

Gastropods Colour Patterns in Cassiopids and Naticids from Romualdo Formation, Araripe Basin, Northeast Brazil

Padrões de Coloração em Gastrópodes Cassiopídeos e Naticídeos da Formação Romualdo, Bacia do Araripe, Nordeste do Brasil

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Abstract

The phylum Mollusca includes one of the most beautiful examples of colour patterns in present-day shells. However, they are rare in the fossil record because they demand excellent fossilization. In Brazil, colour patterns in fossil mollusk shells are recorded in gastropods *Natica* aff. *bulbulus* White, 1887 from the Riachuelo Formation (Aptian-Albian), Sergipe-Alagoas Basin. This paper presents the first gastropod shells from the Romualdo Formation with colour patterns, visible under natural and UV light, belonging to the families Naticidae and Cassiopidae, collected at Santo Antônio outcrop municipality of Exu, Pernambuco and, Pinheiro and Serra do Mãozinha sites, municipality of Missão Velha and Romualdo site, municipality of Crato, Ceará. Among the cassiopids more than 100 specimens were tested, with 1/3 of them showing a residual colour pattern under UV light exposure, after chemical preparation. They correspond to the species *Paraglauconia (Diglauconia) araripensis* (Beurlen, 1964), *Paraglauconia (Diglauconia) lyrica* Maury, 1934, *Gymnentome (Gymnentome) carrezozica* (Maury, 1934) and *Gymnentome (Gymnentome) romualdoi* Beurlen, 1964. The colour pattern is virtually similar in both genera, with fluorescent stripes on a dark background, showing the taxonomic similarity between them. As for the naticids, about 20 specimens were collected and 15 show good preservation, observing the visible colour pattern under natural light in *Natica* sp. and *Euspira* sp.; both new taxa for the Araripe Basin. The residual colour pattern in naticids ranges from spiral stripes to sigmoidal lines and blotches of brown and yellowish tones on a paler background, as observed in fossil species of the same family in the Cenozoic. The new occurrences increase the fossiliferous diversity of mollusks of the Romualdo Formation and extend the understanding of the diversity of colouration patterns of Lower Cretaceous gastropods.

Keywords: Mollusca; South America; Lower Cretaceous

Resumo

O filo Mollusca inclui um dos mais belos exemplos de padrões de cor nas conchas atuais. No entanto, eles são raros no registro fóssil porque exigem excelente fossilização. No Brasil, padrões de cor em conchas de moluscos fósseis são registrados em gastrópodes *Natica* aff. *bulbulus* White, 1887 da Formação Riachuelo (Aptiano-Albiano), Bacia Sergipe-Alagoas. Este trabalho apresenta as primeiras conchas de gastrópodes da Formação Romualdo com padrões de cor visíveis sob luz natural e UV, pertencentes às famílias Naticidae e Cassiopidae, coletadas no sítio Santo Antônio, município de Exu, Pernambuco e, sítios Pinheiro e Serra do Mãozinha, município de Missão Velha e sítio Romualdo, município de Crato, Ceará. Entre os cassiopídeos foram testados mais de 100

espécimes, com 1/3 deles apresentando padrão de cor residual em exposição à luz UV, após preparação química. Estes correspondem às espécies *Paraglauconia (Diglauconia) araripensis* (Beurlen, 1964), *Paraglauconia (Diglauconia) lyrica* Maury, 1934, *Gymnentome (Gymnentome) carregozica* (Maury, 1934) e *Gymnentome (Gymnentome) romualdoi* Beurlen, 1964. O padrão de cor é praticamente semelhante em ambos os gêneros, com listras fluorescentes em fundo escuro, mostrando a semelhança taxonômica entre eles. Quanto aos naticídeos, cerca de 20 espécimes foram coletados e 15 apresentam boa preservação, sendo observado o padrão de cor visível sob luz natural em *Natica* sp. e *Euspira* sp.; ambos novos táxons para a Bacia do Araripe. O padrão de cor residual nos naticídeos varia de listras espirais a linhas sigmoidais e manchas de tons marrons e amarelados em um fundo mais pálido, tal como observado em espécies fósseis da mesma família no Cenozoico. As novas ocorrências aumentam a diversidade fóssilífera de moluscos da Formação Romualdo e ampliam a compreensão da diversidade de padrões de coloração de gastrópodes do Cretáceo Inferior.

Palavras-chave: Molusco; América do Sul; Cretáceo Inferior

1 Introduction

The phylum Mollusca includes one of the most beautiful examples of colouration patterns in shells today. However, because of the rapid decay of their pigments, they are rare in the fossil record and require excellent fossilization (Kobluk & Mapes 1989). The oldest examples of colouration in gastropods date back to the Ordovician (Kobluk & Mapes, 1989; Schneider, Mandic & Harzhauser 2013; Gubanov & Bogolepova 2014), but, as expected, are more common in the Mesozoic and Cenozoic (Bandel & Kiel 2003; Pedriali & Robba 2005; Schneider & Werner 2007; Caze et al. 2011a, 2011b; Caze, Merle & Schneider 2015).

On the other hand, even when shell colouration is invisible in natural light it can still be detected, as some pigments fluoresce under ultraviolet light. This methodology has been especially useful in identifying the variety of colour patterns in paleontology, for example the Jurassic mollusk fossils analyzed by Caze, Merle and Schneider (2015).

While some authors suggest that pigments in shells merely result from the assimilation of metabolic wastes (Comfort 1951; Nuttall 1969; Cox 1960), others believe that they are the results of a biological response to environmental stresses. Colour patterns in shells of present-day gastropods are diverse and frequent, being used for purposes of camouflage, mimicry, aposematism and thermoregulation (Ramírez-Böhme 1974; Miura, Nishi & Satoshi 2007; Williams et al. 2016). According Vermeij (2015) gastropods defenses such as these already were used in the Mesozoic. In addition, different colour patterns in shells can also help distinguish species, for example in present-day and fossil gastropods from the Cenozoic (Dommergues, Dommergues & Dommergues 2006; Caze, Merli & Saint Martin 2012; Hendricks 2015).

In Brazil, the oldest record of colour patterns in fossil mollusk shells are recorded in gastropods from the Riachuelo Formation (Aptian-Albian), Sergipe-Alagoas Basin (Hessel & Carvalho 1988). Of related age, the Romualdo Formation of the Araripe Basin is world-renowned for its diversity and

excellent preservation of fossils (*Konservat-Lagerstätten*, Martill 1988; Maisey 1991). Mollusks are represented by marine gastropods and bivalves. However, to date, colour patterns have not been reported. In this paper, the first gastropod shells from the Romualdo Formation with preserved residual colour pattern, visible under natural and UV light will be presented, including the new record of *Natica* sp. and *Euspira* sp. in the Araripe Basin.

1.1 Geology and Paleontology of Romualdo Formation

The Araripe Basin is located in the Northeast Brazil between the states of Pernambuco, Piauí and Ceará (Figure 1), and rests on Precambrian terrains of the Transversal Zone of the Borborema Province (Brito, dos Santos & Van Schmus 2000), to the south of the Patos Lineament (Assine 2007). It is formed mainly by Mesozoic lacustrine and fluvial strata, grouped in the Pre-rite (Brejo Santo and Missão Velha formations), Rife (Abaiara Formation) and Post-rite I (Barbalha, Crato, Ipubi and Romualdo formations) and II (Araripina and Exu formations) sequences (Assine 2007; Marques et al. 2014). The process of marine ingression during the Lower Cretaceous in the region is recorded mainly in the Romualdo Formation.

The Romualdo Formation of Aptian-Albian age comprises conglomerates, sandstones, siltstones, limestones and mainly shales with fossils that attest a sedimentation in a transitional to shallow marine environment. The paleontological record includes fish, reptiles (pterosaurs, dinosaurs, crocodiles, turtles), crustaceans (ostracods, crabs, shrimps), plants (pteridophytes, gymnosperms and angiosperms), echinoids and mollusks (gastropods and bivalves) (Beurlen 1963, 1964, 1966; Silva-Santos & Valença 1968; Kellner, 2002; Oliveira 2007; Maisey 1991; Bruno & Hessel 2006; Lima, Saraiva & Sayão 2012; Pinheiro, Saraiva & Santana 2014; Pereira, Cassab & Barreto 2016, 2017; Prado, Fambrini & Barreto 2018).

Invertebrates are commonly found in shell beds generated from storm events at the top of the formation, and are the main evidence of typical marine sedimentation in the basin (Beurlen 1963; Sales 2005; Prado, Fambrini & Barreto 2018).

Mollusks have drawn attention since the 1960s when Karl Beurlen described the first gastropod species of the basin, the cassiopids *Craginia araripensis* Beurlen, 1964 and *Gymnentone romualdoi* Beurlen, 1964 collected in the municipality of Crato (Romualdo site) and Missão

Velha (Pinheiro site), respectively, both in the state of Ceará (Beurlen 1964). After almost half a century, these species have been revised and so many other cassiopids have been described (Pereira et al. 2016). In fact, in the last ten years the molluscan fauna has gained notorious visibility with the discovery of new gastropod taxa, including the only naticid described in the basin *Tylostoma ranchariensis* and some bivalves (Pereira, Cassab & Barreto 2016, Pereira, Cassab & Barreto 2018; Fürsich et al. 2019; Rodrigues et al. 2020).

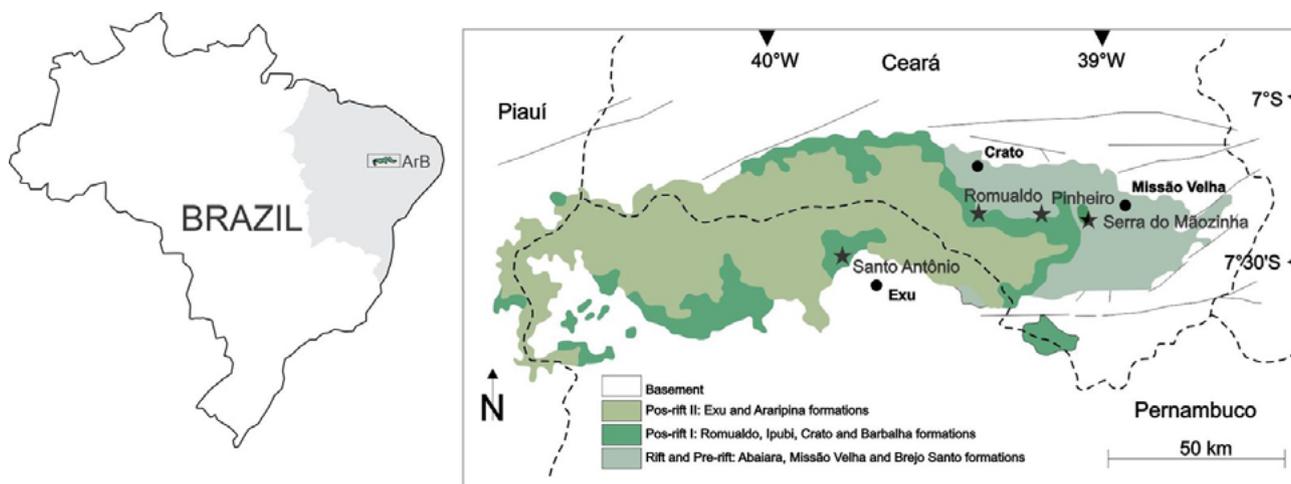


Figure 1 Location of the Araripe Basin (ArB) in the Northeast Brazil and outcrops of the Romualdo Formation with cassiopids and naticids with colour patterns (stars). (modified from Assine, 2007)

2 Materials and Methods

The mollusks come from the shale levels intercalated with fine siltstone/sandstone of the Romualdo Formation in the municipalities of Missão Velha and Crato (Ceará state) and Exu (Pernambuco state) (Figure 1). Cassiopid and naticid shells analyzed are in the Coleção Paleontológica do Departamento de Geologia, Centro de Tecnologia e Geociências, Universidade Federal de Pernambuco, Brazil (DGEO-CTG-UFPE).

In Exu, specifically at the Santo Antônio site, 15 shells of the naticid gastropods were collected with preserved residual colour pattern. In Serra do Mãozinha (Missão Velha), a few hundred cassiopid gastropods without visible pigmentation were collected. Dozens of cassiopid shells from the Pinheiro (Missão Velha) and Romualdo (Crato) sites already deposited at the DGEO-CTG-UFPE were also studied.

In order to observe residual colour patterns in cassiopid shells, we separated the best preserved shell, with

apparently unaltered original mineralogical composition. Subsequently, these shells were observed under 3600 Å ultraviolet light. Following the procedure described by Merle et al. (2008), shells with remnants of UV responsive residual pigments were soaked in a concentration of sodium hypochlorite (9.6% Chlorine) for 24 hours to enhance the residual colour patterns. After being washed to completely remove the chlorine solution, the shells were again analyzed under UV light of the same amperage and photographed. In the naticid gastropods, the residual colour patterns was preserved and could be seen under natural light. However, in order to highlight any unobservable pattern, the specimens were subjected to the same methodology.

The cassiopid specimens (DGEO-CTG-UFPE-7528, 8831, 8832, 8833, 8834, 8796, 8797, 8798) fluoresced under incidence of ultraviolet light, unlike the naticids (DGEO-CTG-UFPE-8592, 8593, 8594, 8595, 8596, 8597) which did not fluoresce.

For taxonomic identification, specimens were mechanically prepared and observed under a stereoscope, which allowed visualization of the morphological characters necessary for identification, measurement and photography. The shell terminology for the family Naticidae was adopted and adapted from several authors

(Cernohorsky 1971; Huelsken et al. 2008; Robba, Pedriali & Quaggiotto 2016), *Paleobiology Database* (accessed at <https://paleobiodb.org/#/>) and *MolluscaBase* (accessed at <http://www.molluscabase.org> on 2021-01-21). The terms and measurements utilized are given in Figure 2 and Table 1.

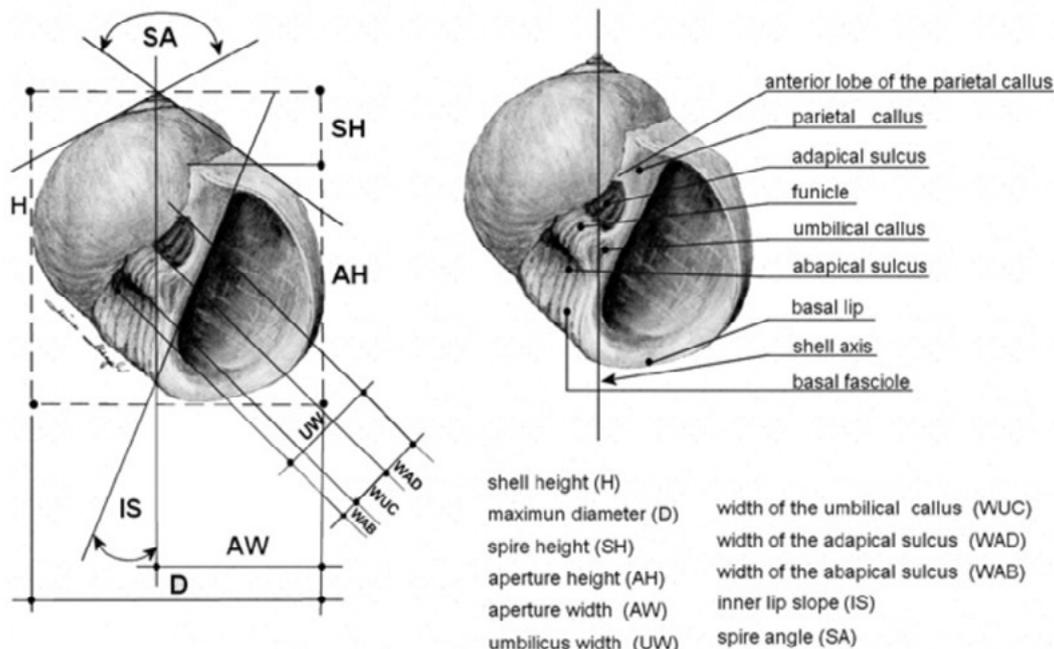


Figure 2 Standard measurements and illustrated glossary of the terms used for parts of naticid shell (from Robba et al. 2016).

Table 1 Measurements of Naticidae specimens analyzed in millimeters (mm). H, shell height; D, maximum diameter; SH, spire height; AH, aperture height; AW, aperture width.

Species	Specimens	Locality	H	D	SH	AH	AW
<i>Natica</i> sp.	DGEO-CTG-UFPE-8592	Santo Antônio site	13,7	12,4	3,2	10,0	6,6
	DGEO-CTG-UFPE-8593		14,3	13,5	3,5	10,6	7,6
<i>Euspira</i> sp.	DGEO-CTG-UFPE-8597	Santo Antônio site	9,8	9,2	1,9	7,0	5,0

2.1 Descriptive terminology

Background: a dark non-fluorescent or paler background that contrasts with elements that form the different colour patterns.

Stripes: Continuous vertical or horizontal lines throughout the shell that either emit fluorescence or represent natural tones (yellows and browns).

Blotches: Any area of a colour with no defined shape.

3 Results

Colour pattern was observed in four species of the Cassiopidae: *Paraglauconia (Diglauconia) araripensis* (Beurlen 1964), *Paraglauconia (Diglauconia) lyrica* Maury, 1934, *Gymnentome (Gymnentome) carregozica* (Maury 1934) and *Gymnentome (Gymnentome) romualdoi* Beurlen, 1964 and in the genera of the Naticidae: *Natica* sp. and *Euspira* sp.

3.1 Systematic palaeontology

Phylum Mollusca Linne, 1758

Class Gastropoda Cuvier, 1797

Family Cassiopidae Kollmann, 1979

Genus *Paraglauconia* Steinmann, 1929

Subgenus *Diglauconia* Mennessier, 1984

Type species. *Diglauconia picteti* Coquand, 1863

Paraglauconia (Diglauconia) araripensis (Beurlen, 1964)

(Figure 3A-F)

1964 *Craginia araripensis* Beurlen, p. 21 and 29, Figure 4.

1964 *Craginia araripensis* var. 'Alta' Beurlen, p. 27, Figure 4A.

1964 *Craginia araripensis* var. 'Lata' Beurlen, p. 27, Figure 4A-C.

2016 *Paraglauconia (Diglauconia) araripensis* Pereira et al., Figure 4 and 8A-C.

Material: DGEO-CTG-UFPE-8834A-I; Serra do Mãozinha, Missão Velha, Ceará; DGEO-CTG-UFPE-8797A-B, Pinheiro site, municipality of Missão Velha, Ceará. Romualdo Formation (Aptian-Albian), Brazil.

Description: Turriculate conical shell displaying eight to ten whorls, well-marked suture straight to concave flank. Initial whorls with three spiral cords, marked suture and straight flank. Main ornamentation consists of two subequal cords, one cord lies above the suture, the other one third down the suture, slightly concave flank.

Remarks: the specimens present some diagnostic characteristics for the species, such as three thin cords in the initial whorls and shell growth only with two equals to sub equals spiral cords, one cord $\frac{1}{4}$ away from the suture and the other near the suture and, base with one peripheral cord and two thin internal secondary cords (Pereira, Cassab & Barreto 2016).

Geographic and stratigraphic range: Cretaceous, Aptian-Albian, Romualdo Formation, Araripe Basin.

Paraglauconia (Diglauconia) lyrica Maury, 1934

(Figure 3G-I)

1936 *Paraglauconia lyrica* Maury; p. 210, pl. 12, Figure 11.

1964 *Craginia lyrica* Beurlen; p. 14 and 17, Figure 1B.

1984 *Paraglauconia (Diglauconia) lyrica* Menessier; p. 19, 20, pl. 2, Figure 42.

Material: DGEO-CTG-UFPE-8831B-C; Serra do Mãozinha, municipality of Missão Velha, Ceará; Romualdo Formation (Aptian-Albian), Brazil.

Description: The whole shell presents in its whorls two main cords as ornamentation. In the initials these cords are close to the suture, in the course of the growth of the shell the cords are moving away from the suture, with almost central positioning, which is well observed in the two last whorls. Well-marked sigmoidal growth lines can be observed at the base and in the last two whorls. These lines when cutting the cords of the last two whorls form false nodules. Base with peripheral cord showing the same thickness as the main ones of the last whorl and two thin inner secondary cords.

Remarks: the specimens have the diagnostic characteristics of the specie pointed out in Maury (1936) and complemented by Pereira, Cassab and Barreto (2016), which refer to cords near the sutures, main ornamentation with two spiral cords, a cord above the suture, and another, remote one third suture, suture well marked, with a concave flank and sinuous growth lines marking all shell cords and forming false nodules.

Geographic and stratigraphic range: Cretaceous, Aptian-Albian, Romualdo Formation, Araripe Basin.

Colour pattern: The species *P. (Diglauconia) araripensis* e *P. (Diglauconia) lyrica* present the same colour pattern. The species has a dark non-fluorescent background and a fluorescent area between the main cords. At the base there is fluorescence between the main cord and the peripheral cord of the base, and no fluorescence near the aperture. The fluorescence can be shaped like continuous stripes (Figure 3A-B) or show discrete sinuosities accompanying the growth lines (Figure 3C).

Genus *Gymnentome* Cossmann, 1909

Subgenus *Gymnentome* Cossmann, 1909

Type species. *Craginia turritiformis* Stephenson, 1952

Gymnentome (Gymnentome) carregozica (Maury, 1934)

(Figure 3J-M)

1936 *Turritella carregozica* Maury; p. 204, pl. 12, Figure 15.

1964 *Gymnentome carregozica* Beurlen; p. 30, Figure 6A.

2016 *Gymnentome (Gymnentome) carregozica* Pereira et al.; Figure 5C-D and 9C.

Material: DGEO-CTG-UFPE-8833; Serra do Mãozinha, municipality of Missão Velha, Ceará; DGEO-CTG-UFPE-8796B, Pinheiro site, municipality of Missão Velha, Ceará;

DGEO-CTG-UFPE-7528, Romualdo site, municipality of Crato, Ceará. Romualdo Formation (Aptian-Albian), Brazil.

Description: Turriculate conical shell, medium-sized, with 3 to 7 whorls, smooth teleoconch, descendants. Suture flush, straight flank, growth lines not observed, cylindrical base, with three cords on the periphery.

Remarks: the specimens present conical turriculate shell, with angular sutures and cylindrical base with three thin cords on the periphery and a shell smooth, with spiral planes resembling a slightly concave shape, all of them diagnostic characters for the species (Pereira, Cassab & Barreto 2016).

Geographic and stratigraphic range: Cretaceous, Aptian-Albian, Romualdo Formation, Araripe Basin and Riachuelo Formation, Sergipe Basin.

Colour pattern: Although there are no cords along the whorls, it is possible to observe that the parts before and after the suture are dark non-fluorescent and between them there is a fluorescent strip. Highlight for the fluorescence between the three cords of the base.

Gymnentome (Gymnentome) romualdoi (Beurlen 1964)
(Figure 3N-O)

1964 *Gymnentome romualdoi* Beurlen; p. 34, Figure 7.

2016 *Gymnentome (Gymnentome) romualdoi* Pereira, Cassab and Barreto; Figure 5A-B and 9F.

Material: DGEO-CTG-UFPE-8832; Serra do Mãozinha, municipality of Missão Velha, Ceará. Romualdo Formation (Aptian-Albian), Brazil.

Description: Conical shell turriculate, specimen with three whorls. Initial whorls absent. Concave flank, flush suture. Teleoconch with two tenuous cords in the third anterior and posterior.

Remarks: The specimens have the diagnostic characteristics of the species, such as two thin and faint cords and straight suture as main ornamentation and base with two faint spiral cords (Beurlen 1964; Pereira, Cassab & Barreto 2016).

Geographic and stratigraphic range: Cretaceous, Aptian-Albian, Romualdo Formation, Araripe Basin.

Colour pattern: The species has a dark non-fluorescent background with fluorescent area in the form of continuous stripes between the two cords present in each whorl. The fluorescent stripes are discrete, but are most easily observed in the last two preserved whorls.

Discussion on the colour patterns of the Cassiopidae:

The only record of Cassiopidae with a colour pattern is *Cassiope kefersteinii* from the Cretaceous of Austria (Gosau Group). In Cleavelly and Moris (1988) there is a citation from Zekeli (1852: 27), in which the author reports the development of nodes in the whorls of this species by regularly spaced brown growth lines. When the specimens analyzed in this work were subjected to UV light, it was noted that the pattern is maintained with the fluorescence emission occurring in pigmented parts. According to Caze et al. (2011a) the residual colour patterns are most frequently revealed by pale fluorescence, yellow-beige to white and sometimes very bright, being commonly found in Caenogastropoda, as in all cassiopids studied from the Romualdo Formation.

The residual colour pattern is virtually similar in both cassiopid genera, with fluorescent longitudinal stripes forming bands on a dark non-fluorescent background, showing the taxonomic similarity between them. All fluorescent stripes are found between the cords, with the exception of *Gymnentome (Gymnentome) carregoica* which lacks cords, but has these fluorescent stripes between the sutures. This pattern, therefore, shows a positive relationship with the sculptural elements of the shell.

In *Paraglauconia (Diglauconia) araripensis* and *Paraglauconia (Diglauconia) lyrica* the colour pattern contributed to the prominence of diagnostic features of the species. In *P. (D.) araripensis* the peripheral cord at the base is thinner than the cord of the last whorl and closer to the last cord. In *P. (D.) lyrica* the peripheral cord has the same caliber as the main cords of the last whorl and are the three cords, equidistant. Regarding the main ornamentation, in *P. (D.) lyrica*, due to the centering movement of the main cords in the adult whorls that moving away from the sutures, the space between the cords is smaller than in *P. (D.) araripensis*, which does not show centralization of cords (Figure 3). In *Gymnentome (Gymnentome) carregoica* even though the shell had no visible ornamentation, it was possible to see the same residual colour pattern on each whorl, in which the fluorescent region is in the center of each of them. Also highlighted in the species the fluorescence is between the three cords present at the base. Based on the description of the species *Gymnentome (Gymnentome) romualdoi* it is noted that the main cords are not clear, being vestigial and in high relief. With fluorescence it was possible to confirm that there are cords in the main ornamentation of *G. (G.) romualdoi*, but possibly are not so marked as in the genus *Paraglauconia* (Figure 3).

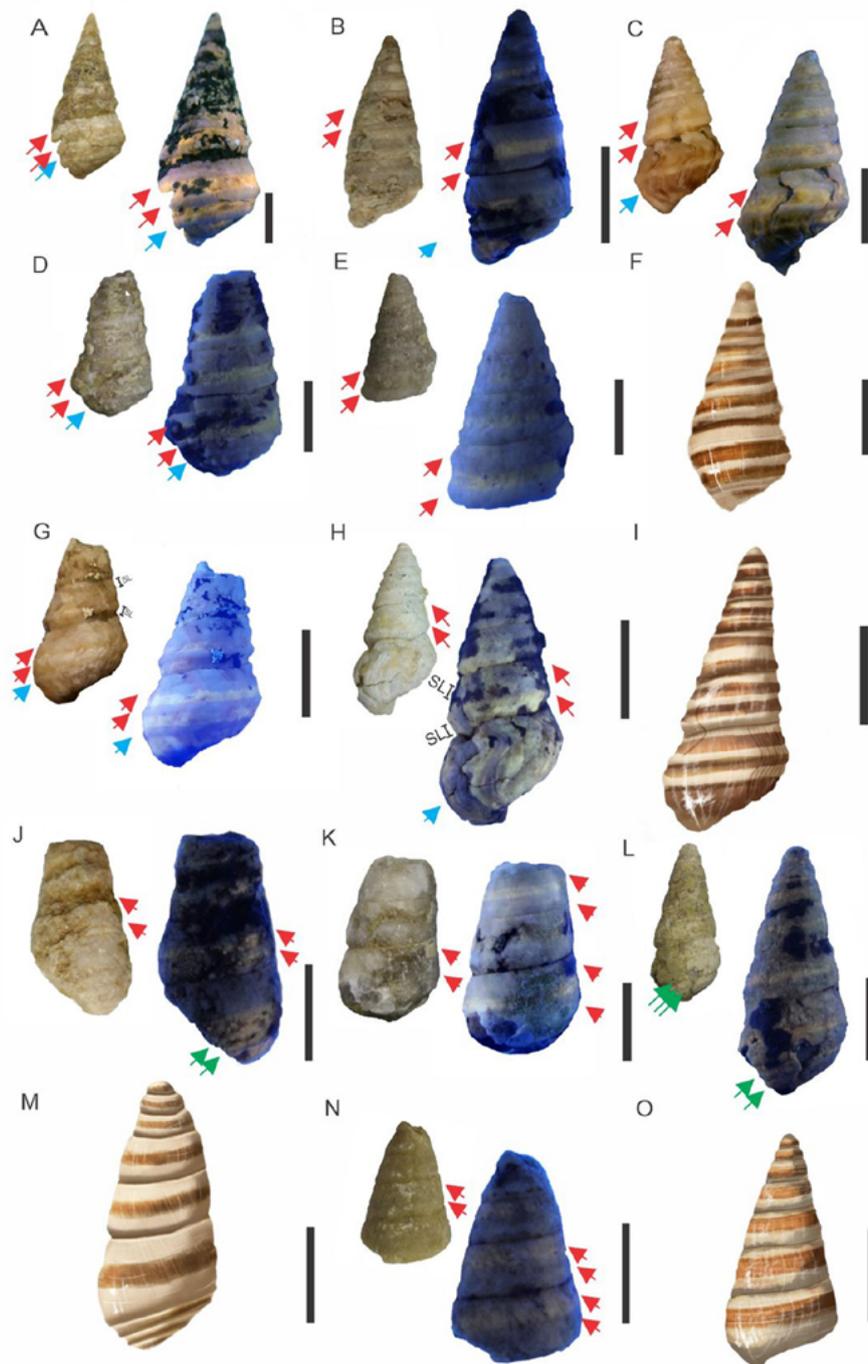


Figure 3 Cassioid gastropods with residual colour pattern from Romualdo Formation, Brazil: A-F. *Paraglauconia (Diglauconia) araripensis*; A. DGEO-CTG-UFPE-8834F; B. DGEO-CTG-UFPE-8834H; C. DGEO-CTG-UFPE-8834I; D. DGEO-CTG-UFPE-8797A; E. DGEO-CTG-UFPE-8797B; F. Reconstitution of the colour pattern and original tones; G-I. *Paraglauconia (Diglauconia) lyrica*; G. DGEO-CTG-UFPE-8831B; H. DGEO-CTG-UFPE-8831C; I. Reconstitution of the colour pattern and original tones; J-M. *Gymnentome (Gymnentome) carregoza*; J. DGEO-CTG-UFPE-8833; K. DGEO-CTG-UFPE-7528; L. DGEO-CTG-UFPE-8796B; M. Reconstitution of the colour pattern and original tones; N-O. *Gymnentome (Gymnentome) romualdoi*; N. DGEO-CTG-UFPE-8832; O. Reconstitution of the colour pattern and original tones; A-C, G-H, J, N. Serra do Mãozinha site; D-E, L. Pinheiro site; K. Romualdo site; Scale bars: 1 cm. Red arrows indicate the main ornamentation pattern of the species. Blue arrow indicates the peripheral cord of the base. Green arrows indicate the base ornamentation pattern for *Gymnentome (Gymnentome) carregoza*.

Longitudinal stripes are colour patterns known since the Paleozoic (Kobluk & Mapes 1989) to the present day. In the Jurassic of France, the same banded colour pattern observed in specimens from the Romualdo Formation is observed in the superfamily Cerithioidea, which includes among others the family Cassiopidae. In Procerithiidae, for example, the fluorescent stripes (3 to 4 per whorl) are located on or between spiral nodular cords (Caze, Merle & Schneider 2015). Currently, still within Cerithioidea, coloured bands on a paler background are present in the family Turritelidae. *Neohaustator fortilirata* (Sowerby 1914) is one of the species that, like cassiopids, presents pigmented stripes between spiral cords in each turn (Hasegawa 2009, p. 253).

Superfamily Naticoidea Guilding, 1834

Family Naticidae Guilding, 1834

Subfamily Naticinae Guilding, 1834

Genus *Natica* Spoli, 1777

Type species. *Natica vitellus* (Linnaeus, 1758)

Natica sp.

(Figure 4A-H)

Material: DGEO-CTG-UFPE-8592-8593; all from Santo Antônio site, municipality of Exu, Pernambuco, Brazil. Romualdo Formation (Aptian-Albian).

Description: Shell globose, 13.7 mm to 14.3 mm high. Protoconch plus three turns, low spirals, the last corresponds to 4/5 of the shell. Sutures well marked. Aperture subelliptical to semi-circular with more rounded area in the basal posterior part of the aperture, upper anterior part of the aperture rounded, outer lip thin. In the specimen DGEO-CTG-UFPE-8592 (Figure 4A-D) it is possible to observe remnant of the parietal anterior lobe and parietal callus. The umbilical callus is absent. There is a narrow half-moon shaped filled umbilicus, below slight abapical groove. In the specimen DGEO-CTG-UFPE-8593 (Figure 4E-H) the parietal lobe and remnant of narrow parietal callus are visible. The umbilical callus is also absent. The umbilicus is narrow, deep and half-moon shaped. Abapical grooves are worn out, but light grooves are visible.

Dimensions: For a list of measurements see Table 1.

Remarks: The genus *Natica* is characterized by higher whorls, subelliptical aperture, thin outer lip and absence of denticles in the inner and outer lips, presence of umbilicus, sometimes covered by parietal callus (Cernohorsky 1971) and absent or vestigial umbilical callus (Cernohorsky 1971; Pedriali & Robba 2009).

In the described species, the umbilicus is filled, and it is possible to observe a narrow-slit mark (Figure 4C) with absence of parietal or umbilical callus in both. A characteristic present in specimens that congrue with the genus *Natica* is the anterior lobe (Figure 4A-E) well marked next to the one that refers to the parietal callus. Despite not showing the preservation of the parietal callus, the presence of a well-marked anterior lobe allows us to infer it's probably narrow, as seen in the extant Brazilian species *Natica juani* Costa and Pastorino 2012. The specimen does not correspond to the genus *Polynices* Montfort, 1810 because it has low turns, last turn corresponding to 4/5 of the shell and globose. *Polynices* is characterized by thick and wide parietal and umbilical callus, sometimes covering the umbilicus. It was not possible to attribute the fossils to a described species due to the absence of characters that indicate affinities and the need for a revision in the identification of the naticid species described for the Cretaceous.

In the Lower Cretaceous, for the sedimentary basins of northeastern Brazil, only in the Sergipe Basin specimens of *Natica* were recorded. The genus was also reported in the Turonian-Campanian in the Potiguar Basin, Jandaíra Formation, but because they were represented in the form of deformed internal molds, it was difficult to identify the morphotypes (Cassab 2003). The species *Natica bulbulus* identified by White (1887) and redescribed by Maury (1936), collected in the Riachuelo Formation, Sergipe Basin, does not correspond to *Natica* sp. due to its lower spirals and a poorly printed suture, besides the presence of a wide callus that completely covers the umbilicus. The species described by White and Maury needs a revision regarding the genus, since they present diagnostic characters that do not fit the genus *Natica*, such as the parietal and umbilical callus fused covering the entire umbilicus. It stands out that the specimens described by Hessel and Carvalho (1988) as *Natica* aff. *bulbulus* from Riachuelo Formation (Figure 4I) were later attributed to the genera *Neritoma* and *Mesoneritina* in Hessel (2005) without further explanation for the identification.

Geographic and stratigraphic range: Cretaceous, Aptian-Albian, Romualdo Formation, Araripe Basin and Riachuelo Formation, Sergipe Basin; Turonian-Campanian, Jandaíra Formation, Potiguar Basin.

Colour pattern: the specimens present differences in their coloration, a common characteristic for the genus. The specimen DGEO-CTG-UFPE-8592 features a paler background with two dark brown horizontal stripes, one

near the suture with 2.5 mm and the other near the base with 1.9 mm in the last turn, equidistant in 2.5 mm. In the two whorls next to the protoconch, we can observe the continuity of the dark stripe far from the suture. On the other hand, the specimen DGEO-CTG-UFPE-8593

has a paler background with yellowish blotches and thin brown axial growth lines, visible throughout the shell. A single horizontal brown strip is at the top of the last whorl, about 3 mm thick, near the suture, in the same position on subsequent whorls near the protoconch.

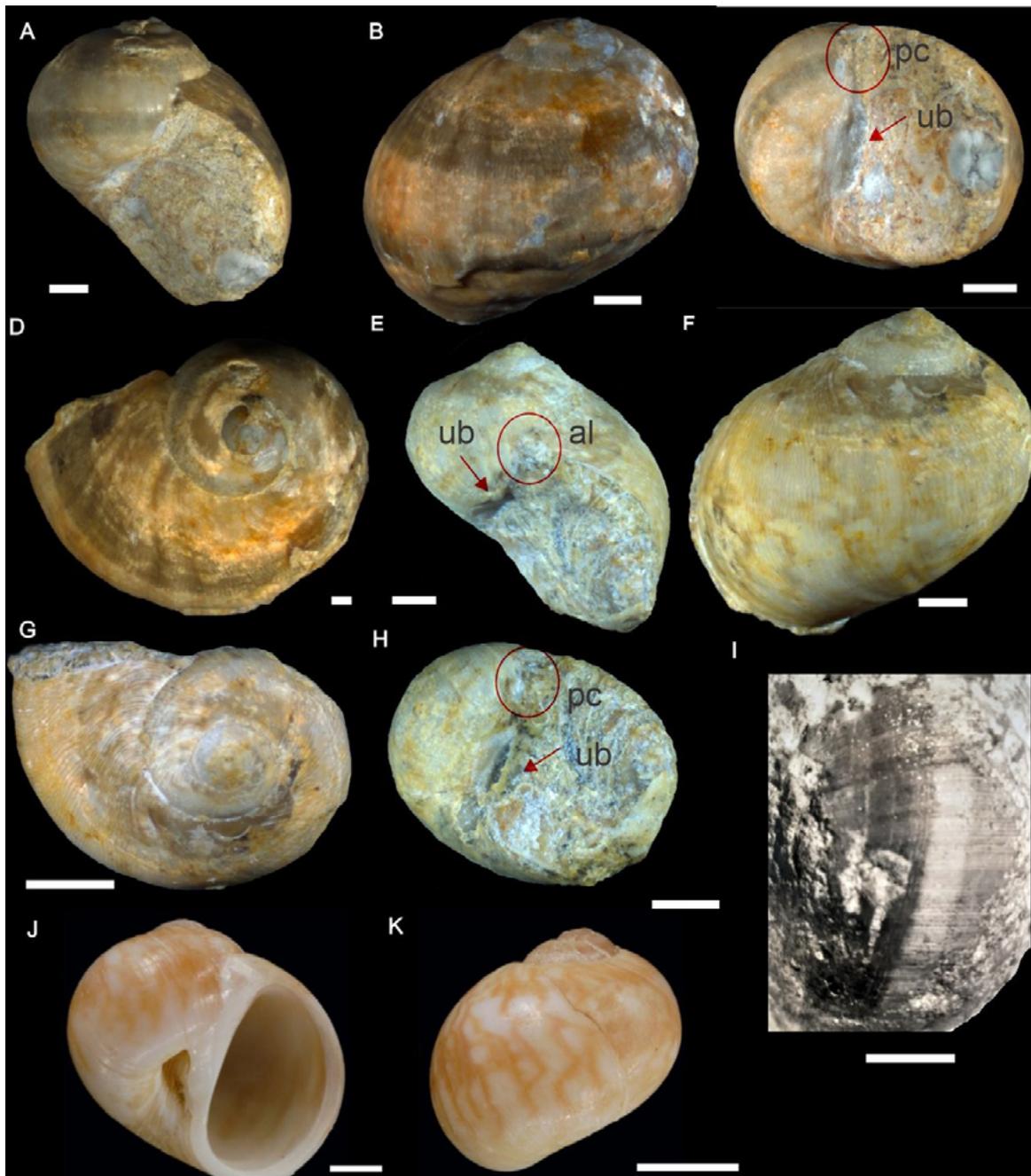


Figure 4 Gastropods Naticidae with colour pattern: A-H. *Natica* sp; A-D. DGEO-CTG-UFPE-8592; E-H. DGEO-CTG-UFPE-8593, Romualdo Formation, Santo Antônio site, Brazil; I. *Natica* aff. *bulbulus* (Neritidae?), Riachuelo Formation, Brazil (photo courtesy of Dr. Helena Hessel; Hessel 2005); J-K. *Natica juani* Costa & Pastorino 2012, extant taxa from Brazil (Costa & Pastorino 2012). Scale bars: 2 mm. pc: parietal callus; al: anterior lobe of the parietal callus; ub: umbilicus. Note the narrow and thin parietal callus and the location of the umbilical opening slit-like in *Natica juani* (J).

Subfamily Polinicinae Gray, 1847

Genus *Euspira* Agassiz, 1837

Type species. *Euspira glaucinoides* (J. Sowerby 1812)

?*Euspira* sp.

(Figure 5A-B)

Material: DGEO-CTG-UFPE-8597. Santo Antônio site, municipality of Exu, Pernambuco. Romualdo Formation (Aptian-Albian), Brazil.

Description: Small and conical-long shell, protoconch plus three whorls. Shallow suture. Protoconch and following spirals without preservation of colouration, only the last whorl is been present. It is not possible to identify the presence or absence of an umbilicus, but the large space where the callus, funiculus and umbilicus would be present indicate the probable presence of unpreserved parietal and umbilical callus.

Dimensions: For a list of measurements see Table 1.

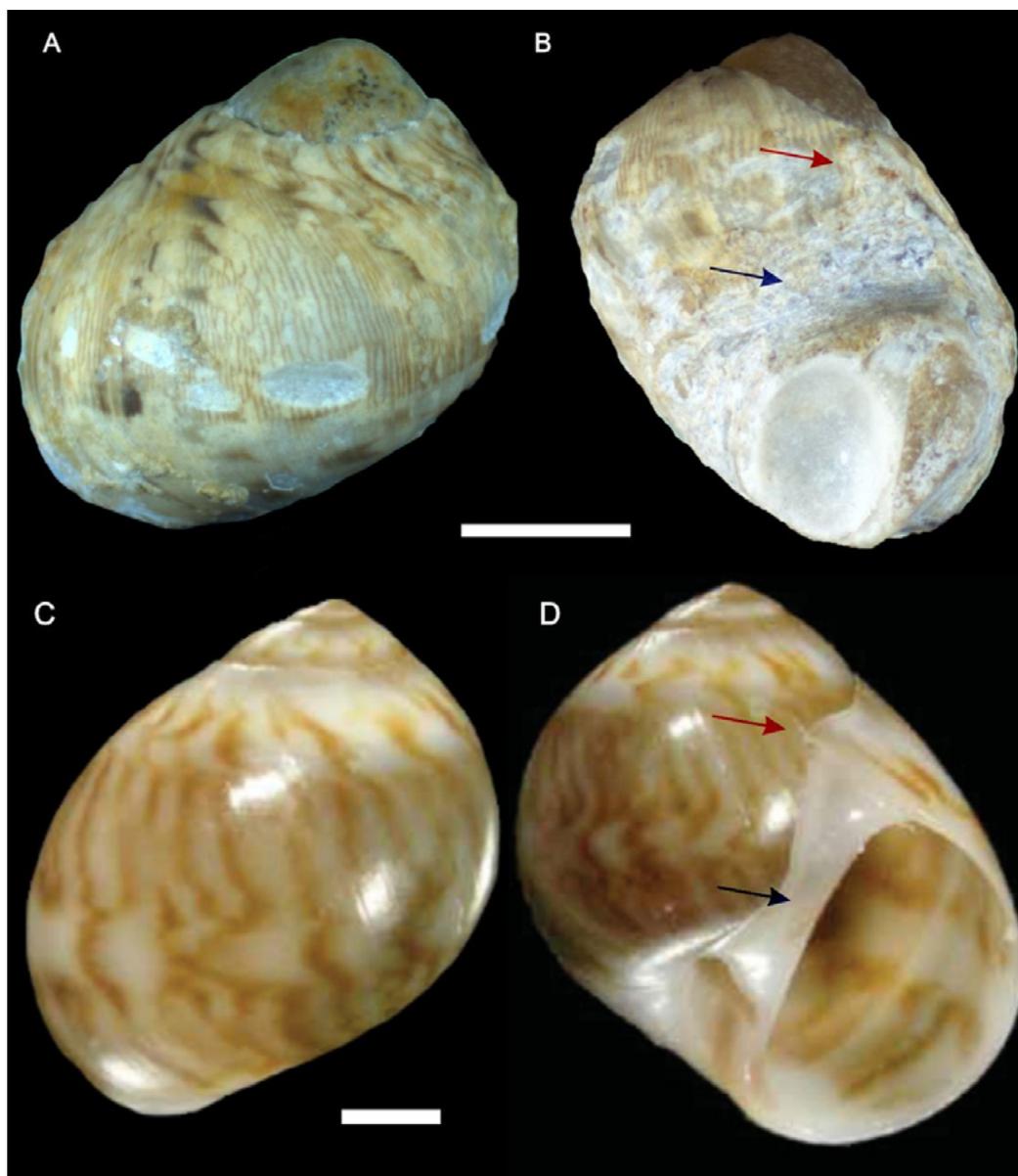


Figure 5 Gastropods Naticidae with colour pattern: A-B. ?*Euspira* sp. DGEO-CTG-UFPE-8597; C-D. *Euspira macilenta* (Philippi 1844) (Huelsen et al. 2008; Figure 9b, p. 30); A-B. Romualdo Formation, Santo Antônio site, Brazil; C-D. Italy. Scale bars: 2 mm. Note the anterior lobe in both species (red arrow), the callus in *E. macilenta* and the space possibly corresponding to the callus in ?*Euspira* sp. (blue arrow).

Remarks: The specimen was assigned to the genus *Euspira* due to the number of turns, shell shape and opening. The specimen does not correspond to the Neritidae Family since these specimens have a very globose shell, indistinct initial turns, shallow sutures, last turn corresponding to practically the entire shell, columellar callus well developed and teeth.

The analyzed specimen has characteristics that resemble *Polinices* Montfort, 1810, but the inconsistencies in the shape of the shell, especially in the last whorl, more rounded in *Polinices*, besides the significant absence of parietal and umbilical callus that in *Polinices* is quite thick and striking allows it to be classified in the genus *Euspira*. This difficulty in identification is justified, since *Euspira* has already been considered a subgenus of *Polinices* by some authors (Marwick 1924; Kilburn 1976; Marincovich 1977; Garvie 2013). After molecular and shell morphology analyses (Huelsen et al. 2012) it was concluded to be a valid genus.

Pedrali and Robba (2009) highlighted diagnostic features for the genus that are: thin to moderately thick, globose or globose-long shell and depressed to moderately raised spiral, somewhat stepped in some species. Suture almost close to compressed, parietal callus moderately thick in width and slender in length, with protrusion of the anterior lobe more or less distinct in the adaptive part of the umbilicus. Umbilicals open and deep, narrow to wide, umbilical callus thin to indistinct, better developed in some species, merging with the anterior lobe of the parietal callus or demarcated by a faint groove. The authors further point out that it is a genus that accommodates species with an open umbilicus practically devoid of funiculus and with a reduced to absent umbilical callus. The absence of parietal and umbilical callus preserved may indicate a) narrow parietal callus and absence of umbilical callus; b) umbilical callus fused to the anterior lobe and the narrow parietal callus; c) narrow parietal and umbilical callus, which best suits the genus *Euspira*.

When comparing ?*Euspira* sp. and *Euspira macilenta* from Mediterranean (Figure 5C-D) (Huelsen et al. 2008), it is noted that both have the same globose-long shell and moderately raised spiral shape and opening in the same outline and oblique position. Although it is not possible to visualize the presence of parietal and/or umbilical callus in the fossil specimen, it is possible to verify the similarity in the positioning of the anterior lobe in relation to the last turn, and similar width where the mentioned calluses would be located.

Members of the genus *Euspira* were described by Maury (1930) from the Riachuelo Formation, Albian of the Sergipe Basin and in the Gramame Formation, Maastrichian of the Paraíba Basin. The species *Euspira parahybensis*

(Maury 1930), previously attributed to the genus *Natica*, was reclassified by Muniz (1993) when collecting new specimens near João Pessoa and Alhandra, Paraíba.

Colour Pattern: Paler background, irregular and equidistant brown stripes that follow the growth lines in the last turn. In the upper portion of the last whorl, the stripes are thinner, almost parallel and close to each other. The anterior portion of the last whorl, in its turn, has the background whitish and the stripes thicker, short and sigmoidal forming randomly distributed waves.

Discussion on the colour patterns of the Naticidae: Although naticids to have originated in the Late Triassic or the Early Jurassic (Wenz 1941; Carriker & Yochelson 1968; Marincovich 1977; Bouchet & Warén 1993), the description of colour pattern in the family is only seen from the Cretaceous, but rare. One such example is the description of the species *Natica conradian* Gaab, 1864 from the Turonian of California and British Columbia, which presents a zig zag pattern, formed by prosocline stripes (Popenoe, Saul & Susuki 1987).

Patterns formed by longitudinal and axial stripes and blotches, such as those present in naticids of the Romualdo Formation, only become more frequent in naticid fossils in the Cenozoic, although they were already common in neritimorphs gastropods during the Cretaceous possible including the Brazilian occurrences (Figure 4I) (Hessel & Carvalho 1988; Hessel 2005; Saul & Squires 1997; Bandel & Kiel 2003; Bandel 2016; Erickson 2019). In the Eocene of France, naticids with colour patterns are identified from the fluorescence emission under Ultraviolet, including some with horizontal stripes, but does not represent a pattern frequently found in fossils of the family (Le Meur 2009).

From the Pliocene, the patterns present in naticids, including those seen in the Romualdo Formation, are organized in the most different ways, somehow sharing similarities (spots, axial and longitudinal stripes and blotches). Examples including the fossil species *Cochlis propinqua* Pecchioli, 1864 from the Pliocene of Italy (Pedrali & Robba 2005) and recent occurrences, such as *Natica perlineata* Dall, 1889 and *Natica juani* Costa and Pastorino 2012 (Figure 4J-K) from Brazil (Costa & Pastorino 2012) and *Euspira macilenta* (Philippi 1844) (Figure 5C-D) from Mediterranean (Huelsen et al. 2008).

4 Conclusion

Colour patterns represent one of the most useful shell morphological features in taxonomic classification within the phylum Mollusca. However, they are rarely cited in paleontological works, with the exception of those

from the Cenozoic, due to the rarity of their preservation. According to Hollingworth and Barker (1991), features indicative of *Lagerstätten* conservation, including rapid sedimentation and cementation, favor the preservation of colour in the shells. This may explain the occurrence of cassiopids and naticids studied here with a preserved residual colour pattern, since these preservational conditions would also be present at Romualdo Formation.

Colour secretion in shells occurs in specialized secretory cells along the edge of the mantle (Oberling 1968; Tichy 1980; Budd et al. 2014) and can be continuous and interruptive (Schneider & Werner 2007). When the secretion is continuous the patterns are simpler like radial stripes and spirals. Interruptive secretions generate more complex patterns such as blotches and spots (Schneider & Werner 2007). Gastropods from the Romualdo Formation show three basic types of colour patterns: longitudinal stripes, axial stripes parallel to the shell margin growth and blotches. Therefore, the cassiopids *Paraglauconia (Diglauconia) araripensis*, *Paraglauconia (Diglauconia) lyrica*, *Gymnentome (Gymnentome) carrezozica* and *Gymnentome (Gymnentome) romualdoi* that present a banded pattern would have their pigments secreted constantly. *Euspira* sp., in its turn, that exhibit vertical and wave stripes in the last turns would result from the continuous secretion of pigments marked by interruption moments. On the other hand, *Natica* sp. exhibit specimens with both types of secretion: one with banded-patterned and other with blotches in the last turn.

If in Cassiopidae there is a maintenance of the banded pattern between species and genera, the patterns in the Naticidae family are discreetly distinct, representing an intraspecific variability or colour polymorphism (Williams 2016). It is possible that this variability has an ecological background (camouflage, mimicry or other), which could favor certain forms over others in the environment. However, it is important to note that even patterns that at first sight would have no ecological function (i.e., “non-functional”; Seilacher 1972), such as colour patterns in shells of infaunal species, could reduce the intensity of penetrating light in the shells (Kobluk & Mapes 1989). According to Miura, Nishi and Satoshi (2007), from the study of colour patterns in the gastropod *Batillaria*, the colour polymorphism may derive from variations in temperature. While forms of *Batillaria* that are dark are predominant in colder regions, the brighter forms are more frequent in hot places, as they reflect heat. It is noteworthy that although they live on the substrate, all naticid species bury in the sand (Huelsen et al. 2008).

Thus, considering the hot and humid climate that prevailed during the deposition of the Romualdo Formation

(Melo et al. 2020; Araripe et al. 2021; Bom et al. 2021) it is possible that the gastropods analyzed here exhibit a colour pattern in response to biological and climatic pressures.

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Priscilla Albuquerque Pereira: conceptualization; formal analysis; methodology; validation; visualization; writing – original draft. **Ludmila Alves Cadeira do Prado:** conceptualization; formal analysis; methodology; validation; visualization; writing – original draft; writing – review and editing. **Rilda Verônica Cardoso Araripe:** writing – review and editing. **David Holanda de Oliveira:** writing – review and editing. **Flávia Azevedo Pedrosa Lemos:** writing – review and editing. **Luiz Ricardo da Silva Lobo:** writing – review and editing. **Maria Emília Travassos Rios Tomé:** writing – review and editing. **Alcina Magnólia Franca Barreto:** writing - original draft; validation; writing – review and editing; supervision.

Conflict of interest

The authors declare no potential conflict of interest.

Data availability statement

All data included in this study are publicly available in the literature.

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