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; Bahlínský, 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; Fryda, 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).

GEOLOGICAL SETTING

The present paper describes a Carboniferous gastropod shell of Naticopsis (Naticopsis) planispira (Phillips, 1836) with a preserved colour pattern, from the Golonóg 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.
Fig. 1. Location of outcrops and stratigraphical position of the Golonóg 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 Golonóg 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 Golonóg 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 Zależ a 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 Golonóg 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 Golonóg Sandstone horizon, are the sandstones of the Sarnów Beds and mudstones with numerous coal seams and marine faunal horizons (Flora Beds and Grodzic Beds; Fig. 1A).

The Golonóg 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. 40, 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 Řehofová: p. 50, pl. 21, figs 6–12.  
*1973* *Naticopsis planispira* (Phillips) – Grumczakiewicz-Lonnicka: p. 44, pl. 9, fig. 4.

**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 prosocinal. Ornamentation consists of slightly strengthened collateral lines, only on the upper flattened subsutural part of the whorl (Fig. 2B). Apical angle equals 130°. The protoconch is not preserved.

**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 collateral lines visible.
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 losing 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 adapertural chevron is located on the one quarter and at an angle of 27° with the adapertural chevron (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 adapertural 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 belts, 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-Lomnicka (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, Kokosova and Gaebler (Rehóf and Rehófová, 1972) and in the older Golonog Sandstone horizon, which is an equivalent of the Stür Faunal Horizon in the Ostrava area (see Kotas, 1995). However, neritopids shells, recognized by Kühne (1930) and sampled from Ptasia Góra and Jugow near Wabrzycz (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: Gałżycze (Holy Cross Mountains). Namurian A: Upper Silesian Coal Basin: Ostrava area (Czech Republic); Dąbrowa Górnica-Laski (Poland).

**REVIEW OF CARBONIFEROUS NATICOPSIS WITH PRESERVED COLOUR PATTERNS**

Among gastropods, colour patterns are most often preserved on neritiform 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 neritiform shells in the form of three rows of oval spots was found in *Paffrathopsis subcostata* (d’Archiac et Verneuil, 1842) at Paffrath (Give-
tion below the suture and break (locally double break) at seven-eighths 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 opisthoclinal 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).

*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 eighth 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-eighths of the whorl height. The slightly narrower third band is situated in the middle of the rounded base (from about three-eighths to one eighth 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 adapatperural direction at a seven-eighths 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 adapatperural 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, 1935. 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-eighths of the whorl height at an angle of 115°. The next break is adapatperural 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 adapatperural break appears slightly above half of the whorl height. Then the belts run strongly opisthoclinally and break twice at about three-eighths 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 eighth to three-eighths 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).

Forste (1930) mentions two taxa of Carboniferous neritids with preserved colour patterns: _Naticopsis (Naticopsis) iridata_ Phillips, 1836 and _Naticopsis (Jedria) pleciastia_ (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, naticopside 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
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 temporally 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 Nugalyyade, 1976; Symonds, 2008). There also has been a large variety of colour patterns in neritiform shells of the same species. For this reason, the colour pattern may not be a diagnostic feature for neritiform shells. Examples are Cenozoic fresh- or brackish-water neritimorpha 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 Triassic Theodoxus danubialis (Pfeiffer) from Hungary (see Bandel, 2001, figs. 27–31) and the Recent Neritina gagates Lamarrick 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 adaptive 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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**Table 1**

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

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


Salamon, M., 1997. *Górnośląskaja fauna piskowców z Golonogaw w*
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