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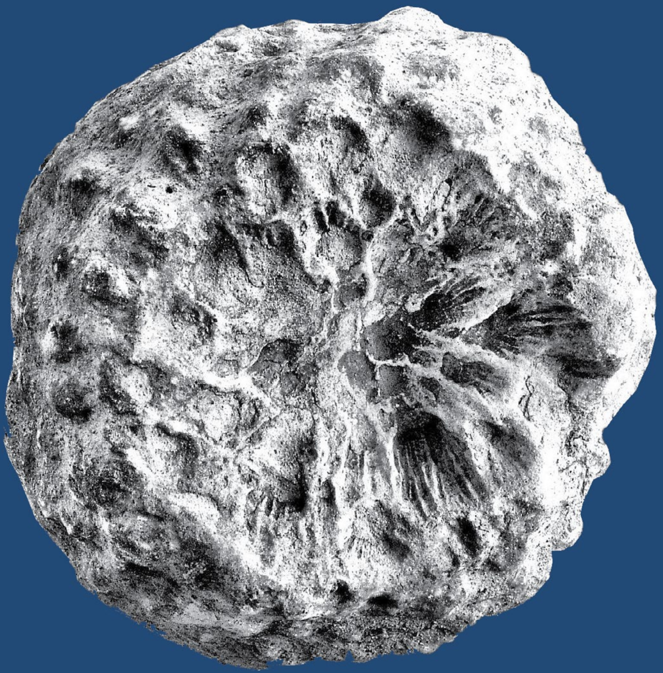
Revision of the Family Chiastoclonellidae Rauff, 1895 (Porifera, Orchocladina)



Freek Rhebergen† and Percy van Keulen

Scandinavian University Press

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Cover picture: *Chiastodiscus verrucosus* n. sp.

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*) The Lethaia Foundation and the publisher regret to announce that our Editor-in-Chief Svend Stouge unexpectedly passed away on April 12th this year. Svend had been the editor of *Fossils and Strata* since 2008. The present volume is the last that he managed to complete as editor.

Revision of the Family Chiastoclonellidae Rauff, 1895 (Porifera, Orchocladina)

by

Freek Rhebergen[†] *and Percy van Keulen*

Acknowledgements

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Within the sponge family Chiastoclonellidae (Rauff, 1895) two new sub-families are erected: (1) the early Palaeozoic Eochiastoclonellinae; (2) the Late Palaeozoic Neochiastoclonellinae. This study focuces on the Eochiastoclonellinae, which mainly originate from Baltica. All in all, six genera and eleven species are distinguished within this taxon. Information derived from new material leads the authors to split *Chiastoclonella* sp. Van Kempen, 1990 into the new species *C. globula* n. sp. and *C. incrustans* n. sp. The unique specimen of *Domospongia silurica* Schlüter, 1887, which was re-assigned by Rauff in 1895 to *Aulocopium aurantium* Oswald, 1847, is restored to its original name. Based on the evidence of new specimens, the diagnosis of *Syltispongia ingemariae* Van Kempen, 1990 is revised and *Diotricheum vonhachti* Van Kempen, 1990 is moved from the Anthaspidellidae to the Eochiastoclonellinae.

The eochiastoclonellid Baltic sponges comprise calcareous sponge bodies from bedrock strata in Estonia and West Russia and silicified erratic sponges from glacial/fluvial deposits in the Netherlands, Germany, and Gotland, Sweden. The erratic chiastoclonellids form part of a large body of erratic sponges, dominated by Astylospongiidae and Anthaspidellidae. On both lithological and palaeontological grounds, this group can be divided into 'blue' sponges, associated with Lavenderblue Chert of Sandbian and Katian age, and 'brown' sponges, associated with Brown Pirgu Chert of Katian age. Most erratic chiastoclonellids are 'brown' sponges, but there is a significant minority of 'blue' specimens. The 'brown' and 'blue' sponge assemblages have a different provenance, but probably all originate from within the North Estonian confacies belt. Their body shape suggests that the Baltic eochiastoclonellids lived on a seabed of loose carbonate sediment in shallow, moderately warm water. Two new genera and five new species are described: *Wilsumispongia*, represented by *W. cylindrica*, *W. cratera* and *W. conica*, and *Chiastodiscus*, represented by *C. verrucosus* and *C. regularis*. ☐ *Ordovicican, Sponges, Chiastoclonellidae, Baltica.*

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Introduction

The Late Ordovician sponge fauna of Baltica includes many taxa which have long awaited description and its overall picture is still incomplete. Thus, up to now erratic Ordovician chiastoclonellid sponges of undoubtedly Baltic origin from German and Dutch sand-pits have not properly been studied. This is also true of the small number of chiastoclonellid sponges known from Ordovician strata in Estonia. The two associations are different in composition but since they contain kindred taxa and share a North-Baltic origin, there are good reasons to treat them together.

The aim of the present study is threefold. First, it seeks to provide a revision of the Early Palaeozoic Chiastoclonellidae Rauff, 1895. This revision will also take into account recently discovered sponges, which represent new genera and species. The second aim is to describe hitherto undescribed or unrecognized chiastoclonellid sponges, both from Ordovician strata in Estonia and the St. Petersburg region (western Russia) and from Neogene fluvial deposits in Germany, the Netherlands and Gotland. By comparing the latter group with the group of endemic Baltic chiastoclonellids, some light may be thrown on the provenance of the erratic chiastoclonellids. Finally, this study aims to discuss the palaeobiogeography of the two chiastoclonellid sponge associations. In particular the palaeobiogeography of the Dutch-German chiastoclonellids has not been studied well, probably because these sponges are erratics, which cannot be matched with known Ordovician formations in Baltica.

In comparison with the Anthaspidellidae Miller, 1889, the Streptosolenidae Johns, 1994, and the Astylospongiidae Zittel, 1877, the Chiastoclonellidae Rauff, 1895 are only a small family within the order of the Orchocladina Rauff, 1895. The oldest chiastoclonellid known to date is the Middle Ordovician *Craterospongiella sinensis* Rigby, Kessel, Ritts & Friedman, 2006, represented by a single specimen from Mongolia. *Chiastoclonella* was the first genus described by Rauff (1894). The description is based on three specimens of Silurian (Wenlock) age from Decatur County, Tennessee.

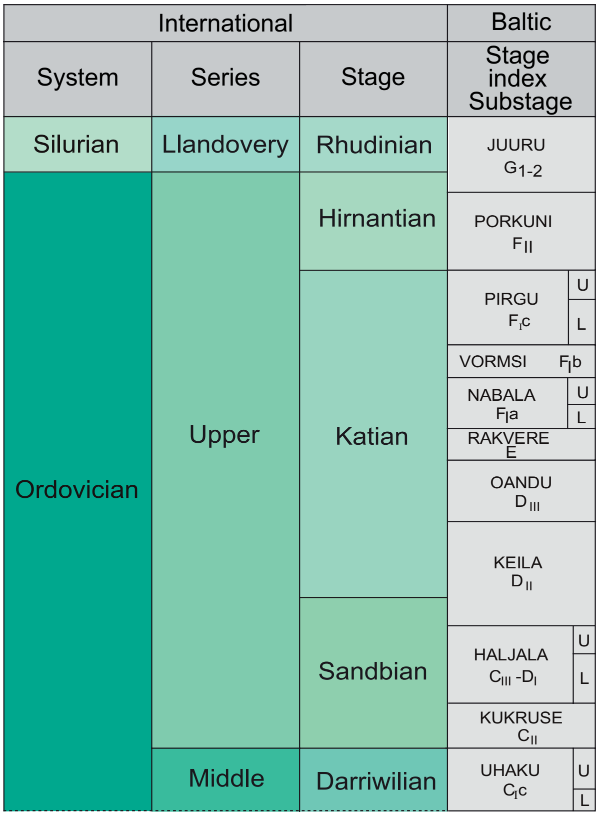
Van Kempen (1990) described two Late Ordovician specimens from Sylt, Germany: *Chiastoclonella* Rauff, 1894 in open nomenclature and *Syltispongia ingemariae* Van Kempen, 1990. At present, these are the oldest representatives of the Chiastoclonellidae and the first (erratic) specimens described from Baltica. Rhebergen (1997) mentioned more specimens from lower Pleistocene fluvial deposits in westernmost Germany and the Netherlands. The taxa represented by these sponges will be treated below in the section Systematic Palaeontology.

The majority of the chiastoclonellid genera are Late Palaeozoic. Established taxa are *Allassospongia* Rigby, 1986 from West Australia and *Rutkowskiella*, Rigby, 1977 from Michigan, USA, both from Devonian strata. Of Permian age are: *Actinocoelia* Finks, 1960 from the west of the USA and Guangxi, China; *Insulipora* Finks, 1960 and *Defordia* King, 1943 from Texas, USA (Finks 1960) and Venezuela (Rigby 1984); *Pseudovirgulopsis* Deng, 1981 from Guangxi.

Van Kempen (1990) observed essential differences between Ordovician/Silurian and Devonian/Permian chiastoclonellids. He proposed to assign the former group to a separate taxon at (sub-)family level (Van Kempen 1990) but made no formal proposal for a new taxon as he felt that he had too little material at his disposal (Van Kempen, pers. comm. 1998).

Geological setting

The erratic chiastoclonellids from the Netherlands, Germany and Gotland, Sweden and the endemic ones from the bedrock of Estonia and the St. Petersburg region, western Russia form part of Ordovician sponge assemblages of widely different geological settings, which for that reason will be described separately. Below, indications of stratigraphy are according to the Estonian regional stratigraphic framework (Männil 1966; Meidla *et al.* 2014; Meidla *et al.* 2023) (Fig. 1), which is commonly used for the East Baltic Ordovician and for Ordovician errata believed to derive from that region. Corresponding series and stages of the global stratigraphic standard (Goldman *et al.* 2020, 2023) will be mentioned where this is opportune (Fig. 1).



International			Baltic	
System	Series	Stage	Stage index Substage	
Silurian	Llandovery	Rhudinian	JUURU G_{1-2}	
Ordovician	Upper	Hirnantian	PORKUNI F_{II}	
		Katian	PIRGU $F_{I}c$	U
				L
			VORMSI $F_{I}b$	
			NABALA $F_{I}a$	U
				L
			RAKVERE E	
			OANDU D_{III}	
			KEILA D_{II}	
		Sandbian	HALJALA C_{III}-D_{I}	U
				L
			KUKRUSE C_{II}	
	Middle	Darriwilian	UHAKU $C_{I}c$	U
				L

Fig. 1. Regional and International series and stages.

Setting of the erratic sponges

Most erratic sponges are found as loose silicifications, but several sponges are still enveloped in their matrix, and these render it possible to link the sponges to particular types of Upper Ordovician (Sandbian and Katian) erratic, silicified limestones. The massively silicified limestone goes by the name 'Hornstein', a term denoting Palaeozoic chert. Henceforth we will designate these 'Hornsteine' as cherts. The loose specimens and the erratic silicified limestones are found together in lower Pleistocene fluvial sand- and gravel deposits. They have been transported and deposited by the Baltic River System, which currently goes by the name Eridanos (e.g. Overeem *et al.* 2001; Suuroja 2007). As a vast river valley system, it drained large parts of Balto-Scandia from the late Oligocene until the early Pleistocene.

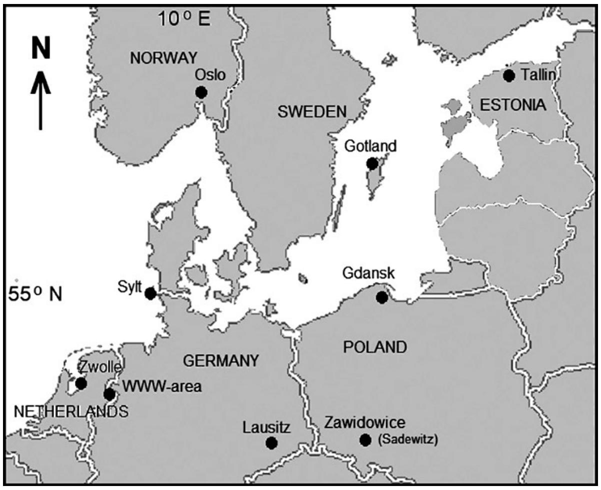


Fig. 2. Map of Northern Europe indicating locations of important assemblages of erratic Ordovician sponges: Lausitz-Sylt assemblage; Gotland assemblage; German-Dutch (WWW-) assemblage; Sadewitz assemblage.

Von Hacht & Rhebergen (1997) and Rhebergen & von Hacht (2000) grouped the erratic Ordovician sponges into four sponge assemblages, each with its own set of genera and species, on the basis of geographical distribution (Fig. 2): (1) the Lausitz-Sylt assemblage occurring in Miocene to Pliocene fluvial deposits in Germany; (2) the Gotland assemblage of sponges (Rhebergen & Van Kempen 2002), which were glacially reworked during the late Pleistocene (Weichselian); (3) the German-Dutch assemblage, a combination of species found in the above-mentioned assemblages, deriving from lower Pleistocene fluvial deposits along the Dutch-German border, in particular the so-called WWW-area, named after the villages Wilsum (Germany), Wielen (Germany) and Westerhaar (Netherlands) (Fig. 3); (4) the Sadewitz assemblage, about 100 to 200 carbonate sponges, containing one chiastoclonellid, from Saalian glacial deposits in Sadewitz (currently Zawidowice, east of Wroclaw, Poland).

This division has lately been replaced by one in which assemblages are primarily distinguished on the basis of palaeontological and lithological aspects: (1) sponges, associated with Haljala/Keila Lavenderblue Chert ($D_{I\text{-}II}$ = upper Sandbian), the 'blue' sponges (henceforth: blue sponges); (2) sponges, associated with Brown Pirgu Chert *sensu* Van Keulen & Rhebergen 2017 (F_{Ic} = upper Katian), the 'brown' sponges (henceforth: brown sponges); (3) sponges, associated with Vormsi/Pirgu erratic carbonates (F_{I}, 'Lyckholmsche Schicht' = upper Katian). Geographically, these assemblages are distributed as follows: blue sponges: Lausitz and Sylt, Germany; brown sponges: Gotland, Sweden; brown and blue sponges combined: the WWW-area, Netherlands; carbonate sponges: Sadewitz, Silesia (Poland).

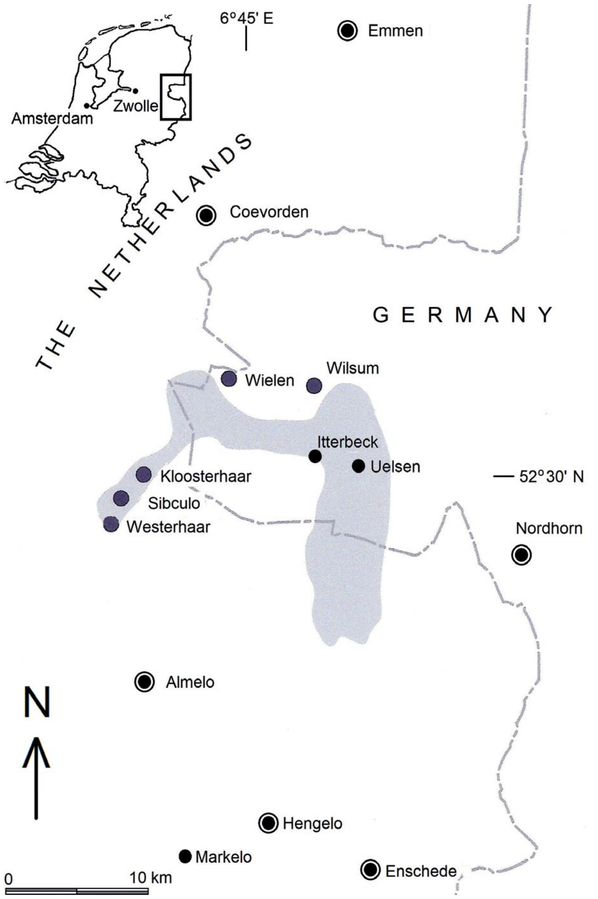


Fig. 3. Map of the so-called WWW-area, a major site of erratic chiastoclonellid sponges.

The distribution of erratic silicified chiastoclonellids is directly linked to the occurrence of the two aforementioned groups of erratic silicified carbonates, i.e. Lavenderblue Haljala/Keila Chert and Brown Pirgu Chert.

Setting of the sponges from Estonia and West Russia

In the Ordovician of Estonia, sponges are not common. Geographically they are restricted to a few localities in northern Estonia (Fig. 4) and stratigraphically to a few stages. This may explain why little research has been done on them. Part of them originate from the Haljala Stage (C_{III} –D_{I}, comprising the substages Idavere and Jöhvi) and the Keila Stage (D_{II}), another part from the Pirgu Stage (F_{Ic}). The sponge taxon *Astraeospongium patina* Roemer, 1861 occurs through the Volkhov–Kunda (B_{II}-B_{III}) to Keila (D_{II}) stages (= Dapingian to Sandbian) (Rhebergen 2009, 2012), but the species is extremely rare in the fossil record.

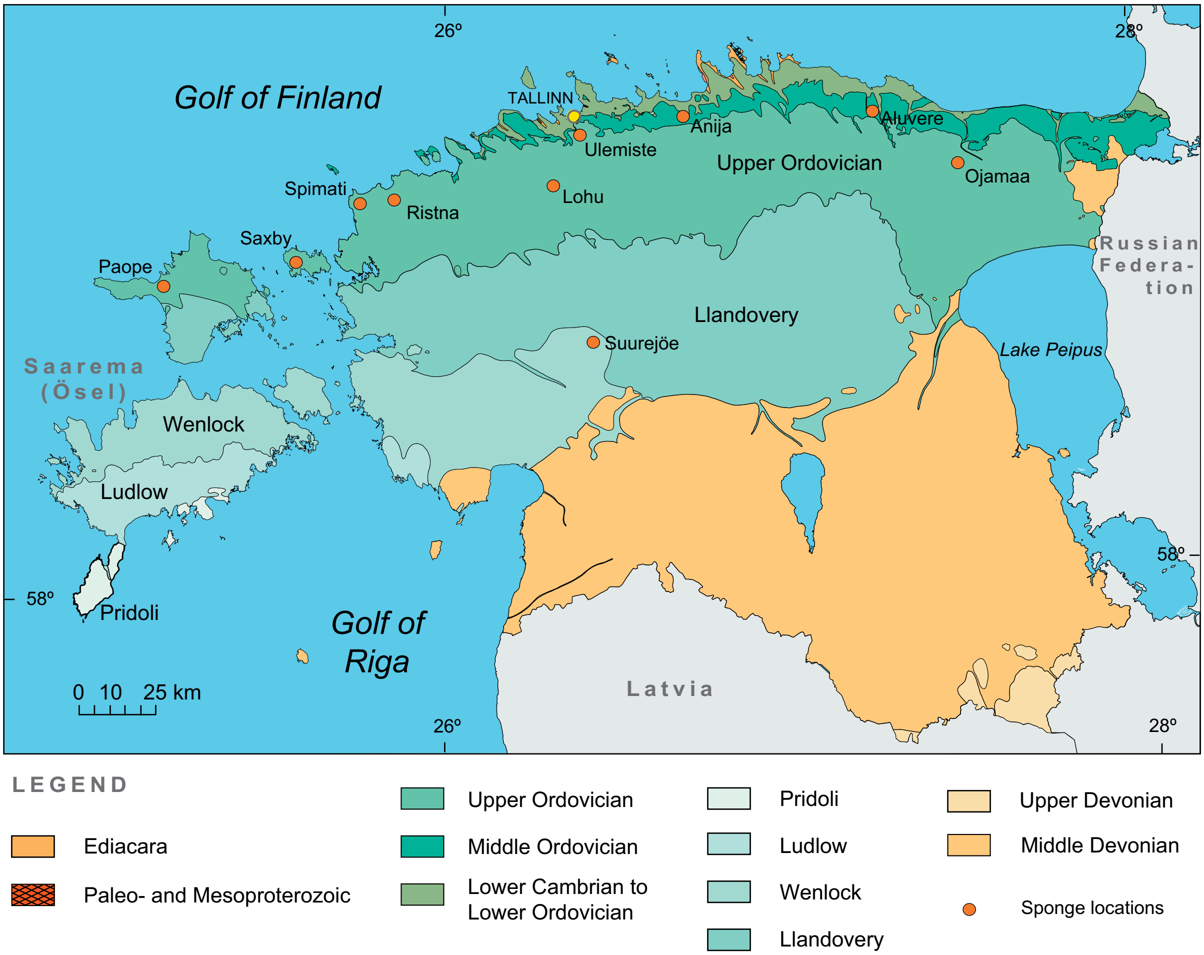


Fig. 4. Map of Estonia indicating areas where Ordovician sponges have been found.

Sponges from the upper Idavere (= lower D_I) can be correlated with coeval sponges from the Russian Shundorovo Formation, described by Asatkin (1931, 1949). This palaeontologist placed them stratigraphically in his C_{IV}-stage, which he called the Sponge Layer. Recently, Iskyul & Fedkovets (2008) collected some 200 sponge specimens from the Kas'kovo quarry, southwest of St. Petersburg, and briefly described the regional geological setting.

The erratic sponge assemblages and the Estonian-Russian sponge faunas each have their own distinct character. In particular the blue assemblage shares several species of astylospongiids with the endemic Estonian-Russian faunas. It is the Anthaspidellidae and Streptosolenidae where these groups show the most conspicuous differences. Thus, *Aulocopium aurantium* Oswald, 1847, which is quite common in the erratic assemblages, has not been found in the Ordovician of Estonia and the St. Petersburg region. The Estonian *Aulocopium discus* (Roemer, 1861), re-assigned to *Aulocopium aurantium* by Rauff (1895), is re-identified here as a chiastoclonellid, namely as the new genus *Chiastodiscus*. As regards the chiastoclonellids, the 'erratic' genera *Domospongia* Schlüter, 1877, *Chiastoclonella* Rauff, 1894, *Syltispongia* Van Kempen, 1990 and a new genus, presented in the sequel as *Wilsumispongia*, have not been found in the Ordovician of Estonia and the St. Petersburg region. Only one genus, introduced in the sequel as *Chiastodiscus* n. gen., can be recognized among sponges of both assemblages.

Apart from a difference in composition, the erratic assemblages and the indigenous Baltic faunas also differ as to the number of specimens known. From West Russia and Estonia a few hundred specimens have been recorded. On Gotland, several thousand erratic brown specimens were collected, but private collections from erratic sponges from Poland, Germany and the Netherlands include more than 100,000 specimens (both blue and brown sponges). These constitute only a small part of the sponges that endured the transport over more than 1,200 km.

Methods, material and repository

Methods

The erratic chiastoclonellid sponge bodies described here show a kind of preservation different from that of other taxa among the erratic Ordovician sponges. The sponges belonging to the Anthaspidellidae, Streptosolenidae and Astylospongiidae use to be massively silicified and they mainly consist of chalcedony. Spicules are mostly preserved as hollow spaces filled with powdery material. By contrast, the matrix of the chiastoclonellid sponges — save for their basal parts of dense chalcedony — usually consists of a yellow-greyish, powdery mass, in which bluish chalcedonic spicules are conspicuous. In addition, small chiastoclones in canal-like tubes are preserved as fragile internal moulds, forming dense structures (see below). Due to this kind of preservation, most sponge bodies are porous and thus susceptible to absorption of iron-oxide, either throughout the matrix or as a film on the surface. The iron-oxide that has precipitated in the sponges derives from Pliocene marine glauconitic deposits which got mixed up with the lower Pleistocene fluvial sands as a result of the late Pleistocene glaciation. More than 50% of the sponges were treated with Sodium Dithionite (Sodium Hydrosulfite, $Na_2S_2O_4$) in a solution of 1.5% in water, in order to remove the film of iron-oxide.

In order to study the sponge skeleton and aquiferous system, the authors had a few specimens cut and their surfaces polished. If possible, powdery surfaces were slightly ground.

In about 50% of the sponges assigned to *Chiastodiscus* n. gen., the matrix is not homogeneous but consists of silt-like bedrock containing a debris of numerous fossil fragments. In many specimens, clay has filled in the space between radially arranged ridges, hiding possible skeletal structures. The infill of clay has been left in place because it proved difficult to determine the exact boundary between infill and sponge surface.

Material

More than 300 specimens were available for investigation. They are grouped into erratic sponges and sponges from bedrock.

Erratic sponges. – Most of the specimens were borrowed from private collectors in the Netherlands and Germany. The majority, including twenty specimens collected by the first author, are from sand-pits in the WWW-area. Fourteen specimens were collected in the Haerst sand-pit near Zwolle (Netherlands). In old collections of erratic sponges housed in Dutch museums, no chiastoclonellids were found. Three specimens were collected by Ulrich von Hacht in Pliocene fluvial deposits on Sylt. One specimen in the Steinmann Institut Goldfuss-Museum, Bonn, is from Sadewitz. Five specimens are from Gotland; four of these have been reposited in the National Museum of Natural History in Stockholm.

Sponges from bedrock. – Thirty-five calcified, dolomitized and/or slightly siliciferous specimens originate from Ordovician strata in Estonia and Russia. Fourteen specimens were borrowed from the Geological Museum of the Technical University of Tallinn, sixteen from the Geological Museum of the University of Tartu, three from the Geological Research Institute in St. Petersburg and two from the private collection of Adrian Popp, Quarnbek (Germany).

Repository

Repositories of material are indicated as follows:

AGH	Archiv für Geschiebekunde; housed in the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg
GIT	Geological Institute Technical University Tallinn
GPIMH	Geologisch-Paläontologisches Institut und Museum der Universität Hamburg
MNDTW	Museum Natura Docet Twente Wonderryck, Denekamp
MTW	Museum Twentse Welle, Enschede
NMB PO	Museum für Naturkunde, Berlin
NRM	Swedish Museum of Natural History, Department Palaeozoology, Stockholm
RGM	Naturalis Biodiversity Center, Leiden
StIPB	Steinmann Institut Goldfuss-Museum, Bonn
TUG	Tartu University Geological Museum
VHC	Von Hacht collection, reposited in the Archiv für Geschiebekunde, University of Hamburg
VSEGEI (GBE)	Geological Research Institute, St. Petersburg

Systematic palaeontology

Phylum Porifera Grant, 1836

Class Demospongea Sollas, 1875

Order Orchocladina Rauff, 1895

Family Chiastoclonellidae Rauff, 1895

Emended diagnosis. – Principal spicules chiastoclones; major skeletal canals radial, concentrical or irregularly winding; sponge sub-globular, massive, disc- or cup-shaped; sponges often attached to substrate basally by overgrowth; imperforate, concentrically wrinkled basal layer often present (emendation from Finks & Rigby 2004, p. 118).

Remarks. – The first chiastoclonellid sponge ever described is *Chiastoclonella headi* Rauff, 1895 (Rauff 1895, pl. 17, fig. 5) (Fig. 5). The description is based on three North American specimens, originating from the middle Silurian Niagara group, Decatur County, Tennessee. Rauff also erected two genera in two subtribes in which he placed several new species, coeval with and originating from the same locality as *C. headi*. One was *Anomoclonella* with *A. zitteli* (Rauff, 1895) as the only species, represented by one specimen; the other was *Pycnopegma*, comprising the species *P. pileum* (Rauff, 1895), *P. callosum* (Rauff, 1895), and *P. stromatoporoides* (Rauff, 1895) (Rauff 1895, pp. 226–242; figs 78–97), each represented by one to three specimens. The taxonomic position of these taxa has been disputed by many authors over several decades (e.g. de Laubenfels 1955; Finks 1960; Reid 1970). Finks, for example, suggested that the genera *Anomaclonella* and *Pycnopegma* were more closely related to the Chiastoclonellidae than to the Jurassic Anomalocladines. Van Kempen (1990, p. 154) summarized this debate and argued that re-examination of Rauff's material would certainly provide conclusive information. The debate resulted in the assignment of both genera, i.e. *Anomoclonella* and *Pycnopegma*, to *Chiastoclonella* (Finks & Rigby 2004).

In addition to these Silurian taxa, there are genera of middle (Devonian) to late Palaeozoic (Permian) age, predominantly from North America and China (Rauff 1894; King 1943; Finks 1960; Rigby 1977, 1986; Deng Zhan-Qiu 1981). They all have a radial canal system, according to the diagnosis of the family. The sponges of the middle and late Palaeozoic are principally composed of small chiastoclones, which often resemble tetraclones, as shown in Figure 6 (Finks 1960, pl. 11, figs 6–8). They also contain a small share of rhizoclones (Finks 1960, pl. 11, fig. 5). Examples are the Devonian genera *Rutkowskiella* Rigby, 1977 from Michigan and Alberta (Birkhead & Murray 1982); *Allassospongia* Rigby, 1986 from West Australia; the Permian genera *Defordia* King, 1943, *Actinocoelia* Finks, 1960 and *Insulipora* Finks, 1960, all three from Texas; *Pseudovirgulopsis* Deng, 1981 from Guangxi.

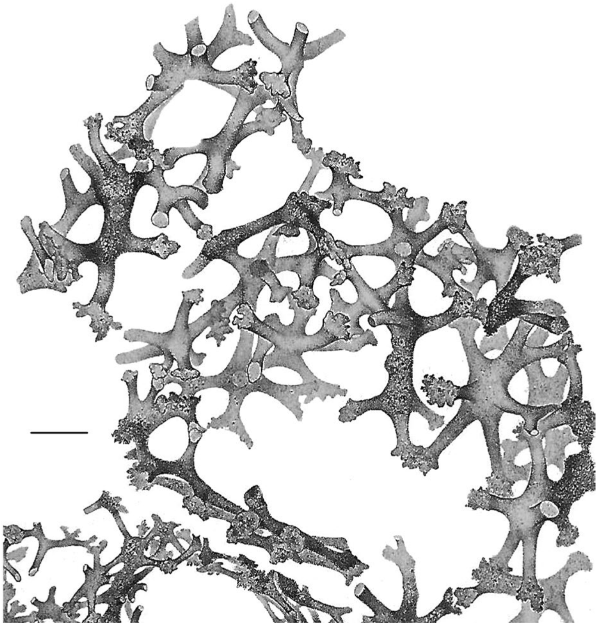


Fig. 5. Chiastoclones as depicted in Rauff 1895 (pl. 17, fig. 5). Scale bar represents 0.1 mm.

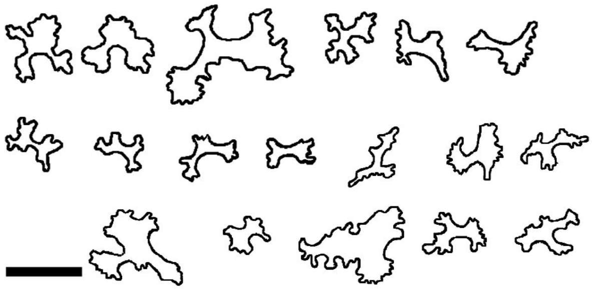


Fig. 6. Tetraclones. After Finks 1960. Scale bar represents 0.2 mm.

Most of the early Palaeozoic chiastoclonellids have a skeleton composed of large chiastoclones in the main skeleton, e.g. *Chiastoclonella headi* Rauff, 1895 (Fig. 5), *Craterospongiella sinensis* Rigby, Kessel, Ritts & Friedman, 2006 (Fig. 7). *Syltispongia ingemariae* Van Kempen, 1990 (Fig. 8), with simple clones lacking the elaborate extensions found in the Devonian and Permian sponges. The skeleton moreover contains a small share of dendroclones, rhizoclones and monaxons, the latter both isolated and in bundles. Examples of desmas commonly found in the materials examined in this study are shown in Figure 9.

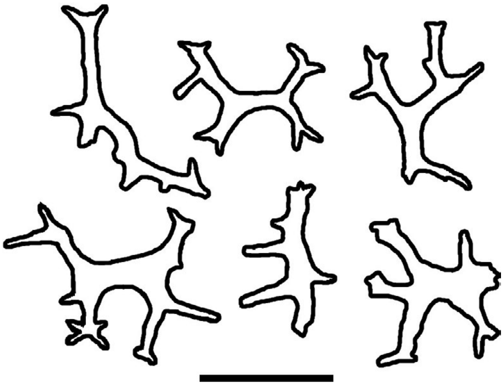


Fig. 7. Chiastoclones of *Craterospongiella sinensis* Rigby, Kessel, Ritts and Friedman, 2006. Scale bar represents 0.2 mm.

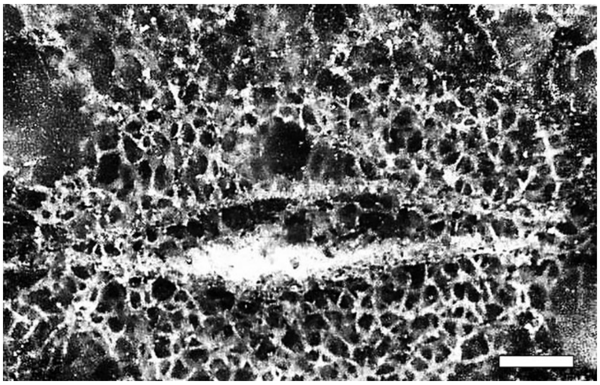


Fig. 8. Chiastoclones in *Syltispongia ingemariae* Van Kempen, 1990, RGM 792 320. Scale bar represents 0.8 mm.

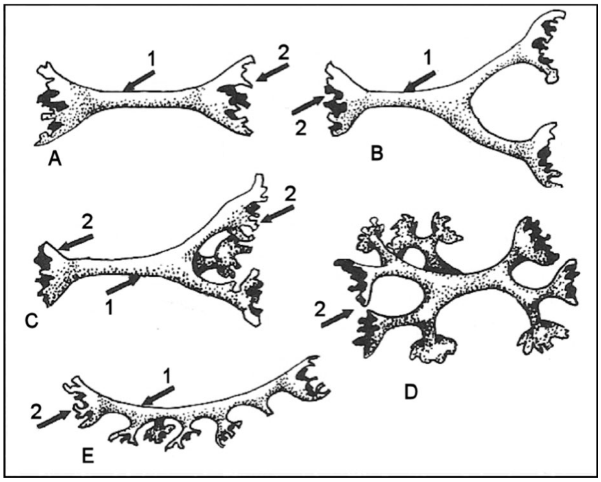


Fig. 9. Examples of desmas which are common to the chiastoclonellid sponges examined in this study (after de Freitas 1991, fig. 3). Spicules are typically 0.3–1.5 mm in length.

According to Schlüter (1877) and Van Kempen (1990), Early Palaeozoic chiastoclonellids might contain rare tetraclone-like chiastoclones, but none have been observed in the eochiastoclonellids studied here. In these regards, they resemble the Middle Ordovician *Craterospongiella sinensis* Rigby, Kessel, Ritts & Friedman, 2006.

According to Finks (1960, p. 63), chiastoclones are derived from the originally monocladine dendroclone, a single-shafted spicule, with arborescent zygoses at both ends: 'Chiastoclones are more complicated spicules derived from dendroclones, in which three long clones, bearing terminal arborescences, radiate from each end of a very short rhabdome' (Finks 2003, p. 69). A different view on the development of the orchocladinid spicules, including chiastoclones, has been put forward by Mehl-Janussen (1999, pp. 38–40). She distinguishes Mesozoic sponge taxa with 'real' tetraclone spicules, comprising four axial filaments, from Palaeozoic taxa composed of anaxial desmas, i.e. spicules without axial filaments. She regards the single-shafted dendroclone as the primary form from which, among others, the monaxonoid desmas and the three- to five-rayed chiastoclonid desmas are derived. This evolution was not a linear development, but a 'mosaic evolution' (Mehl-Janussen 1999, p. 39) in which often intermediate forms arose. Thus, chiastoclonellid sponges may contain dendroclones, rhizoclones and monaxons, whereas anthaspidellids may contain chiastoclones. The irregular, complicated chiasticlonellid desmas are to be distinguished from similarly looking 'real' tetraclones, which did not occur before the Mesozoic. Mehl-Janussen noted that over the Palaeozoic chiastoclones tended to develop shorter clones. Thus, the predominance of long-shafted chiastoclones in the early Palaeozoic is consonant with the observations by Finks and Mehl-Janussen. The Devonian and Permian chiastoclones, then, seem to be derived forms. The latter often show four, usually conspicuously short, clones, resembling four-rayed Mesozoic tetraclones. This explains why in many descriptions chiastoclonellid spicules are named 'tetraclonoid spicules' (Schlüter 1887; Rauff 1895; Finks 1960, 2003; Finks & Rigby 2004). In the present study, it is proposed to put an end to this confusing state of affairs by erecting two sub-families (see below). Mehl-Janussen's proposal to assign all Palaeozoic sponges containing chiastoclones, even those with only a small share of them, to the Chiastoclonellidae, was not followed by Finks & Rigby (2004) and is also declined by the authors.

Skeletal characteristics are so distinctive that the early Palaeozoic Chiastoclonellidae are to be systematically distinguished from the middle and late Palaeozoic ones. Here it is proposed to divide the Chiastoclonellidae into two sub-families, one for the Ordovician and Silurian taxa described below, the other for the Devonian and Permian taxa. It should be stressed that this proposal is a mere elaboration of a suggestion by Van Kempen (1990, p. 159).

Eochiastoclonellinae n. subfam.

Type genus. – Chiastoclonella Rauff, 1894.

Derivation of name. – Eo- (Greek): 'early', referring to the early Palaeozoic types of chiastoclones as distinct from the Late Palaeozoic ones.

Diagnosis. – Medium-sized to large sponges, varying in shape from sub-spherical, sub-cylindrical, conical to discoid, composed predominantly of chiastoclones, of varying dimensions from small to big, usually with relatively straight, slender clones and poorly developed zygomes; monaxons isolated or in small bundles; small amounts of rhizoclones and dendroclones may occur; aquiferous systems vary from simply radial to complicated, irregular; small to wide, tube-like, irregularly winding canals, oriented sub-vertically to sub-horizontally; dense basal part with impermeable cortical layer may be present; deep central spongocoel absent.

Following genera and species are assigned to Eochiastoclonellinae n. subfam.

Genus *Chiastoclonella* Rauff, 1894
    C. headi Rauff, 1895
    C. zitteli Rauff, 1895
    C. pileum Rauff, 1895
    C. callosum Rauff, 1895
    C. stromatoporoides Rauff, 1895
    C. globula n. sp.
    C. incrustans n. sp.

Genus *Domospongia* Schlüter, 1887
    Domospongia silurica Schlüter, 1887

Genus Syltispongia Van Kempen, 1990
    Syltispongia ingemariae Van Kempen, 1990

Genus *Craterospongiella* Rigby, Kessel, Ritts & Friedman, 2006
    Craterospongiella sinensis Rigby, Kessel, Ritts & Friedman, 2006

Genus *Wilsumispongia* n. gen.
    W. cylindrica n. sp.
    W. cratera n. sp.
    W. conica n. sp.

Genus *Chiastodiscus* n. gen.
    C. verrucosus n. sp.
    C. regularis n. sp.

Genus *Diotricheum* Van Kempen, 1989
    Diotricheum vonhachti Van Kempen, 1989

Neochiastoclonellinae n. subfam.

Type genus. – Rutkowskiella Rigby, 1977.

Derivation of name. – Neo- (Greek): 'new', referring to chiastoclonellids of the late Palaeozoic.

Diagnosis. – Irregularly shaped sponges with an aquiferous system of irregularly organized canals, lacking a distinct radial pattern; skeletal net characterized by irregular, short-shafted chiastoclones with extended arborescences, tightly fused; spicules often tetraclone-like chiastoclones, resembling rhizoclones.

Included taxa

Rutkowskiella tumula Rigby, 1977

Genus *Defordia* King, 1943
    D. defuncta King, 1943
    D. digitata Rigby, 1977
    D. foliata Rigby, 1977
    D. verrucula Rigby, 1977

Genus *Actinocoelia* Finks, 1960
    A. meandrina Finks, 1960
    A. verrucosa Finks, 1960

Insulipora elegans Finks, 1960

Pseudovirgulopsis solus Deng Zhan Qiu, 1981

Allassospongia polystromne Rigby, 1986

Remarks. – Rutkowskiella Rigby, 1977 is the first chiastoclonellid of late Palaeozoic (Devonian) age ever described. According to Rigby, the genus is more similar to the Early Palaeozoic *Chiastoclonella* than to Permian genera. It differs from *Chiastoclonella* in two respects. First, it lacks 'the radiating architecture and the pronounced canal structure which is subparalleled by stacked series of spicules in a moderately regular pattern. Such a relationship is distinctly different than seen in the almost irregular, felted net in *Rutkowskiella*' (Rigby 1977, p. 1216). This characteristic applies to all other Devonian and Permian genera. The second difference concerns the shape of spicules. Chiastoclonellids from early Palaeozoic taxa have relatively slender, smooth clones, quite unlike the short-shafted, knobby, sometimes rhizoclone-like and often tetraclone-like clones in Late Palaeozoic taxa.

In the sequel, the Neochiastoclonellinae will be left out of consideration.

Genus *Chiastoclonella* Rauff, 1895

Type species. – *Chiastoclonella headi* Rauff, 1895, pp. 244–247, text-figs 98–102; pl. 17, figs 5–7; pl. 18, fig. 1.

Emended diagnosis. – Sub-globular to fungi-form, acloate sponge with smooth upper surface. Exterior may be smooth without features or with overhanging layers. Incurrent canals indistinguishable from excurrent ones. Skeleton is a dense structure of small chiastoclones of about equal dimensions; monaxons may occur. Indistinct radial skeletal pattern; skeletal radiante within the sponge body. Differentiated basal and dermal layer absent. Concentric zones indicating incremental growth recognizable.

Remarks. – The genus includes sponges from the Upper Ordovician, Llandovery and Wenlock in Europe and the USA. As yet, no other representatives are known. Until recently, the number of erratic sponges from Germany and the Netherlands was too low, and their preservation too poor, to assign them to a particular species. Increased knowledge and a supply of hitherto unknown specimens, mainly discovered in private collections, has led to renewed study, resulting in the proposal of a new species represented exclusively by erratic specimens, but certainly originating from the eastern Baltic.

Chiastoclonella differs from other taxa in the Orchocladina in occurring frequently as an overgrowth of another organism. In those instances, the shape of the sponge body is adapted to the body shape of the host (see below).

Chiastoclonella globula n. sp.

Plate 1, figures 1–6

1990 *Chiastoclonella* sp. Van Kempen, p. 153, fig. 1a–c.
1997 *Chiastoclonella* sp. Rhebergen, p. 138, figs 6, 7.
2001 *Chiastoclonella* sp. Rhebergen, Eggink, Koops & Rhebergen, p. 98, pl. 22, figs 1–5.

Derivation of name. – *Globus* (Latin): 'globe', 'sphere', referring to the sub-globular body form of the species.

Holotype. – RGM 792 305, Wilsum, Germany.

Paratype. – RGM 792 306–308, Wilsum, Germany.

Additional material. – RGM 792 309, RGM 792 329, RGM 792 373, Wilsum, Germany; RGM 792 311, Wielen, Germany, Straaten sandpit.

Diagnosis. – Sub-globular, acloate sponge with smooth exterior and usually one or more small rounded dimples; dense skeletal structure of small chiastoclones of about equal dimensions; monaxons may occur; indistinct radial pattern of canals paralleled by connected chiastoclones; chiastoclones with one elongated arm; isolated or bundle-like monaxons running perpendicular to distal surface; no observable difference between in- and excurrent canals; concentric zonation points to incremental growth; differentiated basal and outer layer absent.

Description. – *Chiastoclonella globula* n. sp. is a somewhat irregularly shaped, sub-spherical to oval sponge, varying in diameter from 30 × 21 mm to 61 × 40 mm. The holotype, RGM 792 305, is 43 × 40 × 34 mm (Pl. 1, figs 1, 2). The diameter of the 20 examined specimens is 35-45 mm. Most of them are slightly flattened. Distally concentric layers, for instance in the holotype, points to incremental growth (Pl. 1, figs 2, 3). RGM 792 309 shows layers partly overlapping older ones (Pl. 1, fig. 4).

The smooth exterior composed of small chiastoclones does not show any characteristic features, apart from usually one or more apical or lateral dimples, about 4–7 mm in diameter and 1–3 mm deep (Pl. 1, fig. 1). Their nature and function are not known.

In specimens is which the interior is exposed, the skeleton can only be discerned in the distal zone, 4–7 mm thick (Pl. 1, fig. 5). In the rest of the interior, canals and skeleton are replaced by dense, opaque or translucent chalcedony. The narrow distal zone, however, is sufficiently clear to establish three characteristics of *Chiastoclonella globula*: (1) the overall structure is indistinctly radial; (2) the skeletal radiante is situated in the centre; (3) the sponge body shows a concentric zonation reflecting incremental growth.

The aquiferous system is composed of an irregular mesh of small canals with diameters of about 0.04–0.06 mm. The irregular shape of chiastoclones reflects the irregularity of the canal system. It is impossible to distinguish in- and excurrent canals from each other, a feature which has also been reported by Rauff (1895, p. 244 [368]) and Van Kempen (1990, p. 153). In this respect, the genus differs from genera in other families of the Orchocladina. The indistinct radial pattern is caused by many chiastoclones having one lengthened arm, pointing to the surface. In some specimens this pattern is strengthened by parallel, isolated or bundle-like monaxons.

The skeletal radiante, which is the point where the sponge larva started to grow, is approximately in the centre. The skeleton is composed of very small chiastoclones, which are connected with adjacent ones at the distal parts of their clones (zygosis). Chiastoclones are of approximately equal dimensions, measuring about 0.12–0.18 mm, on average 0.15 mm. The axial diameter of the clones is about 0.04 mm. In the translucent chalcedony of the dissolved interior, tiny rhizoclones have been observed, as well as rare dendroclones. The latter tend to stack parallel to their axis, thus forming short, radially disposed strands, as are typically found in anthaspidellids and streptosolenids. Rare monaxons may run parallel to lengthened arms of chiastoclones, thus enhancing the radial structure of the sponge. Indistinct concentric zones of chalcedony with variable colour and density do not reflect differences in the skeleton. According to Rauff (1893, p. 216), these were formed diagenetically in the process of silicification.

In RGM 792 308 (Pl. 1, figs 6, 7) the sponge larva appears to have settled on a small bifoliate bryozoan, which is now situated in the centre of the sponge body. This specimen demonstrates that the sponge grew in all directions. Further evidence is provided by two specimens in the Von Hacht collection: In one specimen, the sponge larva settled on a brachiopod valve; in the other, on a stalk fragment of a crinoid. Specimen RGM 792 311 is embedded in a porous, silicified limestone and occurs together with the algae *Vermiporella fragilis* Stolley, 1893, *Palaeoporella variabilis* Stolley, 1893 (Pl. 1, fig. 8), the trilobite *Ectillaenus* sp., the brachiopode *Sowerbyella* sp. and small fragments of an unidentified graptolite. In RGM 792 373, part of the dermal wall of *Archaeoscyphia* sp. can be observed. This specimen is the only one to occur with another sponge species.

Remarks. – The first sponge described as a chiastoclonellid was *Chiastoclonella headi* Rauff, 1895 (Pl. 1, fig. 9), though it was already depicted in Rauff (1894). The description was based on three specimens from the middle Silurian of the Decatur County, Tennessee. *C. headi* is an irregular, oval to subspherical sponge with a layered growth form. Younger layers partly overlap older ones, so that the exterior is irregular. In one specimen, a distinct basal part could be observed (Rauff 1895, fig. 98). The skeletal radiante is situated below the centre. *C. globula* n. sp. differs from *C. headi* in exhibiting a more regular growth form, usually without overlapping layers, in lacking the basal layer and in having the skeletal radiante more or less in the centre.

Van Kempen (1990) described *Chiastoclonella* sp. on the basis of a single, poorly preserved erratic specimen in the Von Hacht collection. It was collected from Pliocene fluvial deposits on Sylt. When Von Hacht and the first author went through this collection between 1995 and 2001, they recognized several more specimens of *Chiastoclonella*, many of them with skeletons that appeared to be better preserved than in the specimen used by Van Kempen. These sponges can now be assigned to *C. globula* n. sp. The description offered above is based on the better preserved specimens from the WWW-area.

The specimens from Germany and the Netherlands reveal two essential features that *C. globula* n. sp. has in common with all other species of *Chiastoclonella* (*C. headi*, *C. zitteli*, *C. pileum*, C. *callosum*, *C. stromatoporoides*): first, a radial pattern of skeleton and canals; second, a skeletal radiante situated within the sponge body, either in the centre or in the lower part. The cylindrical-, conical-, dome- and discus-shaped species all share a complicated aquiferous structure. Moreover, in these taxa the size of chiastoclones widely varies within one specimen, from very large to extremely small.

Due to its smooth, featureless exterior, *C. globula* n. sp. can easily be confused with other spherical sponge species in the erratic assemblages. Especially *Hindia sphaeroidalis* Duncan, 1879 and worn specimens of *Carpospongia* spp. Rauff, 1893 show the same smooth, featureless exterior and a similar radial pattern. In most cases, sound identification is only possible in specimens showing the interior skeleton, since this is what distinguishes *C. globula* n. sp. from *Hindia sphaeroidalis* and *Carpospongia* spp. The skeletons of these species consist of dicranoclones (*Hindia*) or sphaeroclones (*Carpospongia*; see Rauff 1893, 1894, pls 12, 15).

Stratigraphic age. – Based on co-occurrent algae and trilobites (Nitecki *et al.* 2004), *C. globula* n. sp. is assigned to the Katian (Late Ordovician). So far, the species has not been recognized from Estonia and the St. Petersburg region.

Chiastoclonella incrustans n. sp.

Plate 2, figures 1–3

Derivation of name. – *Incrustans* (Latin): 'encrusting', referring to the sponge's habit to overgrow a host organism.

Holotype. – RGM 792 310, Wilsum, Germany, Schroeder sand-pit.

Paratypes. – RGM 792 312, Kloosterhaar, Netherlands, Sierink sand-pit; RGM 792 390-393, RGM 792 397, Braderup, Sylt, Germany.

Other material. – RGM 792 394-396, Braderup, Sylt, Germany.

Diagnosis. – Irregularly shaped body varying from sub-globular to stalked club-shaped, dumb-bell or tripod-like, dependent on the shape of the host organism; sponge composed of thin layers of chiastoclones attached to the surface of the host; growth incremental; skeletal radiante near the point of attachment on the host, from where small canals radiate toward the distal surface or form an agglomeration of sponges, possibly each with its own skeletal radiante; canals of uniform diameter; most chiastoclones of equal size; monaxons parallelling canals may be present.

Description. – RGM 792 310 is a stalked, pear-shaped sponge, 54 mm high, with an upper part 45 mm in diameter. The sponge has adopted the body shape of its host, a rugose coral, by growing over its surface in all directions (Pl. 2, figs 1, 2). Thin concentric layers indicate a process of incremental growth. These layers can be seen along the edge of the cavity formed by natural damage.

A nearly identical pear- to club-shaped body form can be observed in the stalked paratype RGM 792 390. It is 35–42 mm in diameter and 49 mm high, with a slightly tapering ‘stalk part’ 20 mm in diameter. The skeleton of this ‘stalk’ consists of vertically arranged strands of chiastoclones, reminiscent of the ladder-like strands in anthaspidellids. The skeletal radiante seems to be situated near the base of the stalk.

A third example of a sponge being attached to a host is RGM 792 312 (Pl. 2, fig. 3). Here too, the host, in this instance the tabulate *Catenipora* sp., has completely been overgrown by the sponge. Sub-parallel canals, 0.20–0.30 mm in diameter, run to the distal surface and empty perpendicularly or at acute angles. Small canals, occurring as ring-like openings between connected chiastoclones, are 0.05–0.08 mm in diameter. Most chiastoclones are of equal size, measuring 0.12–0.20 mm. Many chiastoclones, especially those which form part of a canal wall, show one elongated clone.

Remarks. – Encrusting orchocladinic sponges are rare. Liu *et al*. (1997) described the Permian *Velellospongia,* from the Hubei Province, China, the first known encrusting sponge in the Anthaspidellidae. Finks & Rigby (2004) mentioned only three genera of Permian age from Wyoming: *Incrustatospongia superficiala* Rigby & Boyd, 2004 and *Virgiaspongiella ramosa* Rigby & Boyd, 2004. The third genus is *Incrustospongia* Molineaux, 1994, of uncertain order and family, from the Carboniferous of Texas. None of these taxa have been assigned to the chiastoclonellids.

Chiastoclonella incrustans n. sp. differs from *C. globula* n. sp. by its manner of growth; unlike the latter species, it completely overgrows the host organism, thereby adopting the body shape of the host. The skeletal radiante of *C. incrustans* is situated at the point of attachment from where skeleton and canals run more or less parallel to the surface of the host. By contrast, the skeletal radiante of *C. globula* is situated in the centre, because the larva used to grow evenly in all directions. Thus, an encrusting mode of growth resulted in an excentrical position of the skeletal radiante. In this study, globular chiastoclinellids showing merely attachments of small organic fragments, such as a juvenile bryozoan or a crinoid ossicle, are all assigned to *C. globula*.

Stratigraphic age. – *C. incrustans* is assigned to the Pirgu Stage ($F_{\mathrm{Ic,}}$) because the tabulate *Catenipora* sp., which occurs in RGM 792 312, is associated with the Brown Pirgu Chert. As yet, no specimens of *C. incrustans* n. sp. have been recognized among the sponge faunas of Estonia and the St. Petersburg region.

***Chiastoclonella* sp.**

Not depicted

2014 *Chiastoclonella* sp. Rauff, 1895; Rhebergen & Botting, p. 39, pl. 11, figs 1–3.

Material. – One specimen, NRM Sp10106, Gnisvärd, Gotland, Sweden.

Description. – NRM Sp10106 is an elliptical, cushion-like sponge with a flat base, measuring 54 × 50 × 32 mm. The distal surface is smooth without pores or other features. The base exhibits a dense, concentrically wrinkled layer. The interior consists of bluish chalcedony, in which most of the skeleton has been dissolved. Sub-horizontal, slightly undulating darker bands correspond to concentric layers on the exterior. The horizontal layering and the concentrically wrinkled base indicate that the skeletal radiante is probably near the base, as depicted in Rhebergen & Botting (2014, Pl. 11, figs 2, 3). The chiastoclonellid skeleton is discernible in a zone of the distal region which is only a few millimeters wide, especially in the basal part of it. It is composed of both isolated and connected chiastoclones, 0.05–0.08 mm long, bearing shafts of usually 0.015 mm in diameter. A radial pattern is present but can only be recognized in two small places in the upper region. Canals could not be observed.

Remarks. – Rhebergen & Botting (2014) described an assemblage of Llandovery (Telychian) sponges from the non-exposed 'Red Layers' on Gotland, which is dominated by the orchocladinid families Anthaspidellidae Miller, 1889 and Astylospongiidae Zittel, 1877. In this assemblage, NRM Sp 101016, a badly eroded specimen from the beach near Gnisvärd, is the only representative of *Chiastoclonella*. Rhebergen & Botting (2014, p. 39) found that 'it has been preserved too poorly to assign it to a species, let alone to propose a new taxon'. Nevertheless, the specimen is important since chronologically it takes an intermediate position between the Late Ordovician *Chiastoclonella globula* n. sp. and *C. incrustans* n. sp. from Baltica on the one hand and the Wenlock species *Chiastoclonella headi* Rauff, 1895 from Tennessee on the other hand.

Genus *Syltispongia* Van Kempen, 1990

Type species. – *Syltispongia ingemariae* Van Kempen, 1990.

Revised diagnosis. – Massive, hemispherical sponges with distinct, flattened, sub-cylindrical basal part composed of thin layers; outer surface with a layered, overhanging appearance produced by irregular layering of skeleton internally; spongocoel absent but with concentration of osculi on summit; principal canals in interior loosely organized into discontinuous, irregularly ascending canals as well as irregularly radially and concentrically arranged canals; skeleton of irregularly oriented chiastoclones producing in some places simple, discontinuous, upward flaring strands; monaxons occurring as minor component forming cores of sections of more complex strands; chiastoclones in the basal part considerably smaller than in the main skeleton; sponge without differentiated dermal layer (revision of diagnosis *in* Finks & Rigby, 2004, p. 124).

Remarks. – The original description by Van Kempen (1990) was based on a single specimen collected from Pliocene fluvial deposits on Sylt (AGH G 50). It was Van Kempen's key-publication that subsequently led the first author to recognize several hundreds of chiastoclonellid sponges, often with well-preserved skeletal parts and canals, in many private collections.

Van Kempen's holotype is a blue sponge. Over the last three decades, sand-pits in the WWW-area and a few other localities in the Netherlands have yielded another 15 to 20 blue specimens of *Syltispongia*, as well as more than 150 brown specimens. In the brown specimens, the skeleton tends to be better preserved than in the blue ones, but the new information derived from the former group does not give cause for a drastic revision of the original description. The only important new insight gained from the examination of the brown specimens is that *Syltispongia* has a characteristic, distinct basal part, consisting of thin, sub-parallel, sub-horizonal layers, which are composed of very small, densely packed chiastoclones. A similar basal part is found in *Aulocopium aurantium* Oswald, 1847, a very common species in the WWW-area. This is probably the main reason that prior to Van Kempen's publication many collectors, including the authors, failed to recognize *Syltispongia* Van Kempen, 1990 as a distinct genus and mistook specimens of it for second- or third-rate *Aulocopiums*.

The only known specimen of *Domospongia* Schlüter, 1887 is similar to *Syltispongia* Van Kempen, 1990, but due to its poor preservation it is impossible to tell if it represents the same genus. Below this sponge will be discussed in more detail.

Syltispongia ingemariae Van Kempen, 1990

Plate 3, figures 1–8

1990 *Syltispongia ingemariae* n. gen. et n. sp. Van Kempen, pp. 156–178, figs 2–9.
1997 *Syltispongia ingemariae* Van Kempen, 1990; Rhebergen, pp. 138–143, figs 1–11.
2001 *Syltispongia ingemariae* Van Kempen, 1990; Rhebergen, Eggink, Koops & Rhebergen, p. 96, pl. 21.
2004 *Syltispongia ingemariae* Van Kempen, 1990; Finks & Rigby, p. 124, figs 88, 89.

Material. – RGM 792 320-323, RGM 792 328, Wilsum, Germany; RGM 792 324, Kloosterhaar, Netherlands; RGM 792 326, Ratzel, Germany, Warrink sand-pit; RGM 792 327, Itterbeck, Germany, Smals sand-pit.

Diagnosis. – As for the genus.

Description. – *Syltispongia ingemariae* varies in size and body shape. More than 100 specimens in about twenty private and museum collections were examined by the first author. The largest one is 140 × 110 mm wide and 70 mm high. The diameter is 80–100 mm in fourteen specimens, 60–80 mm in 60 specimens and 40–60 mm in 25 specimens. Most specimens consist of dense, often opaque to translucent chalcedony. In a few specimens, the skeleton has been preserved extraordinary well.

The body shape varies from hemispherical with a flat (Pl. 3, fig. 1) or a concave base (Pl. 3, fig. 2) to relatively higher than broad, with a conspicuous stalk (Pl. 3, fig. 3; Rhebergen *et al.* 2001, pl. 21, fig. 3a, b). All specimens share a distinctly layered structure, usually with alternation of partly overlapping dense and soft layers. These layers are variable in number and thickness. Layers with many sub-horizontal canals and relatively less spicules in the main skeleton were probably less dense and more liable to erosion (Pl. 3, fig. 4). Few specimens are preserved as porous, yellowish, powdery silicified limestone. In this group, preservation of skeletal details is poor, but the layered frame-work is obvious (Pl. 3, fig. 5).

The aquiferous system is complicated and irregular. Vertical to sub-vertical canals, fed by smaller ones, run from the interior and empty on the summit. Canals use to occur separately, but in a few specimens, they are clustered (Pl. 3, fig. 6). These vertical canals vary in diameter from 0.6 mm to 2.0 mm, most of them having a diameter of 1.4 mm. In RGM 792 324 (Pl. 3, fig. 6), there are more than 30 canals with an average diameter of 1.3 mm.

A second system consists of (sub-)horizontally disposed canals which empty laterally. These canals are concentrated in certain levels, corresponding to less dense layers (Pl. 3, fig. 4). Small canals discharge into larger, tube-like ones (Pl. 3, fig. 7). The diameter of the former is 0.1–0.3 mm, and 0.5–1.6 mm of the latter.

The main skeleton is composed of chiastoclones of relatively equal size. They are connected by zygosis, and clones of adjacent spicules enclose small, probably incurrent canals as seen in Plate 3, figure 8. The longest clones are 0.4 mm, but most clones are 0.30–0.35 mm in length. Where complete chiastoclones could be measured, their length varies from 0.2 to 0.7 mm. Normal length is 0.4–0.5 mm, which is in accordance with the data recorded by Van Kempen (1990). Spicules in the basal part can be measured only with difficulty and vary considerably. Rare, relatively large spicules are up to 0.16 mm long, but most are 0.03–0.08 mm long, on average 0.07 mm. Enclosed small canals are about 0.1 mm in diameter.

Remarks. – As regards their mode of preservation, specimens of *S. ingemariae* differ from other erratic chiastoclonellids. *S. ingemariae* is mostly preserved in dense, often translucent chalcedony, whereas the other chiastoclonellids are usually preserved as a solid powder-like mass, with occasional remnants of chalcedony, and, without exception, with a dense, chalcedonic basal part.

Nearly all examined specimens belong to the brown sponge assemblage; only three specimens can be assigned to the blue sponge assemblage.

S. ingemariae is not extremely rare in the WWW-area (180–200 collected specimens), whereas from Sylt only ten specimens are known, reposited in the Von Hacht collection. The approximately 7,000 erratic brown Ordovician sponges from Gotland examined by the first author yielded only two specimens: one in the collection of Heilwig Leipnitz, Uelzen (Germany) and the other in the collection of Adrian Popp. Compared to the proportion of specimens among the brown sponges of in the WWW-area, this number is surprisingly low. The species is wanting in the major museum collections in Sweden, nor has it been found in the TUG-, GIT- and VSEGEI-collections in Estonia and St. Petersburg.

Stratigraphic age. – The age of *S. ingemariae* could be established on the basis of the alga *Apidium rotundum* Høeg, 1932, which was found to accompany three out of 100 specimens of *S. ingemariae*. *Apidium rotundum* is from the Pirgu Stage (F_{Ic}) (Katian, Upper Ordovician),

Genus *Domospongia* Schlüter, 1887

Type species. – *Domospongia silurica* Schlüter, 1887 pp. 37, 38.

Domospongia silurica Schlüter, 1887

Plate 3, figures 9–11

1887 *Domospongia silurica* Schlüter, n. gen., pp. 37, 38.
1895 *Aulocopium aurantium* Oswald, 1847; Rauff, p. 263 (387), pl. XXI, figs 1, 2.

Material. – A single Upper Ordovician (Katian), erratic specimen from Sadewitz, Poland.

Repository. – Collection Steinmann Institut; Goldfuss-Museum, Bonn; coll. number: StIBP-Schlüter-148.

Diagnosis. – Massive, hemispherical sponge with distinct basal part composed of thin layers; outer surface characterized by stacked, overhanging layers; spongocoel absent; some canals in interior ascending, others radially arranged; skeleton composed of irregularly oriented chiastoclones; chiastoclones in the basal part considerably smaller than in the main skeleton; thin, differentiated dermal layer present.

Description. – Hemispherical sponge body with a concave base, 100 mm in diameter and ca. 50 mm high (Pl. 3, figs 9, 10). In 1885, the specimen was cut axially and a microscopic slide was made. The sponge shows seven concentric, sub-parallel, dome-shaped layers bending more or less horizontally at the margin. Canals have not been preserved due to silicification and dissolution of inner structures. Nevertheless, in some parts indistinctly radiating bluish ‘tubes’ of chalcedony stand out against the brownish matrix. Schlüter (1887, p. 38) observed isolated spicules in the chalcedony, as well as a few spicules connected by zygosis and by little knots, which are the fused tips of clones of adjacent spicules. Chiastoclones can also be observed in weathered distal parts. The spicules are irregular, showing clones of variable length, in accordance with the definition of chiastoclones (see below).

Remarks. – Schlüter collected the specimen before 1885 and described it briefly in 1887. At that time the Silurian System comprised the present Ordovician and Silurian. This accounts for the species name: *silurica.* The sponge is part of an Upper Ordovician assemblage of erratic limestones from the eastern Baltic region, which in older literature is assigned to the Lyckholm stage (e.g. Roemer 1861, p. xiv). Especially the sponge assemblage was thoroughly documented and became well-known among palaeontologists (Oswald 1847; Roemer 1861). Unfortunately, the collections housed in the University of Breslau were largely destroyed during World War II. The specimen described here is one of the few remaining sponges from Sadewitz.

Schlüter recognized some irregular spicules and noted that these differed from the simple clones he knew from other species, like *Aulocopium aurantium* Oswald, 1847. He also found that they resembled tetraclones, spicules he knew well from Mesozoic sponges. In fact, he described chiastoclones, a term which was only introduced by Rauff in 1894. Schlüter announced pictures to be published elsewhere (1887, p. 38), but these could not be traced.

Rauff sought to reduce the number of genera and species in a period most palaeontologists took to endless splitting. Being critical of Schlüter's interpretation of the Sadewitz specimen, Rauff re-assigned it to *Aulocopium aurantium* Oswald, 1847 (Rauff 1895, p. [387] 263). This meant that he reversed the specimen and interpreted it as the lower, basal part of *Aulocopium*, composed of concave concentric layers (Pl. 3, fig. 11) (Rauff 1895, l. 14, figs 1, 2). These concentric layers, which continue in the interior, do not actually fit *Aulocopium*, but Rauff did not attach great importance to this aspect and regarded it as a mere diagenetic phenomenon. Rauff moreover ignored the significance of the unusual spicules he found in the sponge skeleton. In fact, these were chiastoclones which are principally different from the dendroclones in *Aulocopium aurantium* and all other members of the Anthaspidellidae Miller, 1889. It should be noted that the specimen also lacks other features typical of the Anthaspidellidae, such as the pattern of upwardly diverging ladder-like strands and the aquiferous system of converging radial canals emptying into a central gastral spongocoel.

It is obvious that the genera *Domospongia* and *Syltispongia* are closely related and they might in fact be identical. If so, *Syltispongia ingemariae* Van Kempen, 1990 should be regarded as a junior synonym of *Domospongia silurica* Schlüter, 1887.

However, one poorly preserved specimen of *Domospongia* is too slender a basis for assigning 100 specimens of *Syltispongia* with usually, better preserved skeletons to *Domospongia.* Thus, it is preferable to maintain *Syltispongia ingemariae* Van Kempen, 1990 and *Domospongia silurica* Schlüter, 1887 as two closely related but distinct taxa.

Genus *Wilsumispongia* n. gen.

Type species. – *Wilsumispongia cylindrica* n. gen. *et* n. sp.

Included species. – *W. cylindrica* n. sp.; *W. cratera* n. sp. and *W. conica* n. sp.

Derivation of name. – After the village Wilsum, Germany, located in an area with numerous sandpits which have yielded most of the specimens of the genus introduced here.

Diagnosis. – Moderately large sponges varying in shape from cylindrical to sub-hemispherical; dense, basal part with impermeable cortex; upper part containing vertical, sub-horizontal and concentric tubes transecting the sponge body, irregularly branching and converging, emptying laterally and apically, either isolated or in clusters; aquiferous system complicated, composed of tubes usually with a hollow cylinder, the space between the inner wall of the tube and the hollow cylinder filled with a mesh of tiny chiastoclones; monaxons, either isolated or in small bundles, may line the inner walls of tubes, parallel to large chiastoclones forming the outer wall; monaxons also extant along the margin between the inner cylinder and the filling of micro-chiastoclones; main skeleton of large chiastoclones, usually connected by zygosis; canal system in the main skeleton irregular; incurrent canals indistinguishable; dendroclones and rhizoclones rare; skeletal radiante not discerned, but probably located at the base or at the plane separating basal and upper parts.

Remarks. – *Wilsumispongia* n. gen. differs from the late Palaeozoic Neochiastoclonellinae n. sub-family by its main skeleton composed of large chiastoclones with long, thin shafts and by its irregular aquiferous system.

The genus is to be distinguished from *Chiastoclonella* Rauff, 1894, the latter being sub-spherical and marked by a radial structure of canals and indistinct strands of spicules.

It is also markedly different from *Domospongia* Schlüter, 1887 and *Syltispongia* Van Kempen, 1990, which are both composed of conspicuous, sub-parallel, convexly arranged layers.

In *Wilsumispongia*, the occurrence of monaxons forming a kind of tissue along the distal walls of the large tubes and possibly also along the walls of smaller canals, is remarkable. Such monaxons, which should not be confused with the isolated, coring monaxons in ladder-like trabs of dendroclones, have not been reported from other families in the Orchocladina. In the astylospongiid *Carpospongia* Rauff, 1894 isolated or bundled monaxons occur in large excurrent canals of sponges, but their function seems to be defensive against parasites (Johns 1994).

***Wilsumispongia cylindrica* n. sp.**

Plate 4, figures 1–10

Derivation of name. – Named after the common cylindrical appearance.

Holotype. – RGM 792 332, Itterbeck, Germany, Smals sand-pit.

Paratypes. – RGM 792 333-334, RGM 792 336, Wilsum, Germany; RGM 792 335, Kloosterhaar, Netherlands.

Other material. – RGM 792 337-342, RGM 792 344-348, RGM 792 374, RGM 792 389, Wilsum, Germany; RGM 792 343; Itterbeck, Germany, Smals sand-pit.

Diagnosis. – Small to moderately large, high sponge with a well-developed flattened to obconical dense basal part, with a concentrically wrinkled cortical layer, composed predominantly of small chiastoclones; upper part usually cylindrical; top and lateral wall with outlets of large canal-like tubes transecting the sponge body irregularly, both sub-vertically and laterally; tubes bifurcating and converging irregularly; smaller canals merging into them; tubes in cross section ringlike, with an originally hollow inner cylinder surrounded by a mesh of tiny, often concentrically arranged chiastoclones; many hollow inner cylinders diagenetically filled with consolidated mud, visible as central protrusions in hollow surficial outlets; outer wall of tubes composed of large chiastoclones; monaxons isolated or bundle-like, lining outer and inner walls of hollow tubes; main skeleton a loose arrangement of large chiastoclones with relative long, thin shafts, connected by zygosis; incurrent canals and skeletal radiante not distinguished.

Description. – The holotype of *W. cylindrica*, RGM 792 332 (Pl. 4, figs 1, 2), is 52 mm in diameter and 42 mm high. However, the average height measured in ca. 70 specimens is twice the diameter (Pl. 4, fig. 3).

In *W. cylindrica*, the basal part can be clearly distinguished from the upper part. In the holotype, the dense basal part is slightly obconical with irregular horizontal annulations, forming an impermeable cortex. The basal part is composed of a dense skeleton of tiny chiastoclones and probably a few even smaller rhizoclones (Pl. 4, fig. 4). Its thickness varies from a few millimeters to a few centimeters.

The sharp boundary between the basal and the upper part is a more or less horizontal plane, which could be studied in detail in a few damaged or incomplete specimens (Pl. 4, fig. 5).

The upper part consists of a main skeleton of loosely arranged large chiastoclones (see below) and a tangle of irregularly arranged, slightly winding tubes and canals. Some run vertically or sub-vertically, others horizontally or obliquely upward or inward, converging and diverging at random (Pl. 4, fig. 6). Smaller canals empty into larger ones or into tubes which in turn merge or bifurcate (see below). The median wall shows both large and small openings where sub-horizontal canals and tubes empty distally (see below). The vertical tubes end in a number of deep holes at the top (Pl. 4, fig. 7). These tubes are irregularly scattered over the top. They can hardly be regarded as canals, considering their average diameter of 3–4 mm, which appears to be independent of the dimensions of the sponge body. The outer skeletal wall of the tubes is composed of large chiastoclones of the same dimension as in the adjacent main skeleton. Most tubes are filled with a fine structure of powdery casts of tiny chiastoclones. Cross sections show that these fillings are often arranged concentrically (Pl. 4, fig. 8). Natural fractures indicate that most tubes are ring-shaped in cross section. The centres of these tubes consist of cylinders filled with a more solid matrix than the surrounding mesh. As a result, at their outlets, either on the top or in the lateral wall, the fillings form protrusions, conical in shape, 3-10 mm long, about half the diameter of the tubes (Pl. 4, fig. 9). Probably, the central cylinders were originally hollow and their filling is diagenetic.

Two or three inner tubes may merge into a large one. The large tubes formed deep outlets in which organisms settled, such as bryozoans and the alga *Vermiporella fragilis*. This might have already occurred when the sponge was still living, since there are a few instances of algae having been overgrown by their host.

Small canals are hardly discernible. Owing to their bad preservation and chaotic organization, it proved impossible to distinguish between in- and excurrent canal systems in a reliable way.

The main skeleton is composed of large chiastoclones showing zygosis (Pl. 4, fig. 10). The distance between two centres (i.e., the little knobs of fused zygomes) is 0.30–0.38 mm. In some cases, only the length of one of the clones could be measured. The large chiastoclones are found in three diagenetic modifications: (1) As hollow casts in the powdery matrix of intensely weathered specimens; (2) as desmas of greyish-blue chalcedony in the powdery matrix; (3) as hollow casts filled with greyish-white powder in specimens with a matrix consisting of dense greyish-blue chalcedony. In the second and third instances, desmas contrast with the matrix. The tiny chiastoclones in the fillings of the tubes are considerably smaller, approximately 0.10–0.15 mm. They consist of powdery moulds only. The chiastoclones in the dense basal part proved difficult to measure.

Undefined monaxons can sometimes be found aligned with the walls of tubes, running parallel to the large chiastoclones that make up these walls. They are probably the remains of bundle-like tissues which have not been preserved due to selective dissolution. The longest measurable specimens are 1.5 mm. Their diameter is 0.05–0.08 mm.

The skeletal radiante could not be obtained due to the chaotic internal organisation and the absence of distinct growth patterns, but it is believed to lie at the base of the upper part.

Remarks. – The great majority of specimens consist of granular, porous silicifications in which the skeletal desmas are discernible by their different preservation in greyish-blue chalcedony. In this respect, the specimens of *W. cylindrica* differ from most sponges in the other taxa of orchocladinids under consideration.

The age of *W. cylindrica* could be established on the basis of co-occurring fossils. The most frequent species are the algae *Vermiporella fragilis* Stolley, 1893 and *Apidium rotundum* Høeg, 1932. *Rhabdoporella* sp. Stolley, 1893 and *Palaeoporella variabilis* Stolley, 1893 were noticed only once. The latter algal segment shows traces of an epibiont, possibly the bryozoan *Corynotrypa* sp. Bassler, 1911. Other co-occurring fossils include the bryozoan *Chasmatopora* sp. Eichwald, 1855, the tabulates *Paleofavosites* sp. Twenhofel, 1914 and *Catenipora* sp. Lamarck, 1816 and the gastropod *Loxonema* sp. Phillips, 1841. No accompanying ostracods and brachiopods could be identified. One block (RGM 792 348) was found to contain *Aulocopella* sp. Roemer, 1861, a hitherto undescribed sponge species having affinities with the American *Aulocopella dactylos* Rigby & Bayer, 1971. The co-occurrent fossils point to the Katian, in particular to the Pirgu stage.

W. cylindrica shares its dense basal part with streptosolenid genera as *Aulocopella* Rauff, 1894 and *Aulocopium* Oswald, 1847. Often the dense basal part is all what is left of these sponges, and in these instances their identity cannot be established beyond doubt. The vast majority are likely to be remains of *Aulocopium* Oswald, 1847, which is extremely common in the WWW-area, but a small minority may derive from *W. cylindrica*.

***Wilsumispongia cratera* n. sp.**

Plate 5, figures 1–8

Derivation of name. – *Crater* (Latin): referring to the apical and lateral crater-like clusters of excurrent canals.

Holotype. – RGM 792 349, Wilsum, Germany.

Paratypes. – 1, RGM 792 350: Wilsum, Germany; 2, RGM 792 351, Itterbeck, Germany, Jansen sand-pit; 3, RGM 792 352, Zwolle, Netherlands, Haerst sand-pit; other paratypes: RGM 792 353-354, Wilsum, Germany.

Other material. – RGM 792 355-357, RGM 792 359-362, RGM 792 371, Wilsum, Germany; RGM 792 358, Zwolle, Netherlands, Haerst sand-pit.

Diagnosis. – Moderately large, conical sponge, with greatest diameter at the base; flat basal part consisting of dense, thin, parallel layers and gradually sloping sides; apical part usually with a crater-like hollow into which a cluster of tube-like canals empty; similar clusters occurring laterally between smaller canals; clusters emptying more or less perpendicular to the lateral surface; sharp transition between dense basal and upper part; small canals rising from just above the basal part, merging rapidly to form tubes that run irregularly sub-vertically and obliquely upward towards one of the clusters; tubes with a hollow inner cylinder, the space between the inner walls of tubes and the central cylinder filled with a mesh of fine chiastoclones; outer wall of tubes formed by large chiastoclones; inner side of walls covered with tissue of aligned monaxons; main skeleton composed of large, loosely arranged chiastoclones; rhizoclones and dendroclones subsidiary, mainly present in the basal part; skeletal radiante and system of incurrent canals not observed.

Description. – The holotype of *W. cratera*, RGM 792 349, is a regularly conical sponge, 72 × 61 mm in diameter and 40 mm high (Pl. 5, figs 1, 2). The slightly eroded sponge body has a shallow apical crater and laterally numerous tube-like canals converging to the apex. Sub-circular outlets on the sides are part of a sub-horizontally to upward oriented system of smaller canals. Remains of the dense basal part are visible, as in most of the other specimens. In the basis of the holotype, there is a conspicuous, 60 mm long, 13 mm wide and 5 mm deep cylinder-like cast of a cephalopod (Pl. 5, fig. 2).

Most specimens of *W. cratera* are rather flat-based, conical sponges with the largest diameter at or near the base. A typical feature is the top with its crater-like cluster of holes where tubes rising from the interior end. Paratype 1 shows the crater-like apex into which vertical and obliquely converging canals empty (Pl. 5, fig. 3). Similar clusters of excurrent tubes can be seen on the slanting sides, as shown in Paratype 2 (Pl. 5, fig. 4).

The average diameter at the base is twice the height, as measured in over 50 specimens. In the highest specimens the height-diameter rate is about 1:1.3, in the flattest complete specimens about 1:3. The size of the largest specimen is 93 × 83 mm in diameter and 43 mm in height.

The flat basal part is usually only a few millimeters thick. It may consist of a single layer, but more often it is built of a number of thin, sheet-like layers (Pl. 5, fig. 5). The basal part is composed of very small, densely packed chiastoclones and, possibly, a few rhizoclones. Several specimens have a dense, impermeable cortex. Canals are not detectable. The transition from the basal part to the upper part is always abrupt. It proved impossible to obtain a skeletal radiante.

The diameter of the tubes at the top and at the sides is 2–5 mm. Most tubes are filled with fine, sometimes concentrically arranged, tissue of what seem to be small chiastoclones. The large chiastoclones forming the wall of the tubes are lined on the inside by monaxons, which occur either isolated or in small bundles. The diameter of monaxons is rather constant at 0.03–0.04 mm. It proved impossible to measure their length. A few smaller canals, feeding the tubes and without elaborate fillings, are detectable. There are two systems of tubes, which may be linked internally. One is converging from the base and the sides to the cluster at the top, the other is diverging from the base to one of the lateral clusters. Thus, the aquiferous system forms a jumble of merging and dividing, irregularly winding tubes. One specimen shows a number of horizontal canals just above the transition from the basal to the upper part of the sponge body (Pl. 5, fig. 6). Apparently, these canals do not arise from the basal part. As they converge to form the lower end of a tube, they are to be considered excurrent canals. Observations like this one could not often be made; due to diagenetical processes, sponge bodies have usually been preserved as powdery matter.

The sponge contains chiastoclones of three different sizes: (1) The main skeleton consists of large chiastoclones, 0.30–0.38 mm long. (Pl. 5, fig. 7). Desmas are interconnected by zygosis. They also form loosely constructed walls of tubes. The diameter of the clones of the chiastoclones in the main skeleton is 0.05–0.07 mm; (2) The dense lower basal part is formed by smaller chiastoclones and, probably, subsidiary rhizoclones; (3) The smallest chiastoclones make up the fillings of the tubes. They have only been found as powdery moulds in a usually concentric arrangement, suggesting a skeletal function. This is in accordance with the structure of the tubes, which in cross section is ring-like.

A few interconnected dendroclones in translucent chalcedony could be observed, but these strands are only a few millimeters long.

The skeletal radiante is probably located at the base of the upper part, just above the dense basal part.

Remarks. – Paratype 3 is a small, incomplete, regularly conical, dark-grey to black sponge with a distinct crater-like apex (Pl. 5, fig. 8). It is the only blue specimen and in the hollow tubes it exhibits remains of kaolinite and grains of quartz, both deriving from eroded Baltoscandian cristalline rock and typical of the blue assemblage. The cross section of the natural fracture shows light-grey fillings of tubes. More densely silicified cylinders represent inner tubes (see above). The densely silicified matrix shows a skeleton consisting of a mesh of tiny, white chiastoclones. Distally located chiastoclones are considerably larger.

W. cratera differs from *W. cylindrica* in three respects. The first difference concerns body shape. *W. cylindrica* as a rule grows in a vertical direction, thus building a predominantly vertically oriented aquiferous system. *W. cratera*, on the other hand, grows by forming a wide basal surface on which it builds a conus-like body with converging sides. Hence, *W. cratera* has a diameter-height ratio different from that of *W. cylindrica*. Second, in *W. cratera*, the basal part is not as thick as in

W. cylindrica; it is sheet-like and usually only a few millimeters thick. Finally, unlike *W. cylindrica*, the sides of *W. cratera* show various clusters of excurrent, discharging tubes. Transitional forms between the two species are extremely rare.

Compared with *W. cylindrica,* co-occurrent fossils are relatively rare, but algae, unidentified bryozoans and crinoids occur. Fragments of monaxons on the base, sides and top are allochtonous, washed-in spicules.

Stratigraphic age. – *W. cratera* is Late Ordovician (Katian). The presence of the algae *Apidium rotundum* and *Vermiporella fragilis* point to the Pirgu Stage (F_{Ic}).

***Wilsumispongia conica* n. sp.**

Plate 6, figures 1–6

Derivation of name. – *Conica* (Latin): referring to the conical form of the sponge body.

Holotype. – RGM 792 363, Wilsum, Netherlands.

Paratypes. – RGM 792 364-365, RGM 792 368, RGM 792 372, Wilsum, Netherlands.

Other material. – RGM 792 366-367, Wilsum, Netherlands; RGM 792 398-399, RGM 133 2212, Braderup, Sylt, Germany.

Diagnosis. – Conical, in cross section sub-triangular sponge; basal part poorly developed, flat, layered, with an impermeable dermal layer composed of tiny chiastoclones; sides rising upward from the base at angles varying from 45° to 70°, forming a cone with a small cluster of excurrent canals at the apex; tube-like canals running sub-parallel to the lateral surface, emptying into the apical cluster; smaller canals diverging from the base upward and outward to meet the lateral surface at angles between 70° and 90°; main skeleton formed by chiastoclones interconnected by zygosis; chiastoclones with elongated clones and rare dendroclones forming strands, often supported by bundles of monaxons; strands diverging parallel to the canal system; skeletal radiante either in the centre of the base or in the centre of the sponge body.

Description. – The holotype, RGM 792 363, has a flat, sub-circular base (Pl. 6, figs 1, 2). It measures 62 × 68 mm in diameter and 35 mm in height. The form of the sponge body is triangular in cross section (Pl. 6, fig. 2). The aquiferous system comprises three types of canals at least. The largest ones run sub-parallel to the lateral surface and empty into the apical cluster. Smaller canals fan out from the centre of the base, diverging upward and outward to meet the lateral surface at angles between 70° and 90°. These canals are interconnected by poorly developed skeletal strands (see below). The smallest canals are surrounded by connected chiastoclones and rhizoclones. Their average diameter is 0.14 mm. The cross section of RGM 792 372 (Pl. 6, fig. 3) shows the canal system consisting of small canals which rise from above the dense basal part to converge into wider canals, which in turn empty into the largest ones.

The conical body form is found in all specimens of *W. conica*. Cross sections show a regular triangle with sides between 45° to 70° at angle with the flat base (Pl. 6, figs 2–4). All specimens have a tiny apical cluster of excurrent canals. Along the lateral surfaces, irregularly winding canals converge at the top but lateral clusters as found in *W. cratera* are absent. Plate 6, figure 4 shows the median section of RGM 792 364, with the most pronounced canals being preserved as powdery fillings parallel to the lateral surface.

In specimens RGM 792 363-364, the skeleton of chiastoclones is excellently preserved. Chiastoclones are 0.3–0.6 mm in length, averaging 0.4 mm, and their average diameter is 0.1 mm. Most chiastoclones are arranged in strands, in which one clone is longer than the other clones. The elongated clones are always oriented in the same direction, rising upward and outward from a point in the centre of the base of the sponge. The strands of chiastoclones are often accompanied by bundles of very thin monaxons, measuring 0.03–0.04 mm in diameter (Pl. 6, fig. 5). They appear as isolated bundles in which monaxons are densely packed, only slightly separated from each other. The main direction of strands and monaxons is more or less perpendicular to the outer surface. Short, diverging, ladder-like strands of dendroclones or dendroclone-like spicules also appear in both specimens.

The main canals and skeleton, diverging from the middle of the base to the lateral sides, indicate that the skeletal radiante is located just above the upper basal part.

Remarks. – In *W. conica*, monaxons form invididual bundles between ladder-like strands of chiastoclones and rare, short strands of dendroclones. They are to be distinguished from so-called coring monaxons, i.e. bundles monaxons interwoven with the zygomes of ladder-like, vertically stacked strands of dendroclones, as in the anthaspidellids and streptosolenids.

Bundles of monaxons like those in *W. conica* have not been observed in the usually powdery specimens of *W. cratera*. *W. conica* also differs from *W. cratera* in internal organization. Whereas *W. conica* has a more or less regular structure of canals and strands fanning out from a skeletal radiante which is usually located just above the basal part, the general structure of the canal system in *W. cratera* is irregular, with one apical, crater-like cluster and several lateral clusters of excurrent canals.

Even greater are the differences with *W. cylindrica* with its predominantly vertically oriented canals. On the basis of the present material, *W. conica* seems to be more closely related to *W. cratera* than to *W. cylindrica.* At any event, the mutual differences between *Wilsumispongia cylindrica*, *W. cratera* and *W. conica* are too profound to be ascribed to environmental conditions.

A few more specimens of *W. conica* are worthy of note. In two blue specimens from the Von Hacht collection, RGM 792 398 and RGM 792 399, no lateral outlets of separate or cluster-like canals can be detected. RGM 792 399 is the smallest specimen recognized so far. On the surface, about ten canals can be seen to run toward the apical crater. The open canal walls show a network of chiastoclones. In RGM 792 365, one of the tube-like canals contains pellets, similar to the fecal pellets known as *Coprulus* Mayer, 1952 (Pl. 6, fig. 6). Most are 0.8 mm long and 0.4 mm in diameter. A few broken specimens show a small central hollow. The sponge body shows the remnants of desintegrated desmas. The predominance of rhizoclones is remarkable. Apparently, the sponge body desintegrated on the seafloor before being covered with sediment, which is in keeping with the slow sedimentation rate assumed for the Baltic shelf sea.

Apart from *Coprulus*, no co-occurrent fossils have been observed. Given the appearance of *W. conica*, it is beyond doubt that the brown specimens are to be associated with the Brown Pirgu Chert. The scarce blue specimens may be coeval and in that case are to be associated with Lavenderblue Pirgu/Porkuni Chert.

Genus *Chiastodiscus* n. gen.

Type species. – *Chiastodiscus verrucosus* n. sp.

Derivation of name. – Combination of *chiasto* and *discus*, in which *chiasto* alludes to the chiastoclone as the dominant spicule and *discus* to the form of the sponge body.

Following genera and species are here assigned to *Chiastodiscus* n. gen.

1859 (?) *Scyphia reticulum* Eichwald, 1859, (1), p. 327, pl. 22, fig. 1a, b.
1859 *Cnemidium radiatum* Eichwald, 1860 (1), p. 340, pl. 22, fig. 4 a, b.
1861 *Aulocopium discus* Roemer, 1861, p. 8, pl. 3, fig. 1a, b.
1895 *Aulocopium aurantium* Roemer, 1861; Rauff 1895, p. 381, pl. 19, fig. 1.
1930 *Aulocopium* cf. *A. aurantium* Oswald, 1847; Öpik 1930, p. 5.
1931 *Aulocopium aurantium* Oswald, 1847; Asatkin 1931, p. 1215.
1949 *Aulocopium aurantium* Oswald, 1847; Asatkin 1949, p. 69.
1970 *Aulocopium aurantium* Oswald, 1847; Rõõmusoks 1970, p. 218, p. 242.
1970 *Aulocopella cepa* Rauff, 1895; Rõõmusoks 1970, p. 218, p. 242.
2009 *Aulocopium discus* Roemer, 1861; Rhebergen 2009, p. 32.
2012 *Aulocopium discus*, Roemer, 1861; Rhebergen 2012, pp. 6–10.
2012 *Aulocopella cepa* Rauff, 1895; Rhebergen 2012, p. 10.

Diagnosis. – Small to large, flat sponge, 46–175 mm wide and 20–40 mm high; central spongocoel absent; dense basal part poorly developed or absent; thick, sub-circular tubes forming part of the excurrent system, radiating from the centre towards the distal margin, gradually widening and terminating in hollow tubercles; tiny parallel canals emptying into tubercles; second system of sub-vertically arranged tubes, anastomising irregularly throughout the sponge body, emptying into the upper surface; small radial canals, belonging to the incurrent system, rising from the skeletal radiante at or just below the centre of the sponge body; main skeleton and walls of tubes and canals predominantly composed of chiastoclones; spicules often organized in long regular series, supported by isolated or bundle-like monaxons; rhizoclones and dendroclones scarce.

Remarks. – The oldest reports of Ordovician sponges of Baltic provenance are by Eichwald (1840) and Roemer (1861), who introduced *Aulocopium discus*, based on three large, flat specimens as glacial erratics from Sadewitz. Rauff (1895, p. 257) re-assigned these specimens, which were lost during WW II, to *Aulocopium aurantium* Oswald, 1847, together with a similar specimen from bedrock near Kukruse, Estonia (Rauff 1895, p. 257). Öpik (1930, p. 5) mentioned an abundant occurrence ('massenhaftes Vorkommen') of *Aulocopium* in the Aluvere Quarry near Kunda and assigned it to the D_I-stage. Asatkin (1949, table 1, fig. 3) depicted a sponge, which he identified as *Aulocopium aurantium* Oswald, 1847. This specimen could not be studied since it, too, has been lost. In his fauna lists covering Estonian strata of Haljala to Keila age, Rõõmusoks (1970) mentioned *Aulocopium aurantium* Oswald, 1847 and *Aulocopella cepa* (Roemer, 1861) Rauff, 1894.

In 2008 Rhebergen, i.e. the first author, made a brief inventory of the sponges in the museum collections in Tallinn and Tartu. He found disc-shaped sponges, which he at first assigned, like Rõõmusoks, to *Aulocopella* sp., merely on account of the position of their skeletal radiante (Rhebergen 2009). Then he recognized similar disc-shaped sponges in private and museum collections in the Netherlands, as well as in the Von Hacht collection from Sylt. In most collections these entirely silicified, erratic sponges are labelled as specimens of *Aulocopium*.

Upon examining the disc-shaped Estonian sponges and the erratic specimens more closely, Rhebergen found that both groups complemented each other in revealing different anatomical details. The non-eroded Estonian specimens show surficial details, but, being calcified or dolomitized, few, if any, skeletal details. The silicified erratics from the Netherlands and Germany, for their part, often have well-preserved skeletal structures but exhibit few or unclear surficial details. A few erratic Dutch-German sponges show remains of a poorly developed dense basal layer, a feature rarely observed in Estonian and Russian specimens. These observations led Rhebergen to erect a new genus, dubbed *Chiastodiscus*, for the disc-shaped sponges under consideration, since they cannot be assigned to *Aulocopium* or *Aulocopella*. A few specimens of *Aulocopium* and *Aulocopella* (i.e. *A. cepa* and *A. hemisphaericum*) are depicted here to show that their skeletal organisation and canal system are fundamentally different from that of *Chiastodiscus* (Fig. 10A-D).

Both *Aulocopium* and *Aulocopella* use to have a well-developed, dense basal layer and a deep spongocoel, often extending to the base. The skeleton is principally composed of dendroclones, arranged in a typically anthaspidellid manner, as pinnately organized ladder-like trabs rising from the base, bending upward and outward to the lateral surface, or bending inward to the gastral surface, thus forming a plane of pinnation; excurrent radial canals bend inward to empty into the gastral wall of a deep spongocoel (Fig. 10A, B). This description, however, does not fit the specimens which are assigned here to *Chiastodiscus*. In *Chiastodiscus* there is neither a

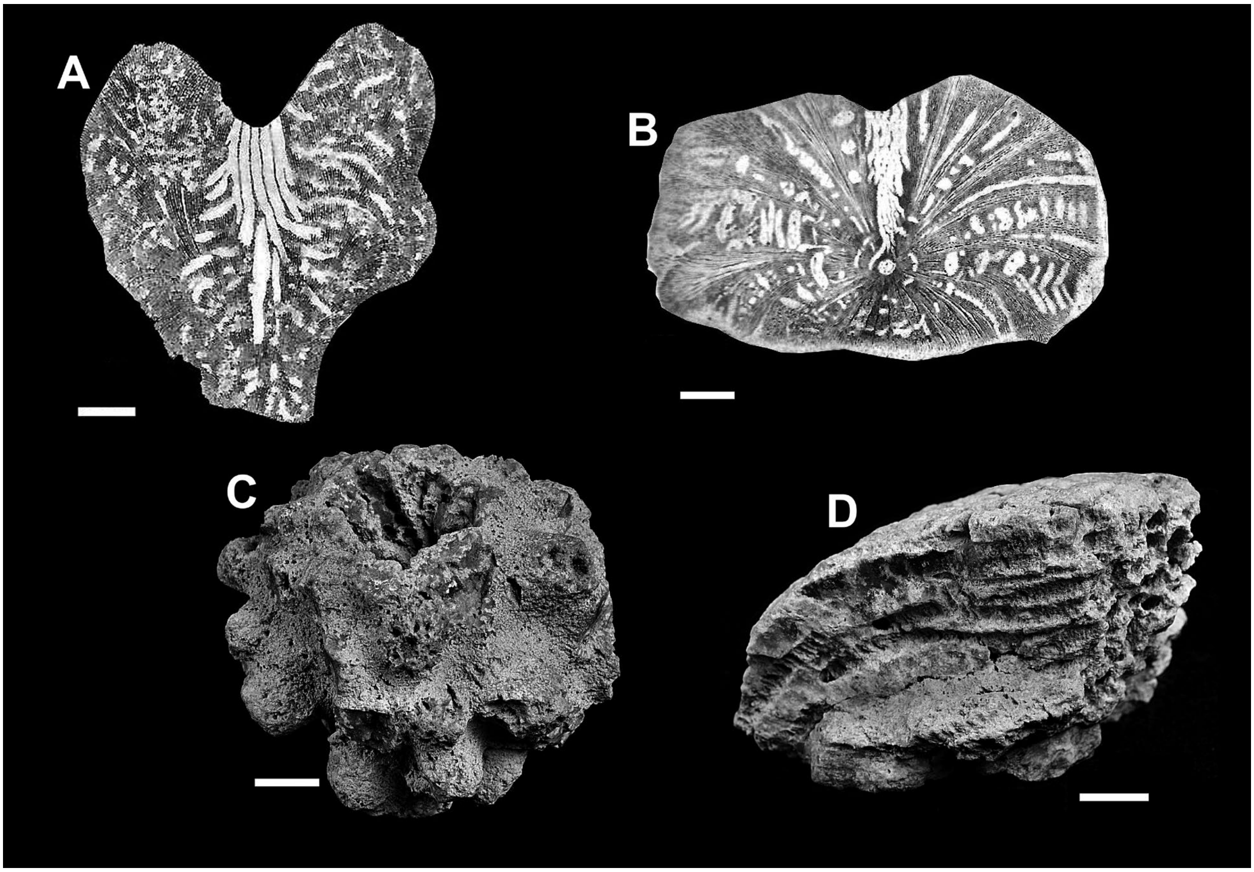


Fig. 10. Examples of *Aulocopium* and *Aulocopella*. **A**. *Aulocopium* sp. Rauff, 1895. Drawing of axial section of *Aulocopium* sp. *in* Rauff 1895 (plate XXII, fig. 6). **B**. *Aulocopella cepa* Rauff, 1895. Drawing of axial section of in Rauff 1895 (plate XXII, fig. 7). **C**. *Aulocopella cepa* Rauff, 1895. Oblique top view; RGM 133 2213. **D**. *Aulocopella hemisphaericum* Roemer, 1861. Fragment, showing concentrically arranged canals emptying in the spongocoel on the right; RGM 332 2220. Scalebar is 1 cm.

deep gastral spongocoel nor a plane of pinnation. The arrangement of excurrent canals, quite regular in *Aulocopium* and *Aulocopella*, is chaotic in *Chiastodiscus*. Whereas in *Aulocopium* the skeletal radiante is situated at the base, it lies at the centre or just below it in *Chiastodiscus*. Unlike *Aulocopium*, *Chiastodiscus* has an arrangement of indistinct strands of chiastoclones supported by monaxons. Furthermore, in *Aulocopium* and *Aulocopella* the excurrent canals converge to empty into the gastral spongocoel, whereas in *Chiastodiscus* they diverge to empty into the lateral or upper surface.

A notable difference between erratic specimens of *Chiastodiscus* and erratic specimens of Anthaspidellidae and Streptosolenidae concerns the presence of remains of the substrate on which the sponges lived. In the former, environmental debris of the seafloor has usually been preserved, especially in the interspace between the irregularly winding tubes (see below); in the latter, remains of the substrate are rare.

Chiastodiscus arose in the Sandbian, but in all likelihood *Aulocopium* and *Aulocopella* did not make their appearance until the Katian. Whereas in the erratic assemblages of Pirgu age of Gotland, Germany and the Netherlands *Aulocopium aurantium* Oswald, 1847 is the predominant species (Rhebergen *et al.* 2001), the presence of *Aulocopium* and *Aulocopella* in Estonian and West Russian bedrock has so far not been demonstrated.

***Chiastodiscus verrucosus* n. sp.**

Plate 7, figures 1-8

Derivation of name. – *Verruca* (Latin): 'small wart'; *verrucosus* (Latin): 'full of warts', referring to the wart-like ends of radiating tube-like canals on the upper surface and sides.

Holotype. – GIT 413-11, Saxby shore, Vormsi, Estonia.

Paratypes. – 1, GIT 399-987, 2, GIT 399-1689, 7, TUG 1306-32, Aluvere Quarry, Estonia; 3, TUG 1306-25, Alliku, Estonia; 4, TUG 1589-189, Ristna, Estonia; 6, TUG 860-1371 Anija, Estonia; 5, GIT 413-10, locality unknown, Estonia.

Other material. – TUG 1306-26, Alliku, Estonia; TUG 76-83, Aluvere quarry, Estonia; TUG 80-453, Suurejöe, Estonia; GIT 413-47, Ülemiste borehole (17.92-18.02 m), Estonia; NMB PO 203, Kukruse ('o Jewe' according to label by Dames, 1876), Estonia; TUG 1306-19, Söjamäe paljand, Estonia.

Diagnosis. – Moderately large to large disc-shaped sponge with a flat or concave base; diameter 100–160 mm (average 113 mm), average height 44 mm (at distal margins); basal cortex absent or poorly developed; upper surface concave or nearly flat to slightly convex; apical concave space may be filled with dense, skeletal 'tissue' of disordered chiastoclones; minimal thickness usually in the centre; spongocoel and gastral wall with accompanying system of converging canals absent; tube-like canals radiating from the centre upward and outward to meet the distal surface; sides usually provided with large, vertically stacked tubercle-like protrusions, being the distal ends of the radiating tube-like canals, of which the diameter increases distally; smaller canals, rising in the sponge body, emptying into the tube-like canals; irregularly winding canals run sub-vertically to the upper surface or empty into the radiating canals; main skeleton composed of chiastoclones fused by zygosis; indistinct strands radiating from the skeletal radiante near the centre into all directions, meeting the distal surface perpendicularly or at acute angles, probably enclosing numerous incurrent canals; skeletal strands mainly composed of chiastoclones with one or two elongated clones, supported by paralleling monaxons, occasionally by dendroclones and rhizoclones.

Description. – The holotype of *Chiastodiscus verrucosus* is sub-circular, 110 mm in diameter and 40 mm high (Pl. 7, fig. 1). The central part of the upper surface, 45 mm in diameter, is slightly convex, composed of probably small chiastoclones. The distal margin, about 35 mm wide, consists of a wreath of radially arranged, circular or oblong wart-like tubercles which increase in size toward the lateral margin. Most tubercles show a circular or oblong opening of an excurrent canal at the top and some of them also show tiny canals at their flanks. The base is covered by marl. Paratype 1 shows that the sharp boundary between the apical ring and the upper central part continues in the sponge body itself without breaking the continuity of the skeletal structure and the course of canals (Pl. 7, figs 2, 3).

The paratypes are large, discus-like sponges, with flat or concave upper surfaces and bases. The largest specimen, NMB PO 203, preserved as cast (Pl. 7, fig. 4), is 160 mm in diameter, 60 mm high and ca. 35 mm thick in the centre. Measurements of 30 specimens from Estonian strata produced an average diameter of 113 mm and an average height of 44 mm at the distal margins and of 28 mm in the centre. The ratio between diameter, distal height and thickness is about 4 : 2.5 : 1 in the centre. In various specimens, the upper surface is flat to slightly convex, with the same filling of unstructured skeletal material as in the holotype. In a few specimens, the central part of the upper surface is covered by matrix and debris. Other specimens have a concave upper surface, with a pattern of diverging tubes and fanning bundles of skeletal structures exposed (Pl. 7, figs 4–6). In TUG 1306-25 and NMB PO 203 a small circle in the centre indicates the skeletal radiante (Pl. 7, figs 4, 5). There is no spongocoel. The tubes terminate in conspicuous, randomly stacked knobs at the distal margins. Axial sections also reveal the presence of sub-vertical canals and canals diverging from the skeletal radiante (Pl. 7, figs 3, 7).

The base is usually concave, which causes the central part of the sponge to be rather thin. *C. verrucosus* differs from other genera of the sub-family in having a base without dense cortical layer. The base rather shows the same pattern of radially diverging tubes, terminal knobs and tubercles that is seen in the upper surface.

The aquiferous system is complicated and its details are not well understood. Most prominent are the radiating, irregular, slightly winding tubes. They are 3–5 mm in diameter with walls composed of large chiastoclones (see below) and they cross the sponge body from the centre to the distal wall. The tubes appear to be composed of several sub-parallel canals. Where the diameter of tubes increases, new canals are intercalated. In a few specimens, the arrangement of bifurcations and intercalations is visible on the surface, e.g. in NMB PO 203 and TUG 1306-26 (Pl. 7, figs 4, 6). In the skeletal strands forming the walls of the canals chiastoclones are exposed.

The rounded distal margins of *C. verrucosus* are tuberculate in appearance. The circular or oblong tubercles appear to be complicated terminations, with small, parallel canals running along the steep sides of the tubercles and emptying at their tops. The average dimensions of 30 terminate tubercles in two specimens, TUG 860-1371 (not depicted) and GIT 399-1689 (Pl. 7, fig. 8), are: 6 mm wide, 9.5 mm long and 2 mm high. In fact, these structures, by which the surface is considerably enlarged, are to be regarded as mini-sponges. In several specimens, tubes and tubercles occur both on the upper surface and at distal regions of the basal surface.

A second system consists of the irregularly winding, sub-vertically arranged canals, 1-3 mm in diameter. Although they could not be studied in detail, they do not seem to be related to the radiating tubes described above. From median sections it appears that they had a hollow central axis, which is now filled with dense calcite or quarz cristals. These canals occur on both upper and basal surfaces, sometimes in regularly arranged rows, 3–5 mm apart from each other, with a diameter of about 2.4 mm.

The skeleton consists of chiastoclones which, due to their irregular shape, do not show the strict, ladder-like organization, known from the dendroclones in the Anthaspidellidae (see below). Clones of adjacent spicules are firmly connected by zygosis, forming little knots. The vast majority of spicules inside the Estonian specimens are calcified and few, if any, can be distinguished. Spicules can more frequently be recognized on weathered surfaces, especially when they are pyritized.

The skeletal radiante is situated at, above or below the centre of the sponge body, occasionally near the base. From this point, indistinct strands of spicules run into all directions, initially straight, fanning out near the distal surface, which they meet at about right angles.

There is a third, undefined system of radiating canals running parallel to these indistinct skeletal strands. These canals may have had long, hollow axial centres. As yet, it cannot be established whether they were part of the incurrent or the excurrent system. No monaxons could be observed.

Remarks. – The tuberculate surface of the sponge, especially at its margins, combined with the skeletal radiante inside the sponge body, explains why palaeontologists mistook it for *Aulocopella* sp. or *A. cepa* (see above; Fig. 10B, C).

Specimen NMB PO 203 (Pl. 7, fig. 4) commands special attention because of its history and re-assignment. According to its label, it originates from the Haljala stage (Jöhvi substage) near Kukruse (Estonia) and was legated by Dames to the Museum für Naturkunde in Berlin in 1876. Rauff (1895, p. 261; Pl. XIX, Fig. 1) assigned it to *Aulocopium aurantium* Oswald, 1847. He took it to be the basal part of *Aulocopium*. In his view, canals and skeletal strands converge to a deep circular centre, which he interpreted as the lower part of the central spongocoel. He admitted that the skeleton did not show any strands of dendroclones. Rauff did not mention that the specimen also lacked the ‘wrinkled cortical layer’ that he had observed in erratic specimens of *Aulocopium* from other localities. The fact that he had only one specimen at his disposal may explain his failure to recognize it as a representative of a new sponge.

Stratigraphic age. – The holotype derives from the Vormsi Stage (Katian); the paratypes are recorded from strata assigned to the Haljala Baltic Stage (Sandbian).

***Chiastodiscus regularis* n. sp.**

Plate 8, figures 1–11

Derivation of name. – The name refers to the regular arrangement of radiating tubes.

Holotype. – GIT 413-71, Ojamaa River outcrops, Estonia (coordinates N 59° 08' – E 27° 08'), Haljala Stage, Idavere Substage (C_{III}). Reposited in the collection of the Institute of Geology of the Technical University Tallinn.

Paratypes. – RGM 792 375, Itterbeck, Netherlands; GBE 4118, Kas'kovo quarry, Nizkovitsky village, St. Petersburg region, Russia; RGM 792 376, Markelo, Netherlands; RGM 792 377, Sylt, Germany.

Other material. – GBE 4094, Paritsy village, St. Petersburg region, Russia; RGM 792 378, RGM 792 381, Sylt, Germany; RGM 792 379-380, RGM 792 382, RGM 792 387-388, Wilsum, Germany; RGM 792, RGM 792 385-386, RGM 133 2216 Zwolle, Netherlands, Haerst sandpit; NRM Sp10832, Lickershamn, Gotland, Sweden; RGM 792 384, Spitham, Estonia.

Diagnosis. – Disc-shaped sponges of moderate size with dense basal layer; exterior smoothly hemispherical; top slightly convex with small apical dip but without central spongocoel and gastral wall; canals vertically stacked parallel to the upper surface, distributed sub-regularly, terminating in small tubercles distally; skeletal radiante at or just below the centre of the sponge body; small skeletal strands diverging from the skeletal radiante into all directions, distally curving to meet the exterior perpendicularly; skeleton composed of chiastoclones, with isolated or small bundles of monaxons and few dendroclones and rhizoclones; dendroclones prone to form series of short ladder-like strands; chiastoclones arranged in strands by parallel elongated clones, often supported by parallel monaxons; basal cortex present, probably composed of small chiastoclones and rhizoclones.

Description. – *Chiastodiscus regularis* n. sp. is a macaroon-shaped sponge with a slightly convex upper surface and a thin, impermeable basal cortex. The holotype is 82 mm in diameter and 35 mm high (Pl. 8, fig. 1). Other specimens are 40-110 mm in diameter and 20-50 mm in height, usually in a rate of 2.5 : 1. Numerous vertically stacked tube-like canals radiate from the apical centre toward the sides in a regular arrangement (Pl. 8, figs 2-4). Although there is a shallow apical depression, only a few millimeters deep, a central spongocoel and a central gastral wall are absent. In cross sections the skeletal radiante appears to be situated in or near the centre of the sponge body (Pl. 8, figs 5, 6) respectively.

In the interior, indistinct strands of spicules radiate into all directions, initially straight, but distally curving upward or downward to meet the distal wall perpendicularly or at angles of 70°-80°. These strands enclose small canals, here interpreted as incurrent canals. Canals could not be measured accurately, neither in the calcified specimens from Estonian bedrock nor in silicified erratic ones. A few irregular, slightly sinuous canals rise from the base to meet the upper surface perpendicularly (Pl. 8, fig. 7).

The diameter of the radiating tube-like canals is 2–3 mm near the centre, increasing to 4–8 mm at their distal ends. In the distal wall, the ends of canals often appear as protruding tubercles, 5–10 mm in diameter. The pattern of radiating tube-like canals is most conspicuous in some erratic blue specimens, due to partial erosion of the skeleton between the more resistant tubes (Pl. 8, figs 3, 4, 8). These specimens also show remains of small canals emptying laterally into the tube-like canals.

The skeleton is composed of chiastoclones measuring 0.15–0.30 mm. Chiastoclones in the canal walls are smaller. The radiating strands were probably supported by isolated or bundle-like monaxons running parellel to the elongated clones of chiastoclones. The basal layer is composed of tiny, densely packed chiastoclones and rhizoclones, possibly with a few dendroclones. It could be studied in a few specimens only because in most specimens chalcedony has erased all traces of spiculae in the basal layer.

Remarks. – Among the erratic specimens, those from the blue sponge assemblage show a peculiar state of preservation. Whereas in these specimens of almost black chalcedony many anatomical details have been erased due to diagenesis and weathering, the system of vertically stacked tubes and the overall internal structure has survived relatively well (Pl. 8, figs 2–4).

Belonging to the oldest erratic Ordovician sponges known to date, these specimens are coeval with Haljala sponges from Aluvere Quarry and the Ojamaa River in Estonia as well as sponges from the Shundorovo Formation (as exposed in Kas'kovo quarry in the western St. Petersburg region; Iskyul pers. comm. 2017; Iskyul & Fedkovets 2008). A comparison of endemic and erratic specimens of *C. regularis* shows that body shape and canal system are quite similar. Thus, compare GIT 413-71 from Ojamaa river (Pl. 8, fig. 1); GBE 4118 from Nizkovitsky village (Pl. 8, fig. 10); RGM 792 377 from Sylt (Pl. 8, fig. 2); RGM 792 383 from Haerst

(Pl. 8, fig. 11). The similarity supports the assumption, previously advanced by the first author (Rhebergen 2009), that there are points of contact between the erratic blue sponge assemblage and Asatkin's 'C_{IV} sponge layers' (Asatkin 1931, 1949).

C. regularis differs from *C. verrucosus* in its overall body form and aquiferous system. The dense basal layer of a few millimeters thickness in *C. regularis* has no counterpart in *C. verrucosus*. The upper side of *C. regularis* is convex, contrary to the usually concave or occasionally flat upper side in *C. verrucosus*. In *C. regularis*, outwardly radiating tube-like canals are more regularly arranged and terminating tubercles are less conspicuous than in *C. verrucosus*.

Stratigraphic age. – *C. regularis* is of Haljala-Keila age, because of the presence of *Coelosphaeridium sphaericum* (Kjerulf, 1865) in matrix attached to RGM 792 376 (Pl. 8, fig. 9) and RGM 133 2216.

Genus *Diotricheum* Van Kempen, 1989

Diotricheum vonhachti Van Kempen, 1989

Plate 9, figures 1–9

Material. – RGM 792 313, RGM 792 319, Itterbeck, Netherlands, Smals sand-pit; RGM 792 314-317, RGM 792 320, Wilsum, Germany; RGM 792 318, Westerhaar, Netherlands, De Boer sand-pit.

Emended diagnosis. – Medium-sized, thick-walled, obconical sponge with narrow, pointed base; upper part probably sub-hemispherical; lateral walls smooth, dense, and differentiated from inner skeleton, marked with upwardly fanning folds or ribs and rhythmic, concentric growth increments; spongocoel moderately deep and narrow; sub-horizontal, radial canals merging into clustered, vertical, axial exhalant canals; irregularly disposed ostia on summit from upwardly divergent, more peripherally disposed, inhalant canals which originate near the base; system of axial and radial canals separated from the more peripheral, diverging inhalant canals; irregular skeleton of predominantly chiastoclones; monaxons, rhizoclones and dendroclones also present; dendroclones occasionally stacked, forming short ladder-like strands (from emendation by Finks & Rigby 2004).

Remarks. – Van Kempen (1989) introduced *Diotricheum vonhachti* to include orchocladinid sponges of the Late Ordovician, known exclusively as erratics from Neogene glacio-fluvial deposits of Sylt. His material comprised about 50 specimens in the Von Hacht collection, now in the AfG. Of these, 29 selected specimens are reposited as type-material in the collections of the GPIMH. All of these sponges belong to the blue sponge assemblage. A typical example, although from the WWW-area, is shown in Plate 9, figure 1. Unfortunately, skeletons are usually poorly preserved due to diagenetical processes as silicification, oxydation and the forming of spherules of chalcedony in cavities, resulting from dissolution of the matrix. Nevertheless, Van Kempen succeeded in giving sound descriptions and drawings, which effectively substantiate his view that these sponges represent a new taxon distinct from the known Anthaspidellids.

However, ever since Van Kempen's study, new material with better-preserved skeletons and details in the aquiferous system has been found in the erratic brown sponge assemblage of the WWW-area. This material challenges Van Kempen's views regarding the taxonomical position of *Diotricheum*. RGM 792 314 may serve as an illustration (Pl. 9, fig. 2). In this relative small, obconical sponge, an irregular mesh of chiastoclones of the distal interior region is exposed where the characteristic impermeable dermal layer is missing. The walls of axial excurrent canals are even more telling, as they exhibit an elaborate network of connected spicules consisting of chiastoclones rather than dendroclones (Pl. 9, fig. 3). This observation and other ones on the new material imply that *Diotricheum* should be moved from the Anthaspidellidae to the Chiastoclonellidae, in particular to the Eochiastoclonellinae n. subfam. The evidence for the chiastoclonellid nature of *Diotricheum* can be specified as follows:

First, the predominance of chiastoclones over dendroclones is overwhelming. Van Kempen already noted this phenomenon. He observed that the skeleton in *Diotricheum* is extremely irregular, and that only 20–25% of the 400 measured spicules are dendroclones, often with Y-shaped clones. The majority comprise irregular desmas, both chiastoclones and a minority of rhizoclones (Van Kempen 1989, p. 140). He also observed that the ladder-like strands formed by dendroclones are generally short and become irregular after a short distance, but he refrained from drawing systematic conclusions from this observation. To Van Kempen, the presence of dendroclones, even though they constitute only a small part of all spicules, was sufficient reason to assign *Diotricheum* to the Anthaspidellidae. In this, he overrated the importance of the short strands of stacked dendroclones. New observations indicate that these strands are restricted to the distal region (Pl. 9, fig. 4), in particular the dense cortical layer (Pl. 9, fig. 5).

Second, in most anthaspidellids, coring monaxons occur between zygomes of stacked dendroclones, their purpose being to strengthen ladder-like strands. Such coring monaxons can also be noticed in *Diotricheum* (Van Kempen 1989, pl. 5a). However, some of the monaxons in *Diotricheum* are not coring monaxons, but more or less 'free' ones (Pl. 9, figs 6, 7). The presence of free monaxons, either isolated or in small bundles, is typical of the Eochiastoclonellinae n. subfam. and sets them apart from the other Orchocladina. Van Kempen did not observe these free monaxons in the specimens he had at his disposal, which may be due to the poor preservation of these blue sponges.

A third indication for the chiastoclonellid nature of *Diotricheum* concerns the preservation of skeletal parts in the aquiferous system. In the recently studied material from the WWW-area, canals are clearly preserved. Whereas in the blue sponges they are either hollow or filled with silicified lime mud (Van Kempen 1989, p. 136), in the brown sponges from the WWW-area, several canals are filled with the delicate, fibre-like skeletal tissue that is also found in canals of other chiastoclonellids described in this study (Pl. 9, figs 7, 8). This preservation of delicate tissue is due to an exceptional combination of silicification, leaching and weathering. Similar skeletal structures have not been observed in other orchocladinids.

Another aspect of the canal-system, too, is indicative of the chiastoclonellid character of *Diotricheum* (Pl. 9, fig. 9). In his paper on *Diotricheum*, Van Kempen drew attention to the presence of sub-vertical canals running parallel to the lateral wall, which he considered to be incurrent canals. In his opinion, the impermeable cortical layer forced the canals to take this unusual direction. Van Kempen (1989, pl. 2, fig. 1a, b), depicted an incurrent canal provided with little branchlets. A striking detail is a narrow cylinder of chalcedony running through the centre of the channel. The chalcedony is the secondary filling of a long central cavity surrounded by fine tissue. In various brown specimens of *Diotricheum* from the WWW-area, similar cylinders of chalcedony can be seen to protrude from the centre of exhalant canals (Pl. 9, fig. 7). This phenomenon proved to be common to some of the taxa assigned here to the Eochiastoclonellinae n. subfam chiastoclonellids, such as *Wilsumispongia*, but it is unusual in the Anthaspidellidae and Streptosolenidae.

To understand Van Kempen's identification of *Diotricheum* as an anthaspidellid sponge, it is important to note that up to 1989 no species except anthaspidellid and astylospongiid ones had been recognized in the Baltic assemblages. This may have prevented Van Kempen from assigning *Diotricheum* to the chiastoclonellids. However, one year later did Van Kempen actually describe two chiastoclonellid species of Ordovician age, i.e. *Chiastoclonella* sp. and *Syltispongia ingemariae* (see above). Since this would place the rise of the chiastoclonellids considerably earlier than indicated by Finks (Fig. 2 in Finks 1960, p. 13), Van Kempen consulted Finks prior to the publication of the paper (Van Kempen, pers. comm. 2000).

Palaeoecology

Most Estonian chiastoclonellid sponges are large, flat and discus-like. They lived on the shallow carbonate platform on the northern flank of the epicontinental sea named the Baltic Palaeobasin (also known as the Baltoscandian Basin; Nestor & Einasto 1997; Meidla *et al.* 2023). Their flat shape secured a stable and secure life position on a sea-floor composed of fine-grained bioclastics and lime mud. It also provided the sponges with an enlarged area for internal filtration (Seilacher *et al.* 2015, p. 160).

During the Ordovician, Northern Estonia formed part of the North Estonian Confacies Belt, a zone characterized by a similar lithofacies and fauna, stretching from the region slightly east of Gotland to the St. Petersburg region (Jaanusson 1995) (Fig. 11). The erratic chiastoclonellids are thought to originate from the same Confacies Belt as the endemic chiastoclonellids. Their habitat must have been close to Estonia, since the silicified limestones of Haljala, Keila and Pirgu age with which they are associated show remarkable faunal affinities with coeval strata in northern Estonia and West Russia (Rõõmusoks 1970; Krueger 2003; Rhebergen 2012; Van Keulen & Rhebergen 2017). The occasional association of dasycladean algae with erratic chastoclonellids indicate that these sponges lived in the photic zone, like the endemic chiastoclonellids did.

The marine environment of the North Estonian Confacies Belt had a low sedimentation rate, an estimated few millimeters per one thousand years (Jaanusson 1972). This may explain both the occurrence of numerous epibionts and the absence of well preserved, fragile hexactinellid sponges. As it took quite a while for the (dead) sponges to be covered by sediment, epibionts had ample opportunity to settle on them. The low sedimentation rate is also reflected by the occurrence of the encrusting sponge *Chiastoclonella incrustans* n. sp. It is generally agreed that the growth of siliceous sponges was very slow, about a few millimeters per century or less (Johns 1994).

Perhaps future investigation will solve the nature of the dimples on the surface of several sponges, in particular *Chiastoclonella*. In view of the current state of knowlegde, it is impossible to tell whether these

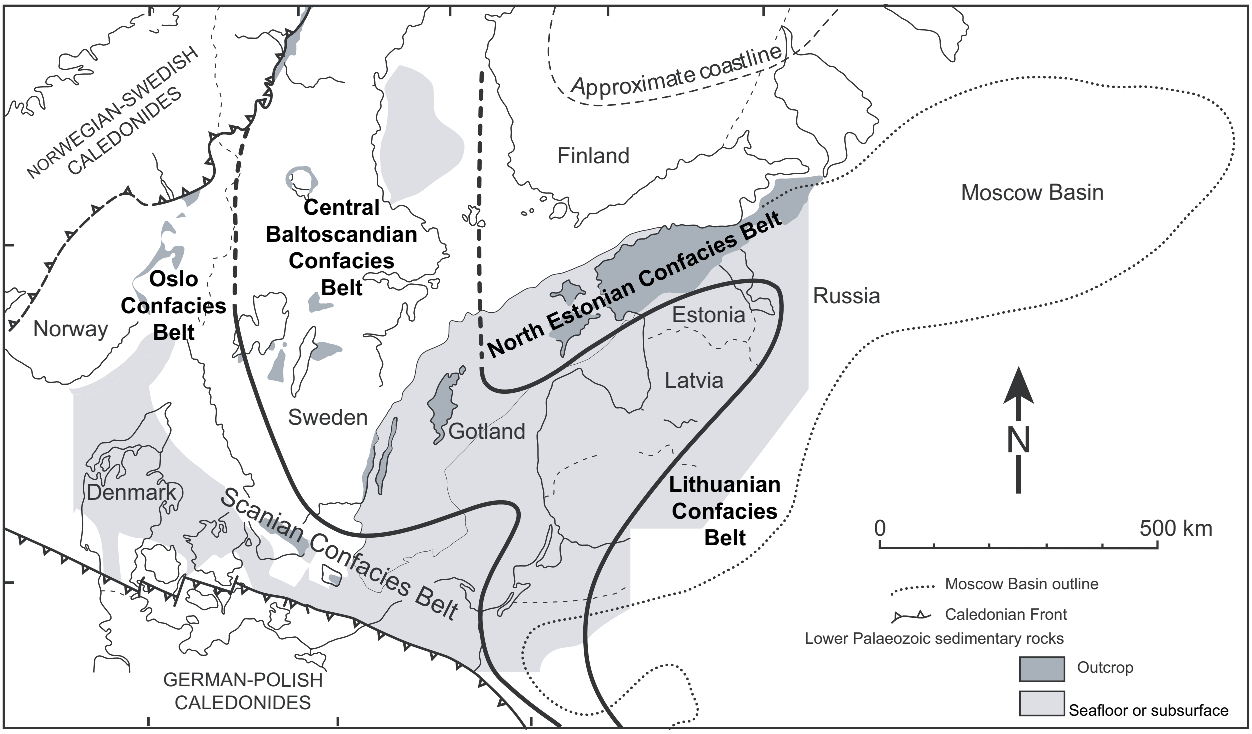


Fig. 11. Map of confacies belts in Baltica (after Jaanusson 1976, 1995) and the possible extension into the Moscow Basin (modified from Nielsen 1995; Stouge 2004).

dimples constitute an anatomical feature or are traces of a kind of 'nibbling' by a tube-like organism.

Hints (1997) described the stratigraphical section of the Aluvere Quarry from which most of the Haljala sponges derive. It comprises a succession of strata of limestone and marl. The different properties of these rocks are reflected in the manner of preservation of the sponges associated with them. Those preserved in marl show neither skeletal details nor traces of a canal system. Only their body form and associated fossil debris do enable us to recognize them as sponges. Remarkably, the same is true of some of the erratic specimens from the Netherlands, as mentioned above.

Stratigraphy of the chiastoclonellid sponge faunas

As stated above (pp. 2–5), the taxa assigned to the new family Eochiastoclonellidae form part of two geographically separated groups of Ordovician sponges, i.e. sponges from bedrock in Estonia and the St. Petersburg region and erratic sponge assemblages from the WWW-area, Sylt, and Gotland.

Eochiastoclonellidae from Estonia and St. Petersburg region

The two species of *Chiastodiscus* comprising this group are somewhat differently distributed, both stratigrafically and geographically. *C. verrucosus* seems to be confined to Estonian strata. The oldest specimen is coll. nr. GIT 413-47 recovered from bore hole 12 at Ülemiste (Estonia) at ca. 18 m depth. It dates from the early Sandbian (Kukruse Stage (C_{II})). About 70% of the Estonian specimens studied herein date from the Haljala Stage (C_{III}-D_I). These are mainly from Aluvere Quarry and the Põõsaspea (Spitham) peninsula coast. A few specimens are from the Keila and Oandu stages (D_{II}-D_{III}). *C. regularis* has a wider geographical but a narrower stratigraphical range, extending from the Russian Shundorovo formation (C_{IV}) to the Estonian Haljala (D_I).

Erratic Chiastoclonellidae

Chiastodiscus regularis is known from the Dutch-German WWW-area and, represented by one specimen only, from Gotland. The brown specimens among them are thought to originate from the western margin of the North Estonian Confacies Belt or from even farther north, from the Southern Bothnian Basin (Van Balen 1996); the blue ones from the Pra-Neva drainage area (Rhebergen 2009). The stratigraphical range of the erratic *C. regularis* is Haljala-Keila (C_{III}-D_{II}) for the blue specimens and (probably) Pirgu (F_{Ic}) for the brown ones. The co-occurring alga *Coelosphaeridium sphaericum* in the rock surrounding RGM 792 387 points to the Haljala-Keila stages. It is tempting to assume a connection with the Russian C_{IV} stage (Rhebergen 2009). One of the brown erratic specimens, RGM 792 375, shows an extremely porous preservation, which is typical of pebbles and blocks of the Pirgu stage (F_{Ic}).

To date, *Chiastoclonella globula*, *Syltispongia ingemariae*, *Diotricheum vonhachti*, *Wilsumispongia cylindrica, W. cratera* and *W. conica* have only sparsely been found outside the WWW-area. From Sylt several examples of *Syltispongia ingemariae* and *Diotricheum vonhachti* are known. The about 5,000 sponges from Gotland in the museum collections in Stockholm, Uppsala and Visby, have yielded no more than one specimen of *W. cylindrica* and one of *Syltispongia ingemariae*. These sponges are from the Pirgu Stage (F_{Ic}). Schlüter (1887) assigned the single *Domospongia silurica* from Sadewitz to the Lyckholm stage (currently Nabala, F_{I}).

Palaeobiogeography

The sponge assemblages discussed here fall into two different global Time Slices (TS), as Webby *et al.* (2004) defined for the Ordovician. One assemblage falls into TS 5b, which corresponds to the regional Baltoscandian Haljala stage and belongs to the global Sandbian Stage; the other assemblage falls into TS 6, predominantly TS 6b, which matches the regional Pirgu Stage and the global upper Katian Stage.

During the Sandbian, a small sponge community developed in the moderately warm waters of the shallow platform of Baltica, situated in a latitude of about 30^0–40^0 south (Nestor & Einasto 1997). The community included Astylospongiidae, Chiastoclonellidae, *Hindia sphaeroidalis* Duncan, 1879, as well as rarely occurring Anthaspidellidae, the hexactinellid *Haljalaspongia inaudita* Botting & Rhebergen, 2011 and the heteractinellid *Astraeospongium patina* Roemer, 1861. During the Sandbian, only a few new orchocladinid sponges appeared, among them *Chiastodiscus*. The chiastoclonellids seem to have been concentrated in certain areas.

During the Katian, new groups of Orchocladiniidae, such as Anthaspidellidae and Streptosolenidae, invaded the western part of the North Estonian Confacies belt. A rich sponge community developed, dominated by the anthaspidellid *Aulocopium aurantium* Oswald, 1847. This community also saw the emergence of the chiastoclonellid genera *Wilsumispongia*, *Syltispongia*, *Chiastoclonella*, *Domospongia* and *Diotricheum*. Astylospongiidae increased substantially, both in numbers of genera and species and in abundance. The cosmopolitan *Hindia* kept its stable position, whereas the Hexactinellidae and Heteractinidae remained rare.

Over the Hirnantian, this sponge fauna must have impoverished considerably and may even have ceased to exist. None of the Ordovician communities seems to have survived the transition to the Silurian. The first Silurian sponge community worldwide from Gotland (Rhebergen & Botting 2014) developed during the late Telychian (Llandovery). It has a markedly endemic character, showing little connection with the preceding Ordovician communities.

Conclusions

The (East) Baltic Ordovician sponge fauna comprises endemic sponges from North Estonia and the St. Petersburg region and erratic sponges from Gotland, Poland, Germany and the Netherlands. Chiastoclonellids form a small but significant part of both groups. The present study seeks to describe these chiastoclonellids, which long have gone unnoticed in palaeontology. Since they share structural features, which set them apart from the late Palaeozoic chiastoclonellids, they are placed in the new sub-family Eochiastoclonellinae.

The endemic assemblage includes *Chiastodiscus verrucosus* and *C. regularis* and its stratigraphical range is Kukruse-Haljala. The erratic assemblage is more diverse and, on the basis of co-occurrent fossils, must be assigned to the Pirgu Stage (Katian). It comprises *Chiastoclonella globula*, *C. incrustans, Wilsumispongia cylindrica*, *W. cratera*, *W. conica*, *Syltispongia ingemariae*, *Chiastodiscus regularis* and *Diotricheum vonhachti*.

The modest common ground between the erratic and the endemic chiastoclonellid assemblages is made up by *Chiastodiscus regularis*. Discoveries made in the past twenty years have shown that the erratic blue Haljala(/Keila?) sponge assemblage shares various species of Astylospongiidae with the coeval endemic Estonian and West Russian sponge communities, suggesting a substantial affinity between the two (Rhebergen 2009, 2012). This affinity is now enhanced by the presence of a blue *Chiastodiscus regularis* in the erratic assemblage.

There is no obvious connection between the erratic Pirgu chiastoclonellids and the Katian fauna of Estonia, which to date has not yielded chiastoclonellid sponges. Most erratic chiastoclonellids belong to the group of brown Pirgu sponges. The presence of such brown sponges, including a few chiastoclonellids, in glacial deposits on Gotland renders it likely that they originate from Ordovician strata northeast of Gotland, that is, the western margin of the North Estonian Confacies Belt. Whatever the exact place of origin of this Pirgu sponge community, more than 100,000 specimens of erratic brown sponges known to date indicate that it must have been extremely rich, both in abundance and diversity. The place of origin of the group of erratic blue Pirgu sponges is believed to be closer to Estonia because they share with the older blue Haljala(/Keila) sponges appearance, colour and nature of silicification. The only blue chiastoclonellid believed to belong to the Pirgu group is *Diotricheum vonhachti*.

The present study confirms the independent position of the Baltic sponge communities in comparison with those from Laurentia. It proves that the erratic component, which has often been neglected in research, is important for getting a full picture of the development and distribution of these communities. The erratic sponges are witnesses to a marine community of which hardly any traces are left in the Baltic Ordovician due to the disappearance of the sedimentary formations from which they originated. As such, they may contribute to filling the information gap pertaining to a substantial part of the Confacies Belts between Estonia and Sweden.

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PLATES 1–9

Plate 1

1–7: *Chiastoclonella globula* n. sp.

1–3 Holotype; 1, oblique top view; 2, cross section; 3, detail of cross section (lower right), showing skeleton of chiastoclones; RGM 792 305.

4 Top view, showing new layers overlapping older ones; RGM 792 309.

5 Paratype; detail of cross section, showing the massively silicified core and the skeleton of chiastoclones in the distal zone; RGM 792 306.

6, 7 Paratype; 6, two halves, median plane; 7, detail, showing a bifoliate bryozoan in the centre of the sponge body; RGM 792 308.

8: *Palaeoporella variabilis* Stolley, 1893

The alga occurring together with RGM 792 311 in a silicified limestone.

9: *Chiastoclonella headi*, Rauff, 1895.

Drawings of different specimens in Rauff 1895, p. 244. Left: lateral view (text-fig. 100); right: median plane (text-fig. 99).

Scale bars represent 1 cm (Figs 1, 2, 4, 6, 9) and 1 mm (Figs 3, 5, 7, 8).

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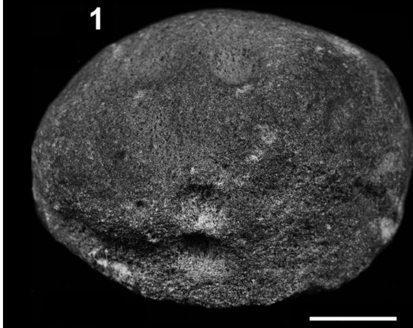

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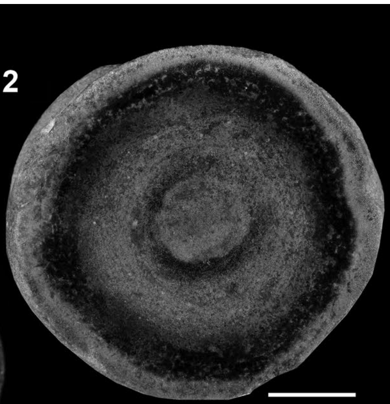

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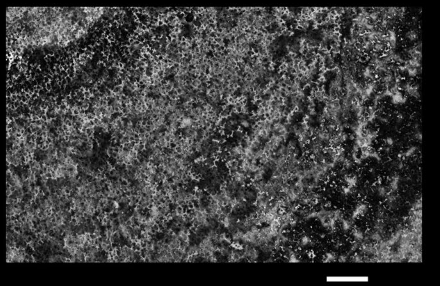

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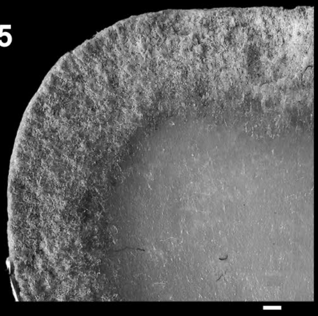

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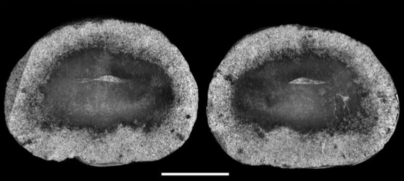

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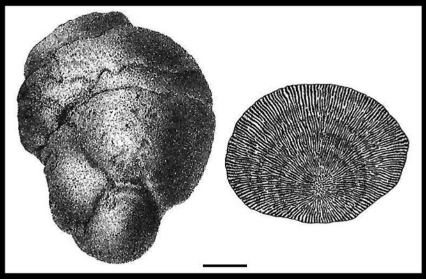

Plate 2

1–3: *Chiastoclonella incrustans* n. sp.

1, 2 Holotype; 1, lateral view. Part of the cortex has broken off, revealing that the sponge has grown around a rugose coral; 2, detail of layered structure; RGM 792 310.

3 Paratype; lateral view. Two fragments of the tabulate *Catenipora* sp. are embedded in the cortex; RGM 792 312.

Scale bars represent 1 cm.

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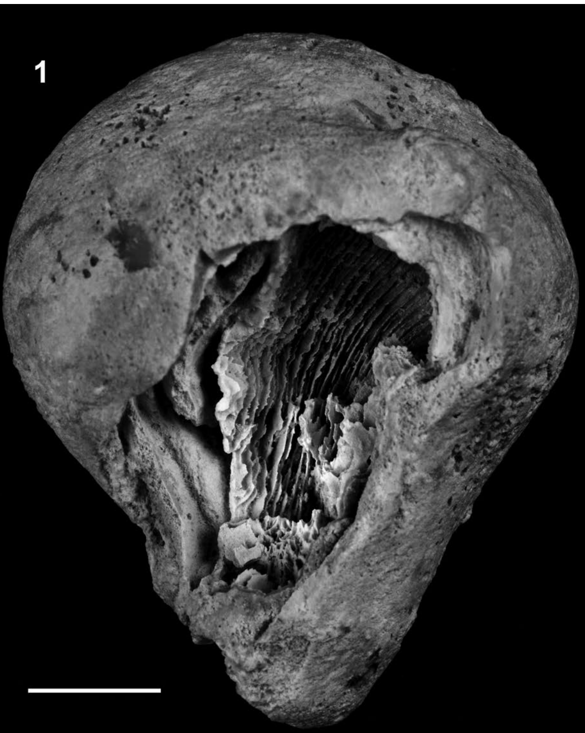

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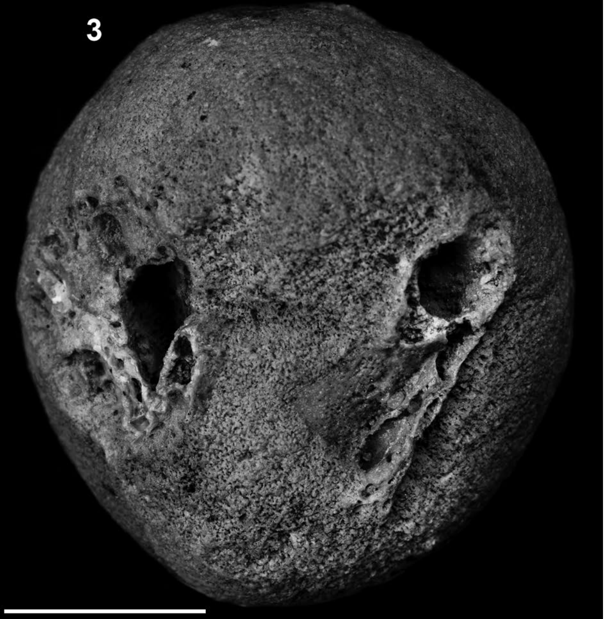

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Plate 3

1–8: *Syltispongia ingemariae* Van Kempen, 1990
1 Lateral view; RGM 792 320.
2 View of concave base; RGM 792 324.
3 Lateral view; RGM 792 323.
4 Lateral view, showing 'pancake'-structure of the specimen; RGM 792 322.
5 Oblique top view; RGM 792 326.
6, Detail of upper surface, showing a cluster of vertical canals, RGM 792 324.
7 Lateral view of a weathered specimen, showing (sub-)horizontal canals; RGM 792 328.
8 Detail of canal enclosed by clones; RGM 792 320.

9–11: *Domospongia silurica* Schlüter, 1887
9 Median view of polished surface; StIBP-Schlüter-148.
10 Fragment showing bottom and cross section, StIBP-Schlüter-148.
11 Drawing of the intact sponge in Rauff 1895 (pl. XXI, fig. 1); StIBP-Schlüter-148.

Scale bars represent 1 mm (Fig. 8) and 1 cm (remaining figures).

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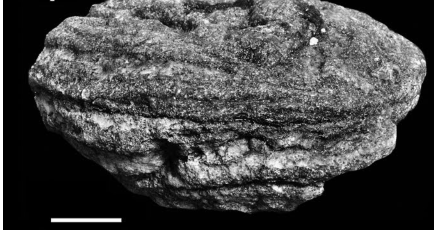

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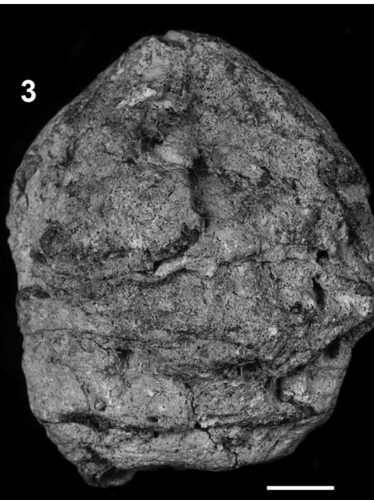

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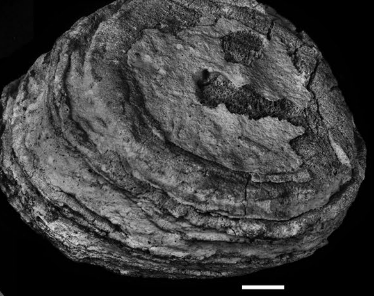

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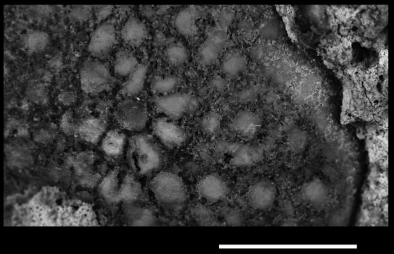

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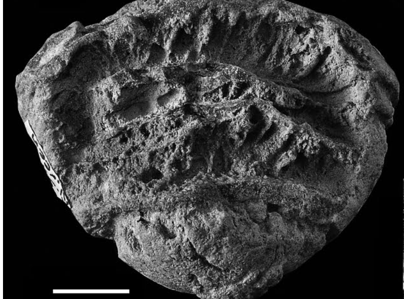

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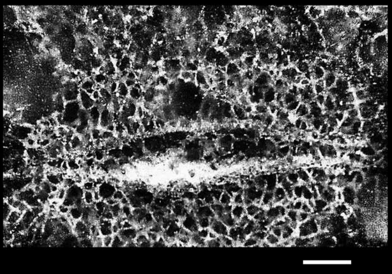

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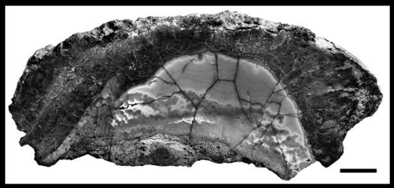

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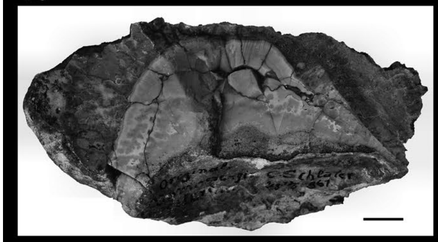

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Plate 4

1–10: *Wilsumispongia cylindrica* n. sp.

1, 2 Holotype in lateral view (1) and top view (2); RGM 792 332.

3 Paratype, lateral view; RGM 792 333.

4 Detail of basal part with skeleton of chiastoclones and rhizoclones (centre); RGM 792 339.

5 Lateral view. The basal part is slightly worn. The boundary between the basal part and the upper part is situated at the widest point of the sponge; RGM 792 337.

6 Paratype, polished surface of median plane showing the canal system; RGM 792 334.

7 Polished surface of median plane. At the top there are deep holes where vertical tubes empty; RGM 792 345.

8 Detail, showing the concentric powdery filling of tubes at the bottom of the two holes in the centre; RGM 792 341.

9 Paratype, detail. The sediment fillings of the central cavities of the tubes have been preserved as cylindrical protrusions; RGM 792 336.

10 Detail of RGM 792 345. View of large chiastoclones showing zygosis.

Scale bars represent 1 cm (Figs 1–3, 5–7) and 1 mm (Figs 4, 8–10).

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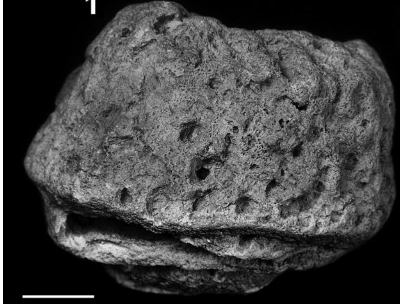

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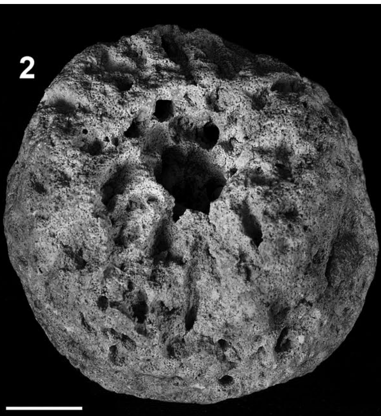

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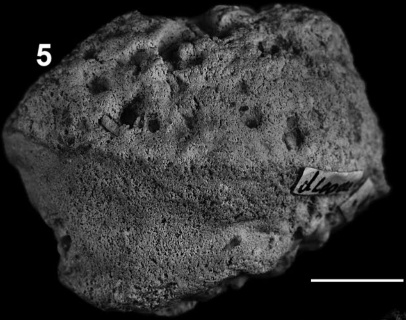

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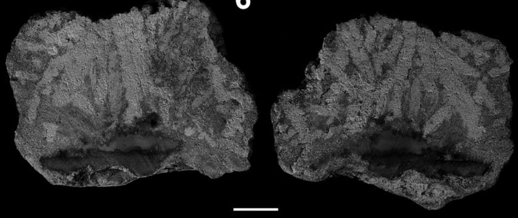

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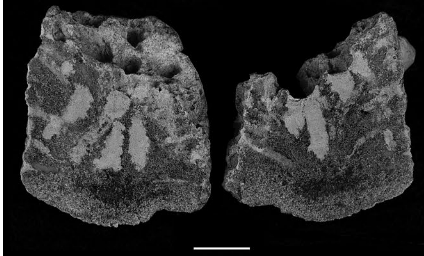

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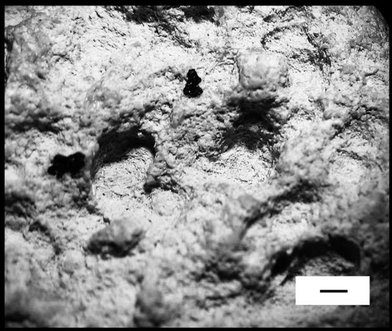

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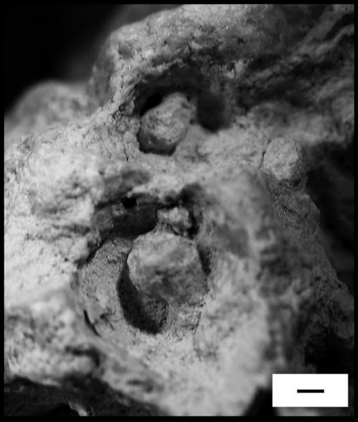

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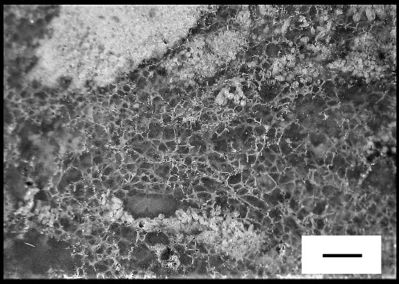

Plate 5

1–8: *Wilsumispongia cratera* n. sp.

1, 2 Holotype; oblique top view (1) and (2) view of base with cast of a cephalopod on the left; RGM 792 349.

3 Paratype; lateral view; RGM 792 350.

4 Paratype; top view; RGM 792 351.

5 Specimen RGM 792 356, oblique view of the base.

6 Paratype; lateral view. Remnants of horizontal canals can be seen above the base; RGM 792 353.

7 Detail, showing skeleton of large chiastoclones with desmas connected by zygosis; RGM 792 360.

8 Paratype; median section; RGM 792 352.

Scale bars represent 1 cm.

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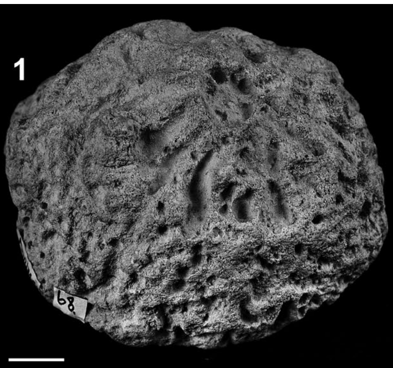

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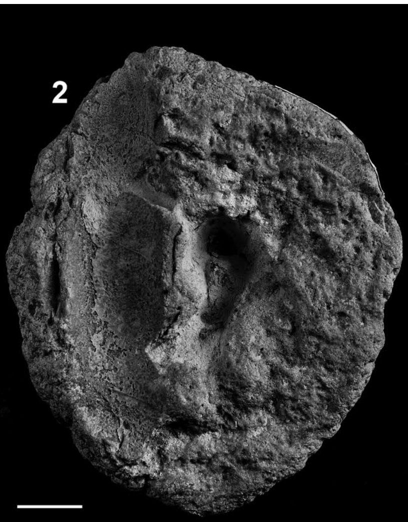

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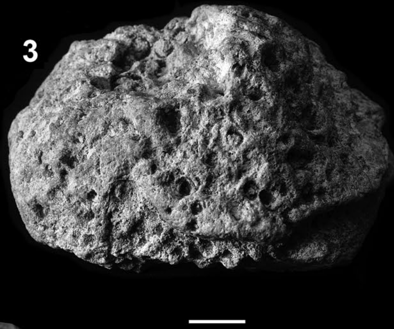

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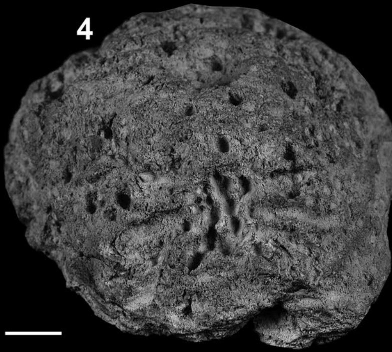

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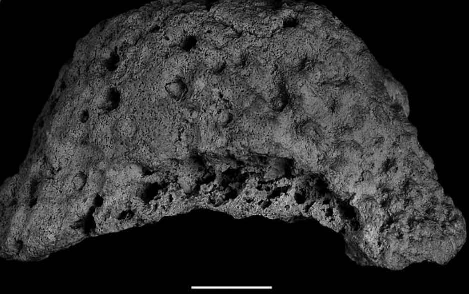

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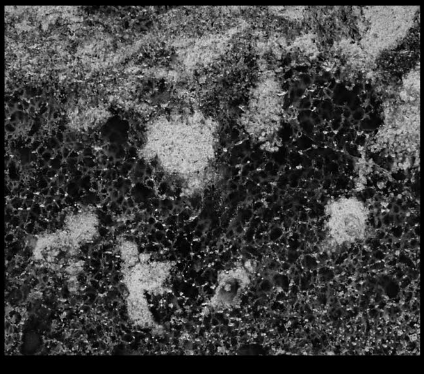

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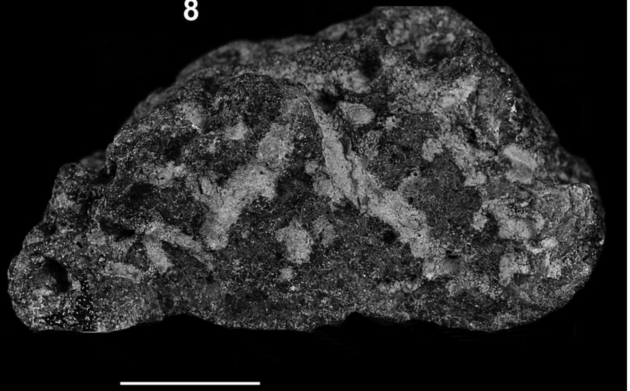

Plate 6

1–6: *Wilsumispongia conica* n. sp.

1, 2 Holotype; (1) oblique top view and (2) median view of polished surface; RGM 792 363.

3 Paratype; median section of partly preserved specimen, showing canal system; RGM 792 372.

4, 5 Paratype; (4) median view of polished surface. (5) detail. On the left strands of chiastoclones accompanied by tiny monaxons; RGM 792 364.

6 Paratype; detail. The arrow points to a canal filled with specimens of *Coprulus* Mayer, 1952; RGM 792 365.

Scale bars represent 1 cm (Figs 1–4, 6) and 1 mm (Fig. 5).

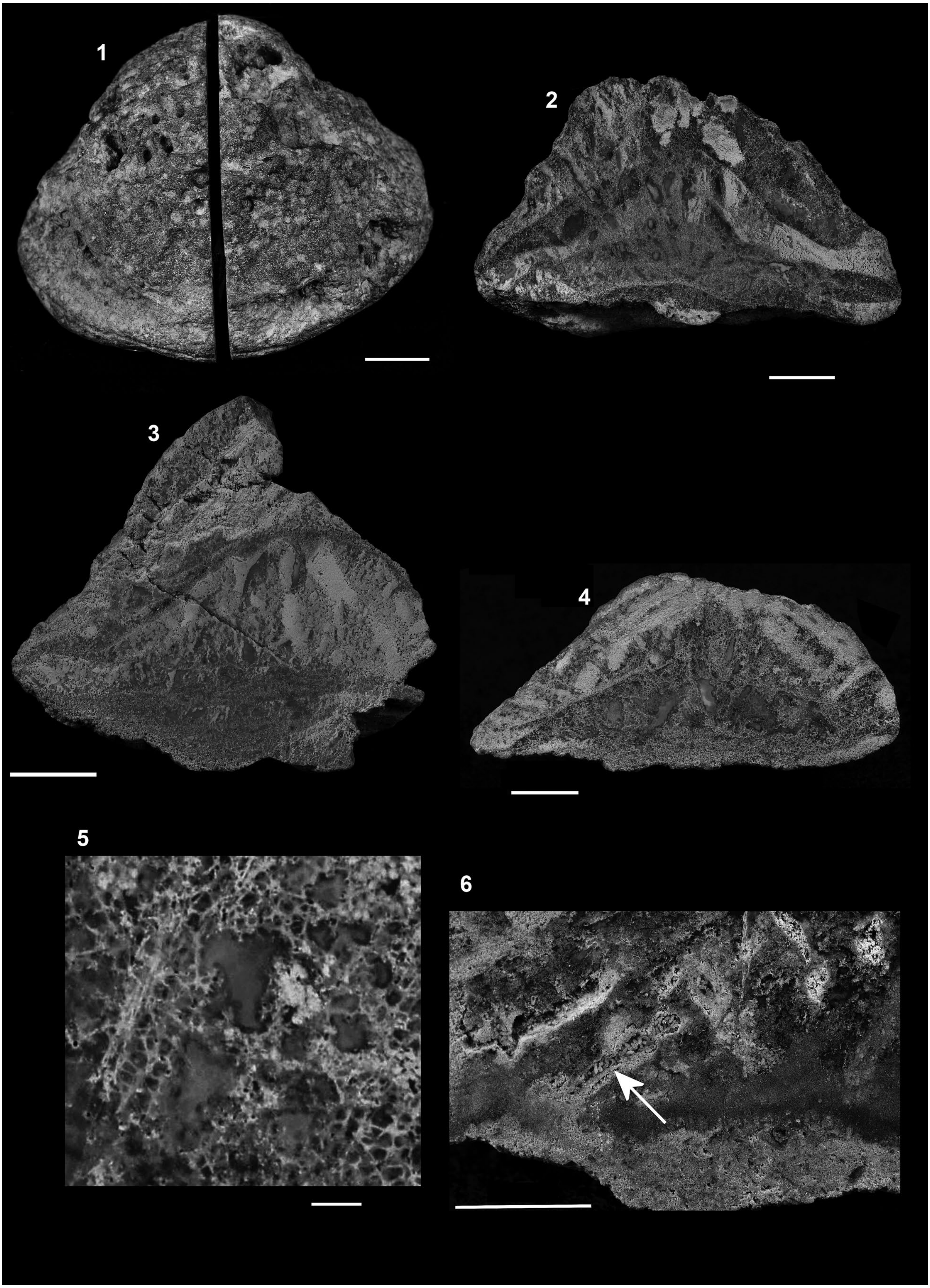
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Plate 7

1–8: ***Chiastodiscus verrucosus* n. sp.**
1 Holotype, top view; GIT 413-11.
2 Paratype, top view, one half of sawed specimen; GIT 399-987.
3 Paratype, polished surface of axial plane; GIT 399-987.
4 Top view of NMB PO 203; only preserved as cast. Drawing *in* Rauff 1895 (pl. XIX, fig. 1).
5 Paratype, top view; TUG 1306-25.
6 Top view; TUG 1306-26.
7 Polished surface of median section; GIT 413-47.
8 Top view, showing wart-like terminations of tubes; GIT 399-1689.

Scale bars represent 1 cm.

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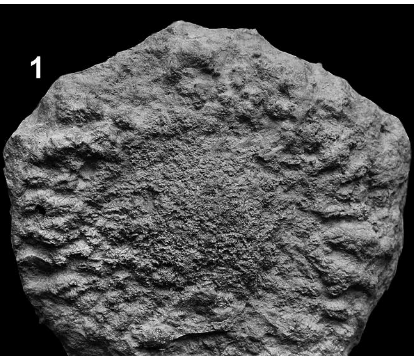

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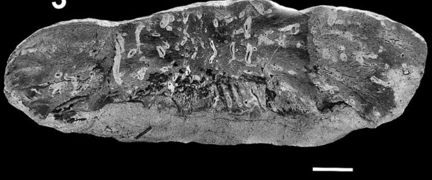

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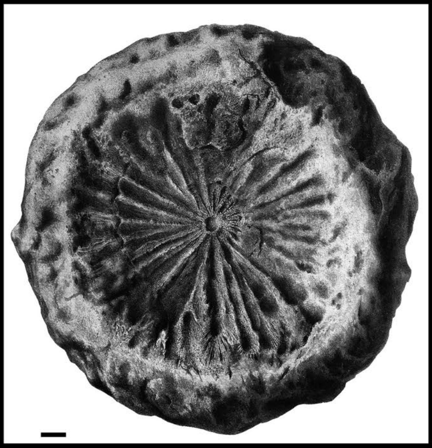

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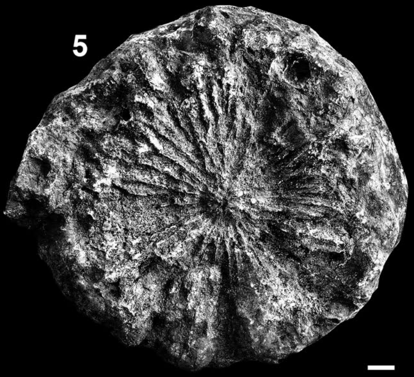

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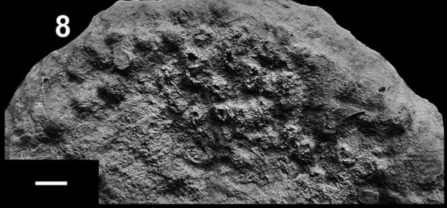

Plate 8

1–11: ***Chiastodiscus regularis*** **n. sp.**

1	Holotype, oblique top view; GIT 413-71.
2	Paratype, oblique top view; RGM 792 377.
3	Paratype, top view; RGM 792 376.
4	Top view of RGM 792 378.
5	Paratype, axial section of broken specimen; RGM 792 375.
6	Polished surface of axial section; RGM 792 384. The dashed line indicates the boundary between matrix (infilling) and sponge body.
7	Tangential section; NRM Sp 10832.
8	Oblique top view of RGM 792 379.
9	Paratype, RGM 792 376; oblique view of base with specimens of the alga *Coelosphaeridium sphaericum* (Kjerulf, 1865).
10	Paratype, oblique lateral view; GBE 4118.
11	Top view of RGM 792 383.

Scale bars represent 1 cm.

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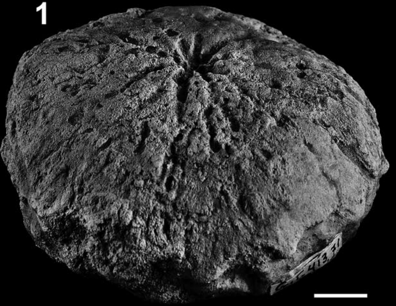

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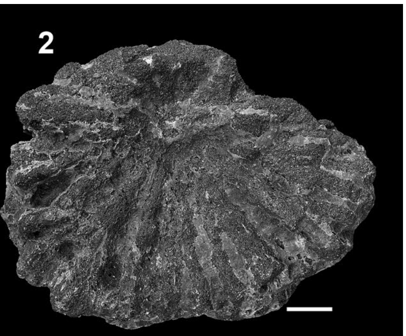

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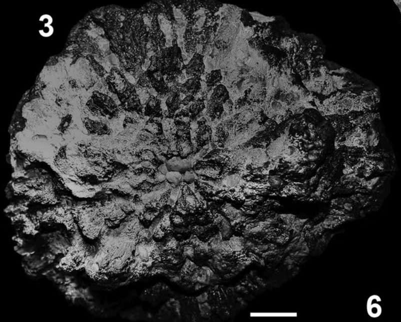

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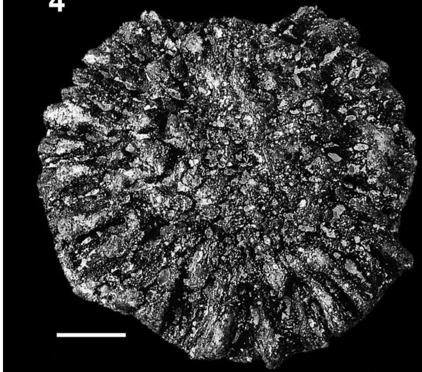

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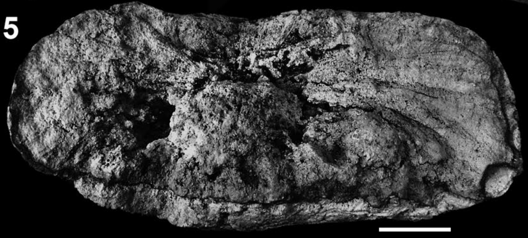

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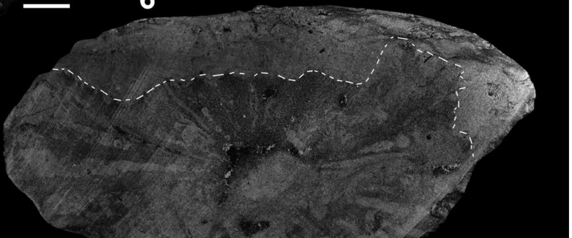

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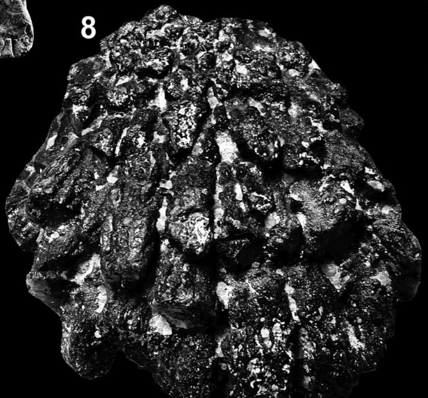

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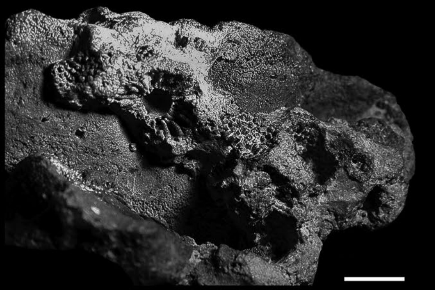

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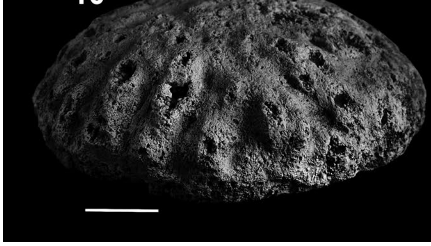

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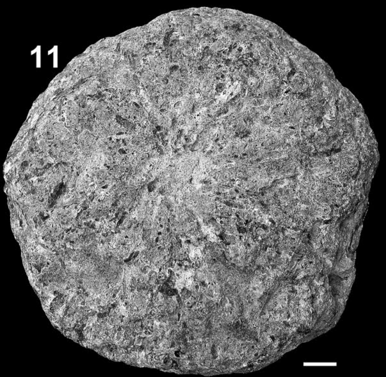
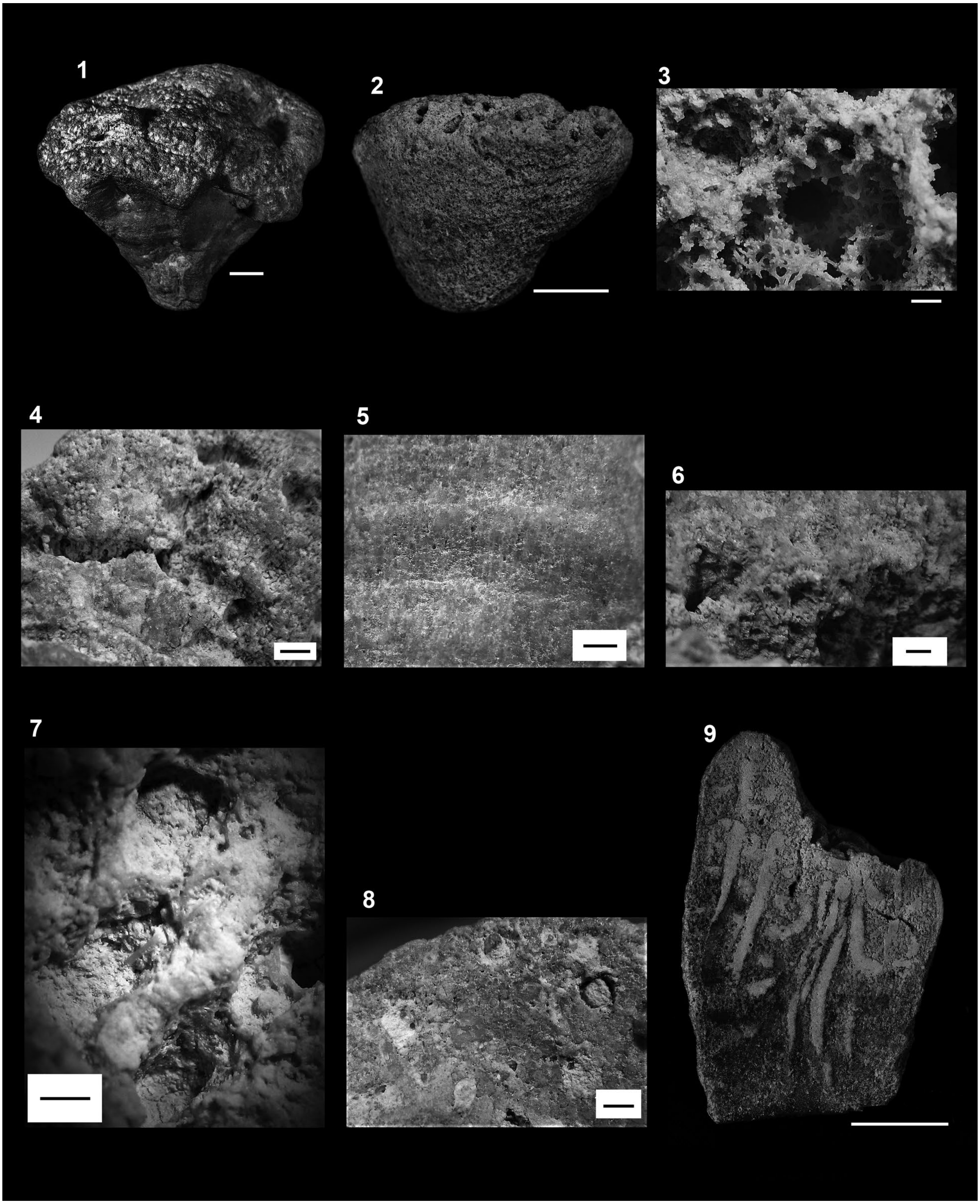


Plate 9

1–9: *Diotricheum vonhachti* Van Kempen, 1989

1 Oblique lateral view; RGM 792 313.
2 Lateral view; RGM 792 314.
3 Detail of upper surface, showing a mesh of chiastoclones around axial excurrent canals; RGM 792 314.
4 Detail of strands of dendroclones in the distal region; RGM 792 317.
5 Detail of strands of dendroclones forming the lateral cortical layer; RGM 792 315.
6 Detail of upper surface showing monaxon on the left; RGM 792 319.
7 Detail of upper surface showing monaxons and canals filled with fibre-like tissue. Bottom right a cylinder of chalcedony can be seen to protrude from an excurrent canal; RGM 792 317.
8 Detail of upper surface showing canals filled with fibre-like tissue; RGM 792 330.
9 Canal system in median view; RGM 792 316.

Scale bars represent 1 cm (Figs 1, 2, 9) and 1 mm (Figs 3–8).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