GERTRUDA BIERNAT

Colour pattern in the Middle Devonian rhynchonellid brachiopods from the Holy Cross Mts

ABSTRACT: Specimens of ?Solidipontirostrum radwanskii sp. n. occurring an the Middle Devonitan brachiopod shales from the Holy Cross Mits, Central Polanid, exhibit peculiar, spotted to acutely-angular-banded colour patterns, slightly differing on each valve of the shell. This patterning is interpreted as a relic of original colouration preserved in the fossil state.

INTRODUCTION

Within the Middle Devonian brachippods from the Skaly Beds in the Holy Mts, Central Poland (cf. Biernat 1959, 1966), one shell of a rhynchonellid retaining very few and weak markings of an amazing brown-coloured, spotted to acutely-angular banded pattern has been recorded. This finding was supplemented by a few specimens coming from the same exposure, collected by Professor A. Radwański, A. Piotrowski, M. Sc., and T. Wrzołek, M. Sc. As a result, a collection of twelve specimens sligthly differentiated in individual age and its surface pattern was received

Insofar, no rhynchonellid or other brachiopods with such an intricate colour pattern have been recorded from the Palaeozoic, particularly from the Devonian deposits. The shells of "Pugnax" pugnoides pugnoides (Schnur) from the Middle Devonian of Germany, as reported by Kayser (1871), discussed by Richter (1919, 1924), illustrated by Schmidt (1941), and recently studied in the original Kayser's collection housed at the Museum of the Humboldt University (Berlin), bear only a spotted pattern. As to the Lower Devonian rhynchonellid from Canada, a subradial colourbanding noted by Boucot & Johnson (1968) appears to be an example having much in common with that of the investigated specimens.

Traces of colour pattern in fossil brachiopods have been noted and discussed e.g. by Richter (1919, 1924), Foerste (1930), Schmidt (1941), Cloud

(1941, 1942), Reimann (1945), Stehli (1955), Niteckii & Sadlick (1968), Boucot & Johnson (1968). The brachiopod shells retaining colouration are still of interest especially when they come from the Palaeozoic strata. Although recently there have been considerably more specimens yielding traces of colour, many questions connected with i.a. their preservation in fossil state, differentiation, and taxonomic value remain unclear.

The collection concerned is housed at the Institute of Palaeobiology of the Polish Academy of Sciences, the abbreviation of which is ZPAL.

MATERIAL

The collection comprises two juvenile shells, ten adults and old individuals, length ranging from 13.7 m — 30.1 mm, all being articulated, thick-walled, and in various state of preservation. These specimens bear, as a rule, rather evident mechanical breakage in contrast to the other, in general, well preserved co-occurring brachiopods (cf. Biernat 1959, 1966). Nevertheless, among the rhynchonellids seriously damaged, and even crushed, there are shells nearly complete (Pls 4—5). All shells are decorticated, to some degree, and weathered, with the primary layer sometimes much reduced. Some specimens bear traces of the restored shell with the concentric lines often stepwise arranged, generally thickened and accumulated, especially on the places of restoration.

Internally, the matrix of the shells is ferrugineous-argillaceous, sometimes with calcitic drusy infilling. Elements of internal structure are usually incomplete, and

the interior studied from peels is not easily interpretable.

All shells display evidences of colour pattern but in different state of preservation. In places, seriously altered, the colour markings such as spots, subradial and accurtely-angular bands indicate the original array of the pattern. This band-having state is much incomplete, especially along the midline of the brachial valve, and its exact pattern becomes rather to be faithfully reconstructed (Pl. 6, Fig. 1a).

The preserved colour markings are dark-brown and, as a rule, distinctly elevated due to its resistance to weathering. This is, in all probability, due to the melanoid group of pigment, the commonest in shells (Comfort 1951), insoluble in most liquid media (Kříž & Lukeš 1974) and hardened in the coloured shell elements. The lighter, colourless intervals are, in contrast, usually much lowered, and often strongly effected by weathering. In addition, the preserved markings are sunken in the outer prismatic layer to a depth of about a half of milimeter, and this matches well to the former data (Newton 1907).

Some shells are encrusted by epifauna, primarily by bryozoans Condranema, Vinella, Ceramoporella, crimoids, and Spirorbis.

COLOUR PATTERN

The investigated specimens exhibit three general kinds of pattern, each being confined to particular shells of the collection. These patterns are: complete spotting, partial spotting to subradial banding, and complete subradial to acutely-angular banding.

The spotting is, as a rule, of almost equal appearance. Some small variations occur in the size and outline of spots. On the younger shells

about 17.5 mm long, the spots are small, usually round in outline and rather irregularly scattered (Pl. 3, Fig. 1). They become larger with growth, on shells to about 30 mm long, thus more densely packed, and keeping their rounded outline on the median part of shell (Pl. 1, Fig. 1a), rounded to ovate on the lateral slopes (Pl. 1, Fig. 1e), and often distinctly transverse at the anterior margin (Pl. 1, Fig. 1c). The spots on a major part of the shell are arranged in a quincuncial pattern; on the anterolateral slopes, occasionally, in the form of discontinuous, slightly concave (bended) rows (Pl. 4, Fig. 1g), and at the anterior part of shell densely packed in the short intercostal furrows or on the crets of costae forming discontinuous rows perpendicular to the anterior commissure (Pl. 1, Fig. 1c).

The spots are known, up to now, as ornamenting im a much similar way and regardless the growth stage of the two German forms (cf. Schmidt 1941), viz. "Pugnax" pugnoides pugnoides (Schnur) and "P." pugnoides latus (Schmidt). Their spots are red-brown, smaller, not so densely packed and usually distinct on the anterior part of the shell.

The transitional pattern is characteristic of the younger specimens, about 13.7 mm long, and very adult shells, about 29 mm long (Pl. 3, Figs 2—3; and Pl. 5). The spots usually cover the posterior half of the shell length, their outline and arrangement being much in correspondance with that of adult shells which bear the former pattern (Pl. 4, Fig. 1a—b). The remaining anterior part of the shell bears a few subradial bands followed by short longitudinal ones confined to the anterior margin (Pl. 5, Fig. 1a, g), with the one central (intercalated) on the pedicle valve and correspondingly with the two central bands on the brachial valve. Arrangement of subradial bands is dissimilar along the midline of both valves. They are widely divergent from the midpoint of the pedicle valve to the lateral slopes, in contrast to the brachial valves where they are convergent medially (Pl. 5, Fig. 1a, 1c). Single, longitudinal bands lie in the intercostal furrows (Pl. 5, Fig. 1e) and correspond with the crests of zigzag line of the anterior commissure (Pl. 5, Fig. 1d).

The spotted/concentrically-banded pattern is known in the brachiopods, being recorded in the Middle Pennsylvanian Chonetinella jeffordsi Stevens from Colorado, and defined as the most spectacular for all the fossil brachipods (Stevens 1965). However, the spotted/subradial-banded pattern displayed by the investigated specimens appears to be unknown in the brachiopods.

The acutely-angular-banded pattern is confined to old shells. It consists of alternating darker and lighter subradial bands (Pl. 6 and Pl. 7, Figs 2—3) covering almost the whole shell surface, except for the umbonal parts on which the eventual spots could become obliterated. The bands are, fairly stout, arranged at almost regular intervals about twice as narrow as the intervening lighter spaces (Pl. 7, Fig. 3b).

Along the middle of the pedicle valve there are about nine subsequent pairs of angularly disposed bands, their apices being directed posteriorly (as in the Canadian rhynchonellid, cf. Boucot & Johnson 1968), widely divergent laterally in a straight or slightly concave way. Each pair starts to divaricate from a single larger median spot. On the slopes of the valves, the bands appear to correspond with the crests of zigzag line.

Along the middle of the brachial valve the pattern is doubled in comparison with that on pedicle valve (Pl. 6, Fig. 1a; Pl. 7, Figs 2, 3a) There are two subsequent larger median spots, each of which starts to divaricate in two directions and giving both short bands somewhat converging anteriorly and one longer, diverging toward the lateral margins in a concave or, in places, zigzag way (Pl. 6, Fig. 1e). Longitudinal single bands lie, like those of the former two patterns, in the short intercostal furrows, arranged alternately when viewing from the anterior commissure.

This striking pattern is unknown in the brachiopods, but, undoubtedly there is some tendency to develop it among the rhynchonellids. This may be confirmed by a Lower Devonian indeterminate rhynchonellid species from Canada (Boucot & Johnson 1968, p. 1208, Pl. 160, Figs 16—17) with marks of subangulary banded patterns. The Canadian shell is very poorly preserved as a pedicle valve only (not a brachial one, suggested by Boucot & Johnson). This is a juvenile valve (15 mm long) having only one pair of bands developed.

The three kinds of colour pattern can be a good illustration of wide intraspecific variability when arranging them in a sequence of gradual transitions, beginning with the spotted pattern, and ending with the subradial one.

When considering the colour patterns in the context of the shell morphology, two general patterns are recognized:

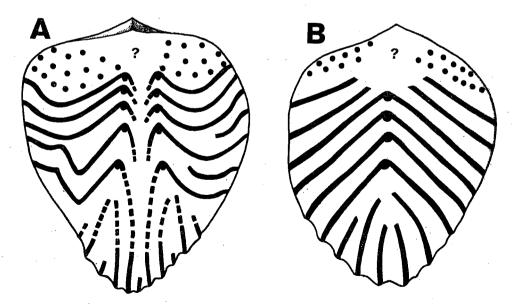


Fig. 1. ?Solidipontirostrum radwanskii sp. n.; stylized picture of the adult shell with colour banding; A — brachial valve, B — pedicle valve

- A the spotting applied to shells of distinctly subquadrate outline, with lateral margins longer and almost parallel, anterior margin widely outlined (morphotype A; see Text-fig. 3A, and Pl. 1, Figs 1a, 2a),
- by shells of pentagonal outline, with lateral margins shorter, more arched, anterior margin narrowed; the banding in the juvenile shell, 13.7 mm long, covers about two-thirds of its anterior shell length (Pl. 3, Figs 2, 3c), that means it replaces the spots rather early in the process of growth (morphotype B; see Text-fig. 3B and Pl. 3, Fig. 3c; Pl. 4, Fig. 1d).

To mention, Schmidt (1941) also noted some correspondance of the shell morphology with the appearance of spotting, and recognized two subspecies: "Pugnax" pugnoides pugnoides (Schnur) with narrowed anterior commissure which is zigzag and densely spotted colour pattern (Schmidt, Pl. 7, Fig. 29) and "P." pugnoides latus (Schmidt) with zigzag anterior commissure and colour pattern composed of small spots scattered sparsely over the whole shell (Schmidt 1941, p. 29, PL. 7, Fig. 30).

The spotting appears to be an uncommon pattern within the Palaeo-zoic brachiopods. As it is shown by Blodgett & al. (1983), of the thirty nine coloured Devonian species only three are completely spotted, viz. "Pugnax" pugnoides pugnoides (Schnur), "P". pugnoides latus (Schmidt), and Terebratula sp., and two other forms, Hamburgia sp. and Granaena maculata Belanski, bear radial rows of spots.

The spots, a result of cyclical activity of special groups of cells of the mantle (Comfort 1951), can be generally defined as indicating a regular pattern in the investigated shells. No serious disturbances in the deposition of pigment occur as can be judged from the rather regularly disposed thickened concentric macrolines, 4—5 per mm in the shells. The rounded and smaller spots on the posterior half of shell are a result of a faster shell increment while anteriorly, where the shell increment becomes much more slow and the secretion of pigment is more intense (Comfort 1951), the spots are larger, more elongate and/or more transverse and densely packed.

Radiating colour pattern in fossil brachiopods (Newton 1907, Nitecki & Sadlick 1968, Blodgett & al. 1983), is in striking contrast to the discussed spotted and/or acutely-angular-banded pattern. The latter seems to be a result of the continued activity of special cells of the mantle which can give, in places, a zigzag pattern. However, such pattern is not easily explained. It may be related to the pallial sinuses as a result of physiological reaction (Cloud 1942), although the bands do not coincide with the traces of the pallial sinuses.

When analyzing this colour pattern one can assume that there is some relationship with the costation, a feature displayed by the anterolateral parts of the adult shells. Support for such a suggestion is as follows:

G. BIERNAT

- (i) With the first appearance of the costation (shell at about 13.7 mm long) developed as very fine marginal foldings, the spotted pattern is replaced by subradial banding;
- (ii) Number of pairs of bands (diverging and converging) in adult and old shells appears to be, in general, in correspondence with the number of short costae, about seven to nine on a particular valve;
- (iii) The bands appear to be confined to the untercostal furrows (in the Canadian form being, in all probability, confined to the crests of costae, as mentioned by Blodgett & al., 1983) and always in correspondence with the crests of the commissural line, arranged alternately when viewing from the shell commissure;
- (iv) Central larger spots always appear in a constant number and site corresponding with the central intercostal furrows, i.e. invariably one of them at the midline of the pedicle, and two others at the midline of the brachial valve.

It is judged here, that the spotting was, in all probability, the basic in the investigated shells. It occurs in many specimens being confined to the younger (faster growing) parts of shell. Replacement of spots by the bands occurs early in adolescence (?early in adult stage) and in this way may depend upon the individual age. With growth the intensity of concentration of pigment increases in contrast to the decreasing rate of growth of the shell. There occur also some longer periods of diapauses (judging upon the thickened and in some cases closely arranged concentric growth lines) with the shell closed, stopping to grow (Brunton 1968). This latter state could favour the special concentration of the pigment and give rise to the continuation of the bands.

No doubt, all the discussed colour markings could play a protective function for the brachiopods (Křiž & Lukeš 1974), supposedly the camouflage. Differentiation of the colour patterns could also be a dimorphic feature.

SYSTEMATIC DESCRIPTION OF THE SPECIES

Genus SOLIDIPONTIROSTRUM Sartenaer, 1970

Remarks. — Sartenaer (1970) proposed Solidipontirostrum as a new generic name for some of the Devonian "pugnaxes". The spotted Middle Devonian "Terebratula" pugnoides (Schnur) from Germany was chosen as a type species of this genus. Among the diagnostic features, Sartenaer (1970) mentions the dental plates, and especially, the robust "connectivum" as a highly characteristic structural element of the genus.

The Carboniferous genus Pugnoides is very close internally to Solidipontirostrum. It also bears the diagnostic connectivum and dental plates but differs in
its external appearance, especially in the smaller size and in having the whole

shell surface costate (Weller 1914, Sartenaer 1970).

With regard to the studied specimens, they are, internally, very much of the Pugnoides-type, possessing dental plates, septal thickening, which is broad, septalium comparatively deep but, in all probability, not covered. No connectivum can be stated in the sectioned shell (see Text-fig. 3 and Pl. 8).

Externally, the investigated specimens correspond more or less with "Pugnax"

Externally, the investigated specimens correspond more or less with "Pugnax" pugnoides pugnoides (Schnur), differing in somewhat larger size, of more variable shape and, especially outline, and more differentiated colour pattern. A few shells (morphotype A) appear to be extremely close to "P." pugnoides latus (Schmidt),

another spotted, Middle Devonian subspecies from Germany (Schmidt 1941). They are of similar shell outline and shape, they possess similarly costate anterior part of the shell and zigzag but widely outlined anterior commissure, differing in being

larger and in having much more densely spotted colour pattern.

As a matter of fact, the generic assignement of the investigated forms is difficult. Due to not very adequate material, their generic identification is based on characters of rather secondary significance, such as shell shape, outline, slize, colour patterning. Internal structure remains insufficiently known. It is possible that they represent a separate genus, but tentatively they are assigned to the genus Solidipontirostrum Sartenaer.

?Solidipontirostrum radwanskii sp. n. (Text-figs 1—3 and Pls 1—8)

Holotype: The specimen No. ZPAL Bp. XVIIII2, presented in Pl 4 ,Fig. 1a-g, as displaying spotted to acutely-angular colour pattern.

Type locality: Skaly, exposure 73 (see Biernat 1966, Text-fig. 2); Lysogóry region, Holy Cross Mountains, Central Poland.

Type horizon: Marly shales ("Brachiopod Shales"), Middle Devonian.

Derivation of the name: To honour Professor Andrzej Radwański, from whom the majority of specimens come, and for his interest with their spectacular features of colour pattern.

Diagnosis: Shell medium-sized, of varying outline from subquadrate to pentagonal, anteriorly costate, spotted to acutely-angular banded.

Description. — Shell of medium size, plano-convex, subquadrate to subpentagonal in outline; lateral margins almost parallel to distinctly arcuate; anterior margin widely outlined to nearly acute, usually with tongue-like elongation, always costate with zigzag commissural line; shell surface bearing very delicate radiate ornamentation and distinct colour markings. Internally, the dental plates rather short and comparatively thin, subparallel (somewhat arcuate); hinge-teeth small; the dorsal median thickening very short, broad; septalium rather deep, not covered (Text-fig. 2 and Pl. 8A—C).

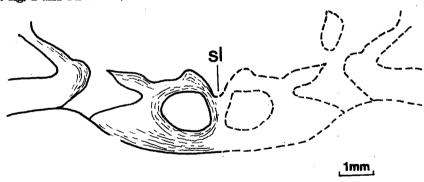


Fig. 2. Interior of the adult shell of ?Solidipontirostrum radwanskii sp. n.; slightly reconstructed (comp. P1. 8B), septalium (sl) not covered

Remarks. — Two morphotypes (A and B) are recognized upon the morphological differing characters, including the colour pattern. In general, they do correspond to the German spotted forms (Schmidt 1941) with some exception of three of them (morphotype A) which seem to be somewhat separate.

MORPHOTYPE A (Text-fig. 3A; Pl. 1 and Pl. 2, Fig. 1)

Material: Three specimens including one of smaller size. Approximate dimensions (in mm):

	shell length	length curvata pedicle l val	orachial	thickness of shell posteriorly	shell width	apical angle
ZPAL Bp.XVIII/7	17.5	18.0	21.0	6.0	17.1	112
ZPAL Bp.XVIII/6	24.4	27.0	34.0	12.9	24.6	119
ZPAL Bp.XVIII/11	27.2	26.0	34.9	9.6	24.4	120

The morphotype A is distinguished for specimens of distinctly subquadrate outline with length slightly exceeding the shell width, lateral margins almost parallel to incipiently arcuate; anterior margin widely rounded to almost straight; beak small, acute; pedicle foramen small, round, subapical; area evenly marked. Adult shell bears six to nine ventral costae. The whole shell surface is spotted. MORPHOTYPE B [Text-fig. 3B; Pl. 2, Figs 2—4 and Pls 3—7)

Material: Eight specimens including one of smaller size. Approximate dimensions (in mm):

	shell length	pedicle	along cure of brachial ves	thickness of shell posteriorly	shell width	apical angle
ZPAL Bp.XVIII/1	13.7	16.0	14.0	5.2	15.9	121
ZPAL Bp.XVIII/2	21.3	31.0	22.0	13.8	24.5	111
ZPAL Bp.XVIII/3	21.4	30.0	23.0	11.3	22.7	117
ZPAL Bp.XVIII/5	?23.7	25.0	30.0	14.3	23.4	117
ZPAL Bp.XVIII/9	30.1	37.0	30.0	11.7	28.7	122
ZPAL Bp.XVIII/10	27.2	34.0	26.0	9.6	24.4	120

The morphotype B is distinguished for specimens of pentagonal outline, narrowing anteriorly, sometimes more or less acutely; tongue-like elongation distinct, in general as wide as long or width slightly exceeding the shell length, the widest part about midlength to just anterior to the cardinal margins (Pl. 5, Fig. 1c); lateral margins rather short, and distinctly to a different degree, arouate exteriorly and well converging anteriorly. The whole shell surface is acutely-angular-banded or, in some specimens spotted to subradially banded.

Discussion. — The two morphotypes have different features which, however, are not of taxonomic value. It is possible that they demonstrate the individual variability (due to ecological factors) or may evidence a dimorphism, not hitherto understood within the brachiopods.

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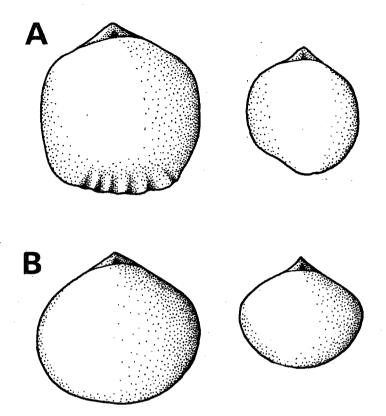


Fig. 3. Dorsal view of ? Solidipontirostrum radwanskii sp. n.; adult and young shells of the distinguished morphotypes A and B

Cross Mountains; to Dr. H. Bolton, Geological Survey of Canada (Ottawa) for the photographs of an indeterminate coloured rhynchonellid from the Lower Devonian of Canada; to Professior Z. Walenczak (University of Warsaw) for the spectroscopic photographs; to Dr. E. Owen (Palaeontological Department, British Museum, London) for critical reading the manuscript.

The photographs were taken by Mrs. G. Podbielska, Institute of Palaeobiology.

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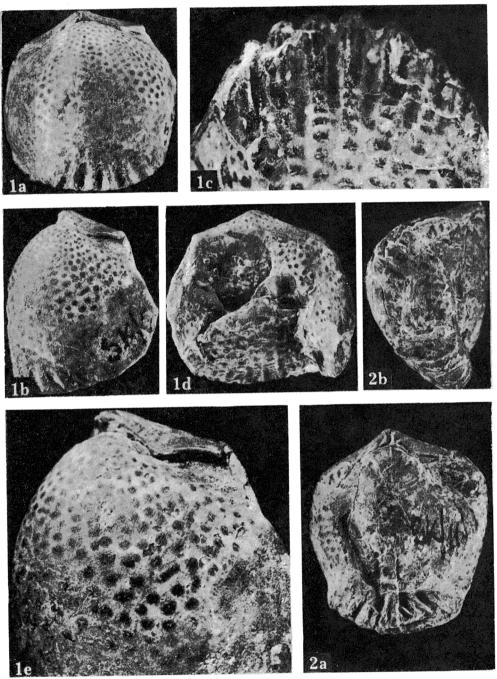
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G. BIERNAT

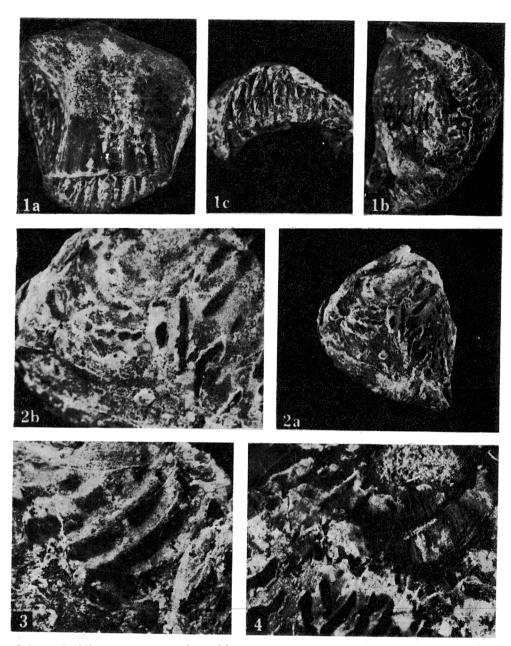
ŠRODKOWO-DEWOŃSKIE RYNCHONELLIDY Z ZACHOWANA BARWNA ORNAMENTACJA

(Streszczenie)

Z środkowo-dewońskich łupków brachiopodowych odsłaniających się w profilu Grzegorzowice-Skały w Górach Świętokrzyskich opisano nowy gatunek rynchonellida, ?Solidipontirostrum radwanskii sp. n., zachowującego na powierzchni muszli ślady bardzo zróżnicowanej barwnej ornamentacji (patrz fig. 1-3 oraz pl. 1-8). Składają się na nią: ciemnobrązowe okrągłe bądź owalne plamki oraz pasy rozchodzące się pod kątem ostrym od środka długości muszli ku jej brzegom bocznym. Poszczególne elementy barwnej ornamentacji wydają się być związane z zarysem muszli, gdyż plamki pokrywają muszle o prawie prostokątnym zarysie (morfotyp A), natomiast pasy występują u okazów o zarysie bardziej pięciokatnym (morfotyp B). Zróżnicowanie takie nie ma znaczenia taksonomicznego; może natomiast wskazywać ono na istnienie dymorfizmu w obrębie nowo ustanowionego gatunku.

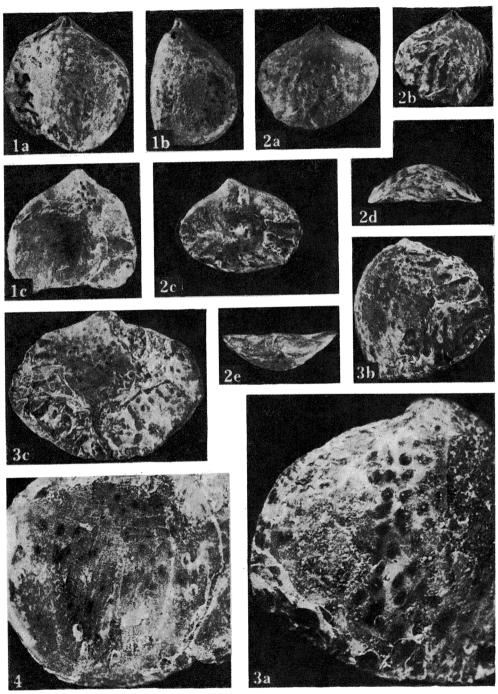


1-2 — ?Solidipontirostrum radwanskii sp. n. (morphotype A); appearance of spots on two adult shells (Bp. XVIII/6 and Bp. XVIII/11) in brachial valve (a), lateral (b, e), anterior margin (c), and pedicle valve (d) views; all taken \times 2, except of 1c and 1e taken \times 4



1-4 — ?Solidipontirostrum radwanskii sp. n.; appearance and state of preservation of four adult shells (Bp. XVIII/11 — morphotype A; and Bp. XVIII/8, Bp. Bp. XVIII/9, Bp. XVIII/3 — morphotype B) in pedicle valve (a), lateral (b), and anterior margin (c) views, \times 2

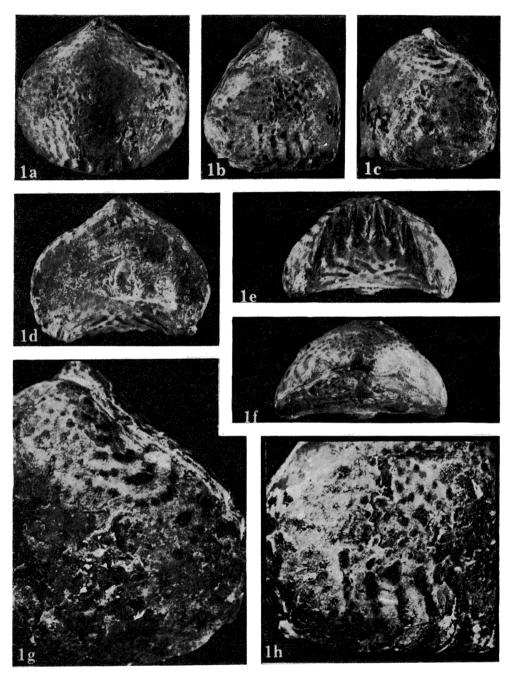
2b — enlarged part of Fig. 2a, to show the rows of lateral spots and subradial bands, 3 — subradial bands on the dorsal right-side (morphotype B), 4 — fragments of subradial bands and thickened growth lines on the ventral left-side (morphotype B), \times 4



1-4 — ?Solidipontirostrum radwanskii sp. n.; colour markings on three young shells (Bp. XVIII/7 — morphotype A; Bp. XVIII/1 and Bp. XVIII/10 — morphotype B) in brachial valve (a), lateral (b), pedicle valve (c), and anterior margin (d) views, × 2

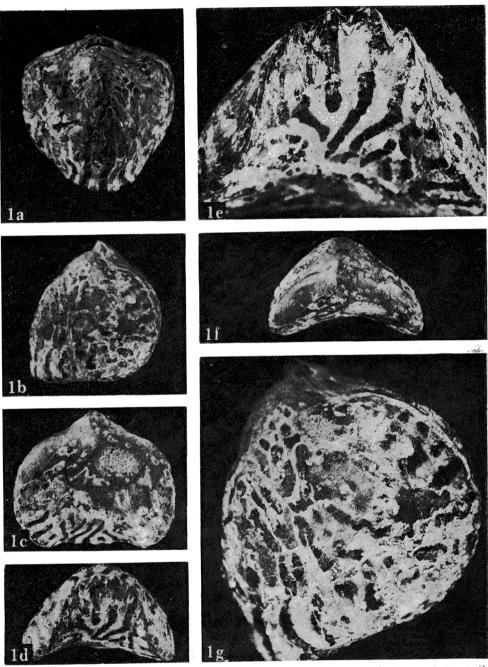
1d — enlarged part of Fig. 1a, to show scattered spots on the posterior part of

shell, 3a — spots on the ventral left-side (morphotype B), taken \times 4



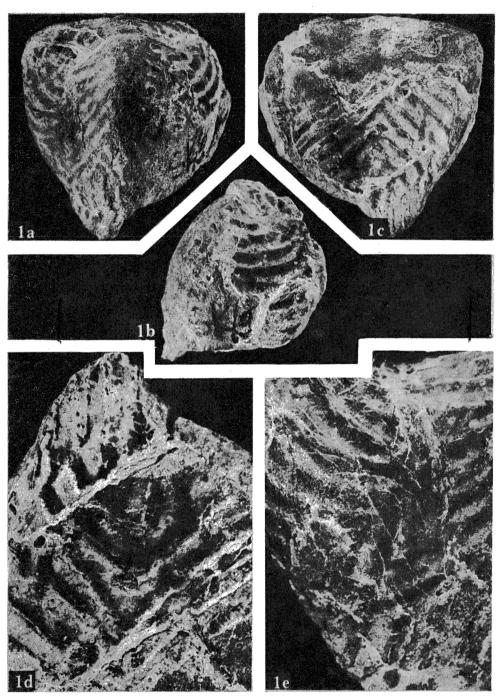
- ?Solidipontirostrum radwanskii sp. n. (morphotype B); spots/subradial bands, colour pattern of the type specimen (Bp. XVIII/2) in: brachial valve (1a), lateral (1b, 1c), pedicle valve (1d), anterior margin (1e), and posterior (1f) views, \times 2

1g, 1h — enlarged part of Figs 1c and 1b, to show lateral rows of spots and anterior subradial bands, both taken \times 4



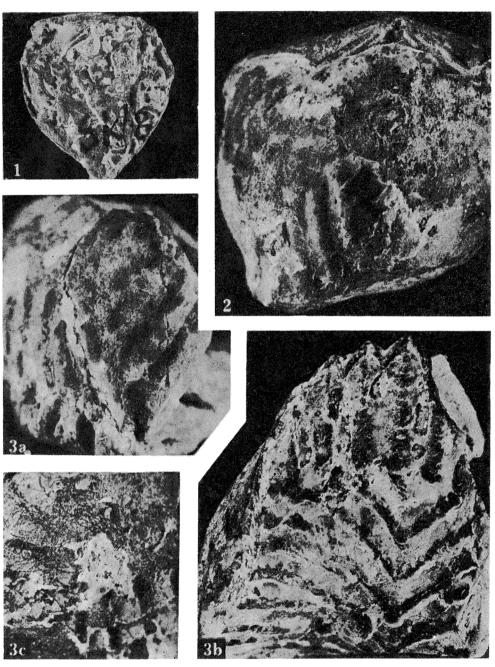
1 — ?Solidipontirostrum radwanskii sp. n.; colour markings in the adult shell (Bp. XVIII/3 — morphotype B) in: brachial valve (Ia), lateral (Ib), pedicle valve (Ic), anterior margin (Id), and apical margin (If) views, × 2
1e — enlarged Fig. 1b, to show arrangement of subradial and longitudinal bands at the anterior part of shell, and concentric lines especially thickened; 1g — dorsal right-side showing distribution of the fragmentary preserved subradial bands; both

taken × 4



- ?Solidipontirostrum radwanskii sp.n.; acutely-angular banding of the adult shell (Bp. XVIII/9 — morphotype B) in: brachial valve (1a), lateral (1b), and pedicle valve (1c) views, \times 2

1d — fragment (cf. Fig. 1c) with colour pattern preserved on the anterior half of pedicle valve, 1e — dorsal left-side (cf. Fig. 1a), to show zigzag arrangement of subradial bands, \times 4

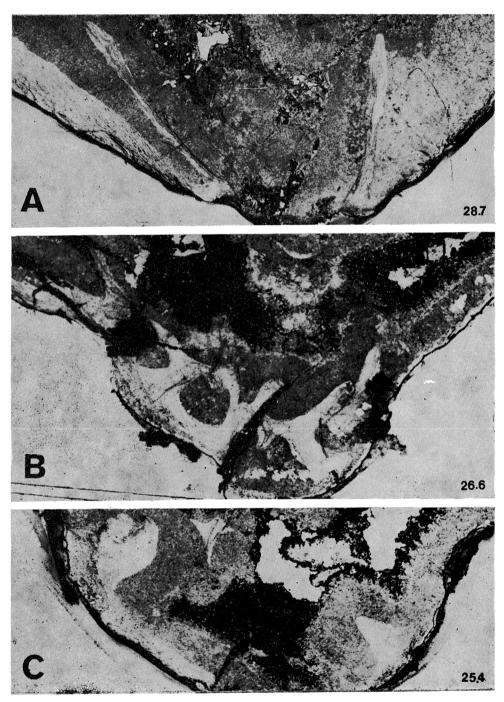


1-4 — ?Solidipontirostrum radwanskii sp. n.; colour markings on three adult shells (Bp. XVIII/8, Bp. XVIII/8, Bp., XVIII/5, Bp. XVIII/4 — morphotype B)

1 — dorsal right-side of bally preserved shell, ×2; 2 — dorsal view showing traces

of somewhat convergent anteriorly bands; 3a — dorsal view, specimen slightly anchylosed to the right with traces of banding, 3b — anterior view, pedicle valve with acutely angular and longitudinal bandings, 3c — fragment of dorsal left-side

(Fig. 3a), to show thickened concentric lines, \times 4



A-C — ?Solidipontirostrum radwanskii sp. n.; cross sections of the adult specimen (Bp. XVIII/12), 30 mm long, and showing: A — dental plates, B — septalium, C — crural bases, all taken \times 10