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COLOUR PATTERN OF *NATICOPSIS PLANISPIRA* (NERITIMORPHA, GASTROPODA) SHELL FROM UPPER CARBONIFEROUS OF UPPER SILESIAN COAL BASIN, SOUTHERN POLAND

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Krawczyński, W., 2013. Colour pattern of *Naticopsis planispira* (Neritimorpha, Gastropoda) shell from Upper Carboniferous of Upper Silesian Coal Basin, southern Poland. *Annales Societatis Geologorum Poloniae*, 83: 87–97.

Abstract: A zigzag colour pattern with additional collabral belts and irregular spots was observed on a shell of *Naticopsis* (*N.*) *planispira* (Phillips, 1836) found in the Gołonóg Sandstone marine faunal horizon (Namurian A, the Upper Silesian Coal Basin, Poland). A disruption in the colour pattern was also observed to have occurred during ontogenetic shell growth. In this specimen, it appeared in the healed shell damage on the outer lip. So far, only nine Carboniferous species of *Naticopsis* have been reported with the colour pattern preserved. The most common are the zigzag-type and the spiral band-type. Individual taxa clearly differ in the morphology of the chevrons (direction and angles of breaks) and the location and width of the spiral bands on a whorl. However, the color patterns may not be diagnostic features for the *Naticopsis* species, because of the large intraspecific variation and colour pattern polymorphism on the neritimorph shells. Colour patterns on Palaeozoic neritimorph shells most likely served as camouflage with respect to the bottom surface in the photic zone.

Key words: Gastropoda, Neritimorpha, colour pattern, Carboniferous, Poland.

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INTRODUCTION

Specimens of Palaeozoic marine invertebrates with colour patterns preserved on their shells or carapaces are rare. They were described from the shells of brachiopods (e.g., Kříž and Lukeš, 1974; Blodgett *et al.*, 1988; Baliński, 2010), bivalves (e.g., Hoare *et al.*, 1988; Mapes and Benstock, 1988), nautiloids (e.g., Manda and Turek, 2009; Turek, 2009), and also from trilobite carapaces (e.g., McRoberts *et al.*, 2013).

Colour patterns on Palaeozoic mollusc shells, including gastropods, are preserved relatively seldom, owing to the frequent recrystallization of the original aragonite shells. The oldest gastropods with preserved colour patterns (*Straparollina harpa*) have been found in the Middle Ordovician deposits of the USA (Raymond, 1906; Foerste, 1930). Individual finds have also been recorded from the Silurian (e.g., Kříž and Lukeš, 1974), Devonian (e.g., Yochelson and Kříž, 1974; Rohr and Smith, 1978; Frýda, 2000; Basse and Heidelberger, 2002; Jankovský, 2003) and Permian deposits (e.g., Yochelson, 1956; Batten, 1958, 1972; Plas, 1972). Their greatest diversity, however, is noted in Carboniferous formations (e.g., Knight, 1932, 1933; Batten, 1966; Hoare and Sturgeon, 1978; see also Kobluk and Mapes, 1989).

The present paper describes a Carboniferous gastropod shell of *Naticopsis* (*Naticopsis*) *planispira* (Phillips, 1836) with a preserved colour pattern, from the Gołonóg Sandstone marine faunal horizon. The diverse faunal assemblage, consisting of about 50 taxa (including bivalves, gastropods, brachiopods, and nautiloids), has been studied by Cramer (1910), and Weigner (1938) and was revised by Bojkowski (1972). Additional faunal research was conducted by Schwarzbach (1935), Přibyl (1951), and Salamon (1997). Among the ten recognized gastropod taxa, *Naticopsis planispira* has not been listed previously.

GEOLOGICAL SETTING

The Upper Silesian Coal Basin is mainly located in the southern part of Poland and only its most SW part stretches into the territory of the Czech Republic (Fig. 1B). The Upper Carboniferous coal-bearing series rests on the Lower Carboniferous mudstone-sandstone deposits (Culm facies) in the W part and limestones (Carboniferous limestone facies) in its eastern part. The Upper Carboniferous deposits of the Upper Silesian Coal Basin consist of the Paralic Series (the lower part of the Coal-bearing Series) in its lower

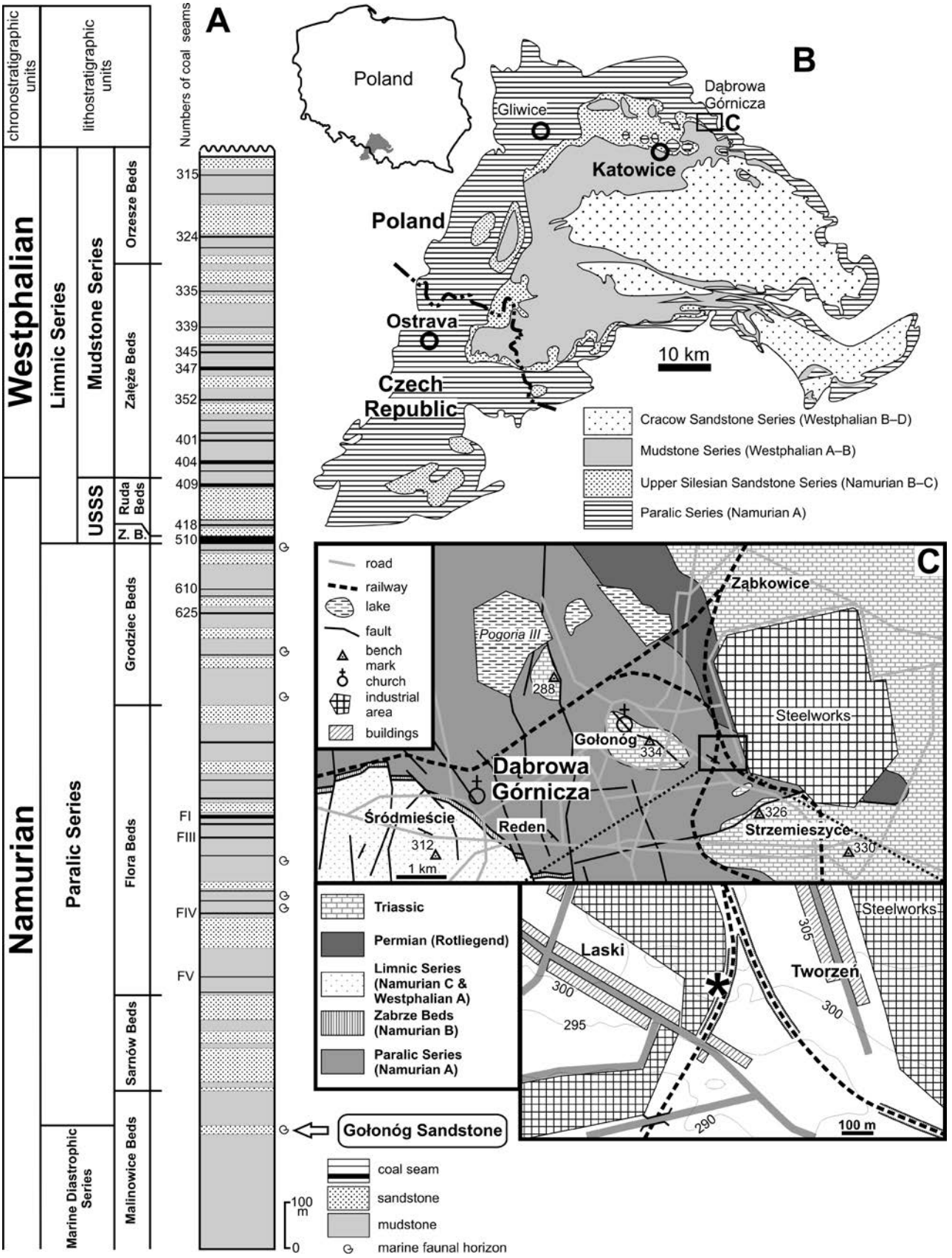

Fig. 1. Location of outcrops and stratigraphical position of the Gołonóg Sandstone marine faunal horizon. **A.** Stratigraphic sequence of the Upper Carboniferous in the NE part of the Upper Silesian Coal Basin, showing position of the Gołonóg Sandstone marine faunal horizon (after Kotas, 1995); Z. B. – Zabrze Beds. USSS – the Upper Silesian Sandstone Series. **B.** Location and geological features of the Upper Silesian Coal Basin (after Jureczka *et al.*, 1995). **C.** Geological map of the NE part of Dąbrowa Górnicza with sample location of *Naticopsis* shell (see asterisk) at the Gołonóg Sandstone horizon outcrop (after Doktorowicz-Hrebnicki, 1954)

part with numerous marine faunal horizons (Namurian A). Above is the Limnic Series with the Upper Silesian Sandstone Series (Zabrze Beds and Ruda Beds; Namurian B and C) and the Mudstone Series (the Załęże Beds and the Orzesze Beds; Westphalian A and B). The Kraków Sandstone Series (Westphalian C and D), which is present only in the eastern part of the basin, forms the last deposit of the Coal-bearing Series (see Kotas, 1995; Fig. 1A).

In the NE part of the basin, the upper Malinowice Beds form the lower part of the Paralic Series. The marine faunal horizon of the the Gołonóg Sandstone occurs locally within the Malinowice Beds. This horizon corresponds to the Štúr Faunal Horizon, present in the Czech part of the basin (Kotas, 1972, 1995). Above the Gołonóg Sandstone horizon, are the sandstones of the Sarnów Beds and mudstones with numerous coal seams and marine faunal horizons (Flora Beds and Grodziec Beds; Fig. 1A).

The Gołonóg Sandstone marine faunal horizon was first described by Roemer (1866, 1870). The Namurian age was determined by Doktorowicz-Hrebnicki (1935), Czarniecki (1959), and Kotas (1972). Currently, the horizon is exposed in the NE part of the Upper Silesian Coal Basin in the area of the Dąbrowa Górnicza city, in the W rail-cut between Laski and Tworzeń districts (GPS co-ordinates: 50°19'55.6"N, 19°15'35.3"E; Fig. 1C). The marine fauna belongs to two assemblages (see Weigner, 1938), preserved in the form of imprints and internal moulds in yellow-gray sandstones (bivalve-brachiopod assemblage with crinoids, corals, and trilobites) and as partially preserved shells in gray mudstones (gastropod assemblage with nautiloids), from which the shell of *Naticopsis planispira* comes.

MATERIAL AND METHODS

In order to better illustrate the colour pattern on the shell, a UV quartz lamp (EMITA VP-60) was used. To enhance the morphological details, the shell was powdered with ammonium chloride before being photographed.

The specimen is housed at the collection of the Department of Palaeontology and Stratigraphy of the University of Silesia in Sosnowiec (abbreviated GIUS).

SYSTEMATIC PALAEONTOLOGY

Order NERITIMORPHA Koken, 1896
Family NATICOPSIDAE Waagen, 1880
Genus *Naticopsis* M'Coy, 1844
Type species *Naticopsis phillipsii* M'Coy, 1844

Naticopsis (*Naticopsis*) *planispira* (Phillips, 1836)
Figs 2A, B, 3A–F

*1836 *Natica planispira* sp. nov. – Phillips: p. 244, pl. 14, fig. 24.
1843 *Nerita spirata* Sowerby – de Koninck: p. 484, pl. 42, fig. 3d.
1881 *Naticopsis*(?) *planispira* (Phillips) – de Koninck: p. 20, pl. 2, figs 23–24, pl. 3, figs 9–10.
non 1930 *Naticopsis* cf. *planispira* (Phillips) – Kühne: p. 98, pl. 4, fig. 4.
1966 *Naticopsis* (*Naticopsis*) *planispira* (Phillips) – Batten: p. 62, pl. 7, figs 4–5.
1972 *Naticopsis planispira* (Phillips) – Řehoř and Řehořová: p. 50, pl. 21, figs 6–12.
1973 *Naticopsis planispira* (Phillips) – Gromczakiewicz-Łomnicka: p. 44, pl. 9, fig. 4.

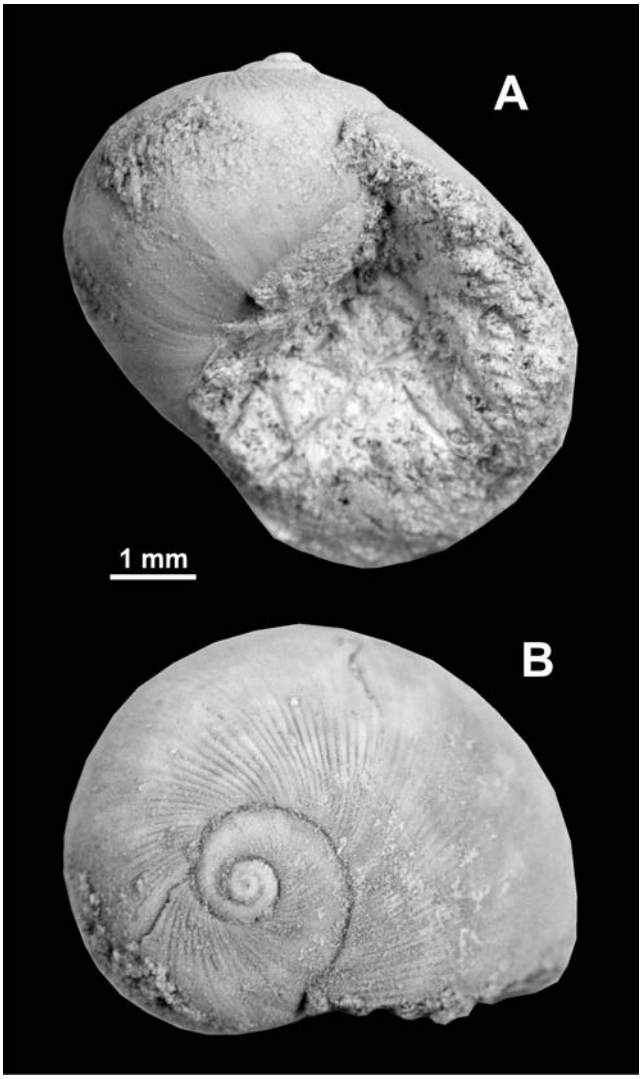

Fig. 2. *Naticopsis* (*Naticopsis*) *planispira* (Phillips, 1836) from the Upper Silesian Coal Basin (Namurian A), Poland, GIUS 5-3605 DG-1. The specimen was powdered with ammonium chloride. **A.** Apertural view of shell. **B.** Apical view with slightly thickened collabral lines visible

Material. One very well-preserved shell (GIUS 5-3605 DG-1).

Measurements of the shell: 6.4 mm height and 6.4 mm width (0.9 mm height of spire).

Description. The shell is globular and consists of three, strongly increasing whorls, covering three quarters of the shell height. The base is rounded and anomphalous. The spire is low and the suture is relatively shallow, but distinct. On the parietal part of aperture, a thickened smooth inductura is located (Fig. 2A). The upper part of the shell surface is gently flattened. The whorls are evenly rounded and distinctly convex. Growth lines are strongly prosoclinal. Ornamentation consists of slightly strengthened collabral lines, only on the upper flattened subsutural part of the whorl (Fig. 2B). Apical angle equals 130°. The protoconch is not preserved.

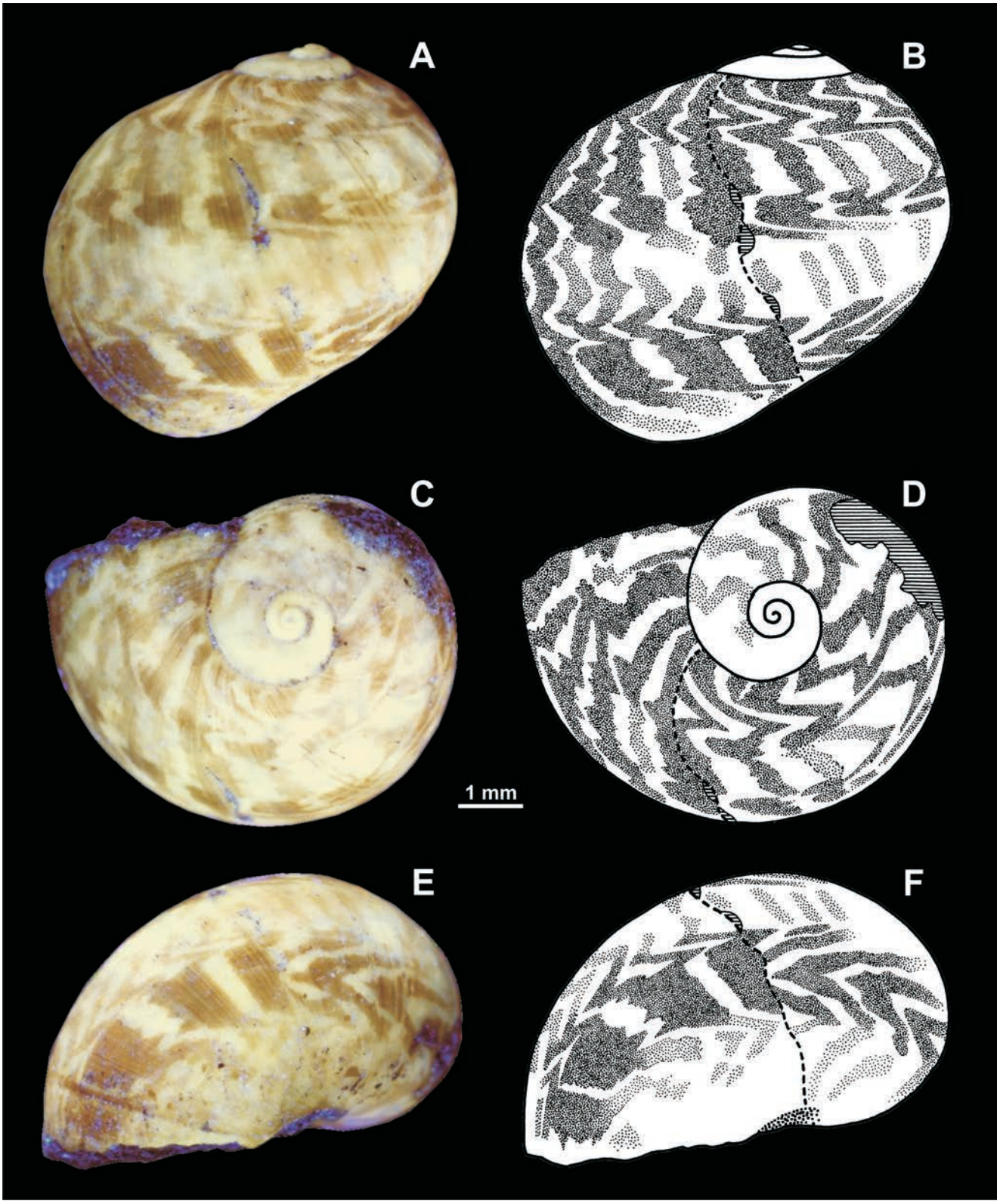

Fig. 3. Zigzag-type colour pattern of *Naticopsis* (*Naticopsis*) *planispira* (Phillips, 1836) from the Upper Silesian Coal Basin (Namurian A), Poland, GIUS 5-3605 DG-1. A, C, E. Photographs under UV light. B, D, F. Hand-made drawings of shell views, based on photographs. **A, B.** Lateral view of the shell with a damage visible. C–D. Apical view of shell. **E, F.** Basal view of the shell

Colour pattern. On the surface of the last whorl and partially on the spire whorls, the colour pattern is preserved in the form of brown markings on a light background. A zigzag-type pattern is dominant. In addition, there are prosoclinal belts and also two rows of trapezoidal or irregular spots in later ontogenetic stage. The colour pattern is relatively regular in the earlier ontogenetic stage.

Generally narrow coloured belts of different widths (about ten on a whorl) run from the suture in a opisthoclinal direction, and then break (sharply bend without loosing its continuity) at an angle

of 80° in a prosoclinal direction with the chevron edge directed adaperturally (Fig. 3C, D). Another double break at an angle of 33° occurs at a whorl height of seven-eights, followed by irregular prosoclinal belts. These belts break again adaperturally at an angle of 27° on the periphery of the whorl. Sometimes, the breaking neighbouring belts merge into irregular spots. After the last break, narrow belts run strongly opisthoclinally and transversely again to irregular prosoclinal belts just below the periphery of the whorl. Another break of the coloured belts is formed at a whorl height of one quarter and at an angle of 27° with the adapertural chevron (Fig. 3A, B). The last visible abapertural chevron is located on the base of the shell and then belts bend arcuately in the direction to the basal part of the aperture (Fig. 3E, F).

A mechanical damage of the shell labrum running irregularly to prosoclinally is visible in later ontogenetic stage of the shell growth. This damage causes a clear change in a relatively regular colour pattern (see Fig. 3). Double breaks of belts at the whorl height of seven-eights become very indistinct and prosoclinal arched belts of irregular width appear in their place. Adapertural bent chevrons on the whorl periphery merge into irregular spots. However, the breaks occurring at the whorl height of one quarter pass into relatively large trapezoidal spots, above which there are double break of narrow strips. Below trapezoidal spots with belts of irregular width break to abapertural direction and they are not visible on the base of the shell (see Fig. 3E, F).

Remarks. The shell of *Naticopsis* (*N.*) *planispira*, characterized by a low spire and a slightly flattened upper part of the whorl with thickened collabral lines, has been described by Phillips (1836) from the Visean of England for the first time. It also occurs in the Hotwells Limestone from Compton Martin (Somerset, England; Batten, 1966). This taxon, initially classified as *Nerita spirata* Sowerby (see de Koninck, 1843), has been found in the Visean limestones in the eastern part of the Namur Syncline in Belgium, from where its concentric operculum was described as well (de Koninck, 1881). Gromczakiewicz-Łomnicka (1973) also noted *N. planispira* in the Visean crinoid-coral limestones from the Holy Cross Mountains, central Poland. This species was also found in the Paralic Series (Namurian A) in Ostrava part of the Upper Silesian Coal Basin. It appears in marine faunal horizons of Naneta, Františka, Enna, Koksova and Gaebler (Řehoř and Řehořová, 1972) and in the older Gołonóg Sandstone horizon, which is an equivalent of the Štúr Faunal Horizon in the Ostrava area (see Kotas, 1995). However, neritopsid shells, recognized by Kühne (1930) and sampled from Ptasia Góra and Jugów near Wałbrzych (The Sudetes), have a much higher spire and a smaller apical angle (105°).

Occurrence. Visean: England: Bolland (Yorkshire), Compton Martin (Somerset); Belgium: Vise and Lives-sur-Meuse near Namur (Namur Syncline); Poland: Gałęzice (Holy Cross Mountains). Namurian A: Upper Silesian Coal Basin: Ostrava area (Czech Republic); Dąbrowa Górnicza-Laski (Poland).

REVIEW OF CARBONIFEROUS NATICOPSIDS WITH PRESERVED COLOUR PATTERNS

Among gastropods, colour patterns are most often preserved on neritimorph shells, owing to the presence of the outer calcitic prismatic layer, containing the remains of pigments (see Cox, 1960; Nützel *et al.*, 2007; Frýda, 2012).

The oldest colour pattern on neritimorph shells in the form of three rows of oval spots was found in *Paffrathopsis subcostata* (d'Archiac et Verneuil, 1842) at Paffrath (Givetian; Renish Slate Mountains, Germany; see Frýda, 2000). Frequently, colour patterns are observed in Carboniferous neritimorph shells, especially in *Naticopsis* M'Coy, 1844 and *Trachydomia* Meek et Worthen, 1866, which is probably a member of the Trachyspiridae Nützel, Frýda, Yancey et Anderson, 2007. Specimens of *Trachydomia*, with a colour pattern, consisting of either irregular collabral belts or dark spots on the tops of numerous nodes, were found at the Buckhorn Asphalt Quarry near Sulphur in Oklahoma, USA (Bandel *et al.*, 2002). Single finds of shells with the colour pattern preserved have also been reported from the Permian. Kemp (1957) described a taxon of the genus *Naticopsis* with narrow collabral belts, coming from the lower Permian deposits of Texas (USA). *Naticopsis minima* (Brown) with a zigzag-type colour pattern has been described by Hollingworth and Barker (1991) from the Zechstein reef limestones of England.

Different types of colour pattern preserved on neritimorph shells were also recorded from the Mesozoic (e.g., Tichy, 1980; Squires, 1993; Bandel and Kiel, 2003; Bandel, 2007; Kaim *et al.*, 2013) and Cenozoic (e.g., Bandel, 2001; Wesselingh, 2006; Symonds and Pacaud, 2010).

The genus *Naticopsis* has a globular or oval shell, which has a relatively low spire with a strongly expanded last whorl in a direction oblique to the axis and an anomphalous base. There are two subgenera within the genus *Naticopsis*. *Naticopsis* (*Naticopsis*) M'Coy, 1844 has a globular shell with a rounded convex profile of the whorl, while *Naticopsis* (*Jedria*) Yochelson, 1953 has a pronounced swelling below the suture and a flattened upper surface of the whorl. The Triassic genus *Marmolatella* Kittl, 1894, classified by Knight *et al.* (1960) as a subgenus of *Naticopsis*, now is a separate genus within the subfamily Platychilininae Bandel, 2007. Colour patterns are preserved on the shells of both subgenera *Naticopsis* and *Jedria*.

Naticopsis (*Naticopsis*) *subovata* Worthen, 1873
Fig. 4C

The zigzag-type colour pattern consists of dark, broad belts of irregular width (about eight on the last whorl). At the beginning, below the suture, the belts run opisthoclinally and break doubly in the adapertural and abapertural directions at an angle of 100°. The largest break in the adapertural direction at an angle of 80° appears just above the periphery of the whorl and the next abapertural one at three-eights of the whorl height, at an angle of 105°. The colour belts are not preserved on the base.

N. subovata was described by Worthen (1873) from the Upper Pennsylvanian (Missourian) of Illinois, USA. It was also recorded from the Pennsylvanian of Arkansas (as *Strophostylus subovata*; Mather, 1915), the Middle Pennsylvanian of Missouri, USA (Knight, 1933), and the Upper Pennsylvanian (upper Virgilian) of Kansas, USA (Mudge and Yochelson, 1962). Poorly preserved specimens of this taxon were found in the lowermost Permian of New Mexico, USA (Kues, 1991).

Naticopsis (*Naticopsis*) *picta* Girty, 1912
Fig. 4D

The zigzag-type colour pattern consists of numerous (about twelve on last whorl) narrow and relatively regular belts. At the beginning, wide, irregular colour belts run in a prosoclinal direc-

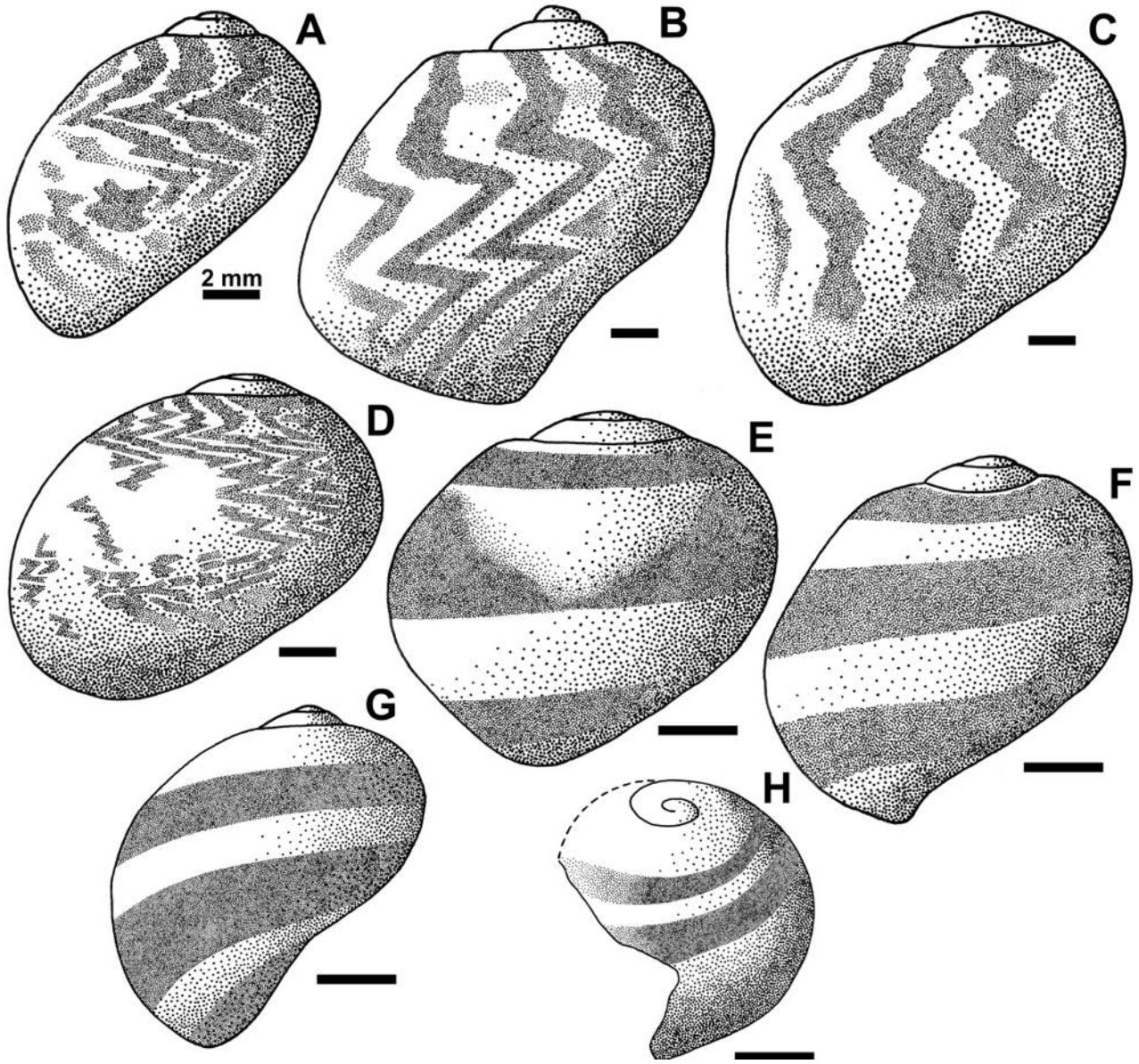

Fig. 4. Review of colour pattern types on lateral views of the Carboniferous *Naticopsis* shells. **A.** *Naticopsis* (*Jedria*) *meeki* Knight, 1933, Middle Pennsylvanian of St. Louis, Missouri, USA (after Knight, 1933, pl. 42, fig. 1c). **B.** *Naticopsis* (*Jedria*) *ventrica* (Norwood et Pratten, 1855), Middle Pennsylvanian of Pontotoc, Oklahoma, USA (after Knight, 1933, pl. 41, fig. 2d). **C.** *Naticopsis* (*Naticopsis*) *subovata* Worthen, 1873, Upper Pennsylvanian of Illinois, USA (after Knight, 1933, pl. 43, fig. 2j). **D.** *Naticopsis* (*Naticopsis*) *picta* Girty, 1912, Upper Mississippian of Perry County, Indiana, USA (after Girty, 1912, pl. 1, fig. 9). **E.** *Naticopsis* (*Naticopsis*) *wortheniana* Knight, 1934, Middle Pennsylvanian of the Buckhorn Asphalt Quarry, Oklahoma, USA (after Squires, 1976, fig. 1a). **F.** *Naticopsis* (*Naticopsis*) *virgata* Knight, 1933, Middle Pennsylvanian of St. Louis, Missouri, USA (after Knight, 1933, pl. 44, fig. 6g). **G.** *Naticopsis* sp., Middle Pennsylvanian of the Buckhorn Asphalt Quarry, Oklahoma, USA (after Seuss *et al.*, 2009, fig. 16a). **H.** *Naticopsis* (*Naticopsis*) *pulchella* Morningstar, 1922, Middle Pennsylvanian of Stark County, Ohio, USA (after Knight, 1933, pl. 44, fig. 3)

tion below the suture and break (locally double break) at seven-eights of the whorl height at an angle of 60°, forming a chevron in an abapertural direction. Then the belts become narrow and regular with many small secondary chevrons. They run strongly opisthoclinally and break again at an angle of 23° in an adapertural direction and continue quite far in an abapertural direction. Narrow belts break a few times at a constant angle of 23° just above and below the periphery of the whorl. From there they continue in an opisthoclinal direction and break again at one third of whorl height in adapertural direction. The direction of the belts is not visible on the base of the shell.

Naticopsis picta was described only from the Upper Mississippian (Chesterian) of Indiana, USA (Girty, 1912; see also Hayasaka, 1953).

Naticopsis (*Naticopsis*) *wortheniana* Knight, 1934
Fig. 4E

The colour pattern consists of dark spiral bands, which are only visible on the last whorl. The adapical band is located just below the upper suture. The central and widest band has constant width in the early ontogenetic stages, while in later stages its width

becomes variable and triangular spots are present. This belt is located on the upper surface of whorl from a height of three quarters to periphery of the whorl. The third spiral band has a continuous width that is similar to the width of the first band. It appears on the rounded base from one quarter to one eight of the whorl height.

Naticopsis wortheniana was first described by Knight (1933) from the Pennsylvanian of St. Louis (Missouri, USA) as *Naticopsis wortheni*. This name proved to be a younger homonym of *Naticopsis wortheni* Weller, 1916 (see Knight, 1934). Several specimens of very well-preserved shells with colour patterns were also found in the Middle Pennsylvanian of the Buckhorn Asphalt Quarry, Oklahoma, USA (Squires, 1976).

Naticopsis (*Naticopsis*) *virgata* Knight, 1933
Fig. 4F

The colour pattern consists of three spiral dark bands. The first band occurs at half of a distance between suture and periphery of the whorl (see Knight, 1933, pl. 44, fig. 6b). The widest band is located just below periphery at five-eights of the whorl height. The slightly narrower third band is situated in the middle of the rounded base (from about three-eights to one eight of the whorl height).

N. virgata was only recorded in the Middle Pennsylvanian of St. Louis, Missouri, USA (Knight, 1933).

Naticopsis (*Naticopsis*) *pulchella* Morningstar, 1922
Fig. 4H

The shell has a colour pattern consisting of spiral dark bands. There are two wide spiral bands on the upper surface of the whorl: a narrower band is located at three-quarter of the whorl height and a wider band is situated just above periphery of the whorl.

This taxon was found in black shales of the Middle Pennsylvanian Pottsville Formation from Ohio, USA (Morningstar, 1922; see also Knight, 1933; Yochelson and Saunders, 1967).

Naticopsis (*Jedria*) *meeki* Knight, 1933
Fig. 4A

The zigzag-type colour pattern consists of about eight dark belts on the last whorl. Wide, irregular belts start in the prosoclinal direction at the suture and run archwise as chevrons (break angle is 27°) in adapertural direction at a seven-eights of the whorl height. The next belts with numerous irregular secondary breaks are directed strongly prosoclinally and break in the abapertural direction at an angle of about 60° on the periphery of the whorl. A further adapertural break is situated at a quarter of the height of the whorl with an angle of 80°, after which the belts run prosoclinally toward the base. Colour belts are not visible on the base.

This taxon is the type species of the subgenus *Naticopsis* (*Jedria*) Yochelson, 1953. It occurs in the Middle Pennsylvanian of St. Louis and Barton Counties, in Missouri, USA (Knight, 1933; Hoare, 1961). Poorly preserved specimens of *Naticopsis* (*Jedria*) *meeki* was also recorded from the Lower Permian limestones of New Mexico, USA (Kues, 1991).

Naticopsis (*Jedria*) *ventrica* (Norwood et Pratten, 1855)
Fig. 4B

The zigzag-type colour pattern consists of eight dark belts on the last whorl. Irregular wide belts (about twice as wide as on the base of the shell) run prosoclinally from the suture and then they break at seven-eights of the whorl height at an angle of 115°. The next break is adapertural at two-third of the whorl height, at an angle of 70°. From this point onward the belts are clearly narrower and more regular. A further abapertural break appears slightly above half of the whorl height. Then the belts run strongly opisthoclinally and break twice at about three-eights of the whorl height, at an angle of 40°. From the last break onward, the belts run strongly opisthoclinally toward the basal part of the labrum.

This species is fairly widespread in Upper Carboniferous sediments. *Naticopsis altonensis* (McChesney, 1865), *N. ventricosus* Meek et Worthen, 1873, *N. pricei* Shumard, 1858, *N. torta* (Meek, 1871) proved to be younger synonyms of this species (see Yochelson and Saunders, 1967). *Naticopsis* (*Jedria*) *ventrica* was first described from the Upper Carboniferous of Indiana, USA (Norwood and Pratten, 1855). The species was also recorded in the Middle and Upper Pennsylvanian of St. Louis, Henry County (Missouri, USA; Knight, 1933), Summit, Muskingum, and Vinton Counties (Ohio, USA; Morningstar, 1922; Knight, 1933), San Juan region (Colorado, USA; Girty, 1903), New Mexico, USA (Kues and Batten, 2001).

Naticopsis sp.
Fig. 4G

The colour pattern is composed of three dark spiral bands. The upper band ranges from periphery of the whorl to at three-quarter of the whorl height. The middle band is the widest one. It is situated at one eight to three-eights of the whorl height. The third band is about as wide as the upper band. It is situated at the lower part of the base.

This specimen was found in the Buckhorn Asphalt Quarry, in Oklahoma, USA (Middle Pennsylvanian; Seuss *et al.*, 2009), and clearly differs with respect to both the proportion of shell and the colour banding of the species *N. wortheniana* Knight, 1934, which was described earlier from the same deposits (Squires, 1976).

Foerste (1930) mentions two taxa of Carboniferous neritids with preserved colour patterns: *Naticopsis* (*Naticopsis*) *lirata* Phillips, 1836 and *Naticopsis* (*Jedria*) *plicistria* (Phillips, 1836), but there are no descriptions of these patterns.

DISCUSSION

Among numerous Carboniferous species of the genus *Naticopsis* only nine exhibit colour patterns on their shells. The predominant pattern is the zigzag-type which is recognized in five taxa. Four taxa have the spiral band-type pattern (see Fig. 4; Tab. 1). Zigzag-type colour patterns clearly differ from each other with respect to the morphology of belts, their width, repeatability, break angle and location of chevrons on the whorl (see Figs 3, 4A–D). Differences are also observed among specimens with spiral band-type patterns, and in particular their relative width and position on the whorl (see Fig. 4E–G).

Up to now, naticopsid shells with the dotted-type colour patterns, appearing on Triassic shells of *Naticopsis* (see Tichy, 1980, pl. 3, fig. 2; Kaim *et al.*, 2013, fig. 4), were not known from the Palaeozoic. Probably, the development of new types of colour pattern could be related to the biotic recovery of gastropods after the end-Permian mass extinction (see Nützel, 2005) and the increasing importance of predation in the early stages of the Mesozoic marine revolution (see Vermeij, 1977).

A colour pattern is formed by temporal activity of pigment-secreting cells in the mantle margin at the edge of labrum. A specific pattern is formed, depending on the location of these cells and their current activity (see Cox, 1960). In

Table 1

Review of Carboniferous taxa of Naticopsis with type of colour pattern, age and locality of findings

Taxon	Type of colour pattern	Age	Locality	Reference
Naticopsis (*N.*) *subovata* Worthen, 1873	zigzag	Upper Pennsylvanian (Middle Pennsylvanian–Lower Permian)	Chanute Shale, Turkey Creek, Kansas City, Missouri, USA	Knight, 1933
Naticopsis (*Jedria*) *ventrica* (Norwood et Pratten, 1855)	zigzag	Middle Pennsylvanian (Middle Pennsylvanian–Lower Permian)	middle Boggy Fm, Pontotoc County, Oklahoma, USA	Knight, 1933
Naticopsis (*Jedria*) *meeki* Knight, 1933	zigzag	Middle Pennsylvanian	St. Louis County, Missouri, USA	Knight, 1933
Naticopsis (*N.*) *pulchella* Morningstar, 1922	spiral bands	Middle Pennsylvanian	Lower Mercer Black Shale, Stark County, Ohio, USA	Morningstar, 1922; Knight, 1933
Naticopsis (*N.*) *virgata* Knight, 1933	spiral bands	Middle Pennsylvanian	St. Louis County, Missouri, USA	Knight, 1933
Naticopsis sp.	spiral bands	Middle Pennsylvanian	Buckhorn Asphalt, Oklahoma, USA	Seuss *et al.*, 2009
Naticopsis (*N.*) *wortheniana* Knight, 1934	spiral bands	Middle Pennsylvanian	St. Louis County, Missouri, USA; Buckhorn Asphalt, Oklahoma, USA	Knight, 1933; Squires, 1976
Naticopsis (*N.*) *planispira* (Phillips, 1836)	zigzag	Namurian A (Visean–Namurian)	Paralic Series, Upper Silesian Coal Basin, Poland	this paper
Naticopsis (*N.*) *picta* Girty, 1912	zigzag	Upper Mississippian	Chester Group, Perry County, Indiana, USA	Girty, 1912

the case of spiral bands, the pigment-secreting cells are in a fixed position and permanently produce pigment. The zigzag-type pattern forms, when cell activity changes over a specific period of time, whereas the collabral-type pattern arises, when all the cells located at the labrum are temporarily active or inactive (see Kobluk and Mapes, 1989).

Colour patterns may change during ontogeny, owing to external, environmental changes. This is known as colour pattern polymorphism and is observed relatively frequently among modern and fossil neritimorphs (see Grüneberg and Nugaliyade, 1976; Symonds, 2008). There also has been a large variety of colour patterns in neritimorph shells of the same species. For this reason, the colour pattern may not be a diagnostic feature for neritimorph species. Examples are Cenozoic fresh- or brackish-water neritimorphs with various zigzag-type colour patterns: the Eocene *Clithon* (*Pictoneritina*) *pisiformis* (Ferussac) from the Blackheath Beds, Abbey Wood, England (see Symonds, 2008, figs. 10–12), the Pliocene *Theodoxus danubialis* (Pfeiffer) from Hungary (see Bandel, 2001, figs. 27–31) and the Recent *Neritina gagates* Lamarck from South Africa (see Bandel, 2001, figs. 68–71).

On the shell of *Naticopsis planispira* from the Upper Silesian Coal Basin, there is a clear change in the morphology of individual elements from a relatively regular zigzag-type pattern to additional rows of irregular or trapezoidal spots (see Fig. 3A, B, E, F). This change in the colour pattern is not a result of colour pattern polymorphism, because it abruptly appears along the site of clear mechanical damage to the shell. The mechanical damage probably resulted from environmental factors (e.g., water turbulence) or predation (see Jeffery *et al.*, 1994). This phenomenon also has been observed, for example, among the Eocene neritid species *Clithon* (*Pictoneritina*) *pisiformis* (Ferussac). One of the specimens of the latter species clearly shows a disruption of the regular zigzag-type pattern into a more irregular pattern, caused by some damage of the outer edge of the shell labrum (see Symonds, 2008, fig. 11).

A colour pattern is an adaptative feature, depending on the environment. In the case of gastropods, it can be important as camouflage, making the animal indistinguishable from the substrate in the photic zone. Zigzag-type and band-type patterns harmonize well with a striped net of shadows on the bottom, created by waves at the surface of the water. The zigzag-type pattern can also be a warning sign to potential predators, because it is similar to the zigzag-type patterns on nautiloid shells. As well, it cannot be excluded that the colour pattern could be created to retain toxic metabolic products in the shell (see Tichy, 1980; Kelley and Swann, 1988; Kobluk and Mapes, 1989).

CONCLUSIONS

1. *Naticopsis* (*Naticopsis*) *planispira* (Phillips, 1836) has a dominant zigzag-type colour pattern, combined with collabral belts.

2. The change of the colour pattern was caused by mechanical damage to the shell, and was not related to colour pattern polymorphism.

3. Zigzag-type and spiral band-type colour patterns are the most common among the Carboniferous *Naticopsis* species. These colour patterns were probably used for shell camouflage on the sea-floor in the photic zone.

4. Despite a significant differentiation of colour patterns within the Palaeozoic *Naticopsis* shells, they cannot be regarded as diagnostic features for the *Naticopsis* species, owing to a high intraspecific variability of colour patterns on their shells.

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