

A new Silurian *Avicenia* (Tabulata): taxonomy, growth pattern, and colony integration

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ABSTRACT

A new heliolitid tabulate coral *Avicenia kocyani* n. sp. is described from Silurian erratic boulders from Pomerania (Poland). The new species has higher intracolony variation than other heliolitids. The growth pattern in corallites of the new species is not correlated with the growth pattern in coenenchymal tubes. This phenomenon is probably caused by different gene expressions in corallites and common tissue. Coenenchymal corals with a common skeleton, developed as polygonal tubes may have two levels of colonial integration: lower, with uncoordinated growth of corallites and common tissue (as for example in *Avicenia kocyani* n. sp.) and higher, with a unified growth pattern throughout the colony (as for example in *Heliolites diligens* Bondarenko, 1966). Heliolitids are known to show strong provincialism during the Silurian. The discovery of *Avicenia* Leleus, 1974 in Europe (previously known only from Central Asia) shows that at least some of them had a wider distribution than previously thought.

KEY WORDS

Tabulata,
Heliolitida,
Silurian,
growth pattern,
colony integration.

RÉSUMÉ

Un nouvel Avicenia (Tabulata du Silurien): taxonomie, croissance et intégration de la colonie.

Un nouveau tabulé héliolitide, *Avicenia kocyani* n. sp., est décrit en provenance des galets erratiques siluriens de Poméranie (Pologne septentrionale). La variation intra-coloniale de cette nouvelle espèce est plus grande que chez les autres héliolitides. La croissance des corallites d'*A. kocyani* n. sp. n'est pas corrélée avec celle des tubes coenenchymaux. Ce phénomène s'explique probablement par

MOTS CLÉS

Tabulata,
heliolitida,
silurien,
croissance,
intégration de la colonie.

une expression différente des gènes dans les corallites et le coenenchyme (tissu commun). Les coraux à coenenchyme dont le squelette commun est composé de tubes polygonaux peuvent avoir deux degrés d'intégration de la colonie: soit la croissance des corallites et du coenenchyme n'est pas coordonnée (comme dans le cas d'*A. kocyani*), soit toute la colonie croît au même rythme (on observe ce plus haut degré d'intégration par exemple chez *Heliolites diligensis* Bondarenko, 1966). On admet généralement que le provincialisme des héliolitides siluriens est assez fort; la découverte d'un *Avicenia* Leleshus, 1974 en Europe (alors que ce genre n'était connu auparavant qu'en Asie) montre qu'au moins certains d'entre eux avaient une répartition géographique plus large.

INTRODUCTION

Heliolitid tabulates are common fossils found throughout the world, ranging from the Middle Ordovician to the Middle Devonian (Hill 1981). Some of them may show provincialism, especially from the late Ordovician to the early Silurian (Leleshus 1976). Due to their relatively complicated anatomy they form an interesting group for studies on intracolony variation and environmental influences on the growth patterns.

The aim of this paper is to describe a new species of the genus *Avicenia* Leleshus, 1974, from Silurian erratic boulders of Poland, with its intracolony variation, growth patterns, as well as to analyze distribution and potential endemism of Silurian heliolitid faunas.

The investigated specimens were collected by A. Nowiński and the late A. Stasińska near the coastal cities (Międzyzdroje, Kołobrzeg, Jastrzębia Góra) of Pomerania (Fig. 1).

ERRATIC BOULDERS OF POLAND AND THE AGE OF *AVICENIA KOCYANI* N. SP.

Erratic boulders in Northern Poland are common and large part of them is formed by sedimentary rocks. These contain abundant faunas ranging stratigraphically mainly from Ordovician to Silurian. They were a subject of detailed

studies (e.g., Kielan-Jaworowska 1966; Stasińska 1967). Boulders containing corals are also common; Stasińska (1967) described 52 coral taxa. According to Kielan-Jaworowska (1966), most of Pomeranian boulders are derived from the moraines of the Baltic (Würm) glaciation. They are strongly diversified in size, but most often are of fist size.

The coral faunas of erratic boulders of northern Poland are of Late Ordovician to Silurian age (Stasińska 1967) and coral assemblages can be correlated with these known from Estonia and Sweden. Ordovician *Sarcinula-Paleofavosites* assemblage is rare and generally does not occur in Pomerania. Moreover, Ordovician corals are often silicified, while our samples are not; we can therefore exclude the Ordovician age of our corals. Earliest Silurian deposits are argillaceous without coral faunas. The investigated Pomeranian coral limestones are most probably early to middle Silurian (Stasińska 1967); also light grayish colour of our samples suggests this age. Unfortunately there is no sediment around investigated colonies, precise determination is therefore not possible. We can estimate that the age of *Avicenia kocyani* n. sp. is most probably latest Llandovery to Wenlockian. Their estimated age and provenance might correspond to Upper Visby or Högkint Formations (see Calner *et al.* 2004), however there is no direct evidence for such statement.

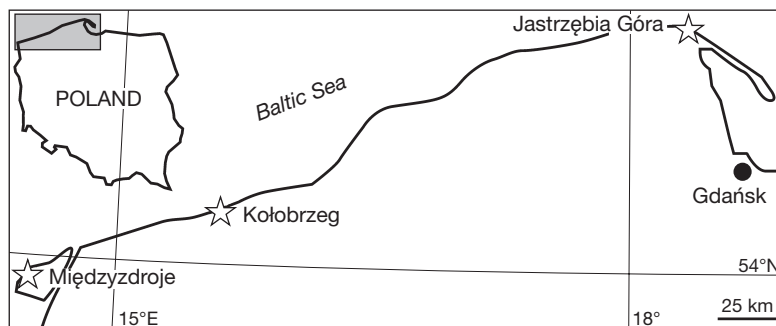


FIG. 1. — Sketch map showing erratic boulder collecting sites in northern Poland (marked by stars).

MATERIAL AND METHODS

The material analyzed here contains four coralla from erratic boulders. They are not complete, although well preserved, clearly displaying anatomical features. Altogether 20 thin sections were prepared. The investigated material is housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw under the repository number ZPAL T.26.

SYSTEMATIC PALAEOONTOLOGY

Order HELIOLITIDA Frech, 1897

Suborder KHANGAILITINA Bondarenko, 1992

Family AVICENIDAE Ospanova, 1986

Genus *Avicenia* Lelehus, 1974

TYPE SPECIES. — *Avicenia aseptata* Lelehus, 1974 from the Turkestan Ridge, Late Silurian.

DIAGNOSIS. — see Lelehus (1974), Hill (1981) and Bondarenko (1992).

OCCURRENCE. — Silurian: Central Asia, Europe.

REMARKS

Two previously described species of the discussed genus (*A. aseptata* Lelehus, 1974 and *A. secunda* Ospanova, 1986) were known only from Central Asia. The discovery of *A. kocyani* n. sp. in the Silurian of Europe extends the geographic range of this genus.

Avicenia kocyani n. sp.

(Figs 2-4)

TYPE MATERIAL. — Holotype: ZPAL T. 26 AVI-1; 3 paratypes: ZPAL T. 26 AVI-2 to AVI-4, altogether 20 thin sections.

ETYMOLOGY. — In honour of Antoni Kocyan (also Anton Kocian, Antal Koczyan; *1836 †1916), Polish zoologist working in the Tatra Mountains.

TYPE LOCALITY AND AGE. — Międzyzdroje, Pomerania, Poland; erratic boulders; Silurian, probably latest Llandovery to Wenlockian.

OCCURRENCE. — Erratic boulders of Pomerania: Międzyzdroje, Kołobrzeg and Jastrzębia Góra; most probably Llandovery to Wenlockian.

DIAGNOSIS. — Corallites round to polygonal in cross section, 0.48-0.52 mm in diameter (mean values for coralla), very often in contact. Coenenchymal tubes often elongated in cross section, irregular, 0.04-0.42 mm (largest diameter). Walls uniformly thin, 0.02 mm in thickness. Septal apparatus absent.

DESCRIPTION

Coralla large, with the largest diameter of up to about 15 cm. Corallites long, in cross sections they are oval or round in some regions of corallum, in other regions subpolygonal, 7 to 12 sided, with slightly rounded corners. Corallites show strong dimetrisism, these of large diameters grouped in aggregates of 8-12 individuals placed between corallites of smaller diameter. They are very often in contact, in some places separated by coenenchymal tubes, spaced unevenly up to

TABLE 1. — Biometrical values of *Avicenia kocyani* n. sp. Abbreviations: **CD**, corallite diameter; **PD x**, diameters of parasiphonolites; **TS**, tabulae spacing; **DS**, diaphragm spacing; **SWT**, single wall thickness.

Material	CD	PD 1	PD 2	TS	DS	SWT
ZPAL T.26 AVI-1 (holotype)						
min value	0.34	0.04	0.04	0.16	0.06	0.02
max value	0.92	0.20	0.42	1.06	0.38	0.02
mean value	0.518	0.225	0.216	0.540	0.195	0.02
SD	0.109	0.103	0.098	0.252	0.076	0
V	0.21	0.46	0.45	0.47	0.39	0
N	90	32	32	40	45	25
ZPAL T.26 AVI-2						
min value	0.34	0.06	0.12	—	—	0.02
max value	0.44	0.36	0.40	—	—	0.02
mean value	—	—	—	—	—	—
SD	—	—	—	—	—	—
V	—	—	—	—	—	—
N	10	9	9	—	—	12
ZPAL T.26 AVI-3						
min value	0.38	0.04	0.12	0.14	0.04	0.02
max value	0.66	0.46	0.30	0.52	0.30	0.02
mean value	0.481	0.214	0.191	0.303	0.135	—
SD	0.081	0.095	0.065	0.092	0.055	—
V	0.169	0.447	0.342	0.305	0.406	—
N	35	19	19	30	31	15
ZPAL T.26 AVI-4						
min value	0.42	0.06	0.08	—	—	0.02
max value	0.60	0.36	0.42	—	—	0.02
mean value	0.481	0.209	0.201	—	—	—
SD	0.047	0.090	0.087	—	—	—
V	0.10	0.43	0.43	—	—	—
N	19	23	23	—	—	10

0.30 mm, with 20 to 42 corallites per 10 mm². Tabulae in corallites very thin, flat, horizontal or inclined, most often complete, spaced unevenly (showing faint cyclomorphosis).

Coenenchyme is composed of tubes (parasiphonolites), very variable in form: usually three to seven sided; triangular, square-shaped, rectangular, rhomboidal or irregular in cross section. Parasiphonolites may form incomplete ring of 7-12 tubes (rarely to 15) around tabularia, but they are frequently weakly developed; they are often strongly elongated in cross section. Walls very thin and very even, sometimes faceted (walls of corallite and coenenchymal tubes are of the same thickness). In places where corallites are in contact the median line is invisible. Diaphragms in coenenchymal tubes flat, rarely slightly meniscus-shaped. In two places of the holotype connecting

pores were found (Fig. 1D), measuring about 0.10 mm in diameter. Septal apparatus absent. Microstructure invisible in polarized light. Biometrical data is given in the Table 1.

COMPARISON WITH OTHER SPECIES

The type species, *Avicenia aseptata* has thicker walls (0.03-0.11 mm, most often 0.05-0.07 mm) and rare small septal spines (absent in new species). Corallites of the type species are somewhat larger (0.7-0.8 mm); the parasiphonolites are more uniform in size and do not show strong elongation in cross section (data after Leleshus 1974). *Avicenia secunda* from the Ludlovian of Asia has much larger corallites (1.5-1.7 mm) and thicker walls (0.07-0.15 mm; data after Ospanova 1986).

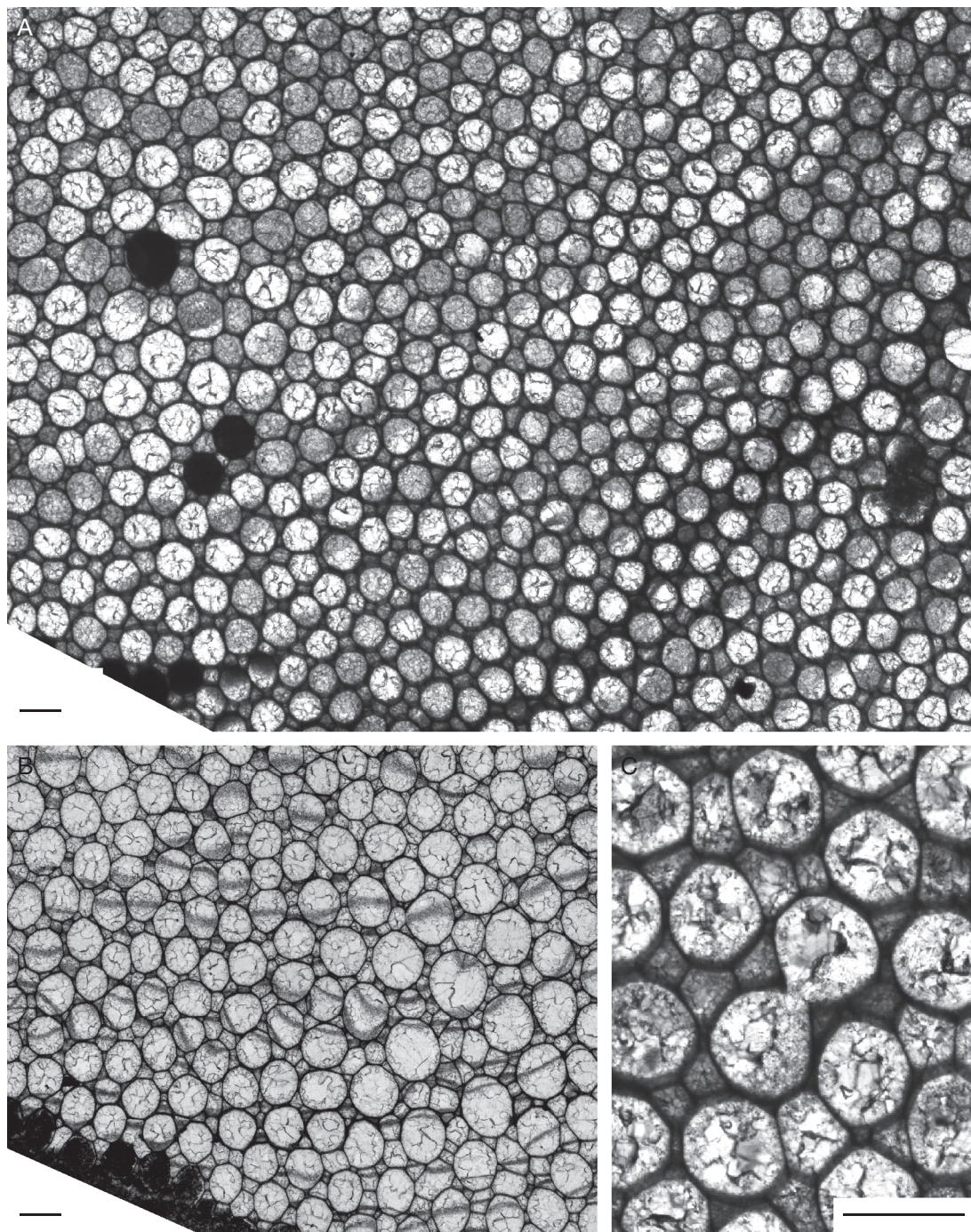


FIG. 2. — Transverse section of *Avicenia kocyani* n. sp. (holotype; ZPAL T. 26 AVI-1) from the erratic boulder of Międzyzdroje, probably latest Llandovery-Wenlockian: **A, B**, general view (notice the dimetrium of corallites and differences in coenenchymal tissue distribution); **C**, a detail showing the connecting pore, polarized light. Scale bars: 500 µm.

PROVINCIALISM OF TABULATE CORALS DURING THE SILURIAN

The Silurian tabulate corals, especially heliolitids have been considered as showing provincialism (Leleshus 1976). There are numerous examples of taxa restricted to Asia: *Baitalites* Chekhovich, 1977; *Ducdonia* Leleshus, 1974; *Innapora* Leleshus, 1974; *Rotalites* Leleshus, 1974, or *Sibiriolitella* Bondarenko, 1977 (for data concerning these genera see Hill 1981). To such genera also belongs *Avicenia* (Leleshus 1974, 1976; Ospanova 1986).

The suggested provincialism does not necessarily reflect the restricted palaeobiogeographical distribution. The Asian faunas were principally investigated by Soviet and Russian researchers (e.g., Leleshus 1974, 1976; Bondarenko 1977, 1992; Ospanova 1986); their papers were poorly known in Western countries; conversely, papers published outside the former Soviet Union were rarely cited in the articles concerning tabulates. Moreover, Silurian heliolitids were never a subject of focused studies in Europe, with exception for a classic monograph by Lindström (1899) (there are some papers dealing with selected species, or listing taxa, as for example Môtus [2004, 2006]). Heliolitid names appear also in numerous papers devoted to erratic boulders, as for example Dreyer Jørgensen (1944), Krul (1954) and Gaba & Pek (1999). The discovery of *Avicenia* in Europe seems to suggest that these faunas had much wider distribution than previously thought.

Such a conclusion seems to be confirmed by observations on distribution of other Silurian benthic faunas. For example brachiopods, at least during the Early Llandovery-Early Wenlock are widely distributed in the northern hemisphere (Boucot & Johnson 1973; Sheehan & Coorough 1990). The paper by Kaljo & Klaamann (1973) states that many tabulate corals were broadly distributed during the Silurian, contrary to the work by Leleshus. The former paper was however published before the studies on tabulate faunas distribution and their provincialism (Leleshus 1976).

INTRACOLONIAL VARIATION, GROWTH PATTERN AND GENE EXPRESSION

Recognition of the intracolony variation in corals is fundamental in coral taxonomy – both in extant and fossil forms. It can be assumed that a colony arises

from an initial individual through asexual reproduction. Following this, a colony can be regarded as genetically homogenous (Dixon 1989: 821); its form depends, however, also on the environment (phenotypic expression; see Young & Scrutton [1991] for heliolitid data). Intracolony variation is therefore a mixture of genetically and environmentally controlled components (Dixon 1989). Recognition of elements controlled genetically can be crucial for taxonomy (see for example a study on extant scleractinians by Todd [2008]); yet it may differ from group to group.

The new species displays very high intracolony variation when compared to other heliolitids, both in qualitative and quantitative characters. The most evident is dimetrisism of the corallites (Fig. 2). As a consequence the coefficient of variation (V) values (calculated as in Zapalski in press) of corallites can reach $c. 0.2$. Such a variation is linked to large differences in corallite density – 20 to 42 corallites per 10 mm². Also coenenchymal tissue displays very large variation – both in shape and size. On the other hand, the single wall thicknesses remain unusually stable – no thickening is visible throughout the investigated material.

These V values are much higher than average in other heliolitids, having usually 0.05 to 0.08 for the tabularium diameter (Môtus 2006). Watkins (2000), however, noticed that heliolitids display large intracolony and intraspecific variation; but this paper does not provide the V values. The investigated species has similar coefficient of variation values as Devonian favositid tabulates (about 0.15–0.25 for corallite diameter, 0.20–0.35 for the double wall thickness in alveolitids and coenitids, see Zapalski [in press]). Wall thickness variation in Silurian heliolitids from Estonia is much higher, reaching $V = 0.2$ (Môtus 2006). It needs to be noticed that larger thicknesses of the wall seen on some of our illustrations here are caused by faint obliquities of cutting. In summary, it can be stated that the new species has high intracolony variation, higher than in other members of the order Heliolitida. As there are no large differences in V values between colonies coming from different, distant localities (it can be assumed that also origin of these erratics cannot be the same) it can be presumed that observed variation is of genetic, not environmental origin.

Young & Kershaw (2005) introduced a scale of growth banding (adopted from Insalaco [1996]),

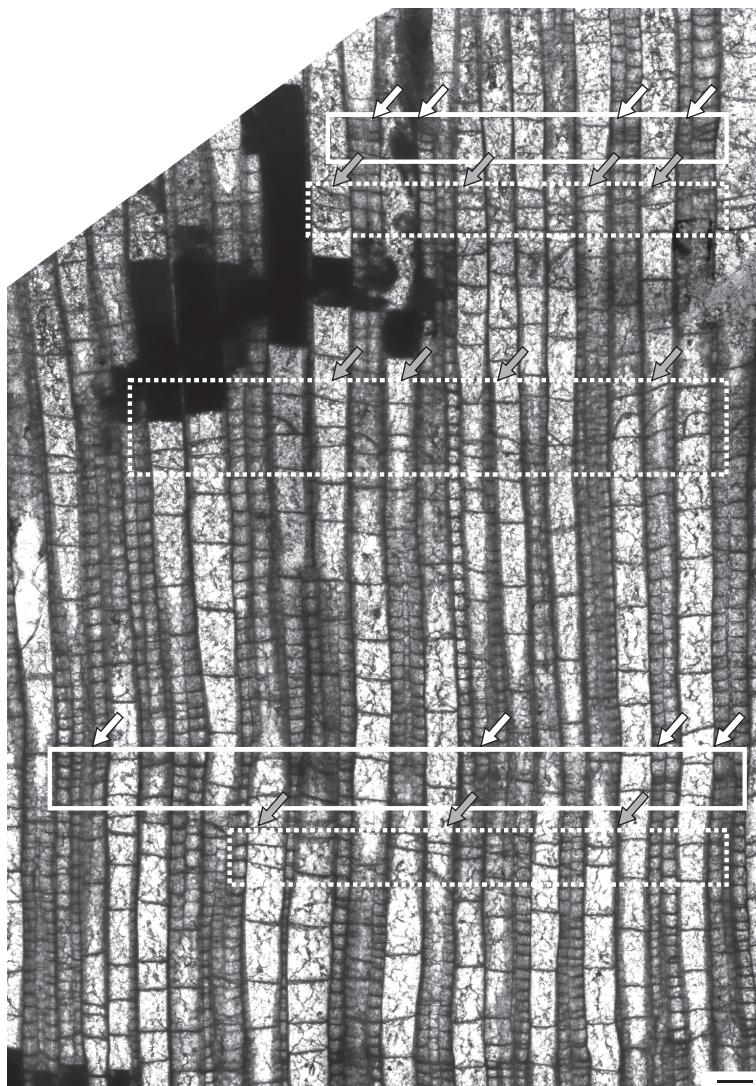


FIG. 3. — Longitudinal section of *Avicenia kocyani* n. sp. (holotype; ZPAL T. 26 AVI-1) from the erratic boulder of Międzyzdroje, probably latest Llandovery-Wenlockian: high density zones in corallites (**dashed line**) do not correspond to high density zones in diaphragm distribution in coenenchymal tubes (**continuous line**). Scale bar: 500 μ m.

where D0 corresponds to absence of banding, and D5 corresponds to a distinctly visible banding with clear borders between the HD (High Density) and LD (Low Density) zones. *Avicenia kocyani* n. sp. shows faint growth periodicity. Tabulae in corallites in HD zones are slightly more densely distributed than in LD zones, the borders between zones are

gradual and blurred. There is also difference in development of tabulae: in the HD zones tabulae are more often inclined or incomplete – in LD zones tabulae are horizontal and complete. Following the Young and Kershaw (2005) scale, the growth periodicity in the discussed species can be evaluated as D1/D2.

It needs to be emphasized that distribution of diaphragms in coenenchymal tubes does not reflect the distribution of tabulae in corallites. These discordances cannot be investigated quantitatively, as the coralla of the new species come from the erratic boulders and do not have a common reference level (such as surface of the coralla, for example). This feature is however, well seen on the thin sections, where pattern of distribution of tabulae is not followed by the pattern of distribution of diaphragms (see Figure 3; Zapalski 2010).

Uncoordinated distribution of tabulae and diaphragms in tabularia and coenenchymal tubes is a feature not described so far. Such phenomena may be, however found in illustrations of several genera (e.g., *Heliolites* [Nowiński 1992: text-fig. 15b]; *Paraheliolites* [Bondarenko 1992: pl. 40, fig. 3a, b]; *Pachyhelioplasma* [Bondarenko 1985: text-fig. 2b, s, zh]). There are a number of possible causes of this phenomenon. First of all it can be caused by different gene expressions in corallite and coenenchyme. This seems to be most possible, as it follows and emphasizes the anatomical differences between these two skeletal structures. Environmental influence causing such differences can be excluded, as neighbouring individuals, due to their millimetric size were influenced by the same environmental factors (such as temperature, salinity or insolation). Also pathogens could be probably excluded, as the skeleton seems to not be modified in other way. If a pathogen would change the growth pattern, this could be also regarded as a change in gene expression (phenotype behaves in a different way than it should). It is also difficult to imagine that a pathogen could result in the same modifications in distinct taxa spread in time and space).

Discordances in growth rhythm correlation have been already observed in alveolitids (Zapalski 2007; Zapalski *et al.* in press), in this group the causes of such a phenomenon seem to be external rather than internal, as in alveolitids there is no coenenchymal tissue for the colony. Therefore the physiological control over this phenomenon seems to be different in both groups.

COLONY INTEGRATION

Coenosteid colonies have the highest levels of integration, comparing to other types of colony

organization (Coates & Oliver 1973); also Noble & Lee (1990) concluded that in heliolitids all individuals were linked and coordinated. Within the coenenchymal corals, those with the common tissue developed as closed polygonal tubes have highest possible level of integration (Bondarenko 1975). Therefore colony integration in *Avicenia* is high, as compared to other heliolitids. Young (1999) states, however, that “it is unlikely that a hierarchical model of colony integration based on colony type alone will withstand a more refined analysis”. Here we attempt to analyze colony integration within selected coenenchymal corals-heliolitids.

Heliolitids with coenenchyme developed as closed polygonal tubes are not homogenous in terms of colony integration. They can be divided into two distinct groups: 1) corals with differences in growth pattern between corallites and coenenchymal tubes (examples given above); and 2) those with coordinated growth throughout the colony.

Avicenia kocyani n. sp. can be an example of the first group. The second group can be exemplified by *Heliolites diligensis* Bondarenko, 1966 from Douro Fm. (Late Silurian) of Somerset and Griffith Islands (Canada) – this species displays similar pattern of diaphragms and tabulae distribution (Dixon 1989: figs 4.4, 5.8). Also *H. spongiosus* Foerste, 1906 from the Silurian of Indiana (Stumm 1964: pl. 57, fig. 1) repeats growth pattern in tabularia and coenenchymal tubes.

The process of colony integration involves a weakening of the individuality of zooids (Beklemishev 1969). In the group with coordinated growth the individuality of polyps is weakened and the physiology and phenotypical response to the environment of the colony can be regarded as homogenous. The different growth patterns in the second group seem to be symptoms of unhomogenous physiology and gene expression.

It can therefore be stated that taxa with a growth pattern in the coenenchymal tubes differing from the corallites are less integrated in terms of colony integration. Conversely, those with growth rhythm unified morphologically within the colony had also unified physiology and following this – higher colony integration.

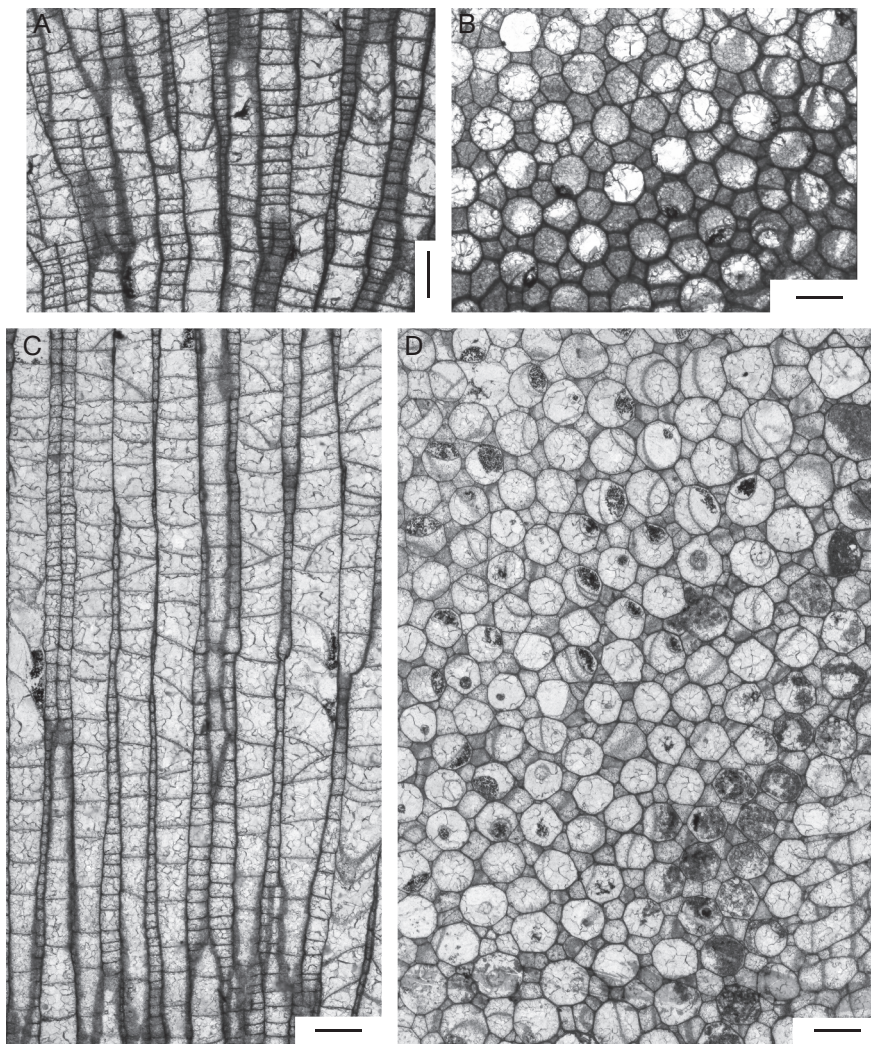


FIG. 4. — *Avicenia kocyani* n. sp., paratypes: **A, B**, specimen (ZPAL T. 26 AVI-2) from Jastrzębia Góra; probably latest Llandovery-Wenlockian; **C, D**, specimen (ZPAL T. 26 AVI-4) from Kołobrzeg; probably latest Llandovery-Wenlockian; **A, C**, longitudinal sections; **B, D**, transverse sections. Scale bars: 500 μ m.

CONCLUSIONS

A new species of *Avicenia* is described from the Silurian of Europe. This discovery shows that heliolitids had a wider geographical distribution than previously thought.

– The new species has high intracolony variation as compared to other heliolitids and similar to members of Alveolitidae and Coenitidae.

– The growth pattern in corallites of the new species is not coordinated with the growth pattern of coenenchymal tubes. This phenomenon is probably caused by different gene expressions in these two anatomical units.

– Coenenchymal corals with the common skeleton developed as tubes may have two levels of colonial integration: lower, with uncoordinated growth of corallites and common tissue (as for example in

Avicenia kocyani n. sp.) and higher, with a unified growth pattern throughout the colony (as for example in *Heliolites diligensis*).

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