To my mother

PIOTR MIERZEJEWSKI

ULTRASTRUCTURE, TAXONOMY AND AFFINITIES OF SOME ORDOVICIAN AND SILURIAN ORGANIC MICROFOSSILS

(Plates 19—37)

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The work presents the results of morphological and ultrastructural (TEM and SEM) studies on Ordovician and Silurian organic (non-calcareous) fossils among which representatives of scyphozoans, hydrozoans, pogonophorans and pterobranchs are recognized. A few forms of uncertain systematic position are also described. Scyphozoa: well preserved scyphothecae of *Byronia robusta* (KOZŁ.) are described along with ultrastructural observations made on other *Byronia* species. Part of the so-called dithecoid graptolites is recognized as colonial scyphopolyps. Hydrozoa: forms described by R. KOZŁOWSKI and A. EISENACK as hydroids are revised. The astogenesis of *Rhabdohydra tridens* KOZŁ. is reconstructed. Two new taxa are designated. The periderm ultrastructure of five species is described and interpreted. Some forms known as dithecoid graptolites and the group Chaunograptidae are recognized as colonial hydropolyps. Pogonophora: *Beklemishevites grandis* gen. et sp. n. is described. Tube ultrastructure is studied for two species revealing in one case the presence of a chitin-protein complex. Pterobranchia: forms described by R. KOZŁOWSKI are revised and a new taxonomy is proposed for Rhabdopleurida. Some forms classified previously as hydroids are identified as rhabdopleurids and five new taxa are designated. The astogenesis of *Rhabdopleurites primaevus* KOZŁ. is reconstructed and new types of stolonal tubes (without zig-zag suture and fuselli) are described. The ultrastructure of cysts, stolons and stolonal tubes is studied in several forms. A congenerity of *Rhabdopleurites* with some forms described previously as tuboid or stolonoid graptolites and hydroids is suggested. Miscellanea: ultrastructure of five problematic microfossils are studied. A few new taxa are described including two new genera.

Key words: Ultrastructure, taxonomy, microfossils, Scyphozoa, Hydrozoa, Pogonophora, Pterobranchia, Graptolithina, Miscellanea, Ordovician, Silurian, glacial erratics, Baltic Region, Poland.

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ULTRASTRUKTURA, TAKSONOMIA I POKREWIEŃSTWO NIEKTÓRYCH ORDOWICKICH I SYLURSKICH MIKROSKAMIENIAŁOŚCI ORGANICZNYCH

Streszczenie — Opracowano, przy wykorzystaniu technik elektronowo-mikroskopowych ordowickie i sylurskie mikroskamieniałości organiczne, rozróżniając wśród nich krążkopławy, stułbiopławy, pogonofory, pióroskrzelne i rozmaite formy *incertae sedis*.

Scyphozoa. — Opisano dobrze zachowane scyfoteki *Byronia robusta* (Kozł.), zbadano ultrastrukturę peridermy 2 gatunków, w jednym przypadku ujawniono jej chitynowo-proteinowy charakter. Część tzw. graptolitów ditekoidowych uznano za kolonijne scyfopolipy.

Hydrozoa. — Przeprowadzono rewizję form opisanych przez R. Kozłowskiego i A. Eisenacka. Zrekonstruowano kormogenezę *Rhabdohydra tridens* Kozł., wyróżniono 2 nowe taksony, zbadano ultrastrukturę peridermy 5 gatunków. Część tzw. graptolitów ditekoidowych i Chaunograptidae uznano za kolonijne hydropolipy.

Pogonophora. — Opisano *Beklemishevites grandis* gen. n., sp. n., zbadano ultrastrukturę rurek 2 gatunków, w jednym przypadku ujawniono obecność kompleksu proteinowo-chitynowego.

Pterobranchia. — Przeprowadzono rewizję form opisanych przez R. Kozłowskiego, przedstawiono nową koncepcję taksonomii Rhabdopleurida, wykazano rabdopleuridowy charakter szeregu form uważanych dotąd za Hydroida, wyróżniono 5 nowych taksonów. Zrekonstruowano kormogenezę *Rhabdopleurites primaevus* Kozł., opisano nieznane dotąd typy rurek stolonalnych (bez szwu zygzakowatego i bezfuzellarne), zbadano ultrastrukturę cyst, stolonów i rurek stolonalnych niektórych form. Sugeruje się kongeneryczność *Rhabdopleurites* z niektórymi domniemanymi graptolitami tuboidowymi lub stolonoidowymi oraz Hydroida.

Miscellanea. — Zbadano ultrastrukturę 5 problematyków i opisano kilka dalszych, ustanawiając dwa monotypowe nowe rodzaje.

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INTRODUCTION

In 1973, the late Professor ROMAN KOZŁOWSKI kindly passed me for further study some organic microfossils he had extracted by chemical methods from Baltic erratics of Ordovician and Silurian age. The material comprised various microfossils, usually in the form of branching or simple tubes. Some specimens of that collection have been previously described as Hydroida by KOZŁOWSKI (1959*a*). In discussions, he repeatedly suggested that some of the forms previously interpreted by him as Hydroida may actually have nothing in common with coelenterates. He also used to emphasize the necessity of revising some taxa described by him. My studies show a high degree of homeomorphy of tubular organic skeletons or fragments of such, often representing quite distant systematic groups, thus confirming his opinion than revision was necessary.

This paper deals with animal microfossils built of organic matter and of debatable or unknown systematic position. An attempt to establish their taxonomic affinities has resulted in an inevitable break in the compactness of the paper. However, I regarded it necessary to present as complete as possible an analysis of the taxonomy of the microfossils that represent different systematic groups but are poorly known, similar in shape and often very difficult to distinguish and to classify.

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The studies were conducted at the laboratories of electron microscopy of the following institutions: M. Nencki Institute of Experimental Biology and Centre of Experimental Medicine (Polish Academy of Sciences), Zoology and Botany Departments of Warsaw University and the Anatomy Department of the St. George's Hospital Medical School (London).

MATERIAL

The material studied comes from one locality *in situ*, four borings, and some dozens of glacial erratics (fig. 1). *Sokolovites pogonophoroides* KOZŁ. was derived from the chalcedonites of Chojnów Dół by Zbilutka. The age of these chalcedonites was estimated by SZANIAWSKI (1979) as Upper Tremadoc. Some fossils were extracted from the following borings:

Biała Podlaska 2. Middle Ordovician (W. BEDNARCZYK, personal information). Depth 680—687 m. *Rhabdohydra tridens* KOZŁOWSKI, ?*Rhabdopleurites* sp. *Kystodendron* ex gr. *longicarpus* (EISENACK) *sensu* KOZŁOWSKI.

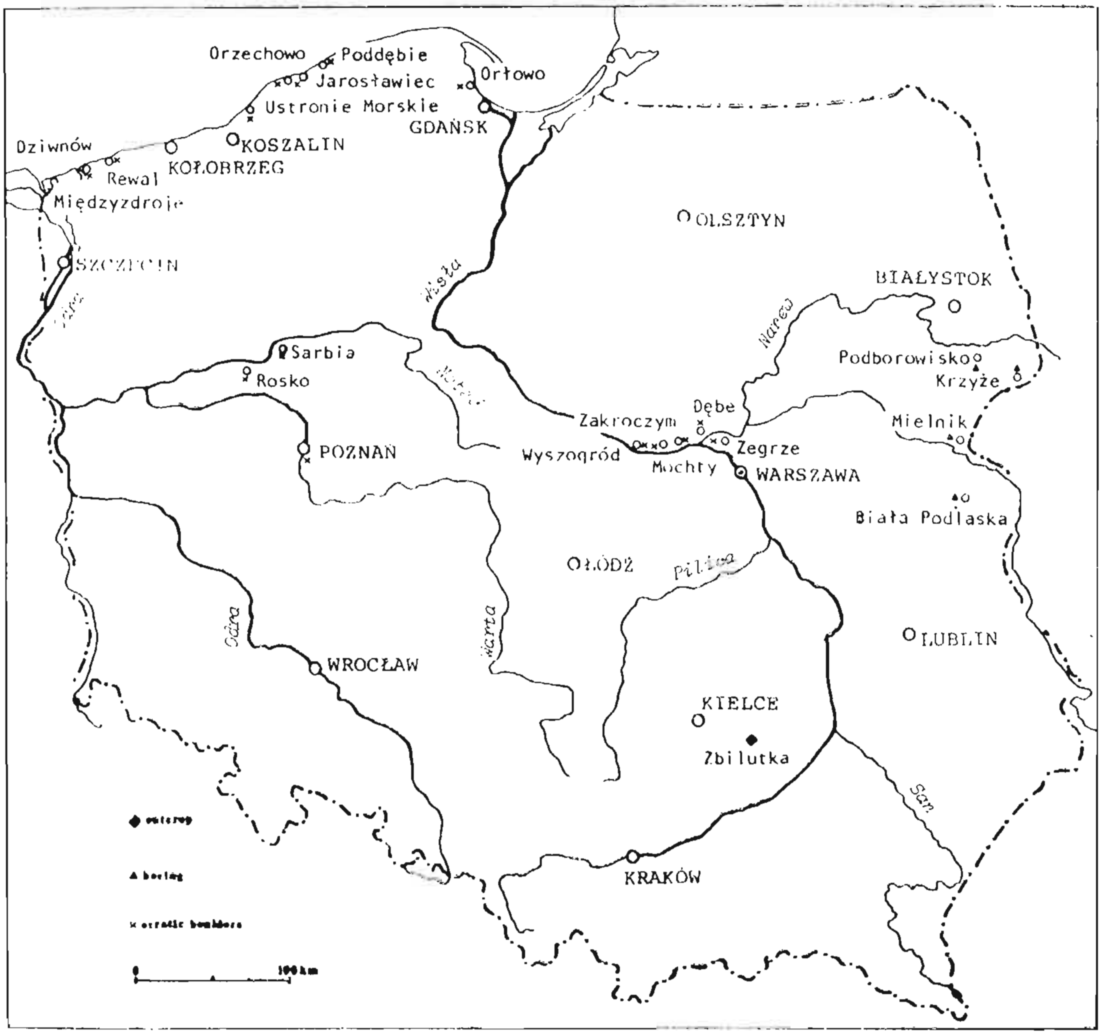

Fig. 1.

Sketch-map of Poland showing: outcrops (black square), situation of deep boring (black triangle) and localities where described erratic boulders were collected (crosslet).

Krzyże 4. Llandeilo (TOMCZYK 1964, ZNOSKO 1964, BEDNARCZYK 1966). Depth 471—473 m: *Rhabdohydra tridens* KOZŁOWSKI, 477—479 m: *Chitinodendron bacciferum* EISENACK.

Mielnik 1. Upper? Ordovician (TOMCZYK 1964). Depth 1118—1124 m: *Byronia* sp. A, *Rhabdopleuroides expectatus* KOZŁOWSKI, *Xenohydra labiata* KOZŁOWSKI.

Podborowisko 1. Arenig (TOMCZYK 1964, ZNOSKO 1964). Depth 396—397 m: *Inocaulis* sp., *Kystodendron longicarpus* (EISENACK) *sensu* KOZŁOWSKI.

The bulk of the material comes from calcareous erratic boulders of Ordovician and Silurian age. The boulders were gathered at various localities in central and northern Poland. Boulders from the collections of the Institute of Paleobiology of the Polish Academy of Sciences are marked with symbol ZPAL, and those I gathered during work in the Museum of Earth, Polish Academy of Sciences — with the symbol MZ. The list of erratic boulders, given below, shows: symbol and number of boulder, its locality, geological age, lithological characteristics (or references to papers where relevant data may be found), list of accompanying fossils (or references to relevant publications), and list of microfossils discussed here.

Boulder no. ZPAL 0.15, Orłowo (province of Gdańsk). Ordovician. The lithological characteristic and the assemblage of fossils in Kozłowski (1954, 1959*a*), Górka (1969). *Flexihydra undulata* Kozłowski.

Boulder no. ZPAL 0.22, Sarbia (province of Poznań). Ordovician. The lithological characteristic and the assemblage of fossils in Kozłowski (1954, 1959*a*, 1961, 1962) and Górka (1969). *Rhabdopleuroides expectatus* Kozłowski.

Boulder no. ZPAL 0.25. Poznań. Ordovician. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*). *Rhabdohydra tridens* Kozłowski, ?*Kystodendron* sp.

Boulder no. ZPAL 0.26, Poznań–Czerwonak. Middle Ordovician. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*, 1962, 1963*a*, 1966*b*), Urbanek (1959) and Górka (1969). *Chaunograptus adhaerens* (Kozłowski), *Rhabdohydra tridens* Kozłowski.

Boulder no. ZPAL 0.29. Stara Warka (province of Warszawa). Llandeilo?. The lithological characteristic and the assemblage of fossils in Kozłowski (1954, 1959*a*, 1962, 1963*b*) and Kielan-Jaworowska (1966). *Calyxhydra irregularis* Kozłowski, *Chitinodendron bacciferum* Eisenack, *Diplohydra solida* Kozłowski, *Diplohydra gonothecata* Kozłowski, *Kystodendron longicarpus* (Eisenack) *Rhabdohydra tridens* Kozłowski.

Boulder no. ZPAL 0.31, Poznań–Czerwonak. Llanvirn. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*, 1962, 1963*a*) and Kielan-Jaworowska (1966). *Diplohydra gonothecata* Kozłowski, *Chitinodendron bacciferum* (Eisenack) *Rhabdohydra tridens* Kozłowski.

Boulder no. ZPAL 0.42, Zakroczym (province of Warszawa). Ordovician? The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*) and Kielan-Jaworowska (1966). *Diplohydra gonothecata* Kozłowski, *Lagenohydra phragmata* Kozłowski, *Phragmohydra articulata* Kozłowski, *Rhabdopleuroides expectatus* Kozłowski.

Boulder no. ZPAL 0.44, Poznań–Czerwonak. Ordovician? Silurian? The lithological characteristic in Kozłowski (1959*a*). *Xenohydra labiata* Kozłowski.

Boulder no. ZPAL 0.52, Ustronie Morskie (province of Koszalin). Ordovician. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*). *Rhabdohydra tridens* Kozłowski.

Boulder no. ZPAL 0.60, Rewal (province of Szczecin). Ashgill. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*, 1961, 1963*a*). *Rhabdopleuroides expectatus* Kozłowski.

Boulder no. ZPAL 0.62, Orlowo (province of Gdańsk). Organogenic limestone with *Mastigograptus* sp., *Dictyonema* sp. and *Discograptus schmidti* Wiman. The presence of *D. schmidti* suggested Upper Ordovician age of boulder (see Urbanek and Towe 1974: 2). *Kystodendron complicatus* sp. n.

Boulder no. ZPAL 0.66, Dziwnów (province of Szczecin). Ashgill. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*). *Rhabdohydra tridens* Kozłowski.

Boulder no. ZPAL 0.90, Rewal (province of Szczecin). Ordovician? Light grey, compact limestone with *Acanthograptus* sp. (Kozłowski 1961). *Rhabdopleuroides expectatus* Kozłowski.

Boulder no. ZPAL 0.94, Jarosławiec (province of Słupsk). Ordovician. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*, 1962, 1967) and Górka (1969). *Rhabdohydra tridens* Kozłowski.

Boulder no. ZPAL 0.110, Orłowo (province of Gdańsk). Ordovician ? Fine-grained limestone with tuboid graptolites (Kozłowski 1959*a*). *Phragmohydra articulata* Kozłowski.

Boulder no. ZPAL 0.121, Wyszogród (province of Warszawa). Middle Caradoc. The lithological characteristic and the assemblage of fossils in Kozłowski (1959*a*, 1967) and Górka

(1969). *Kystodendron subtilis* (KOZŁOWSKI), ?*Kystodendron* sp. B, *Chaunograptus adhaerens* (KOZŁOWSKI), Chaunograptidae ? Gen. et sp. indet.

Boulder no. ZPAL O.123, Wyszogród (province of Warszawa). Ordovician? The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Diplohydra gonothecata* KOZŁOWSKI.

Boulder no. ZPAL O.129, Wyszogród–Zakroczym (province of Warszawa). The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Chaunograptus flexuosus* (KOZŁOWSKI), *Chaunograptus adhaerens* (KOZŁOWSKI), *Diplohydra micropedunculata* KOZŁOWSKI.

Boulder no. ZPAL O.137, Wyszogród–Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1962) and GÓRKA (1969). *Ascosyrinx tenuis* KOZŁOWSKI.

Boulder no. ZPAL O.153, Wyszogród–Zakroczym (province of Warszawa). Ordovician? The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Kystodendron subtilis* (KOZŁOWSKI).

Boulder no. ZPAL O.158, Wyszogród–Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Kystodendron longicarpus* (KOZŁOWSKI), *Kystodendron subtilis* (KOZŁOWSKI).

Boulder no. ZPAL O.163, Wyszogród–Zakroczym (province of Warszawa). Ordovician? The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). ?*Kystodendron* sp. B.

Boulder no. ZPAL O.166, Wyszogród–Zakroczym (province of Warszawa). Ordovician? The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*, 1960, 1962). *Kystodendron longicarpus* (EISENACK).

Boulder no. ZPAL O.167, Wyszogród–Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*, 1962) and GÓRKA (1969). *Rhabdohydra tridens* KOZŁOWSKI, *Chaunograptus adhaerens* (KOZLOWSKI), *Diplohydra gonothecata* KOZŁOWSKI.

Boulder no. ZPAL O.168, Wyszogród–Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL O.169, Wyszogród–Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*, 1961, 1962). *Kystodendron longicarpus* (EISENACK), *Rhabdopleuroides expectatus* KOZŁOWSKI.

Boulder No. ZPAL O.170, Wyszogród–Zakroczym (province of Warszawa). Ordovician. The litological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*) and GÓRKA (1969). *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL O.179, Mochty (province of Warszawa). Upper Ordovician? Llandovery? The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*) and KIELAN-JAWOROWSKA (1966). *Ascosyrinx tenuis* KOZŁOWSKI, *Chaunograptus adhaerens* (KOZŁOWSKI), *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL O.181, Mochty (province of Warszawa). Upper Llanvirn or Lower Llandeilo. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*, *b*) and URBANEK (1959). *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL O.182, Mochty (province of Warszawa). Middle Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*, 1962), KIELAN-JAWOROWSKA (1962, 1966), ADAMCZAK (1963) and GÓRKA (1969). *Chaunograptus adhaerens* (KOZŁOWSKI), *Palaeotuba polycephala* EISENACK, *Rhabdohydra tridens* KOZŁOWSKI, *Diplohydra solida* KOZŁOWSKI, *Kystodendron longicarpus* (EISENACK), *Kystodendron subtilis* (KOZŁOWSKI), Chaunograptidae? Gen. et sp. indet.

Boulder no. ZPAL O.184, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Chitinodendron bacciferum* EISENACK, *Kystodendron longicarpus* (EISENACK), Chaunograptidae? Gen. et sp. indet.

Boulder no. ZPAL O.185, Mochty (province of Warszawa). Upper Ordovician? The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*) and KIELAN-JAWOROWSKA (1966). *Byronia naumovi* KOZŁOWSKI, *Ascosyrinx tenuis* KOZŁOWSKI.

Boulder no. ZPAL O.186, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*) and GÓRKA (1969). *Rhabdohydra multiplex* sp. n.

Boulder no. ZPAL O.218, Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1962) and GÓRKA (1969). *Kozlowskisyrinx graptovermiformis* gen. n., sp. n.

Boulder no. ZPAL O.240, Zakroczym (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*) and GÓRKA (1969). *Chaunograptus flexuosus* (KOZŁOWSKI), *Chitinodendron bacciferum* EISENACK.

Boulder no. ZPAL O.242, Zakroczym (province of Warszawa) Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Palaeotuba polycephala* EISENACK.

Boulder no. ZPAL O.244, Rewal (province of Szczecin). Ashgill. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1967). *Ascosyrinx tenuis* KOZŁOWSKI.

Boulder no. ZPAL O.262, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1959*a*). *Kystodendron longicarpus* (EISENACK.)

Boulder no. ZPAL O.320, Mochty (province of Warszawa). Middle? Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1962). Gen. et sp. indet. (Pterobranchia).

Boulder no. ZPAL O.322, Mochty (province of Warszawa). Light, coarse grained limestone with *Leiosphaera* sp., *Climacograptus* sp., *Rhabdohydra tridens* KOZŁOWSKI and thelodont scales (KOZŁOWSKI, unpublished). Silurian?

Boulder no. ZPAL O.324, Mochty (province of Warszawa). Ordovician? Limestone with conularid fragments, *Tasmanites* sp., Chitinozoa, scolecodonts, *Diplograptus* sp., *Mastigograptus* sp., *Beklemishevites grandis* gen. n., sp. n.

Boulder no. ZPAL O.331, Mochty (province of Warszawa). Ordovician. Grey, fine grained limestone with *Conotreta* sp., *Dendrograptus* sp., *Dictyonema* sp., *Byronia naumovi* KOZŁOWSKI.

Boulder no. ZPAL O.334, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1960). *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL O.366, Zakroczym (province of Warszawa). Middle Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1962), KIELAN-JAWOROWSKA (1962, 1966) and GÓRKA (1969). *Ascosyrinx tenuis* KOZŁOWSKI and *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL O.389, Zegrze (province of Warszawa). Ashgill? Baltic limestone with Porifera, Radiolaria, scolecodonts, *Climacograptus* sp., *Rhabdohydra tridens* KOZŁOWSKI (KOZŁOWSKI, unpublished).

Boulder no. ZPAL O.390, Zegrze (province of Warszawa). Ordovician? Light compact limestone with brachiopods, conodonts and scolecodonts (KOZŁOWSKI, unpublished). *Byronia naumovi* KOZŁOWSKI.

Boulder no. ZPAL O.392, Zegrze (province of Warszawa). Ordovician? The lithological characteristic and the assemblage of fossils in GÓRKA (1969). *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL 0.400, Mochty (province of Warszawa). Middle Ordovician. The lithological characteristic and the assemblage of fossils in KIELAN-JAWOROWSKA (1962, 1966), KOZŁOWSKI (1967) and GÓRKA (1969). *Rhabdopleurites primaevus* KOZLOWSKI.

Boulder no. ZPAL 0.424, Międzyzdroje (province of Szczecin). Ordovician. Grey, fine grained, compact limestones with conodonts and scolecodonts (KOZLOWSKI, unpublished). *Byronia robusta* (KOZLOWSKI).

Boulder no. ZPAL 0.468, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in GÓRKA (1969). ?*Rhabdopleurites* sp. B.

Boulder no. ZPAL 0.469, Mochty (province of Warszawa). Middle? Ordovician. The lithological characteristic and the assemblage of fossils in KIELAN-JAWOROWSKA (1966) and GÓRKA (1969). *Ascosyrinx tenuis* KOZŁOWSKI.

Boulder no. ZPAL 0.470, Mochty (province of Warszawa). Middle? Ordovician. The lithological characteristic and the assemblage of fossils in KIELAN-JAWOROWSKA (1966) and GÓRKA (1969). *Kozlowskisyrinx graptovermiformis* gen. n., sp. n.

Boulder no. ZPAL 0.498, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in GÓRKA (1969). *Ascosyrinx tenuis* KOZŁOWSKI, *Rhabdohydra tridens* KOZŁOWSKI, *Sokolovites pogonophoroides* KOZŁOWSKI.

Boulder no. ZPAL 0.499, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in GÓRKA (1969). *Rhabdohydra tridens* KOZŁOWSKI, ?*Rhabdopleurites* sp.

Boulder no. ZPAL 0.501, Mochty (province of Warszawa). Ordovician? Light grey, coarse grained limestone with *Tasmanites* sp., foraminifers, chitinozoans, *Dictyonema* sp. and *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL 0.533, Mochty (province of Warszawa). Middle? Ordovician. The lithological characteristic and the assemblage of fossils in KOZŁOWSKI (1970*a*). *Rhabdopleurites primaevus* KOZLOWSKI.

Boulder no. ZPAL 0.542, Mochty (province of Warszawa). Organogenic, coarse grained limestone with scolecodonts, brachiopods, chitinozoans and graptolites (*Graptolodendrum* sp., *Mastigograptus* sp., *Dictyonema* sp., *Climacograptus* sp., Diplograptidae, Tuboidea), *Rhabdopleurites primaevus* KOZŁOWSKI, Ordovician.

Boulder no. ZPAL 0.544, Mochty (province of Warszawa). Grey, compact limestone with foraminifers, scolecodonts, brachiopods (*Conotreta* sp.) and graptolites (*Dictyonema* sp. and others). *Rhabdopleurites primaevus* KOZLOWSKI.

Boulder no. ZPAL 0.555, Mochty (province of Warszawa). Ordovician. The lithological characteristic and the assemblage of fossils in GÓRKA (1969). *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL 0.642, Wolin (province of Szczecin). Ordovician? Compact, fine grained limestone with scolecodonts, chitinozoans, conularids and graptolites. *Rhabdohydra tridens* KOZŁOWSKI.

Boulder no. ZPAL 0.693, Mochty (province of Warszawa). Ordovician? Light, compact limestone. ?*Rhabdopleurites* sp.

Boulder no. ZPAL 0.695, Mochty (province of Warszawa). Ordovician? No information on lightology and fossils. *Kystodendron* aff. *subtilis* KOZLOWSKI.

Boulder no. MZ/2, Orzechowo (province of Słupsk). Ordovician or Silurian. Grey, fine grained limestone with scolecodonts and chitinozoans. *Problematicum* B.

Boulder no. MZ/11, Orzechowo (province of Słupsk). Light grey limestone with glauconite, partly silicified. Caradoc. Algae — *Coelosphaeridium cyclocrinophilum* Roemer, *Cyclocrinites porosus* STOLLEY, *Mastopora concava* EICHWALD, *Tasmanites* sp., Chitinozoa — *Desmochitina* sp., *Conochitina proboscifera* EISENACK, *Cyathochitina* cf. *kukersiana* EISENACK, Foraminifera — *Blastammina* sp., Hydrozoa — *Chaunograptus flexuosus* (KOZLOWSKI). Polychaeta — *Luno-*

prionella symmetrica Eisenack, *Atraktoprion* sp., *Polychaetaspis* sp., *Pistoprion* sp., Tentaculitida — *Homoctenus* sp., Graptolithina — ?*Epigraptus* sp.

Boulder no. MZ/14, Orzechowo (province of Słupsk). Ordovician. Light grey limestone with glauconite. Algae — *Baltisphaeridium* sp., Chitinozoa — *Cyathochitina campanulaeformis* Eisenack, *C. calyx* Eisenack, *Conochitina robusta* Eis., Hydrozoa — *Rhabdohydra tridens* Kozłowski, Polychaeta — *Tetraprion* sp., *Xanioprion* sp., Graptolithina — *Kozlowskitubus erraticus* (Kozłowski), Dendroidea.

Boulder no. MZ/18, Orzechowo (province of Słupsk). Limestone lithologically similar to the Baltic limestone. Ordovician (Caradoc?). Melanosleritoidea — *Melanocyathus dentatus* Eis. and others, Foraminifera — *Blastammina* sp., Chitinozoa — *Cyathochitina campanulaeformis* Eis., *Conochitina* sp., *Lagenochitina* sp., Polychaeta — ?*Mochtyella* sp., *Polychaetaspis* sp., Hydrozoa — *Rhabdohydra tridens* Kozłowski, Pterobranchia — *Kystodendron* sp., Graptolithina — *Kozlowskitubus erraticus* (Kozłowski), *Mastigograptus* sp., *Dendrotubus* sp., Problematicum — *Parachitina curvata* Eis.

Boulder no. MZ/24, Orzechowo (province of Słupsk). Limestone lithologically similar to the Baltic limestone. The presence of *Discograptus schmidti* Wiman suggested Upper Ordovician age of the boulder (see Urbanek and Towe 1974: 2). Melanoscleritoidea — *Melanorhachis brachycladus* Eisenack, ?*Melanorhachis* sp. and others, Chitinozoa — *Conochitina* sp., *Lagenochitina* sp., Hydrozoa — *Chaunograptus flexuosus* (Kozłowski), Polychaeta — *Mochtyella fragilis* Szaniawski, *Atraktoprion* sp., *Polychaetaspis* sp., *Lunoprionella* aff. *asymmetrica* Eisenack, Graptolithina — *Discograptus schmidti* Wiman.

Boulder no. MZ/30, Orzechowo (province of Słupsk). Light grey, fine grained limestone. Ordovician (Caradoc?). Algae — *Tasmanites* sp., Hydrozoa ?*Rhabdohydra* sp., Polychaeta, Graptolithina — *Micrograptus* sp.

Boulder no. MZ/38, Poddębie (province of Słupsk). Light grey, coarse grained limestone, Silurian. Melanoscleritoidea — *Melanorhachis brachycladus* Eisenack and others, Chitinozoa — *Ancyrochitina primitiva* Eisenack and others, Polychaeta — *Mochtyella* ex gr. *trapezoidea* Kielan-Jaworowska, *Vistulella* sp., *Xanioprion* sp., *Lunoprionella* sp., *Polychaetaspis* sp., *Symmetroprion* sp., Pterobranchia — *Kystodendron* sp., Graptolithina — *Epigraptus kozlowskii* Mierzejewski, Problematica — *Chitinodendrum bacciferum* Eisenack.

Boulder no. MZ/39, Ustka (province of Słupsk). Light grey, coarse grained limestone. Ordovician or Silurian. Foraminifera, tabulates, Scyphozoa — *Byronia robusta* (Kozłowski), Polychaeta — *Polychaetaspis* sp., *Paulinites* sp., ?*Xanioprion* sp.

Boulder no. MZ/42, Orzechowo (province of Słupsk). Llanvirn — *Eoplacognathus pseudoplanus* Zone. The lithological characteristic and the assemblage of fossils in Mierzejewski (1977, 1978*a*). *Eisenackisyrinx curvatus* gen. n., sp. n., *Problematicum* A.

Boulder no. MZ/61, Rewal (province of Szczecin). Grey, organogenic limestone. Ordovician? Scolecodonts, Pterobranchia — *Rhabdopleurites primaevus* Kozłowski, Graptolithina — *Epigraptus* sp., *Mastigograptus* sp., *Kozlowskitubus erraticus* (Kozłowski).

Boulder no. MZ/96, Jarosławiec (province of Słupsk). Light, organogenic limestone. Ordovician (Caradoc?). Foraminifers, chitinozoans, Problematica — *Ascosyrinx tenuis* Kozłowski, *Parachitina curvata* Eisenack.

Boulder no. MZ/116, Orzechowo (province of Słupsk). Pyritized, light grey, fine grained limestone. Ordovician? Foraminifers, Chitinozoa — *Cyathochitina campanulaeformis* Eisenack, Hydrozoa — *Rhabdohydra tridens* Kozłowski, Polychaeta — *Mochtyella fragilis* Szaniawski, Pterobranchia — *Kystodendron longicarpus* (Eisenack), Graptolithina — diplograptid graptoloids.

Boulder no. MZ/125. Poddębie (province of Słupsk). Grey, pyritized, coarse grained limestone. Ordovician? Algae — *Baltisphaeridium longispinosum* (Eisenack), *Tasmanites* sp., Chitinozoa — *Desmochitina minor ovulum* EISENACK, *Cyathochitina* sp., Polychaeta — *Mochtyella fragilis* SZANIAWSKI, *Rhytiprion magnus* KIELAN-JAWOROWSKA, *Rakvereprion balticus* (EISENACK), *Xanioprion* sp., *Pistoprion* sp., Pterobranchia — *Kystodendron longicarpus* (EISENACK), tuboid and crustoid graptolites, graptoblasts, remnants of eurypterid cuticle, Problematicum — *Xenotheka klinostoma* EISENACK.

Boulder no. MZ/142, Poddębie (province of Słupsk). Upper Silurian. The lithological characteristic and the assemblage of fossils *in* MIERZEJEWSKI (1978*c*). *Kystodendron tener* sp. n.

Boulder no. MZ/148, Poddębie (province of Słupsk). Upper Ludlow. The lithological characteristic and the assemblage of fossils in MIERZEJEWSKI (1977). Pterobranchia — *Kystodendron tener* sp. n.

Boulder no. MZ/151, Warszawa. Dark grey, coarse grained limestone. Ordovician? Hydrozoa — *Rhabdohydra tridens* KOZŁOWSKI, Graptolithina — *Kozlowskitubus erraticus* (KOZŁOWSKI), Problematicum C.

METHODS

Chemical methods

Methods of etching organic microfossils from carbonate rocks were exhaustively discussed by KIELAN-JAWOROWSKA (1966). Specimens from the collection of KOZŁOWSKI were obtained using these methods as were the majority of specimens extracted by me. However, in some cases I had to introduce some modifications to methods of treatment of the residuum. In the course of work I came to the conclusion that forms described in the literature as hydroids of the genera *Cylindrotheca* EISENACK and *Kystodendron* KOZŁOWSKI actually represent stolons with cysts of sterile buds of *Rhabdopleura*. My hypothesis seemed to be supported by the fact that sporadic narrow and fragile zooidal tubes of Ordovician and Silurian Rhabdopleurida were accompanied by the above mentioned fossils. Such cases were described by EISENACK (1976*a*) and MIERZEJEWSKI (1977). This suggested that tubes of that type were previously washed out of the residuum along with clay particles in the course of laboratory work. If this conclusion is correct, zooidal tubes should be found in unwashed residuum yielding fragments of *Kystodendron* and *Cylindrotheca*. Therefore, after finding the supposed stolons in the residuum, I used a different technique for the remaining part of a boulder. This technique involved searching through the residuum before its washing. This extremely laborious method gave positive results — finding of numerous highly fragile zooidal tubes of Rhabdopleurida.

Electron microscopy

Morphological and ultrastructural studies were done with scanning electron microscopes, Jeol JSM 1, Stereoscan and COATES and WELTER. For some years paleontologists have successfully used SEM in studies on ultrastructure of inorganic skeletons. The SEM methods appeared so easy to use that there were attempts to introduce them in studies on ultrastructure of organic microfossils (e.g. RICKARDS, HYDE and KRINSLEY 1971, CORRADINI, RUSSO and SERPAGLI 1974). However, it was soon found that the methods are rather of limited applicability and even deceptive. This question was discussed in relation to examples of graptolite periderm (URBANEK 1976*b*) and polychaete jaws by MIERZEJEWSKA and MIERZEJEWSKI (1978).

The main part of the present study was done with the methods of transmission electron microscopy. The microfossils were embedded in Durcupan or Epon 812 epoxide resin according to the procedures recommended by the manufacturers or by prolonging several times the time of infiltration. Ultrathin sections were cut by diamond knives with L.K.B. I, L.K.B. III and Tesla BS 490 A ultramicrotomes. Staining tests of sections were conducted by Reynolds' methods with the use of a 2% uranyl acetate, 2% potassium permanganate and lead citrate. The studies were conducted in the JEM 7A, Jem 100B and Tesla BS 500 transmission electron microscopes, with an accelerating voltage of 60 kV and 80 kV.

The resulting differences between the SEM and TEM methods in studies on organic microfossil ultrastructure may be easily noted by comparing of micrographs (pl. 19: 2—7 and pl. 30: 1—6).

TEM is sporadically used in morphological studies on organic microfossils (e.g. KWIECIŃSKA and SIEMIŃSKA 1974). Wider use in taxonomic studies is impeded by its disadvantageous feature — the loss of objects analysed by the replica method. Therefore, the specimens analysed by the method cannot be used as taxonomic types.

During studies of organic microfossils, the TEM is mainly used in analysing their structure. The results of TEM may widen the knowledge of the structure of a given form suggesting a basis for more accurate comparisons of the microfossils studied and, sometimes, drawing some conclusions concerning their affinity. Occasionally, the results make it also possible to identify the chemical character of the skeleton-building matter (TOWE and URBANEK 1974, MIERZEJEWSKA and MIERZEJEWSKI 1979*a*, MIERZEJEWSKI herein) or even to draw some conclusions on the nature of biochemical processes (MIERZEJEWSKA and MIERZEJEWSKI 1975, 1978).

The studies carried out with the use of SEM raise some questions of both technical and interpretational nature. The quality of the data obtained depends very closely on the type of knife used for cutting. Glass knives, often used in biological and medical studies, should generally be avoided in cutting organic microfossils. They appeared almost completely useless in the case of graptolite periderm (A. URBANEK, oral inf.) and other microfossils which I studied. Ultrathin sections obtained using glass knives very often display mechanical deformations, obscuring actual ultrastructure. For wider discussion of that phenomenon in the case of fossil polychaete jaws and Chitinozoa see MIERZEJEWSKA and MIERZEJEWSKI (1978) and MIERZEJEWSKI (1981).

Contrasting of sections represents a separate question. Nowadays it is difficult to imagine biological or medical studies without gorgeously expanded contrasting methods[1]. However, all attempts to contrast early Paleozoic material appeared fruitless. This is the case with graptolites (A. URBANEK, oral inf.), fossil polychaete jaws (MIERZEJEWSKA and MIERZEJEWSKI 1977, 1978) as well as other organic microfossils. Mummified muscle cells of Oligocene spider from Baltic amber also appeared insusceptible to constrasting (MIERZEJEWSKI, unpublished data). The lack of susceptibility of early Palaeozoic materials to contrasting may be explained in terms of the highly advanced or even complete degradation of its original biochemical structure. This statement is rather surprising in the light of records of aminoacids in graptolite periderm (FOUCART and JEUNIAUX 1965, FOUCART, BRICTEUX-GRÉGOIRE, JEUNIAUX and FLORKIN 1965). It may be necessary now to repeat paleobiochemical studies on the periderm.

In the course of TEM studies it is sometimes possible to note the phenomenon contrast of material as a result of a strong electron beam. This phenomenon has been recorded in graptolites studies (URBANEK, oral inf., and my own observation) found in studying chitin structures. The classic method of identifing of chitinous structures in modern material requires use of 2% potassium permanganate solution (NEVILLE and LUKE 1969). The structures are easily noted in TEM micrographs of Ordovician material without contrasting. It may be said that fossilization was here accompanied by the process of "self-contrasting" of tissue. In comparison

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[1] Contrasting is connected with separation of atoms with high atomic number, i.e. those more capable to bend electron beam than the majority of organisms building atoms, in a given object.

with the negative contrasting of LUKE and NEVILLE, we are dealing here with positive contrasting. A sudden pulse with a strong electron beam results in marked increase in contrast (see pl. 19: 2, 5 and pl. 30: 5—6). I suppose this increase to be due to partial or complete destruction of basic matter and contraction of fibrous building matter.

The highly specialized histo- and ultrahistochemical methods cannot be used in studies of early Paleozoic organic structures which is highly disadvantageous for their interpretation. Some conclusions on the nature of organic matter may be only drawn by comparing fossil and modern ultrastructures. This method has been successfully used in studies on graptolites (TOWE and URBANEK 1972, URBANEK and TOWE 1974, URBANEK 1976*a*) and it also appeared useful in those on the ultrastructure of scolecodonts (MIERZEJEWSKA and MIERZEJEWSKI 1975, 1977, 1978). However, its applicability appears confined to specific cases. This is due to the fact that several biochemically different types of organic matter may appear completely homogeneous in TEM micrographs. In turn, biochemically different matters may form identical, morphologically complex ultrastructures. The "parabolic pattern" ultrastructure, formed by chitin-protein complexes as well as protein-cholesterol liquid crystals, tunicine fibrils and chromosomal DNA, may serve as examples here. However, I treat the "parabolic pattern" images obtained in studies on *Byronia robusta* (KOZLOWSKI) and *Beklemishevites grandis* gen. n., sp. n. as a premise of protein-chitin nature of their skeletons. In that interpretation I take into account the fact that the protein-chitin complex is the only one of these substances playing an important role as a component of organic skeletons of invertebrates. Moreover, it is present in scyphothecae of scyphozoans and tubes of pogonophores.

Another question arising in TEM studies is the estimation of the degree of preservation of original ultrastructure by a given fossil object. The possibility of obliteration or deformation of original structures in the course of fossilization should be always taken into account. The difficulties in estimating the degree of advancement of these changes are generally increased by the fact that we do not know with which modern tissues the studied objects may be compared. A large part of the objects studied by me appear highly homogeneous. However, it is not excluded that the homogeneity is of secondary character. Studies on the state of preservation of periderm of the dendroid graptolite *Dictyonema wysoczkianum* KOZLOWSKI extracted from chalcedony from Wysoczki (URBANEK and MIERZEJEWSKI, in press), showed that this form is characterized by an entirely different cortex than *Dictyonema* sp., from a carbonate erratic boulder, previously studied by TOWE and URBANEK (1972). The specimen extracted from chalcedony displays obliteration of the original fibrous structure and, locally, advanced homogenization of the cortex. Interpretation of this phenomenon is additionally complicated by the fact that diagenetic changes did not affect the fusellum which is biochemically close to cortex (URBANEK 1976*b*).

The contribution of early- and late-diagenetic agents to changes in the original structure of the wall of Chitinozoa vesicles was recently discussed by WRONA (1980*a*).

SYSTEMATIC PART

SCYPHOZOA

Scyphozoans (Scyphozoa) are marine cnidarians, almost completely metagenetic. Within their life cycles one finds commonly free-living forms (scyphomedusae) as well as sedentary ones (scyphopolyps, scyphostomae). However, some species are devoid of free or sedentary stages in the life cycle. The distinct tetramerous symmetry, sometimes combined with incompleted octomerous or multiplicated octomerous symmetry, is a characteristic feature of both scyphomedusae and scyphopolyps (BEKLEMISHEV 1957). Living scyphozoans are not represented by numerous taxa in comparison with other cnidarians. NAUMOV (1961) was of opinion that there are only about 200 species in present seas.

A number of authors (KIDERLEN 1937, HARRINGTON and MOORE 1956, CHAPMAN 1966, WERNER 1966, 1967, 1973) assumed close phylogenetic affinities between Scyphozoa and Conulata, a group of enigmatic organisms known from the Cambrian to Triassic. They interpreted Recent polyps of the order Coronata, allocated in the genus *Stephanoscyphus* ALLMAN, as a link connecting the two groups. The structure of conulariids from the Baltic erratic boulders was studied in detail by KOZŁOWSKI (1968). He concluded that this group cannot be regarded as related with any hitherto described group of the animal world. KOZŁOWSKI's opinion has been recently discussed by BISCHOFF (1978), who placed conulariids definitely within the Scyphozoa.

The records of undoubted scyphozoans in the fossil state are relatively rare. Medusoids undoubtedly belonging to Scyphozoa are known from the Jurassic onwards, mainly from the specimens from Solnhofen (KIESLINGER 1939). Questionable specimens were reported from the Precambrian and Cambrian (see e.g. KIESLINGER 1939). KOZŁOWSKI (1967) described fossil thecae of scyphopolyps from Ordovician erratic boulders under the name *Byronia naumovi* KOZŁOWSKI. He also noted that the fossil previously described as *Byronia annulata* MATTHEW also represents thecae of scyphozoan polyps.

In zoological literature Coronata scyphopolyps are included under the generic name *Stephanoscyphus* ALLMAN, treated as an informal collective group. *Stephanoscyphus* scyphothecae have the form of high, reversed cones, attached to the basement with apex ending with basal disc. Scyphothecae vary from a few mm to some cm in height. Individual scyphopolyps often use scyphothecae of other individuals as a base, forming in this way apparent colonies. Moreover, some species such as *Stephanoscyphus allmani* KIRKPATRICK (fig. 2a) are capable of forming colonies proper.

In some species characteristic teeth of unknown functional significance may be noted at inner side of periderm. The presence or lack of these teeth, shape of scyphotheca and character of its ornamentation, and capability to form colonies are the basic criteria for identification of recent species (NAUMOV 1961). These features may be also easily used in paleontological studies. It is worth noting that the majority of *Stephanoscyphus* species were described on the basis of scyphothecae only.

The structure and chemical composition of scyphothecae are still poorly known. Using chitosan test, D. M. CHAPMAN (1966) discovered the presence of chitin in scyphothecae of *Stephanoscyphus* sp. However, it should be remembered that JEUNIAUX (1971) showed this test to be ambiguous. In studies on microstructure of periderm of *S.* cf *simplex*. KIRKPATRICK, D. M. CHAPMAN (1966) found it to be two-layered, with inner layer 2.5 times thicker than the outer. These observations were subsequently confirmed by D. M. CHAPMAN and WERNER (1972). The latter studies showed that the thick inner layer of periderm is secreted by calyx and stalk of scyphopolyp and the thin inner layer by so-called "junctional secretory band". The inner layer is always smooth and the outer — has the characteristic sculpture. Secretion of the two layers is independent in character. D. M. CHAPMAN and WERNER (1972) also studied ultrastructure of scyphotheca periderm with the use of TEM. They published only a single electron micrograph, not indicating which periderm layer it represents. The ultrastructure they described as "thin (12 μm) lamellae separated by about the same distance but bridged at 8 μm intervals by 14 μm wide processes whose shape was not determined" (D. M. CHAPMAN and WERNER 1972: 416). This makes the possibility to compare ultrastructures of modern scyphothecae and those of fossil *Byronia naumovi* KOZŁOWSKI and *B. robusta* (KOZŁOWSKI), studied by me, rather limited.

Dithecoidea — primitive graptolites or colonial scyphopolyps?

OBUT (1964) ascribed a specific role in early phylogenetic development of graptolites to the graptolite order Dithecoidea, proposed by him. The order was characterized as comprising graptolites with bushy to tree-like colonies budding in diads, and dimorphism of thecae (bithecae missing). According to him, Dithecoidea were the stem group for all the remaining graptolites [2], giving rise to the most primitive Dendroidea of the family Dendrograptidae in the Late Cambrian. The transition from Dithecoidea to Dendroidea was, in this concept, connected with differentiation of thecae, leading to the origin of thecal trimorphism and budding in triads. Within the order Dithecoidea, OBUT (1964, 1974) differentiated four families (Dithecodendridae, Siberiograptidae, Chaunograptidae and Bulmanidendridae), to which he assigned 7 genera and 6 other with reservation. It is worth noting that all the genera, except for *Mastigograptus* RUEDEMANN, are known on the basis of imprints or carbonized remains of flattened rhabdosomes preserved at rock surface.

The above hypothesis concerning the origin of the Dendroidea and systematic position of Dithecoidea did not get support from graptolite workers. It was treated with marked scepticism by BULMAN (1970) who treated the genera placed in Dithecoidea by OBUT as Dendroidea, Tuboidea, Crustoidea, Stolonoidea as taxonomically uncertain. He also doubted whether all of them represent graptolites. QUILTY (1971) described genera assigned to Dithecoidea by OBUT (1964) from the Cambrian of Tasmania, treating them as either Hydroidea or graptolites of the order Dendroidea. URBANEK and TOWE (1974) and ANDRES (1980) treated the genus *Mastigograptus* RUEDEMANN as graptolite *incertae sedis*. A. URBANEK (1975, oral inf.) and R. KOZŁOWSKI (1975, oral inf.) held that it is possible that Dithecoidea (except for the genus *Mastigograptus*) do not belong to graptolites at all.

SDZUY (1974) described some fossils from the Middle Cambrian of Spain which he treated as dithecoid graptolites. He proposed seven new species allocated in three new genera and described genus *Archaeolafoea* CHAPMAN, previously known from Australia only. The affiliation of these forms with graptolites was assumed mainly with reference to alleged finding of traces of fuselli on some of them. The affiliation was highly questionable for both R. KOZŁOWSKI and A. URBANEK (oral inf., 1974). In looking through Recent coelenterate collections in the Institute of Zoology of the Soviet Academy of Sciences, Leningrad, I noted some colonial scyphopolyps strikingly similar to the alleged graptolites of SDZUY (1974). The forms, when found in Early Paleozoic deposits would be undoubtedly interpreted as corresponding to dithecoid graptolites of OBUT and SDZUY in morphology. Figure 2 shows the striking similarity of "graptolite" colony of SDZUY (1974) and that of Recent scyphopolyps of the order Coronatae. Moreover, the alleged fuselli of the Spanish Dithecoidea may be easily compared with annulation of scyphopolyp periderm (fig. 3).

OBUT (1964) has drawn too far-reaching conclusions with respect to possibilities of interpretation of his material from the Cambrian of Siberia and those described by some other authors. The major drawback of these materials is connected with the fact that the affiliation of these forms (except for those of the genus *Mastigograptus* RUEDEMANN which, actually, do not match the concept of Dithecoidea) with graptolites may be seriously questioned. Even if the fossils assigned to Dithecoidea were proved to be graptolites, their preservation precludes tracing the course of stolons and even finding their presence. The only solution to verify OBUT's (1964) hypothesis is to study branching details of the stolon system. The course of stolons in the rhabdosome of *Chaunograptus sphaericola* (ÖPIK) as shown by OBUT (1964, fig. 36) should not be treated as observation but rather hypothesis (see also KOZŁOWSKI 1962). The state of

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[2] Subsequently, OBUT (1974) proposed another order of graptolites, Archaeodendrida, the morphology of which is similarly poorly known as in the case of Dithecoidea.

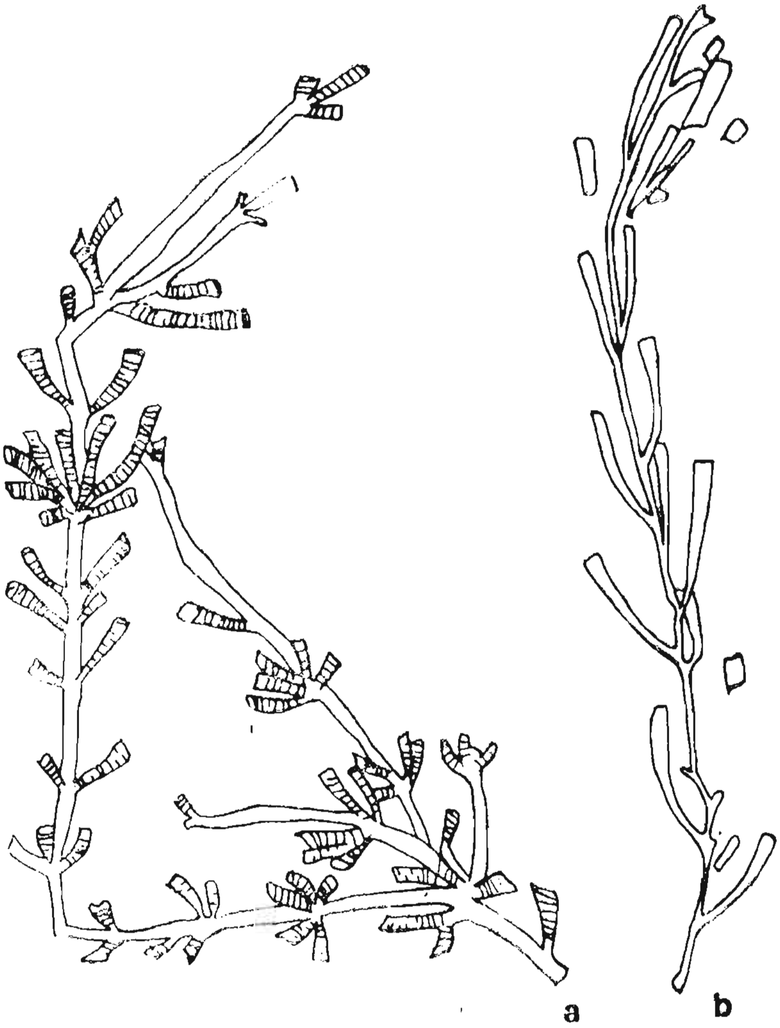

Fig. 2.
Comparison of the colony morphology of *Stephanoscyphus allmani* Kirkpatrick, Recent (*a*) and *Tarnagraptus palma* Sdzuy, Middle Cambrian (*b*). After Leloup in Naumov and Sdzuy.

preservation of Soviet specimens interpreted as dithecoid graptolites is best shown by the fact that Obut (1974) found the alleged traces of fuselli only in those of the species *Bulmanidendrum magnificum*.

Obut (1964) and Sdzuy (1974) accept the general shape of the colony as one of features characterizing Dithecoidea, so I would like to draw attention to Bulman's (1970) print that a number of graptolites traditionally regarded as representatives of the order Dendroidea may actually belong to the order Tuboidea. Dendroid and tuboid graptolites form very similar colonies so that, when flattened and carbonized in the course of fossilization, the nature of budding becomes unclear and, therefore, unequivocal identification is often impossible.

The majority of dendroids described on the basis of such material do not represent actual taxa but rather "form-genera" (Bulman 1970). Practically, the only criterion used by Obut (1964, 1974) to differentiate Dithecoidea from other graptolites is the general shape of the colony or rather the presence of one type of thecae as the presence of stolothecae was not proved. If representatives of pterobranchs of the genus *Rhabdopeluroides* Kozłowski or hydroids *Epallohydra* Kozłowski or *Desmohydra* Kozłowski were preserved flattened and carbonized among remains of other colonial organisms, the use of this criterion would result in their allocation in Dithecoidea "graptolites". It is not excluded that such assignation has already taken place. The genus *Chaunograptus* Ruedemann, interpreted as hydroid by Ruedemann (1947) and dithecoid graptolite by Obut (1964), is most probably congeneric with the above mentioned hydroids *Epallohydra* and *Desmohydra* (see p. 162).

Similarly as some of the above mentioned authors, I consider Dithecoidea as an artificial group, comprising organisms of various, taxonomically distant groups. I am inclined to regard all forms described as graptolites from the Cambrian of Spain by Sdzuy (1974) as colonial scyphopolyps of the order Coronata. My hypothesis is undoubtedly much easier to accept than that of Sdzuy (1974) as it does not require any additional assumptions. Such additional assumption in Sdzuy's conception is the alleged existence of primitive graptolites, budding in diads and devoid of bithecae, unsubstantiated by any observations. Moreover, the presence of scyphopolyps Coronata in the Cambrian fully agrees with their modern interpretations as the most primitive polyps of coelenterates (Werner 1973).

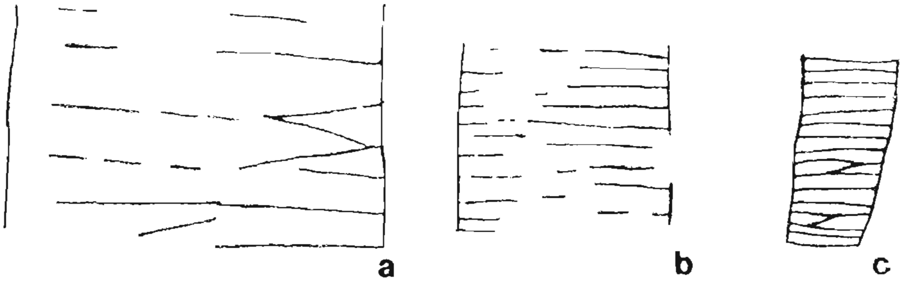

Fig. 3.

Comparison of the periderm annulation in the Dithecoidea *(a—b)* and in the Coronata scyphopolyp *(c)*: *a Tarnagraptus thomasi* Sdzuy, *b Sotograptus flexilis* Sdzuy, *c Stephanoscyphus* sp; *a* and *b* after Sdzuy.

The reinterpretation of the Sdzuy (1974) "graptolites" as colonial scyphopolyps has far going nomenclatoric consequences. Differences between individual taxa of these "graptolites" are not significant when they are treated as scyphopolyps and, theoretically, they all may be placed in the genus *Stephanoscyphus* Allman. Taxonomy of recent Scyphozoa polyps from the Order Coronata was not long ago solely based on the structure of skeleton, since the features connected with metageny were not used for taxonomical purposes prior to Werner (1971). As I mention above (p. 141), *Stephanoscyphus*, a formal genus, is used as a collective name in zoological practice. However, *Stephanoscyphus mirabilis* Allman, 1874, the type species, appears to be the junior synonym of *Nausithoë punctata* (Kölliker, 1853), so that the name *Stephanoscyphus* lost its validity as it appeared to be junior synonym of the name *Nausithoë*. This was not noted by zoologists who, instead of formal introduction of collective group name for sessile generation of Coronata, traditionally use the invalid name *Stephanoscyphus* Allman.

In zoological practice, the name *Stephanoscyphus* is used for both colonial and individual forms. The species at present described under that generic name will undoubtedly be allocated to a few separate families in the future (Naumov 1961). In this respect, zoologists link the future prospects with the existing possibilities to reconstruct metageny of these forms. The lack of such prospects for those studying fossil Scyphozoa must have some effect on the taxonomic approach of paleontologists, as there is no hope of classifying fossil scyphopolyps at the family or generic level in the biological sense. In this work I use the generic name *Byronia* Matthew for all the solitary species of scyphopolyps as well as those forming encrusting colonies but I am treating it as a name for informal collective group. It is obvious that for me each of the species of *Byronia* listed below belongs in a separate genus but there is no way of verifying that assumption. That is why I consider as justified, from the point of view of both taxonomy and usability of classification, a description of all the fossil solitary and encrusting-colony-forming scyphopolyps under the name *Byronia* MATTHEW. In turn, dendroidal forms such as "graptolites" of SDZUY (1974) should be allocated in the genus *Archaeolafoea* CHAPMAN, and also treated as an informal collective group. When there appears a need to create additional ranks in this classifications, it would be the best solution to use other informal taxonomical units such as species groups or sections. This would prevent formation of a break between the taxonomy of modern forms and that of fossil ones.

One of the genera assigned to the Dithecoidea by OBUT (1964), *Mastigograptus* RUEDEMANN, seems to require a separate discussion. This cosmopolitan genus comprises a significant number of species, mainly Ordovician ones, reported from the North and South Americas, North Africa, Europe and Australia. This is the only group form of Dithecoidea, whose affiliation with graptolites appears unquestionable. On the basis of material from Ordovician erratic boulders, ANDRES (1961) evidenced a distinct thecal trimorphism, i.e. differentiation of thecae into auto-, bi- and stolothecae, in *Mastigograptus.* When this is the case, the treatment of *Mastigograptus* as a dithecoid graptolite (OBUT 1964) appears completely unsubstantiated. However, it should be noted that OBUT and SOBOLEVSKAYA (1967) strongly question the affiliation of ANDRES' specimens with the genus *Mastigograptus.*

Summing up, I would like to note that the so called dithecoid graptolites may be interpreted as proposed on the basis of superficial similarities to organic fossils representing distantly related systematic groups. In the Dithecoidea were placed colonial scyphopolyps, encrusting hydroids (Chaunograptidae, see p. 162), graptolites with well-developed thecal trimorphism (*Mastigograptus*) and various incertae sedis organisms (e.g. *Dithecodendrum* OBUT, *Siberiodendrum* OBUT, *Siberiograptus* OBUT), some of which may represent green algae.

DESCRIPTION

Type **Cnidaria** HATSCHEK, 1888
Class **Scyphozoa** GÖTTE, 1887
Subclass **Scyphomedusae** LANKESTER, 1881
Order? **Coronata** Maas, 1903
Incertae familiae
Genus *Byronia* MATTHEW, 1899

Type species: *Byronia annulata* MATTHEW, 1899

Emended diagnosis. — Scyphothecae long, circular to suboval in cross-section, gradually widening in distal direction. Scyphorhiza in the form of basal disc; colonial forms also with stolons. Periderm organic, sculptured with transversal rings, longitudinal striated or smooth. Solitary or encrusting colonial forms.

Species assigned. — *Byronia annulata* MATTHEW, 1899, *B. naumovi* KOZŁOWSKI, 1967 and *B. robusta* (KOZŁOWSKI, 1967).

Remarks. — Because of insurmountable difficulties in the taxonomy of fossil scyphopolyps, I treat this genus as an informal collective group (see p. 144).

Occurrence. — Upper Cambrian of Canada (MATTHEW 1899) and Ordovician of Poland (KOZŁOWSKI 1967).

Byronia naumovi KOZŁOWSKI, 1967

(pl. 19: 1; fig. 4)

1967. *Byronia naumovi* KOZŁOWSKI; KOZŁOWSKI 107, figs. 2—3.

Diagnosis (after KOZŁOWSKI 1967: 107, orig. French). — Scyphothecae conical, circular in cross-section, more or less bent, with basal discs in proximal part; surface smooth, indistinctly transversally striated with growth lamellae in distal part.

Material. — Type series (19 scyphothecae varying in preservation and various scyphotheca fragments from boulders no. ZPAL 0.121, ZPAL 0.185, ZPAL 0.331 and ZPAL 0.390).

Description. — Scyphothecae of this species were discussed in detail by Kozłowski (1967), so only some supplementary remarks are given here.

Distal parts of scyphothecae sometimes display fairly distinct annular sculpture, resembling that of *B. annulata* and modern species of "*Stephanoscyphus*". Periderm variable in morphology connected with both of annular structure and differences in its gloss. Some scyphothecae are smooth and glossy, others — rough and matt, with intermediates. Material from boulder 0.331 displays scyphothecae with extremely thin discs (Kozłowski 1967, fig. 2b, c) and those with discs with diameter markedly smaller than thickness (fig. 4).

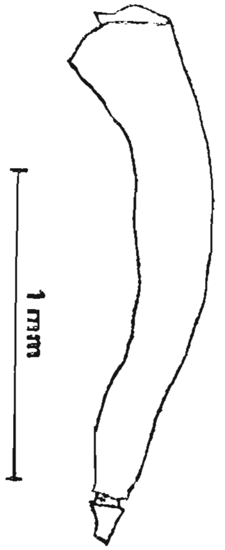

Fig. 4.
Byronia naumovi Kozłowski (ZPAL Sc. I/1); boulder no. ZPAL 0.331, Mochty, Ordovician.

Ultrastructure. — TEM shows periderm to be fully homogeneous (pl. 19: 1).

Remarks. — Kozłowski (1967) reported boulder 0.121 from Wyszogród (Middle Ordovician) as the type locality and type horizon of this species. However, these data are invalid as the holotype was derived from boulder 0.390 from Zegrze and its age may be only generally referred to the Ordovician, as the type locality and type horizon.

The presence of weak annular sculpture on the scyphothecae of some specimens of *B. naumovi* brings this species to a position morphologically intermediate between *B. annulata* and *B. robusta*.

Occurrence. — Ordovician erratic boulders in Poland.

Byronia robusta (Kozłowski, 1967)

(pl. 19: 2—7; fig. 5)

1967. *Ascosyrinx robustus* Kozłowski; Kozłowski 114, fig. 6.

Emended diagnosis. — Scyphothecae varying in height, distally widening, circular in cross-section, unsculptured. Scyphorhiza strongly developed, usually in the form of flat-convex disc. Stolons present in colonial forms.

Material. — Type series comprising 9 scyphothecae and some fragments from boulder ZPAL 0.424 and 7 scyphothecae from boulder MZ/39.

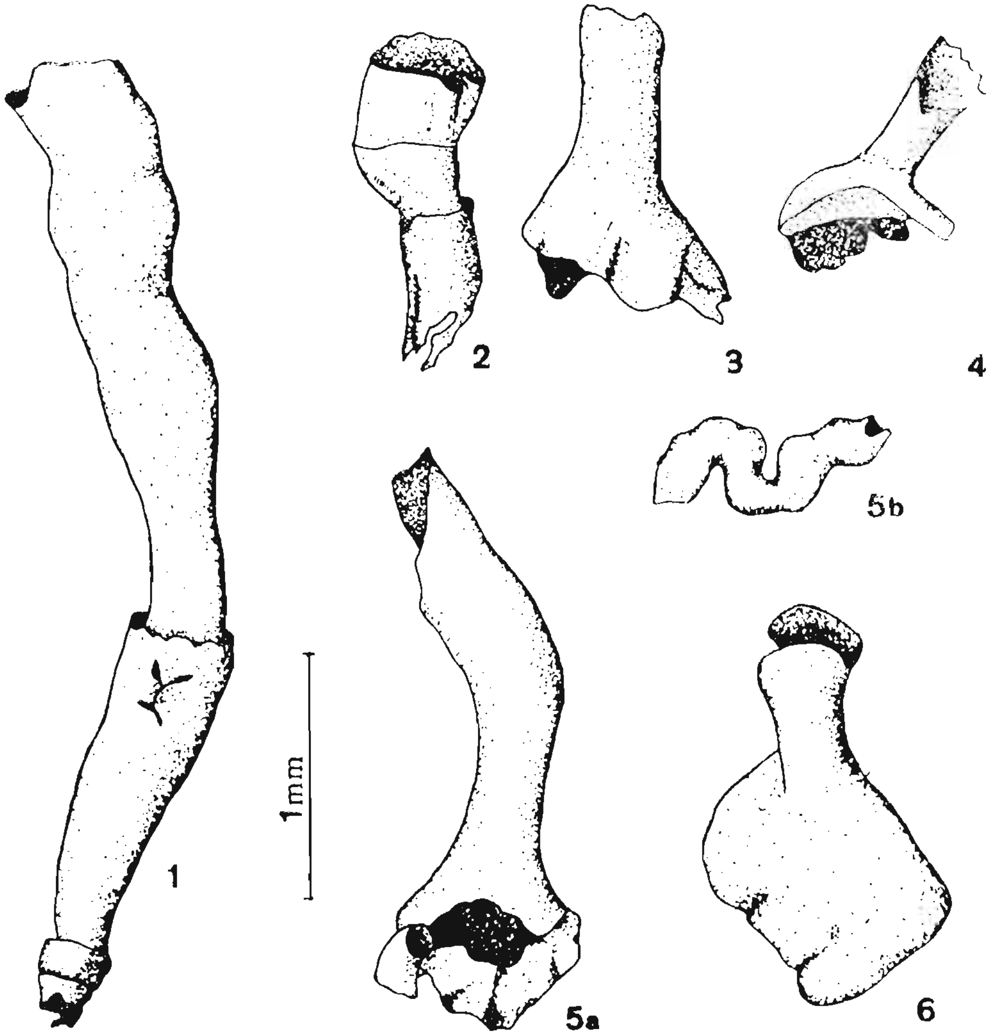

Fig. 5.
Byronia robusta Kozłowski (ZPAL Sc. I/2); boulder no. MZ/39, Ustka, Ordovician or Silurian. *1—2* distal parts of scyphothecae, *3—4*, *5* fragment of the scyphotheca with the stolon remnant, *6* proximal parts of scyphothecae.

Revised description. — Scyphotheca circular in cross-section, strongly widening in distal direction. On the basis of the largest specimen (fig. 5: 1) it may be assumed that scyphotheca together with scyphorhiza were over 5 mm high. Scyphotheca morphology suggests that scyphopolyp, similar to modern ones, was repeatedly subjected to regeneration related to budding of scyphomeduses (fig. 5: 1—2 here, see also Kozłowski 1967, fig. 6b—d). Scyphothecae ranging from 0.20 to 0.52 mm in diameter.

Scyphorhiza strongly developed in form of flat-convex disc and stolons. Basal disc varying from almost hemispherical, irregular to subquadrangular in outline and 0.72 mm to 1.07 mm in diameter. Scyphotheca branching off from disc in its central or peripheral parts. Stolons, about 15 μm in diameter, branching sporadically from basal discs (fig. 5: 5).

The periderm thickness decreases towards distal part of scyphotheca. Periderm unsculptured, with mat and somewhat rough surface.

Ultrastructure. — The SEM studies showed lamellar structure of periderm but they failed to give more detailed data on the structure (pl. 19: 6). Details of ultrastructure appeared easier to trace in the TEM studies on ultrathin sections (pl. 19: 2—5, 7). Lamellae found in periderm fragments range from 30 to 35 in number in periderm the total thickness of which equals 10—

15 μm (pl. 19: 4). Individual lamellae are built of electron-dense, arcuately bent fibres embedded in a matrix of low electron density (pl. 19: 7). The fibre pattern forms a specific image known in the literature as "parabolic pattern" or "Bouligand pattern". Depending on the angle at which periderm is cut, the ultrastructural image varies (see pl. 19: 3, 7). Fibres vary in thickness from 250 to 370 Å, and lamellae — from 0.15 to 1.10 μm.

Some fragments display fibres slightly denser that the basic matter (pl. 19: 2). A sudden pulse with a strong beam of electrons of such preparations usually results in a marked increase of contrast (pl. 19: 5). This may be explained by breakage of the basic matter and, possibly, shrinkage of fibres (see also p. 140, pl. 30: 5—6).

The ultrastructure recorded appears identical with some images of chitin-protein complexes (see p. 140). Taking into account the reservations made on p. 140, I state that the results of electron microscope studies suggest chitin character of *B. robusta* periderm.

Remarks. — *Byronia robusta* (KOZLOWSKI, 1967) was originally described under the generic name *Ascosyrinx* KOZLOWSKI (KOZLOWSKI 1967) and treated as an organism with enigmatic systematic position. This was connected with the fact that the type series of this species was comprising incomplete specimens with missing distal parts of scyphothecae which made them somewhat similar to *A. tenuis* KOZLOWSKI, 1967.

Byronia robusta (KOZLOWSKI) differs from *B. naumovi* KOZLOWSKI in stronger development of scyphorhiza. It is not clear whether or not the differences in ultrastructure of the scyphothecae of the two species are of primary nature and what is their eventual taxonomic value (see also p. 141).

Occurrence. — Erratic boulders of Ordovician age in the area of Poland.

Byronia sp. A

Material. — A single specimen from the borehole Mielnik IG 1, depth 1118—1124 m,? Upper Ordovician.

Description. — A fragment of flattened scyphotheca 6 mm long. Basal disc missing. Periderm surface black, smooth and glossy.

Remarks. — The specimen has been identified by KOZLOWSKI and labelled in his own handwriting as *Byronia ordoviciana* n. sp., similarly as the type series of *Byronia naumovi* KOZLOWSKI. Undoubtedly, KOZLOWSKI had been studying this specimen along with the *B. naumovi* type series and the decision to change the name *B. ordoviciana* to that of *B. naumovi* had been taken after labelling all the specimens. The resasons why that specimen was finally left aside the *B. naumovi* type series remain unknown. In the light of the above revision of *B. robusta* (KOZLOWSKI), identification of a single specimen of scyphotheca without basal disc at the specific level is impossible.

HYDROZOA

The scope of this study comprises only those of early Paleozoic hydrozoans which were capable of building organic perisarc, i.e. Hydroida (as Siphonophorida) are hitherto unknown from Poland. They were described from the Cambrian (F. CHAPMAN 1919, F. CHAPMAN and SKEATS 1919, F. CHAPMAN and THOMAS 1936, RUEDEMANN 1947), Ordovician and Silurian (EISENACK 1932, 1934, 1968*b*, 1970*a*, 1976, KOZLOWSKI 1959*a*, SKEVINGTON 1965*b*, BEHR, JORDAN and MALCOLM 1966, LAUFELD 1979*a*, Devonian (RUEDEMANN 1947, DECKER 1948, 1952), and Carboniferous (NITECKI and RICHARDSON 1972, SCHRAM and NITECKI 1975). Still less has been said about Mesozoic Hydroida with organic perisarc. Single forms were described by Eisenack (1935) and Voigt (1973) and some findings were reported by Kozłowski (1956*a*), Kulicki (1969), Gochi (1970), Kulicki and Szaniawski (1972).

From all the works on fossil Hydroida, a special attention should be paid to that of Kozłowski (1959*a*). This work, the largest of the above, was based on material extracted from Ordovician and possibly Silurian erratic boulders found in central and northern Poland. Kozłowski described there 22 species (including 19 new ones), assigned to 14 genera (including 11 newly proposed). He also described several specimens as gonothecae or hydrorhizae of Hydroida. However, the allocation of the majority of these forms in Hydroida appears questionable as the microfossils described by him include stolons and cysts of sterile buds of pterobranchs (Pterobranchia) and various problematica the taxonomic position of which is very difficult to decipher. A number of forms hitherto regarded as Hydroida are here discussed in various places, so it becomes necessary to give their list along with some short comments and references. These are the following genera:

Calyxhydra Kozłowski, 1959. Hydroida? Rhabdopleurida? — p. 168
Chitinodendron Eisenack, 1937. Foraminifera? — p. 196
Cylindrotheca Eisenack, 1934. Rhabdopleurida. *Nomen dubium*. p. 183
Desmohydra Kozłowski, 1959. Hydroida, Chaunograptidae, junior synonym of the name *Chaunograptus* Hall, 1882 — p. 163
Diplohydra Kozłowski, 1959. *Problematicum* — p. 197
Epallohydra Kozłowski, 1959. Hydroida, Chaunograptidae, junior synonym of the name *Chaunograptus* Hall, 1882, p. 163
Flexihydra Kozłowski, 1959. Hydroida — p. 168
Kystodendron Kozłowski, 1959. Rhabdopleurida — p. 182
Lagenohydra Kozłowski, 1959. Pterobranchia? — p. 193
Palaeotuba Eisenack, 1934. Hydroida, Rhabdohydridae — p. 160
Phragmohydra Kozłowski, 1959. Problematicum — p. 199
Rhabdohydra Kozłowski, 1959. Hydroida, Rhabdohydridae — p. 152
Trimerohydra Kozłowski, 1959. Graptolithina, Acanthograptidae; junior synonym of the name *Koremagraptus* Bulman, 1927 (see Kozłowski 1963*a*).
Xenohydra Kozłowski, 1959. Problematicum — p. 199

The taxonomy of Ordovician and Silurian hydroids is troublesome. In modern forms, taxonomy is carried out with reference to such features as structure of body of polyps and medusae, the nature of metagenesis, arrangement of colony, and details of perisarc structure (Naumov 1960). The material available for studies on early Paleozoic Hydroida consists, as a rule, of strongly crushed fragments of perisarc which makes impossible analysis of the majority of the above features. The difficulties in analysing the material are best shown by the fact that even differentiation of Athecata and Thecaphora may be highly debatable. It follows that the presence or lack of thecae is not fully reliable as a criterion for differentiation of the suborders. There is a modern hydroid of the suborder Thecaphora which is devoid of both hydrothecae and gonothecae — *Melicertum campanula* (Fabricius) of the family Campanulinidae. Naumov (1960) interpretes that lack as secondary, drawing attention to a trend to reduction of thecae in another genus of the same family (*Campanopsis*). The two forms may be assigned to Thecaphora essentially thanks to the knowledge of their medusae only.

In the light of the above data it is clear that taxonomical decisions fossil Hydroida workers are inevitably highly arbitrary in character.

SOME REMARKS ON THE HYDROIDA SKELETON

The ability to develop external skeleton by sessile stages became factor of decisive significance for evolutionary success of the Hydroida and the direction of their phylogenetic development. The skeleton may be either organic (Limnomedusae, Athecata, Thecaphora) or mineral (Hydrocorallia) but always of ectodermal origin. So, the long-held and widely accepted idea of the existence of mesogleal skeleton in Solandendriidae appeared erroneous (VERVOORT 1966). The organic skeleton of the Hydroida originates due to activity of specialised ectodermal cells, randomly distributed among epitheliomuscular ones (LENDENFELD 1883). They secret a matter called periderm or cuticle, which surrounds the coenosarc and, to greatest or smaller degree, the polyps. The overwhelming majority of colonial hydroids are characterized by elastic, translucent or yellow- to brown-coloured or, sometimes, colourless periderm. With the passage of time, the periderm may become black and opaque. The mechanism of this phenomenon remains unknown but changes of this type may be due to increase in degree of sclerotization or secretion of granular bodies markedly enriched in iron as in the case relic periderm of scyphistome theca (D. M. CHAPMAN 1968).

The chitinous nature of the Hydroida (actually Thecapora) periderm was experimentally shown by HYMAN (1940). Her results were further supported by results of chitinosan tests of RICHARDS (1951). The presence of chitin was also suggested by x-ray studies (RUDALL 1955). Accurate data given by JEUNIAUX (1963, 1965, 1971) show that chitin content in the periderm of some Hydroida is varying from 3.2 to 30.3%. Chitin occurs in the periderm in association with some unidentified albumens, sometimes hardened with tannin acid (RUDALL 1955, JEUNIAUX 1971).

Typical periderm of the Hydroida, characteristic of Thecaphora and some Athecata and Limnomedusae, originated in phylogeny by hardening of gelatinous sheaths of primitive forms (REES 1957). The sheaths were presumably very similar to the perisarc of some modern Corymorpinae, *Tricyclusa* and some species of *Myriothela*. The latter hydroids produce perisarc in the form of irregular, gelatinous sheaths mainly consisting of mucopolysaccharids and an insignificant admixture of chitin (VERVOORT 1966 and written note on unpublished results). According to VERVOORT (1966), further evolution was connected with increase in share of chitin at the expense of mucopolysaccharids, and sclerotization involving secretion of proteins. REES (1957) suggested the possibility of independent evolution of perisarc in some hydroid groups, treating various Athecata sheaths as some kind of "natural experiments" aimed at producing a rigid skeleton.

The question of development of perisarc in onto -and phylogeny appears underestimated by REES (1957) and VERVOORT (1966). This is suggested by some data on secretion ectodermal cells in Hydrozoa, mainly obtained with the use of electron microscopy techniques. MACKIE (1960) found both typical thick periderm developed around pneumatophore and a very thin cuticle formed by unspecialized ectodermal cells in *Physalia* (Siphonophora). Similar cuticle was reported in *Hydra* by LENTZ and BARNATT (1965) and LENTZ (1966). In the latter genus, the cuticle covers a typical "unit membrane" and it consists of a thin (0.1 μm) lower layer built of homogeneous matter with high electron density, and an upper layer (0.5 μm thick), built of granular or fibrillar matter. D. M. CHAPMAN (1969) found cuticle of that type in *Clava* (Athecata). In that genus it is also two-layered but ultrastructurally different. Lower layer is thin (0.3 μm thick), fairly loose in structure and penetrated by microvilli at its whole thickness, and the upper — 0.8 μm thick, built of tightly packed indistinct fibrils, set parallel to cell surface.

D. M. CHAPMAN (1969) proposed the following classification of Cnidaria cuticle:

I. Relatively thin cuticle
    a) with microvilli,
    b) without microvilli.
II. Relatively thick, chitinous cuticle
    a) with desmocytes,
    b) without desmocytes.

Studies of the structure of periderm of modern forms were hitherto very random in character. This is especially the case of those of BROCH (1929), MANTON (1941) and NAUMOV (1960).

The differences in chemical composition should be reflected by the micro- and ultrastructure of the periderm but no data on that subject is found in the literature.

My studies on the ultrastructure of the Hydroida periderm, initiated some years ago (MIERZEJEWSKI 1974), were aimed at checking whether or not they supply some important data for taxonomy and far the evolution of this group of Cnidaria. The studies covered two modern species — *Eudendrium capillare* ADLER, 1857 (Athecata, Eudendriidae) and *Sertularia argentea* ELL. et SOLL, 1786 (Thecaphora, Sertulariidae) — and six fossil forms which were at that time interpreted as representatives of the Hydroida, in accordance with the point of view of KOZLOWSKI (1959*a*). The results obtained showed ultrastructural studies on the periderm completely useless for solving taxonomical problems. Ultrastructure of periderm in modern representative of Athecata appeared equally homogeneous (pl. 34: 8) as in modern representative of Thecaphora (pl. 24: 5), not differing in a significant way from that of stolons of Ordovician graptolites or some pterobranchs.

DESCRIPTIONS

Class **Hydrozoa** OWEN, 1843

Order **Hydroida** JOHNSTON, 1836

Suborder **Athecata** HINCKS, 1868

Family **Rhabdohydridae** fam. n.

Type genus: *Rhabdohydra* Kozlowski, 1959

Diagnosis. — Hydroida forming monopodial colonies with coenosarc growth zones. Colony with thick, monosiphonal stem. Sheaths of polyp stalks long and narrow. Polyps distributed regularly or randomly within colony.

Genera assigned. — *Rhabdohydra* KOZLOWSKI, 1959; *Palaeotuba* EISENACK, 1934.

Remarks. — The systematic position of the new family in the order Hydroida is rather unclear. Although KOZLOWSKI (1959*a*) did not place the suborder affiliation of the genus *Rhabdohydra*, he used the term "theca" in description of that form. It should be also noted that SKEVINGTON (1965*b*) assumed the presence of gonothecae in the periderm of that genus. The use of the terms "theca" and "gonotheca" unequivocally indicates that these authors interpreted Rhabdohydra as a representative of the suborder Thecaphora. My detailed studies on the morphology of the perisarc of *Rhabdohydra tridens*, based on very rich material, showed that the so-called thecae actually represent sheaths of the polyp stalks and gonothecae — small fragments of lateral branchings of colonial stem. It follows that the morphology of polyp perisarc argues against allocation of *Rhabdohydra* in this suborder. On the other hand, monopodial colonies with coenosarc growth zones, typical of that genus, are at present found only in the Thecaphora. No equivalents of the shape and organization of colony of *Rhabdohydra* are known in modern Hydrozoa.

Rhabdohydridae fam. n. is here assigned to the Athecata, taking into account the lack of thecae and high organization of colony. The latter feature speaks against its eventual assignation to the suborder Limnomedusae. However, it cannot be excluded that Rhabdohydridae fam. n. may represent an extinct, hitherto unknown suborder of Hydroida. Data on the anatomy of polyps and the nature of metagenesis are, unfortunately, missing. So any further considerations on that subject would be merely speculative.

Genus *Rhabdohydra* KOZŁOWSKI, 1959

Type species: *Rhabdohydra tridens* KOZŁOWSKI, 1959

Emend. diagnosis. — Polyps developing on common base[3] or, less frequently, directly at colonial stem and hydrorhiza stolons. Stem rigid, monosiphonal, usually straight, sometimes branching. Hydrorhiza filamentous.

Species assigned. — *Rhabdohydra tridens* KOZŁOWSKI, 1959, *Rhabdohydra multiplex* sp. n.

Remarks. — The reconstruction of the astogenesis and studies on the taxonomy of this genus were hitherto markedly impeded by unsatisfactory preservation of hydrosomes and the unknown range of variability of the type species. The situation was made worse by the fact that the use of material from various erratic boulders and drillings in reconstructions of hydrosomes would be inappropriate. It appears impossible to exclude, *a priori*, the possibility that the recorded variability in the morphology of branches coming from different localities actually reflects differentiation of the genus in a few species of different age. Wide stratigraphic range of that genus support these apprehensions. That is why I decided to redescribe the type species and to establish its variability range mainly on the basis of material coming from a single erratic boulder. This seemed to be the only way to be assured of the isochronous character of the material. The material also had to be rich enough for sufficiently complete evaluation of inter-colonial variability in this species. It was also possible that the sample comprised remains of more than one species of *Rhabdohydra* but that risk was unavoidable. Despite of the above reservations, I am sure that the reconstruction of *R. tridens* colony and the evaluation of inter-colonial variability has been carried out on conspecific material. Single fragments of branches derived in the course of my studies from different localities often differ so much from one another that I was initially inclined to ascribe a specific rank to the differences. The study on the *R. tridens* colony, carried out in the way described above, made it possible to state that the differences fall within the limits of intra-colonial variability of this species. Only in one single case were they so high that it was necessary to propose a new species.

Rhabdohydra colonies differ markedly in morphology from those of all hitherto described modern and fossil coelenterates. They appear strikingly similar to rhabdosomes of the graptolite *Mastigograptus* RUEDEMANN, described from an erratic boulder by ANDRES (1961), in the shape and distribution of colonies within them. The similarity should be interpreted as convergence only.

Occurrence. — Ordovician in the Baltic Region.

Rhabdohydra tridens KOZŁOWSKI, 1959

(pl. 20, pl. 21: 1—6, pl. 22, figs. 6—10)

1959*a*. *Rhabdohydra tridens* KOZŁOWSKI; KOZŁOWSKI: 235, fig. 14 A—D, G—H.
1959*a*. Fragment d'hydrorhize; KOZŁOWSKI: 261, fig. 31C.
1965*b*. *Rhabdohydra tridens* KOZŁOWSKI; SKEVINGTON: 156, figs. 6—8.
1976. *Rhabdohydra tridens* KOZŁOWSKI; EISENACK: 185, pl. 1: 6.

New diagnosis. — Polyps mainly grouped at common bases, as a rule in threes and fours.

Material. — Some hundreds of fragments of stems and about 30 fragments of hydrorhizae from erratic boulders:
ZPAL 0.25, ZPAL 0.26, ZPAL 0.29, ZPAL 0.31, ZPAL 0.52, ZPAL 0.66, ZPAL 0.94, ZPAL 0.167, ZPAL 0.168, ZPAL 0.170, ZPAL 0.179, ZPAL 0.181, ZPAL 0.182, ZPAL 0.322, ZPAL 0.334,

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[3] The name "common base" is here given to short projections of colonial stem on which polyps were developing in *Rhabdohydra* (see pl. 21: 3—4).

ZPAL 0.366, ZPAL 0.389, ZPAL 0.392, ZPAL 0.498, ZPAL 0.499, ZPAL 0,501, ZPAL 0.555, ZPAL 0.642, MZ/14, MZ/18, MZ/151 and boreholes Krzyże 4 (depth 471—473 m) and Biała Podlaska 2 (depth 680—687 m).

Description. — Type material (holotype and two paratypes) of *Rhabdohydra tridens* was studied without much precision by KOZLOWSKI (1959*a*). Consequently, the description of this species, based on its morphology, is inaccurate with reference to such features as distribution of nodes on stems and structure of the nodes, i.e. common bases. This made it necessary to redescribe the type material here.

The holotype (see KOZLOWSKI 1959*a*, fig. 14A) is a fragment of a straight stem 2.54 mm long. The stem displays 4 common bases, diverging from it at an angle of about 45°. Each of the lower three common bases displays 3 sheaths of hydranth stalks, and the clearly damaged fourth only a single one. All the common bases are arranged at one side of the stem but this is only due to its twisting and flattening after death of the colony. The reconstruction of original shape of the stem shows common bases to be situated on its different sides, so the above one-sided distribution is an artefact.

The type locality and horizon of this species remain unknown as KOZLOWSKI (1959*a*) did not give any data on that subject. The original label of the specimen also fails to solve this question. It is only certain that the holotype has been extracted from an erratic boulder found in Poland. There is no reason to assume that the holotype comes from the same boulder as the paratypes (i.e. boulder no. ZPAL 0.182) as KOZLOWSKI (1959*a*) often placed specimens coming from different boulders in a single type series. Cotypes and paratypes of *Cylindrotheca subtilis* KOZLOWSKI may serve as an example here.

The two paratypes of *Rh. tridens* completely fail to match the diagnosis of that species and they differ markedly from the holotype. KOZLOWSKI (1959*a*) neither figured nor described these specimens, giving only the number and spacing of nodes. The specimen treated as the paratype I is a fragment of curved stem 6.1 mm long and about 67 μm wide (pl. 20: 3). It displays 7 nodes, none of which is situated on common bases and only three with single sheaths of polyp stalk. The remaining nodes are very strongly damaged and devoid of stalk sheaths. The paratype II is almost a straight fragment of stem, 6.4 mm long and 67—72 μm wide (pl. 20: 2), with nine nodes, only one of which is similar in morphology to those of the holotype. The node is in the form of common base with two sheaths of polyp stalks, whereas the remainings ones display single stalk sheaths sometimes thickened at the base. On both paratypes, nodes are distributed on various sides of branches. However, some regularity may be found as the nodes seem to mark various points of helisa apparently running at surface of stem of colony.

The hydrorhiza of *Rh. tridens* was hitherto unknown. It is formed of by a twine of filamentous stolons (fig. 6; pl. 20: 8—11; pl. 21: 5—6). Stolons have the form of flattened tubes 80—200 μm in diameter, with irregular widenings and narrowings along their whole length. Single sheath of hydranth stalks sporadically grow directly upwards from stolon surface (fig. 6: 1, fig. 8: 2). Stolons of large hydrorhiza fragments are sometimes intertwined so densely that it is impossible to trace their course. The stolon surface is mat and rough. Stolons are often branching, always by bifurcation. This results in origin of pairs of descendant hydrorhizal stolons (fig. 6: 6),whereas stolons acting as the stem of colony (hydrocaulus) rise upwards from lateral surface of the hydrorhizal stolon. The process of branching of the colony stem may be traced in detail in individual phases. The stem runs for some time along the hydrorhizal stolon at the base. In this growth phase, it is possible to identify stem stolons on the basis of their circular section and smooth, glittering periderm. It subsequently rises above the basement and begins to grow markedly faster than the accompanying hydrorhizal stolon (fig. 6: 2). When the stem rises, the hydrorhizal stolon describes a loop around it. The loop, either dextral or sinistral, is an extremely characteristic morphological feature of the *Rh. tridens* colony. Periderm of loop is at first markedly less strongly sclerotized than that of the young stem around which the loop is developed.

Fig. 6.

Rhabdohydra tridens Kozłowski. *1* Fragment of the hydrorhiza with the hydranth sheath and the proximal part of the stem (ZPAL Hz. I/16), boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician, × ca. 25; *2* Young stem with the fragment of the hydrorhiza (ZPAL Hz.I/17), boulder no. ZPAL 0.555, Mochty, Ordovician, × ca. 25; *3* Fragment of the hydrorhiza with the proximal part of the stem (ZPAL Hz.I/18), boulder no. ZPAL 0.366, Zakroczym. Middle Ordo-

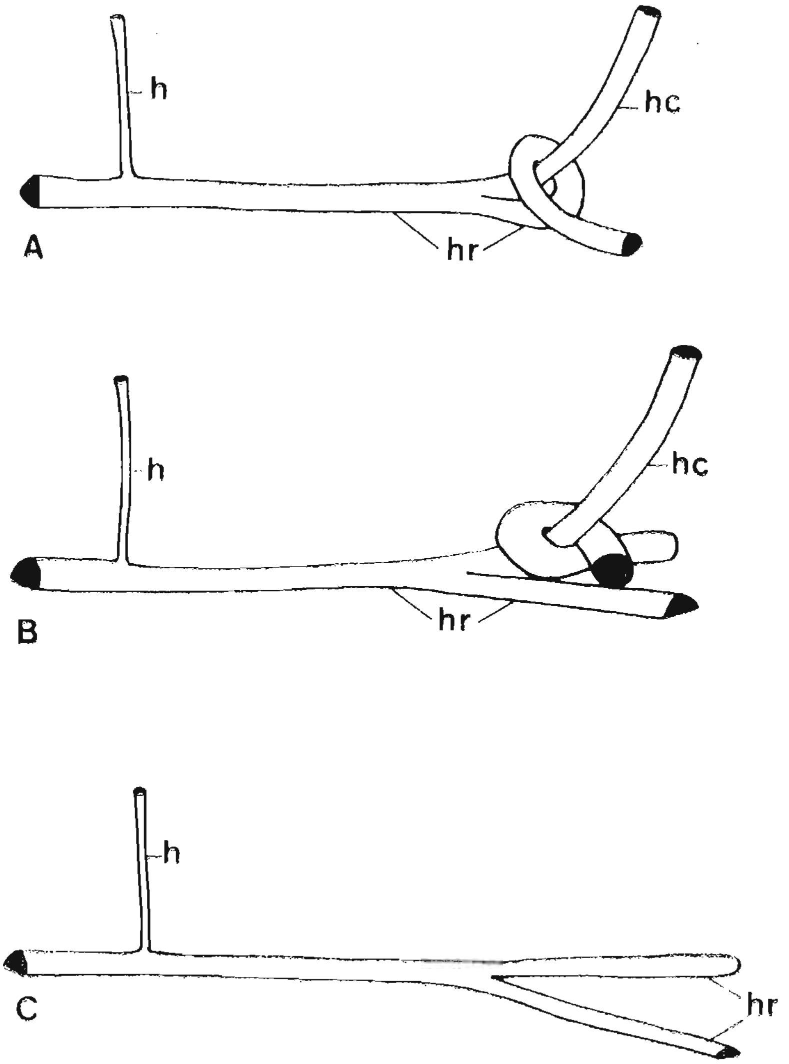

Fig. 7.

Rhabdohydra tridens Kozłowski. Three different types of hydrorhiza stolon branching. Abbreviations: *h* hydranth sheath *hc* stem, *hr* hydrorhiza stolon.

Sporadically, the loop is not formed by a "sister", stem-accompanying stolon but by one of those passing nearby (fig 7B).

The hydrocaulus branches out much less often than the hydrorhizal stolons. It bifurcates in the upper parts of colony (pl. 20: 5) or, exceptionally, just after rising above the substratum (fig. 8: 2). The stem varies from 50 to 90 μm in diameter, quite clearly thickening upwards. The colony displays marked heteropolarity in structure: almost only single hydranths are found in lower part of the colony stem, whereas almost all occurring in the upper parts are grouped on common bases.

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vician, ×ca. 30;. *4* Fragment of the hydrorhiza with the proximal part of the stem (ZPAL Hz.I/19), boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician, ×ca 30; *5* Young stem with the fragment of the hydrorhiza ZPAL Hz.I/20, boulder no. ZPAL 0.555, Mochty, Ordovician, ×ca. 30; *6* The largest fragment of the hydrorhiza with preserved proximal part of the stem (ZPAL Hz.I/21), boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician, ×ca. 25; *7* Fragment of the hydrorhiza with the proximal part of the stem (ZPAL Hz.I/22), boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician, ×ca. 30. Abbreviations: *H* hydranth sheath, *HC* stem, *HR* hydrorhiza stolon, dotting shows translucent part of the periderm.

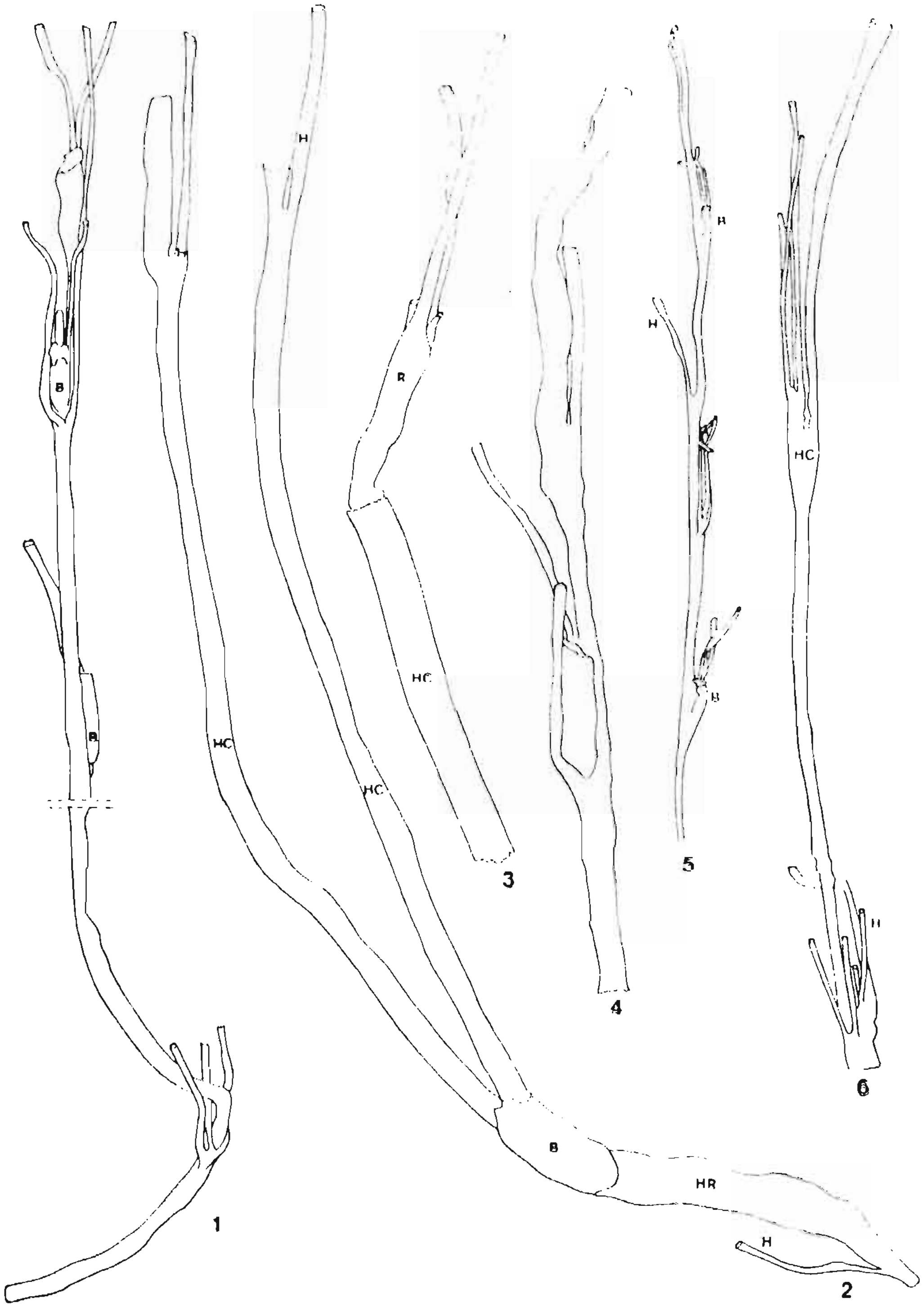

Fig. 8.

Rhabdohydra tridens Kozłowski. Fragments of stems. *1* long fragment with three young lateral branches (ZPAL Hz.I/23), ×ca. 30, *2* early bifurcated young stem with young lateral branch (ZPAL Hz.I/24), ×ca. 60, *3* fragment of stem partly regenerated (ZPAL Hz.I/24), ×ca. 60, *4* distal part of the stem with lateral branch (ZPAL Hz.I/25), ×ca. 60, *5* fragment of the stem with two lateral branches (ZPAL Hz.I/26), ×ca. 30, *6* fragment of the stem (ZPAL Hz.I/27), ×ca. 40. All specimens from the boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician. Abbreviations: *B* lateral branch, *HC* stem, *HR* hydrorhiza stolon, *H* hydranth sheath, *R* regenerated part of the stem.

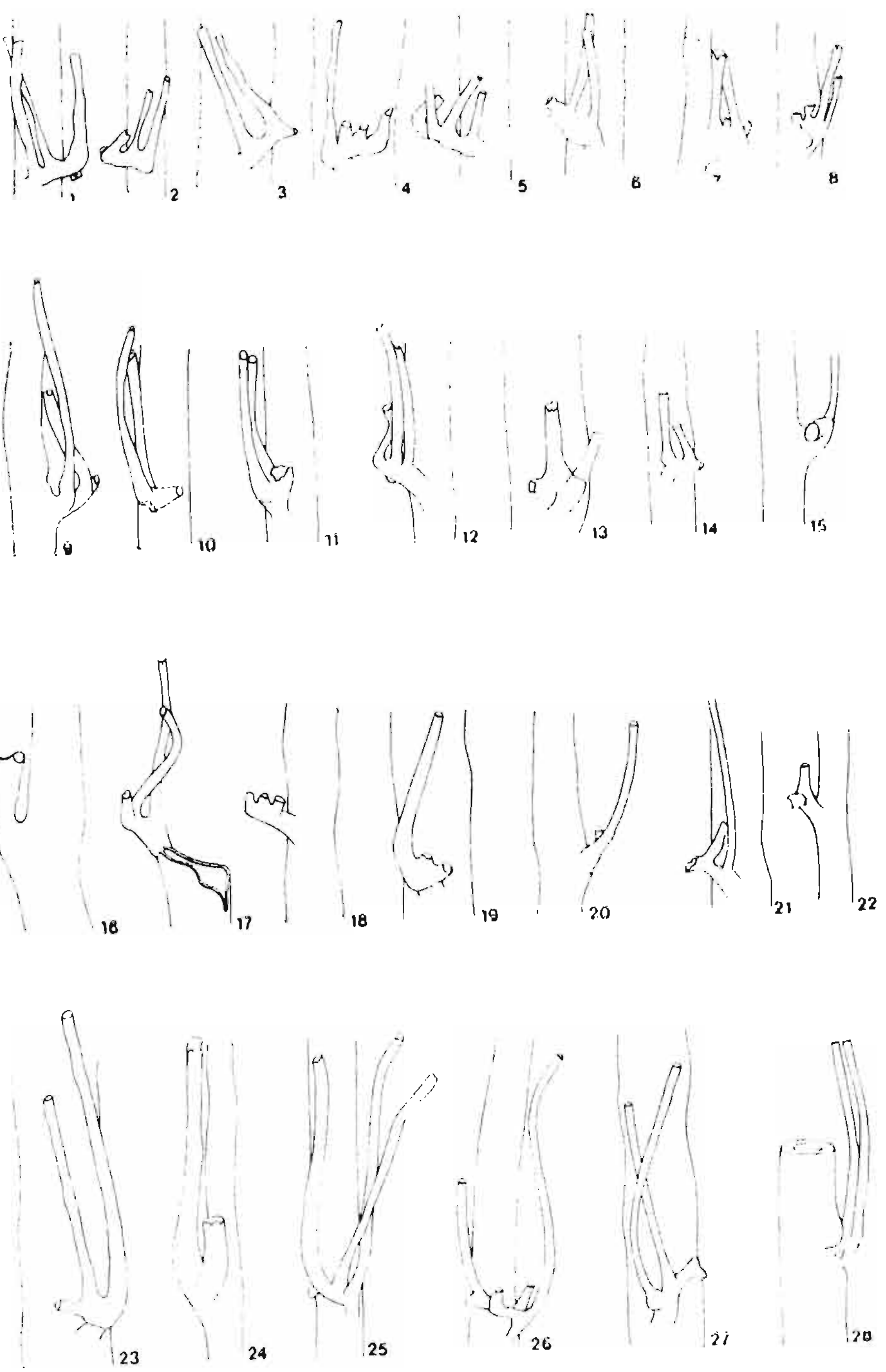

Fig. 9.
Rhabdohydra tridens Kozłowski. Differentiation of nodes, ×ca 35. Boulder no. MZ/18, Orzechowo, Ordovician.

Groups of polyps rising from common bases comprise 3—4 or, rarely, 2 individuals. Figure 9 shows the variability in morphology of groups in colony. Spacing of the groups is also highly variable but there may be a marked trend to their arrangement along the helisa. Hydranth groups are sporadically accompanied by single individuals growing up directly from the stem (fig. 8: 4—5). Sheaths of polyp stalks are up to 450 μm long and 20—35 μm in diameter.

The stem sometimes bifurcates at the height of nodes. Sometimes the origin of branch has negative effect on diameter of the major stem, leading to its decrease in its diameter even to that of the hydranth stalk sheath (fig. 8: 4). Along with further growth, the major stem regains its former diameter. It should be noted that the major stem impedes growth of lateral branchings in a similar way as does its accompanying hydrorhizal stolon at an early growth stage. That is why it is possible to find fragments of stems with short lateral branchings (fig. 8: 1, 4, 5). The latter were misidentified as gonothecae by SKEVINGTON (1965: 158, fig. 7b).

The major stem is usually straight. Its course appears undisturbed by budding polyps (pl. 20: 2—4, 9; fig. 8: 6), except when a single hydranth develops along the axis of growth of the colony stem (pl. 21: 2). The apex of the growing colony (fig. 6: 2) is characterized by translucent stem periderm above the highest-positioned group of polyps. The growth of the stem presumably ends with the origin of group of polyps at its apex (see KOZŁOWSKI 1959*b*: 236, fig. 14b).

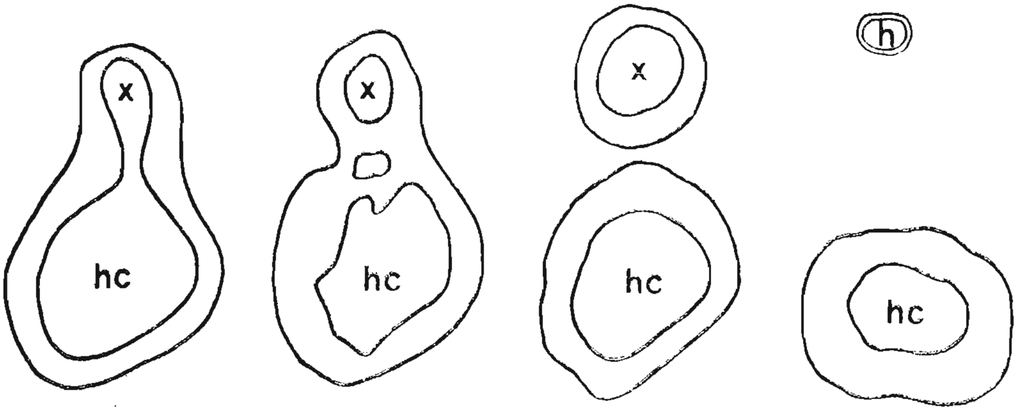

Fig. 10.
Rhabdohydra tridens KOZŁOWSKI. Four transverse sections at the node level. Abbreviations: *h* hydranth sheath, *hc* stem, *x* common base.

Microstructure. — Studies on transverse, 1—2 μm thick sections (fig. 10) failed to show any differences in microstructure of the periderm. Sections of colony stem periderm are dark-brown to cherry-red in colour, opaque, and those of the periderm of hydranth stalk sheaths-light-brown and translucent. Colony stem and hydrorhiza are characterized by periderm 6—15 μm thick, and sheath of hydranth stalk 1—2 μm thick. Accumulations of pale-yellow material may be often found inside stems and stolons.

Ultrastructure. — Studies on periderm ultrastructure were carried out with the use of SEM and TEM. SEM analysis of fractured stems and hydrorhiza stolons failed to show any ultrastructural differences. Preliminary results of TEM studies on periderm ultrastructure have been presented previously by MIERZEJEWSKA and MIERZEJEWSKI (1974). The periderm seemed to be completely homogeneous at low magnifications. High magnifications revealed some ultrastructural details, showing that apparently homogeneous periderm is built of fine granules of high electron density, embedded in electronically less dense ground material. The granules are usually fairly well ordered along lines concentric to the axis of the branch line (pl. 22: 1, 4). In older parts of colony branches are characterized by periderm with a thin layer of high electron density, built of lumps varying in size but generally large, on its inner side. Some of the lumps seem to be aggregates composed of smaller units. The boundary between the basic, fine-granulated layer and the upholstering, coarse-granulated one is blurred. Integration of the two layers must be insignificant as they very often diverge (pl. 22: 2).

The outer surface of stem periderm is most often smooth (pl. 22: 4) or, sometimes, covered with large isolated bodies which do not form any continuous layer (pl. 22: 1).

The periderm of hydranth stalk sheaths is devoid of inner coarse-granular layer, being primarily built of ground material with insignificant admixture of granules.

The periderm of hydrorhiza stolons appears to be essentially the same as that of the branches. The fine-granular layer, forming its major mass, displays concentrically spaced granules, the number and size of which decrease towards its interior. It is covered with numerous large bodies of high electron density (pl. 22: 6). The upholstering coarse-granulated layer is missing here and the inner part of the periderm is relatively poor in granules.

Accumulations of a material characterized by an electron density markedly lower than that of surrounding periderm, are found inside the stems and hydrorhizal stolons. The matter is granular in structure in the stems (pl. 22: 5, 7) and amorphous in the hydrorhiza (pl. 22: 3); and its accumulations appear to be closely connected with periderm in some places.

The ultrastructural features of the periderm of branches and hydrorhiza, especially the concentric arrangement of granules, suggest gradual, prolonged formation of skeleton. The process of formation of colony stem periderm ended with the appearance of the upholstering coarse-granular layer, known from old parts of a colony only.

The material infilling interior of hydrorhiza stolons and stems should be treated as relics of periderm forerunners, accumulated in ectodermal cells. Wide distribution of this matter suggests that epithelio-muscular cells were most capable to secrete periderm. Some electron micrographs seem to reveal the act of secretion of single cells (pl. 22: 7).

Occurrence. — The Lower Ordovician of the Öland Id (Skevington 1965*b*, Eisenack 1976), Middle and Upper Ordovician of Poland.

Rhabdohydra multiplex sp. n.

(pl. 20: 1)

Holotype: A fragment of colony stem with seven nodes, shown in pl. 20: 1 (ZPAL Hz. I/1).

Type horizon and locality: Ordovician erratic boulder no. ZPAL O.186 from Mochty.

Derivation of the name: Lat. *multiplex* — numerous, on account of large number of polyps in individual nodes.

Diagnosis. — Hydranths seated on complex common bases. Periderm of stem displays single openings circular to subovate in outline at the height of some nodes.

Material. — Holotype only.

Description. — The holotype represents a fragment of slightly bent colony stem 2600 μm long and 50 μm wide, displaying five nodes (II—VI) and traces of two others (I and VII). Common bases are distributed on convex side of the stem, roughly one above another. Close to the node I, II, III, IV and VII, there exist (or existed — see below) subovate to almost circular openings in periderm, 40 to 80 μm in diameter. Periderm translucent, yellow-brownish due to chemical decolouring. Nodes spaced in intervals equal (in μm) respectively to: 400, 420, 400, 380, 360, 350.

Common bases from nodes II, III and IV, the best preserved, appear complex in character. Each of them seems to be composed of two common bases typical of *Rh. tridens*. Sheaths of hydranth stalks are here relatively well preserved and often complete. On each common base, there are sheaths wider and darker-coloured (which suggests larger thickness of periderm) than the remaining ones. The former are about 20 μm in diameter, and the latter — about 15 μm. The number of hydranth stalk sheaths on common bases is 6, 6 and 5 (?), respectively. Nodes V and VI display some remains of common bases only. At the height of nodes I and VII, there may be noted traces after openings only (see below).

Remarks. — *Rhabdohydra multiplex* sp. n. differs from *Rh. tridens* in the presence of complex common bases and enigmatic openings at the height of individual nodes.

The holotype of *Rh. multiplex* sp. n. has been undoubtedly studied by Kozłowski along with material subsequently described under the name of *Rh. tridens*. This is shown by the label attached in his handwriting: "*Rhabdohydra tridens* n. sp. var. multithecata?". Unfortunately, the specimen was not described nor figured in his publication. The specimen was subsequently passed to me along with other material in Spring 1973 but its state of preservation soon deteriorated. The photo (pl. 20: 1) shows its appearance in 1977. My sketch drawings from 1973 show that the specimen was displaying complete openings at the height of nodes I and VII, relics of common base I and much better preserved fragments of common bases V and VI. Moreover, there was no longitudinal fracture of periderm at that time. The changes of the specimen are undoubtedly due to its chemical decolouring which has presumably taken place more than 20 years ago.

The nature of circular to subovate openings remains enigmatic. I suppose that they represent traces of medusoids existing at these places. Because of a high degree of integration of the colony, the occurrence of free-living medusoid stage in its metageny is doubtful.

Occurrence. — The species is hitherto known from a single erratic boulder in the area of Poland (Mochty) only.

?*Rhabdohydra* sp.

(fig. 11)

1959*a*. *Rhabdohydra tridens* KOZŁOWSKI; KOZŁOWSKI, fig. 14 E—F.

Material. — Three fragments of stems from Ordovician erratic boulders MZ/30.

Description. — Fragments of straight stems 700—900 μm long and 70—90 μm in diameter, with single, short, irregularly spaced second-order branchings 35 μm in diameter.

Remarks. — KOZŁOWSKI (1959*a*) assigned to *Rhabdohydra tridens* two fragments of branches with short, knee-like second-order branchings, atypical of this species. The affinity of these specimens to the genus *Rhabdohydra* could be regarded as proved by the record of a specimen displaying both hydranth stalks sheaths typical of it and knee-like second-order branchings characteristic of these specimens, but such an intermediate form has not yet been found. Therefore, it is difficult to make assumptions concerning actual systematic position.

SKEVINGTON (1965*b*) interpreted the specimens as branches from which Gonothecae Formae A—C KOZŁOWSKI *sensu* SKEVINGTON were growing. The similarity of ?*Rhabdohydra* sp. and branches bearing Gonothecae A—C is of little significance. Short, hook-like legs of some "gonothecae" (more precisely, cysts of sterile buds of Rhabdopleurida, see p. 174) diverge from branches of the same width or slightly wider (see KOZŁOWSKI 1959*a*, figs. 26 and 29 A—C and SKEVINGTON 1965*b*, figs. 9—16), whereas branches of ?*Rhabdohydra* sp. are several times thicker than its second-order branchings.

Occurrence. — Ordovician erratic boulder from the area of Poland.

Genus *Palaeotuba* EISENACK, 1934

Type species: Palaeotuba polycephala EISENACK, 1934

Remarks. — Three species were hitherto allocated to this genus: *P. polycephala* EISENACK, 1934, *P. dendroidea* EISENACK, 1934, and *P. dichotoma* KOZŁOWSKI, 1959.

Palaeotuba polycephala EISENACK, first described from the Kukruse in Estonia (EISENACK 1934), was also reported from two erratic boulders in Poland (KOZŁOWSKI 1959*a*). One of the boulders was subsequently dated as presumably Kukruse horizon (KOZŁOWSKI 1962).

Palaeotuba dendroidea EISENACK was described from the *Orthoceras* Limestone on the basis of two small fragments (EISENACK 1934). According to KOZŁOWSKI (1959*a*), the type material is so fragmentary that identification of the species becomes hazardous. For me it is even difficult to prove that the two specimens of *P. dendroidea* represent the same taxon. The specimen figured by EISENACK (1934, fig. 1) appears strikingly similar to fragments of various "hydro-

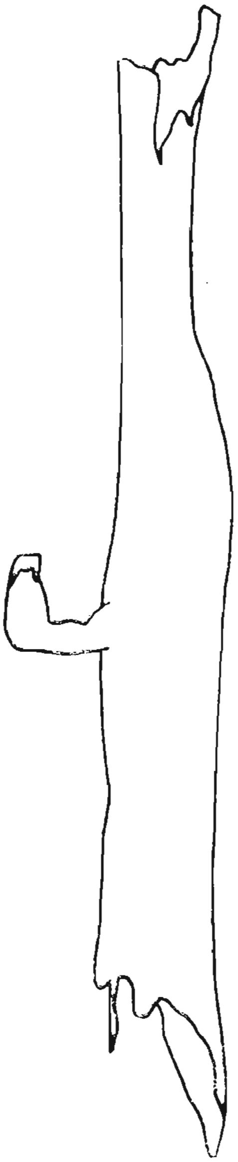

Fig. 11.
?*Rhabdohydra* sp. Fragment of a stem, ×200. Boulder no. MZ/30, Mochty, Ordovician.

rhizae" collected by KOZŁOWSKI (1959*a*) or even stolons of *Rhabdopleurites primaevus* KOZŁOWSKI (Pterobranchia).

Palaeotuba dichotoma Kozłowski, described from Ordovician erratic boulders in Poland by KOZŁOWSKI (1959*a*), was tentatively allocated in the genus *Palaeotuba*. It is not excluded that under that name he described stolons of *Rhabdopleurites primaevus* KOZŁOWSKI (see. p. 179). That is why I treat the specific names *Palaeotuba dendroidea* EISENACK, 1934 and *P. dichotoma* KOZŁOWSKI, 1959 as *nomina dubia* and the genus *Palaeotuba* EISENACK, 1934 as monotypic.

Palaeotuba polycephala EISENACK, 1934

1934. *Palaeotuba polycephala* EISENACK; EISENACK 54, fig. 3a, b; pl. 4: 5.
1959*a*. *Palaeotuba polycephala* EISENACK; KOZŁOWSKI: 233, fig. 12.
non 1976. *Palaeotuba* cf. *polycephala* EISENACK; EISENACK 185, pl. 1: 19—20.

Material. — Two specimens reported from erratic boulders no. ZPAL 0.182 and ZPAL 0.242 by KOZŁOWSKI (1959*a*) do not exist (they underwent disintegration in glycerine due to chemical decolorization of the periderm).

Remarks. — It is not excluded that the nominal species *Palaeotuba polycephala* EISENACK, 1934 and *Rhabdohydra tridens* KOZŁOWSKI, 1959 are conspecific. The specimens of the former may represent atypically developed fragments of stems of colony *Rh. tridens.*

The specimens described under the name *Palaeotuba* cf. *polycephala* from the Lower Ordovician of Öland Island by EISENACK (1976) are not congeneric with those described by that author (EISENACK 1934) and KOZŁOWSKI (1959*a*). They differ markedly from the latter in shape of second-order branchings and I consider that they represent sets of stolons of *Rhabdopleurida.*

Occurrence. — Ordovician (Kukruse) of Estonia (EISENACK 1934) and Ordovician erratic boulders from the area of Poland (KOZŁOWSKI 1959*a*).

Suborder **Thecaphora**

Family **Chaunograptidae** BULMAN, 1955

Type genus: *Chaunograptus* HALL, 1882

Remarks. — Chaunograptidae were initially defined as: "Free dendroid or irregularly branching encrusting rhabdosome with free conical thecae" (BULMAN 1955: V 36). BULMAN (1955) assigned to that family the following genera: *Chaunograptus* HALL, *Mastigograptus* RUEDEMANN and *Haplograptus* RUEDEMANN, Chaunograptidae were initially treated as graptolites of the order Dendroidea. BOUČEK (1956: 149) held a different point of view, stating that "it would be better to treat these genera (and the family on the whole) for the present separately as dendroid graptolites incertae sedis (or i. ordinis)". Subsequently, OBUT (1964) allocated this family in the graptolite order Dithecoidea Obut (see p. 142).

Chaunograptidae as interpreted by BULMAN (1955) represent clearly artifical groups and as such they were later treated (BULMAN 1970) when he neglected this name and placed the genera previously allocated to the Chaunograptidae in "Dendroidea, Tuboidea, Crustoidea, Camaroidea and Stolonoidea — taxonomic position uncertain".

I present here a new concept of the Chaunograptidae. I treat this family as Hydroidea, assigning to it only the type genus with its junior synonyms (*Desmohydra* KOZŁOWSKI and *Epallohydra* KOZŁOWSKI).

The similarity of *Chaunograptus* to Hydroidea was indicated by CHAPMAN (1919) and BULMAN (1938); RUEDEMANN (1947) regarded this genus as hydroid. The genus *Chaunograptus*, to which were assigned several species from the Cambrian, Ordovician, Silurian and Devonian from various continents, is known from imprints and carbonized remains on rock surfaces only. The species were assigned here taking into account similarities in shape of colony and tubular form of thecae. Because of poor preservation, some hydroids, rhabdopleurids (*Rhabdopleuroides* KOZŁOWSKI) or crustoid graptolites could be described under that generic name. I do not doubt that this was often the case as *Chaunograptus* has never been described on the basis of material chemically extracted from rock and *Desmohydra*, *Epallohydra* and *Rhabdopleuroides* — on the basis of imprints or carbonized remains. The lack of remains of representatives of the three last-named genera preserved in a similar form as those of *Chaunograptus* is simply improbable, so I suppose here a typical dualism in nomenclature used for a part of hydroids, rhabdopleurids and crustoid graptolites. The origin of this may be explained in the following way: encrusting, irregularly branching colony with thecae creeping on their whole length, when preserved as imprints or carbonized remains, used to be assigned to the genus *Chaunograptus*, whereas the colony identical in shape and form of thecae, when extracted from rock could be subjected to studied on morphological details and, therefore, assigned to Hydroida, Rhabdopleurida or Crustoidea. If follows that *Chaunograptus* is one more "form-genus". The ordering of the taxonomy of species assigned to this genus is therefore significant but troublesome. The significance of this question is connected with the fact that several specific names of hydroids, rhabdopleurids and crustoids most probably are junior synonyms of species of *Chaunograptus* and the troubles which may be expected in this taxonomical revision are related to difficulties in comparing the type specimens of individual *Chaunograptus* species and forms extracted by chemical methods due to poor preservation of microanatomical details in the former.

The congeneric character of species assigned to *Chaunograptus* is questionable, so the taxonomic position of that genus may be reconstructed on the basis of an analysis of its type species only. The type species, *Ch. novellus* (HALL) from the Silurian of the USA, was originally defined as: "Fossils occurring free in the shales, or upon other fossil bodies, in slender branching fronds. Branches diverging, lax and slender, with numerous branchlets, both marked by numerous cellules which are usually indicated by the appearance of abrupt expansion and contraction of the branches. The angular projection of the cell apertures can be observed in many parts of the fossil" (RUEDEMANN 1947: 254). The presence of expansions and contractions of branches and thecae (branchlets) is of marked significance for discussion on systematic position of this form, as such shapes of branches and thecae are found in neither graptolites nor pterobranchs, but rather in various hydroids. When this is the case, the species *Ch. novellus* and, thus, the genus *Chaunograptus* should be treated as hydroid.

From Ordovician erratic boulders, KOZŁOWSKI (1959*a*) described the genera *Desmohydra* KOZŁOWSKI and *Epallohydra* KOZŁOWSKI, differing in the presence or lack of short stalk of hydrotheca. The rank of this difference is too small for discrimination of genera. In modern Thecaphora, a single genus may comprise species with hydrotheca seated or with stalkes. Moreover, the two types of seating may be found even in a single species (e.g. in *Thyroscyphoides biformis* NAUMOV). The type species of *Desmohydra* and *Epallohydra* appear strikingly similar to *Chaunograptus novellus*. According to me, the names *Desmohydra* KOZŁOWSKI, 1959 and *Epallohydra* KOZŁOWSKI, 1959 should be treated as junior subjective synonyms of the name *Chaunograptus* HALL, 1883.

I propose here a new diagnosis of Chaunograptidae: Hydroida with encrusting, irregularly branching colonies; thecae creeping along their whole length.

Genus *Chaunograptus* HALL, 1882

Type species: *Chaunograptus novellus* (HALL)

1959*a*. *Desmohydra* KOZŁOWSKI; KOZŁOWSKI: 227.
1959*a*. *Epallohydra* KOZŁOWSKI; KOZŁOWSKI: 230.

New diagnosis. — Hydrorhiza tubular. Stolons of hydrorhiza of the same or almost the same diameter as hydrothecae. Hydrothecae long, creeping, tubular.

Species assigned. — *Chaunograptus novellus* (HALL), *Chaunograptus flexuosus* (KOZŁOWSKI), *Chaunograptus adhaerens* (KOZŁOWSKI).

Remarks. — *Desmohydra* (KOZŁOWSKI, 1959 and *Epallohydra* KOZŁOWSKI, 1959 are junior synonyms of *Chaunograptus* HALL, 1882 (see pp. 162—163). The taxonomic position of *Desmohydra zigzag* KOZŁOWSKI, 1959 and *Desmohydra*? *recta* SKEVINGTON, 1965 is unclear. There is a large number of species assigned to the genus *Chaunograptus* HALL (see pp. 162—163). In my opinion this genus should be confined to the species enumerated above, until detailed revision of the remaining ones, previously assigned to it, is made. In that situation it would be useful to use "*Chaunograptus*" as comprehensive name for the latter.

Chaunograptus flexuosus (Kozłowski, 1959)

(pl. 23: 1—3)

1959*a*. *Desmohydra flexuosa* Kozłowski; Kozłowski: 227, fig. 8.

Material. — About a dozen specimens from erratic boulders ZPAL 0.129, ZPAL 0.240, MZ/11 and MZ/24.

Diagnosis. — See Kozłowski (1959*a*: 227).

Description. — The specimens available are morphologically identical with those described by Kozłowski (1959*a*).

Ultrastructure. — TEM studies showed the periderm of the hydrothecal walls to be homogeneous in structure, without differentiation in ultrastructure (pl. 23: 1, 2). The periderm displays a distinct trend to form layers, and varying from 0.5 to 1.5 μm in thickness. Inside hydrothecae there may be noted accumulations of organic matter, locally gaining "cellular" appearance, with marked electronically dense "nucleus" inside "cell" (pl. 23: 3). Periderm of stolons does not differ from that of thecae, except for being markedly thicker (pl. 23: 1). No accumulations of organic matter were found inside stolons.

The data on ultrastructure appear insufficient for drawing more detailed conclusions on the character of periderm building organic matter.

Occurrence. — Ordovician erratic boulders from the area of Poland (Kozłowski 1959*a*, Mierzejewski 1978*b*).

Chaunograptus adhaerens (Kozłowski, 1959)

(pl. 23: 4—6)

?1934. *Chitinoröhre (Hydrorhiza?)*; Eisenack 56, fig. 7, pl. 4: 8.
1959*a*. *Epallohydra adhaerens* Kozłowski; Kozłowski: 230, fig. 10.
1965*b*. *Epallohydra adhaerens* Kozłowski: Skevington 155, figs. 4—5.

Diagnosis. — See Kozłowski (1959*a*: 230).

Material. — The available specimens are morphologically identical as those described by Kozłowski (1959*a*) and Skevington (1965*b*).

Ultrastructure. — TEM studies showed periderm of hydrothecae to be homogeneous in structure, without any differentiation in ultrastructure (pl. 23: 4—6). The periderm displays a distinct trend to fall into layers.

Some organic matter may be found close to inner surface of hydrothecae (pl. 23: 4—6). It is possible to differentiate three modes of development of the organic matter: 1) as more or less regular lumps of homogeneous material not differing from peridermal ultrastructure, 2) accumulations of irregularly distributed spongy material, and 3) innumerous membranous forms.

The data on the ultrastructure appear insufficient for drawing more detailed conclusions on the character of periderm building organic matter.

Remarks. — *Chaunograptus adhaerens* appears strikingly similar to the modern hydroid *Filellum serpens serpens* (Hassel) (see Naumov 1960, fig. 170) in morphology of hydrosome and hydrothecae. It also resembles *Chaunograptus novellus* (Hall), especially in contractions and widenings displayed by some specimens.

Occurrence. — Ordovician erratic boulders from the area of Poland (Kozłowski 1959*a*), Lower Ordovician of the Öland Island (Skevington 1965*b*).

?*Chaunograptus* sp.

1959*a*. *Gonotheca* Forma E; KOZŁOWSKI: 258, fig. 29F.

Material. — A fragment of hydrosome with one hydrotheca and two isolated hydrothecae from boulders nos. ZPAL 0.121, ZPAL 0.182 and ZPAL 0.184.

Remarks. — The material, previously described in detail by KOZŁOWSKI (1959*a*), differs from that of the type species of *Chaunograptus* HALL as well as the species *Chaunograptus flexuosus* (KOZŁOWSKI) and *Chaunograptus adhaerens* (KOZŁOWSKI) in having thecae markedly wider than stolons. This feature brings it close to "*Chaunograptus*" *contortus* RUEDEMANN, "*Ch.*" *gonothecatus* DECKER or "*Ch.*" *vermiformis* RUEDEMANN. Moreover, it displays contractions and widenings of the stolons and hydrothecae, similarly but on somewhat smaller scale than in *Ch. novellus* (HALL).

The form presumably represents a new species but the material available is so fragmentary that it would be hazardous to propose a new specific name on the basis of it.

Family **Inocaulidae** RUEDEMANN, 1947

Type genus: *Inocaulis* HALL, 1861

Remarks. — RUEDEMANN (1947) established graptolite family Inocaulidae allocating in it the genera *Inocaulis* HALL, *Thallograptus* RUEDEMANN, *Medusaegraptus* RUEDEMANN and *Diplospirograptus* RUEDEMANN. BOUČEK (1957) excluded the genus *Thallograptus* from that family, allocated the genus *Palmatophycus* BOUČEK, and rised its rank to the order Inocaulida with the following characteristics: "Thick main branches, simple or infrequent bifurcating, rarely distally a bundle of secondary branchlets, with abundant filamentous thecal tubes" (BOUČEK 1957: 145). OBUT (1964) widened the range of Inocaulidae to comprise also the genera *Boucekocaulis* OBUT, *Crinocaulis* OBUT and *Estoniocaulis* OBUT et RYTZ. According to the latter author, Inocaulidae developed from dendroid graptolites, more precisely those of the family Dendrograptidae. BULMAN (1970) assigned the genus *Inocaulis* to dendroid graptolites (family Acanthograptidae), treating the remaining genera together as "Dendroidea, Tuboidea, Camaroidea, Crustoidea, Stolonoidea — taxonomic position uncertain".

I doubt the graptolitic nature of *Inocaulis* and other forms regarded as related to it by the authors mentioned above. Anatomy of all these genera is very poorly known as they have been described on the basis of imprints or carbonized, flattened remains. The only features in which they may resemble graptolites include: a) a bushy shape of colony displayed by some of them, and b) the presence of long, narrow "thecae". Both features are without much importance for analysis of eventual affiliation of inocaulids and graptolites, as bushy colonies are known from various groups of colonial invertebrates and the so-called "thecae" fail to display any traces of fusellar structure. The "thecae" and branches actually somewhat resemble morphology of autothecae of such graptolites as *Acanthograptus* SPENCER or *Koremagraptus* BULMAN but, up to the present, no elements which could be interpreted as bithecae were found in inocaulids. *Inocaulis plumulosa* HALL, the type species of the genus *Inocaulis*, display branches formed of bunches of undifferentiated long tubes (see RUEDEMANN 1947, pl. 32: 9—11).

BULMAN (1970: V55) stated that *Diplospirograptus* displays "superficial resemblance to algal forms, though it is perhaps doubftul whether such delicate filamentous algae could survive under the given conditions of preservation of these fossils". According to me, the algal nature of this genus may be regarded as quite sure. I consider *Diplospirograptus* as an alga of the class Chlorophyceae, close to Dasycladaceae, especially Batophoreae. In the "rhabdosome" of *D. goldringae* RUEDEMANN, type species of *Diplospirograptus*, it is possible to note morphological elements identical to the thallus of modern *Batophora oerstedi* AGARTH (fig. 12).

Elements of the "rhabdosome" of *D. goldringae*, named as "theciferous branches" by RUEDEMANN (1947), are essentially identical to lateral branchings of the above-mentioned green alga. These forms essentially differ in the presence of single major axis in *Batophora*, similarly as in all Dasycladaceae, and double, spirally coiled and branching axis in *Diplospirograptus*. This makes possible treatment of the latter as a representative of the Dasycladaceae which it so closely resembles in morphology of "theciferous branches". It is worth to note here that I found a thallus of alga with polysiphonal axes and lateral branchings similar to those of Dasycladaceae in one of Silurian erratic boulders. According to Dr. J. KAŹMIERCZAK (1978, oral inf.) the algae represent hitherto unknown group, intermediate between Dasycladaceae and Codiaceae. It seems that the genus *Diplospirograptus* would be best accomodated in that group.

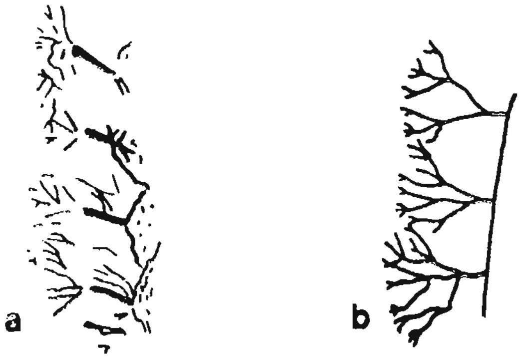

Fig. 12.
Lateral branches in *Diplospirograptus goldringae* RUEDEMANN (*a*) and *Batophora oerstedi* AGARDH (*b*). After RUEDEMANN and NITECKI.

Other inocaulid, Ordovician-Silurian *Medusaegraptus* RUEDEMANN may also represent Chlorophyceae. RUEDEMANN (1925: 29) characterized it as follows: "rhabdosome consisting of a simple, not branching stipe, which is a uniformly thick tube, ending in a blunt point at the base and terminating distally in a dense mass of simple, unbranched flexuosus thin tubes, the thecae". *Medusaegraptus* may be easily classified as representative of Codiaceae. Thallus of Codiaceae is sometimes built of stem and brush-like top part, formed of numerous thallus threads. The so-called thecae of *Medusaegraptus* I treat as equivalents of these threads, and "not branching stips". In an identical way I interpret the Silurian *Palmatophycus* BOUČEK, actually originally described as an alga (BOUČEK 1941).

In considering the systematic position of *Diplospirograptus*, *Medusaegraptus* and *Palmatophycus*, the record of the first fossil representatives of Batophoreae (*Archaeobatophora* NITECKI) from the Ordovician of the USA (NITECKI 1976) is of marked significance. The morphology and state of preservation of this form are strikingly similar to those of "inocaulid graptolites".

Among inocaulids, special attention should be paid to the genus *Inocaulis* HALL. RUEDEMANN (1947: 236) characterized it in the following way: "Very thick branches, bifurcating infrequently, composed of an extremely large number of fine tubes, which project freely distally as hairlike processes". I suppose that this genus represents hydroids with polysiphonal colonial stems and branches. Species assigned to the genus *Inocaulis* have hydrosomes simply identical as those of modern hydroid species of the genus *Grammaria* STIMPSON, 1854 (family Lafoeidae) (fig. 13). I do not know of any differences in structure of the hydrosomes of species of the two genera. Both genera are characterized by: (a) identical tree-like shape of colony, (b) stems and branches polysiphonal along their whole length, (c) root-like hydrorhizae, (d) tubular thecae with basal parts embedded in stems and branches of colony, (e) thecae regularly or randomly arranged, (f) free part of theca diverging from stem and branches, or (g) distal part of theca embedded up to aperture in stems and branches, and (h) the same diameter of distal parts (0.05—0.4 mm in *Inocaulis* and 0.15—0.4 mm in Grammaria). Moreover, the differentiation in morphology within these genera is so similar that it is possible to find fossil equivalents for modern species of *Grammaria* among those of *Inocaulis*. The species *G. immersa* NUTTING, *I. simplex* RUEDEMANN and *G. stentor* ALLMAN, *I. arborescens* RUEDEMANN may serve as examples. In discussing the two genera it is even possible to state that their hydrosomes display no morphological features which would question their congeneric nature. I suppose, however, that in the light of gap in their records, extending from the Devonian to the present times, it will be more appropriate to treat them as separate taxa.

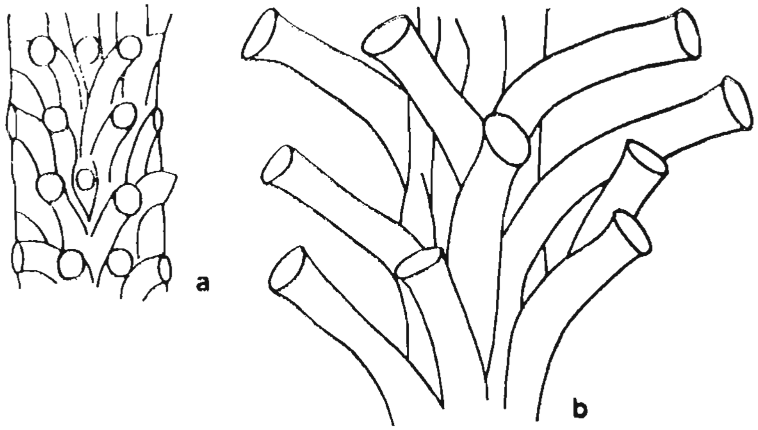

Fig. 13.
Recent species of the genus *Grammaria* STIMPSON: *a Grammaria immersa* NUTTING, *b Grammaria stentor* ALLMAN. After Naumov.

In this work I am confining the range of the family Inocaulidae to the genus *Inocaulis* HALL.

Genus *Inocaulis* HALL, 1852

Type species: *Inocaulis plumulosa* HALL, 1852

Remarks. — Taxon related or even congeneric with the modern genus *Grammaria* STIMPSON 1854 (see above). From that genus I exclude the species *Inocaulis kirki* RUEDEMANN, 1916 the affiliation of which with hydroids seems at least questionable.

Inocaulis sp.

(pl. 35: 5)

Material. — Basal part of colonial stem with hydrorhiza and three small fragments of stems (? lateral branches) from borehole Podborowisko IG 1, depth 396.30—397.30, Arenigian.

Description. — The largest specimen represents a fragment of colonial stem with hydrorhiza (pl. 35: 5). Hydrorhiza root-like, formed of tightly packed stolons. Stolons strongly flattened (diagenetic changes), 140—180 μm wide. Some stolons rise above surface of hydrorhiza, forming stem of colony. Colonial stem stolons less flattened, 80—100 μm wide, interweaved one with another.

The remaining specimens include fragments of stems or branches, consisting of 3—6 stolons. It so not excluded that all the specimens represent fragments of a single colony, disintegrated in the course of dissolving rock.

Remarks. — The thecae are unknown, so specific identification of this form is not possible.

Incertae familiae

Genus *Calyxhydra* KOZŁOWSKI, 1959

Type species: *Calyxhydra gemellithecata* KOZŁOWSKI, 1959

Remarks. — KOZŁOWSKI (1959*a*) assigned to this genus three species: *C. gemellithecata* KOZŁOWSKI, 1959, *C. constricta* KOZŁOWSKI, 1959, and *C. irregularis* KOZŁOWSKI, 1959. I interpret similar forms as stolons and cysts of sterile buds of Rhabdopleurida (e.g. *Cylindrotheca* EISENACK), so the species listed above require redescription and possibly also reinterpretation. Unfortunately, the type series of the species *Calyxhydra* are nowadays represented by broken holotype and paratypes only and attempts to gather new material failed. However, the possibility that *Calyxhydra* represents rhabdopleurids cannot be excluded.

Genus *Flexihydra* KOZŁOWSKI, 1959

Type species: *Flexihydra undulata* KOZŁOWSKI, 1959

Diagnosis. — See KOZŁOWSKI (1959*a*: 225).

Remarks. — Monotypic genus. Systematic position within Thecaphora unclear.

Flexihydra undulata KOZŁOWSKI, 1959

(pl. 24: 1—4)

1959*a*. *Flexihydra undulata* KOZŁOWSKI; KOZŁOWSKI: 225, fig. 7.

Material. — Six specimens from boulder ZPAL 0.15.

Description. — Detailed morphological description of this species was given by KOZŁOWSKI (1959*a*).

Ultrastructure. — TEM studies showed homogeneity of hydrothecae periderm. Hydrothecae are infilled with accumulations of organic material highly specific in form and ultrastructure (pl. 24: 1—4).

The outer part of the matter is markedly condensed and it seems to form some kind of membrane (pl. 24: 4). At larger magnifications it may be noted that this membrane is of granular character (pl. 24: 1). Identical granules as those forming the membrane occur directly beneath it, differing in less dense spacing only.

I am inclined to interpret these accumulations of organic matter inside hydrothecae as a possible outline of the hydranth body, formed of remains of periderm precursors occurring inside ectoderm cells. It also appears possible to interpret the external membrane of these accumulations as remains of so-called "thin pellicle" of D. M. CHAPMAN (1969), covering the hydranths of some hydrozoans, independently of thick periderm (see also p. 150).

Data on ultrastructure are, however, insufficient for making any statements on the chemical nature of periderm forming matter.

Occurrence. — The species is known from a single erratic boulder from the area of Poland (KOZŁOWSKI 1959*a*).

POGONOPHORES (POGONOPHORA)

Pogonophores are a relatively poorly known group of marine worm-like invertebrates, related to annelids (Annelida). SOKOLOV (1965, 1972) interpreted Sabellitida, known on the basis of organic tubes from the Lower Cambrian, as a fossil group of Pogonophora. From Ordovician erratic boulders, KOZŁOWSKI (1967) described two fragments of tubes, on the basis of which he proposed two monotype genera: *Ivanovites* KOZŁOWSKI and *Sokolovites* KOZŁOWSKI, assigned to Pogonophora.

Living tubes are the elements of pogonophores with the greatest chances of preservation in the fossil state. Biochemical studies on Recent pogonophores showed that a chitin-protein complex is the basic structural component of these tubes (BRUNET and CARLISLE 1958, BLACKWELL, PARKER and RUDALL 1965, FOUCART, BRICTAUX-GRÉGOIRE and JENNIAUX 1965). Pogonophore tubes were also examined by ultrastructural and ultrahistochemical techniques, carried out by GUPTA and LITTLE (1975), GEORGE (1977) and URBANEK and MIERZEJEWSKA (1977).

The morphology of tubes is of importance for the taxonomy of Pogonophora. Features such as length, diameter and ornamentation of the tubes and their differentiation into sections are helpful in identification of species and genera (IVANOV 1960, 1963), whereas they appear insufficient as criteria for families and orders. Therefore, I consider that all the fossil pogonophores should be treated as forms of incertae ordinis et familiae. The treatment of Sabellitida as an order of fossil Pogonophora (see SOKOLOV 1965) appears at least questionable and that group would be best treated as an informal taxonomic unit. In working on fossil pogonophores one should bear in mind the possibility of essential differences between individual sections of a given tube. The situation is additionally complicated by the fact that all the fossil tubes hitherto described are known only on the basis of fragments. The case of the Recent Pogonophora is not dissimilar because the material coming from seas is usually crushed (IVANOV 1960, 1963).

Toothed bristles of Pogonophora were not hitherto described in the fossil state and this may represent an example of selective fossilization. It is worthy of note that an enigmatic microfossil described as a probable gastropod radula from the Cretaceous of France by TAUGOURDEAU (1976) resembles fairly closely the bristles mentioned above.

Pogonophora JOHANSSON, 1937
Incertae ordinis et familiae
Genus *Sokolovites* KOZŁOWSKI, 1967

Type species: *Sokolovites pogonophoroides* KOZŁOWSKI, 1967

Diagnosis. — "Tube chitinoids, droit, subcylindrique, à surface irrégulière, garni de collerettes transversales membraneuses, disposées plus ou moins perpendiculairement à l'axe du tube" (KOZŁOWSKI 1967: 121).

Sokolovites pogonophoroides KOZŁOWSKI, 1967
(pl. 31)

1967. *Sokolovites pogonophoroides* KOZŁOWSKI; KOZŁOWSKI: 121, fig. 10.

Material. — Over a dozen specimens from the Upper Tremadoc of Zbilutka.

Description. — Fragments of tubes 0.4—3.1 mm long and 70—325 μm in diameter. External surface displays weakly marked transversal rings (pl. 31: 1, 4) and, locally, adjoining fragments of membrane (pl. 31: 1—3).

Ultrastructure. — SEM studies showed tube wall to be of granular structure (pl. 31: 2, 6).

Remarks. — The species was hitherto known on the basis of a single specimen from Ordovician erratic boulder ZPAL 0.498 (KOZLOWSKI 1967).

Genus *Beklemishevites* gen. n.

Type species: *Beklemishevites grandis* sp. n.

Derivation of the name: In honour of V. N. BEKLEMISHEV, an outstanding Soviet zoologist.

Diagnosis. — As for the type species.

Remarks. — Monotypic genus.

Beklemishevites grandis sp. n.

(pl. 30; pl. 32: 6—11)

Holotype: A fragment of living tube shown in pl. 32: 6 (ZPAL Po. I/2).

Type locality and horizon: Ordovician erratic boulder ZPAL 0.324 from Mochty.

Derivation of the name: Lat. *grandis* — great, on account of tube dimensions large in comparison with other known Ordovician Pogonophora.

Diagnosis. — Straight thick-walled tubes, circular in cross-section, 0.3—0.4 mm in diameter. External surface unornamented. Tube wall with laminar structure, displaying typical "Bouligand pattern".

Material. — Twenty seven fragments of tubes from the boulder ZPAL 0.324.

Description. — The holotype represents a fragment of unflattened tube, 18 mm long and 0.4 mm in diameter (pl. 32: 6). The remaining fragments vary from 1 to 8 mm in length and 0.3 to 0.4 mm in diameter. Some tubes are strongly flattened (pl. 32: 11). Tubes black, with mat, rough and unornamented outer, and smooth and shiny inner surface. External surface of two fragments of tubes display ovate openings, presumably representing traces after epibionts.

Ultrastructure. — SEM studies show laminar structure of the wall (pl. 30: 4). However, the micrographs obtained did not give any additional information on the nature of laminae. Electron micrographs obtained with the use of TEM clearly show that the laminae are built of characteristic parabolic fibres, forming the so-called "Bouligand pattern" (pl. 30: 2—3). This suggests that the tube of *B. grandis* gen. et sp. n, was built of chitin-protein complex.

Remarks. — The total tube length of *B. grandis* gen. et sp. n. remains unknown but it may be assumed that they were about a dozen or so cm long. The Recent species *Siboglinum cinctum* IVANOV is characterized by tubes of a similar diameter, 0.3—0.4 mm, and up to 15 cm long (IVANOV 1960).

Occurrence. — The species is hitherto known from a single erratic boulder from Mochty.

PTEROBRANCHIA

Pterobranchs (Pterobranchia) are treated as an order of the class Hemichordata by the majority of authors. BEKLEMISHEV (1951, 1957) assumed their affiliation to hemichordates, regarding them as representatives of the class Graptolithina. Phylogenetic relations between pterobranchs and graptolites have been the subject of discussions for several decades. The hypothesis of direct affinity between the two groups has been put forward on the begininng of this century by SCHEPOTIEFF (1905). It draw much attention and it even seemed to be fully supported by results of studies by KOZŁOWSKI (1938, 1947, 1949*a*, 1966*a*). According to the latter, this problem was solved by the discovery of homologous nature of fusellar tissue of graptolites and pterobranchs. However, the hypothesis of SCHEPOTIEFF and KOZŁOWSKI was questioned in the mid-seventies by URBANEK (1976*a*). This author presented results of his studies on ultrastructure of coenecium of modern and fossil Pterobranchia and a comparison with those obtained in the course of previous studies on ultrastructure of graptolite periderm (TOWE and URBANEK 1972, URBANEK and TOWE 1974, 1975). URBANEK found very large differences in ultrastructure and the mode of secretion of fusellar tissue in the two groups. According to him, the rank of these differences precludes homologization of fusellar tissue of Pterobranchia and Graptolithina and, therefore, casts some doubts on any close phylogenetic relations between these groups. The paper by URBANEK (1976*a*) initiated a new stage in discussion on relations between Pterobranchia and Graptolithina (ANDRES 1977, 1980, CROWTHER 1978, 1981, URBANEK 1978, and others), but this question still remains open.

The modern Pterobranchia form a small group of marine invertebrates represented by three genera only: *Cephalodiscus* M'INTOSH, 1882, *Atubaria* SATO, 1936, and *Rhabdopleura* ALLMAN, 1868. The first two of these are assigned to the order Cephalodiscida, and the third one — to the order Rhabdopleurida.

Both orders of Pterobranchia are known from the fossil material, from the Upper Ordovician upwards. From the Ordovician of Poland, KOZŁOWSKI (1949*a*, 1967) reported two monotypic genera of Cephalodiscida: *Eocephalodiscus* KOZŁOWSKI, 1949, and *Pterobranchites* KOZŁOWSKI, 1967. The latter genus is interpreted recently as an aberrant graptolite (MIERZEJEWSKI, 1984*a*). Moreover, some disputable remains of Cephalodiscida have been described from the Eocene of France and tentatively assigned to the genus *Cephalodiscus* M'INTOSH (BULMAN 1970).

Remains of Rhabdopleurida are much more common in the fossil record. They have been described for the first time from the Maastrichtian, Danian and Montian[4] of Poland (KOZŁOWSKI 1949*b*, 1956*a*), the Eocene of Great Britain (THOMAS and DAVIS 1949*a*, *b*), and subsequently from the Ordovician of Poland (KOZŁOWSKI 1961, 1967, 1970*a*), Öland (EISENACK 1976*a*) and W. Germany (ANDRES 1977), the Silurian of Poland (MIERZEJEWSKI 1977), Carboniferous of Belgium (MORTELMANS 1955) and Jurassic (KULICKI 1969, 1971) and Cretaceous of Poland (KULICKI and MIERZEJEWSKI, in preparation). Moreover, ANDRES (1977) and MIERZEJEWSKI (1977) noted that microfossils described as ?*Graptovermid* sp. gen. and sp. indet. by SKEVINGTON (1965*a*) actually represent tubes of Rhabdopleurida. Identical fragments of tubarium of Rhabdopleurida were described as thecae of the graptolite *Mastigograptus* RUEDEMANN by ANDRES (1961) who later (ANDRES 1977) corrected this misidentification.

In citing undoubted records of fossil representatives of the Rhabdopleurida it is worth mentioning an enigmatic fossil described from the Carboniferous of Mazon Creek (USA) by NITECKI and SCHRAM (1976). The form, known as *Etacystis communis* NITECKI and SCHRAM, is without coenecium but, nevertheless, it clearly resembles the zooid of *Rhabdopleura* in body shape.

Fossil remains of Pterobranchia may markedly vary in the state of preservation. There are known single findings of imprints of tubarium (MORTELMANS 1955) as well as pyritized and silicified tubaria (THOMAS and DAVIS 1949*a*, *b*, and BULMAN 1970, respectively). However, most of the Palaeozoic, Mesozoic and Cenozoic forms have been obtained by etching carbonate rocks with acids. Material obtained with the use of that method is usually strongly crushed but, nevertheless, it appears sufficient for studying very fine morphological details as well as ultrastructure.

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[4] KOZŁOWSKI (1949*b*, 1956*a*) found the remains in rocks dated as the Maastrichtian and Danian; a part of the latter were subsequently shown to represent the Montian by POŻARYSKA (1968).

THE STRUCTURE OF THE RHABDOPLEURIDA COENECIUM

The skeleton of modern Rhabdopleurida, called as either tubarium or coenecium, represents a system of elements, comprising stolonal and zooidal tubes, stolons and cysts of sterile buds. The morphology of these elements in modern *Rhabdopleura* has been studied in detail by SCHEPOTJEFF (1907, 1909). All the elements of tubarium are built of organic matter. The chemical nature of that matter still remains disputable but it may be already stated that chitin is missing here (SUNDARA-RAJULU, JENNIAUX and VOSS-FOUCART 1982). Moreover, aminoacid analysis has shown protein character of the organic matter (FOUCART, BRICTEUX-GRÉGOIRE, JENNIAUX and FLORKIN, 1965) and electron microscope and x-ray studies — the presence of proteins of the keratin group (DILLY 1971 and his data reported by URBANEK 1976*a*). However, the results were questioned by BAIRATI (1972) and HARE (unpublished data reported by URBANEK 1976*a*).

The knowledge of the skeleton structure of Palaeozoic Rhabdopleurida still remains unsatisfactory as it is based mostly on results of studies by KOZŁOWSKI (1961, 1967, 1970*a*). The structure of the coenecium of *Rhabdopleuroides expectatus* KOZŁOWSKI was exceptional as it was found to be characterized by trailing zooidal tubes, unknown in modern forms (KOZŁOWSKI 1961). Moreover, colonies of *Rhabdopleurites primaevus* KOZŁOWSKI were assumed to be characterized by dendroid structure (KOZŁOWSKI 1970*a*). The comparisons of fusellar tissue of Ordovician *Rhabdopleurites primaevus* KOZŁOWSKI, Jurassic *Rhabdopleura kozlowskii* KULICKI and modern *Rhabdopleura compacta* HINKS, carried out by URBANEK (1976*a*), showed that the ultrastructure of periderm in Rhabdopleurida has not changed at least since the Ordovician.

The Mesozoic Rhabdopleurida found hitherto are represented by two species of the genus *Rhabdopleura* ALLMAN: Jurassic *Rh. kozlowskii* KULICKI and Cretaceous-Tertiary *Rh. vistulae* KOZŁOWSKI. They do not display any significant differences in relation to modern species of that genus but it should be noted that *Rh. vistulae* is an important link between early Palaeozoic and modern Rhabdopleuridae (see p. 183).

After analysing the available material I concluded that two basic types of structure may be differentiated for both fossil and modern Rhabdopleuridae:

— fusellar type, with fully fusellar stolonal tubes; and

— partly nonfusellar type, with partly nonfusellar stolonal tubes.

The fusellar type is typical of the genera *Rhabdopleura* ALLMAN, *Rhabdopleuroides* KOZŁOWSKI and most probably *Kystodendron* KOZŁOWSKI. Stolonal tubes are fully fusellar, trailing, with clearly marked zig-zag suture in the first two genera. Tubes of *Kystodendron* are almost unknown but the structure of the remaining elements of tubarium implicates that their development was identical as in *Rhabdopleura* and *Rhabdopleuroides*.

The partly nonfusellar type is known in the genus *Rhabdopleurites* KOZŁOWSKI only, but it is not excluded that it was also present in the species *Stolonodendrum parasiticum* KOZŁOWSKI (see p. 176). Tubaria of that type were hitherto unknown in the Rhabdopleurida. KOZŁOWSKI (1967, 1970*a*) and ANDRES (1977) described partly nonfusellar tubes in *Rhabdopleurites* but they failed to interpret them correctly. KOZŁOWSKI (1970*a*) compared the nonfusellar part to "embryonal vesicle" of *Rhabdopleura* and the graptolite prosicula. The specimens described by these authors actually represent stolonal tubes with partly nonfusellar structure. All the stolonal tubes of Rhabdopleurida known hitherto are characterized by purely fusellar structure, with marked zig-zag suture, and they represented creeping structures. In turn, *Rhabdopleurites* was found to display creeping and erect nonfusellar stolonal tubes as well as creeping and erect stolonal tubes with all the features of fusellar structure, except for zig-zag suture.

In differentiating, partly nonfusellar type of coenecium, I have taken into account the possibility that such character of stolonal tubes may be apparent, due to specific preservation of fusellar periderm only, i.e. phenomenon noticed sometimes in graptolites. However, the following data speak against that hypothesis, giving further support to originally nonfusellar character of the structure:

1) In specimens displaying nonfusellar part, a sharp boundary may be traced between clearly a nonfusellar and fusellar parts (see KOZŁOWSKI 1970*a*, pl. 2: 3 and here pl. 26: 12—16).

2) The nonfusellar parts contact the fusellar at one side only. If the lack of fusellar structure was due to preservation only, there should occur fusellar tubes with "intercalations" not displaying such structure. The analysis of some hundred of fusellar tubes of *Rhabdopleurites* failed to show a single case of nonfusellar part contacting the fusellar ones at its both ends.

3) The studies by URBANEK (1976*a*) cited above, unequivocally showed that structural units of periderm and their spatial arrangement have remained unchanged in the Rhabdopleurida at least since the Ordovician. If the lack of fusellar structure was due to preservation only, one could expect its presence in tubaria of other rhabdopleurids. However, this is not the case, as such structures have not been found in any other fossil forms.

4) Preliminary electron microscope studies (see p. 179) showed that the nonfusellar periderm differs essentially from the fusellar (see URBANEK 1976*a*) in ultrastructure.

The coenecium of modern Rhabdopleurida is characterized by the presence of cysts of sterile buds, fairly common within a colony. They have been described for the first time under the name hybernacula by LANKESTER (1884). He assumed that they represent normal buds, the growth of which had been impeded. Subsequently, SCHEPOTIEFF (1907) interpreted them as sterile buds, stating that they become most common in the autumn and, therefore, may be interpreted as a mode of adjustment of colony to survive the winter. Detailed studies on sterile buds have been carried out quite recently by STEBBING (1970), who described the mode of their origin in the colony and the process of enveloping by cysts. He found a bud to represent ovoidal to spherical yolk mass with pigment spots in the outer zone and initially without cysts. Cysts starts to develop some time after the bud is formed, growing distally from the stolon to which the bud is attached. With time the cyst became completely closed, being connected with the colony by a stolonal opening. Yolk matter accumulated in the cyst is subjected to resorption, so the latter becomes empty except for some small spherical tissue mass. The buds may turn into zooids in *Rhabdopleura compacta* but, nevertheless, STEBBING (1970) regards them as most important for storage of nutrients for the colony. Further studies on sterile buds and their cysts were carried out by DILLY (1975) with the use of the electron and light microscopes.

Cysts of sterile buds of the Rhabdopleurida, reported from the Bathonian (Jurassic) of Poland by KULICKI (1971) are the oldest hitherto found. This seems somewhat enigmatic as:

1) fossil fusellar tubes of the Rhabdopleurida are known from the Ordovician upwards in the geological column;

2) cysts of sterile buds are most massive elements of the coenecium and, therefore, their fossilization potential is the highest;[5]

3) Ordovician *Eorhabdopleura urbaneki* KOZŁOWSKI, 1970 does not differ in any significant way from zooidal tubes of modern species of the genus *Rhabdopleura*.

The question of either real or apparent lack of cysts in Ordovician and Silurian rocks may be explained in two ways:

1) Early Palaeozoic forms still did not develop cysts; or

2) Early Palaeozoic forms had cysts but the latter used to be erroneously assigned to other group of organisms.

A third possibility, i.e. that the cysts exist but are still to be found, may be neglected if we take into account the vast literature dealing with organic microfossils and their high resistance to the diagenetic agents.

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[5] A high resistance of cysts to diagenetic agents was noted by KULICKI (1969), who found that *Rh. kozlowskii* is represented in some samples by cysts only.

The analysis of very rich material, review of the literature and the experience gathered in the course of extraction of microfossils from rocks (see p. 138) made it possible to state that the Rhabdopleurida cysts were repeatedly described in the literature but as gonothecae or hydrothecae of hydrozoans. An example is the paper by EISENACK (1976), in which zooidal tubes are described as ?Rabdopleuridae stolons (sic!); and original stolons with cysts as a hydrosome of hydrozoan *Cylindrotheca profunda* EISENACK!

The available data indicate, however, that Ordovician and Silurian rocks yield both cyst-bearing forms and those without cysts, i.e. Rhabdopleuroididae fam. n. and Rhabdopleuritidae fam. n. At present it is difficult to state whether or not the lack of cysts in the latter also means the lack of sterile buds as there remains a theoretical possibility of the presence of buds incapable of forming cysts. This theoretical possibility could be neglected if it is proved that cysts are necessary for buds for physiological reasons.

Cysts of sterile buds of Ordovician and Silurian Rhabdopleuridae are highly varying in morphology. The differences are so high that we may even speak about polymorphism. Cysts of *Kystodendron tener* sp. n. and *Kystodendron* sp. B appear most similar to those of modern species of the genus *Rhabdopleura*. The former are ovoid in shape, sometimes fairly elongate, and either seated or peduncular stolons variable in length or separated from them (pl. 29: 25—27). Cysts of *Kystodendron longicarpus* (EISENACK) *sensu* KOZŁOWSKI often develop stolons, here called secondary peduncular stolons, in their distal part. Such stolons pass into the next cyst, here termed "composite" to distinguish the relationship from simple ones of *Rhabdopleura* and *Kystodendron tener* sp. The extent of composite cysts is highest in *K. complicatus* sp. n.

Composite cysts have not been found in modern species of *Rhabdopleura* but their equivalent may be noted in fossil *Rh. vistulae* KOZŁOWSKI (see p. 181) and as yet undescribed *Rhabdopleura* sp. from a Cretaceous erratic. I consider the following interpretation of composite cysts may be plausible. The sterile bud of *Rhabdopleura* is nothing less than a specialized fragment of a stolon, adjusted to store nutrients. However, it may turn into zooid (STEBBING 1970) which means that the loss of the original properties of the final section of stolon is not complete. As the sterile bud retains the capability to reorganization, there is no reason to exclude recurrent reorganization of sterile buds into stolons as an alternative of reorganization into zooids in fossil forms. When this is the case, it follows that stolons retain the ability to grow and eventually form zooids and sterile buds.

REMARKS ON THE SYSTEMATICS OF THE RHABDOPLEURIDA

Problems of the systematics of the Rhabdopleurida were essentially beyond discussion in past literature. This may be explained by the fact that untill 1961 the known range of this order was limited; the only genus known then times, was *Rhabdopleura* ALLMAN, with a few species differing little from one another. In years, KOZŁOWSKI (1961, 1967, 1970*a*) described new genera of the Rhabdopleurida but he left aside the question of their affiliation to a taxon at family rank. It should be noted here that KOZŁOWSKI was presumably rather against the use of the family as a taxonomic unit and review of his papers on Dendroidea, Camaroidea and Stolonoidea (KOZŁOWSKI 1949*a*, 1966*b*), Crustoidea (KOZŁOWSKI 1962), Pterobranchia (KOZŁOWSKI 1961, 1967, 1970*a*), Polychaeta (KOZŁOWSKI 1956*b*) and other organic microfossils (KOZŁOWSKI (1967) show that he was consistent in that approach.

The taxonomy of the fossil Rhabdopleurida at the suprageneric level was analysed by BULMAN (1970) who placed all the genera of that order in the family Rhabdopleuridae.

On the basis of the newly-obtained data on the morphology of fossil Rhabdopleurida I am inclined to present a different approach to the systematics of this group of pterobranchs. First of all I think that attention should be paid to the presence of nonfusellar part in tubarium of *Rhabdopleurites*. The presence of nonfusellar tubes in old parts of colonies and their absence in the youngest, indicates that a specific metamorphosis of a terminal bud must have taken place in the course of that astogeny. In the Rhabdopleurida colony the terminal bud is responsible for both its growth and formation of stolonal tubes. The phenomenon of rapid transition from nonfusellar to fusellar structure within a single stolonal tube indicates metamorphosis of the terminal bud, reflected by a change in the mode of secretion of periderm. Taking into account this specific metamorphosis of the terminal bud, I assume a markedly isolated position of *Rhabdopleurites* among Rhabdopleurida. I regard this genus as representing a separate, blind phylogenetic line, here differentiated as the family Rhabdopleuritidae nov. The family Rhabdopleuroididae nov., comprising the genus *Rhabdopleuroides* only, represents another offshoot, and the family Rhabdopleuridae, comprising the genera *Kystodendron* and *Rhabdopleura* — a third phylogenetic line.

The available data suggest that expansion of the Rhabdopleurida took place in the Ordovician, when this order was represented by three families. Of these families, the Rhabdopleuridae survived until the present, whereas the two remaining families presumably became extinct by the end of the Ordovician.

The taxonomy of fossil Rhabdopleurida at the specific and generic levels appears fairly difficult and complex. This is due to the following reasons: a) taxonomy of the modern forms is not much help from the point of view of methodological premises as it deals with three species and one genus only, b) the morphology of the skeletal elements is highly variable within a given species or genus and both the diagnostic value and the reasons of that variability remain debatable, and c) skeletons of fossil forms are as a rule preserved as small isolated fragments which further impedes their interpretation. That is why I abandoned revision of some taxa for taxonomic decisions taken in the present state of knowledge, and on the basis of insufficient material, could not be convincing but rather contributing to the existing mess in the taxonomy of this group. This is the case with the possible synonymy of *Stolonodendrum parasitum* KOZŁOWSKI, 1949, *Conitubus siculoides* KOZŁOWSKI, 1949 and *Rhabdopleurites primaerus* KOZŁOWSKI, 1967 and the systematic positions of forms treated below as incertae sedis (?Pterobranchia)

STOLONOIDEA — GRAPTOLITES OR PTEROBRANCHS?

The order Stolonoidea has been proposed on the basis of material from the Tremadoc in the Wysoczki locality by KOZŁOWSKI (1949*a*). The forms, fairly fragmentary and rare, are placed in a single genus *Stolonodendrum* KOZŁOWSKI, comprising two species. KOZŁOWSKI (1949*a*) regarded the Stolonoidea as a group of primitive graptolites, which developed independently of other orders. In turn, OBUT (1964) assumed that the Stolonoidea evolved from the same ancestors as dendroid graptolites of the family Dendrograptidae. URBANEK (*in*: KUŹNICKI and URBANEK 1967) noted that there are no marked differences in the morphology of the Stolonoidea and the Rhabdopleurida. Similarly the Stolonoidea are characterized by the lack of apertural modifications, the presence of autho- and stolothecae, and a perforational mode of budding. According to him "Stolonoidea presumably represent an offshoot which evolved from a group close to the Rhabdopleurida, independently of other groptolites, to form a tribe subjected to minor modifications only" (URBANEK *in*: KUŹNICKI and URBANEK 1967: 433).

The hypothesis of affiliation of the Stolonoidea to graptolites may be very seriously questioned in the light of the present state of knowledge of fossil Rhabdopleurida. It should be noted that colonies of *Rhabdopleurites primaevus* and *Stolonodendrum parasiticum* appear strikingly similar. The fragments of *Stolonodendrum parasiticum* colonies found hitherto have the form of branching creeping tubes. The tubes, initially nonfusellar, gradually widen and smoothly pass into fusellar ones. Nonfusellar parts of the tubes were interpreted by KOZŁOWSKI (1949*a*) as stolons and the fusellar — as thecae. BULMAN (1955, 1970) also regarded Stolonoidea as graptolites but he noted that such smooth transition between stolon and theca is not known in other graptolites. It is worth noting here that such transition is also unknown in the Rhabdopleurida.

I think that the known fragments of *S. parasiticum* colonies should be interpreted in an entirely different way then in KOZŁOWSKI (1949*a*). I regard the supposed stolons of this species as homologous to nonfusellar stolonal tubes in *Rhabdopleurites primaevus* and the supposed thecae to fusellar stolonal tubes in the latter. Therefore, I do not regard *Stolonodendrum parasiticum* as a primitive graptolite but rather a rhabdopleurid of the family Rhabdopleuritidae.

The above interpretation of fragments of *Stolonodendrum parasiticum* colony makes it possible to assume that stolons and zooidal tubes of that species are not represented in its type series. I think that stolons have been independently described as such elements of *Stolonodendrum* sp. A—F by KOZŁOWSKI (1949*a*) and erect fusellar parts served as the type material for describing the tuboid graptolite *Conitubus siculoides* KOZŁOWSKI, 1949 [6]. The stolons of *Stolonodendrum* sp. A—F do not differ from those of *Rhabdopleurites primaevus*. In turn, the presence of a nonfusellar part of periderm in the basal part of "autotheca" and its transition into the creeping tube, markedly smaller in diameter, were interpreted as characteristic morphological features of *Conitubus siculoides* KOZŁOWSKI (see KOZŁOWSKI 1949*a*, fig. 46b and pl. 15, fig. 9).

Doubts concerning the graptolitic nature of *Conitubus siculoides* KOZŁOWSKI and some reservations in relation to the taxonomy of the genus *Epigraptus* EISENACK (=*Idiotubus* KOZŁOWSKI), put forward elsewhere (MIERZEJEWSKI 1978*b*), show that it would be desirable to revise the Tuboidea described by KOZŁOWSKI (1949*a*).

DESCRIPTION

Class **Pterobranchia** Lankester, 1877
Order **Rhabdopleurida** Fowler, 1892
Family **Rhabdopleuroididae** fam. n.

Type genus: *Rhabdopleuroides* KOZŁOWSKI, 1961

Diagnosis. — Coenecium exclusively composed of creeping stolonal and zooidal tubes and stolons without cysts of sterile buds.

Remarks. — Monotypic family.

Genus *Rhabdopleuroides* KOZŁOWSKI, 1961

Type species: *Rhabdopleuroides expectatus* KOZŁOWSKI, 1961 (monotype)

Diagnosis. — As for family.

Occurrence. — Ordovician of Poland.

Rhabdopleuroides expectatus KOZŁOWSKI, 1961

1961. *Rhabdopleuroides expectatus* KOZŁOWSKI; KOZŁOWSKI: 4, figs. 1—3.
1970*a*. *Rhabdopleuroides expectatus* KOZŁOWSKI; KOZŁOWSKI: 5, pl. 1: 1—2.

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[6] KOZŁOWSKI (1949*a*) placed this genus in the family Idiotubidae (=Cyclograptidae). However, it differs from all the other tuboid graptolites in the lack of a zig-zag suture. This feature brings it closer to graptolites *Mastigograptus* RUEDEMANN and *Micrograptus* EISENACK and it should be noted that is was regarded as related to the latter by ANDRES (1977).

Diagnosis. — See Kozłowski (1961: 4—5).

Material. — About a dozen decoloured and strongly crushed fragments of coenecium from erratic boulders ZPAL 0.22, ZPAL 0.25, ZPAL 0.42, ZPAL 0.60, ZPAL 0.90 and ZPAL 0.169 as well as from the borehole at Mielnik (depth 1118—1124 m).

Remarks. — No additional material was found and some of the specimens gathered by Kozłowski became crushed or even completely destroyed as a result of intense decolouring.

The holotype of *Rhabdopleuroides expectatus* has become dissolved in glycerine in which it had been kept and in this way Kozłowski (1970*a*) designated the neotype. However, this designation appears invalid in the light of the principles of zoological nomenclature. According to Article no. 75 of the International Code of Zoological Nomenclature, a neotype may be designated only when a type series has been destroyed or lost and providing that certain formal requirements are met. In the present case all the specimens of type series except for the holotype were available. Therefore only one of them could be chosen as neotype. However, Kozłowski (1970*a*) designated a specimen coming from a new locality (Mielnik borehole). For this reason I designate as a lectotype a specimen from the type series, described, figured and designated as paratype by Kozłowski (1970*a*: 7; fig. 2).

Occurrence. — Ordovician of Poland.

Family **Rhabdopleuritidae** fam. n.

Type genus: *Rhabdopleurites* Kozłowski, 1967

Diagnosis. — Dendroidal-encrusting coenecium. Stolothecal tubes nonfusellar in some parts. Cysts of sterile buds missing.

Remarks. — Monotypic family.

Genus *Rhabdopleurites* Kozłowski, 1967

Type species: *Rhabdopleurites primaevus* Kozłowski, 1967

Emend. diagnosis. — As for the species.

Remarks. — Monotypic genus. From the biological point of view, it is worth noting an interesting convergence of colonies of *Rhabdopleurites* Kozłowski and the tuboid graptolite *Kozlowskitubus* Mierzejewski. The forms resemble one another mainly in the organization of the colonies as both of them were forming dendroid encrusting colonies. The colonies consist of an encrusting part, comprising stolonal tubes, and a dendroid part, also comprising a system of stolons. Colonies of that type are unknown in any other Rhabdopleurida or Graptolithina which is very difficult to explain in terms of phylogeny. However, it is worth to note here that Kozłowski (1949*a*) regarded the Tuboidea as graptolites most closely related to pterobranchs.

Rhabdopleurites primaevus Kozłowski, 1967

(pl. 26, pl. 27: 1—2, pl. 29: 1—13)

?1959*a*. *Palaeotuba dichotoma* Kozłowski; Kozłowski: fig. 13.
1961. Art Nr 3; Andres: 641, figs. 7—8, 10d.
1965*a*. *?Graptovermid* sp., gen. et sp. indet.; Skevington: 63, figs. 68—72.
1967. *Rhabdopleurites primaevus* Kozłowski; Kozłowski: 126, fig. 15.
1970*a*. *Rhabdopleurites primaevus* Kozłowski; Kozłowski: 6, pl. 2.
1977. *Rhabdopleurites*: Andres: 72, figs. 23—25.

Emend. diagnosis. — Fusellar tubes varying from 0.3 to 0.6 mm in width and fuselli 60 to 100 μm wide. Fusellus collars varying in size, sometimes very large. Some stolonal tubes nonfusellar. Stolons without diaphragms. Sterile bud cysts missing. Colony encrusting-dendroidal, with dendroidal part underdeveloped, composed of stolonal and zooidal tubes.

Material. — Some hundred of fragments of coenecium (fusellar and nonfusellar tubes, isolated and with stolons) from Ordovician erratic boulders ZPAL 0.400, ZPAL 0.533, ZPAL 0.542, ZPAL 0.544 and ZPAL 0.601.

Revised description. — The material comprises fragments identifiable as encrusting and dendroid parts of coenecium as well as practically unidentifiable fragments.

The encrusting part of the coenecium is preserved as an entangled mass of stolonal tubes and stolons (pl. 26: 17). The periderm of stolonal tubes poorly preserved, translucent, yellow to brown in colour, usually nonfusellar except for locally traceable fusellar parts. No zig-zag suture was found in the fusellar portions. Stolons highly variable in thickness (20—75 μm), black and opaque or yellow-brown and translucent. Branchings of stolons fairly chaotic in appearance; their more detailed analysis is precluded by insufficient preservation of material. Dichotomous branchings of stolons sporadically found.

The dendroid part represented by fusellar are tubes circular in cross-section (pl. 26: 1—8), and the most common element of coenecium of *Rh. primaevus.* The longest of them, up to 1500 μm, and from 300 to 600 μm in diameter (about 400 μm on average). Apparent diameter of tubes flattened in the course of diagenesis may exceed 1 mm. Some tubes display marked changes in diameter (pl. 26: 3—5).

The periderm of tubes well preserved, light-brown or yellow, translucent. Fuselli highly variable, varying from 60 to 100 μm and occasionally even from 40 to 110 μm in width. The collars of fuselli also highly varying in development (pl. 26: 1—8). The fuselli usually ring-like, only sporadically with an oblique suture.

Zoodial tubes are indistinguishable from fusellar stolonal tubes of the dendroid part when the latter are preserved without stolons. They may be identified with certainty only when connected to large fragments of coenecium. The specimen shown in pl. 29: 13 represents a fragment of coenecium consisting of zooidal tube (zt), two stolonal tubes (st) and bifurcating stolon (s, s_1, sp). The zooidal tubes in this specimen is clearly wider than the stolonal (300 μm and 45—125 μm in diameter, respectively). It may be assumed that the widest of the fusellar tubes found represent fragments of zooidal tubes. This is further supported by the fact that unquestionable stolonal tubes are below 400 μm in diameter. Transition of stolonal tube into the zooidal appears gradual and the boundary between the tubes is marked by the end of a peduncular stolon. Peduncular stolons are long (up to 410 μm long), characterized by a more or less strongly marked widening in the distal part (pl. 29: 13), and are sometimes globular in shape (pl. 26: 11). The distal part of that stolon is usually more transparent than the rest of stolonal system suggesting a thinner wall. The dendroid parts are also represented by nonfusellar-fusellar tubes (pl. 26: 12—16) which, however, are less common than the fusellar. The stolons of the encrusting part appear mainly related to nonfusellar tubes which suggests that the tubes represent fragments of stolonal ones in which we are dealing with passage from nonfusellar to fusellar structure. Boundary between nonfusellar and fusellar parts is fairly sharp and strikingly similar to that between the nonfusellar prosicula and the fusellar metasicula in graptolites. Collars of fuselli are very poorly developed in such tubes. No marked changes in diameter were found in the proximity of the passage from nonfusellar to fusellar tube.

Nonfusellar tubes sometimes display openings located at the top of small conical projections. Identical projections were described from fusellar tube by Kozłowski (1970*a*, fig. 13 D). I think that this is a structure connected with perforatory budding.

The material comprises numerous stolons with fragments of periderm (pl. 29: 1—12). Identical stolons but lacking even minute fragments of the periderm of stolonal tube are also common. It is highly probable that they also represent fragments of *Rh. primaevus.*

Ultrastructure. — Electron microscope studies of fusellar tubes of *Rh. primaevus*, carried out by URBANEK (1976*a*), showed that elementary structural units of periderm and their spatial arrangement are consistent with the ultrastructural image of periderm in modern Pterobranchia. Moreover, ANDRES (1980) found secondary, unfusellar periderm layers, typical of Rhabdopleurida, on the inner surface of fusellar tubes. Taking this into account I limited the range of my studies to TEM analysis of periderm of nonfusellar tubes and stolons.

Nonfusellar tubes are built of periderm with clearly laminar structure (pl. 27: 1). The periderm is formed of closely packed thin membranes, the number of which is difficult to precise but surely exceeds 10. Because of laminar structure, the periderm displays distinct trend to fragment into layers.

The structure of the stolons is fairly compact but sometimes it is possible to see that they are built of homogeneous matter, formed as a result of cementation of long straight fibres (pl. 27: 2).

Remarks. — The revised description of *Rhabdopleurites primaevus* given above is based on an analysis of the type material (erratic boulder ZPAL 0.400) as well as a newly collected specimens. The studies showed that the type series of this species did not comprise the whole material extracted from the boulder ZPAL 0.400 by KOZŁOWSKI (1967) who proposed that taxon on the basis of isolated fusellar tubes, generally termed by him zooidal, leaving aside a large part of the material. My studies on the material gathered by KOZŁOWSKI showed that it comprises stolonal tubes with stolons and isolated fusellar tubes and stolons.

The record of fusellar stolonal tubes circular in cross-section in the material studied gave support to the hypothesis of dendroid nature of the coenecium of *Rhabdopleurites primaevus*, put forward by KOZŁOWSKI (1970 *a*). The analysis showed that in this species coenecia are partly developed in encrusting and partly in dendroid form. The fragments recorded suggest that the dendroid part was here poorly developed (see e.g. pl. 29: 13).

On the basis of a few fragments of dichotomously branching stolons from the erratic boulder ZPAL 0.31, KOZŁOWSKI (1959*a*) described the species *Palaeotuba dichotoma* KOZŁOWSKI, 1959, interpreting it as a hydroid. This form is practically undistinguishable from stolons of *Rhabdopleurites primaevus* which sometimes also display dichotomous subdivision. I regard *Palaeotuba dichotoma* as stolons of Rhabdopleuritidae and they are most probably conspecific with *Rhabdopleurites primaevus*. However, it is inadvisable to recognize *Rh. primaevus* KOZŁOWSKI, 1967 as a junior synonym of *Palaeotuba dichotoma* Kozłowski, 1959 as there is no information on the presence of fusellar tubes in the boulder ZPAL 0.31. Moreover, stolons of the two nominal species are too simple in morphology to give a reliable basis for specific identification, especially as they are very similar to those of *Stolonodendrum* sp., described by KOZŁOWSKI (1949*a*) from the Tremadoc of Wysoczki. Electron microscope studies showed that the stolon of *P. dichotoma*, coming from the type series of this species, has an homogeneous structure (MIERZEJEWSKI 1974) which makes it unimportant for taxonomic discussion. I think that the specific name *Palaeotuba dichotoma* KOZŁOWSKI, 1959 should be treated as *nomen dubium*.

Fusellar tubes of *Rhabdopleurites primaevus* have been described by ANDRES (1961). They were originally described as thecae of the graptolite *Mastigograptus* RUEDEMANN but his misidentification was corrected later (ANDRES 1977). Fusellar stolonal tubes with stolons of *Rh. primaevus* were also found by SKEVINGTON (1965*a*) who assigned them to Graptovermida. I regarded the specimens as related to Rhabdopleurida, erroneously placing them in the species *Eorhabdopleura urbaneki* KOZŁOWSKI (MIERZEJEWSKI 1977). Their correct identification was made by ANDRES (1977).

As noted above, *Rh. primaevus* differs from all the remaining fossil and modern Rhabdopleurida in the presence of partially nonfusellar coenecium. A typical structure of the coenecium may raise some doubts as it may possibly be due to diagenetic factors. It should be noted here that in his description of the discovery of nonfusellar-fusellar tube, KOZŁOWSKI (1967) tried to explain the nonfusellar structure as due to fossilization processes. Subsequently he found another specimen, interpreting it as initial part of colony, similar to the graptolite sicula, composed of nonfusellar prosicula and fusellar metasicula (KOZŁOWSKI 1970*a*). The existence of nonfusellar-fusellar tubes has been confirmed by ANDRES (1977). I found such tubes in the material from all the *Rhabdopleurites*-bearing erratic boulders. Therefore, I think that partially nonfusellar character of the tubarium is not an artifact, i.e. effect of diagenetic changes (see also p. 173). This seems to be fully confirmed by TEM micrographs. Ultrastructural studies make possible a full comparison of nonfusellar periderm of *R. primaevus* and secondary periderm layers of *Rhabdopleura* (ANDRES 1980, DILLY, unpublished data) and *Cephalodiscus* (ANDRES 1980, URBANEK, DILLY and MIERZEJEWSKI, unpublished data). The secondary layers, strewing fusellar tube from the inside and covering from the outside, are built of densely packed membranes and display laminar structure. The ultrastructural similarity of these secondary layers and nonfusellar periderm of *Rhabdopleurites primaevus* is unquestionable. As this is the case, the nonfusellar character of periderm can not be treated as evidence for qualitatively different skeletal matter in *Rh. primaevus*.

In biological terms the presence of nonfusellar periderm may be explained in two ways:

1) The fusellar phase was left out and secretion of periderm started with deposition of secondary layers.

2) The fusellar phase was very strongly reduced in the process of secretion of periderm at the advantage of the phase of formation of secondary layers. Poorly developed fuselli either could not be fossilized or they underwent resorption during the lifetime of an individual.

In the former case, the above mentioned metamorphosis of the terminal bud would be connected with achieving the ability to secrete fuselli, and in the latter with sudden increase of resistance of fuselli to the influence of diagenetic agents or the ability to be resorbed. TEM studies on the passage from nonfusellar part of tube to the fusellar should give a basis for solving the question of the mechanismus responsible for nonfusellar nature of periderm.

In discussing the question of partially nonfusellar nature of the coenecium in *Rh. primaevus*, it is worth comparing that case and a similar phenomenon in the graptolite *Mastigograptus* sp. URBANEK and TOWE (1974) found the lack of a fusellar layer in large parts of the periderm of that graptolite, assuming that this may be due to resorption during life. The similarity is interesting, especially if one accepts the hypothesis of direct phylogenetic relations of pterobranchs and graptolites.

Rhabdopleurites primaevus remains the only hitherto described species of the genus *Rhabdopleurites* KOZŁOWSKI. Taking into account the marked variability in development of fusellar collars and the diameter of fusellar tubes, ANDRES (1977) stated that his material may comprise more than one species. However, the variability may be intra-specific type. The analysis of the type series of this species also showed high variability in both the mode of development of the fusellar collars (pl. 26: 1—8) and the diameter of the fusellar tubes. The variability in diameter of the tubes within a single colony is best displayed by the specimen shown in pl. 29: 13.

Occurrence. — Ordovician of Poland, W. Germany and Sweden (Öland).

?*Rhabdopleurites* sp.

(pl. 32: 4—5)

Material. — Six bunches of stolons from erratic boulders ZPAL 0.499, ZPAL 0.693 and the borehole Biała Podlaska 2 (depth 680—687 m), Ordovician.

Description. — Strongly branching bunches of stolons, up to 4.1 mm long. Periderm black, opaque, except for terminal parts of lateral branchings — brown and translucent. Surface of stolons smooth or with membrane-like patches. Terminal parts of lateral branchings widened. Stolons 43—71 μm thick, branching in various planes.

Remarks. — Affiliation of the form described above to the Rhabdopleurida, especially *Rhabdopleurites* seems highly probable. The microfossils may correspond to the stolon system of the dendroid part in the *Rhabdopleurites* colony. This is supported by the presence of characteristic membrane-like patches on stolons, which resemble remains of the periderm of stolonal tubes, as well as the similarity of the distal portions of branchings to peduncular stolons of *Rh. primaevus*.

Family **Rhabdopleuridae** HARMER, 1905

Type genus: *Rhabdopleura* ALLMAN, 1869

Diagnosis. — Creeping coenecia. Stolonal tubes and proximal parts of zooidal ones creeping, distal parts of zooidal tubes erect. Sterile buds surrounded by cysts.

Remarks. — The family Rhabdopleuridae comprises two genera: *Rhabdopleura Allman*, 1869 and *Kystodendron* KOZŁOWSKI, 1959.

Fossil remains of *Rhabdopleura* are known from strata not older than the Jurassic (KULICKI 1969, 1971). MORTELMANS (1955) described *Rhabdopleura delmeri* MORTELMANS from the Lower Carboniferous of Belgium but generic affinity of that form, represented by imprint only, remains questionable. ?*Rhabdopleura* sp. described by me from the Upper Silurian of Poland (MIERZEJEWSKI 1977) represents in fact the genus *Kystodendron*.

The genus *Eorhabdopleura* KOZŁOWSKI, 1970 is a junior synonym of *Kystodendron* KOZŁOWSKI, 1959 (see p. 184).

The record of the undoubted genus *Kystodendron* is limited to the Lower Palaeozoic (Ordovician and Silurian) but it is not excluded that a form from the Middle Devonian of Sahara, identified as *Rhabdopleurites* sp. by TAUGOURDEAU (1978) also belongs to that genus.

Of the modern and fossil species of the genus *Rhabdopleura*, *Rh. vistulae* KOZŁOWSKI, 1956 appears especially interesting. This species is known from the Maestrichtian, Danian and Montian of Poland. KULICKI (1969) noted that the structure of the tubarium of that form differs more strongly from modern species than from *Rh. kozlowskii* described by him from the Jurassic of Poland. Thanks to the courtesy of Prof. KRYSTYNA POŻARYSKA, I got small samples of core material from the borehole Góra Puławska, from which the type series of *Rh. vistulae* was derived. Material extracted from these samples (pl. 25) indicated that stolons and sterile bud cysts of Cretaceous-Tertiary *Rh. vistulae* very closely resemble Ordovician-Silurian species of *Kystodendron*.

KOZŁOWSKI (1956*a*) found that the major stolons of *Rh. vistulae* are circular in cross-section. My studies carried out with the use of SEM showed that lower surfaces of stolons are sometimes slightly flattened in this species (pl. 25: 7). Some stolons are strongly flattened but his may be explained by diagenesis as they are accompanied by similarly preserved cysts of sterile buds (pl. 25: 5—6). It follows that *Rh. vistulae* occupies an intermediate position between *Kystodendron* and the remaining species of *Rhabdopleura* on account of the type of transversal section of major stolon (fig. 14).

In *Rhabdopleura*, cysts of sterile buds are characterized by convex upper surface and almost flat lower one. The lower surface is thin and is not preserved in *Rh. kozlowskii*. Cysts of *Rh. vistulae*, often almost circular in cross -section (pl. 25: 2—3), are almost identical in morphology to those of the Silurian *Kystodendron tener* sp. n. (pl. 29: 24—26). It should be noted that some cysts of *Rh. vistulae*, here termed "composite" (see p. 174), are connected by a terminal stolon (pl. 25: 1—2). Cysts of this type are also known in the Ordovician *K. longicarpus* and *K. complicatus* sp. n. From the description of *Rh. vistulae* (KOZŁOWSKI 1956*a*) it follows that peduncular stolons of cysts are not attached to their proximal ends but rather to the lower surface. The available material shows both types of connections of peduncular stolons and cysts (pl. 25: 3, 5) but the second one appears much more common.

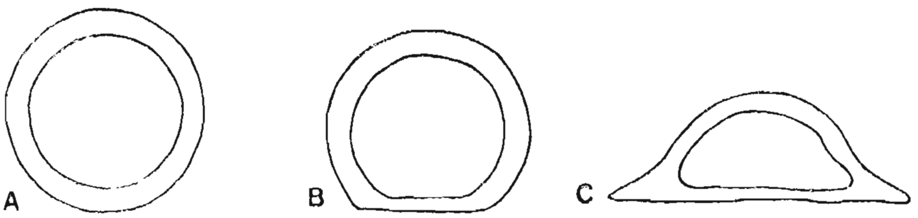

Fig. 14.
Comparison of transversal sections of main stolons in *Kystodendron longicarpus* (Eisenack) *sensu* Kozłowski (*A*), *Rhabdopleura vistulae* Kozłowski (*B*) and *Rhabdopleura normani* Allman (*C*).

The presence of diaphragms makes the structure of peduncular stolons of *Rh. vistulae* close to that of the remaining species of this genus. I did not find peduncular stolons with diaphragms in *Kystodendron* but it should be noted that some peduncular stolons of cysts of *K. longicarpus* (Eisenack *sensu* Kozłowski (fig. 15) appear some what similar to such stolons. Moreover, diaphragms may be found in terminal stolons of cysts of this species (see Kozłowski 1959*a*, fig. 24 D_2).

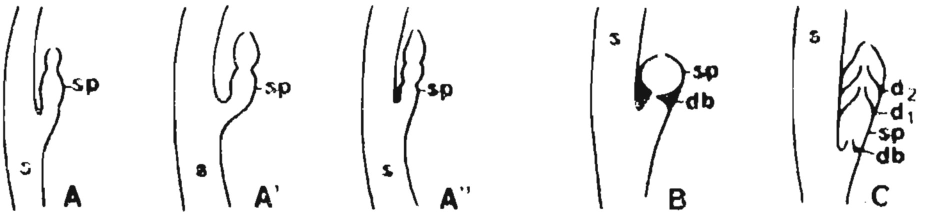

Fig. 15.
Comparison of longitudinal sections of peduncular stolons in *K. longicarpus* (*A*), *Rh. vistulae* (*B*) and *Rh. normani* (*C*). Abbreviations: d_1, d_2 secondary diaphragms, *db* basal diaphragm, *s* main stolon, *sp* peduncular stolon. *B* and *C* after Kozłowski.

The above comparisons clearly suggest that the genus *Kystodendron* is very closely related to *Rhabdopleura*. Moreover, it can not be excluded that the former is the ancestor of the latter. It may be even discussed whether or not the recorded differences are sufficiently high to treat *Kystodendron* and *Rhabdopleura* as separate genera.

Genus *Kystodendron* Kozłowski, 1959

Type species: Chitinodendron longicarpus Eisenack, 1937

Emend. diagnosis. — Major stolon and peduncular stolons of cysts of sterile buds without diaphragms. Sterile bud cysts circular in cross-section, simple or composite. Zooidal and stolonal tubes similarly developed as in *Rhabdopleura*.

Species assigned. — *Kystodendron longicarpus* (Eisenack, 1937), *Kystodendron subtilis* (Kozłowski, 1959), *Kystodendron complicatus* sp. n., *Kystodendron tener* sp. n.

Remarks. — The genus was proposed by Kozłowski (1959*a*), according to whom differences between the species *Chitinodendron bacciferum* Eisenack, 1937 and *Ch. longicarpus* Eisenack, 1937 are too great to accept allocation of both species to the same genus. He interpreted the former species (Kozłowski 1959*a*, p. 251) as a form of unknown systematic position, and the latter as a coelenterate of the order Hydroida. The two species also differ in the ultrastructure of periderm (Mierzejewski 1974).

The taxonomy of the genus *Kystodendron* is fairly complex because of some problems connected with nomenclature, methodology, etc. Its type species, *Chitinodendron longicarpus*

EISENACK was described on the basis of an unknown number of specimens. EISENACK (1937) figured only three of them: two fragments of stolons with two cysts each and a single isolated cyst. Moreover, he gave only brief and rather imprecise remarks on the morphology and variability of the type series. I analysed several hundred specimens of that genus to find that the holotype and the remaining specimens figured by EISENACK are insufficient for unequivocal definition of specific features. Long and smooth peduncular stolons of cysts displayed by the specimens do not differ from corresponding ones in such species as *Kystodendron subtilis* (KOZŁOWSKI) or *K. tener* sp. n. In turn, cysts identical in the figured specimens of *Ch. longicarpus* EISENACK may be found in *K. subtilis* but also in *Rhabdopleura vistulae* (see pl. 25: 2 and EISENACK 1937, fig. 20). Designation of this species as the type of the genus *Kystodendron* resulted in significant nomenclatoric complications. Forms described as *K. longicarpus* (EIS.) by KOZŁOWSKI (1959*a*) markedly differ from typical specimens of this species. This is especially the case of peduncular stolons of cysts of sterile buds, long and smooth in the material of EISENACK, and short with swellings and constrictions in the specimens of KOZŁOWSKI. The differences raise serious doubts as to the conspecific character of specimens described by these authors.

The above data show that KOZŁOWSKI (1959*a*) misidentified the type species in proposing the genus *Kystodendron*. When this is the case, the matter should be brought to the International Commission on Zoological Nomenclature, in accordance with the Article no. 70. Until the questions of the name and authorship of the type species of *Kystodendron* are solved, I propose

a) to use the name *Kystodendron longicarpus* (EISENACK) *sensu* KOZŁOWSKI for forms described as *K. longicarpus* (EISENACK), i.e. those displaying features making possible correct identification of the real species;

b) to describe forms named as *Chitinodendron longicarpus* EISENACK by EISENACK (1937), i.e. those not displaying features characteristic for specific rank, with the use of open nomenclature category, under the name *Kystodendron* ex gr. *longicarpus* (EISENACK) *sensu* KOZŁOWSKI.

The genus *Kystodendron* KOZŁOWSKI, 1959 is most probably congeneric with the genus *Cylindrotheca* EISENACK, 1934. EISENACK proposed the genus *Cylindrotheca* with *C. profunda* EISENACK, 1934 as a single species. The type material of that species comprises three fragments of stolons each with a single incomplete cyst, coming from the Silurian of Czechoslovakia. However, the present state of knowledge of diagnostic features, makes it possible to state that the type material of *C. profunda* is clearly insufficient to be used as the basis for a new taxon. This material does not make possible unequivocal interpretation of the taxon so the name *C. profunda* should be treated as a *nomen dubium*. Unfortunately, this species is at the same time the type of the genus *Cylindrotheca* EISENACK so this genus has to be also as *nomen dubium* treated.

The specific name *C. profunda* was not used for new findings for thirty two years, until EISENACK described under that name some forms from the Lower Ordovician of Öland Islands. One of these specimens has been designated as neotype by that author. Unfortunately, the above mentioned lack of features of specific rank in the holotype, conspecific relations between it and neotype are highly debatable. Moreover, the designation of neotype is invalid according to the rules of zoological nomenclature as it failed to meet formal limitations and requirements of the International Code of Zoological Nomenclature — Article 75, points a, b and c (1—5). That is why I regard it necessary to bring the above case to the International Commission of Zoological Nomenclature with a suggestion to place the names *Cylindrotheca* EISENACK, 1934 and *Cylindrotheca profunda* EISENACK, 1934 in the index of invalid and rejected names.

KOZŁOWSKI (1970*a*) proposed the genus *Eorhabdopleura* KOZŁOWSKI with a single species *E. urbaneki* KOZŁOWSKI on the basis of a single fragment of zooidal tube with part of its creeping part. He claimed that these were the only fragments of coenecium found but the analysis of accompanying fossils showed the presence of cyst-bearing stolons of *Kystodendron longicarpus*

(EISENACK) *sensu* KOZŁOWSKI. The holotype, (i.e. the only known specimen of *Eorhabdopleura urbaneki*) has been lost but an almost identical specimen, representing creeping part as well as fragment of erect zooidal tube, was found among microfossils extracted from the erratic boulder ZPAL 0.166. This specimen was also accompanied by stolons and cysts of *K. longicarpus* (EISENACK) *sensu* KOZLOWSKI.

The zooidal tube of *Eorhabdopleura urbaneki* KOZŁOWSKI does not display any features which would be of diagnostic value for a species. Therefore, both the generic name *Eorhabdopleura* KOZŁOWSKI and the specific name *Eorhabdopleura urbaneki* may be treated as *nomina dubia*. In turn, the fact that the holotype of the nominal taxon has been accompanied by remains of *K. longicarpus* (EISENACK) suggests that the taxa are conspecific.

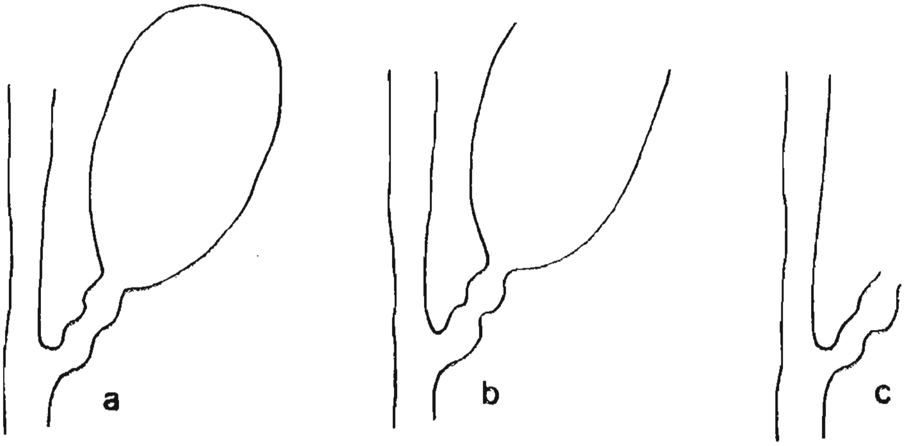

Fig. 16.
The same fragment of tubarium of *Kystodendron*, depending on the mode of preservation of cysts, was interpreted by previous authors as gonotheca (*a*), hydrotheca (*b*) or hydranth stalk sheath of Athecata (*c*).

The taxonomy of *Kystodendron* appears complicated from the point of view of methodology. Tubaria of that taxon, as those of fossil species of *Rhabdopleura*, are as a rule represented by isolated, small fragments of fusellar tubes and short fragments of stolons, usually with cysts of sterile buds. Isolated cysts with fragments of peduncular stolons are also common. Stolons are poorly differentiated and without diaphragms which make it impossible to state whether their short lateral branchings represent peduncular stolons (on which either zooid or sterile bud cyst was seated) or simply fragments of broken branches of major stolons. Remains of *Kystodendron* are accompanied by numerous microfossils, often tubular in shape, the relation of which to the tubarium remains debatable. Determination of species on the basis of such material is identical from the point of view of methodology as discrimination of fossil species of *Rhabdopleura* by KOZŁOWSKI (1956*a*) and KULICKI (1969, 1971) as there always remains some probability that the sample comprises remains of more than one species of Rhabdopleuridae. This problem was faced by KULICKI (1971) when he found in Bathonian nodules from Blanowice near Zawiercie, both *Rhabdopleura kozlowskii* and remains which he finally decided to describe under the name *Rhabdopleura* species.

As in *Rhabdopleura*, zooidal tubes of *Kystodendron* are of limited value for the identification of species. KULICKI (oral inf.) is inclined to treat the structure of stolonal system, especially that of peduncular stolons, as of diagnostic value for discrimination of species in *Rhabdopleura*. My studies on *Kystodendron* showed that diagnostic features for species of this genus include morphology of the stolons of cysts of sterile buds, as well as of the structure and size of cysts. However, the situation is complicated by the fact that more than one type of cyst or their peduncular stolons may be found in a single species of *Kystodendron*, as in the *Rhabdopleura* *vistulae* discussed above. When the amount of material is limited, this often makes specific identification hazardous and, therefore, the use of open nomenclature necessary.

In discussing the question of the variability in *Kystodendron*, it is necessary to make a distinction between actual variability and apparent variability, i.e. that resulting from the state of preservation. Stolons with incomplete cysts or lack of cysts may differ markedly from well preserved material and even imitate fragments of hydrosomes of Thecaphora and Athecata (fig. 16, pl. 29: 14—15).

This paper presents descriptions of only a part of the material available. The material requiring further study comprises small fragments of stolons and cysts which may be generally identified only as *Kystodendron* spp. (see e.g. pl. 32: 2).

Occurrence. — Ordovician and Silurian of Central Europe.

Kystodendron longicarpus (EISENACK, 1937) *sensu* KOZŁOWSKI

(Pl. 27: 5, pl. 28: 11—33, pl. 32: 1)

?1937. *Chitinodendron longicarpus* EISENACK; EISENACK 237, figs. 18—20.
1959*a*. *Kystodendron longicarpus* (EISENACK); KOZŁOWSKI: 252, fig. 24.
1970*a*. *Eorhabdopleura urbaneki* KOZŁOWSKI; KOZŁOWSKI: 4, fig. 1.

Material. — Two fragments of zooidal tubes and some dozens of fragments of stolons with cysts of sterile buds and isolated cysts from erratic boulders ZPAL 0.29, ZPAL 0.158, ZPAL 0.166, ZPAL 0.169, ZPAL 0.182, ZPAL 0.262, MZ/116, MZ/125, and core material from the borehole at Podborowisko (depth 396—397 m, Arenigian).

Emend. diagnosis. — Zooidal tubes consisting of erect and creeping parts and with structure similar as in *Rhabdopleura*. Cysts of sterile buds subcylindrical, variable in length (usually 350—700 μm long), closed or ending with terminal stolon (composite cysts). Peduncular stolon of cysts usually short, with constrictions and swellings, rapidly widening and passing into cyst.

Description. — Zooidal tubes similar in structure as those of *Rhabdopleura* (pl. 32: 1). Creeping part partly preserved, 360—450 μm long, with clearly visible regular zig-zag suture. Erect part preserved in the form of fragments 160—220 μm long, circular in cross-section, 110—125 μm in diameter. Fuselli 34 μm wide at the average. Oblique suture occasionally traceable in set-up part. Periderm brown, translucent.

Cysts of sterile buds subcylindrical, with secondary deformations, 350—700 μm (occasionally even 1200 μm) long, 50 to 100 μm in diameter, closed or ending with terminal stolon in distal part. Terminal stolon located centrally or excentrically in relation to cyst (pl. 28: 21b, 32, 33), smooth, with constrictions and even diaphragms (see KOZŁOWSKI 1959, fig. 24 D_2). Branchings of terminal stolons and related composite cysts are also occasionally found (pl. 28: 17—18).

Lumps representing cluster of minute spherules are sometimes found inside cysts the boulder ZPAL 0.166 (pl. 28: 11). The spherules are about 4 μm in diameter and the largest lump of spherules — about 10 μm in diameter.

Peduncular stolons short, usually 40—50 μm long, with marked constrictions and swellings rapidly widening and passing into cysts (pl. 28: 31). Smooth and somewhat longer stolons are less common.

Major stolons varying from 8 to 12 μm in diameter.

Ultrastructure. — SEM studies showed homogeneous character of the matter which builds cysts of sterile buds and stolons. Weak traces of lamination were only occasionally found (pl. 27: 5).

Remarks. — The zooidal tubes of *K. longicarpus* described above appear different from those of *Eorhabdopleura urbaneki*, which I consider conspecific. From the description given by KOZŁOWSKI (1970*a*) it follows that the tube of *E. urbaneki* is markedly wider (280 μm) and built of wider fuselli (about 50 μm wide on average). According to my work the conspecific character of the above two nominal species is suggested by:

a) co-occurrence of typical cysts and stolons of *K. longicarpus* and zooidal tubes in both the material gathered by KOZŁOWSKI and by myself;

b) high variability in diameter of zooidal tubes of Rhabdopleuridae: from 140 to 240 μm in *Rhabdopleura kozlowskii* and from 50 to 170 μm in *Kystodendron* ex gr. *longicarpus* described below.

Taking this into account, I treat the differences between zooidal tube described by KOZŁOWSKI (1970*a*) and those described by myself as due to intraspecific variability of *Kystodendron longicarpus* (EISENACK) *sensu* KOZŁOWSKI. The relation between this species and the type material of the nominal species *Chitinodendron longicarpus* EISENACK was discussed above (pp. 182—183).

The clusters of minute spherules found inside cysts of sterile buds seem to correspond to yolk matter known from modern species of *Rhabdopleura* (see STEBBING 1970: 210, fig. 6). If this is the case, preservation of yolk matter would be an interesting example of fossilization.

Occurrence. — Ordovician of Poland.

Kystodendron ex gr. *longicarpus* (EISENACK) *sensu* KOZŁOWSKI

(pl. 28: 1—10)

Material. — About a dozen fragments of stolons with cysts of sterile buds and a dozen fragments of zooidal tubes from core material from the borehole Biała Podlaska 2 (depth 680—687 m), Ordovician.

Description. — Zooidal tubes represented by fragments of erect parts, 300—1540 μm long and 50—170 μm (113 μm at the average, standard deviation 35.55) in diameter. Fuselli 3 to 8 in number per 100 μm section of tube, narrow (12—35 μm wide, 17 μm at the average, standard deviation 6.24). Collars of fuselli weakly marked. Narrow tubes as a rule displaying narrow fuselli.

Cysts of sterile buds (pl. 28: 6—9) without distal parts, seated on smooth peduncular stolons. Cysts 110—600 μm long (288 μm at the average, standard deviation 154.18) and 30—100 μm in diameter (60 μm at the average, standard deviation 22.61). One of the specimens with composite cysts (pl. 28: 8). Peduncular stolons vary from 20 to 250 μm in length.

Major stolons 7—12 μm thick.

Remarks. — The specimens described above are characterized by peduncular stolons typical of *Kystodendron subtilis* (KOZŁOWSKI) and open cysts of sterile buds, resembling those of *K. longicarpus* (EISENACK) *sensu* KOZŁOWSKI.

Kystodendron subtilis (KOZŁOWSKI, 1959)

(pl. 36: 5—8)

1959*a*. *Cylindrotheca subtilis* KOZŁOWSKI; KOZŁOWSKI: 232, fig. 11.
1959*a*. Gonotheca Forma C; KOZŁOWSKI: 257, figs. 29a—c.
1965*b*. Gonotheca Formae A&C; SKEVINGTON: 158, figs. 9—17.

Emend. diagnosis. — Cysts of sterile buds large, usually 500—1000 μm long, elongate, subcylindrical or, sometimes, spindle-shaped or irregular, with eccentrically displaced long, smooth and gradually widening peduncular stolon. Distal part of cysts usually with terminal stolon.

Fusellar and stolonal tubes unknown.

Material. — Some tens of isolated cysts and a few fragments of stolons from the erratic boulders ZPAL 0.121, ZPAL 0.153, ZPAL 0.158, ZPAL 0.182.

Description. — Fragments of branching stolons with cysts of sterile buds are very rare in the material studied (see KOZŁOWSKI 1959*a*, fig. 11). Isolated cysts with preserved peduncular stolons are most common here (pl. 36: 7—8).

Cysts are very large, 500 to 1000 μm long or even longer. They are accompanied by some smaller ones, merely 200 μm long but some intermediate in size are fairly numerous. Cysts are usually markedly elongate, subcylindrical or, sometimes, spindle-like or irregular in shape. They display marked trend to bending, most probably reflecting bends of stolonal tube in which they have been placed. Typical cysts become narrower in the distal part, gradually passing into a terminal stolon. The lack of the latter in some cysts may be explained by mechanical damage when the periderm is mature (i.e. black and opaque) and distal part missing.

The peduncular stolon of cysts vary in length, being up to 250 μm long in extreme cases. It is eccentrically located in relation to the outline of the cyst. It is always displaced towards the major stolon which makes it possible to identify a part of a cyst directed towards the stolon and the opposite one.

Among the cysts there may be found immature ones, built of markedly finer periderm (immature periderm, i.e. brown and translucent), and with the distal part and terminal stolon lacking (see also SKEVINGTON 1965*b*, fig. 17). Discrimination of such cysts and those displaying mechanical damage (see above) is fairly easy thanks to differences in the periderm from which they are built. There were also found completely closed cysts, with the outlet related to the peduncular stolon as the only one.

Major stolons, 20—40 μm in diameter, are black and glittering or eventually translucent and brown.

Zooidal and stolonal tubes are unknown. Some shreds of translucent periderm were found on some stolons and cysts.

Ultrastructure. — TEM studies failed to show any differentiation in ultrastructure of the matter which forms cysts of sterile buds and stolons, even at magnifications of the order of 60.000× (MIERZEJEWSKI 1974).

Remarks. — The species discussed above was described as two independent forms: *Cylindrotheca subtilis* KOZŁOWSKI and Gonotheca Forma C by KOZŁOWSKI (1959*a*). The former actually comprised stolons with attached cysts. The lack of distal parts made the cysts deceptively similar to hydrotheca of the Hydroida. In turn, Gonotheca Forma C comprised isolated, almost complete cysts with peduncular stolons and distal parts and with only terminal stolons missing. Comparative studies of the type series of both forms and some new material from the relevant type localities showed that they are undoubtedly conspecific. It is worth noting that the erratic boulders ZPAL 0.121 and ZPAL 0.182, from which *Cylindrotheca subtilis* had been described, were also found to yield complete cysts with terminal stolons.

Of the names used for the species *Cylindrotheca subtilis* KOZŁOWSKI is the only taxonomically valid one. As was stated above, the generic name *Cylindrotheca* EISENACK should be treated as *nomen dubium* (see p. 183) and the species in question appears morphologically very close to *Kystodendron longicarpus* (EISENACK) so it is assigned here to the genus *Kystodendron* EISENACK.

Rich material of *Kystodendron subtilis* (KOZŁOWSKI) has been described from the Lower Ordovician of Öland under the name Gonothecae Formae A & C by SKEVINGTON (1965*b*). Of this special attention should be paid to a specimen displaying a cyst with terminal stolon which passes into a branching stolon with two other cysts (SKEVINGTON 1965*b*, fig. 14). In the Lower Ordovician of Öland, SKEVINGTON (1965*b*) also found a form which he identified as *Cylindrotheca subtilis* KOZŁOWSKI. It was not discussed in detail as he regarded it as matching the description given by KOZŁOWSKI (1959*a*). However, it is meaningful that the specimens supposed by him to represent *Cylindrotheca subtilis* were accompanied by Gonothecae A & C. This gives further support to the conspecific character of these forms.

Kystodendron subtilis appears morphologically close to *K. longicarpus*, especially in the presence of terminal stolons in distal part of cysts. The former differs from the latter in its larger size, and slender cysts which seated on smooth peduncular stolons, and a marked eccentric translocation of peduncular stolon in relation to the outline of cyst.

Occurrence. — Lower Ordovician of Öland (SKEVINGTON 1965*b*), Ordovician erratic boulders from Poland (KOZŁOWSKI 1959*a*).

Kystodendron cf. *subtilis* (KOZŁOWSKI, 1959)

(pl. 32: 3)

Material. — Two specimens from the Ordovician erratic boulder ZPAL 0.533.

Description. — Cysts subcylindrical, elongate, without distal part. Peduncular stolon smooth, long, gradually widening. One specimen displays a shred of periderm, most probably corresponding to secondary layer of periderm (pl. 24: 3).

Remarks. — The specimens described above most probably belong to the species *K. subtilis* but the material is too poor and cysts too incomplete for identification without reservation. The preserved shred of periderm confirms affiliation of *K. subtilis* and similar forms to Rhabdopleurida.

Kystodendron aff. *subtilis* (KOZŁOWSKI, 1959)

(Fig. 17)

Material. — Some dozens of fragments, mainly cysts of sterile buds, sometimes connected with relatively long sections of stolons, from the Ordovician erratic boulder ZPAL 0.695.

Description. — Cysts of sterile buds very large, built of black, thick, glittering periderm, usually 600—1050 μm long but sometimes longer (1300—1890 μm), markedly varying in morphology: from very long and narrow (fig. 17: 4, 12) to relatively wide in relation to their length (fig. 17: 2), usually straight (fig. 17: 7—9, 12), sometimes distorted to various degrees. Distal part of cysts relatively rarely preserved (mechanical damage?), best preserved in small cysts. Distal part open to the outside narrowed aperture and without terminal stolons. Peduncular stolons varying from 20 to 110 μm in length, gradually passing into cysts and usually eccentrically located in relation to its periphery, 12 to 80 μm wide. Major stolons 50—150 μm thick.

Remarks. — The form described above is characterized by cysts of sterile buds clearly larger than in all the hitherto known representatives of the genus *Kystodendron* KOZŁOWSKI. In morphology, it is closest to those of the species *K. subtilis* (KOZŁOWSKI, 1959*a*) but they do not seem to be conspecific. It is not clear whether the lack of terminal stolons of cysts is due to their mechanical fracture or a feature characteristic of *K.* aff. *subtilis*. I think that further discoveries of such forms will allow their separation as a new taxon.

Kystodendron complicatus sp. n.

(pl. 29: 35—41, fig. 18)

Holotype: Fragment of stolon with three cysts of sterile buds, from the erratic boulder ZPAL 0.62 (Orłowo) (ZPAL Pb. III/13).

Type horizon and locality: Upper Ordovician, erratic boulder ZPAL 0.62 from Orłowo.

Derivation of the name: Lat. *complicatus* — complicated, on account of fairly complicated morphology of cysts and stolons.

Fig. 17.
Kystodendron aff. *subtilis* (Kozłowski) (ZPAL Pb.I/19). Sterile bud cyst with stolons, boulder no. ZPAL 0.695, Mochty, Ordovician.

Diagnosis. — Cysts of sterile buds composite, small, varying in lenght (180—410 μm). Peduncular stolons with discs.

Material. — Seven fragments of stolons with cysts of sterile buds and one isolated cyst.

Description. — The holotype (pl. 29: 41, fig. 18: 4) represents a fragment of stolon, 1580 μm long, with three cysts seated on separate peduncular stolons and one peduncular stolon without cysts. Major stolon about 10—12 μm thick. Cysts a and b 220 and 230 μm long, respectively, 30—60 μm wide and ended with terminal stolons with cup-shaped discs. Cyst d without distal part but this is probably not due to mechanical damage but rather its immaturity as its wall fairly light. Peduncular stolons of cysts, b, c and d with cup-shaped discs. Connection of cyst a and major stolon indistinct. Periderm black, glittering.

The remaining specimens do not differ from the holotype in the morphology of cysts and stolons. Cysts vary from 180 to 410 μm in length (276 μm at the average, standard deviation 77.34). However, attention should be paid to a specimen with fairly complicated morphology, shown in pl. 29: 37 and fig. 18: 1. This specimen displays a small cyst, c_1, separating from disc

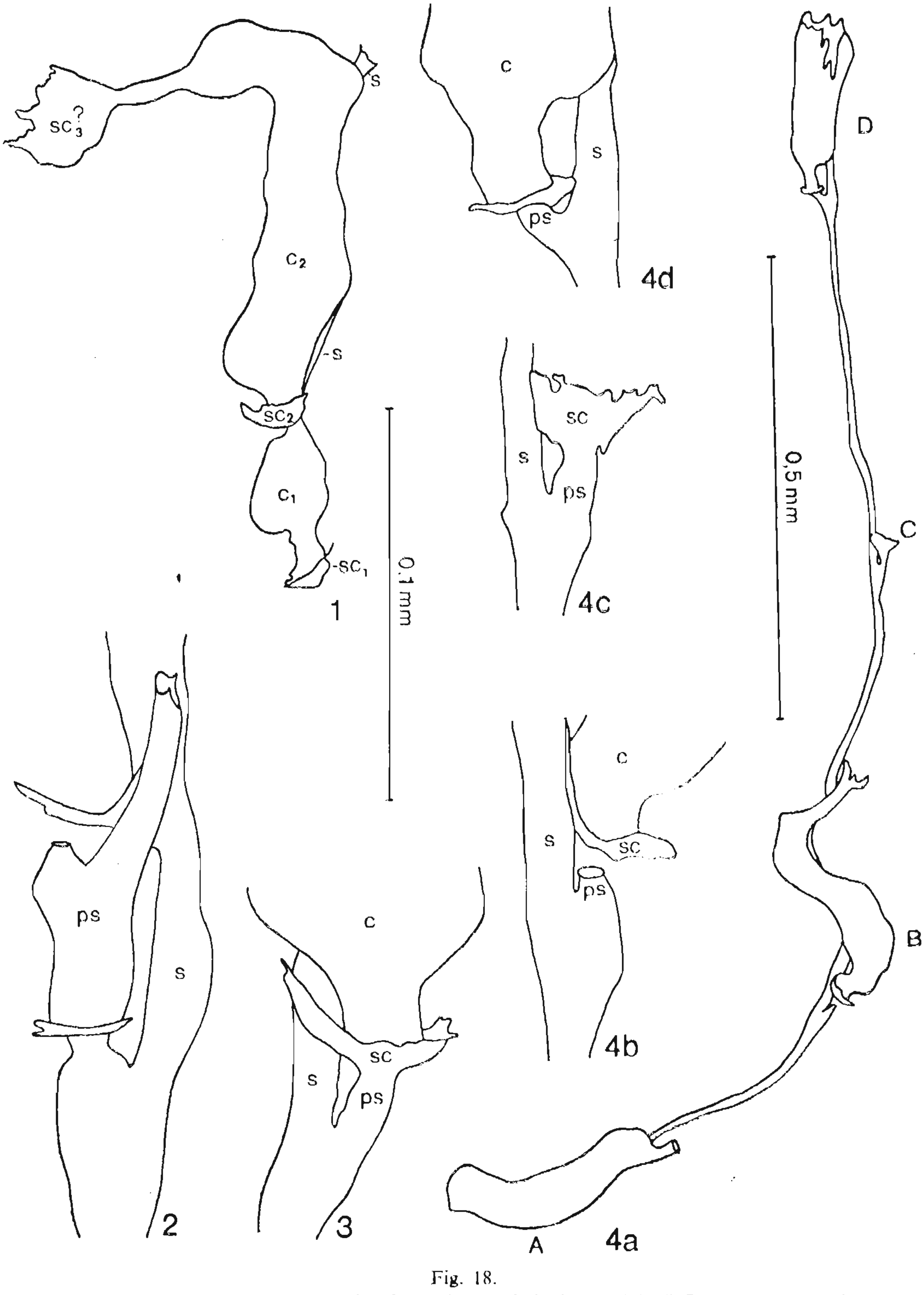

Fig. 18.

Kystodendron complicatus sp. n. Fragments of stolons with sterile bud cysts (ZPAL Pb.I./ 13). 1 — holotype. Abbreviations: *c* — sterile bud cyst, *ps* — peduncular stolon, *s* — main stolon, *sc* — cup-shaped disc

sc_1. In its distal part the cyst passes into two terminal stolons — one long (S) and another short, ending with disc (sc_2) and representing at the same time peduncular stolon of large cyst (c_2). The cyst c_2 ends with terminal stolon which displays bulb-like widening (disc sc_8?).

One of the remaining specimens (fig. 18: 2) displays peduncular stolon with disc. No cyst is attached to that disc but a short stolon (ps), dividing into stolon with disc and another without disc. This pattern somewhat resembles the one described above: $sc_1+c_1+s+sc_2$. Cysts show a marked trend to adjoin stolons.

Typical representatives of *Kystodendron complicatus* sp. n. are accompanied by a fragment of stolon with two cysts of sterile buds (pl. 29: 40). Peduncular stolons of these cysts are without discs. The available material is insufficient to state whether this specimen represents a separate taxon or, as seems more probable an effect of variability of *K. complicatus* sp. n.

Remarks. — *Kystodendron complicatus* sp. n. is closest in morphology to *K. longicarpus* (EISENACK) *sensu* KOZŁOWSKI, from which it differs in the presence of cup-shaped discs on the peduncular and terminal stolons of cysts.

Occurrence. — Known from the erratic boulder ZPAL 0.62 only.

Kystodendron tener sp n.

(pl. 29: 20—34; fig. 19)

1977. ?*Rhabdopleura* sp.; MIERZEJEWSKI: 105, fig. 2.

Holotype: Fragment of major stolon with cysts of sterile buds (pl. 29: 26) (ZPAL Pb. III/9).
Type horizon and locality: Erratic boulder MZ/142 (Poddębie), upper Silurian.
Derivation of the name: Lat. *tener* — fine.

Diagnosis. — Major stolons and peduncular stolons of cysts smooth or with various swellings. Cysts of sterile buds without terminal stolons. Zooidal tubes fine, 140—280 μm in diameter, with weakly marked collars.

Material. — Over a hundred fragments of stolons with cysts of sterile buds and some tens of fragments of zooidal tubes from erratic boulder MZ/140, MZ/112 and MZ/148 (Silurian).

Description. — All the elements of coenecium very fine and translucent.

Major stolons 15—30 μm in diameter, smooth or with various swellings (pl. 29: 21—30). Peduncular stolons of cysts varying in length (40—300 μm long), smooth or with fairly regularly spaced swellings. Cysts of sterile buds without terminal stolons, 130—1100 μm long and 40—80 μm wide.

The preserved fragments of zooidal tubes 300—900 μm long, representing set-up part only (pl. 29: 32—34, fig. 19), 140—280 μm wide; fuselli 35—90 μm wide. Collars of fuselli poorly developed. Periderm translucent, almost colourless.

Remarks. — *Kystodendron tener* sp. n. is close to *K. longicarpus*, differing in the presence of small, irregular widenings of major stolons and the lack of terminal stolons. Fusellar periderm of zooidal tubes differs from that of other Ordovician-Silurian Rhabdopleurida in being exceptionally fine and almost completely colourless.

?*Kystodendron* sp. A

(fig. 20)

Material. — A single specimen from the Ordovician boulder MZ/14.

Description. — Fragment of flattened zooidal tube, 435 μm long and 150 μm wide. Fuselli about 24 μm wide at the average, mainly in the form of rings. Oblique suture traceable on some fuselli only. Periderm light-brown, translucent.

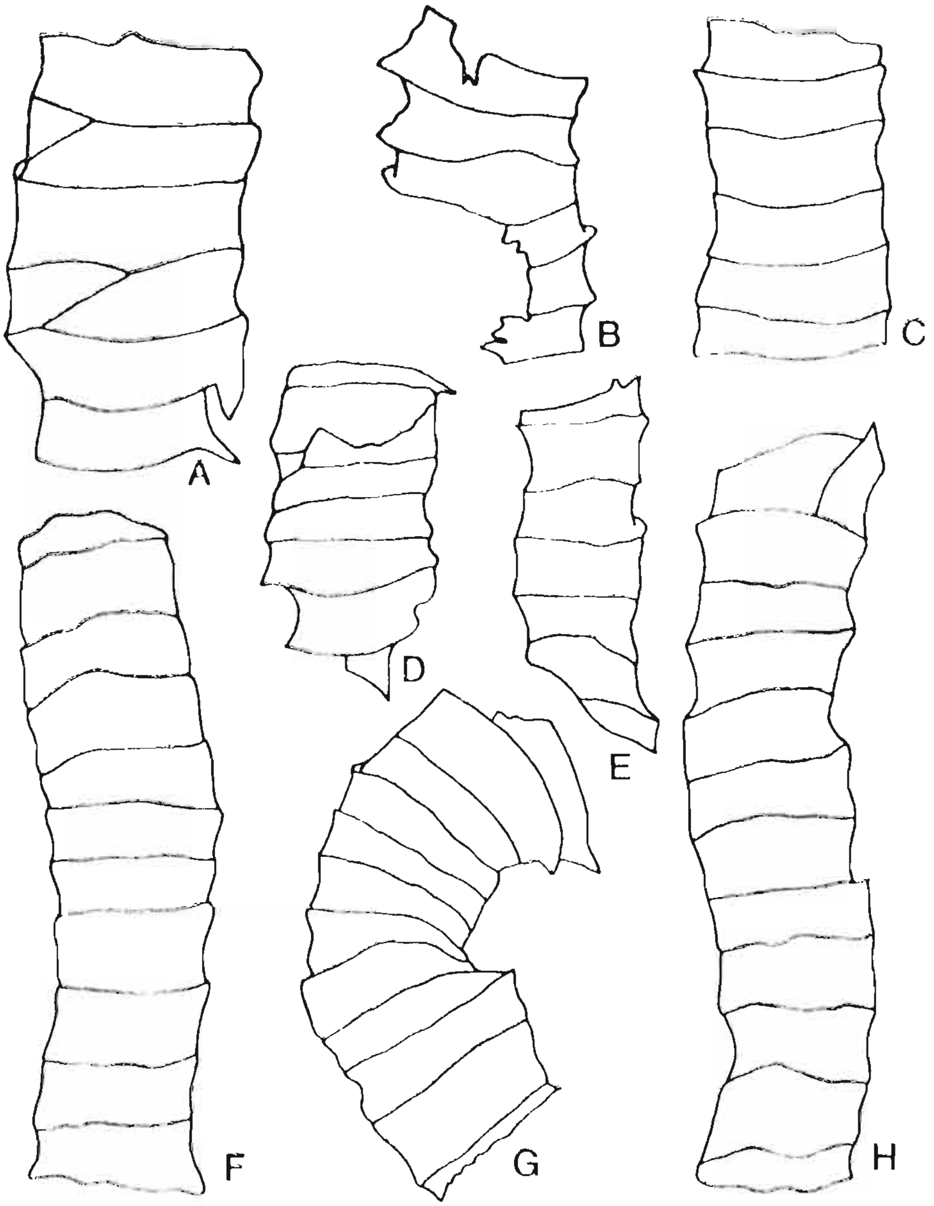

Fig. 19.
Kystodendron tener sp. n. Zooidal tubes (ZPAL Pb.I/ 9), ×160. Boulder no MZ/142, Poddębie, Upper Silurian.

Remarks. — I regard the above specimens as a fragment of erect part of zooidal tube of Rhabdopleurida and I place it tentatively in the genus *Kystodendron*. The possibility that is represents a fragment of graptolite of the genus *Mastigograptus* RUEDEMANN or *Micrograptus* EISENACK appears less probable.

?*Kystodendron* sp. B

1959*a*. *Gonotheca* Forma B; KOZŁOWSKI: 256, fig. 28.

Material. — Fragment of stolon with two cysts of sterile buds, from Ordovician boulder ZPAL 0.163.

Description. — The specimen has been described in detail by Kozłowski (1959*a*). A highly advanced decolouring resulted in its break up.

Remarks. — Kozłowski (1959*a*) assigned this specimen to Hydroida as he interpreted it as a fragment of hydrozoan branch with two gonothecae. However, two facts speak against that interpretation: 1) the supposed gonothecae are closed and 2) one of them is surrounded by shred of membrane which has no equivalents in hydrosomes of Hydroida. In turn, there are no features which would speak against treatment of the specimen as stolon with cysts of sterile buds of Rhabdopleurida. This would also explain apparently enigmatic nature of the shred of membrane as a remain of inner, unfusellar periderm layer of stolonal tube.

Fig. 20.
?*Kystodendron* sp.A. Zooidal tube (ZPAL Pb.I/ 14). Boulder no. MZ/14, Orzechowo, Ordovician.

Incertae sedis (Pterobranchia?)
Genus *Lagenohydra* Kozłowski, 1959
Type species: *Lagenohydra phragmata* Kozłowski, 1959

Diagnosis. — See Kozłowski (1959*a*: 245—247).

Remarks. — Monotypic genus. Kozłowski (1959*a*) regarded this form as a hydroid characterized by distinct dimorphism of thecae. However, *Lagenohydra* is neither related to hydroids nor any other coelenterates. The supposed thecae do not resemble any modern or fossil Coelenterata in morphology and distribution. If we treat this form as hydroid, it should be necessary to assume both coenosarcal and zooidal growth of the colony. Thecae "a" would be of coenosarcal origin and thecae "b" — growing from the former — of zooidal origin (fig. 21). Such mixed type of growth is absolutely unknown in coelenterates (see Beklemishev 1957).

I think that the holotype, i.e. the only hitherto recorded representative of *Lagenohydra phragmata* Kozłowski probably represents a fragment of stolon of the Rhabdopleurida, on which cysts of sterile buds are seated. It can not be excluded that this form is close (if not congeneric) to the *Kystodendron* KOZŁOWSKI, especially *K. complicatus* sp. n. This is shown by the general morphology of cysts, especially the presence of terminal stolons on them and the growth of secondary cysts from the primary.

Lagenohydra phragmata KOZŁOWSKI, 1959

(fig. 21)

1959. *Lagenohydra phragmata* KOZŁOWSKI; KOZŁOWSKI: 258, fig. 33.

Remarks. — The species has been described on the basis of a single specimen from Ordovician boulder ZPAL 0.42. Because of intense chemical decolouring, the specimen was dissolved in glycerin before 1972.

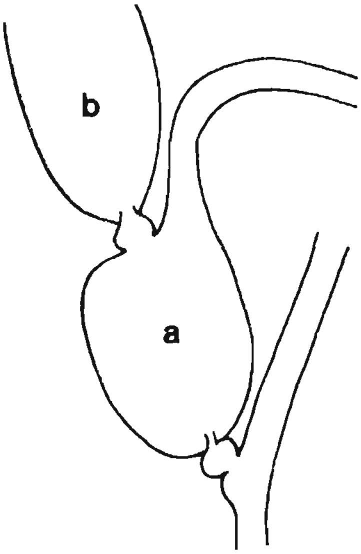

Fig. 21.
Lagenohydra phragmata KOZŁOWSKI. Sketch reconstruction of "thecae" after KOZŁOWSKI.

MISCELLANEA

The chapter presents descriptions of organic microfossils which belong to various groups of invertebrates. Determination of their systematic position is, however, highly troublesome in the present state of knowledge. Of the forms described, the only affiliation which may be regarded as possible are those of *Kozlowskisyrinx graptovermiformis* gen. n., sp. n. to the Polychaeta. The microfossils described below represent only a part of the organic problematic which I found in Ordovician and Silurian rocks or described previously by other authors. Such groups as Acanthastida, Graptoblasti, Graptovermida or Melanoskleritoidea are neglected here. Acanthastida, known from the Tremadoc of Poland only (KOZŁOWSKI 1949*a*), were the subject of ultrastructural studies of URBANEK (unpublished data). Graptoblasti described from the Ordovician (KOZŁOWSKI 1949*a*, 1962) and reported from the Silurian (MIERZEJEWSKI 1977), were also covered by electron microscopy studies (URBANEK and RICKARDS 1974, MIERZEJEWSKI 1984*b*, URBANEK, MIERZEJEWSKI and RICKARDS 1986). Their biological significance was discussed by URBANEK (1986). Melanoskleritoidea, regarded as coelenterates by EISENACK (1942, 1950, 1963) and as algae by GÓRKA (1971) and J. KAŹMIERCZAK (oral inf.) were recently discussed by LAUFELD (1979*b*), SCHALLREUTER (1981) and others.

Genus *Ascosyrinx* KOZŁOWSKI, 1967

Type species: *Ascosyrinx tenuis* KOZŁOWSKI, 1967

Diagnosis. — See KOZŁOWSKI (1967: 112).

Remarks. — Under that generic name, KOZŁOWSKI (1967) described two species: *A. tenuis* KOZŁOWSKI, 1967 and *A. robustus* KOZŁOWSKI, 1967. New findings of such forms make possible a more accurate reconstruction of their morphology and to question their congeneric character. *A. robustus* appeared to be scyphopolyp and it is here transferred to the genus *Byronia* MATTHEW (see p. 146) whereas the systematic position of *A. tenuis* is treated as still unclear.

Ascosyrinx tenuis KOZŁOWSKI, 1967

(pl. 33, pl. 34: 1—4, pl. 35: 2)

1967. *Ascosyrinx tenuis* KOZŁOWSKI; KOZŁOWSKI: 113, fig. 5.

Diagnosis. — As for the genus.

Material. — Several dozen specimens from boulders MZ/86, ZPAL 0.137, ZPAL 0.179, ZPAL 0.185, ZPAL 0.244, ZPAL 0.366, ZPAL 0.469 and ZPAL 0.498.

Description. — Organic test in the form of flat-convex, subconoid or hemispheric chamber with central aperture. Aperture situated at the top of long narrow tube. Base of chamber at the place of attachment to substratum represented by thin flat sole with numerous band-like thickenings (pl. 35: 2). Chamber slightly varying in diameter, from 0.4 to 0.5 mm, and tube — from 0.08 to 0.1 mm. Length of tube is most variable here but this may be due to the fact that it is often broken off. The tube is up to 1.5 mm long at the most.

Periderm black, glittering, opaque, not displaying differentiation in microstructure under the light microscope when decoloured.

Ultrastructure. — Ultrastructure was studied with the use of SEM and TEM methods. Periderm seems to be completely structureless in fractured surfaces studied under SEM (pl. 34: 4) whereas TEM studies make it possible to distinguish two zones in cross-sections of the tubes: a) external, more or less homogeneous, with locally spaced subradial irregular fissures, and b) inner, built of five concentric layers, separated by a material occurring in the form of radially arranged "pillars" (pl. 33: 6, pl. 34: 1). Periderm of the chamber does not display elements known from the tube and it is homogeneous (pl. 34: 2). All the elements of chamber (except for the sole) are built of the same organic material. The material is inhomogeneous in electronic density. In some electron micrographs it appears as irregular narrow bands varying in density and separated by irregularly spaced pores (pl. 34: 2). The substance displays granules of high electronic density (pl. 34: 2—3).

The sole and overlying band-like thickenings are built of spongy organic substance, locally very loose in character (pl. 33: 1—2).

Inside chamber, a significant amount of organic matter varying in shape and structure is found. Some of bodies recorded there are membrane-like or more or less lumpy in shape (pl. 33: 3—5).

Remarks. — *Ascosyrinx tenuis* is almost identical in morphology with some isolated autothecae of camaroid graptolites (Camaroidea) described from the Tremadoc of Wysoczki by KOZŁOWSKI (1949*a*). The similarity, especially to the specimen "Echantillon No. 210" was noted by that author (KOZLOWSKI 1967: 113). However, the forms essentially differ in the lack of fusellum and cortex, typical of graptolites, in periderm of *A. tenuis*. The differences in structure seem to preclude any affinity between this species and Camaroidea. However, the studies carried out by URBANEK and myself (*in press*) showed that dendroid graptolites from Wysoczki essentially differ from the same extracted from erratic boulders in ultrastructure of periderm and that the differences may be due to different conditions of fossilization.

The membrane-like and lumpy bodies found inside the chamber of *A. tenuis* draw attention to ovoid bodies described from authotheca of *Cysticammara accollis* KOZŁOWSKI (Camaroidea) by KOZŁOWSKI (1949*a*, 1971) and interpreted by him as graptolite eggs (URBANEK and MIERZEJEWSKI, in preparation).

Occurrence. — Ordovician erratic boulders from the area of Poland.

Genus *Chitinodendron* EISENACK, 1937

Type species: *Chitinodendron bacciferum* EISENACK, 1937

Remarks. — EISENACK (1937) treated this genus as form of uncertain systematic affinities but he supposed that it may represent organic lining of foraminifer test. He compared this form with foraminifers *Psammatodendron* NORMAN, *Dendrophrya* WRIGHT, *Rhizammina* BRADY, *Aschelmonella* BRADY and *Ramulina* RUPERT JONES. CUSHMAN (1948) and BYKOVA and REITLINGER (1959) assigned the genus *Chitinodendron* to subfamily Dendrophyrinae of the family Hyperamminidae (Foraminifera).

Besides the type species, EISENACK (1937) assigned to this genus also *Ch. longicarpus* EISENACK. Fot the latter, KOZŁOWSKI (1959*a*) proposed a separate genus *Kystodendron* KOZŁOWSKI, treating it as hydroid. This form is here discussed as representative of pterobranchs of the order Rhabdopleurida (p. 182).

The genus *Chitinodendron* is essentially known from the Ordovician and Silurian of the Baltic region only. Uncertain occurrences of forms morphologically close to that genus were reported by ELLER (1964) from the Devonian of Ontario and CHAIFEZ (1974) from the Lower Silurian of Alabama.

Chitinodendron bacciferum EISENACK, 1937

(pl. 24: 6, pl. 32: 12—15, pl. 34: 5—6, pl 37: 8)

1937. *Chitinodendron bacciferum* EISENACK; EISENACK: 236, figs. 9—17, pl. 16: 6.
1959*a*. *Chitinodendron bacciferum* EISENACK; KOZŁOWSKI: 253, fig. 25.

Material. — Several specimens from boulders ZPAL 0.29, ZPAL 0.31, ZPAL 0.184, ZPAL 0.240, ZPAL 0.523, MZ/38 and from the borehole Krzyże 4 (depth 477—479 m).

Description. — The material available fully matches descriptions given by EISENACK (1937) and KOZŁOWSKI (1959*a*). Some more interesting specimens are shown here in pl. 32: 12—14.

Ultrastructure. — Section 1—2 μm thick appear black and opaque under the light microscope. Interior of the vesicles are infilled with concentrations of black substance. Periderm varying from 2.2 to 2.9 μm in thickness.

The periderm seems structureless under TEM at magnifications of the order of a few thousand times (p. 32: 15). At larger magnifications, it is possible to note that structureless basic material forms the bulk of periderm. In that matter there are embedded fine granules of high electron density (pl. 34: 5). The granules, variable in size, are arranged in layer in which their size is markedly less varying. Attention should be paid to a layer formed of especially large granules (pl. 37: 8) and visible even at low magnifications. Outer and inner surfaces of periderm are covered with more or less loosely spaced, relatively large granules (pl. 37: 8).

Interior of vesicles is partly infilled in an irregular way with concentrations of organic substance, sometimes close to that forming periderm. The concentrations may vary from irregular to subcircular in shape in cross-sections. Irregular concentrations display grit-like structure and they are built of lumps of matter varying in electronic density (pl. 37: 8), whereas the subcircular ones may be completely homogeneous (pl. 34: 6) but they usually resemble periderm in ultrastructure. The latter, however, differ from periderm in random arrangement of granules. The concentrations are accompanied by smaller ones, consisting of lumps of high electronic density only. Some of them seem to represent inner linings of periderm, translocated to the interior of vesicle (pl. 32: 15).

Intercalations of the grit-like matter may be locally found in periderm (pl. 37: 8). The intercalations, similarly as regular arrangement of granules in periderm, suggest its prolonged formation.

The techniques used does not allow biochemical interpretation of the ultrastructures recorded.

Remarks. — I regard the systematic position of *Ch. bacciferum* as generally unclear but I treat the hypothesis of its affiliation with Foraminiferida (EISENACK 1937, KOZŁOWSKI 1959*a*) as fairly probable. My unpublished ultrastructural studies on organic linings of Jurassic foraminifers of the Nodosariidae failed to show any structural differentiation but this may be irrelevant.

Occurrence. — Ordovician and Silurian of Poland and Estonia (EISENACK 1937, KOZŁOWSKI 1959*a*).

Genus *Diplohydra* KOZŁOWSKI, 1959

Type species: *Diplohydra longithecata* KOZŁOWSKI, 1959

Remarks. — KOZŁOWSKI (1959*a*: 240) gave the following diagnosis of this genus: "Les espèces groupées dans ce genre sont caractérisées par la présence, le long des rameaux, des thèques de deux catégories, groupées par paires et communiquant entre elles de différente manière". He assigned four species to it: *D. longithecata*, KOZŁOWSKI, *D. micropedunculata* KOZŁOWSKI, 1959, *D. gonothecata* KOZŁOWSKI, 1959 and *D. solida* KOZŁOWSKI, 1959. The type material of these species was rather limited and its greater part underwent destruction in time. The preserved fragments of specimens display some features which make me doubt in both congeneric character of the four species and their affiliation with Hydroida. I think that the supposed pairs of thecae of two categories, grouped at each node, should be rather treated as single "thecae" seated at lateral branchings of major stolon. This is especially the case of *D. gonothecata*, which displays some similarity to some species of the genus *Kystodendron* KOZŁOWSKI. In turn, *D. solida* resembles stolon of *Rhabdopleurites* KOZŁOWSKI in morphology. Highly fragmentary character of the type material and the lack of new ones makes any taxonomical decisions concerning this genus hazardous.

Genus *Eisenackisyrinx* gen. n.

Type species: *Eisenackisyrinx curvatus* sp. n.

Derivation of the name: In honour of ALFRED EISENACK, student of microfossils, and from Gr. *syrinx* — tube.

Diagnosis. — As for the type species.

Remarks. — Monotypic genus.

Eisenackisyrinx curvatus sp. n.

(pl. 35: 3)

Holotype: The specimen shown in pl. 35: 3 (ZPAL V. X/5)

Type horizon and locality: The *Eoplacognathus pseudoplanus* Zone (Llanvirnian), erratic boulder MZ/42 (Orzechowo).

Derivation of the name: Lat. *curvatus* — *curved.*

Diagnosis. — Curved, irregular tubes, narrowing at both ends, up to 2 mm long or longer.

Material. — Nine specimens from the boulder MZ/42.

Description. — Strongly bent irregular tubes built of black, glittering opaque periderm. Tubes about 100—210 μm in diameter, narrowing to 30—50 μm at both ends, with maximum length over 2 mm.

Remarks. — The systematic position of *Eisenackisyrinx curvatus* sp. n. is unclear. This microfossil displays a distant similarity to Gonothecae Forma D, described by KOZŁOWSKI (1959*a*), from erratic boulder of Ordovician age, differing from the latter in the lack of one-sided flattening.

Occurrence. — The specimen is known from the type locality only.

Genus *Kozlowskisyrinx* gen. n.

Type species: *Kozlowskisyrinx graptovermiformis* sp. n.

Derivation of the name: In honour of Professor ROMAN KOZŁOWSKI (1889—1977), an outstanding Polish paleontologist, and from Gr. *syrinx* — tube.

Diagnosis. — As for the species.

Remarks. — Monotypic species.

Kozlowskisyrinx graptovermiformis n. sp.

(pl. 27: 6, pl. 37: 1—6)

Holotype: Specimen shown in pl. 37: 1 (ZPAL V.X/10)

Type locality and horizon: Erratic boulder ZPAL 0.218 of the Ordovician age, Zakroczym.

Derivation of the name: From the generic name *Graptovermis* KOZŁOWSKI, 1949, and from Lat. *forma* — shape.

Diagnosis. — Translucent, not branching tubes tightly coiled mainly in one plane. Tube wall brown, smooth, almost translucent.

Material. — Five specimens from boulder ZPAL 0.218 and one from boulder ZPAL 0.470.

Description. — Fine, brown, almost translucent tubes, optically homogeneous and tightly coiled in one plane. Tube side adhering to substratum thinner and flattened. Coils of tubes thightly to loosely packed. Tubes varying from 80 to 100 μm in diameter.

Ultrastructure. — TEM studies showed granular nature of tube building matter (pl. 27: 6). Fine granules of high electronic density are embedded in homogeneous basic material. Some parts of cuttings display free spaces corresponding to the granules in size. The spaces undoubtedly represent traces after granules broken down by knife in the course of cutting the sample.

Remarks. — *Kozlowskisyrinx graptovermiformis* sp. n. appears strikingly similar to the enigmatic Lower Ordovician genus *Graptovermis* KOZŁOWSKI, 1949, especially the species *G. intestinalis* KOZŁOWSKI, 1949 (see KOZŁOWSKI 1949*a*, pl. 15: 6), differing in the lack of fusellar structure and smaller dimensions. The similarity between these forms appears merely superficial and not connected with their systematic positions.

I am inclined to interpret the forms described above as living tubes of polychaetes. Among modern polychaetes, *Potamilla reniformis* (Müller) of the family Eunicidae *s. l.* and several others build translucent horny tubes.

The living tubes are built by several species representing various families of polychaetes. Individual genera (as e.g. *Eunice* CUVIER) often comprise both errant and sessile species, living in tubes. The tubes may be built of mucus-like, membrane-like or horny matter or they may be calcareous or agglutinated. Among organic microfossils from the Ordovician and Silurian of Poland, there are sometimes found tubes which may belong to Polychaete. The current techniques of dissolving rocks only gives a chance of preservation in the residuum only to tubes of horny matter. Tubes of that type are not characteristic of orders, families or even genera so their taxonomy is immediately impeded. TEM techniques may appear useful in identification of species.

Also tubothecae of benthic graptolites are interpreted as living tubes of sessile polychaetes (KOZŁOWSKI 1970*b*, URBANEK and MIERZEJEWSKI 1982). Fairly rich findings of organic tubes were recently reported from the Silurian of Gotland by BROOD (1979).

Occurrence. — Ordovician erratic boulder from the area of Poland.

Genus *Phragmohydra* KOZLOWSKI, 1959

Type species: *Phragmohydra articulata* KOZŁOWSKI, 1959

Diagnosis. — See KOZŁOWSKI (1959*a*: 238).

Remarks. — Monotypic genus.

Phragmohydra articulata KOZLOWSKI, 1959

1959*a*. *Phragmohydra articulata* KOZŁOWSKI; KOZŁOWSKI: 238, fig. 15.

Remarks. — The genus was described on the basis of a few specimens from Ordovician erratic boulders ZPAL 0.12 and ZPAL 0.110 by KOZŁOWSKI (1959*a*). The whole type series of *Ph. articulata* was lost or dissolved in glycerine before 1972.

KOZŁOWSKI (1959*a*) regarded this species as hydroid but there is no evidence in favour of that point of view. *Ph. articulata* very clearly differs in morphology from all the hitherto described Hydroida. It also differs markedly from the known stolons of graptolites and pterobranchs, I suppose that this form would be best treated as an *incertae sedis* organism until better preserved specimens are found.

Genus *Xenohydra* KOZŁOWSKI, 1959

Type species: *Xenohydra labiata* KOZŁOWSKI, 1959

Diagnosis. — "Rameaux épais, droits, percés d'orifices arrondis, bordés chacun au-dessous par un large et court processus bilobe" (KOZŁOWSKI 1959*a*: 249).

Remarks. — Monotypic genus, the systematic position of which is unclear. KOZŁOWSKI (1959*a*) noted that its affiliation with Coelenterata is uncertain. I suppose that *Xenohydra* represents a group of colonial organism hitherto unknown.

Xenohydra labiata KOZLOWSKI, 1959

(pl. 36: 1—4, pl. 37: 7)

1959*a*. *Xenohydra labiata* KOZŁOWSKI; KOZŁOWSKI: 249, fig. 23.

Diagnosis. — As for the genus.

Material. — 34 flattened fragments of branches from boulder ZPAL 0.44 (Ordovician? Silurian?) and 18 from the borehole at Mielnik (depth 1118—1124 m, Upper? Ordovician).

Description. — The specimens from Mielnik fully correspond to those from erratic boulder ZPAL 0.44, previously described by KOZŁOWSKI (1959*a*). In a single case I found remains of unknown element around opening in branch. The element resembles seated theca of some modern Hydroida (pl. 36: 4).

Ultrastructure of periderm. — SEM micrographs very clearly show the two-layered character of periderm (pl. 36: 1). The image obtained with the use of TEM gives more information on ultrastructure. Differentiation into translucent and opaque layers, traceable under light microscope, appears to be due to differences in distribution of electronically denser deposits in homogenic basic matter (pl. 36 :3). The opaque inner layer, forming about two-thirds of thickness of periderm, displays numerous closely spaced and quite uniformly distributed deposits (pl. 37: 7). The translucent outer layer shows deposits markedly less regularly distributed and less numerous and even absent in its outermost part. The boundary between the two layers is very distinct. A thin layer built of granules of high electronic density covers uneven outer surface of periderm. The granules most probably represent foreign bodies adhering the periderm.

Periderm is about 4—5 μm thick.

Remarks. — The type horizon of *Xenohydra labiata* remains unknown. In the paper by Kozłowski (1959*a*) and his unpublished notes no information may be found on accompanying fossils, on the basis of which the boulder 0.44 was dated as Ordovician. It shoud be also noted that the sample from that boulder and its residuum, housed at the Institute of Paleobiology of the Polish Academy of Sciences, was unfortunately lost. This is important because of the fact that some boulders, dated as Ordovician by Kozłowski (1959*a*), were subsequently shown to yield conodonts indicative of the Silurian (Dzik, oral inf.).

Occurrence. — Ordovician (and Silurian?) of Poland.

Genus *Xenotheka* Eisenack, 1937

Type species: *Xenotheka klinostoma* Eisenack, 1937

Remarks. — Eisenack (1937) noted similarity of these microfossils to some sessile foraminifers. Cushman (1948) interpreted *Xenotheka* as representatives of Ammodiscidae, Loeblich and Tappan (1964) — of the family Allogromiidae, and Jansonius (1964) — as one of *incertae sedis* genera of Chitinozoa. Eisenack (1970*b*, 1971) later supposed that the microfossils were related to the Graptolithina and compared them with graptoblasts. According to him small *Xenotheka* "Fortsatz" described from one of specimens (Eisenack 1970) may represent a homolog of graptoblast filum and the tube to the cryptopyle.

According to my work *Xenotheka* cannot be related to graptoblasts. The fusellar tissue, typical of graptolites (Kozłowski 1962, Urbanek and Rickards 1974) was not hitherto found in *Xenotheka* and the similarity of "Fortsatz" to filum, i.e. stolon fragment, is questionable. Here I would like to draw attention to the striking similarity of this genus to other organic microfossils. The type material of *X. klinostoma*, figured by Eisenack (1937), looks like a sicula of benthic graptolite, ascribed to the Crustoidea by Kozłowski (1971). Both microfossils display elongated, flat-convex globular part attached to substratum, and identically developed basal membrane. In both cases, a tube with annular structure is rising obliquely upwards from the globular part. In *X. klinostoma*, the tube was named a "Mündungsrohr" and the rings — as growth lines by Eisenack (1937), and in sicula of Crustoidea — respectively as metasicula and fusellar rings by Kozłowski (1971). The specimens of the type series of the form studied were lost so it is not possible to check whether or not the name *X. klinostoma* was not given to sicula ascribed to Crustoidea by Kozłowski. The affinity of *Xenotheka* and Ordovician problematic *Chitinolagena* Bykova is also not excluded.

The question of the systematic position of *Xenotheka* was additionally complicated by the neotype of *X. klinostoma*, designated by Eisenack (1970, fig. 1), wery closely resembling other Ordovician organic microfossil — *Ascosyrinx tenuis* Kozłowski, 1967.

Xenotheka klinostoma Eisenack, 1937

(fig. 22)

1937. *Xenotheka klinostoma* Eisenack; Eisenack: 239, figs. 21—22.
1970*b*. *Xenotheka klinostoma* Eisenack; Eisenack: 29, figs. 1—2.

1971. *Xenotheka klinostoma* EISENACK; EISENACK: 342, figs. 13—16.
1976. *Xenotheka klinostoma* EISENACK; EISENACK: 184, fig. 1.

Material. — A single specimen from erratic boulder MZ/125.

Description. — Specimen 640 μm long, without a part attached to substratum. Distal part of tube with weakly marked annular structure. Base trapezoidal in outline, smoothly passing into tube. Periderm black, weakly glittering.

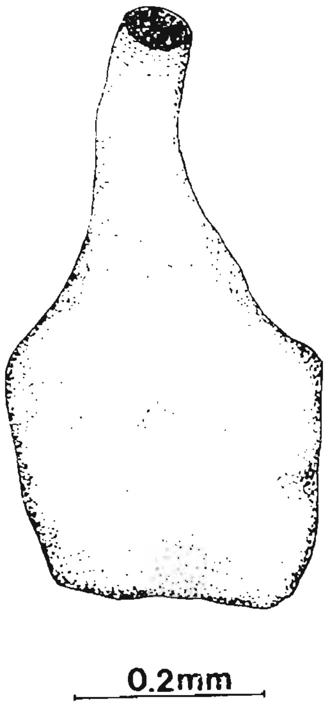

Fig. 22.
Xenotheka klinostoma EISENACK (ZPAL VX/10). Boulder no. MZ/125, Poddębie, Ordovician.

Occurrence. — Ordovician erratic boulders from the Baltic region (the so-called *Ostseekalk*, i.e. Baltic Limestone), Öland Id — Vaginatum (Kunda) Limestone (EISENACK 1937, 1970*b*, 1971, 1976).

Problematicum A
(pl. 35: 6—7)

Material. — Two specimens from erratic boulder MZ/42 (Orzechowo), the *Eoplacognathus pseudoplanus* Zone (Llanvirn).

Description. — Flat-convex microfossils irregular, close to suboval in shape. Periderm black, weakly glittering, with circular perforations.

Remarks. — The nature of the microfossils described above is unclear. They may represent cysts of Rhabdopleurida or Crustoidea.

Problematicum B
(fig. 23)

Material. — A single specimen from erratic boulder MZ/2 (Orzechowo), Ordovician (?).

Description. — Fragment of stolon about 2 mm long and with three nodes. Periderm dark-brown, slightly glittering and somewhat translucent, more translucent in terminal parts of

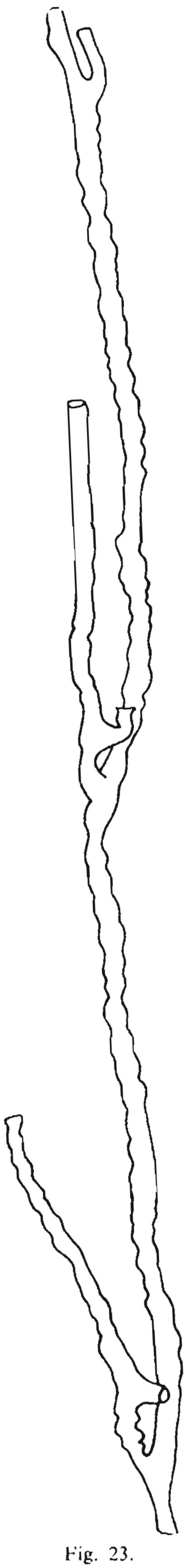

Fig. 23.

Problematicum B (ZPAL VX/11). Boulder no. MZ/2. Orzechowo, Ordovician or Silurian.

branchings only. Annulation of stolon clear, except for the proximity of points of branching, where it is missing or at least less clear.

Remarks. — The stolon appears strikingly similar to fragments of hydrosomes of some modern Hydroida of the suborder Athecata, e.g. *Coryne pusilla* GAERTNER (Corynidae) or *Eudendrium annulatum* NORMAN (Eudendriidae). On the other hand, it is somewhat similar to the stolons of Crustoidea. However, the available material is insufficient for reconstruction of the taxonomic position of the specimen.

Problematicum C
(pl. 35: 4)

Material. — A single specimen from erratic boulder MZ/151, Ordovician (?).

Description. — Thick-walled stolon trifurcating into descendant ones. Descendant stolons Sa and Sb connected with long "thecae", becoming narrower in distal direction, and the stolon Sc — ending with small, cup-shaped appendix.

Remarks. — The specimen undoubtedly represents a fragment of skeleton of a colony. However, it differs markedly in morphology from similar structures known in Coelenterata, Pterobranchia, as well as in the Graptolithina.

Problematicum D
(pl. 21: 7)

1978*b*. ?*Stolonodendrum* sp.; MIERZEJEWSKI: p. 559.

Material. — Two specimens from erratic boulder MZ/88 (of Ordovician age), characterized by MIERZEJEWSKI (1978*b*).

Description. — Clusters of markedly flattened stolons, strongly entangled in one plane. Periderm smooth, black and matt.

Remarks. — The specimens appear very similar to both those described as stolons *Stolonodendrum* sp. by KOZŁOWSKI (1949*a*, pl. 32: 3) and stolons of hydrorhizae of *Rhabdohydra tridens* KOZŁOWSKI, described here (p. 153).

REFERENCES

ADAMCZAK, E. 1963. *Gloecapsomorpha prisca* ZALESSKY (sinice) z ordowickich głazów narzutowych Polski. — *Acta Palaeont. Polonica*, 8, 4, 465—474.

ANDRES, D. 1961. Die Struktur von Mastigograptiden aus einem ordovizischen Geschiebe Berlins. — *N. Jb. Geol. Paläont. Mh.*, **1961**, 12, 636—647.

— 1977. Graptolithen aus ordovizischen Geschieben und die frühe Stammesgeschichte der Graptolithen. — *Paläont. Z.*, **51**, 1/2, 52—93.

— 1980. Feinstrukturen und Verwandtschaftsbeziehungen der Graptolithen. — *Ibidem*, **54**, 1/2, 129—170.

BEDNARCZYK, W. 1966. Uwagi o stratygrafii ordowiku w rejonie Białowieży (Remarks of the Ordovician stratigraphy in the Białowieża Region). — *Kwart. Geol.*, **10**, 1, 33—43.

— 1971. Ordowik wschodniej części obniżenia podlaskiego. — *Acta Geol. Polonica*, **21**, 2, 201—212.

Behr, H. J., Jordan, H. and Malcalm, H. 1966. Chitinozoenfaunen aus dem Altpaläozoikum von Thüringen. — Monatsberichte der D. Akad. Wiss. Berlin, **8,** 5, 347—353.

(Beklemishev, V. N.) Беклемишев, В. Н. 1951. К построению системы животных. Вторноротные (Deuterostomia), их происхождение и состав. — *Усп. совр. биол.* **32,** 347—353.

Bischoff, G. C. O. 1978. Internal structures of conulariid tests and their functional significance, with special reference to Circonulariina n. suborder Cnidaria, Scyphozoa. — *Senckenberg. Lethea,* **59,** 4/6, 275—327.

Blackwell, J., Parker, K. D. and Rudall, K. M. 1965. Chitin in pogonophore tubes. — *J. mar. biol. Ass. U. K.,* **45,** 659—661.

Broch, H. 1929. Hydroidenuntersuchungen. VI. Studien an *Silicularia* Meyen. — *Abh. Norske Vidensk. Akad., m. n. Kl.,* **3,** 1—30.

Bouček, B. 1941. Ueber neue Algenreste aus dem böhmischen Silur. — Vestnik Kral. ceske spol. nauk, tr. mat.-prorod. Praha.

— 1957. The dendroid graptolites of the Silurian of Bohemia. — *Rozprawy Ustr. ust. geol.,* **23,** 5—294.

Brood, K. 1979. Organic tubes. *In*: Jaanusson, V., Laufeld, S. and Skoglund, R. (ed.), Lower Wenlock faunal and floral dynamics — Vattenfallet section, Gotland, 252. Uppsala.

Brunet, P. C. J. and Carlisle, D. B. 1958. Chitin in Pogonophora. — *Nature,* **182,** 1689.

Bulman, O. M. B. 1938. Graptolithina. *In*: Schindewolf, O. H. (ed.), Handbuch der Paläozoologie, Borntraeger, Berlin, Band 2D, Lief. **2,** 1—92.

— 1955. Graptolithina with sections on Enteropneusta and Pterobranchia. *In*: Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, V. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

— 1970. Graptolithina with sections on Enteropneusta and Pterobranchia. *In*: Teichert, C. (ed.), Treatise on Invertebrate Paleontology, V. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

(Bykova, E. V. and Reitlinger, E. A.) Быкова, Е. В. и Райтлингер, Е. А. 1959. Отруад Astrochizida. В: Орлов, Ю. А. (эд.), Основы палеонтологии, Общая часть, простейшие, Недра, Москва.

Chaiffetz, M. S. 1974. Ratios of larger palynomorphs, Red Mountain Formation, Northeastern Alabama. Abstract. — Southeastern Section, Geol. Soc. of America, Section Meeting, April 1974.

Chapman, D. M. 1966. Evolution of the scyphistoma. — *Symp. zool. Soc. London,* **16,** 51—75.

— 1968. Structure, histochemistry and formation of the podocyst and cuticle of *Aurelia aurita*. — *J. mar. biol. Ass. U. K.,* **48,** 187—208.

— 1969. The nature of cnidarian desmocytes. — *Tissue and Cell,* **1,** 4, 619—632.

— and Werner, B. 1972. Structure of a solitary and a colonial species of *Stephanoscyphus* (Scyphozoa, Coronata) with observations on periderm repair. — *Helg. Wiss. Meeresunters.,* **23,** 393—421.

Chapman, F. 1919. New or little-known Vistorian fossils in the National Museum. Part 23: On some hydroid remains of Lower Palaeozoic age from Manegetta, near Lancefield. — *Proc. Roy. Soc. Victoria,* **31,** N. S., 2, 388—393.

— and Skeats, E. W. 1919. On the discovery of fossil hydroid remains of the order Calyptoblastea in the Palaeozoic of Victoria, Australia. — *Geol. Mag.,* **66,** 550—551.

— and Thomas, D. E. 1936. The Cambrian Hydroida of the Heathcote and Monegeeta Districts. — *Roy. Soc. Victoria.* **48,** 2, 193—212.

Corradini, D., Russo, F. and Serpagli, E. 1974. Ultrastructure of some fossil and recent polychaete jaws (scolecodonts.) — *Boll. Soc. Paleont. Ital.,* **13,** 1/2, 122—134.

Crowther, P. R. 1978. The nature and mode of life of the graptolite zooid with reference to secretion of the cortex. — *Acta Palaeont. Polonica,* **23,** 4, 473—479.

— 1981. The fine structure of graptolite periderm. — Spec. Pap. *Palaeontology,* **26.**

Cushman, J. A. 1948. Foraminifera. Their classification and economic use. Harvard University Press. Harvard.

Decker, Ch. E. 1948. A new species of hydrozoan from the Athens shale of Virginia. — *J. Paleont.,* **22,** 4, 528—529.

— 1952. A new hydrozoan from the Devonian of Michigan. — *Ibidem,* **26,** 4, 656—658.

Dilly, P. N. 1971. Keratin-like fibres in the hemichordate *Rhabdopleura compacta*. — *Z. Zellforsch.,* **117,** 502—515.

— 1975. The dormant buds of *Rhabdopleura compacta* (Hemichordata). — *Cell Tiss. Res.,* **159,** 3, 387—397.

Eisenack, A. 1932. Neue Mikrofossilien des baltischen Silurs. II. (Foraminiferen. Hydrozoen, Chitinozoen u. a.). — *Palaeont. Z.,* **14,** 257—277.

— 1934. Neue Mikrofossilien des baltischen Silurs. III. und Neue Mikrofossilien des böhmischen Silurs. I. — *Ibidem,* **16,** 1/2, 56—76.

— 1935. Mikrofossilien aus Doggergeschieben Ostpreussens. — *Z. Geschiebeforsch.,* **11,** 4, 167—184.

— 1937. Neue Mikrofossilien des baltischen Silurs. IV. — *Palaeont. Z.,* 19, 3/4, 217—242.

— 1942. Die Melanoskleritoiden, eine neue Gruppe silurischer Mikrofossilien aus dem Unterstamm der Nesseltiere. — *Ibidem,* **23,** 1/2, 157—180.

— 1950. Nachtrag zum Melanoskleritoiden-Problem. — *N. Jb. Geol. Paläont. Mh.,* **1950,** 12, 371—376.

— 1963. Melanoskleriten aus anstehenden Sedimenten und aus Geschieben. — *Paläont. Z.,* **37,** 1/2, 122—134.

— 1968. Mikrofossilien eines Geschiebes der Borkholmer Stufe, baltisches Ordovizium, F_2. — *Mitt. Geol. Staatsinst. Hamburg,* **37,** 81—94.

Eisenack, A. 1970*a*. Mikrofossilien aus dem Silur Estlands und der Insel Ösel. — *Geolog. Förening. Stockholm*, **92**, 3, 302—322.

— 1970*b*. *Xenotheka klinostoma* und ihre systematische Stellung. — *N. Jb. Geol. Paläont. Mh.*, **1970**, 8, 449—451.

— 1971. Die Mikrofauna der Ostseekalke Ordovizium. 3. Graptolithen, Melanoskleriten, Spongien, Radiolarien, Problematika nebst 2 Nachträgen über Foraminiferen und Phytoplankton. — *N. Jb. Geol. Paläont. Abh.*, **137**, 3, 337—357.

— 1976. Mikrofossilien aus dem Vaginatenkalk von Hälludden, Öland. — *Palaeontographica A*, **154**, 4—6, 181—203.

Eller, E. R. 1964. Scolecodonts of the Delaware Limestone, Devonian of Ohio and Ontario. — *Ann. Carnegie Mus.*, **36**, 229—275.

Foucart, M. F., Bricteux-Gregoire, S. and Jeuniaux, Ch. 1965. Composition chimique du tube d'un Pogonophore *Siboglinum* sp. et des formations squeletiques de deux Pterobranches. — *Sarsia*, **20**, 35—41.

—, —, — and Florkin, M. 1965. Fossil proteins of graptolites. — *Life Sciences*, **4**, 467—471.

— and Jeuniaux, Ch. 1965. Paleobiochimie et position systematique des graptolites. — *Ann. Soc. Roy. Zool. Belg.* **95**, 2, 39—45.

George, J. D. 1977. The pogonophore epidermis, its structure, functions and affinities. — *Symp. zool. Soc. London*, **39**, 195—222.

Gocht, H. 1970. Dinoflagellaten-Zysten aus dem Bathonium des Erdöfeldes Aldorf (NW Deutschland). — *Palaeontographica B*, **129**, 4—6, 178—192.

Górka, H. 1969. Microrganismes de l'Ordovicien de Pologne. — *Palaeont. Polonica*, **22**, 166 pp.

— 1971. Sur les "Melanosclerites" extraits des galets erratiques ordoviciens de Pologne. — *Soc. Geol. Min. Bret. Bull.*, (C), **3**, 1, 29—40.

(Ivanov, A. V.) Иванов, А. В. 1960. Погонофоры. Москва — Леннград. 271 пп.

— 1963. Pogonophora. — Academic Press, London.

Jansonius, J. 1964. Morphology and classification of some Chitinozoa. — *Bull. Can. Petrol. Geol.*, **12**, 4, 901—918.

Jeuniaux, Ch. 1963. Chitine et chitinolyse. Un chapitre de la biologie moleculaire. — Masson, Paris. 181 pp.

— 1965. Chitine et phylogenie: Application d'une methode enzymatique de dosage de la chitine. — *Bull. Soc. Chim. Biol.*, **47**, 12, 2267—2278.

— 1971. Chitinous structures. *In*: Florkin, M. and Stotz, E. H. (ed.), Comprehensive biochemistry, Extracellular and supporting structures, **26C**, 595—632. — Elsevier Publ. Co., Amsterdam.

Kiderlen, H. 1937. Die Conularien. Ueber Bau und Leben der ersten Scyphozoa. — *N. Jb. Min.* etc., Beil-Bd **B 77**, 113—169.

Kielan-Jaworowska, Z. 1962. New Ordovician genera of polychaete jaw apparatuses. — *Acta Palaeont. Polonica*, **7**, 3—4, 291—332.

— 1966. Polychaete jaw apparatuses from the Ordovician and Silurian of Poland and a comparison with modern forms. — *Palaeont. Polonica*, **16**, 152 pp.

Kieslinger, A. 1939. Scyphozoa. *In*: Schindewolf, O. H. (ed.), Handbuch der Paläozoologie, B. 2A, 71—109. Berlin.

Kozłowski, R. 1938. Informations préliminaires sur les Graptolithes du Tremadoc de la Pologne et sur leur portée théorique. — *Ann. Mus. Zool. Pol.*, **13**, 183—196.

— 1947. Les affinitiés des Graptolithes. — *Biol. Rev.*, **22**, 99—108.

— 1949*a*. Les Graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne. — *Palaeont. Polonica*, 3, I—VIII, 71 pp.

— 1949*b*. Découverte du Ptérobranche *Rhabdopleura* à l'état fossile dans le Crétacé supérieur en Pologne. — *C.—R. Acad. Sc. de Paris*, **228**, 1505—1507.

— 1954. O budowie niektórych Dichograptidae. — *Acta Geol. Polonica*, **4**, 4, 423—444.

— 1956*a*. Sur *Rhabdopleura* du Danien de Pologne. — *Acta Palaeont. Polonica*, **1**, 1, 3—21.

— 1956*b*. Sur quelques appareils masticateurs des Annelides Polychetes ordoviciens. — *Ibidem*, **1**, 3, 165—210.

— 1959*a*. Les hydroides ordoviciens à squelette chitineux. — *Ibidem*, **4**, 3, 209—271.

— 1959*b*. Un microfossile enigmatique. — *Ibidem*, **4**, 3, 273—277.

— 1960. *Calyxdendrum graptoloides* n. gen., n. sp. — a graptolite intermediate between the Dendroidea and the Graptoloidea. — *Ibidem*, **5**, 2, 107—125.

— 1961. Découverte d'un Rhabdopleuride (Pterobranchia) ordovicien. — *Ibidem*, **6**, 1, 3—16.

— 1962. Crustoidea — nouveau groupe de graptolites. — *Ibidem*, **7**, 1, 3—52.

— 1963*a*. Le développment d'un graptolite tuboide. — *Ibidem*, **8**, 2, 103—134.

— 1963*b*. Sur la nature des Chitinozoaires. — *Ibidem*, **8**, 4, 425—449.

— 1966*a*. On the structure and relationships of graptolites. — *J. Paleont.*, **40**, 489—501.

— 1966*b*. *Graptolodendrum mutabile* n. gen., n. sp., an aberrant dendroid graptolite. — *Acta Palaeont. Polonica*, **11**, 1, 1—14.

— 1967. Sur certains fossiles ordoviciens à test organique. — *Ibidem*, **12**, 2, 99—132.

— 1968. Nouvelles observations sur les Conulaires. — *Ibidem*, **13**, 4, 497—531.

— 1970*a*. Nouvelles observations sur les Rhabdopleurides (Pterobranches) ordoviciens. — *Ibidem*, **15**, 1, 3—17.

Korzowski, R. 1970*b*. Tubotheca — a peculiar morphological element in some graptolites. — *Ibidem*, **15**, 4, 393—410.

— 1971. Early development stages and the mode of life of graptolites. — *Ibidem*, **16**, 4, 313—343.

Kulicki, C. 1969. The discovery of *Rhabdopleura* (Pterobranchia) in the Jurassic of Poland. — *Ibidem*, **14**, 4, 537—552.

— 1971. New observations on *Rhabdopleura kozlowskii* (Pterobranchia) from the Bathonian of Poland. — *Ibidem*, **16**, 4, 415—429.

— and Szaniawski, H. 1972. Cephalopod arm hooks from the Jurassic of Poland. — *Ibidem*, **17**, 3, 379—419.

Kuźnicki, L. and Urbanek, A. 1967. Zasady nauki o ewolucji, I, PWN, Warszawa.

Kwiecińska, B. and Siemińska, J. 1974. New fossil microorganisms found in the marble of Przeworno (Lower Silesia). — *Ann. Med. Sect. Pol. Acad. Sci.*, **19**, 2, 129—130.

Lankester, E. R. 1884. A contribution to the knowledge of *Rhabdopleura*. — *Q. J. microsc. Sci.*, **24**, 622—647.

Laufeld, S. 1979*a*. "Chitinous" hydroids. *In*: Jaanusson, V., Laufeld, S. and Skoglund, R. (ed.), Lower Wenlock faunal and floral dynamics — Vattenfallet section, Gotland. — *Sver. Geol. Undersökning*, C, **762**, 77—78.

— 1979*b*. Melanosclerites. — *Ibidem*, 762, 79—80.

Lendenfeld, R. 1883. Ueber Coelenteraten der Südsee. IV Mittheil. *Eucopella campanularia* nov. gen. — *Z. wiss. Zool.*, **38**, 497—583.

Lentz, Th. L. 1966. The cell biology of Hydra. — *North-Holland Publ.* Co., Amsterdam. 199 pp.

— and Barnett, R. J. 1965. Surface specialization of hydra cells: The effect of enzyme inhibitors on ferritin uptake. — *J. Ultrastruc. Res.*, **13**, 192—211.

Loeblich, A. R. and Tappan, H. 1964. Protista 2, Sarcodina, chiefly "Thecamoebians" and Foraminiferida. *In*: Moore, R. C. (ed.), Treatise on Invertebrate Paleontology, Lawrence, Kansas.

Mackie, G. O. 1960. Studies on *Physalia physalis* (L.). Part II. Behaviour and histology. — *Discovery Reports*, **30**, 301—408.

Manton, S. M. 1941. On the hydrorhiza and claspers of the hydroid *Myriothela cocksi* (Vigurs). — *J. mar. biol. Ass. U. K.*, **25**, 143—150.

Matthew, G. F. 1899. Upper Cambrian of Mount Stephen, British Columbia: the trilobites and worms. — *Roy. Soc. Canada, Trans.*, Ser. 2, **5**, 4, 39—56.

Mierzejewska, G. Mierzejewski, P. 1974. The ultrastructure of some fossil invertebrate skeletons. — *Ann. Med. Sect. Pol. Acad. Sci.*, **19**, 2, 133—135.

— and — 1975. Breakdown of collagen during phyllogenetic development of Polychaeta. — *Ibidem*, **20**, 2, 99—100.

— and — 1977. Electron microscope investigations of the fossil and recent polychaete jaws from the genus *Glycera* Savigny, 1818. — *Prace Muz. Ziemi*, **26**, 127—130.

— and — 1978. Ultrastructure of the jaws of the fossil and recent Eunicida (Polychaeta). — *Acta Palaeont. Polonica*, **23**, 3, 317—339.

— and — 1979*a*. Chitin-protein complex in the Ordovician organic microfossils. — *Acta Med. Polona*, **20**, 1, 33—34.

— and — 1979*b*. Traces of bacterial activity on the Ordovician polychaete jaws. — *Ibidem*, **20**, 1, 35—36.

Mierzejewski, P. 1974. Ultrastruktura peridermy kopalnych i współczesnych Hydroida (Ultrastructure of the recent and fossil Hydroida periderm). Graduate paper, Institute of Zoology of the Warsaw University. Unpublished.

— 1977. The first discovery of Crustoidea (Graptolithina) and Rhabdopleurida (Pterobranchia) in the Silurian. — *Bull. Acad. Pol. Sci., Ser. Sci. de la Terre*, **25**, 2, 103—107.

— 1978*a*. Molting of the jaws of the Early Paleozoic Eunicida (Annelida, Polychaeta). — *Acta Palaeont. Polonica*, **23**, 1, 73—88.

— 1978*b*. Tuboid graptolites from erratic boulders of Poland. — *Ibidem*, **23**, 4, 557—575.

— 1978*c*. New placognath Eunicida (Polychaeta) from the Ordovician and Silurian of Poland. — *Acta Geol. Polonica*, **28**, 2, 273—282.

— 1981. TEM study on ultrastructure of chitinozoan vesicle wall. — *Cah. Micropaleontologie*, **1981**, 1, 59—62.

— 1982. On the nature of pre-Devonian tracheid-like tubes. — *Lethaia*, **15**, 2, 148.

— 1984*a*. *Pterobranchites* Kozłowski, 1967 — an aberrant graptolite. — *Acta Palaeont. Polonica*, **29**, 1—2, 83—89.

— 1984*b*. *Cephalodiscus*-type fibrils in the graptoblast fusellar tissue. — *Ibidem*, **29**, 3—4, 157—160.

— 1984*c*. *Xenocyathus* Eisenack, 1982 — a crustoid graptolite. — *N. Jb. Geol. Paläont. Mh.* 1984, H. 5, 300—302.

Mortelmans, G. 1955. Découverte d'un ptérobranche, Rhabdopleura delmeri nov. sp., dans les Viseen terminal du sondage de Turnhaut. — *Mém. Mus. Roy. Hist. nat. Belgique*, 52—66.

(Naumov, D. V.) Наумов, Д. В. 1960. Гидроиды и гидромедузы морских, солоноватоводных и пресноводных бассейнов СССР. Изд. АН СССР. Москва — Ленинград.

— 1961. Сцифойдные медузы морей СССР. Определители по фауне СССР, **75**, 1—97.

Neville, A. C. and Luke, B. M. 1969. A two-system model for chitin-protein complexes in insect cuticles. — *Tissue and Cell*, **1**, 4, 689—707.

Nitecki, M. H. 1976. Ordovician Batophoreae (Dasycladales) from Michigan. — *Fieldiana*: *Geology*, **35**, 4, 29—40.

— and Richardson, E. S. 1972. A new hydrozoan from the Pennsylvanian of Illinois. — *Ibidem*, **30**, 1, 1—7.

— and Schram, F. R. 1876. *Etacystis communis*, a fossil of uncertain affinities from the Mazon Creek fauna (Pennsylvanian of Illinois). — *J. Paleont.*, **50**, 6, 1157—1161.

(Obut, A. M.) Обут, А. М. 1964. Подтип. Стомохордовые. В: Орлов, Ю. А. (эд.), Основы палеонтологии. Недра, Москва.

— 1974. New graptolites from the Middle Cambrian of the Siberian Platform. — *Spec. Pap. Palaeont.*, **13**, 9—13.

— and Sobolewskaya, R. F.) Обут, А. М. и Соболевская, Р. Ф. 1967. Некоторые стереостолонаты позднего Кембрия и ордовика норильского района. В: Новые данные по биостратиграфии нижнего палеозоя сибирской платформы, 45—160. Изд. Наука, Москва.

Pożaryska, K. 1968. Recherches sur les couches du Tertiaire inférieur en Europe Epicontinentale. — Conferences, Acad. Pol. Sci., Centre Sci. Paris, fasc. 72.

Quilty, P. G. 1971. Cambrian and Ordovician dendroids and hydroids of Tasmania. — *J. Geol. Soc. Australia*, **17**, 2, 171—190.

Rees, W. J. 1957. Evolutionary trends in the classification of capitate hydroids and medusae. — *Bull. Br. Mus. Nat. Hist. Zool.*, **4**, 453—534.

Richards, A. G. 1951. The integument of arthropods. — Univ. of Minnesota Press, Minneapolis.

Rickards, R. B., Hyde, P. J. W. and Krinsley, D. H. 1971. Periderm ultrastructure of a species of *Monograptus* (phylum Hemichordata). — *Proc. Roy. Soc. Lond.*, **B 178**, 347—356.

Rudall, K. M. 1955. Distribution of collagen and chitin. — *Symp. Soc. Experim. Biol.*, **9**, 49—71.

Ruedemann, R. 1925. The Utica and Lorraine formations of New York. Part II. Systematic paleontology. No. 1. Plants, sponges, corals, graptolites, crinoids, worms, bryozoans, brachiopods. — *N. Y. State Mus., Bull.*, **262**, 1—171.

— 1947. Graptolites of North America. — *Geol. Soc. Amer., Mem.*, **19**, 1—652.

Schallreuter, R. 1981. Mikrofossilien aus Geschieben. I. Melanoskleriten. — *Der Geschiebesammler*, **15**, 3, 107—130.

Schepotieff, A. 1905. Ueber die Stellung der Graptolithen im Zoologischen System. — *Neues Jb. Min. Geol. Paläont.*, **2**, 79—90.

— 1907. Die Pterobranchier. — *Zool. Jb., Abt. Anat. Ontogen. Tiere*, **23**, 3, 463—534.

— 1909. Die Pterobranchier des Indischen Ozeans. — *Zool. Jb., Abt. Systematik*, etc., **28**, 4, 429—445.

Schram, F. R. and Nitecki, M. H. 1975. *Hydra* from the Illinois Pennsylvanian. — *J. Paleont.*, **49**, 3, 549—551.

Sdzuy, K. 1974. Mittelkambrische Graptolithen aus NW-Spanien. — *Paläont. Z.*, **48**, 1/2, 110—139.

Skevington, D. 1965*a*. Graptolites from the Ontikan limestones Ordovician of Öland, Sweden. II. Graptoloidea and Graptovermida. — *Bull. Geol. Inst. Univ. Uppsala*, **43**, 3, 1—74.

— 1965*b*. Chitinous hydroids from the Ontikan limestones Ordovician of Öland, Sweden. — *Geol. Fören. Stockh. Förh.*, **89**, 275—349.

(Sokolov, B. S.) Соколов, 1965. Древнейшие отложения раннего кембрия и сабеллитиды. Всесоюзный симпоз. по палеонт. докембрия и раннего кембрия (тезисы докладов), 78—91. Новосибирск.

— 1972. Vendian and Early Cambrian Sabelliditida (Pogonophora) of the USSR. — Proc. IPU, 23 Int. Geol. Congress 1968, 79—86.

Stebbing, A. R. D. 1970. Aspects of the reproduction and life cycle of *Rhabdopleura compacta* (Hemichordata). — *Mar. Biol.*, **5**, 3, 205—212.

Sundara-Rajulu, G., Jeuniaux, Ch., Poulicek, M. and Voss-Foucart, M. F. 1982. Comparative value of chitosan test and enzymatic method for chitin detection. *In*: Hirano, S. and Tokura, S. (ed.), Chitin and Chitosan, Proceed. 2d. Intern. Conf. on Chitin and Chitosan, Sapporo.

Szaniawski, H. 1979. Conodonts from the chalcedony beds, Holy Cross Mountains (Poland). — *Acta Palaeont. Polonica*, **25**, 1, 101—122.

Taugourdeau, Ph. 1976. Sur une radula presumée de gasteropode trouvée dans le neocomien. — *Rev. Micropaleont.* **19**, 1, 54—58.

— 1978. Incertae sedis et microfossiles divers conserves en matière organique du paleozoique saharien. — *Ibidem*, **21**, 3, 149—159.

Thomas, H. D. and Davis, A. G. 1949*a*. A fossil species of the pterobranch *Rhabdopleura*. — *Abstr. Proc. Geol. Soc. Lond.*, **1450**, 79.

— and — 1949*b*. The pterobranch *Rhabdopleura* in English Eocene. — *Bull. Brit. Mus. Nat. Hist., Geol.*, **1**, 1, 1—19.

Tomczykowa, E. 1964. Ordowik platformy wschodnioeuropejskiej na obszarze Polski. — *Kwart. Geol.*, **8**, 3, 491—505.

Towe, K. M. and Urbanek, A. 1972. Collagen-like structures in Ordovician graptolite periderm. — *Nature*, **237**, 443—445.

Urbanek, A. 1959. Studies on graptolites, II. On the development and structure of graptolite genus *Gymnograptus* Bulman. — *Acta Palaeont. Polonica*, **4**, 3, 279—338.

— 1976*a*. The problem of graptolite affinities in the light of ultrastructural studies on peridermal derivatives in pterobranchs. — *Ibidem*, **21**, 1, 3—36.

— 1976*b*. Ultrastructure of microfuselli and the evolution of graptolite skeletal-tissues. — *Ibidem*, **21**, 4, 315—331.

— 1978. Significance of ultrastructural studies for graptolite research. — *Ibidem*, **23**, 4, 595—629.

— and Mierzejewska, G. 1977. The fine structure of zooidal tubes in Sabelliditida and Pogonophora with reference to their affinity. — *Ibidem*, **22**, 3, 223—240.

URBANEK, A. and MIERZEJEWSKI, P. 1982. Ultrastructure of the tuboid graptolite tubotheca. — *Paläont. Z.*, **56**, 1/2, 87—93.

—, — and RICKARDS, R. B. (in press). New observations on the fine structure of graptoblasts. — *Lethaia.*

— and RICKARDS, R. B. 1974. The ultrastructure of some retiolitids and graptoblasts. — *Spec. Pap. Palaeont.*, **13**, 177—186.

— and TOWE, K. M. 1974. Ultrastructural studies on graptolites, 1: The periderm and its derivatives in the Dendroidea and in *Mastigograptus*. — *Smith. Contr. Paleobiology*, **20**, 1—48.

— and — 1975. Ultrastructural studies on graptolites, 2: The periderm and its derivatives in the Graptoloidea. — *Ibidem*, **22**, 1—24.

VERVOORT, W. 1966. Skeletal structure in the Solanderiidae and its bearing on hydroid classification. — *Symp. zool. Soc. Lond.*, **16**, 373—396.

VOIGT, E. 1973. *Hydrallmania graptolithiformis* n. sp., eine durch Biomuration erhaltene Sertulariidae (Hydroz.) aus der Maastrichter Tuffkreide. — *Paläont. Z.* **47**, 1/2, 25—31.

WERNER, B. 1966. *Stephanoscyphus* scyphozoa, Coronatae und seine direkte Abstammung von den fossilen Conulata. — *Helgoländer wiss. Meeresunters.*, **13**, 317—347.

— 1967. Morphologie, Systematik und Lebensgeschichte von *Stephanoscyphus* (Scyphozoa, Coronatae) sowie seine Bedeutung für die Evolution der Scyphozoa. — *Zool. Anz.* (Suppl.), **30**, 297—319.

— 1971. *Stephanoscyphus planulophorus* n. spec., ein neuer Scyphopolyp mit einem neuen Entwicklungsmodus. — *Helgoländer wiss. Meeresunters.*, **22**, 120—140.

— 1973. New investigations on systematics and evolution of the class Scyphozoa and the phylum Cnidaria. — *Publ. Seto Marine Biol. Lab.*, **20**, 35—61.

WRONA, R. 1980. Microarchitecture of the chitinozoan vesicles and its paleobiological significance. — *Acta Palaeont. Polonica*, **25**, 1, 123—163.

ZNOSKO, J. 1964. Ordowik obszaru Białowieży i Mielnika. — *Kwart. Geol.* **8**, 1, 60—72.

EXPLANATION OF PLATES 19—37

PLATE 19

Byronia naumovi KOZŁOWSKI, 1967

1. Ultrastructure of the outer part of the periderm; boulder no. ZPAL 0.121, Wyszogród, Caradoc; TEM, ×22000

Byronia robusta (KOZŁOWSKI, 1967)

2. Ultrastructure of the periderm before the stroke of a strong electron beam; TEM, ×64000.
3. Inner part of the periderm; TEM, ×36000.
4. Transverse section of the periderm; TEM, ×12000.
5. Ultrastructure of the periderm after the stroke of a strong electron beam; TEM, ×120000.
6. Longitudinally fractured periderm; SEM, ×7800.
7. Parabolic pattern in the fibre arrangement; ×54000.

Boulder no. MZ/39, Mochty, Ordovician.

Abbreviations: *c* inner cavity of the scyphotheca, *e* outer part of the periderm, *i* inner part of the periderm.

PLATE 20

Rhabdohydra multiplex sp. n.

1. Holotype (ZPAL Hz. I/1); *a* general view; ×50; *b—d* best preserved nodes; ×200; boulder no. ZPAL 0.186, Mochty, Ordovician.

Rhabdohydra tridens KOZŁOWSKI, 1959

2. Paratype no. II (ZPAL Hz.I/2); boulder no. ZPAL 0.182, Mochty, Middle Ordovician; ×30.
3. Paratype no. I (ZPAL Hz.I/3); Boulder no. ZPAL 0.182, Mochty, Middle Ordovician; *a* general view; ×30; *b—c* best preserved nodes; ×120.
4. Distal part of the stem (ZPAL Hz.I/3); boulder no. MZ/14, Orzechowo, Ordovician; ×30.
5. Bifurcated proximal part of the stem (ZPAL Hz.I/4); boulder no. ZPAL 0.334, Mochty, Ordovician, ×25.
6. Regeneration of the stem (ZPAL Hz.I/5); boulder no. MZ/116, Orzechowo, Ordovician?; ×30.
7. Proximal part of the stem with the fragment of hydrorhiza (ZPAL Hz.I/7); boulder no. 0.334, Mochty, Ordovician; ×30.
8. Fragment of the hydrorhiza (ZPAL Hz.I/8); boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician; ×30.
9. Proximal part of the stem with the fragment of hydrorhiza (ZPAL Hz.I/9); boulder no. ZPAL 0.334, Mochty, Ordovician; ×30.
10. Small fragment of the stem and hydrorhiza (ZPAL Hz.I/10); boulder no. ZPAL 0.366, Zakroczym, Middle Ordovician; ×30.
11. Small fragment of the stem and hydrorhiza (ZPAL Hz.I/11); boulder no. ZPAL 0.334, Mochty, Ordovician; ×30. Abbreviations: *f* fissure in the periderm, *h* sheaths of the hydranth stalk, *hc* stem, *hr* hydrorhiza, *o* subcircular opening in the periderm, *r* regenerated part of the stem, *I, II, III,* etc. node numbers.

PLATE 21

Rhabdohydra tridens KOZŁOWSKI, 1959

1. Top of the young stem (ZPAL Hz.I/11); SEM, ×300.
2. Deviation of the stem growth direction at the node level (ZPAL Hz.I/12); SEM, ×300.

3—4. Typical common bases with hydranth sheaths (ZPAL Hz.I/12—13); SEM, ×300.

5. Fragment of the hydrorhiza with the initial part of the stem (ZPAL Hz.I/14); a — general view, ×50, b fragment of the specimen, ×300, SEM.
6. Fragment of the hydrorhiza with the initial part of the stem (ZPAL Hz.I/15); SEM, ×100.

All specimens from the boulder no. MZ/18, Orzechowo, Ordovician (Caradoc?).
Abbreviations: *h* hydranth sheath, *hc* stem, *hr* hydrorhiza, *x* common base of hydranth sheaths.

Problematicum D

7. Tightly coiled stolons (ZPAL V.X/1); boulder no. MZ/88, Poddębie, Ordovician; SEM, ×120.

PLATE 22

Rhabdohydra tridens KOZŁOWSKI, 1959

1. Transverse section of the outer part of the stem periderm; TEM, ×16000.
2. Transverse section of the inner part of the stem periderm; TEM, ×18000.
3. Transverse section of the hydrorhizal stolon inner part; TEM, ×22000.

4. Regular distribution of electron dense granules in the stem periderm; TEM, ca ×50000.
5. Material infilling the inner cavity of the stem; TEM, ca ×45000.
6. Transverse section of the hydrorhizal stolon outer part; TEM, ca ×35000.
7. Material infilling the stem inner cavity connected with the periderm; TEM, ×35000.

Boulder no. ZPAL 0.334, Mochty, Ordovician.

Abbreviations: *c* inner cavity of the stem or hydrorhizal stolon, *f* foreign body, *g* coarse-granular layer, *p* periderm, *s* material infilling inner cavities of the stem or hydrorhizal stolon.

PLATE 23

Chaunograptus flexuosus (KOZŁOWSKI, 1959)

1. Transverse section of the theca and stolon; TEM, ×6000.
2. Ultrastructure of the theca periderm; TEM, ×36000.
3. Material infilling the theca cavity; TEM, ×12000.

Boulder no. ZPAL 0.240, Zakroczym, Ordovician.

Chaunograptus adhaerens (KOZŁOWSKI, 1959)

4—6. Ultrastructure of the periderm and the organic matter infilling the theca cavity; TEM, 4 — ×2700, 5 — ×2700, 6 — ×9300.

Boulder no. ZPAL 0.179, Mochty, Ordovician? Llandovery?

Abbreviations: *o* organic matter infilling theca cavities, *p* periderm, *s* stolon cavity, *t* theca cavity.

PLATE 24

Flexihydra undulata KOZŁOWSKI, 1959

1. Accumulation of the organic matter from the theca cavity, comp. with pl. 24: 4; TEM, ×22000.
2. Theca — fragment of the transverse section; TEM, ×8000.
3. Ultrastructure of the organic matter infilling the theca cavity; TEM, ca ×50000.
4. Transverse section of the theca with the inner accumulation of the organic matter (outline of the hydranth's body?), comp. with pl. 24: 1; TEM, ×2000.

Boulder no. ZPAL 0.15, Orłowo, Ordovician

Abbreviations: *m* organic matter infilling the theca cavity, *p* periderm, *s* organic matter — outline of the hydranth body?

Sertularia argentea ELL. and SOLL, 1786

5. Ultrastructure of the periderm; Mediterranean, recent, TEM, ca ×40000.

Chitinodendron bacciferum EISENACK, 1937

6. Irregular and subcircular accumulations of the organic matter from the vesicle cavity; boulder no. ZPAL 0.29, Stara Warka, Llandeilo?; TEM, ca ×10000.

PLATE 25

Rhabdopleura vistulae KOZŁOWSKI, 1956

1. Composite cysts of sterile buds; SEM, *a* ×100, *b*—*c* details of cysts, ×350.
2. Sterile bud cyst with the peduncular and terminal stolons; SEM, ×100.
3—4. Fragments of main stolon with sterile bud cysts; SEM, ×200.
5—6. Fragments of main stolon with sterile bud cysts; SEM, ×250.
7. One-sided flattening of the main stolon; SEM, ×1500.
Góra Puławska borehole, 8 m in depth, Montian.
Abbreviations: *c* sterile bud cyst, *ps* peduncular stolon, *s* main stolon.

PLATE 26

Rhabdopleurites primaevus KOZŁOWSKI, 1967

1—8. Fragments of zooidal and/or stolonal fusellar tubes; ×150.
9—10. Fragments of fusellar stolonal tubes with stolons; ×100.
11. Fragment of coenecium composed of zooidal and stolonal tubes and stolon; ×ca 80
12—16. Nonfusellar-fusellar fragments of stolonal tubes; ×150.
17. Large fragment of coenecium composed of stolonal tubes and stolons; ×50.
Abbreviations: *f* fusellar part of the stolonal tube, *s* stolon, *sp* peduncular stolon, *st* stolonal tube, *uf* nonfusellar part of stolonal tube, *x*—*x* boundary between nonfusellar and fusellar parts of stolonal tubes, *zt* zooidal tube.
Boulder no. ZPAL 0.400, Mochty, Middle Ordovician.

PLATE 27

Rhabdopleurites primaevus KOZŁOWSKI, 1967

1. Ultrastructure of the nonfusellar stolonal tube, transverse section; TEM, ×12000.
2. Ultrastructure of the stolon; TEM, ×45000.
Boulder no. ZPAL 0.400, Mochty, Middle Ordovician.

Koremagraptus sp.

3. Fragment of the transverse section of the stolon trifurcation, transverse section; TEM, ×2000.
4. Local porosity of the stolon material; TEM, ×45000.
Boulder no. ZPAL 0.186, Mochty, Ordovician.
Abbreviations: *c* cavity of the stolon, *w* wall of the stolon.

Kystodendron longicarpus (EISENACK) *sensu* KOZŁOWSKI

5. Ultrastructure of the sterile bud cyst; boulder no. ZPAL 0.182, Mochty, Middle Ordovician; TEM, ×10000.

Kozlowskisyrinx graptovermiformis gen. n., sp. n.

6. Wall of the tube, fragment of the transverse section; boulder no. ZPAL 0.218, Zakroczym, Ordovician; TEM, ×ca 6000

PLATE 28

Kystodendron ex gr. *longicarpus* (EISENACK) *sensu* KOZŁOWSKI

1—5. Fragments of zooidal tubes (ZPAL Pb.III/1); ×47.
6—10. Sterile bud cysts with fragments of stolons (ZPAL Pb.III/2); ×47.
Biała Podlaska 2 borehole, 680—687 m in depth, Middle Ordovician.

Kystodendron longicarpus (EISENACK) *sensu* KOZŁOWSKI

11. Sterile bud cyst with yolk (?) substance (ZPAL Pb.III/3); *a* ×47, *b* ×470.
12—29. Sterile bud cysts (17—20 composite cysts) (ZPAL Pb. III/4); ×47.
30. Distal part of the sterile bud cyst (ZPAL Pb. III/4); ×470.
31. Proximal part of the sterile bud cyst: (ZPAL Pb.III/4); ×470.
32—33. Distal part of the sterile bud cysts with terminal stolons (ZPAL Pb. III/4); ×470.
Specimens from the boulder no. ZPAL 0.166, Wyszogród—Zakroczym, Ordovician.
Abbreviations: *c* sterile bud cyst, *cc* composite cysts of sterile buds, *ps* peduncular stolon, *s* main stolon, *ts* terminal stolon, *y* yolk (?) substance.

PLATE 29

Rhabdopleurites primaevus KOZŁOWSKI, 1967

1—12. Stolons with stolonal tubes (ZPAL Pb. III/5); ×50.
13. Fragment of coenecium composed of the zooidal and stolonal tubes, main and peduncular stolons (ZPALPb. III/6); ×65.
Boulder ZPAL 0.400, Mochty, Middle Ordovician.

?*Kystodendron* sp.

14—18. Fragments of main stolons with peduncular stolons and vestiges of sterile bud cysts (ZPAL Pb. III/7); ×80
19. Sterile bud cyst with peduncular stolon (ZPAL Pb. III/7); ×80.
Boulder no. ZPAL 0.25, Poznań, Ordovician.

Kystodendron tener sp. n.

20—30. Sterile bud cysts with stolons, 26 — holotype (ZPAL Pb.III/8—9); ×47.
31. Largest sterile bud cyst (ZPAL Pb.III/10); ×47.
32—34. Fragments of zooidal tubes (ZPAL Pb.III/11); ×47.
Boulder no. MZ/142, Poddębic, Upper Silurian.

Kystodendron complicatus sp. n.

35—41. Sterile bud cyst with stolons, 41 — holotype (ZPAL Pb.III/12—13); ×47.
Boulder no. ZPAL 0.62, Orłowo, Upper Ordovician.
Abbreviations: *c* cyst of sterile bud, *ps* peduncular stolon, *s* stolon, *st* stolonal tube, *ts* terminal stolon, *zt* zooidal tube.

PLATE 30

Beklemishevites grandis gen. n., sp. n.

1. Fragment of the longitudinally fractured living tube; SEM, ×200.
2. Ultrastructure of the outer part of the living tube, transverse section; TEM, ×1600.
3. "Bouligand pattern" in the arrangement of fibres;TEM, ×9600.
4. Fragment of the longitudinally fractured living tube wall; SEM, ×1600.
5. Ultrastructure of the living tube wall before the stroke of a strong electron beam; TEM, ×35000.
6. Ultrastructure of the living tube wall after the stroke of a strong electron beam; TEM, ×35000.

Boulder no. ZPAL 0.324, Mochty, Ordovician?

PLATE 31

Sokolovites pogonophoroides KOZŁOWSKI, 1967

1. Weakly marked transversal rings on the living tube surface (ZPAL Po.I/1); SEM, ×400.
2. Vestige of the membrane (m) and granular ultrastructure (g) of the living tube; SEM, ×5000.
3. Details of the membrane; SEM, ×7400.
4. Fragment of the living tube (ZPAL Po.I/1); SEM, ×120.
5. Fragment of the longitudinally fractured living tube (ZPAL Po.I/2); SEM, ×120.
6. Ultrastructure of the living tube wall; SEM, ×12000.

Chojnów Dół by Zbilutka, Upper Tremadoc.

PLATE 32

Kystodendron longicarpus (EISENACK) *sensu* KOZŁOWSKI

1. Fragment of zooidal tube, *e* erect part, *c* creeping part, note the zig-zag suture (ZPAL) Pb.I/14); boulder no. ZPAL 0.166, Wyszogród—Zakroczym, Ordovician; *a* lateral view, ×50, *b* dorsal view, ×45.

Kystodendron sp.

2. Fragment of the stolon with two sterile bud cysts (ZPAL Pb. I/15); boulder no. MZ/18, Orzechowo, Ordovician (Carodoc?); ×100.

Kystodendron cf. *subtilis* (KOZŁOWSKI, 1959)

3. Fragment of the coenecium composed of stolon (s), sterile bud cyst (c) and remnant of the periderm (p) (ZPAL Pb.I/16); boulder no. ZPAL 0.533, Mochty, Middle? Ordovician; ×240.

?*Rhabdopleurites* sp.

4. Fragment of stolonal system (ZPAL Pb.I/17); *a* general view, ×47, *b* enlargement of the specimen showing remnant of the periderm (p), ×100.
5. Fragment of stolonal system (ZPAL Pb.I/18); ×47.

Boulder no. ZPAL 0.693, Mochty, Ordovician.

Beklemishevites grandis gen. n., sp. n.

6. Holotype (ZPAL Po.I/2); ca ×10.
7—10. Fragments of living tubes (ZPAL Po.I/4); ca ×10.
11. Fragment of diagenetically flattened living tube (ZPAL Po.I/4); ca ×10.
Boulder no. ZPAL 0.324, Mochty, Ordovician?

Chitinodendrum bacciferum EISENACK, 1937

12. Vesicle with stolon vestiges (ZPAL V.I/2); boulder no. ZPAL 0.240, Zakroczym, Ordovician; ×60.
13. Three vesicles connected by stolons (ZPAL V.I/3); boulder no. ZPAL 0.533, Mochty, Middle? Ordovician; ×60.
14. Vesicle with stolons in the transmitted light (ZPAL V.I/4); boulder no. ZPAL 0.240, Zakroczym, Ordovician; ca ×135.
15. Transverse section of the vesicle; boulder no. ZPAL 0.29, Stara Warka, Llandeilo; TEM, ×900.
Abbreviations: *i* organic matter infilling the vesicle (subcircular concentration), *g* organic matter infilling the vesicle (irregular concentration of grit-like matter), *s* stolon, *v* vesicle, *w* wall of the vesicle.

PLATE 33

Ascosyrinx tenuis KOZŁOWSKI, 1967

1. Fragment of the sole, transverse section; TEM, ×4000.
2. Sole surface covered with band-like thickenings; SEM, ×2000.
3—5. Organic matter infilling the chamber; TEM, ×6000.
6. Ultrastructure of the inner zone of the tube; TEM, ×43000.
Boulder no. MZ/96, Jarosławiec, Ordovician, (Caradoc?).
Abbreviations: *b* band-like thickening of the sole, *p* pillar, *s* sole.

PLATE 34

Ascosyrinx tenuis KOZŁOWSKI, 1967

1. Fragment of the tube transverse section; TEM, ×2200.
2. Ultrastructure of the chamber periderm; TEM, ×55000.
3. Ultrastructure of the innermost chamber periderm; TEM, ×5000.
4. Fragment of the longitudinally fractured tube periderm; SEM, ×8000.
Boulder no. MZ/96, Jarosławiec, Ordovician (Caradoc?).
Abbreviations: *i* inner zone of the tube, *m* organic matter infilling the chamber, *o* outer zone of the tube, *p* periderm.

Chitinodendron bacciferum EISENACK, 1937

5. Ultrastructure of the vesicle wall (w) and grit-like matter (m); TEM, ca 16000.
6. Ultrastructure of granular (g) and homogenic (h) subcircular concentrations from the vesicle cavity; TEM, ×9000.
Boulder no. ZPAL 0.29, Stara Warka, Llandeilo.

Hydroida? Gen. et sp. indet.

7. Ultrastructure of the periderm; boulder no. ZPAL 0.26, Poznań—Czerwonak, Middle Ordovician; TEM, ×52000.

Eudendrium capillare ALDER, 1857

8. Ultrastructure of the periderm; Mediterranean, recent; TEM, ca ×50000.

PLATE 35

Dendrograptidae, gen. et sp. indet.

1. Fragment of the rhabdosome with circular perforations (ZPAL G.IX/2); boulder no. MZ/42, Orzechowo, *Eoplacognathus pseudoplanus* Zone (Lanvirn); SEM, ×250.

Ascosyrinx tenuis KOZŁOWSKI, 1967

2. Specimen with the partly preserved tube (ZPAL V.X/5); boulder no. MZ/96, Jarosławiec, Ordovician (Caradoc?), SEM, ×45.
   Abbreviations: *c* chamber, *cc* chamber cavity, *s* sole, *t* tube.

Eisenackisyrinx curvatus gen. n., sp. n.

3. Holotype (ZPAL V.X/6); boulder no. MZ/42, Orzechowo, *Eoplacognathus pseudoplanus* Zone (Llanvirn); SEM, ×200.

Problematicum C

4. Stolon (s) with three secondary stolons (sa, sb, sc) (ZPAL V.X/7); boulder no. MZ/151, Warszawa, Ordovician; SEM, ×200.

Inocaulis sp.

5. Proximal part of the hydrocaulus (h) with the hydrorhiza (hy) (ZPAL Hz.I/16); Podborowisko 1 borehole, 396.30—397.30 m in depth, Arenig; SEM, ×150.

Problematicum A

6—7. Specimens with the perforated periderm ZPAL V.X/8; boulder no. MZ/42, Orzechowo, *Eoplacognathus pseudoplanus* Zone, Llanvirn; SEM, ×200.

PLATE 36

Xenohydra labiata KOZŁOWSKI, 1959

1. Transversely fractured periderm ZPAL V.X/9; SEM, ×350.
2. Fragment of the branch ZPAL V.X/9; SEM, ×180.

3. Ultrastructure of the periderm; TEM, ×2400.
4. Bilobate processus with the theca? remnant ZPAL. X/9; SEM, ×300. Boulder no. ZPAL 0.44, Poznań—Czerwonak, Ordovician? Silurian? Abbreviations: *b* bilobate processus, *e* outer layer of the periderm, *i* inner layer of the periderm, *t* theca? remnant.

Kystodendron subtilis (KOZŁOWSKI, 1959)

5. Distal part of the sterile bud cyst ZPAL Pb.I/18; SEM, ×100.
6. Proximal part of the sterile cyst bud ZPAL Pb.I/18; SEM, ×100.
7—8. Sterile bud cysts: ZPAL Pb.I/18; SEM, ×60.
Boulder no. ZPAL 0.121, Wyszogród, Middle Caradoc.

PLATE 37

Kozlowskisyrinx graptovermiformis gen. n., sp. n.

1. Holotype ZPAL V.X/10; boulder no. ZPAL 0.218, Ordovician, Zakroczym; ×ca 100
2—5. Specimens accompanying the holotype ZPAL V.X/11; boulder no. ZPAL 0.218, Ordovician, Zakroczym; ×ca 100.
6. ZPAL V.X/12; boulder no. ZPAL 0.470, Mochty, Middle? Ordovician; ×ca 100.

Xenohydra labiata KOZŁOWSKI, 1959

7. Ultrastructure of the inner layer of the periderm boulder no. ZPAL 0.44, Poznań—Czerwonak, Ordovician? Silurian?; TEM, ×60000.

Chitinodendron bacciferum EISENACK, 1937

8. Ultrastructure of the vesicle periderm *p* and grit-like matter; boulder no. ZPAL 0.29, Stara Warka, Llandeilo?; TEM, ×18000.

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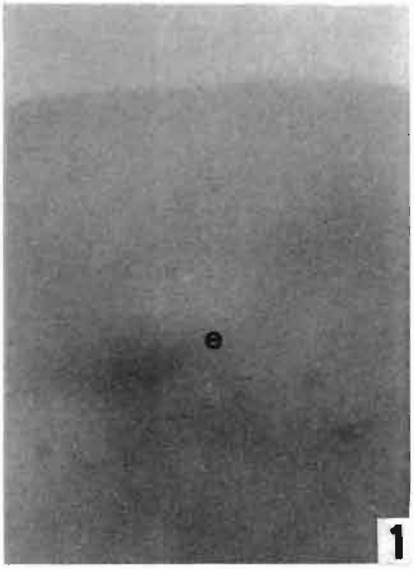

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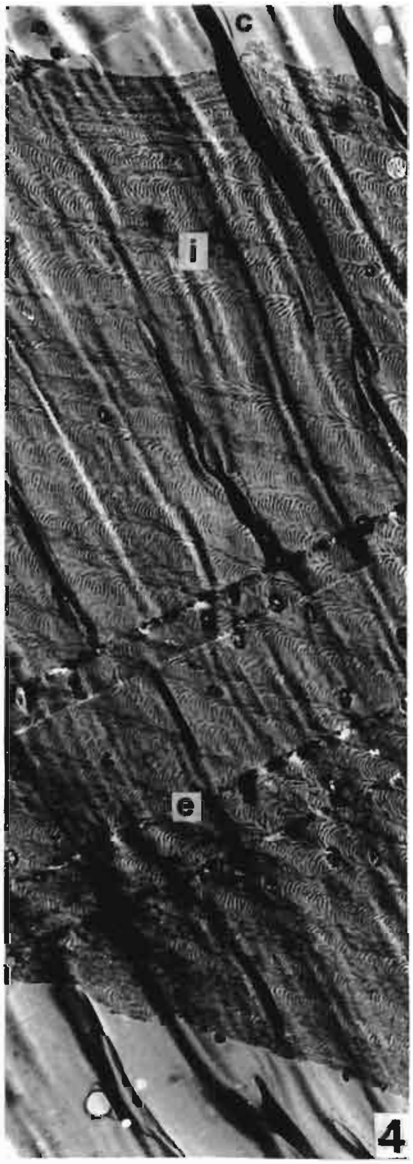

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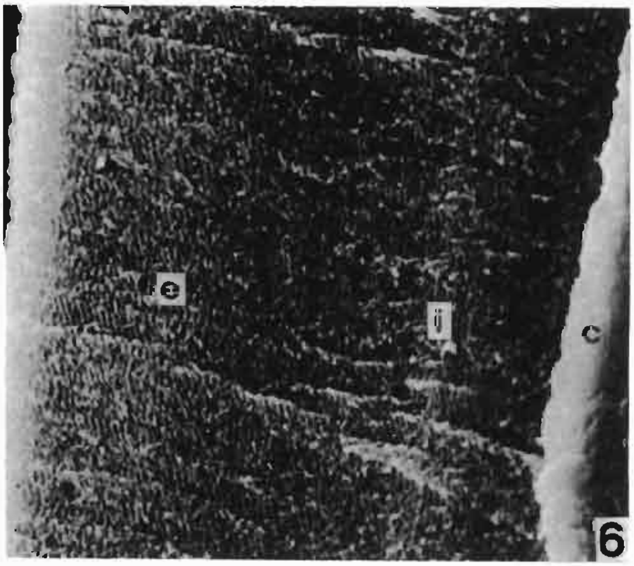

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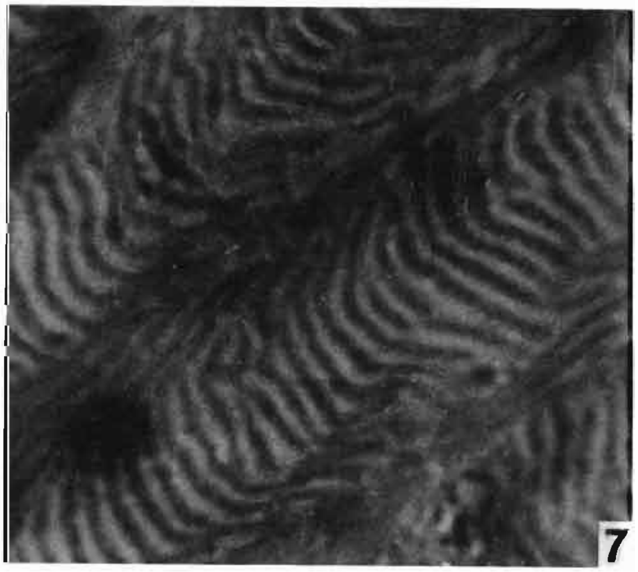

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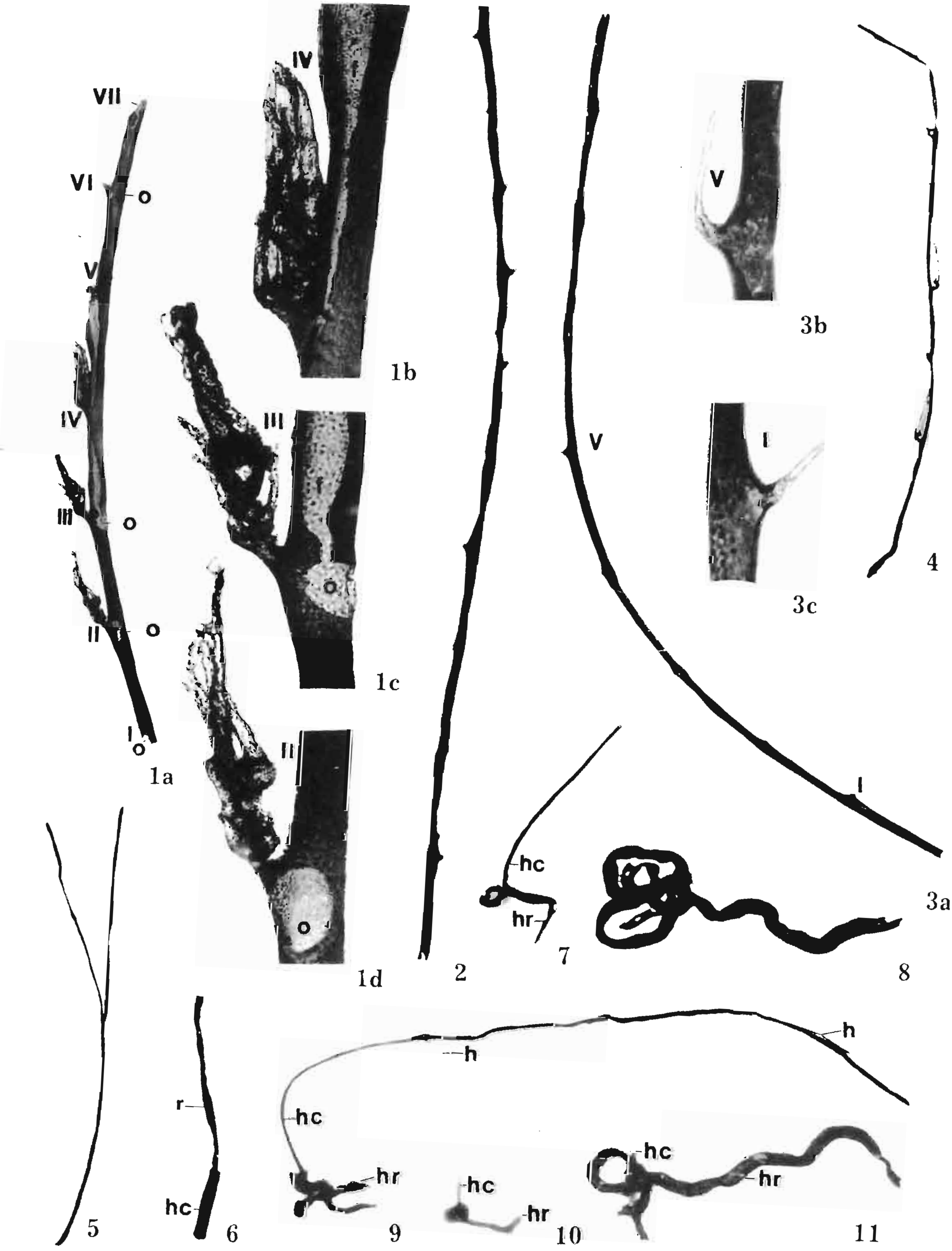
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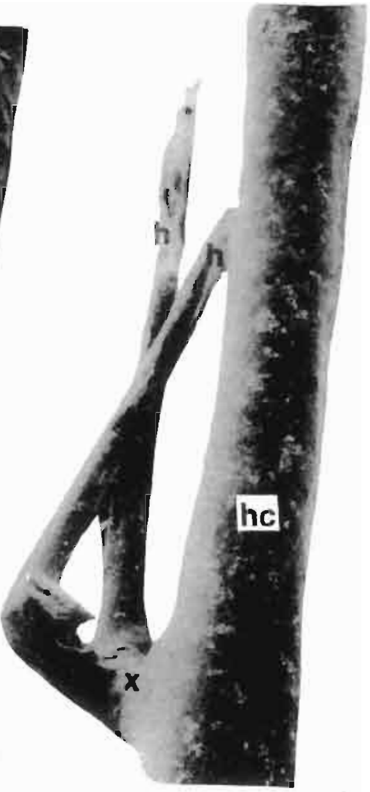

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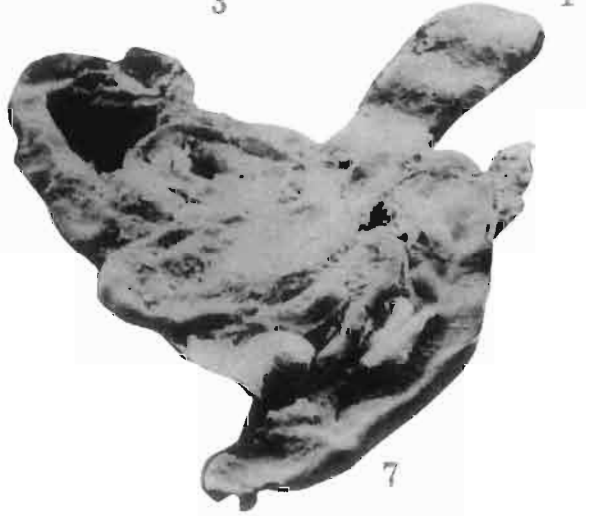
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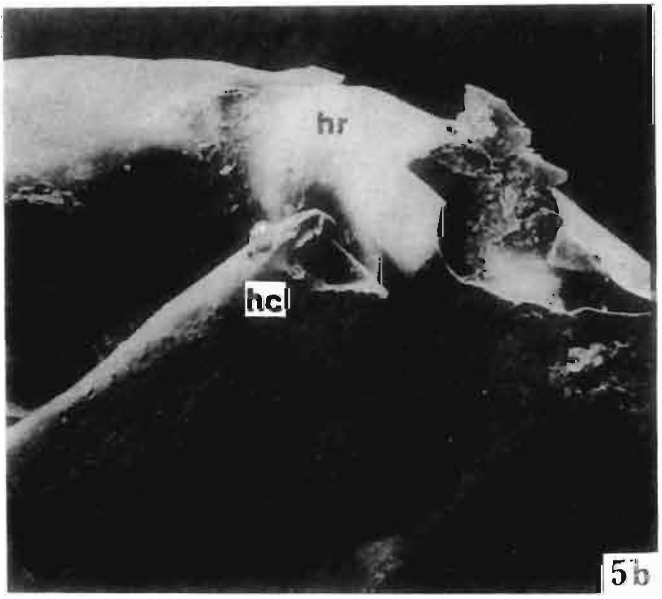

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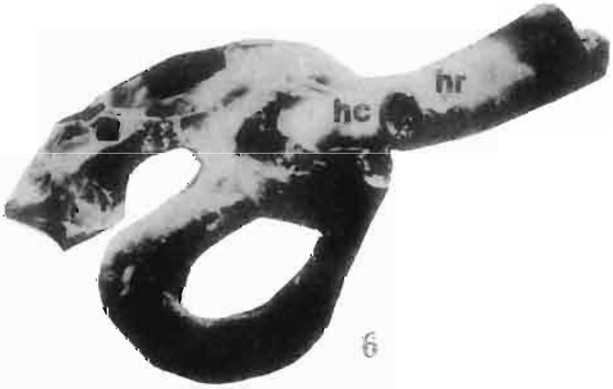

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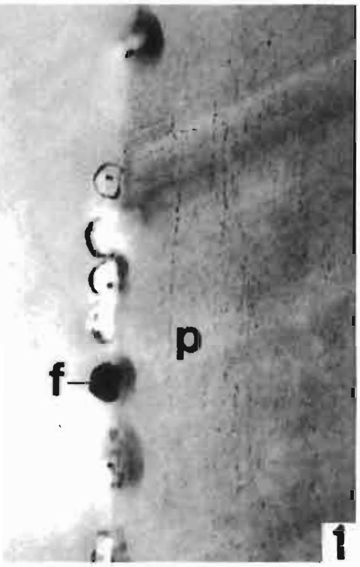

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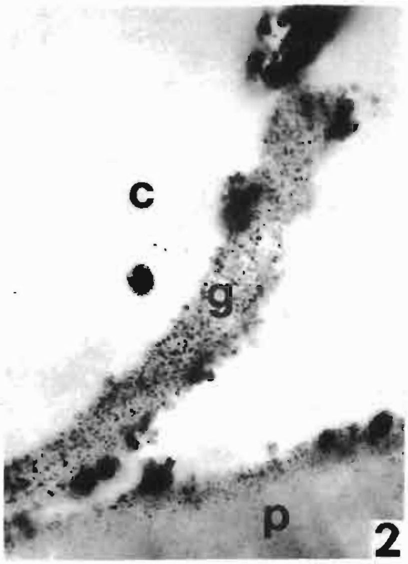

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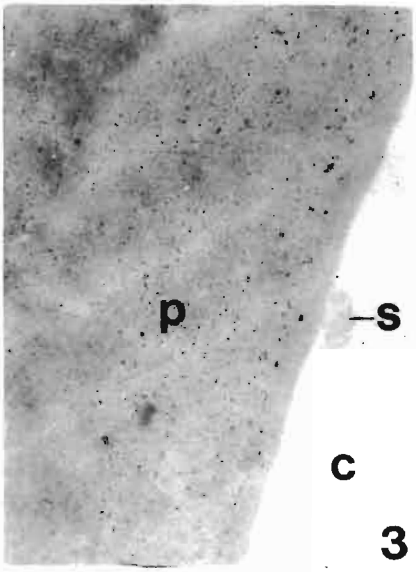

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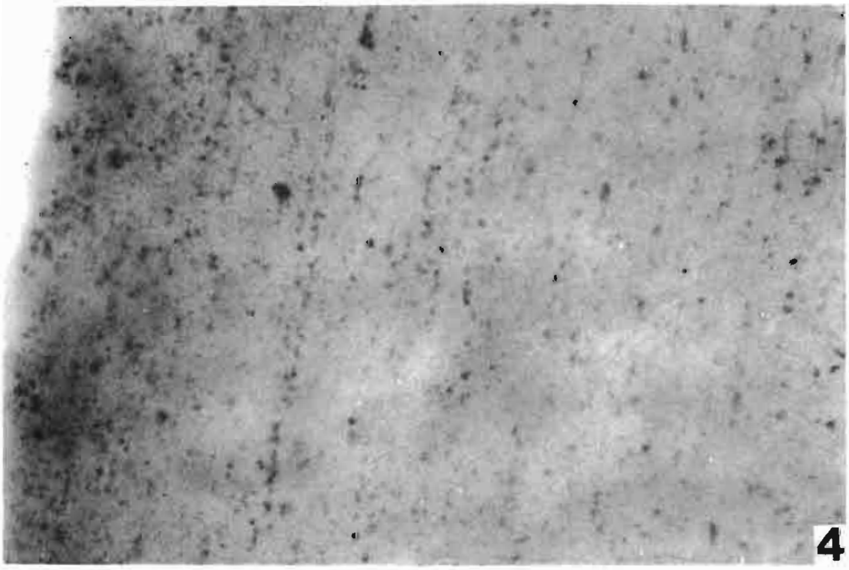

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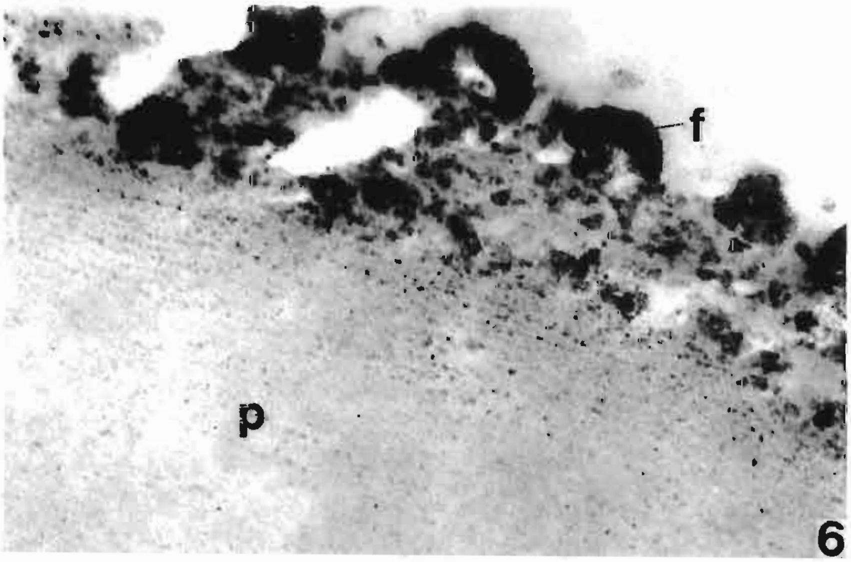

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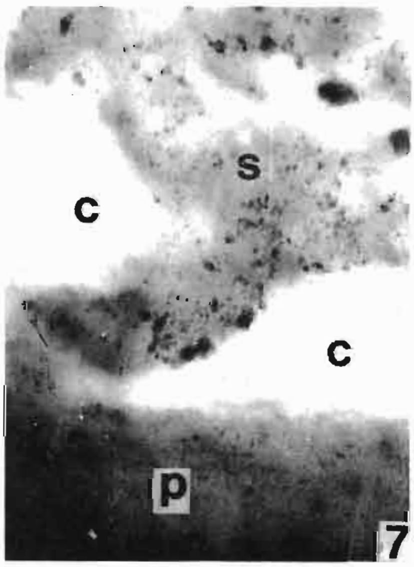

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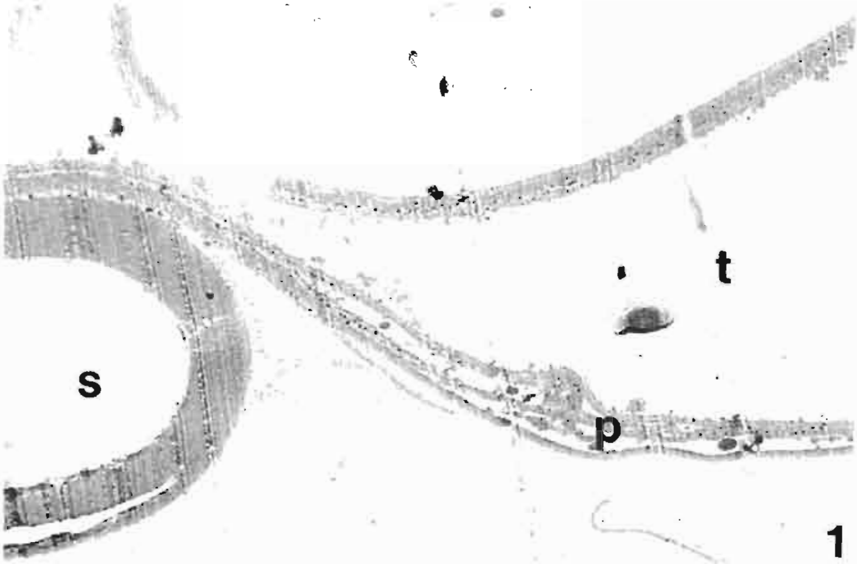
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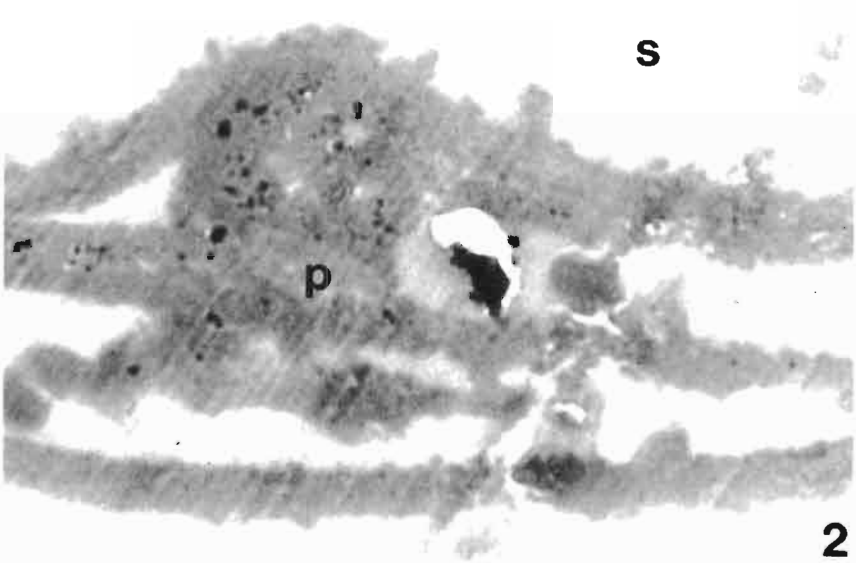
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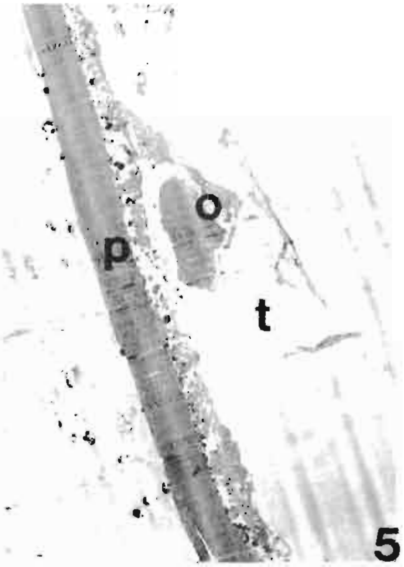
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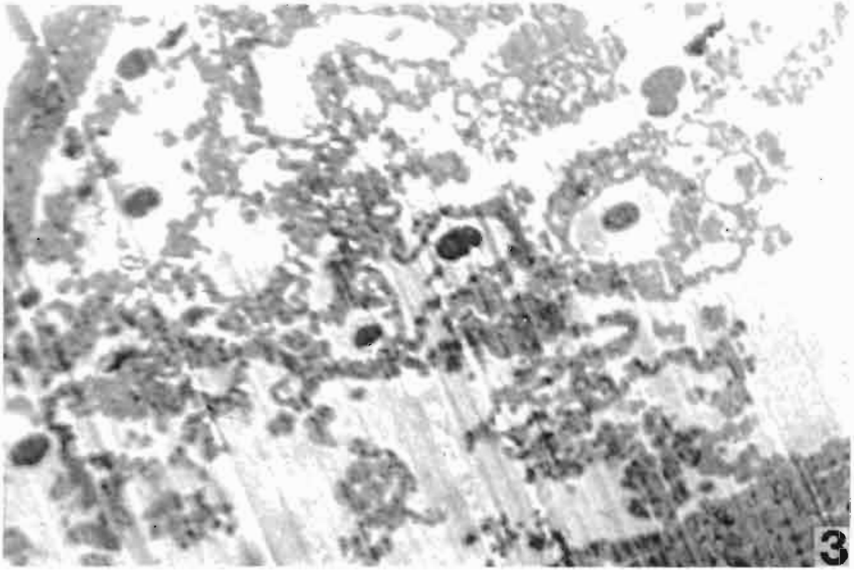
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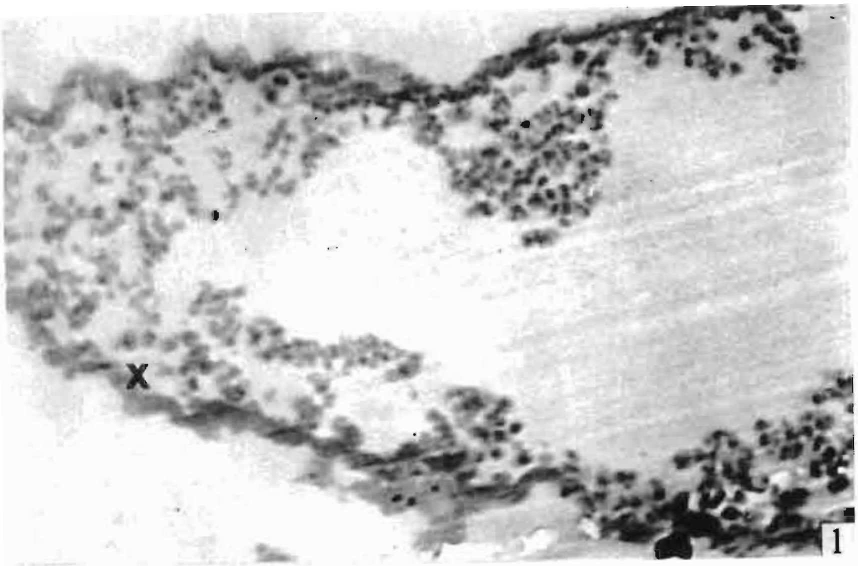
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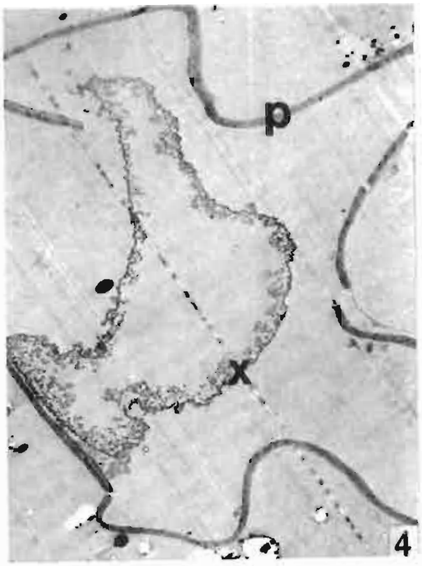
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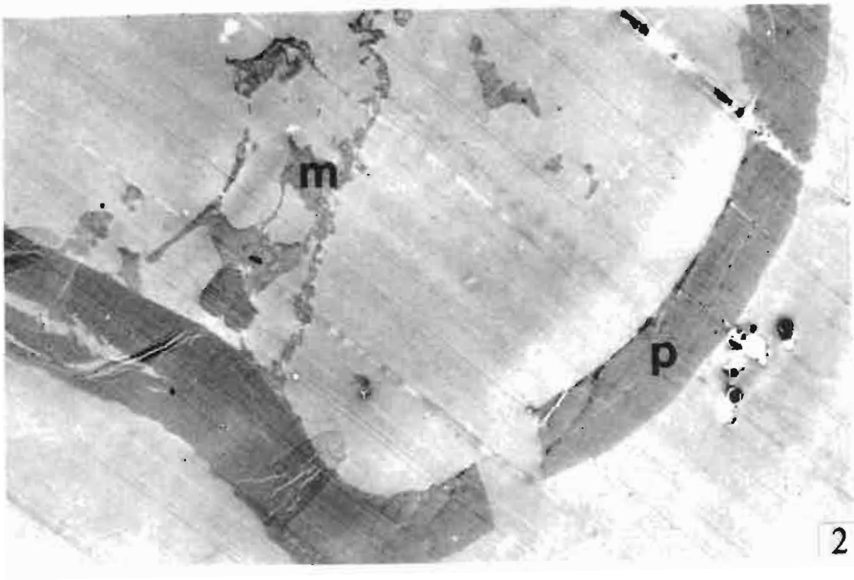
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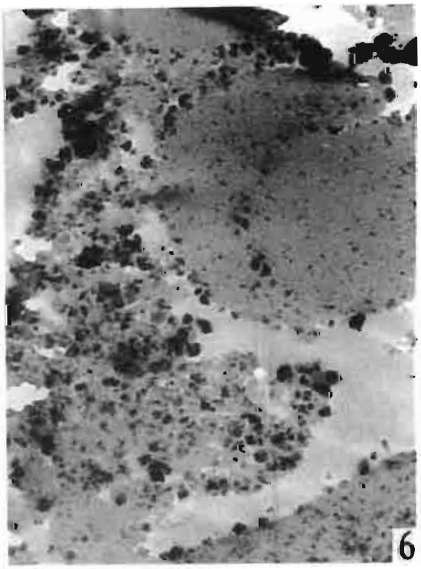
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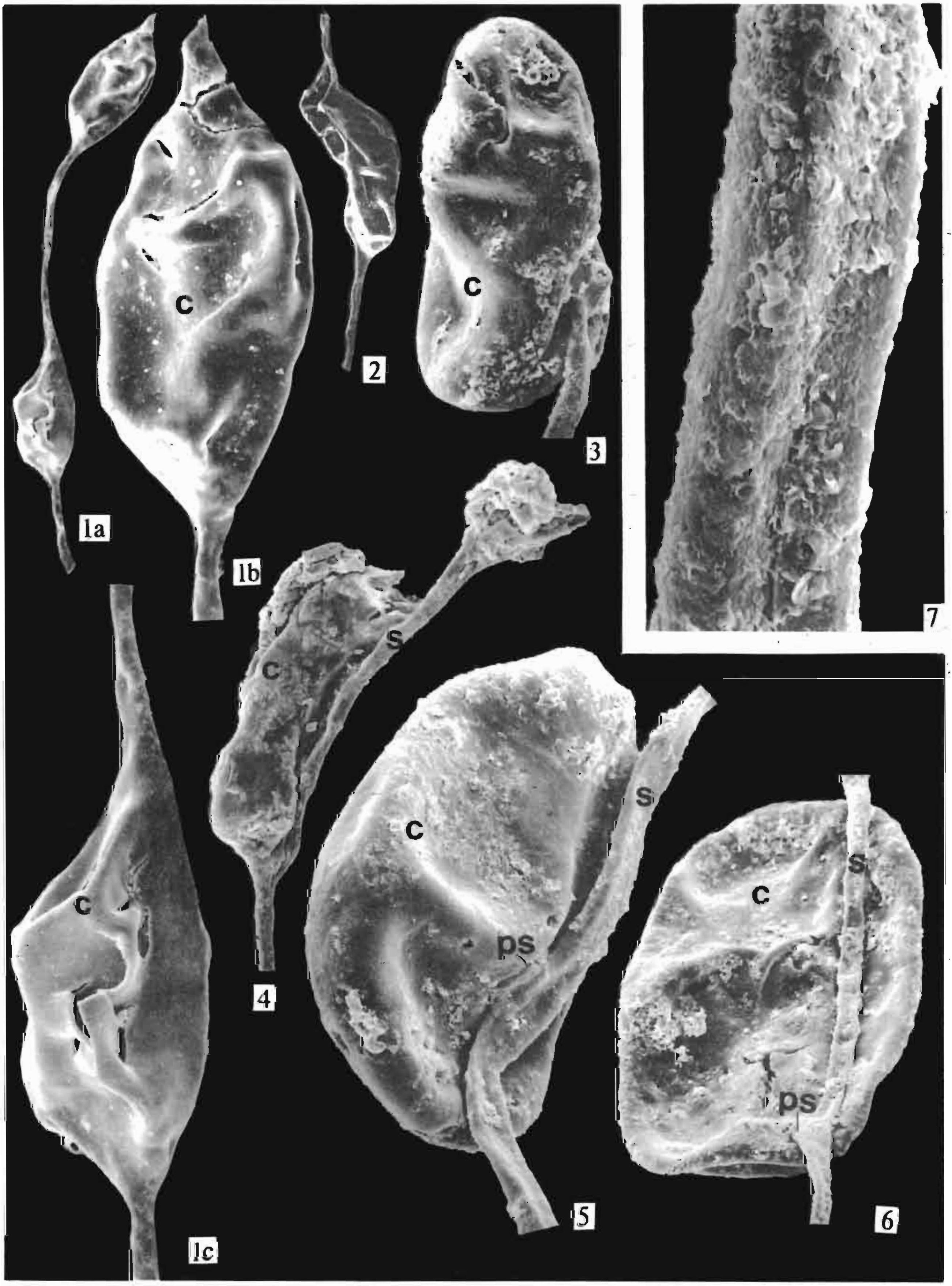
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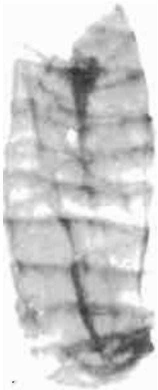
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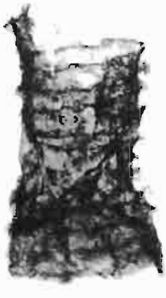
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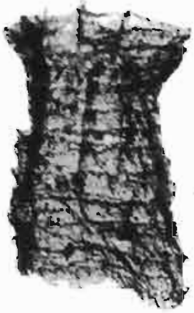
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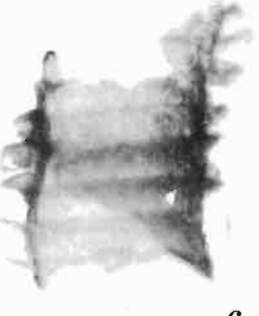
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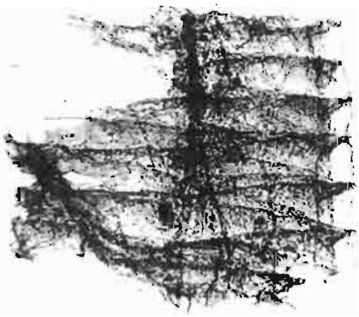
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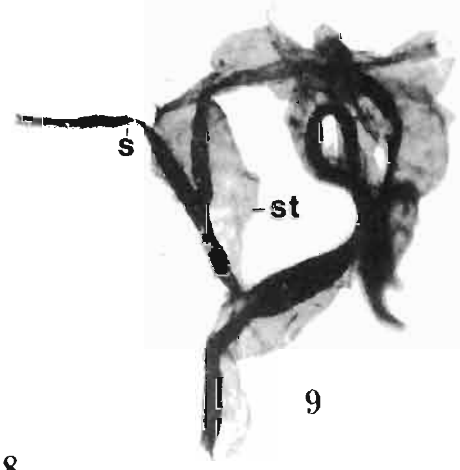

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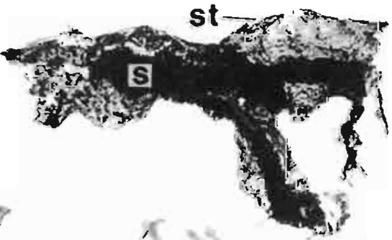

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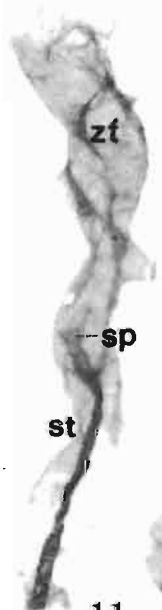

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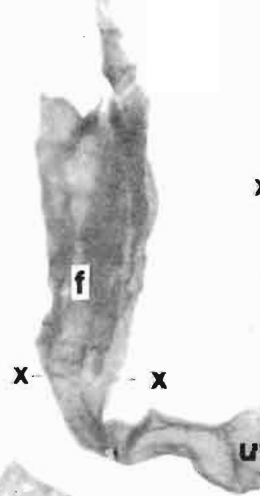

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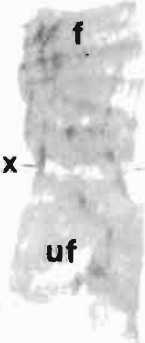

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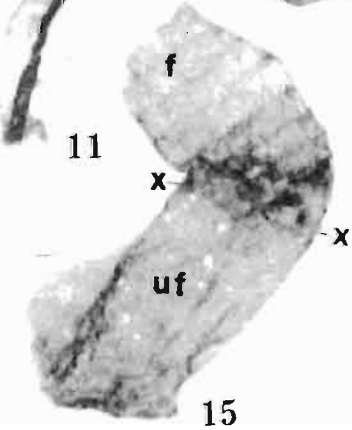

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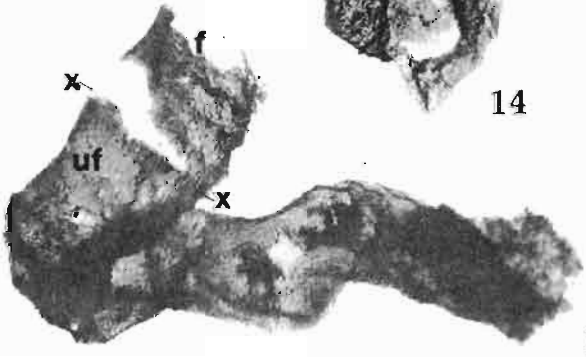

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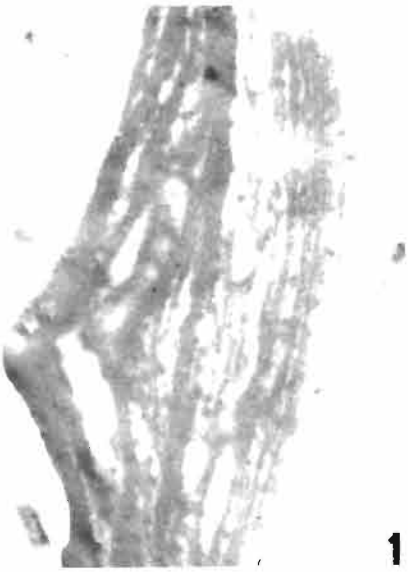
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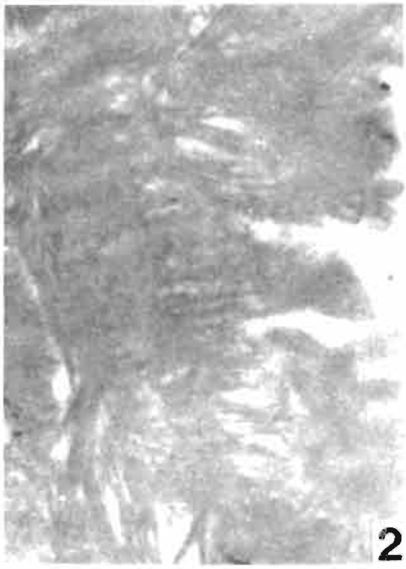
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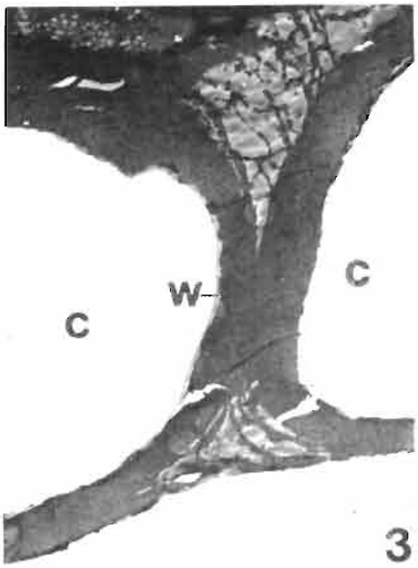
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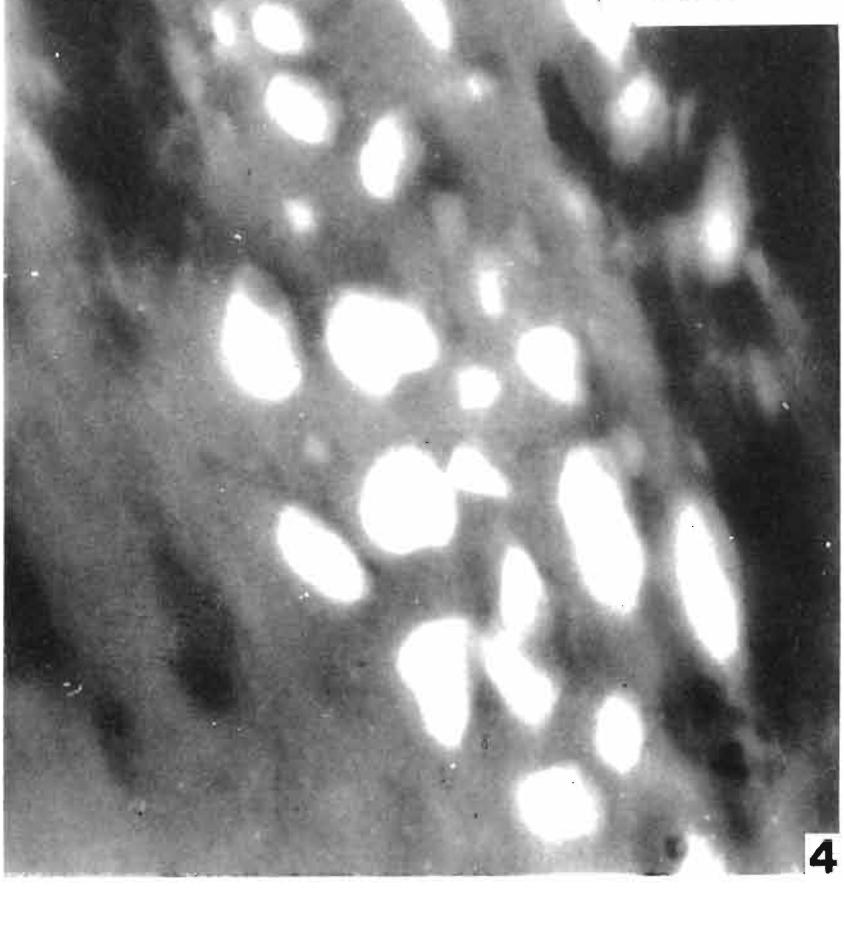
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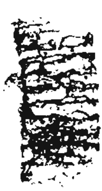
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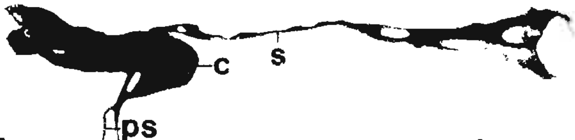

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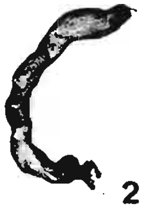
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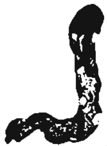
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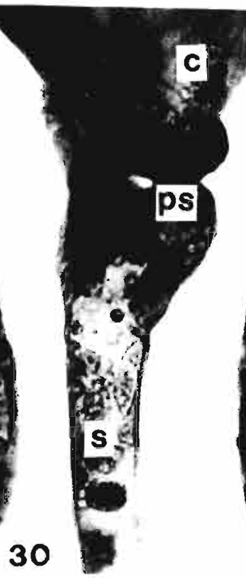

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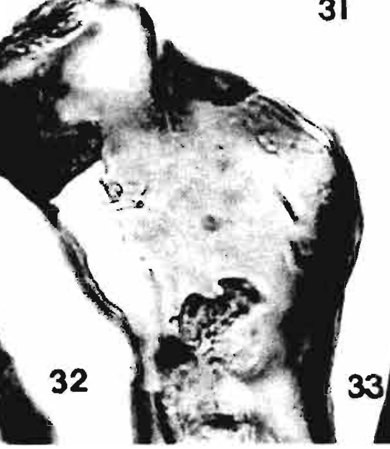

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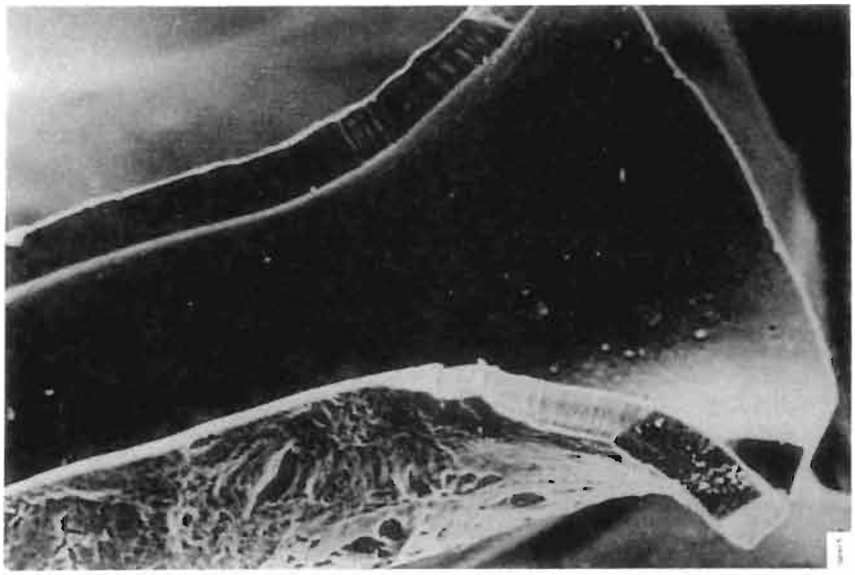
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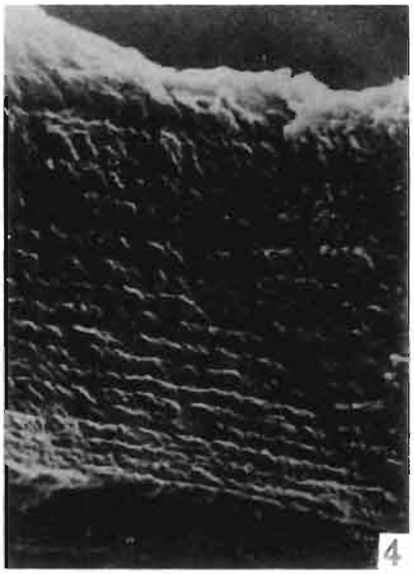
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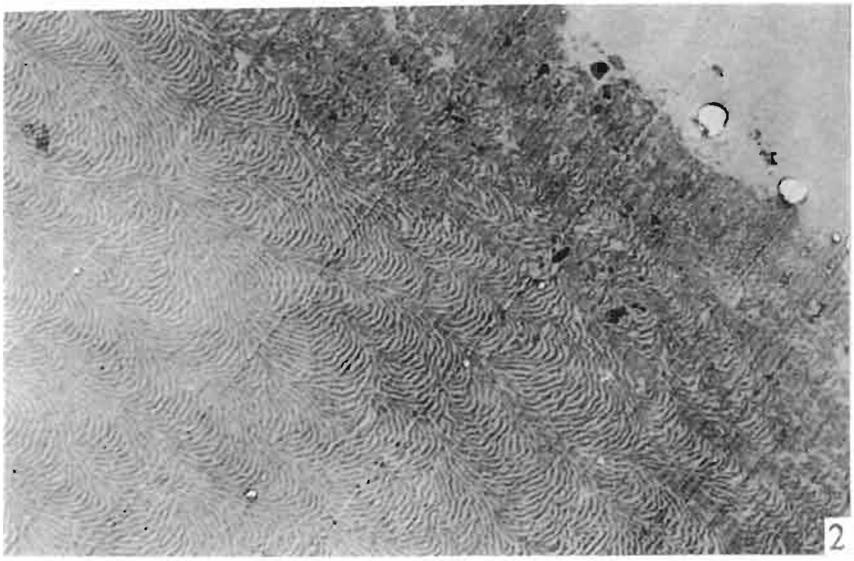
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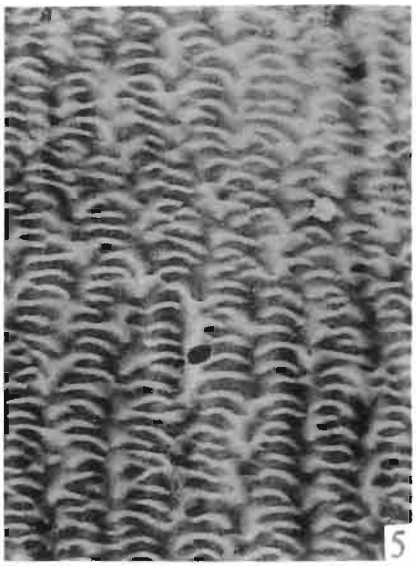
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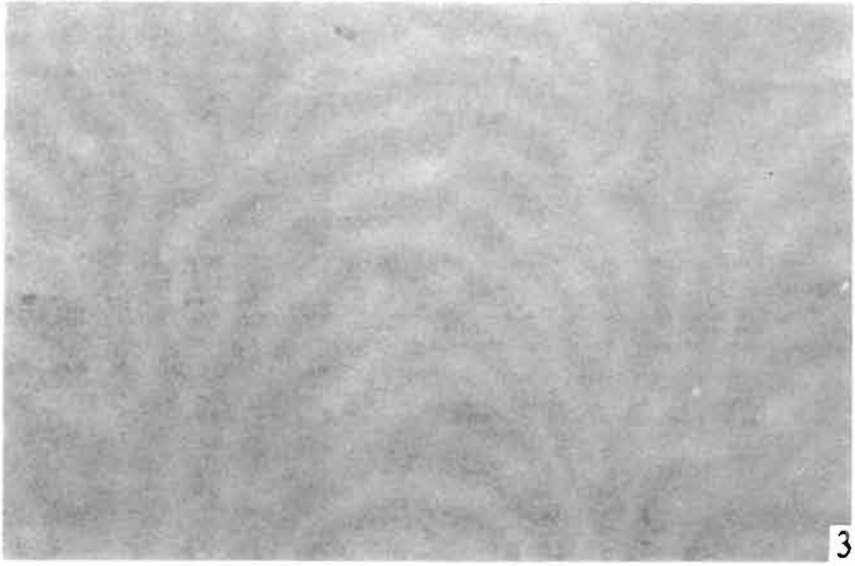
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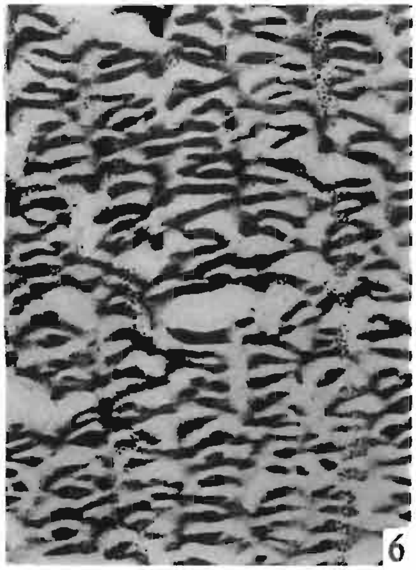
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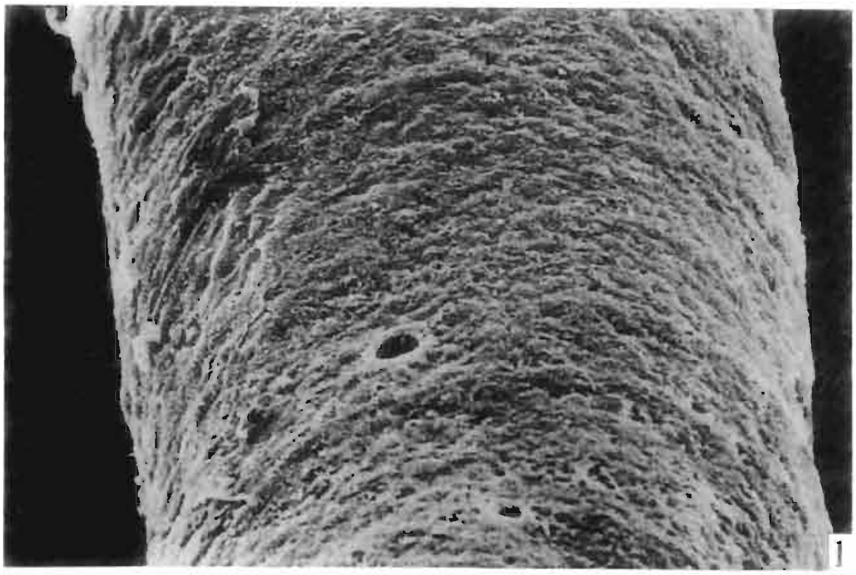

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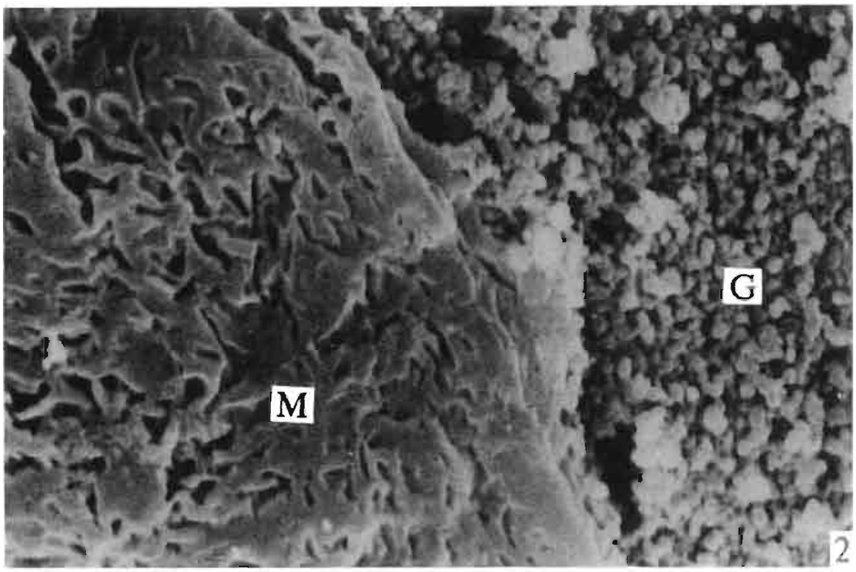

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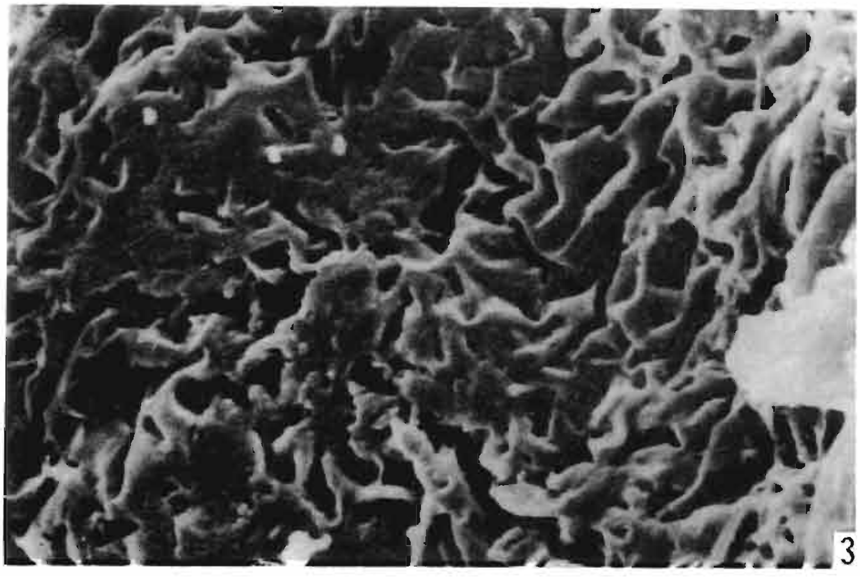

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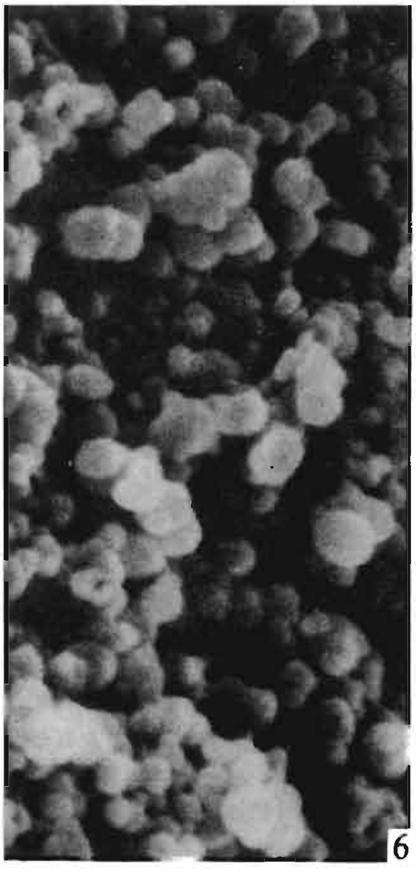

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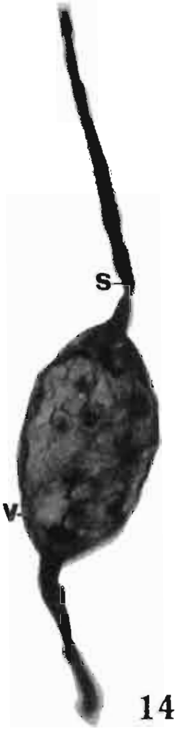

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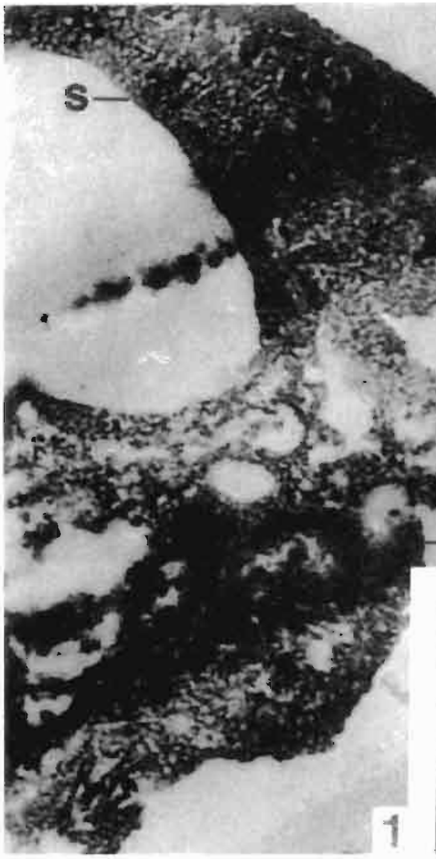
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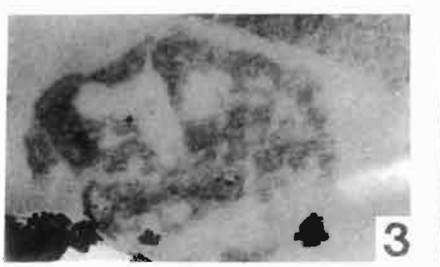
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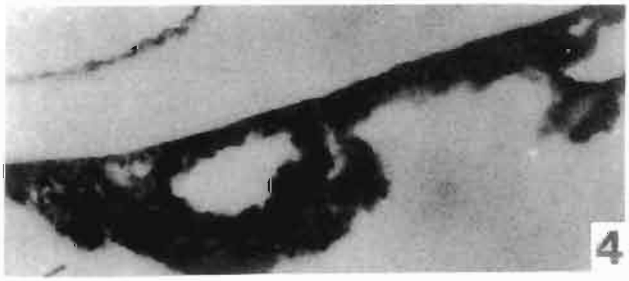
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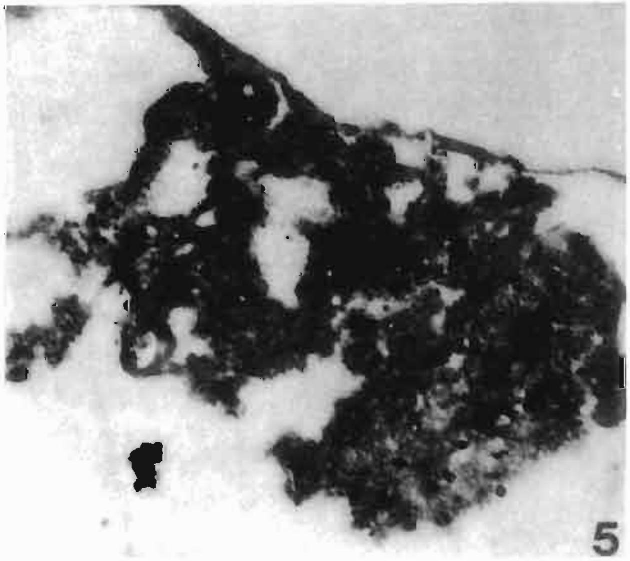
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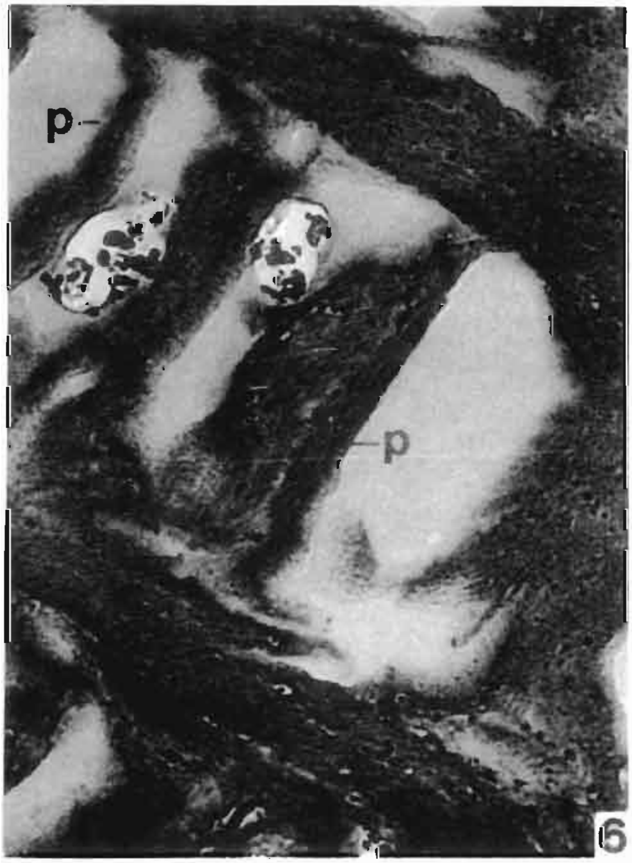
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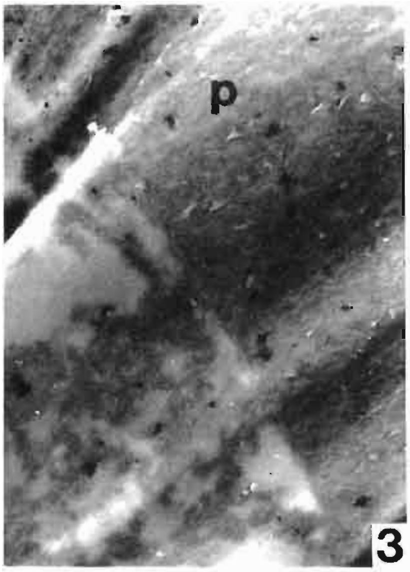

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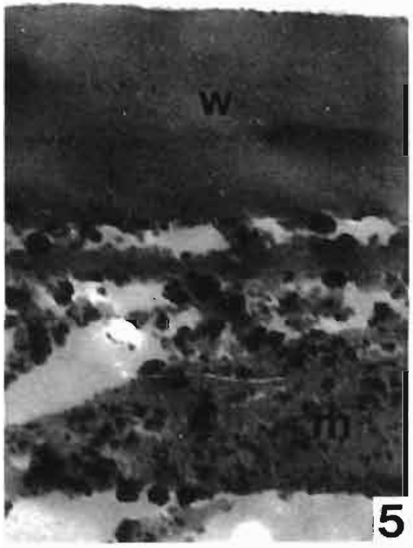

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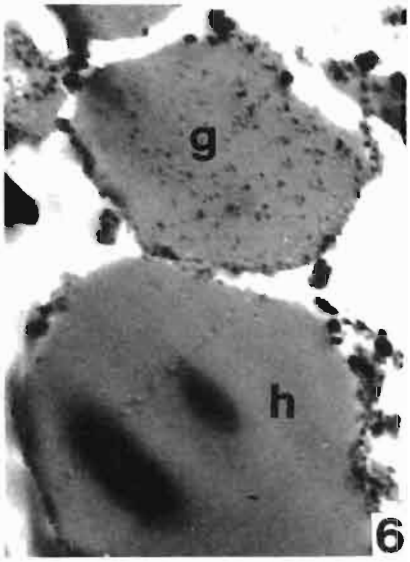

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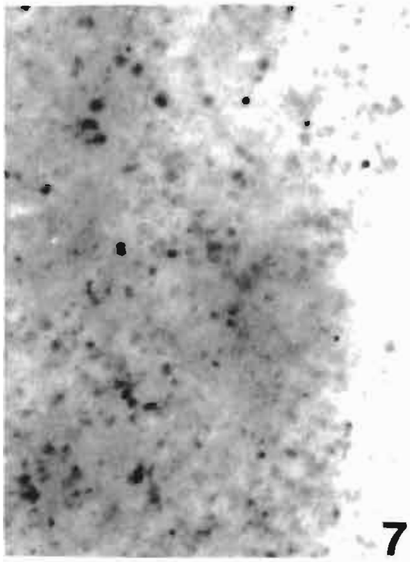

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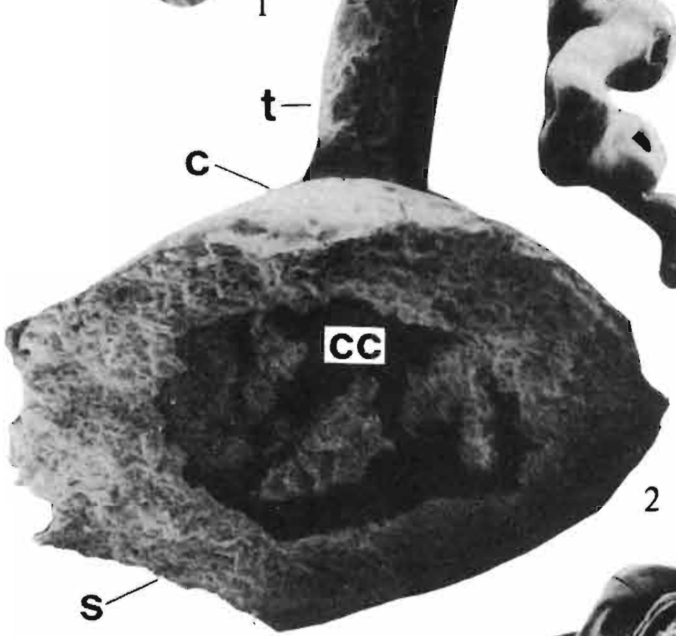

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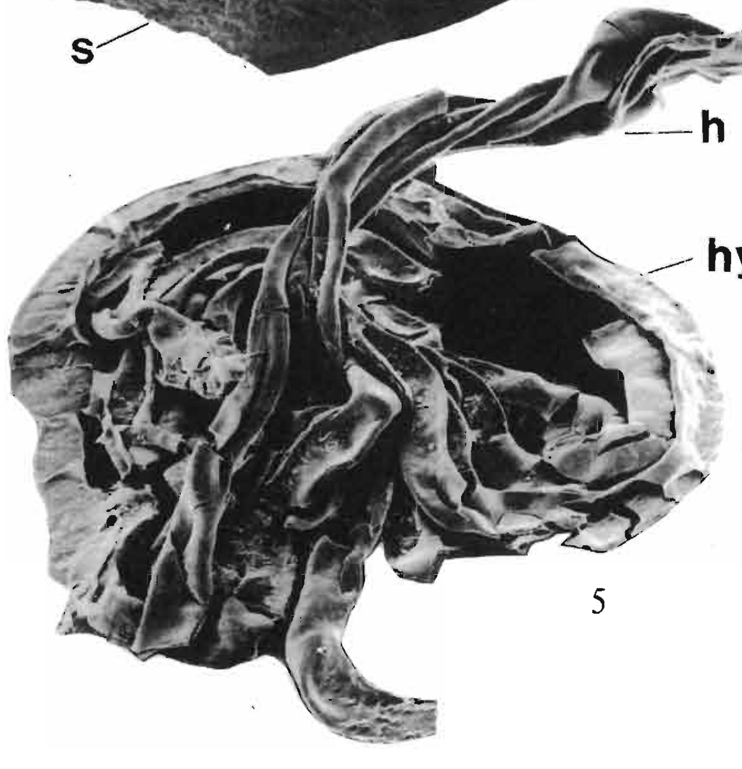

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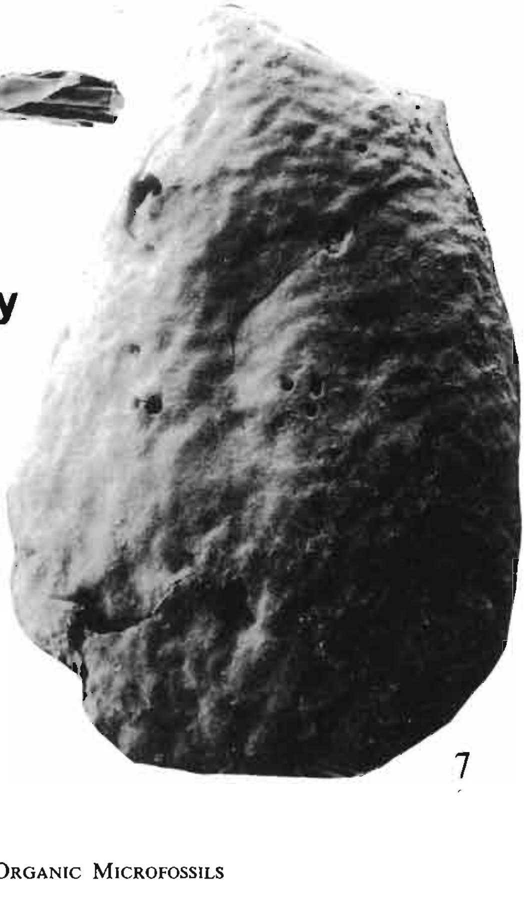

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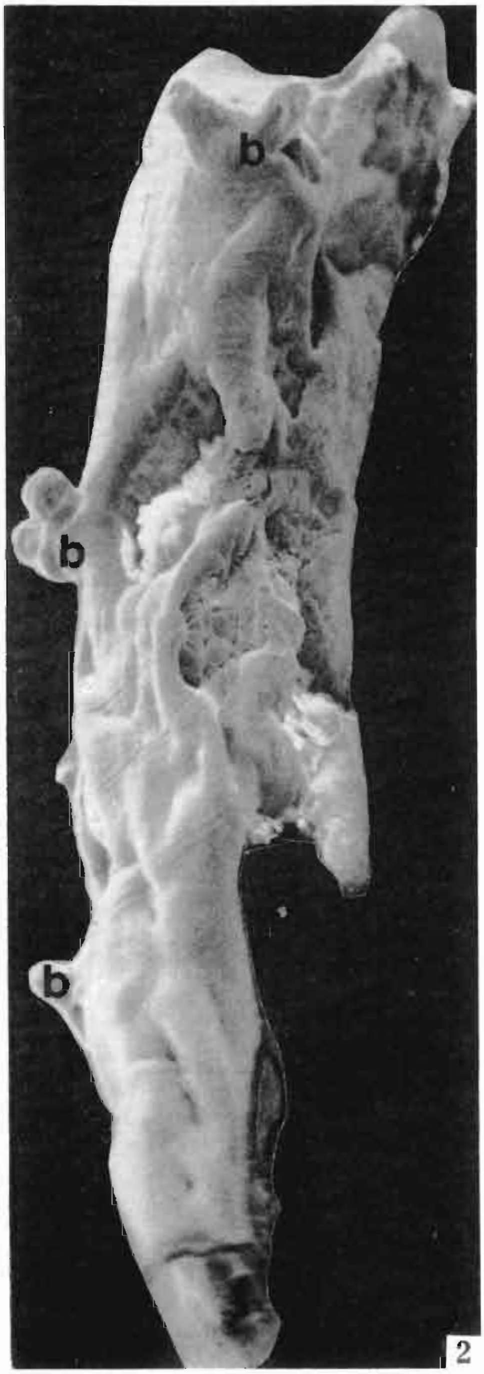

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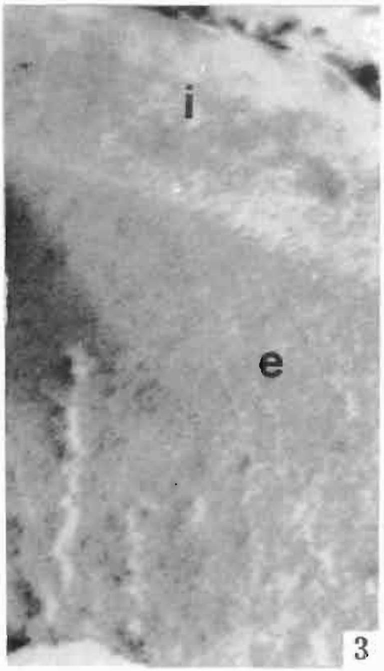

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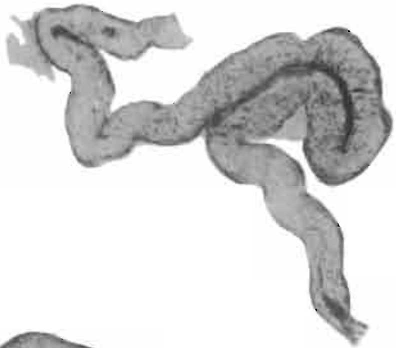

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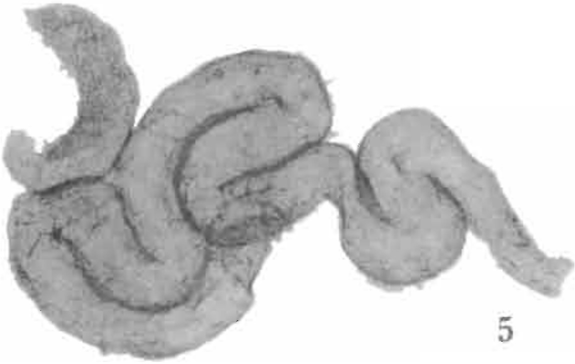

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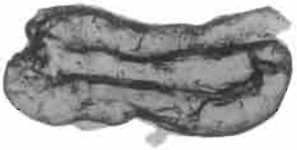

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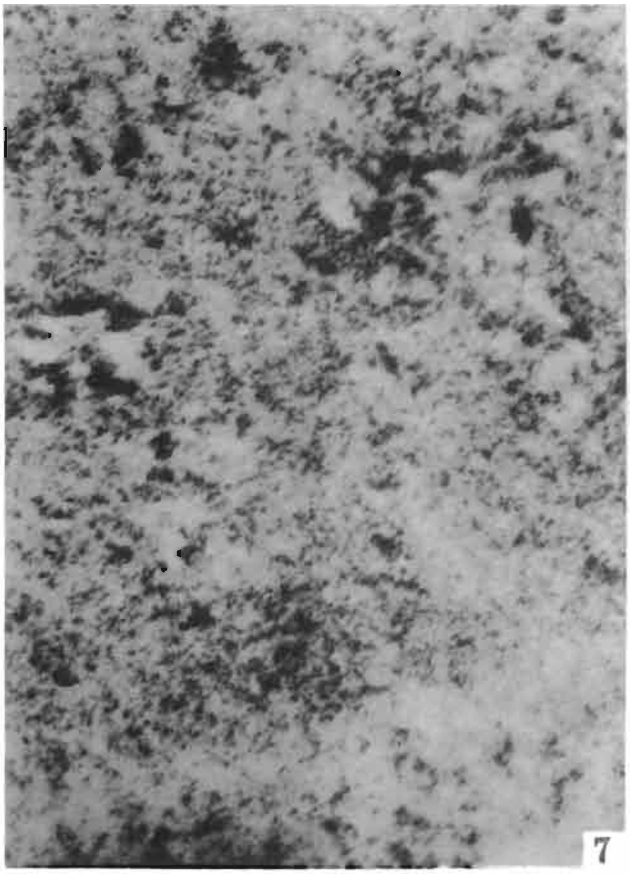

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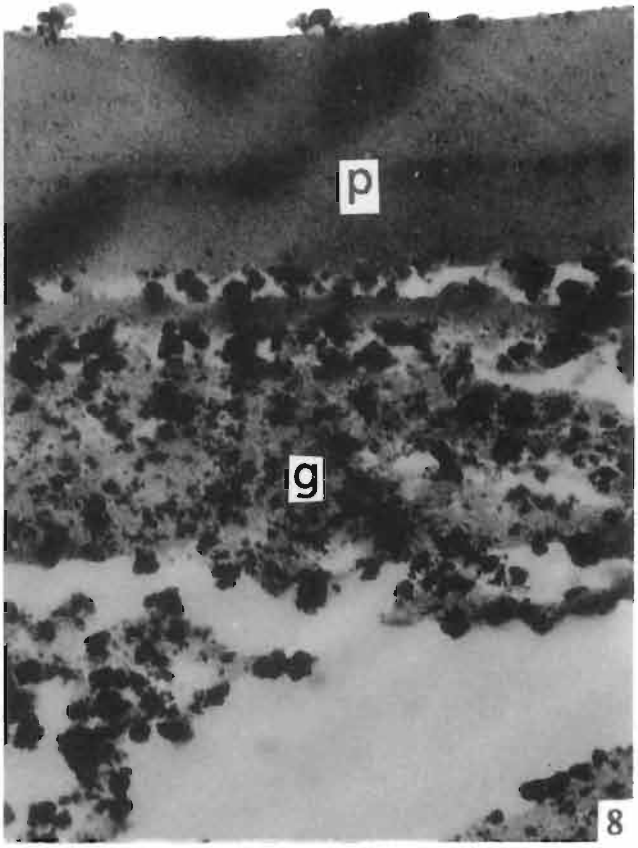

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