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Colour patterns on Silurian orthocerid and pseudorthocerid conchs from Gotland – palaeoecological implications

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Abstract. The longitudinal colour pattern – an adaptively controlled feature functioning in cephalopods as camouflage – is described in two straight-shelled cephalopods from the Silurian of Gotland. A shell of the orthocerid *Dawsonoceras annulatum* (Sowerby) exhibits relatively broad longitudinal colour bands around the entire shell circumference, which in combination with transverse annuli and undulated growth ridges form a visually reticulate ornament. Such a combination is not known in other Silurian straight-shelled cephalopods. *Dawsonoceras annulatum* is the only known Palaeozoic cephalopod retaining an almost identical colour pattern in populations inhabiting different palaeo-continents. The shell of the pseudorthocerid *Lyecoceras*? *columnare* (Marklin) has densely packed narrow longitudinal colour bands on the entire smooth shell. In this feature the species is very similar to other Silurian and Ordovician pseudorthocerids. However, in Ordovician pseudorthocerids colour bands are restricted dorsally. The type of colouration described herein differs from that of Devonian and younger pseudorthocerids where the shell bears zig-zag bands. Longitudinal colouration around the entire shell circumference supports vertical or subvertical life orientation in both described species.

Key words: Silurian, Orthocerida, Pseudorthocerida, colour pattern, palaeoecology.

INTRODUCTION

Shell colouration in extant *Nautilus* consists of transversal irregular bands on the coiled shell and it is widely accepted that shell colouration functioned as a camouflage (for summary see Stenzel 1964 and Kobluk & Mapes 1989). A similar function of shell colouration has been supposed analogically for extinct nautiloids. Post-Triassic coiled shelled nautiloids share a colour pattern very similar to *Nautilus* (Mapes & Davis 1995), but Palaeozoic cephalopods exhibit a large variety of shell colouration (Foerste 1930; Teichert 1964; Turek 2009). Longitudinal, transversal and zig-zag colour bands have been described in straight-shelled cephalopods (for summary see Teichert 1964). Nevertheless, an example of adaptive convergence in shell form/colouration in straight-shelled cephalopods (Manda & Turek 2009a, 2009b) and colour pattern polymorphism related to depth (Flower 1957; Turek & Manda 2011) clearly supports adaptive control of shell colouration in nautiloids as the protective feature. The protective function of shell colouration has also been documented in other Early Palaeozoic externally shelled invertebrates (e.g. gastropods), but causal links between shell colouration of predators and prey are still poorly explained (Kobluk & Mapes 1989; Balinsky 2010).

Colour patterns in straight-shelled cephalopods (orthocerids, pseudorthocerids and lituitids) are rather poorly known in comparison with oncocerids and discosorids (Nautiloidea). The colour pattern in straight-shelled cephalopods consists of longitudinal, transversal or zig-zag bands. Shell colouration is related to biological orientation of the shell; horizontally oriented forms exhibit shell colouration restricted to lateral and dorsal sides, while cephalopods with shells oriented in life vertically are coloured around the entire shell circumference. Currently the vast majority of known Palaeozoic species with the preserved colour pattern belong to the order Pseudorthocerida. Colour patterns in Silurian representatives of the order Orthocerida are known only in the single species – *Dawsonoceras annulatum* Sowerby (Blake 1882). Shell colouration in the orthocerid *Dawsonoceras annulatum* Sowerby was described in a single specimen from Wales (Blake 1882) where the colour pattern is restricted to only part of the shell. Similarly, only a single species of Lituitina (= Palliocerida, Astrovioidea; group of externally shelled cephalopods with lamellar cameral deposits, which was previously included in Orthocerida and now is considered to be a distinct evolutionary lineage; Dzik 1984; Zhuravleva & Doguzhaeva 2002) retaining shell colouration is known (*Sphooceras truncatum* Barrande; Turek & Manda 2012). The colour pattern on oncocerid and disosorid cephalopods from the Silurian of Gotland has been described by Stridsberg (1985) and Turek & Manda (2011). The colour pattern in '*Orthoceras*' *columnare* Marklin was described by Angelin & Lindström (1880) for a small shell fragment from Gotland of uncertain taxonomic affinity. Herein we describe additional specimens of the latter with better-preserved colouration. The shell colouration in two Silurian straight-shelled cephalopods (Orthocerid, Pseudorthocerid) from the Island of Gotland is described in this paper and its implications for the mode of life are discussed.

DESCRIPTIONS AND DISCUSSION

The studied specimens from Gotland are housed in Naturhistoriska Riksmuseet in Stockholm, Sweden (prefix RM Mo).

Order ORTHOCERIDA Kuhn, 1940
Family DAWSONOCERATIDAE Flower, 1962
Genus *Dawsonoceras* Hyatt, 1884

Type species. *Orthocera annulata* Sowerby, 1818 from the middle Silurian of Wales.

Dawsonoceras annulatum (Sowerby, 1816)
Figure 1

Colour pattern. A single specimen RM Mo 47793, Wenlock, *D. annulatum* from the late Wenlock (lower Sheinwoodian) of Gotland (Högklint Beds, Hangvar kanal, Sweden) consists of a fragment of the body chamber, partially filled by light sparitic calcite. The specimen has well-preserved shell sculpture and is moderately dorsoventrally compressed. The colour patterning is observable around the entire circumference of the shell and is characterized by about twenty longitudinal bands subparallel to the shell axis. The bands run through adapically convex segments of growth ridges undulations. Based on shell sculpture it is impossible to determine unequivocally dorsal and ventral sides of the shell. If the white sparitic infilling of the body chamber indicates the dorsal side, the width of dark bands is almost the same as the width of unpigmented interspaces between them. On the opposite, perhaps ventral side (filled by dark micritic limestone), the mid-central part is lighter in colour. Two sub-centrally situated dark strips are markedly narrower than the strips between and bordering them on both sides. A very similar colour pattern was observed and illustrated in *D. annulatum* from the late Wenlock of Wales (Blake 1882, pl. 4, fig. 4) in a specimen showing five dark longitudinal bands each about 3 mm wide; their spacing is equal to the width of the bands. The specimen is slightly flattened so that the biological position of the coloured part of the shell is uncertain.

Classification. The relatively thick siphuncle of *Dawsonoceras* resembles that of pseudorthocerids, but the spherical apex with missing cicatrix and growth lines developed on the apical part of the shell clearly suggests the position of the family Dawsonoceratidae Flower within Orthocerida (Kröger & Isakar 2006).

Mode of life. *Dawsonoceras annulatum* is a rather long-ranging orthocerid from the late Llandovery up to the late Ludlow. It is known from Avalonia (Anglo-Welsh Basin in the Great Britain), Baltica (Gotland, Estonia, Podolia) and Perunica (Bohemia, = *D. barrandei* Horný, 1956). The occurrence in North America is uncertain, but some described species of *Dawsonoceras* are closely

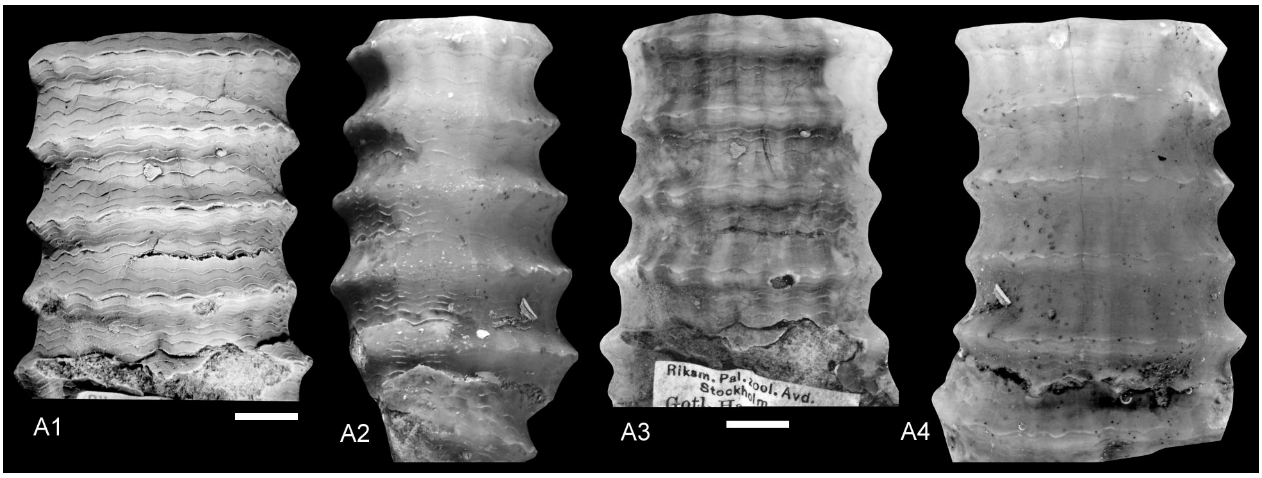

Fig. 1. A1–A4, *Dawsonoceras annulatum* (Sowerby, 1816), RM Mo 47793, Hangvar kanal, Högklint Beds, Wenlock, lower Sheinwoodian. Ventral (A1, A3), lateral (A2) and dorsal (A4) view. Scale bars equal 5 mm. Specimens figured as Fig. A2–A4 were immersed in alcohol before photographing.

related to or conspecific with *D. annulatum* (Foerste 1928). *Dawsonoceras annulatum* is thus restricted to warm-water low-latitude areas of the southern hemisphere. In the Prague Basin, *D. annulatum* was most common in shallow-water environments close to the fair wave base, but occasionally it occurs in deeper-water carbonate facies (cephalopod limestone biofacies, platy limestone with common trilobites) or even off-shore shales. Colour bands around the entire shell circumference document a (sub-)vertical biological orientation supporting evidence supplied by the shell morphology (straight or slightly oblique annulation). The shallow and broad hyponomic sinus in adult stage indicates active pulse-jet propulsion. *Dawsonoceras* was probably a predator preferring quiet, shallow, warm-water environments.

Order PSEUDORTHOCERIDA Flower & Caster, 1935
Family uncertain
Genus *Lyecoceras* Mutvei, 1957

Type species. *Lyecoceras gotlandense* Mutvei, 1957 from the middle Silurian of Gotland.

Lyecoceras? *columnare* (Marklin, 1857) in Boll (1857)
Figure 2

Colour pattern. The colour pattern was observed in five specimens from late Ludlow rocks of Gotland (Fig. 2A: RM Mo 45540, Östergarn, upper Hemse Beds; Fig. 2B: RM Mo 54333, Östergarn; Fig. 2C: RM Mo 50646, Hamra, Hamra or Sundre Formation; Fig. 2D: RM Mo 150461, Östergarn, upper Hemse Beds; Fig. 2E: RM Mo 156201, Östergarn, upper Hemse Beds). It consists of narrow 0.5–2 mm thick densely packed longitudinal bands. The distance between bands is almost equal to band width, sometimes less. The margin of dark-brown bands is sometimes slightly irregular. In none of the specimens the shell colouration is preserved around the entire shell circumference, but the combined observations of all the specimens suggest that bands originally circumscribed the shell surface. The colour pattern of *L.*? *columnare* strongly resembles the shell colouration in *L.*? *pellucidum* (Barrande, 1868) from the latest Ludlow of Bohemia in which the longitudinal bands are variable in width (Barrande 1868, pl. 261, fig. 1; 1870, pl. 400, fig. 8, pl. 420, figs 1, 2, pl. 460, fig. 2). Variation in the width of longitudinal bands is also confirmed in this species in several additional specimens coming from recent collections.

Classification. The inner structure of shells of *L.*? *columnare* (Fig. 2E1), as well as closely related *L.*? *pellucidum*, strongly resembles *Lyecoceras gotlandense* Mutvei, 1961 from the Silurian of Gotland. However, *Lyecoceras* is characterized by faint radial striae appearing later in ontogeny so that the early post-embryonic shell is smooth. Thus, *Orthoceras columnare* may be tentatively placed to *Lyecoceras*. Although Mutvei (1961) did not place his new genus *Lyecoceras* in a family, the slightly curved cup-like protoconch that possesses a cicatrix (Mutvei 1957, pl. 20, fig. 2) suggests a position in the order Pseudorthocerida.

Mode of life. According to Mutvei (1961, p. 231), *Lyecoceras* and allied forms were actively swimming cephalopods with a vertically oriented shell. The colour bands that have developed around the entire shell in *L*?. *columnare* support the hypothesis of a subvertical life position. They also give evidence of the appearance of Silurian pseudorthocerids with subvertical biological orientation and secondary reduced cameral deposits. Data concerning the facies distribution of *Lyecoceras* from Gotland are scarce, but closely related late Ludlow species *L. araneosum* (Barrande) and *L. neptunicum* (Barrande) from the Prague Basin preferred rather shallow-water environments. They occurred in the brachiopod–trilobite-dominant biofacies and adjacent cephalopod limestone biofacies of the Kosov type according to Ferretti & Kříž (1995) (see Manda & Frýda 2014).

CONCLUSIONS

Longitudinal colour bands disrupt the shape of an animal especially in an environment with changing light intensity and shadows (e.g. Cott 1940). Some straight-shelled cephalopods were prominent and successful predators in Early Palaeozoic seas. Very similar colour patterns (longitudinal bands) in Ordovician and Silurian orthocerids, pseudorthocerids, actinocerids and endocerids clearly suggest that this type of shell colouration had an adaptive value. It probably helped to camouflage cephalopods and may be considered as a consequence of adaptive convergence because in nautiloids (i.e. basal cephalopod clade) longitudinal colour bands are very rare and are developed only in conchs resembling orthocerids/pseudorthocerids.

Dawsonoceras annulatum is the only indisputable Silurian orthocerid with a preserved colour pattern. All other previously described orthocerids are in fact pseudorthocerids, or their affinity is unclear (Foerste 1930; Kobluk & Mapes 1989; Turek 2009; Turek & Manda 2012). The same type of colouration was, however, reported in the smooth-shelled Ordovician *Isorthoceras* (Kröger 2013), which probably also belongs to the Orthocerida (D. H. Evans, pers. comm. 2014). Longitudinal bands that developed around the entire shell circumference in *Dawsonoceras* further support

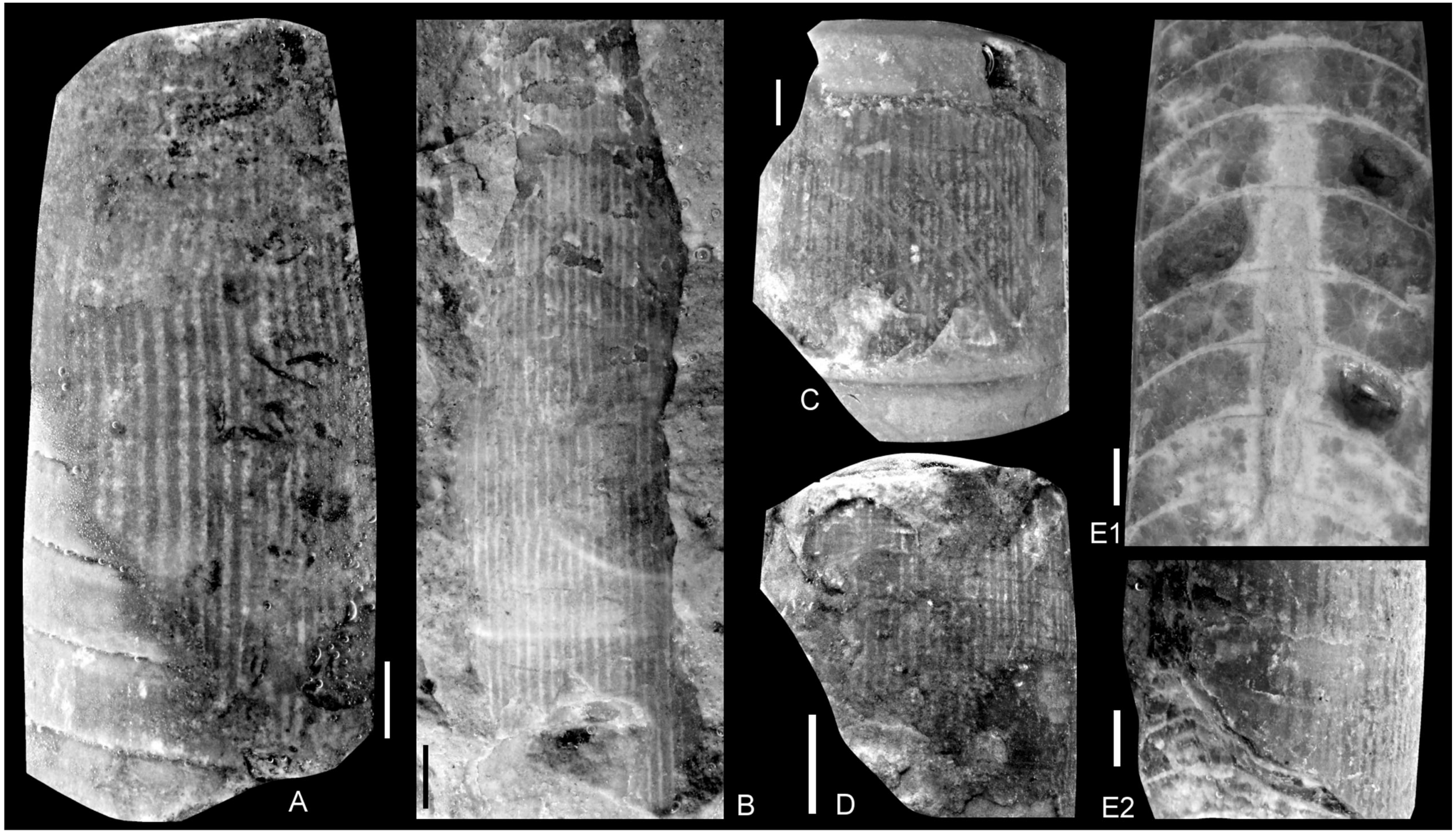

Fig. 2. *Lyecoceras*? *columnare* (Marklin, 1857). **A**, RM Mo 45540, lateral view, Östergarn, upper Hemse Beds, late Ludlow. **B**, RM Mo 54333, ventral view, Östergarn, late Ludlow. **C**, RM Mo 50646, dorsolateral view, Hamra, Hamra or Sundre Formation, latest Ludlow. **D**, RM Mo 150461, original of Angelin & Lindström (1880, pl. 10, fig. 1), lateral view, Östergarn, late Ludlow. **E1**, **E2**, RM Mo 156201, dorsal view, Östergarn, late Ludlow. Scale bars equal 5 mm. All specimens were immersed in alcohol before photographing.

the sub-vertical biological orientation of the shell. Colour bands together with annuli and well-elaborated transverse undulated growth ridges form a reticulate ornament, a combination unknown in other straight-shelled cephalopods. Highly elaborated sculpture not only reinforced the shell but is also considered as another protective feature, analogous in function, to shell colouration (Cowen et al. 1973). Apart from *Dawsonoceras* and the Silurian coiled-shell nautiloid *Peismoceras* Hyatt, no shell colouration was documented in any other species with highly elaborated sculpture. However, in Mesozoic ammonoids a combination of pronounced sculpture and colour bands is relatively common (Mapes & Davis 1996). Identical colour patterns observed in one specimen of *Dawsonoceras* from Gotland and one specimen from Wales is the first evidence of the stability of colouration in straight-shelled cephalopod populations from different Palaeozoic palaeocontinents.

The Silurian pseudorthocerid *Lyecoceras*? *columnare* exhibits smooth, straight or slightly curved endogastric shells. Densely spaced longitudinal colour bands are present around the entire shell circumference. Shell colouration is very similar in the Silurian pseudorthocerid *Lyecoceras*? *pellucidum*. The colour pattern supports vertical or subvertical biological orientation of these pseudorthocerids. The moderately expanding shell of the Early Ordovician cephalopod *Hedstroemoceras haelluddense* Foerste shows narrow zig-zag bands. Although Kröger (2006) placed *Hedstroemoceras* in Pseudorthocerida, the shape of the shell and the position and form of the siphuncle suggest rather an affinity with oncocerids (D. H. Evans, pers. comm. 2014). Middle and Late Ordovician pseudorthocerids with longiconic shells shared a similar colour pattern (longitudinal bands) with Silurian pseudorthocerids, which nevertheless, is restricted to the dorsal side only. Such a distribution of the colour pattern in these pseudorthocerids possessing well-developed cameral deposits supports the view that their shell was oriented horizontally during life (Ruedemann 1921; Foerste 1930; Frey 1988; Kröger et al. 2009). It is highly probable that secondary reduction of cameral deposits in some Silurian pseudorthocerids caused a change in life position. Middle Devonian and younger pseudorthocerids exhibit zig-zag colour bands (Archiac & Verneuil 1842; Foerste 1930; Gordon 1964) which were developed around the entire shell circumference or rarely were restricted dorsally depending on the hydrostatic poise of the shell during life. Consequently, there is a prominent change in the colour pattern between early and middle-late Palaeozoic pseudorthocerids, which may be linked to the radiation of predators starting in the Devonian (e.g. Signor & Brett 1984). Transverse growth bands described in a Late Palaeozoic straight-shelled cephalopod (‘*O.*’ *dunbari* Foerste; Foerste 1930; Teichert 1964) represent another new type of shell colouration. However, the taxonomic affinity of this cephalopod is unknown.

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