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First colour-patterned strophomenide brachiopod from the earliest Devonian of Podolia, Ukraine

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Retained colour pattern on the shells of *Plectodonta* sp. from the earliest Devonian of Podolia (Ukraine) is the first finding for strophomenide brachiopods and the oldest among articulate brachiopods. The colour pattern in *Plectodonta* sp. is composed of small, round, brownish spots scattered rather irregularly on the ventral valve only. This may suggest that the described pattern probably performed a protective function through disruptive camouflage against visual systems of potential predators. The occurrence of the colour pattern in *Plectodonta* sp. exclusively on the ventral valve strongly suggests that these brachiopods lived with the patterned (and convex) ventral valve upwards and the patternless concave dorsal valve facing to the underlying substrate. It thus contradicts a general assumption that concavo-convex brachiopods lived with their convex valves resting on the sediment.

Key words: Brachiopoda, Strophomenida, colour pattern, Devonian, Podolia.

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Introduction

Fossil invertebrates revealing some genuine colouration (when pigment is distributed more or less uniformly within shell matter) or colour patterns (when pigment is concentrated or arranged in bands, lines, spots, patches, etc.) are rather rare because a variety of factors destroys original colouring of the shells during the process of fossilisation. On the other hand, Blumer (1965) remarked that organic pigment compounds from plants and animals are preserved as molecular fossils in a wide range of geologic materials, often of great antiquity. Fossil brachiopods retaining colour pattern are of great interest especially when they come from rocks hundreds of millions years old. Although records of colour pattern in Devonian brachiopods are numerous (see list of citations in Blodgett et al. 1983; Kobluk and Mapes 1989) they invariably exemplify an exceptional state of preservation.

Devonian articulate brachiopods retaining colour markings are represented by eight taxa of Rhynchonellida, six taxa of Athyrididina, and 28 taxa of Terebratulida (see Boucot and Johnson 1968; Blodgett et al. 1983, 1988; Biernat 1984; Baliński 1985; Johnson 1986). The previously oldest articulate brachiopods with preserved colour patterns came from the middle Early Devonian. These are the athyridoid *Merista* Suess, 1851 (Kříž and Lukeš 1974) and two terebratulid genera *?Prionothyris* Cloud, 1942 (Murphy 1972) and *Beachia* Hall and Clarke, 1893 (Blodgett et al. 1988). No Devonian representatives of the order Strophomenida have been reported to retain the colour pattern. The aim of this report is to illustrate specimens of *Plectodonta* sp. from the earliest Early

Devonian of Podolia, which are the first strophomenides and the oldest articulate brachiopods known to the author retaining shell colour pattern.

Colour-patterned fossils have a great potential value for palaeoecologic, palaeogeographic, evolutionary, and taxonomic purposes (Nicol 1967; Blodgett et al. 1983, 1988; see also Newton 1907; Foerste 1930; Kobluk and Mapes 1989; Hagdorn and Sandy 1998; Manda and Turek 2009; Turek 2009). For example, remarkable pattern consistency of a single pair of radial bands on the brachial valve in *Beachia* and *?Prionothyris* prompted Blodgett et al. (1983, 1988) to regard this morphologic feature as a supplementary diagnostic for at least part of the subfamily Eurythyridinae Cloud, 1942.

Institutional abbreviation.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warszawa, Poland.

Material and methods

All material presented here was collected from beds 47–48 representing the lowest part of the Khudykivtsi (former Tajna) Member, about 5.5 m above the Silurian–Devonian boundary, exposed in a trench near the village of Dnistrove (former Volkovtsy) in Podolia (Ukraine; see Małkowski et al. 2009 for details on the locality). The specimens of *Plectodonta* sp. with retained colour pattern occur in a single fossiliferous interval measuring about 18 cm in thickness and belonging to an otherwise poorly fossiliferous, monotonous, 180 m thick complex of platy limestones and variably interbedded dark grey argillaceous shales, marls and marly to

micritic limestones extending from the base of the Lower Devonian through the Khudykivtsi to the top of the Mytkiv members. Beds 47–48 are remarkable in their relatively rich, well-preserved, and taxonomically diversified brachiopod fauna. The fauna yields 15 species, of which the most characteristic are *Resserella elegantuoides* (Kozłowski, 1929), *Dalejina frequens* (Kozłowski, 1929), *Plectodonta* sp., *Glossoleptaena* sp., *Clorinda pseudolinguifera* Kozłowski, 1929, *Sphaerirhyncha gibbosa* (Nikiforova, 1954), *Lanceomyonia borealiformis* (Siemiradzki, 1906), and *Septatrypa* (*Septatrypa*) *secreta* Kozłowski, 1929 (systematic description of the brachiopod fauna from the locality will be published elsewhere). Nearly 170 specimens of *Plectodonta* sp. were recovered from beds 47–48, of which 92 retain variably preserved colour pattern. This species is externally very close to *Plectodonta mariae* Kozłowski, 1929 which occurs in a slightly younger horizon representing the Mytkiv Member (upper part of the Borshchiv Horizon). *Plectodonta* sp. illustrated here is persistently smaller, has less numerous primary costellae, and deeper, more restricted ventral sulcus. According to Nikiforova et al. (1985) the species from the Khudykivtsi Member is not conspecific with *P. mariae* from Mytkiv Member. This species will be studied and described taxonomically in detail elsewhere.

Description

The colour pattern of *Plectodonta* sp. consists exclusively of spots (Figs. 1A–C, E–G, 2). They are scattered more or less evenly, although irregularly, over the whole surface of the valve except for the most posterior 0.4–0.6 mm (umbonal region). On some specimens the spots reveal a weak subradial arrangement but this condition is rather rare and obscure. Usually the size of the spots does not change much during ontogeny although on some shells the spots around the anterior margin are slightly larger from those situated more posteriorly (Fig. 1E). Rarely, some spots show a tendency to coalesce to form larger, irregularly outlined patches (Figs. 1A, F, 2G, R, AG). Spot density varies in a rather wide range from 7 to 17 per mm² and averages at 11 spots per mm². It seems that spot density is more or less uniform over the whole surface of the valve excluding the spotless umbonal region.

The spots are more or less circular in outline, light to dark brown in colour, darkest in their centre and gradually fading away peripherally. The diameter of the spots varies over a wide range from 0.06 to 0.25 mm but most often averages about 0.15 mm. The variability of the pattern and character of the distribution of spots as observed on the 40 best preserved ventral valves are shown diagrammatically on Fig. 2.

One of the most appealing features of the material presented here is the fact that all of the examined colour pattern-bearing shells have this feature retained exclusively on the ventral valve. Although several specimens have the dorsal valve well exposed none of them has the colour pattern clearly visible (Fig. 1D). In the studied material there is a re-

markable specimen of a small rock slab showing on one surface two specimens of *Plectodonta* sp. with exposed ventral valves and one shell with a dorsal valve visible (Fig. 1G): all of the former show distinct colour pattern, whereas the latter does not show any perceptible pattern. This rock slab clearly supports the observation that the colour pattern in *Plectodonta* sp. was probably restricted to the ventral valve only.

Discussion

Reimann (1945) noted that some dark coloured radial pattern observed in a few *Meristella* species from the Middle Devonian of New York was caused by differential absorption and reflection of light by the corrugated prismatic shell layer. In consequence, the angle of view affects the appearance or disappearance of the pattern on such specimens. On the other hand, the appearance of the colour pattern which is caused by a presence of a real pigment or its remnants within shell substance is not affected by the angle of view. Parker (2000: R15) discussed the array of structural colours (selective reflectance of light by the physical nature of a structure) found in animals as early as the Cambrian. Towe and Harper (1966) described iridescent pearly or nacreous lustre in Devonian pholidostrophiid brachiopods that resulted from the crossed lamellar shell structure. Yet some types of colouration or colour patterns of fossil exoskeletons may have been the result of diagenetic alteration (e.g., Klug et al. 2009; Turek 2009). These kinds of colour patterns or colourations should not be confused with the undoubtedly genuine colour retained in fossils. The colour-spotted pattern in *Plectodonta* sp. described here is an example of the last case, i.e., it is caused by retention of a pigment derived from original colour and embedded in the shell matter. Noteworthy is that the colour spots are equally visible from the exterior of the valve as on its interior. This suggests that the colouring substance, as presently preserved, occurs not superficially but is embedded within the shell substance.

There are several kinds of colour patterns which can be found in fossil and Recent articulate brachiopods. One of the most common is radial banding which has been found in the rhynchonellides, athyridides, and terebratulides (Fig. 3E–G, I). Concentric bands are described in orthotetides, productides, athyridides, and terebratulides (Fig. 3B, C, J). Among the Devonian brachiopods with preserved pattern 25 have radial and 5 concentric banding (Blodget et al. 1983). Spotted patterns have been recognised in productides, rhynchonellides, terebratulides, and, in this paper, strophomenides (Fig. 3A, B, D, H). Frequently, the spots are arranged radially, or, as in the Middle Devonian *Solidipontirostris radwanskii* Biernat, 1984, the spots and bands can form a spectacular pattern (Biernat 1984; Fig. 3D). Rarely, spots are combined with banding (Fig. 3B, D). In some brachiopods, the colour pattern consists of large irregular patches, as is observed in the Recent terebratulid *Shimodaia* MacKinnon, Saito, and Endo, 1997 (Fig. 3K).

Plectodonta is a member of the superfamily Plectambonioidea, which is characterised by the presence of a pseudo-

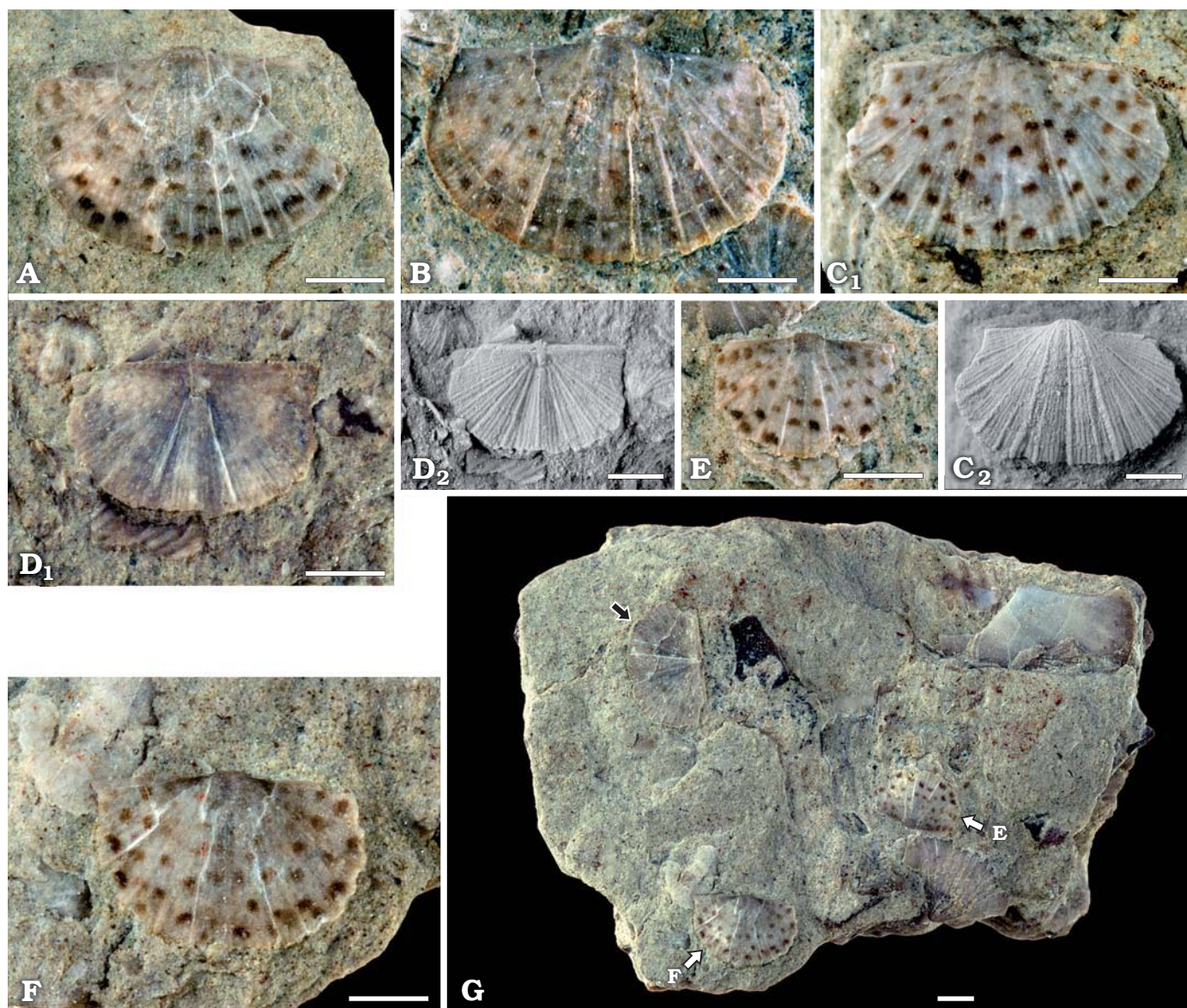


Fig. 1. Shell colour pattern in a strophomenide brachiopod *Plectodonta* sp. from the Khudykivtsi Member, Early Devonian, Dnistrove, Podolia, Ukraine. **A, B, E, F.** External view of four uncoated ventral valves, ZPAL Bp 56/90–93. **C.** External view of uncoated (**C₁**) and coated with ammonium chloride (**C₂**) ventral valve, ZPAL Bp 56/94. **D.** External view of uncoated (**D₁**) and coated with ammonium chloride (**D₂**) dorsal valve, ZPAL Bp 56/95; note the absence of colour pattern on the valve. **G.** Rock slab showing exterior of two ventral valves (white arrows, ZPAL Bp 56/96 and 97, enlarged on **E** and **F**) and one exterior of dorsal valve (black arrow; ZPAL Bp 56/98); note that both ventral valves show evident colour pattern, whereas dorsal valve is without discernible pattern. Specimens in **A, B, C₁, D₁, E–G** immersed in water before photographing. Scale bars 1 mm.

deltidium, chilidium, and supra-apical pedicle foramen. According to an exhaustive description of a type species of the genus, i.e., *P. mariae* Kozłowski, 1929 given by its founder, this pedicle foramen, although comparatively small, was fully functional at earlier growth stages, but then became sealed off and nonfunctional in adults (Kozłowski 1929). The diameter of the foramen in *P. mariae*, as given by Kozłowski (1929), ranges from 0.08 to 0.1 mm. In a few specimens presently studied, in which the pedicle foramen is preserved satisfactorily enough, it attains up to 0.06 mm in diameter. Thus, at an earlier ontogenetic stages *Plectodonta* had a functional pedicle and was anchored to the substrate. At the adult stage, however, individuals lost the pedicle and

became free-living. Generally, it is assumed that free-living concavo-convex brachiopods rested on the soft sediment on the convex valve (e.g., Rudwick 1970). However, Lescinsky (1995) presented epibiontic and taphonomic evidences that concavo-convex orthides and strophomenides lived on probably firm mud bottoms with the convex valve on top.

As described above, the colour pattern of the studied shells of *Plectodonta* sp. is confined to the ventral valve. This may suggest that the life position of the brachiopod was with the patterned (and convex) ventral valve uppermost and the patternless concave dorsal valve lying next to the underlying substrate. This is in agreement with the general life position of many living (as well as fossil) brachiopods with a func-

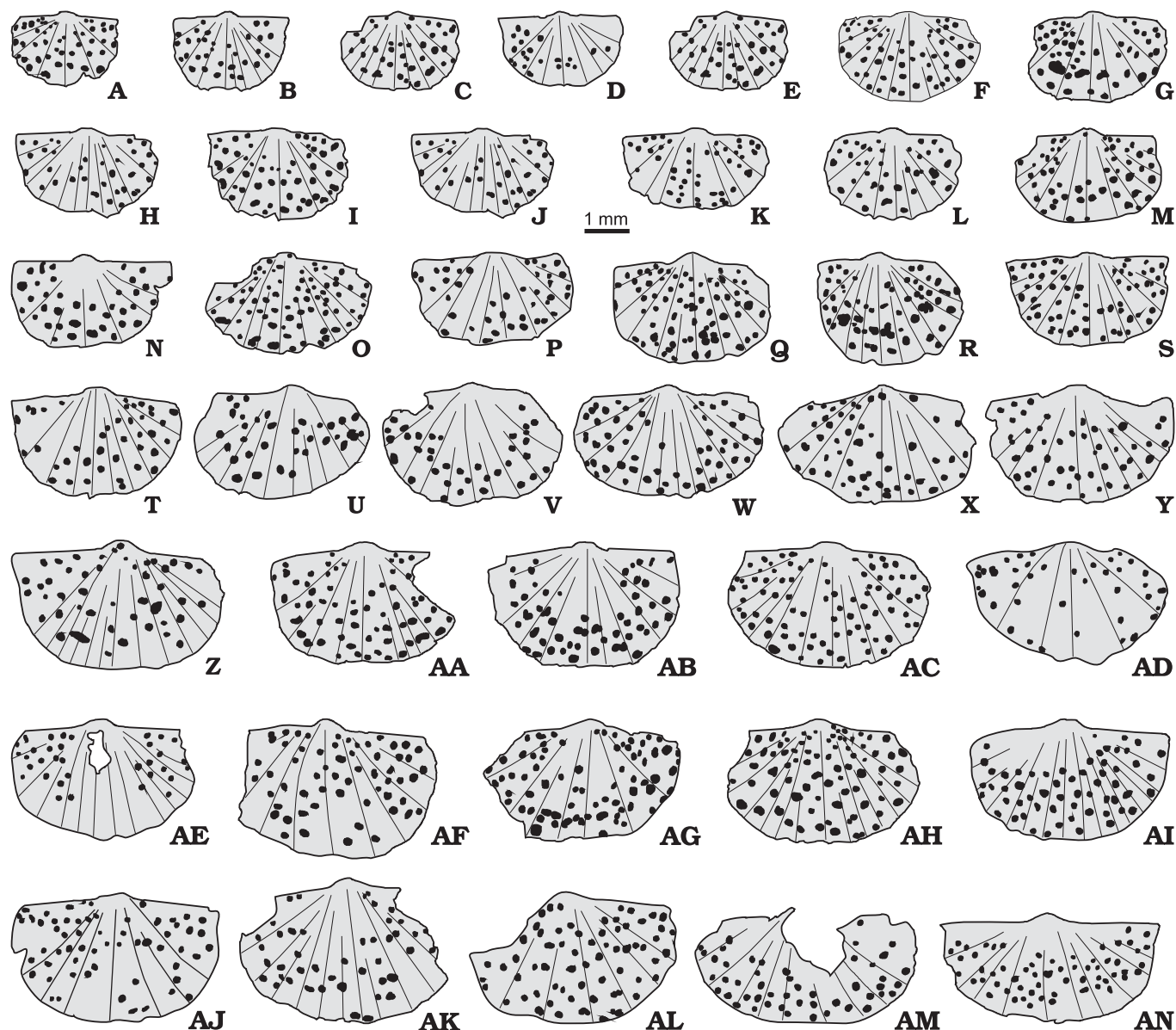


Fig. 2. Diagram showing variability of colour pattern in 40 ventral valves of *Plectodonta* sp. from the Khudykivtsi Member, Early Devonian, Dnistrove, Podolia, Ukraine.

tional pedicle whose shell is inclined above the substrate with ventral valve uppermost. At the adult stage, however, when individuals of the species lost their pedicle, the thickened posterior region of the shell might have helped them maintain a preferred orientation, presumably still with the colour-patterned and convex ventral valve uppermost. The presence of the colour pattern exclusively on the ventral valve seems so meaningful that it justifies supposition of yet another and unknown (not preserved on the shell exterior) mode of anchoring in some adult plectambonitoids which enabled them to stabilise the orientation of the shell above the substrate (for example, by cementing with a short, thin organic pad secreted by a gradually atrophying pedicle).

The colour-patterned ventral valve of *Plectodonta* sp. suggests also, that the pattern may perform a protective function through mimicry or a kind of disruptive camouflage. This

brachiopod lived in shallow waters (photic zone) where a patterned body cover might perform an important protective function against the visual systems of potential predators. Irregularly scattered spots probably blurred the shell outline and distracted potential predators. In other words, the predator's "searching image" (a few visual characters which enable the predator to recognise prey; see Wicksten 1983) may be seriously disturbed by patterned shells of *Plectodonta* sp. as potential prey. Protective function of a camouflage seems to be strongly linked with the development of vision in predators. Kobluk and Mapes (1989) suggest that vision capable of discerning form and colour pattern developed as early as the Late Ordovician. Since then camouflage served as a valuable protective function (Kobluk and Mapes 1989: 75). It needs to be mentioned, however, that the suggested function of the pattern was possible only when the outermost organic shell layer in

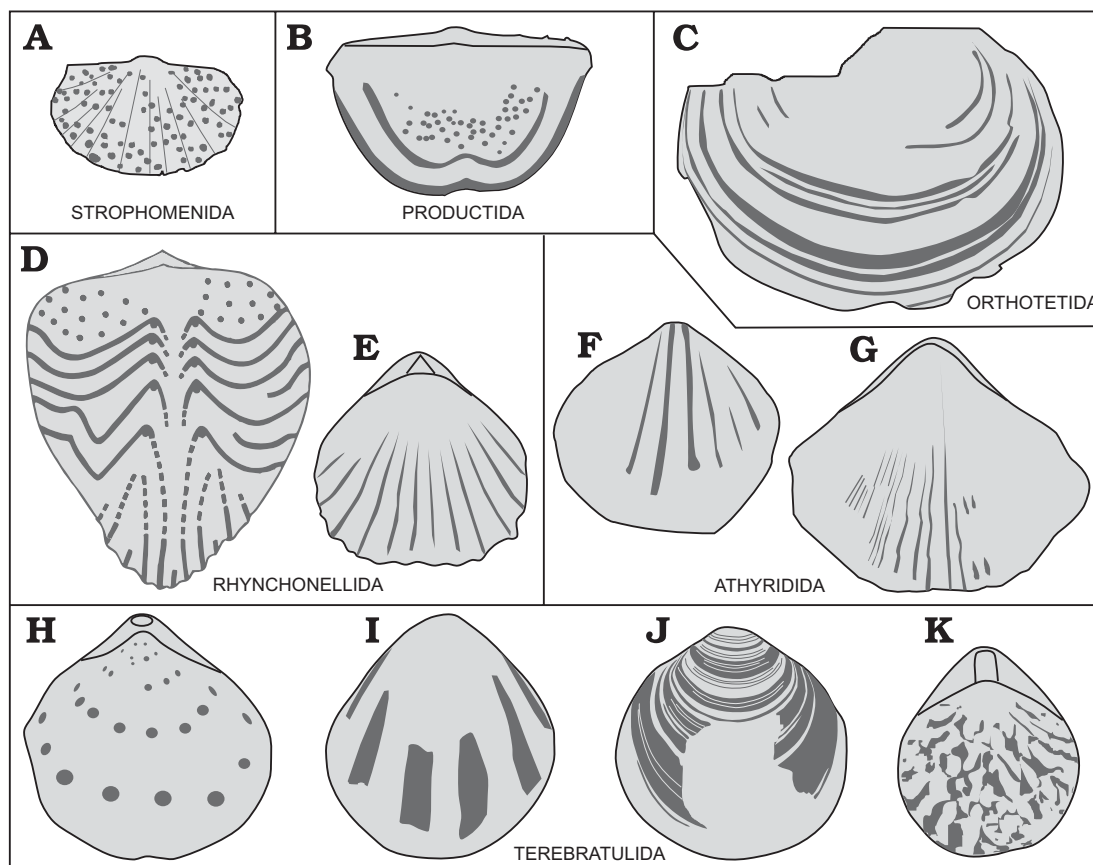


Fig. 3. Diagram showing examples of different types of colour pattern in some articulate brachiopods. **A.** Spotted pattern in strophomenide *Plectodonta* sp. from the lowermost Devonian of Podolia, Ukraine (this paper). **B.** Concentric banding and spots in productide *Chonetinella jeffordsi* Stevens, 1962 from the Middle Pennsylvanian of Colorado, USA (based on Stevens 1965: text-fig. 1). **C.** Concentric banding in orthotetide *Orthotetes kaskaskiensis* (McChesney, 1860) from the Mississippian of Illinois, USA (based on Nitecki and Sadlick 1968). **D.** Spots and irregular banding in rhynchonellide *Solidipontirostrum radwanskii* Biernat, 1984 from the Middle Devonian of Poland (Biernat 1984). **E.** Radial banding in rhynchonellide *Cassidirostrum radiatum* Johnson, 1975 from the late Early Devonian, USA (based on Johnson 1975: pl. 8: 23). **F.** Radial banding in athyridide *Athyris vittata* Hall, 1860 from the Middle Devonian of Michigan, USA (based on Blodgett et al. 1988: fig. 4). **G.** Radial banding in athyridide *Merista herculaea* (Barrande, 1911) from the Pragian Stage of Bohemia (based on Kříž and Lukeš 1974: pl. 1: 8). **H.** Spotted pattern in terebratulide *Cranaena morsii* Greger, 1908 from the Middle Devonian of Missouri (based on Kříž and Lukeš 1974: pl. 2: 14). **I.** Radial banding in terebratulide *Cranaena thomasi* Stainbrook, 1941 from the Middle Devonian of Iowa (based on Kříž and Lukeš 1974: pl. 2: 15). **J.** Concentric bands in terebratulide *Cranaena casei* Foerste, 1930 from the Middle Devonian of Michigan (based on Cloud 1942: pl. 24: 32). **K.** Irregular patches in the Recent terebratulide *Shimodaia pterygiota* MacKinnon, Saito, and Endo, 1997 from Japan Sea (based on MacKinnon and Lee 2006: fig. 1467: 5a). Not to scale.

Plectodonta sp., i.e., periostracum, was thin enough and did not obscure the visibility of the spots. Indeed, a fully developed periostracum in living brachiopods is extremely thin measuring usually up to 5–6 μm in thickness (Williams et al. 1997) and, to a large extent, is translucent.

The occurrence of the colour pattern in *Plectodonta* sp. may be helpful in obtaining useful data about the probable bathymetrical zone of the sea in which the species lived. It has been noted long ago by Forbes (1854; see also Newton 1907, Foerste 1930, and Blodgett et al. 1988) that marine organisms with colour-patterned shells essentially inhabit shallow-water depths related to the photic zone. He noted that marine shelly fauna living below 100 fathoms (about 200 m; 1 fathom = ca. 1.85 m) depth are quite white or colourless whereas those living from 50 fathoms shorewards have colours and patterns well marked (Forbes 1854: 21).

Distribution of colour-patterned marine invertebrates may

also indicate a difference in temperature of water areas. As noted by Nicol (1967), Recent colour-patterned marine pelecypod shells are very common in warm tropical waters and quite common in temperate-water areas, whereas in cold polar regions colour-patterned shells usually do not occur and are rare on shells found in water that never exceeds 12°C. Blodgett et al. (1988) confirm this phenomenon within the distribution of the Devonian marine invertebrates. They noted that all colour-patterned forms occurred in either the Old World Realm or Eastern America Realm, i.e., roughly tropical-subtropical and warm-temperate belts, respectively. High latitude Malvinokaffric Realm of the Southern Hemisphere totally lacks marine colour-patterned invertebrates (Blodgett et al. 1988). Occurrence of colour-patterned brachiopods in the earliest Devonian strata of Podolia, which at that time was situated quite near the equator (Małkowski et al. 2009: fig. 8), supports this distributional model.

Conclusions

- Numerous specimens of *Plectodonta* sp. described here from the earliest Early Devonian of Podolia are the first strophomenide and the oldest known articulate brachiopod retaining shell colour pattern.
- The colour pattern of *Plectodonta* sp. consists of brownish spots scattered more or less evenly, although irregularly, excluding the spotless umbonal region. The pattern is caused by the retention of a pigment derived from original colour and embedded in the shell substance.
- The colour pattern is developed exclusively on the ventral valves.
- The colour pattern on the ventral valve of *Plectodonta* sp. might have performed a protective function through mimicry or a kind of disruptive camouflage against visual systems of potential predators. This suggests that the life position of the brachiopod was with the patterned (and convex) ventral valve uppermost and the patternless concave dorsal valve lying next to the underlying substrate.
- Distributional characteristic of marine invertebrates with colour-patterned shells and carapaces supports the observation that *Plectodonta* sp. inhabited shallow and warm water areas.

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