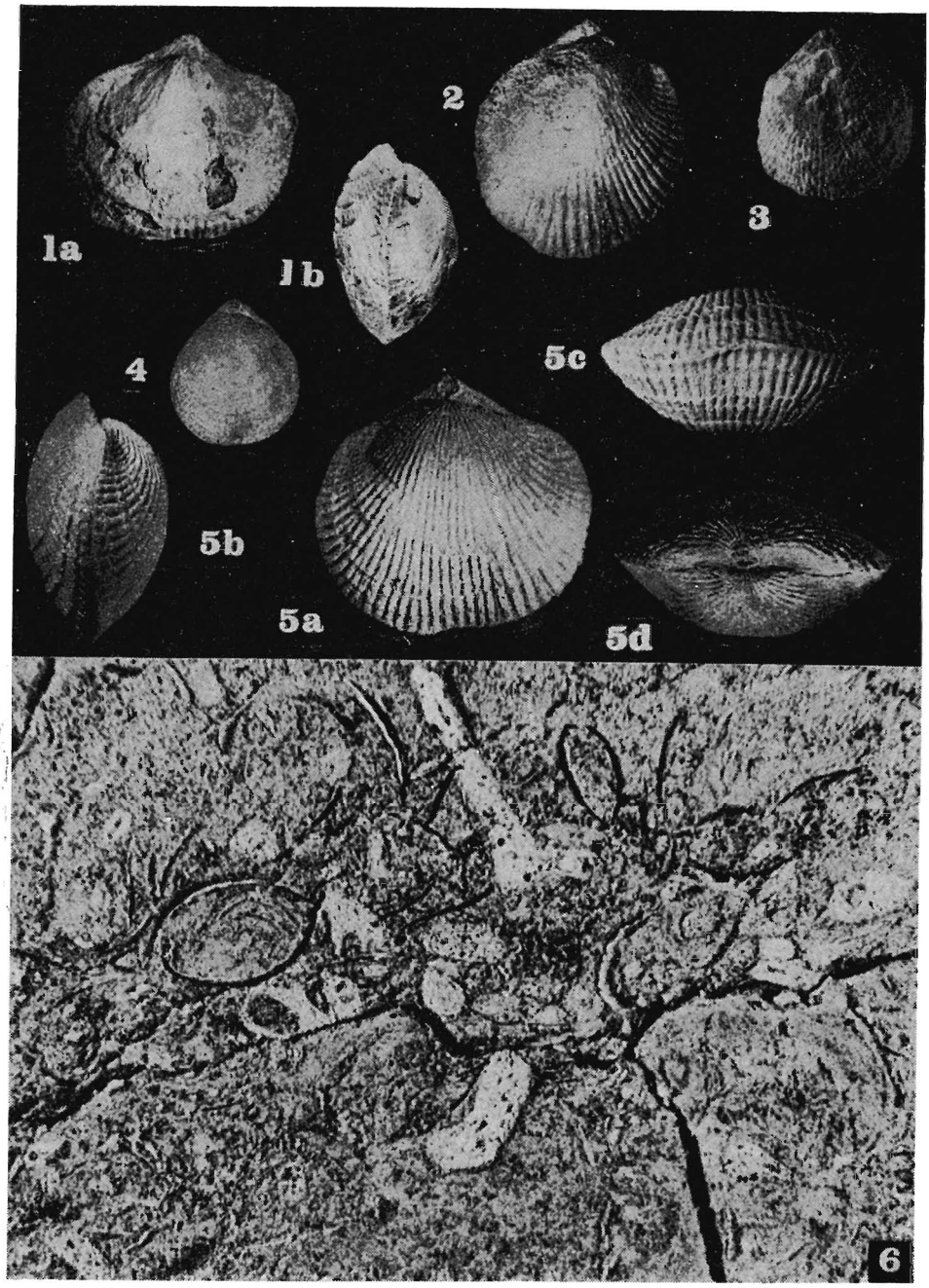


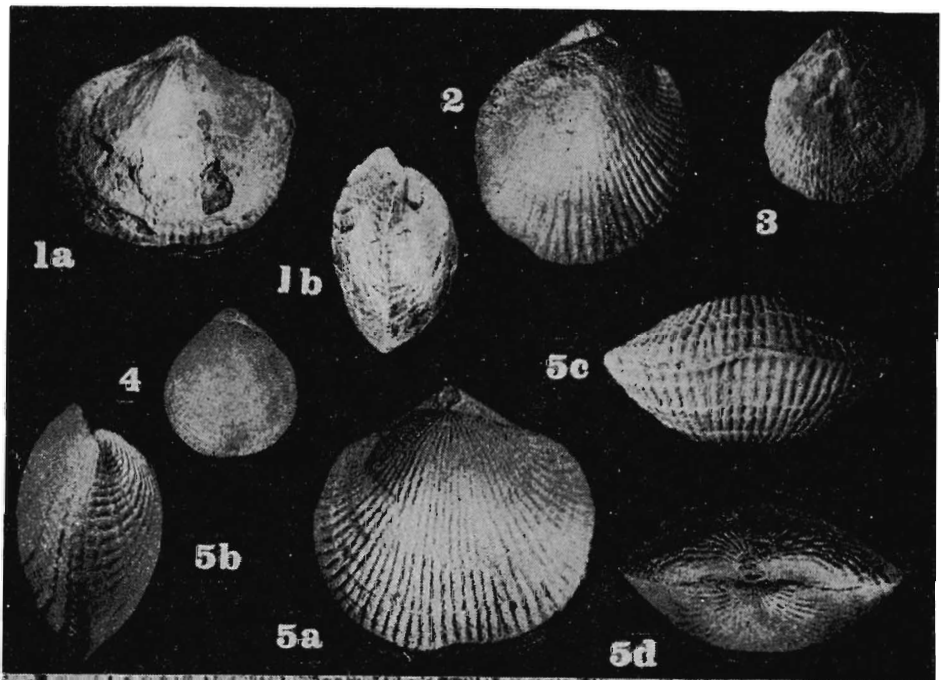
Fig. 5. Transverse serial sections of *Desquamatia macroumbonata* sp. n. for a large specimen from Zelejowa (A) and an adult specimen from Jaźwica (B — details of beak region only); blackened are silicified parts; numbers refer to distance in *mm* from the ventral apex



Desquamatia macroumbonata sp. n.: 1 — holotype in dorsal (*1a*), ventral (*1b*), anterior (*1c*), lateral (*1d*) and posterior (*1e*) views, and a magnified posterior part (*1f*); 2 — large specimen in dorsal (*2a*) and lateral (*2b*) views; 3 — untypical specimen with strong anterior fold in ventral (*3a*) and anterior (*3b*) views; 4—5 — extremely differently shaped specimens in dorsal views; 6 — decorticated shell in ventral view; 7 — damaged shell with exposed spiralia; 8 — posterior part of immature specimen; Jaźwica Quarry, set *H*; all taken × 2, except Fig. 7 (× 3), and Figs 1*f* and 8 (× 10)



Desquamatia macroumbonata sp. n.: 1 — wide specimen in dorsal (*1a*) and lateral (*1b*) views; 2 — thick-ribbed specimen in dorsal view; 3—4 — small, elongated specimens in dorsal views; 5 — large, bilaterally asymmetrical specimen in dorsal (*5a*), lateral (*5b*), anterior (*5c*) and posterior (*5d*) views; 6 — polished slab of atrypid-bearing limestone showing concentration of shells and valves jointly with ramose stromatoporoids; eastern Sowie Hill Quarry (1 and 6); Jaźwica Quarry (2 and 4—5), and western Zelejowa Quarry (3); all taken ×2, except Fig. 5 taken ×2.5



Desquamatia macroumbonata sp. n.: 1 — wide specimen in dorsal (*1a*) and lateral (*1b*) views; 2 — thick-ribbed specimen in dorsal view; 3—4 — small, elongated specimens in dorsal views; 5 — large, bilaterally asymmetrical specimen in dorsal (*5a*), lateral (*5b*), anterior (*5c*) and posterior (*5d*) views; 6 — polished slab of atrypid-bearing limestone showing concentration of shells and valves jointly with numerous stromatoporoids; eastern Skała Mill Quarry (1 and 6); Jaźwica Quarry (2 and 4—5), and western Zelejowa Quarry (3); all taken ×2, except Fig. 5 taken ×2.5

the Givetian of North America (*see* FENTON & FENTON 1930, p. 11, Pl. 2, Figs 10—11; McCOMMON 1960, p. 52, Pl. 8, Figs 13—14; CRICKMAY 1963, p. 15, Pl. 4, Figs 14—20, Pl. 11, Figs 1—4; KESLING & *al.* 1974, Pl. 3, Fig. 18, Pl. 4, Fig. 11) are always larger, thicker-ribbed (in some cases even very conspiciously), and have less equally convex valves (dorsibiconvexity) and better developed anterior fold.

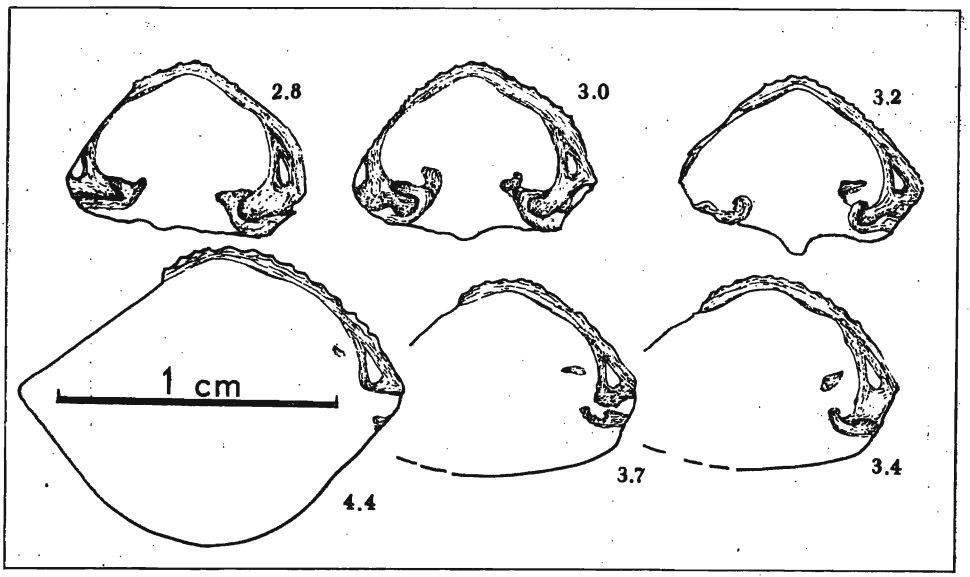


Fig. 6. Transverse sections of *Desquamatia macroumbonata* sp. n. for an adult specimen with damaged beak from Jaźwica; numbers refer to approximate distance in *mm* from the ventral apex

The similarly sized species, *Desquamatia cliipes* (CRICKMAY) from the Upper Frasnian of NW Canada (CRICKMAY 1957, p. 14 and Pl. 1, Figs 1—8 & 15; 1967, p. 5 and Pl. 1, Fig. 3), seems to differ only in having a smaller, more pointed beak and in extensive frill development; COOPER (1978, p. 296) considered this species as belonging to the subgenus *Desquamatia* (*Seratrypa*).

The new species, *Desquamatia macroumbonata* sp. n., can readily be distinguished from *D. globosa* (GÜRICH), the common species in the Givetian/Frasnian boundary beds of the Holy Cross Mts (RACKI & BALIŃSKI 1981), by smaller size, biconvexity, almost rectimarginate anterior commissure and a very large beak. A few large-beaked specimens of *D. globosa* were found at Sitkówka. Seemingly, the new species has evolved from *D. globosa* as result of progressive adaptation to a local, higher hydrodynamic, „reefal" habitat, possibly by paedomorphosis, as exemplified e. g. by *Tegulorhynchia* (*see* McNAMARA 1983).

OCCURRENCE: The species *Desquamatia macroumbonata* sp. n. occurs in strata of lowermost Frasnian age (Upper Sitkówka Beds) at the Jaźwica Quarry, south of Bolechowice, the western Zelejowa Quarry, and the eastern Sowie Hill Quarry near Miedzianka. Fragmentary specimens attributable to *D. macroumbonata* were found in the set *G* (?Givetian) of the Jaźwica section, and in western slope of the Miedzianka Hill, in the Ołowianka Quarry near Miedzianka, and at Sitkówka (*see* Text-fig. 1).

ECOLOGY

The new species, *Desquamatia macroumbonata* sp. n., is thought to be a typical element of a stromatoproid-shoal assemblage. Its lithologic setting are organodetrital limestones composed chiefly of overturned and frequently broken skeletons

of stromatoporoids embedded in fine-grained matrix (*see* Text-fig. 2 and Pl. 2, Fig. 6); high micrite content and the presence of only small lithoclasts suggest a fluctuating hydrodynamic activity in the environment of deposition, what agrees well with an interpretation presented by KAŹMIERCZAK (1971) for all the Sitkówka Beds.

This stromatoporoid-shoal was dominated (Text-fig. 8) chiefly by small, massive, nodular-shaped (possibly *Actinostroma* and *?Pseudodictyon*; *see* KAŹMIERCZAK 1971), and ramose (including *Amphipora*) stromatoporoids; dendroid corals (*Thamnopora*, *Thamnophyllum*, *Disphyllum*) and heteractinid calcareous sponges (as evidenced by numerous octactine spicules) played subordinary function in this buildup.

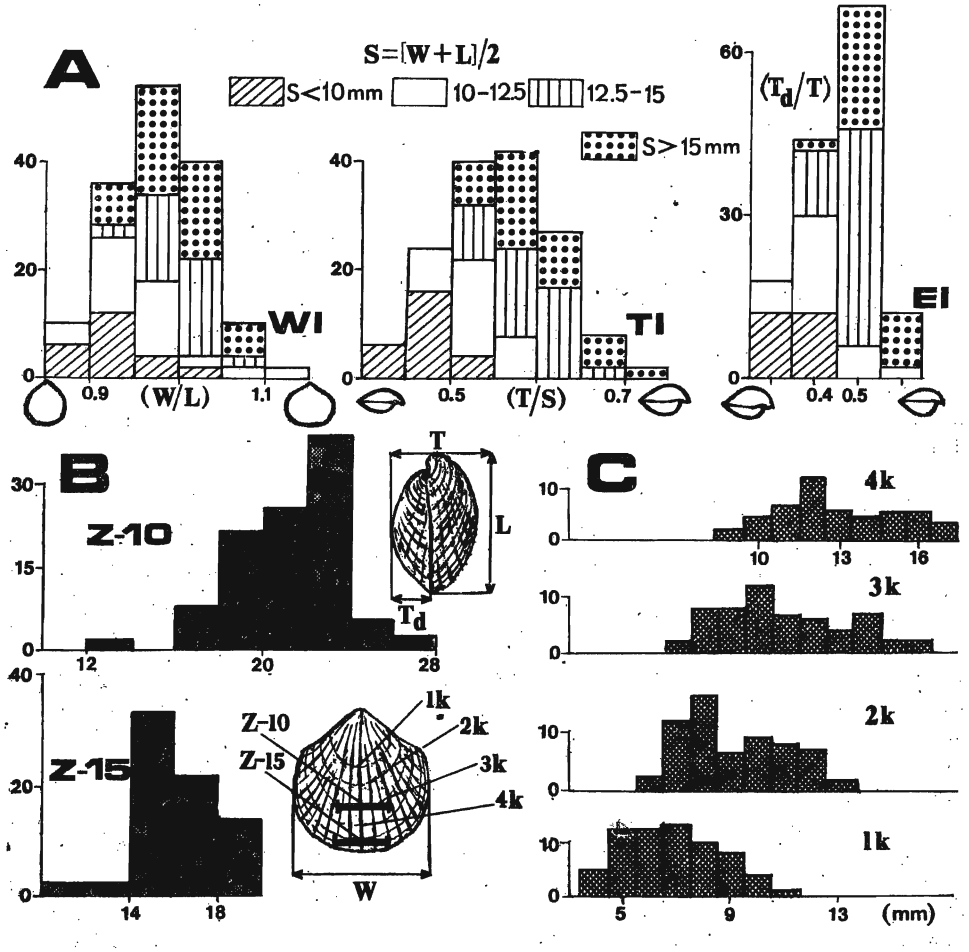


Fig. 7. Variations of the most important external characters for *Desquamatia macroumbonata* sp. n.

A — Variability of width index [WI — width/length ratio], thickness index [TI — thickness/size ratio], and equibiconvexity index [EI — thickness of dorsal valve/thickness of shell ratio]
B — Variability of rib density as measured at 10 mm (Z-10) and 15 mm (Z-15) in distance from the ventral apex per 10 mm of arcs
C — Variability of lengths of the four oldest growth lamellae (numbered 1*k*-4*k*) as measured on ventral valves

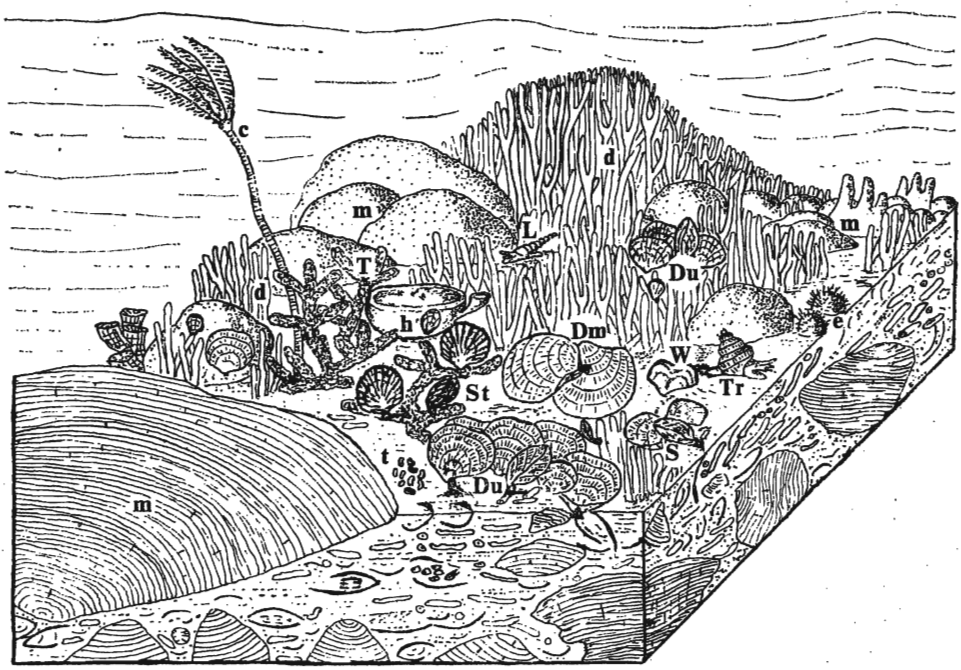


Fig. 8. Idealized reconstruction of bottomscape picturing the biotope of *Desquamatia macroumbonata* association (drawing by W. Bardziński)

m — massive stromatoporoids, **d** — ramose stromatoporoids, **T** — *Thamnopora*, **r** — dendroid rugosans, **Du** — *Desquamatia macroumbonata*, **St** — brachiopod *Spinatrypina* ex gr. *tubaecostata*, **Dm** — *Desquamatia* cf. *magna*, **S** — brachiopod *Schizophoria*, **W** — brachiopod *Warrenella*(?), **L** — gastropod *Loxonema*, **Tr** — gastropod *Trochonema*, **e** — echinoids, **c** — crinoids, **h** — heteractinid sponges, **t** — ostracodes

Concerning the new species, it constitutes almost 85% of brachiopod association which is recognized within this shoal and called here the *Desquamatia macroumbonata* association*. This dominating brachiopod is accompanied by small (up to 13 mm), forms including *Spinatrypina* ex gr. *tubaecostata* (PAECKELMANN), as well as by rare *Schizophoria* and smooth spiriferids (chiefly *?Warrenella*). Larger-sized *Desquamatia* cf. *magna* (GRABAU), *Spinatrypina*, and undeterminated rhynchonellids occur singly.

Less significant dwellers of this shoal are limited to trophically diversified gastropods (*Loxonema*, *Trochonema*, *Mourlonia*, *?Bellerophon*; identified by Dr. L. Karczewski), ostracodes (*Bairdiocypris*, *Microcheilinella*, *Buregia*, *Uchtovia*, *Fabalicypris*, *Cytherelina*, *?Fellerites*; identified by J. Malec, M. Sc.), uncommon crinoids (*Anthinocrinus*, *Kstutocrinus*, *Schyschatocrinus*; determined by Dr. E. Głuchowski), echinoids, and ramose bryozoans.

It is believed that reworking of the assemblage can result from little lateral transport of skeletal material in case of periodic, short-lived strong wave and current

* The last term is taken the same as used by KAUFFMAN & SCOTT (1976), *i.e.* for a group of organisms derived from a single ancient community.

action (?storms), joined with structural or soft substrate instability caused by increasing skeletal size due to the growth of main builders or bioerosion (*cf.* KOBLUK & *al.* 1977; *see also* BRAITHWAITE 1967).

Such morphological characters of the new species *Desquamatia macroumbonata* sp. n., as small size, a protruding beak displaying a large foramen, equal convexity of valves, an almost rectimarginate anterior commissure, and underdevelopment of frills, argue (*see* COPPER 1967a) for the functional pedicle during all phases of its ontogeny. It is probably also the case for other small forms of the discussed *D. macroumbonata* association.

The indicated features of *Desquamatia macroumbonata* sp. n., causing a micromorphic nature ("juvenile aspect") of adult shells, are also plausible attributes of brachiopods inhabiting higher-energy biotopes with numerous firm substrata for anchorage (*see* McMAGARA 1983, ALEXANDER 1984). In fact, the atrypids displaying such features are dwellers of the organic buildups, *e.g.* in the Silurian of Gotland (WATKINS 1975) and the Devonian of western Europe (COPPER 1966). On the other side, successful colonization of a "reef" habitat confirms a high adaptendness of *Desqaumatia*, which is typical of different intershoal biotopes (*see* RACKI & BALIŃSKI 1981).

Micromorphic nature of the *Desquamatia macroumbonata* association corresponds to a well-known feature of many "reef"-dwelling brachiopods (*see* PALMER & FÜRSICH 1981, SZULCZEWSKI & RACKI 1981). It can however be also explained exclusively by a pedunculate habit of the species, eventually controlled by higher hydrodynamic activity of the biotope, as evidenced by some Recent brachiopods (*see* ZEZINA 1976, RICKWOOD 1977, ALDRIDGE 1981).

BIOSTRATIGRAPHIC IMPLICATIONS

Narrow statigraphic range and regional distribution suggest that *Desquamatia macroumbonata* sp. n. may be useful for biostratigraphic subdivision of the Sitkówka Beds and as a marker for the Givetian/Frasnian boundary (*see* Text-fig. 2).

Detailed analysis of the profiles of stromatoporoid-coral deposits points a correlative potential of the brachiopod faunas. In the Jaźwica Quarry, *D. macroumbonata* belongs to the last members of the *Desquamatia* sequence. The species is succeded by the Variatrypinae joined with the well-known Kadzielnia-type fauna (*Fitzroyella alata*&*Parapugnax brecciae* assemblage of SZULCZEWSKI & RACKI 1981; *see also* BIERNAT 1971), and preceded by infrequent *D. globosa* (GÜRICH), chiefly in set *D.* In Miedzianka area, the general succession is similar. Furthermore, small smooth spiriferids of the family Ambocoeliidae and *Stringocephalus* were found below the atrypid-bearing strata. Numerous Ambocoeliidae, with "*Crurithyris inflata*" (SCHNUR) as the last in the sequence (*see* Text-fig. 2), occur also in the lowermost parts of section of the Jaźwica Quarry and of the nearby Łgawa Hill Quarry, directly above the "Givetian" dolomites.

The recognized brachiopod succession, from the ambocoeliid- to the atrypid--dominated ones, is also displayed by other profiles of the Sitkówka Beds, *e.g.* in the Zamkowa Hill at Chęciny (*see* RACKI & BALIŃSKI 1981, Text-fig. 2) and at Sitkówka, over all areas where the Middle/Upper Devonian boundary beds are exposed in the south-western part of Holy Cross Mts.

Acknowledgements

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RAMIENIONÓG *DESQUAMATIA MACROUMBONATA* SP. N. Z POGRANICZA ŻYWETU I FRANU GÓR ŚWIĘTOKRZYSKICH

(Streszczenie)

Przedmiotem pracy jest opis nowego gatunku ramienionoga *Desquamatia macroumbonata* sp. n. z utworów pogranicza żywetu i franu Gór Świętokrzyskich (*patrz* fig. 1—8 oraz pl. 1—2). Cechami diagnostycznymi nowego gatunku jest bardzo duży, ortoklinalny dziób i mała wielkość muszli. Nowy gatunek atrypida zinterpretowano jako formę żyjącą na nóżce w warunkach przynajmniej okresowo podwyższonej turbulencji. Stanowi on główny element asocjacji ramienionogowej związanej z płyciznami stromatoporoidowymi. Wąski zasięg stratygraficzny przy dość znacznym rozprzestrzenieniu regionalnym (co najmniej od Bolechowic po rejon Miedzianki) wskazuje na możliwość wykorzystania go do korelacji i podziału sekwencji stromatoporoidowo-koralowcowej dewonu Gór Świętokrzyskich.
