

A new graptolite, intermediate between the Tuboidea and the Camaroidea

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A new tuboid graptolite, *Camarotubus graptocamaraeformis* gen. et sp.n., is described from a calcareous erratic boulder of middle Ordovician (Caradoc?) age from Poland. This encrusting form combines characters of both the tuboid and the camaroid graptolites, and is regarded as a purely morphological intermediate between them. This finding supports Kozłowski's (1949) concept of a close phylogenetic relationship between the orders Tuboidea and Camaroidea.

Key words: Graptolithina, Camaroidea, Tuboidea, evolution, Ordovician, erratic boulders, Poland.

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Introduction

The order Tuboidea is a small and still very inadequately described group of sessile graptolites, originally erected by Kozłowski (1938, 1949) for some exceptionally well-preserved three-dimensional material etched by chemical treatment from upper Tremadoc cherts, found near Wysoczki (Holy Cross Mountains, Poland). The order comprises forms with encrusting as well as more or less dendroid rhabdosomes, sometimes strikingly similar to those of the Dendroidea. Despite fundamental differences from dendroid graptolites in stolonial budding, the Tuboidea have been very difficult to classify and treat systematically (Bulman & Rickards 1966; Bulman 1968, 1970). Tuboids are known from the Early Ordovician to the end of the Silurian. Their palaeogeographic distribution is restricted to Europe and North America. The Middle Cambrian *Fasciculitubus tubularis* Obut & Sobolevskaya, 1967, from Siberia was identified as the earliest tuboid graptolite by Obut & Sobolevskaya (1967) and most probably represents a rhabdopleurid pterobranch, closely related to the family Rhabdopleuridae (Durman & Sennikov 1993). After their rapid rise, tuboids survived on as a rather conservative group, with few genera.

Tuboid graptolites are characterized by: (i) diad budding, effecting on irregularity of thecal succession; (ii) presence of a thecorhiza or basal disc, composed of the adnate parts of autothecae, stolothecae and bithecae, from which thecae arise (either singly or, in some tuboids, in sheaves); and (iii) a distinct tendency toward intracolony polymorphism (i.e. the presence of conothecae, microthecae or umbellate thecae), and a high level of colonial integration (see Bulman & Rickards 1966; Bulman 1970; Kozłowski in Urbanek 1973; Urbanek 1973). While many aspects of the palaeobiology of tuboid graptolites are still unclear, some important observations on their colonial organization have been made by Urbanek (1973). Moreover, it should be emphasized that the Tuboidea are of great significance in discussions about the origin of graptolites (e.g., Kozłowski 1938, 1949; Urbanek 1986; Bengtson & Urbanek 1986). Some aspects of their fine structure were described by Urbanek (1979), Urbanek *et al.* (1980), and Urbanek & Mierzejewski (1982, and unpublished results). In our present state of knowledge, tuboid taxonomy remains provisional and partly artificial (further tuboids are likely to be identified among some genera attributed traditionally to the Dendroidea or to graptolites of uncertain taxonomic position (Bulman 1968, 1970; Mierzejewski 1978).

The present paper describes a new Ordovician encrusting tuboid graptolite, *Camarotubus graptocamaraeformis* gen. et sp. n. This interesting form represents a stage morphologically intermediate between the Tuboidea and another order of sessile graptolites, the Camaroidea. The new form was discovered in the residue from a calcareous erratic boulder of Baltic origin found in the Pleistocene glacial deposits near Mochty, Vistula River valley (60 km north of Warsaw, central Poland). This boulder O.469 was among the enormous collection of erratic blocks gathered by the late Professor Roman Kozłowski and his co-workers. It contained abundant organic microfossils (acritarchs, chitinozoans, scolecodonts, hydroid-like forms, graptolites, pterobranchs and forms *incertae sedis*, which have been described by several authors (e.g., Kozłowski 1959, 1962; Kielan-Jaworowska 1966; Górka 1969; Mierzejewski 1986). The fauna is not stratigraphically diagnostic, but the boulder is most probably middle Ordovician (Caradoc?) in age. Hints (1998) has suggested a Keilan age or older for the boulder, based on the occurrence of some eunicid polychaete jaws.

The SEM micrographs which illustrate this paper were taken with a Cambridge Stereoscan 180 operating at 30 kV. The material is stored in glycerine in plastic boxes or on SEM stubs at the Institute of Paleobiology of the Polish Academy of Sciences (ZPAL).

General remarks

Since the classic work of Kozłowski (1949), the phylogenetic relationships among primitive (i.e. non-graptoloid) benthic orders of the Graptolithina have only rarely been discussed (e.g., Skevington 1963; Obut 1964; Kozłowski 1962, 1966; Bulman 1968; Mierzejewski 1985; Urbanek 1986; Chapman *et al.* 1996). Bulman (1968, 1970) accepted the validity of only five diverse orders of sessile graptolites (Camaroidea, Crustoidea, Dendroidea, Stolonoidea, and Tuboidea) and considered their interrelationships to be unclear. Other graptolite 'orders', especially the Dithecoidea and the

Inocaulida, were discussed by Mierzejewski (1986) who considered the majority of dithecoids (including the family Chaunograptidae) and inocaulids to be non-graptolitic (presumably colonial scyphopolyps or hydrolyps, and algae). This view received support, at least in part, from subsequent redescrptions of some allegedly sessile graptolite genera (e.g., Lo Duca 1990; Mierzejewski 1991).

Despite the fact that early graptolites are still poorly known, it is possible distinguish two main evolutionary lineages leading from a common pterobranch ancestor (Kozłowski 1949, 1962): (1) Crustoidea → Dendroidea → Graptoloidea; and (2) Tuboidea → Camaroidea. Kozłowski (1938, 1949, 1962, 1966) stressed the importance of budding patterns and stolonal morphology in diagnosing the sessile graptolite orders. Hence lineage (1) is characterized by regular triad budding, whereas lineage (2) exhibits diad budding with no regular succession and variably distributed nodes. However, Kozłowski left open the question of what mode of budding and thecal succession has been adopted by the common ancestor of all graptolites. There are some indications that the Tuboidea and the Camaroidea retained the primary pattern inherited from their pterobranch ancestors, presumably related to the Rhabdopleurida (Urbanek 1986). Mierzejewski (1985) supposed that the common ancestor of both lineages must have been very similar, or even closely related, to the mysterious genus *Maenniligraptus* Mierzejewski, 1985, which exhibits the both diad and triad modes of budding, and represents one of the lowest grades of colonial development. However, the problem is made more difficult and complex by some aberrant *incertae ordinis* graptolites, e.g., genera *Mastigograptus* Ruedemann, 1908, and *Micrograptus* Eisenack, 1974 (see Urbanek 1986). Moreover, Skevington (1963) has even suggested that the Tuboidea was ancestral to the Denroidea, or *vice versa*.

Until recently, little attention has been paid to the Tuboidea → Camaroidea lineage. These graptolites are poorly known in terms of their general morphology and astogeny, and their palaeogeographic and stratigraphic distribution. Their outline morphology was established by Kozłowski (1938, 1949): both are encrusting forms (although some tuboids have more or less dendroid rhabdosomes), exhibit irregularly diad budding, and possess autothecae which are strongly differentiated into two portions – a creeping part embedded in a ‘thecorhiza’ (in tuboids) or ‘extracamara tissue’ (in camaroids), and an erect part, often provided with one or two apertural processes. The Camaroidea are distinguished from the Tuboidea mainly by (1) the stronger differentiation of camaroid autothecae into two (camara and collum); (2) their lack of bithecae (with the exception of *Bithecocamara* Kozłowski, 1949); (3) the lack of autothecal dimorphism; and (4) the common occurrence of extracamara tissue instead of stolothecae. In other words, morphological changes in this lineage were dominated by a significant reduction in polymorphism, a looser integration of the colony, and a broadening of the creeping part of each autotheca from the tubular shape of tuboids to the bulbous camara of most camaroids.

Kozłowski (1949) ascribed a specific role to the tuboid genus *Idiotubus* Kozłowski, 1949, in the Tuboidea → Camaroidea lineage (*Idiotubus* is treated here as a junior synonym of *Epigraptus* Eisenack, 1941; see Mierzejewski 1978 and Urbanek 1986). Kozłowski considered *Idiotubus* to unite certain characters of both orders and to represent a truly transient link, comparable with the role played by *Dictyonema* Hall, 1851 in the Dendroidea → Graptoloidea lineage (see Kozłowski 1949: p. 109).

Epigraptus is especially similar to the camaroid genus *Graptocamara* Kozłowski, 1949. Both have autothecae which arise singly from the surface of a thecorhiza. Moreover, the autothecal apertures of *Graptocamara* possess a distinct, linguiform process, very similar to that of numerous epigraptid species. The main difference between the two genera concerns bithecae, which are abundant in the tuboid but absent in the camaroid.

The encrusting graptolite described here, *Camarotubus graptocamaraeformis* gen. et sp. n., seems to represent a stage morphologically intermediate between the Tuboidea and the Camaroidea. It departs in some respects from typical representatives of both orders, while simultaneously combining in mosaic fashion some of their key characters. In the few well-studied tuboid genera, numerous bithecae outnumber autothecae by several times. As a rule, each tuboid autotheca is surrounded by a few (2–3 or sometimes even 5) bithecae, forming a more or less regular circle. In contrast, all known camaroid graptolites (with the exception of the enigmatic *Bithecocamara* Kozłowski, 1949) are completely devoid of bithecae. In this respect, *Camarotubus* is clearly intermediate in position between the two orders. Its bithecae are few in number distributed irregularly over the surface of the thecorhiza; this is an important difference from typical tuboids. However, the basal part of an autotheca in *Camarotubus* is distinctly tuboid in form, i.e. creeping and elongated. Yet its erect portion is underdeveloped, as in the majority of Camaroidea (with the exception of *Tubicamara* Kozłowski, 1949), and strikingly resembles the collum of the poorly known camaroid species *Graptocamara hyperlinguata* Kozłowski, 1949. Remarkably, the autothecal apertures of *Graptocamara* are sometimes occluded, as in numerous representatives of the Tuboidea and the Camaroidea (see Kozłowski 1949).

It can be stated with certainty that the new *Camarotubus* intergrades from the Tuboidea to the Camaroidea. However, while morphologically intermediate, it cannot be considered a truly transient link because of its age, as is also the case for the tuboid *Epigraptus* Eisenack and the camaroids *Bithecocamara* Kozłowski, *Graptocamara* Kozłowski, and *Tubicamara* Kozłowski. It is notable that intermediate forms between the two orders are relatively numerous in comparison with the small total number of tuboid and camaroid genera. These intergradations make it impossible to define a sharp boundary between both orders. Strikingly, individual genera exhibit different tuboid and camaroid features. For example, *Epigraptus* (= *Idiotubus*), the typical tuboid graptolite, might playfully be described as comprising the camara and apertural apparatus of *Graptocamara*, the collum of *Tubicamara*, and the bithecae of *Bithecocamara* (which is also devoid of extracamaral tissue); it certainly lacks the sclerotized stolons of camaroids, but then some other tuboids do possess this feature. The occurrence of different tuboid and camaroid characters intermediate forms suggests that there were several different evolutionary pathways within the Tuboidea → Camaroidea lineage, as has been shown for the Dendroidea → Graptoloidea lineage. Moreover, it seems clear that there was a certain independence of particular rhabdosome elements in the evolution process of the Tuboidea.

The presence of well-sclerotized stolons in *Camarotubus* gen. n. is of special interest because of the few tuboid genera (*Tubidendrum* Kozłowski, 1949, *Kozłowskitubus* Mierzejewski, 1978, and partly *Reticulograptus* Wiman, 1901) which possess a more or less developed stolonial system with peridermal envelopes (Kozłowski 1949, 1963,

1971; Bulman & Rickards 1966; Bulman 1970; Mierzejewski 1978). The significance of these observations for tuboid evolution remains unclear. Urbanek (1973) pointed out that Kozłowski's (1949) graded series, illustrating successive changes in tuboid spatial organization, are not necessarily closely related because of differences in the degree of sclerotization of the stolon. Later, he suggested that sclerotization of the stolon in the Tuboidea was a gradual process (Urbanek 1986; see also Bengtson & Urbanek 1986: p. 308). In such a situation, *Epigraptus* should be interpreted as distinctly less advanced than *Camarotubus* gen. n., in spite of both representing the same morphoecological type and both exhibiting similar surface features. *Epigraptus* may also be interpreted as a morphological intermediate between tuboid graptolites and some rhabdopleurid pterobranchs (e.g., Middle Cambrian *Rhabdotubus* Bengtson & Urbanek, 1986, or '*Rhabdopleura*' *obuti* Durman & Sennikov, 1993), while *Camarotubus* bridges the Tuboidea and the Camaroidea (and is especially allied with early Ordovician *Graptocamara* Kozłowski).

The discovery of *Camarotubus* gen. n. supports Kozłowski's (1949) view of a close phylogenetic relationship between tuboid and camaroid graptolites. But paradoxically, the existence of the above mentioned morphological intermediates does not necessarily confirm Kozłowski's (1949) simple evolutionary pathway from the Tuboidea to the Camaroidea. The present writer considers the recant data sufficient to cast doubt upon Kozłowski's scheme, and perhaps reject it altogether. Some Ordovician hemichordates combine, in mosaic fashion, characters of cephalodiscid pterobranchs and camaroid graptolites (Mierzejewski 1984, 2000, and unpublished results). This may have significant phylogenetic implications and shed new light on the early evolution of the Graptolithina. The camaroids may, for example, appear not to be the highly specialized and evolutionarily advanced descendants of the Tuboidea, but even more primitive forms, closely related to a common ancestor with cephalodiscid-like pterobranchs. These considerations suggest that *Camarotubus* gen. n. may even have been a primitive tuboid, similar to its immediate camaroid ancestors. Nevertheless, the problem of the origin of the Camaroidea and their phylogenetic relationships is beyond the scope of the present paper and will be discussed elsewhere (Mierzejewski in preparation).

Systematic paleontology

Phylum Hemichordata Bateson, 1885, emend. Fowler, 1892

Class Graptolithina Bronn, 1849

Order Tuboidea Kozłowski, 1938

Family Cyclograptidae Bulman, 1938

Synonym: Idiotubidae Kozłowski, 1949.

Genus *Camarotubus* gen. n.

Type species: *Camarotubus graptocamaraeformis* sp. n.

Derivation of the name: Greek, *kamara* (= space enclosed by an arch, vaulted room) and Latin, *tubus* (tube) are the standard endings for tuboid and camaroid generic names, as proposed by R. Kozłowski; referring to intermediate features between tuboid and camaroid graptolites.

Diagnosis. — As for the type species.

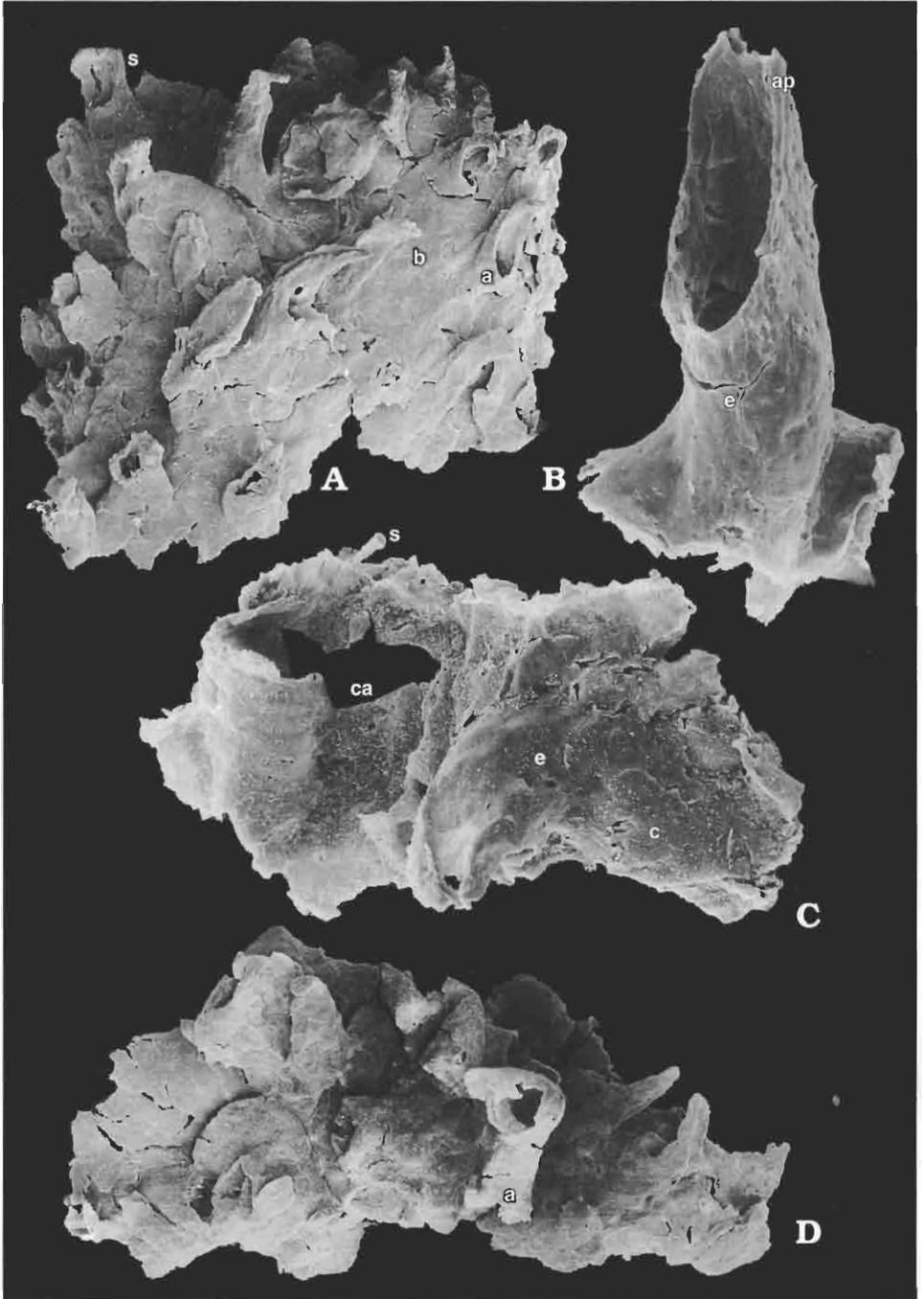


Fig. 1. *Camarotubus graptocamaraeformis* gen. et sp. n. Middle Ordovician (Caradoc?), erratic boulder No. O.469, Mochty (Poland). SEM micrographs. A. General view of the holotype; $\times 25$ (ZPAL G/0/1). B, C, $\times 85$ (ZPAL G/0/2); D, $\times 20$ (ZPAL G/0/3). Abbreviations: a, autotheca; ap, apertural process; b, bitheca; c, creeping part of autotheca; e, erect part of autotheca; s, stolon.

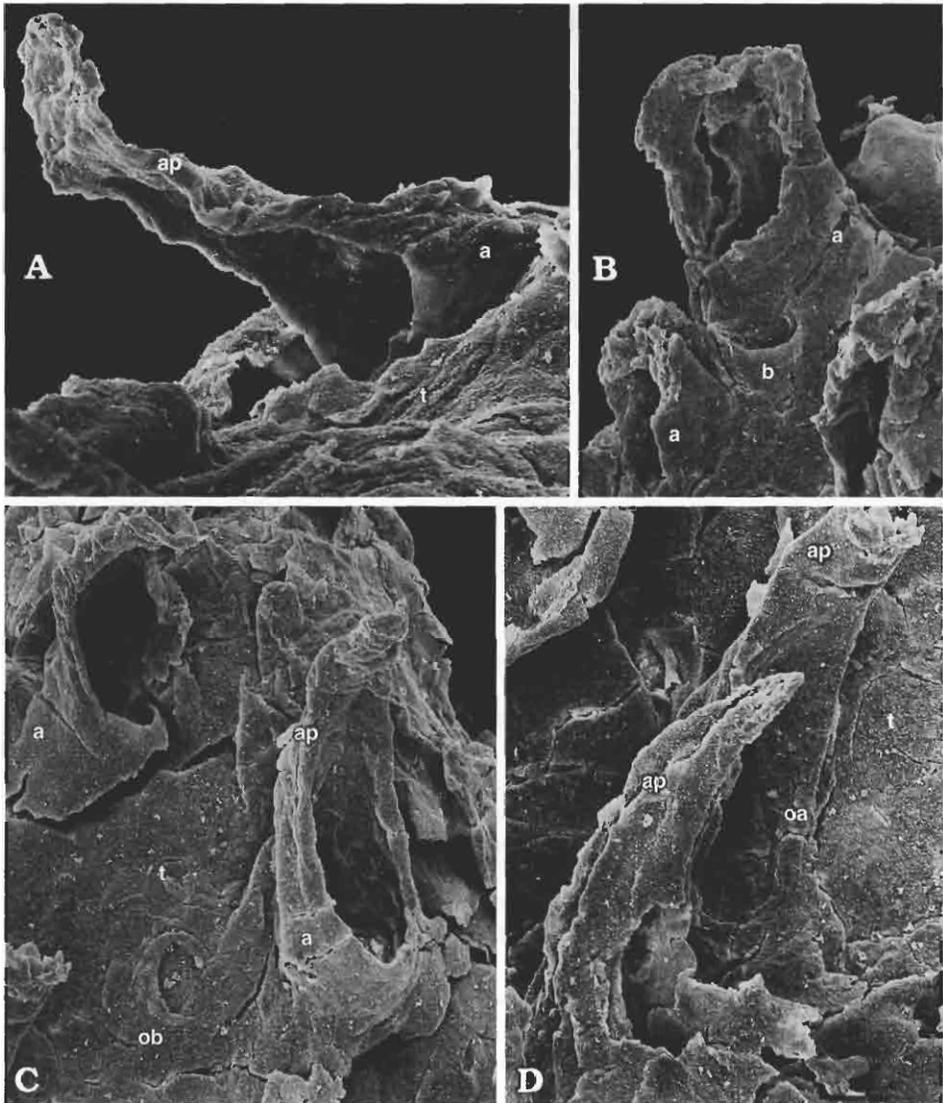


Fig. 2. *Camarotubus graptocamaraeformis* gen. et sp. n. Middle Ordovician (Caradoc?), erratic boulder No. O.469, Mochty (Poland). SEM micrographs. Fragments of the thecorhiza showing erect autothecal portions and bithecae. A, $\times 150$ (ZPAL G/0/3); B–D, $\times 85$ (ZPAL G/0/1). Abbreviations: a, autotheca; ap, apertural process; b, bitheca; ca, cavity of broken autotheca; oa, occluded autotheca; ob, occluded bitheca; s, stolon.

Remarks. — The genus is monotypic, erected to include *Camarotubus graptocamaraeformis* sp.n.; stratigraphic and geographic range as for the type species. The genus may only tentatively be referred to the family Cyclograptidae because this family is not a natural taxon and is in need of revision (see Mierzejewski 1978: p. 562). *Camarotubus* gen.n. resembles superficially some other tuboid genera (especially *Epigraptus* Eisenack, 1941) with isolated erect portions of autothecae, but it differs distinctly in the presence of sclerotized stolons with diaphragms and the striking scarcity of bithecae. It is also superficially similar to the camaroid genus *Graptocamara* Kozłowski, 1949, but differs in the presence of bithecae and stolons.

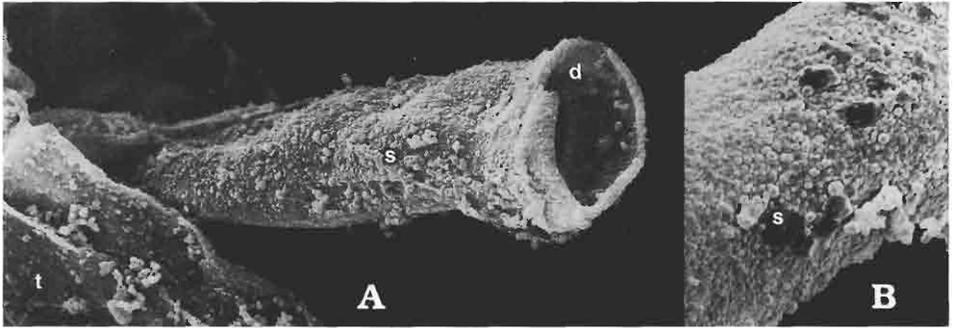


Fig. 3. *Camarotubus graptocamaraeformis* gen. et sp. n. Middle Ordovician (Caradoc?), erratic boulder No. O.469, Mochty (Poland). SEM micrographs. A. Fragment of stolon showing its vesicular diaphragm; $\times 800$ (ZPAL G/0/3). B. Fine structure of the surface of the stolon; $\times 700$ (ZPAL G/0/1). Abbreviations: d, diaphragm; s, stolon; t, thecorhiza.

Camarotubus graptocamaraeformis sp. n.

Figs. 1–3.

?*Graptocamara hyperlinguata* Kozłowski; Skevington 1963: pp. 55–56, figs. 76–77.

Holotype: Fragment of thecorhiza with twenty one autothecae and three bithecae (Figs. 1A, 2 B–D, 3B).

Type locality and type stratum: Middle Ordovician (Caradoc?), glacial boulder No. O.469 found near Mochty, Poland.

Derivation of name: Referring to its superficial similarity with the camaroid genus *Graptocamara* Kozłowski, 1949, and Latin *form* – form.

Diagnosis. — General shape of entire rhabdosome unknown, but essentially encrusting. The colony comprises three types of thecae. Autothecae several times as numerous as bithecae, stolothecae indistinct. Autothecae composed of creeping proximal parts incorporated in thecorhiza and erect distal parts usually reduced to ventral linguiform or subtriangular apertural process. Bithecae limited to thecorhiza and irregularly distributed. Stolon system well developed and strongly sclerotized; autothecal stolons provided with vesicular diaphragms.

Material. — Seven fragments of rhabdosomes from the erratic boulder No. O.469 (ZPAL G/0/1–7), well preserved and showing only mild deformation.

Description. — The general rhabdosomal characters are not yet completely known but sufficiently large fragments are preserved to demonstrate an essentially encrusting character (Fig. 1). However, it is not possible to suggest whether it was tape-like, discoidal or completely irregular. The holotype (Fig. 1A) measuresca 3×3 mm, and is a subquadrangular fragment of a colony comprising a piece of thecorhiza, twenty-one autothecae and three bithecae. No traces of conothecae or other special thecae are found. The majority of the autothecae are arranged in two distinct rows, whereas three bithecae are distributed capriciously. The autothecae are distinctly variable in both the morphology and the height of their erect portions. In general, the erect portion of each autotheca comprises a rising tube and an apertural apparatus in the form of a ventral process. The rising tubes are short, tubular and oval in cross section (Figs. 1B, 2B, C), but are often lacking. Where there is no rising tube, the erect portion of the autotheca is formed entirely of an apertural process (Fig. 2A, D). As a rule the apertural process is subtriangular or tongue-shaped; however, both types of process grade into each other. The autothecal erect portions attain 0.21–0.28 mm in diameter and 0.50–0.85 mm in height. The bithecae are confined to the thecorhiza and their length is uncertain. Bithecal apertures occur at the base of erect portions of the autothecae, and their shape varies from circular to semicircular (Fig. 2B, C); apertural diameter ranges from 0.08 to 0.11 mm. The bitheca illustrated in Fig. 2C has its aperture occluded. Short fragments of stolons can be seen at the margins of some specimens (Fig. 1A, C). They

are provided with distinct vesicular diaphragms or globular swellings (Fig. 3A). The outer surface of the stolon is covered with a granular sculpture (Fig. 3B). The periderm surface is rather smooth and devoid of fusellar structure or cortical bandages (Fig. 2).

Remarks. — Presumably all the specimens described originated from a single colony which was disintegrated during chemical dissolution of the matrix. It is possible that some indeterminate graptolite remnants described by Skevington (1965) as isolated linguiform apertural processes of *Graptocamara hyperlinguata* Kozłowski, 1949 (Ontikan Limestones, Öland) represent *C. graptocamaraeformis* sp. n.

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Nowy graptolit pośredni między Tuboidea a Camaroidea

PIOTR MIERZEJEWSKI

Streszczenie

Znanych jest kilka rzędów osiadłych graptolitów, w większości opisanych przez Kozłowskiego (1938, 1949, 1962). Związki rodowe między tymi rzędami są słabo poznane. Stosunkowo najlepiej wydaje się być udokumentowane pochodzenie kamaroidów (Camaroidea) od tuboidów (Tuboidea), sugerowane przez Kozłowskiego (1949). Zdaniem tego autora, Camaroidea rozwinęły się z inkrustujących Tuboidea, zbliżonych do rodzaju *Epigraptus* Eisenack (= *Idiotubus* Kozłowski). Rodzaj ten przypomina najprymitywniejszego znanego dotąd graptolita kamaroidowego, tj. *Graptocamara* Kozłowski. Zasadnicze różnice pomiędzy tymi dwoma rodzajami polegają na obecności lub braku bitek: liczba bitek w koloniach *Epigraptus* dwu- lub trzykrotnie, czasem nawet wielokrotnie, przewyższa liczbę autotek, podczas gdy *Graptocamara* całkowicie pozbawiona jest bitek (cecha właściwa dla Camaroidea, z wyjątkiem problematycznego rodzaju *Bithecocamara* Kozłowski). W pracy opisano nowego przedstawiciela inkrustujących graptolitów tuboidowych, *Camarotubus graptocamaraeformis* gen. et sp. n., którego uznano za kolejną formę pośrednią między Tuboidea a Camaroidea, a zwłaszcza między rodzajami *Epigraptus* a *Graptocamara*. Charakteryzuje się on silnie zredukowaną liczbą bitek – duże obszary kolonii pozbawione są bitek, a na innych występują one pojedynczo, rozmieszczone rzadko i nieregularnie. Nowy graptolit został opisany z ordowickiego (karadok?) głazu narzutowego, znalezione go w okolicach Mocht (ok. 60 km na północ od Warszawy). *Camarotubus* gen. n. z racji swojego stosunkowo młodego wieku nie może być traktowany jako przypuszczalny przodek rodzaju *Graptocamara*, znanego już z tremadoku. Istnienie jego wskazuje jednak, że proces eliminacji bitek, co jest cechą progresywną, następował w różnych liniach ewolucyjnych Tuboidea i w różnych momentach czasu geologicznego, podobnie jak następowało eliminowanie bitek w szczepach wiodących od Dendroidea do Graptoloidea.