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The XXI[st] Century Edition of the "New studies on Triassic Siphoneae verticillatae, by Julius von PIA"

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24 Text-Figures, 8 Tables, 7 Plates

Algae
Dasycladales
Triassic
Stratigraphy
Taxonomy
Phylogeny

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Die 21. Jahrhundert Edition von Julius von Pia's „Neue Studien über die triadischen Siphoneae verticillatae“

Zusammenfassung

Zum 100. Jahrestag von Julius von Pia's 1912 erschienener Arbeit „Neue Studien über die triadischen Siphoneae verticillatae“ wird eine leicht modifizierte, grafisch verbesserte englische Version der ursprünglichen Arbeit von Pia vorgestellt, die auf einer elektronischen Edition, die 2013 online zur Verfügung gestellt wurde, basiert (Granier & Sander, 2013).

Die Herausgabe der Arbeit, Bearbeitung der Mikro-und 2D-Grafiken stammen von Bruno Granier. Für die 3D-Grafiken ist Alexandre Lethiers verantwortlich, die englische Übersetzung stammt von Nestor J. Sander (Granier, 2012). Die ursprünglichen 24 Abbildungen und sieben Tafeln [II-VIII] wurden in 125 Einzelmikrofotografien und 61 Abbildungen (einschließlich zweiundvierzig 3D-Zeichnungen) umgewandelt.

Abstract

For the 100th anniversary of Julius von Pia's 1912 memoir entitled “Neue Studien über die triadischen Siphoneae verticillatae” a slightly modified, graphically improved English version of the original work by Pia is presented based on an electronic edition that was made available online earlier this year (Granier & Sander, 2013).

The editing, photomicrographs and 2D artwork were due to Bruno Granier, the 3D artwork to Alexandre Lethiers and the English translation to the late Nestor J. Sander (Granier, 2012). The original twenty-four text-figures and seven plates [II-VIII] were converted into one hundred and twenty-five discrete photomicrographs and sixty-one figures (including forty-two 3D drawings).

Preface

This manuscript does not meet the editorial requirements of «Jahrbuch der Geologischen Bundesanstalt». Since this is an English translation of the original work by Pia (1912) the aim is to maintain the original structure of the manuscript. The original text of Pia starts on page 241.

Since Pia's illustrations at the plates were hand drawings, this translation has photomicrographs of the original thin sections which are kept in the Museum of Natural History in Vienna, made by Bruno Granier.

Another improvement concerns the drawings of reconstructions in Pia (1912). Originally Pia made drawings showing 2D vertical sections of the algae with some calcification. In this work every figure of Pia is presented in two 3D views giving a better idea of the calcification and the shape of the algae. Pia's original work, as well as this work, are available as PDF in the catalogue of the Geological Survey of Austria (http://opac.geologie.ac.at). The online version of this work shows the 3D figures as animated videos.

Some additional comments have been added in square brackets, in particular the additional information of localities that are mentioned in the «Areal distribution and range» sections by Pia (1912).

Figures in the plates have been grouped differently to the original work by Pia due to the smaller paper size of the «Jahrbuch der Geologischen Bundesanstalt» in relation to the original article by Pia (1912).

Acknowledgements

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New studies on Triassic Siphoneae verticillatae by Julius v. Pia

(VII Plates [II–VIII] and 24 Text-Figures)

The present study is due mainly to my having found very beautifully weathered-out specimens of *Diplopora annulata* in the course of my reconnaissance field work in the Höllengebirge. At that time the age assigned the Wetterstein Limestones seemed rather doubtful to me, so I tried to determine their age by reviewing older literature. I soon came to the conclusion that this method would not yield the degree of accuracy required, mainly because of the poor quality of the figures. With the encouragement of Prof. UHLIG I first reviewed the literature concerning the fossil occurrences and structure of the Siphoneae verticillatae in general and then studied thoroughly the Diploporid material of the Imperial and Royal (Austro-Hungarian) Geological Survey [= k. k. Geologische Reichsanstalt]. The first survey already revealed that a new and thorough investigation of Triassic Dasycladaceae in no way has as poor prospects of success as common opinion has held to date.

The studies I undertook are based on the collections of the museums of the Imperial and Royal Geological Survey and of the Geological Institute of the University of Vienna as well as a number of specimens that I and others collected. The results of this work are presented below. The examination of an even broader range of material is not possible for the moment as I must stop work temporarily in order to present it as a doctoral dissertation.

For the investigation I used thin sections almost exclusively (193 slides). My experience has shown that from a rock full of Diploporids the best results are obtained by making one or more random sections as large as possible and not too thin. In the sections there are almost always enough examples in positions sufficiently varied to permit easy reconstruction of the thallus. In any event, it is recommended not to use thin sections made for other purposes. Included around every specimen reproduced in the plates is a zone of the surrounding sediment because the boundary between fossil and rock is not always clearly defined everywhere. I emphasize this expressly because in oral communications I have encountered misunderstandings several times due to the above mentioned method of presentation. Weathered specimens were used only secondarily because it is extremely rare that they are well preserved. Admittedly certain characteristics, in particular those of the general outer form, could be only partially determined with sufficient clarity. Further progress may be expected here only through finding accidentally the appropriate favorably oriented and well-prepared sections.

Many are the problems that the present study tackles either to solve them or to prepare for their solution. In the first place it was important to me to allow the field geologist himself to identify the fossils he found. The plates serve this purpose very well. They provide a fairly ample assortment of the 155 drawings I made using a microscope. By the way, it is already widely known that only by the use of thin-sections can a fairly reliable determination be made, a conclusion strongly supported by what has been said above.

Furthermore, my objective of course must be to clarify the stratigraphic significance of each species discussed. Here, where extensive consultation of older literature is inevitably necessary, the difficulties were all but insuperable. Data concerning the geologic level of the localities were in many cases uncertain and unreliable and the same applies to an even greater extent to fossil determinations. Nevertheless, I have come to believe that the Diploporids actually have a stratigraphic value that must not be underestimated. A satisfactory answer may be reached only through the examination of an abundance of materials. It would be very desirable that as much precise data as possible be published on all future finds of Diploporids from accurately known levels. Should their determination not be possible with the help of this present work, I should be very grateful if my esteemed colleagues would turn over such samples for my use.

From a botanist's standpoint the study of fossil calcareous algae has a more intrinsic and a more scientific value, for without a knowledge of fossil Siphoneae verticillatae, especially those of the Silurian and Triassic, we would have a most inadequate conception of the real importance and diversity in form of this Order. Naturally here too very much, if not the most, remains to be done, for the number of Triassic Dasycladaceans is certainly much greater than those described so far, and even of these I have examined only a portion in detail. The purpose of my work would be completely fulfilled if I have succeeded in setting up a systematic framework in which new finds could be inserted and remain there, at least for a long time. As is noted immediately below, it is apparent that the two old genera *Diplopora* and *Gyroporella* cannot be accommodated. Therefore, I annulled the first genus and assembled all the Triassic genera into a special family, the Diploporidae, the full description of which makes up the contents of the next sections. With regard to species names, I took great pains to locate and to identify correctly the forms already described. I even made a trip to Munich especially for this purpose; but unfortunately I did not succeed for GÜMBEL's types were not made available to me. Consequently, I could not be completely secure regarding the validity of the following four species:

- *Gyroporella ampleforata*
- *Physoporella pauciforata*
- *Physoporella dissita*
- *Physoporella minutula*

Should GÜMBEL's original sections turn up again, which by the way there is reason to doubt, the designations of these species would be subject to revision. Otherwise, I can but suggest that new names - to avoid pointless nomenclatural disputes - be assigned in accordance with the methods I have adopted. GÜMBEL's descriptions and drawings (for *Gyroporella ampleforata* there is no figure at all) do not provide adequate characterization; on that point everyone will agree with me. For that reason I have not attached to the designation of the species in question a «conf», but I stress again here the particular uncertainty of the identification. After describing the several species I attempt to present something about what we can assume now concerning the phyletic relationships within our Family and its place in the Order.

After my work had already been completed, through the kindness of Professor ROTHPLETZ I received a rock sample with Dasycladaceans that because of its geologic age (Rhaetian) merited special attention. The species in question proved to be markedly different from my remaining material, so that it probably requires separate handling. On the other hand it has many interesting peculiarities that make it seem almost certain that it presents certain difficulties to my arriving at a definitive view. Shortly, I hope I can report on these and perhaps also some other forms in one of these «Contributions».

Here I set aside everything else to express my most sincere and warmest thanks to all those who from the beginning supported me in carrying out my work. First among them naturally, my admired, unforgettable teacher Professor V. UHLIG, who, in spite of my initial reluctance, invited me to take on this work that later gave me genuine pleasure, and also was always at my side while I was doing it; then Mr. Hofrat TIETZE who most liberally placed at my disposal the fine material of the Austro-Hungarian Geological Survey; also, but not less warmly, those people who helped me either by individually turning over first class material or by supplying bibliographic references. Among the first in this respect I name the Chief Geologists G. v. BUKOWSKI and G. GEYER as well as Prof. ROTHPLETZ, and as seconds Prof. v. WETTSTEIN and Dr. SCHUBERT. Finally I express my grateful thanks to Professors ROTHPLETZ and v. AMMON and the same to all the others who during my stays in Munich gave me such a friendly reception.

I. Anatomy

1. General pattern of construction of the Diploporids

For a first overview of the construction of verticillate siphonids use Pl. VIII, Fig. 8. In the middle we see the main axis, a cylindrical construction that is enclosed in a rather thick membrane while the interior is filled with protoplasm. This contains numerous cell nuclei that are not separated from each other by cell walls. Downward, the main axis terminates in a voluminous and ramified rhizoid. All around this axis are thinner organs, generally of the same fabric as it itself is: these are called branches, verticillated branches or lateral branches. These serve as the major organs of assimilation in the Diploporids (as in many other groups), but also for reproduction. Absence of secondary ramification in the verticillated branches is a characteristic of the Diploporid family, but it occurs frequently in other families. The branches secrete calcium carbonate in a well-defined zone so that a calcareous cylinder develops around the main axis. This is called the calcareous skeleton, the shell, or the calcification. The openings in it that represent the trace of the verticillated branches we call pores or canaliculae. When the plant is fully grown, the calcareous skeleton is closed above in a hemisphere or ogive. The skeleton is all that is fossilized and the main object of our research consists of judging from it the architecture of the plant body.

2. Ontogeny

We know from several recent species that true fertile shoots are preceded by several sterile ones (see Pl. VIII, Fig. 9). These develop one after another from the rhizoid and each is assigned the task of assimilation for awhile, thereby storing reserves in the root cells that alone persist throughout the life of the plant. They then die and are replaced by new shoots. It appears that in their development these juvenile stages reproduce more or less precisely the phylogeny of their ancestors. In the descriptive part of this work we often have occasion to make use of these facts.

One might raise the question of whether or not these juvenile stages of fossil forms have been described as new species. I do not consider it probable, because in all recent species the shoots of the juvenile stage are too weakly calcified to be fossilized. Therefore I believe I must reply in the negative to STEINMANN's question of whether or not *Gyroporella* is the fertile form of some Diploporid (in the old, broad sense) that was in just such a juvenile stage. In the great majority of instances *Gyroporella* occurs by itself, and as STEINMANN himself very justly emphasized, it is absent in the northern and central Alps. On the other hand, today there is not one Diploporid of which some part has not be referred at least speculatively to the sporangium.

After these very preliminary remarks we turn now to a detailed discussion of the individual organs.

3. The main axis

It is generally not fossilized, but there are two exceptions to this rule: when the membrane of the main axis is itself calcified (*Gyroporella ampleforata*) or when the calcareous skeleton is deposited directly on it (*Kantia*). In all such directly observed cases the main axis is completely cylindrical and smooth, without the constrictions that are common in recent forms (*Dasycladus*, *Halicoryne*, *Acetabularia*, *Cymopolia*). It merits special emphasis that even between the discrete annular segments of *Kantia philosophi* no trace of such a constriction can be distinguished (Pl. VI, Fig. 17).

In general, with the exception of some *Macroporella*, the main axis of the Diploporids appears to have been much thicker in relation to the length of the branches (or at least of their calcified portion) than those of recent **Siphoneae verticillatae**.

4. The verticillated branches

a) Form of the verticillated branches

We distinguish two main types:

α) The phloiophore type: In fossils it is characterized by pores that broaden outward. I presume that a little past the outer surface of the calcareous skeleton the verticillated branches were enclosed in a thickened membrane, the external membrane. As proof of it the following facts can be considered:

1. In *Kantia philosophi* this external membrane, at least in many specimens, is calcified and therefore fossilized (see in particular Pl. VI, Fig. 19)
2. Even though most show a clear separation into stem and cortical cells, in principal the secondary ramifications of *Neomeris* and its relatives are analogs of the phloiophorous primary verticillated branches of the Diploporids. Thus we can compare the manner in which the ends of these develop to those of the branches of the Triassic forms.
3. The closest resemblance is with the branches of *Coelosphaeridium*. From Kiesow (see 1896-4) we know that the outer end of the pores is closed by a lid. Thus we are informed about the shape and position of the external membrane.

This type includes *Macroporella* and *Kantia*, of which the reconstructions (Pl. VIII, Figs. 10 & 15) may lead to a better understanding of what has been said.

β) The trichophore type: The pores taper outward. The branches in the form of filaments (hairs) extend well past the thallus as seems probable for the following reasons:

1. *A priori*, such a lengthening must be assumed because an organ of assimilation must try to enlarge its outer surface.
2. In many cases (especially in *Teutloporella*) the whole form of the pore makes the conception of such a lengthening much more likely.
3. If among the recent Dasycladaceans we look for forms in which the verticillated branches taper outwards, the closest relationship with the Triassic species is shown by certain juvenile stages of *Neomeris* (see Pl. VIII, Fig. 9). In these, at the end of each primary verticillated branch (only they are present here) is a multiple-branched filament. Certainly these filaments fall off of the lower verticils, but one must consider that they cannot have the same importance in an almost uncalcified plant as they did in the trichophorous Diploporids. Later we shall have to investigate whether they may represent the degeneration of an ancestral trait. In my reconstructions I was content with drawing unbranched filaments because we know nothing as yet of the probable types of ramification.

Teutloporella and *Oligoporella* belong to this type, along with *Diplopora* which has a somewhat different form with very thin canicules over its entire length.

The verticillated branches have a two-fold function: assimilation and reproduction (see section c, Sporangia). Our two main types of branches represent essentially two distinct adaptations for assimilation, two ways of increasing the outer surface exposed to light. But in both types the reproductive function becomes predominant over that of nutrition. This latter was probably shifted during the juvenile stages. Thus two specific sub-types arise: vesiculiferous and pyriferous. The development of the first type begins with the calcification of the outer membrane of the phloiophorous verticillated branches. When completely developed the ramification divides into a stem and a terminal bladder, the true sporangium. Probably such a branch retains a certain amount of assimilatory activity. Example: *Gyroporella*. The pyriferous type, represented by *Physoporella*, is developed from the trichophorous type through the loss of the filaments while the basal portion of the ramification is more strongly developed and is completely enclosed in $CaCO_3$. In this case assimilation decreases in the adult plants to the point that it is completely gone. In the early stages the sporangium is still tapered outward, later it takes on a more parallel-sided, tube-shaped form.

The openings that represent the verticillated branches of both specialized subtypes are closed at their outer ends. However, I still call them pores, because they are entirely homologous with the open ones.

All reconstructions took as a basic premise that the broader base of the verticillated branches was not attached to the main axis but that their most proximal parts are enlaced. Direct evidence regarding this has not been adduced. At most, one can observe a few indications of it in *Teutloporella herculea* (Pl. II, Fig. 27) and especially in *Physoporella pauciforata* (Pl. V, Fig. 13). More important, it seems to me, is the fact that in recent forms there is a pronounced enlacement at the connection between main axis and verticillated branches.

Perhaps a few remarks concerning the way in which the several types of verticillated branches are recognized in thin section may not be unprofitable. The most informative for judging the form of the branches is an oblique longitudinal section, whereas vertical cross-sections and longitudinal axial sections, if by chance they occur, usually give little information. As a rule, the two principal types of ramification are easy to distinguish because the widest cross sections of the pores of the phloiophorous species are situated near the edge of the slide, while those of the trichophorous forms lie next to the inner space. Vesiculiferous pores differ from true phloiophorous pores in that at their distal ends they are filled by spar calcite while only sediment (from inside the calcareous cylinder) penetrates the proximal part, the stem. If on the other hand all of the cavities in the skeleton are filled with spar calcite it is not a reliable guide according to my observation. This type of preservation occurs not only in the vesiculiferous forms (Pl. II, Figs. 19–21) but also in small phloiophores *s.s.* (see Pl. II, Fig. 2). In the pyriferous type it is significant that in oblique longitudinal sections the sharp ends of the pores do not appear (see Pl. V, Figs. 15–16 & 19). In a tangential section they are confined to a middle zone (Pl. VI, Fig. 2). But caution is not out of place here for often even the narrow distal portion of the pores is not preserved.

Frequently the verticillated branches are curved and almost invariably are inclined in the same direction even near the main axis. I always regard this direction as up, partly from direct observation (see Pl. VIII, Fig. 2 where this disposition is only vaguely hinted at), and partly because of the consideration that organs of assimilation are heliotropically positive.

b) Placement of the verticillated branches

In this respect we divide the Diploporids into three groups:

1. Proverticillatae. The branches are placed randomly.
2. Euverticillatae. The branches are arranged in verticils.
3. Metaverticillatae. The branches within the verticils are arranged in special groupings of tufts.

Euverticillate verticils are either simple, that is the pores are ranged more or less strictly into rows (see Pl. IV, Fig. 16 and Pl. V, Fig. 19) or packed, when the verticillated branches are so numerous that all do not have enough space side by side but must move up or down, crowded out somewhat from the ideal of verticil geometry (see Pl. IV, Figs. 3 & 7 and many others). The extreme of this latter development is presented in the biserial verticil that appears to be two simple verticils set closely together, one above the other (see the reconstructions of Text-Figs. 13 & 17 and Pl. IV, Fig. 11; Pl. VI, Figs. 2 & 10–11), and is linked to single-row forms by every kind of transition.

Where tufts of branches occur, they are always arranged in verticils.

In judging the position of the pores, as a rule only the innermost part of the calcareous skeleton should be used as farther out their regularity gets blurred because of small differences in the inclination of the branches.

In the same genus proverticillate and euverticillate branching arrangements commonly occur together. The metaverticillate arrangement, however, is a characteristic of the subfamily Diploporinae (*Kantia* and *Diplopora*).

c) Sporangia

(see also Section 4α, on the form of the verticillated branches). The reasons for the assumption that the verticillated branches of the Diploporids have a fertility function may be found in part in the descriptions of particular species. Here only the most important points are discussed briefly:

1. We know from STEINMANN's observations on *Triploporella* and *Tetraploporella* (see 1880-5, 1899-1, 1903-1) that fertile primary verticillated branches occur in Mesozoic Dasycladaceans.
2. The shape of the verticillated branches of many trichophorids would be completely incomprehensible if they did not serve as sporangia. Without this assumption especially the strong thickening of the often very clearly defined basal part of the branches of *Teutloporella triasina* would seem an inconceivable waste of material.
3. The interpretation of vesiculiferous and pyriferous lateral branches as fertile can hardly be avoided. On the other hand, both of these forms of branches are connected through transitions respectively to true phloiophorous and trichophorous types.
4. For the moment I should like to attach no great weight to the observations concerning *Kantia philosophi* and *Diplopora annulata*.

As a rule, all or at least the greater part of a verticil is to be interpreted as fertile, and probably the spores of the Phloiophores were produced there, probably in the whole branch or within its distal portion; among the Trichophores they are produced in a proximal segment. The Diploporinae comprise quite an exception. It seems that here, if we generalize the first isolated observations, only a few branches were involved in reproduction and were especially adapted for it. But our knowledge on this point is still in a very tentative early stage.

5. The calcareous skeleton

According to SOLMS-LAUBACH (1887-5) it is formed in recent *Cymopolia* as follows: the outer layers of the membrane of the verticillated branches peel off and turn into muck. In this body of slime that fills the interstices between the branches the formation of $CaCO_3$ takes place. The undegenerated portions of the cell wall remain uncalcified in *Cymopolia*. In other cases, as in *Acetabularia*, we have to do with a true calcification of the membrane.

As a rule (except in *Kantia*) the calcareous skeleton is separated from the main axis by a gap. Its relative thickness is extraordinarily variable. In some cases the entire length of the branches is included (*Macroporella*, *Gyroporella*, *Kantia*), in others it is reduced to a quite narrow zone (*Teutloporella tenuis*). As a rule it is massive. Exceptionally, perhaps as evidence of a reduction, it may also have a cellular or spongy structure (*Teutloporella gigantea*, see Pl. III, Fig. 5).

The function of the calcareous skeleton is clearly twofold, on one hand a support for the plant that lacks internal support by cell membranes, on the other hand as armor, as a protection for soft parts, especially the sporangia. In many living forms protection against too strong a light is involved. We know this from *Acetabularia mediterranea* for it is much more strongly calcified in illuminated locations than in dark ones (see 1895-6, p. 21). However, from the overall configuration of the calcareous skeleton in the Diploporids, it is not probable that this function played a role there.

As the most outstanding identifying characteristic we find that the thallus of many Diploporids has a special structuring. We can distinguish three types:

1. Bulge or undulation (*Undulatio*). It exists in that the thickness of the calcareous skeleton increases near the verticils from which it was already separated whereas between them valleys occur (see Pl. IV, Fig. 6; Pl. VI, Figs. 6–9). This phenomenon seems to be entirely accidental, functionless. However, in an extreme development it can take over the appearance and function of the annulation to be discussed below (Pl. VI, Figs. 1–3). This kind of structuring is naturally restricted to euverticillate species. It appears occasionally in *Oligoporella* and *Physoporella*. Its strongest expression is attained in *Physoporella dissita*.
2. Annulation (*Annulatio*). This is based primarily on the fact that segments of the plant populated densely by verticillated branches are separated by zones free of ramifications. At their junctures there is no deposit of lime; instead there is a deep furrow that may extend inward as far as the inner cavity (Pl. III, Fig. 12; Pl. VI, Fig. 17; Pl. VII, Fig. 7; *etc.*). The purpose of this arrangement might be no other than to equip a frail plant with a certain amount of flexibility as a protection against wave action. This flexibility may also be reached when a thin layer of calcite exists at the bottom of the furrow, for it does not hinder bending. This annulation seems to be general in the Diploporids. Moreover it occurs in some teutloporids (*Teutloporella vicentina* and probably in others not discussed in this study).
3. Inner or inverted annulation (*Intusannulatio*). It involves a periodic change in the thickness of calcification: the cylindrical shape of the outer surface is preserved but the inner surface approaches the main axis at one period and moves away from it at another (see Text-Fig. 4 and Pl. II, Fig. 21). This kind of structuring has no effect on the development of the soft parts. Nothing is known concerning its purpose. Until now it has been observed only in *Gyroporella ampleforata*.

6. The general structure of the Diploporids

The structure of the Diploporids and perhaps of the **Siphoneae verticillatae** in general is controlled by a double set of rules: radial symmetry and the tendency of verticillated branches to segregate into several discrete groups. The first rule is obvious from direct observation of every species. For the second I consider the occurrence of tufts, verticils and segmentation of primary importance in the development of a classification of families. It follows that more highly specialized species have a pronounced metameric structure and in many cases we can distinguish metamers of first and second orders. The former is represented by the disposition of the verticils the latter by the different types of segmentation that we have already in part named in the discussion of the calcareous skeleton. Only the bulge class does not belong here, for no matter what its shape it includes only one verticil. Not yet mentioned is a type of metamers of second order because it cannot be observed on the calcareous skeleton but exists only in the verticils themselves. We range in this group *Teutloporella triasina* and I have called this arrangement the formation of series of verticils. In principle it means that the shape of branches within a group of verticils that I have just now named a series, alternates from one row to another and repeats in each series in the same way resulting in branches in which the several groups of verticils have the same shape. For a better understanding of this somewhat abstract definition I refer you to the text and figures of *Teutloporella triasina*. Among recent forms *Halicoryne* offers a suggestive analog (see 1895-2 and 1895-6) in that fertile and sterile verticils exceedingly different in form alternate sequentially. Something similar holds for *Acetabularia*.

II. Systematics

A. Descriptive section

Before we come to the description of individual genera and species, a few words on the systematic principles I followed. It proved impossible to break up GÜMBEL's genus *Gyroporella* using only one distinguishing characteristic. My endeavor was rather to combine several characters so that related species could be grouped according to their overall habitus. As a general principle I have observed that among the properties of the plant body more importance is to be attached to the systematic value of the pores than to those of the calcareous skeleton. In the preparation of this work it turned out that forms very similar in all other characters are sometimes proverticillate, sometimes euverticillate, so that this characteristic could not be used to distinguish genera, but only to identify species. On the other hand the metaverticillate position occurs only in a completely defined group, also related in other respects.

Tthe following table provides a first digest of the genera I set up:

Family: Diploporidae

Only primary verticillated branches that serve also as sporangia.

Insofar as establishing a species within a genus is concerned, I consider it right that they be set up very sparingly. If there is no special reason against it, in a single piece of rock one can hardly go wrong by considering individuals of the same genus as all of one species too. I shall have repeated opportunities to discuss the great variability of the characteristics, in particular of dimensions.

In order to lighten the text the important ratios are given in a special table (see below). A reconstruction of the genera may be found on Pl. VIII.

I. Proverticillate or euverticillate	
1. Phloiophorous	
a) truly phloiophorous	*Macroporella*
b) vesiculiferous	*Gyroporella*
2. Trichophorous	
a) truly trichophorous	
α) Verticillated branches relatively thin and very numerous	*Teutloporella*
β) Verticillated branches relatively thick and sparse in number	*Oligoporella*
b) pyriferous	*Physoporella*
II. Metaverticillate	
1. Phloiophorous	*Kantia*
2. Trichophorous	*Diplopora*

Macroporella nov. gen.
(Pl. VIII, Fig. 10)

I incorporate in this genus all of the non-metaverticillate Diploporids in which the pores widen outwards and are open at the distal end. Here belong the best examples of the phloiophorous type. Except for one doubtful case all known species of our genus are proverticillate. No segmentation of the calcareous skeleton or of metamerization of a higher order has been observed. All Macroporellids appear to have in common a small size and the smallest Diploporids known belong to this genus. The width of the inner cavity is narrow in most cases, so that more than in other genera the verticillated branches occupy a greater area than the main axis. Spore formation probably occurred in the verticillated branches. In one case I found dubious suggestions of a differentiation between some few fertile branches and a great mass of assimilatory ones (*Macroporella Bellerophontis*).

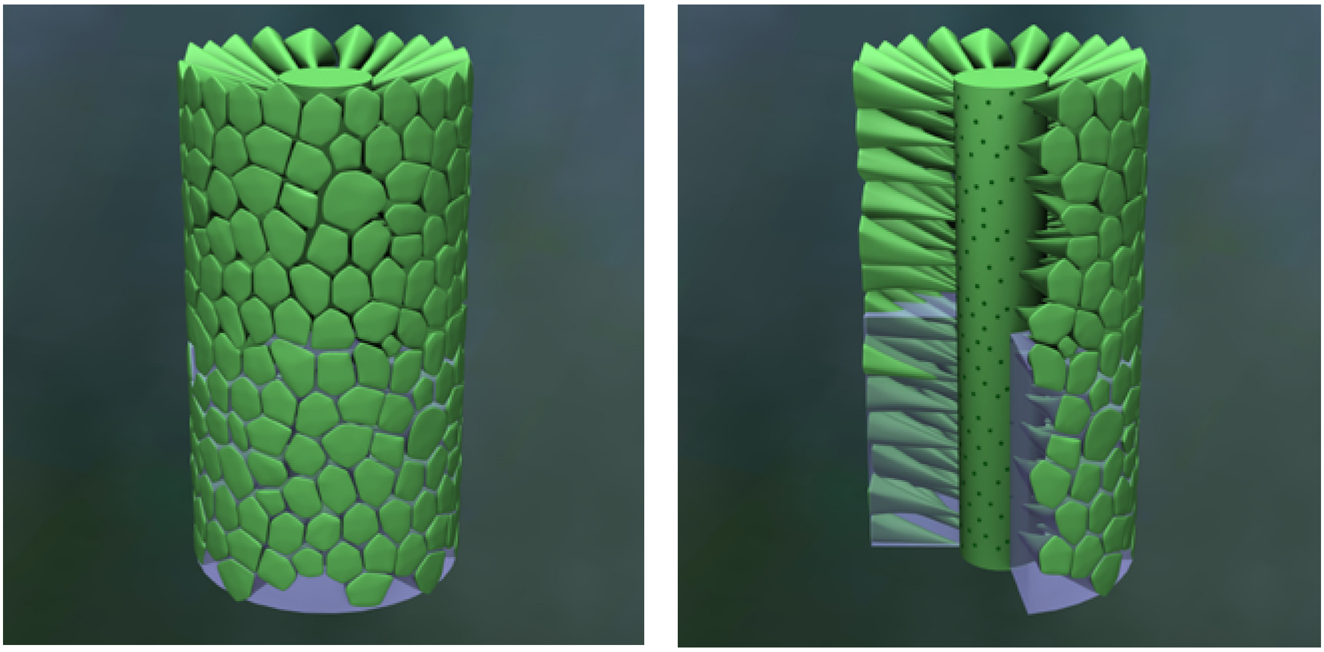
Areal distribution: Dinarides, northern Alps (Swiss Klippes?).

Range: *Bellerophon* Limestone (Permian) to the Muschelkalk (Wetterstein Limestone?). This genus comprises the oldest known undoubted Diploporids.

Macroporella dinarica nov. sp.
(Pl. II, Figs. 1–6 [Text-Fig. 1])

This is the type species of the genus *Macroporella*. Occasionally the small tubules show a slight curvature. Considering the small diameter of the inner cavity, calcification has come quite close to the main axis. While a rather large area for $CaCO_3$ deposition remains on the inner part of the wall between the pores it is deposited only in the distal portion in thin, almost flat lamellae. The cross-section of the pores is polygonal here because the verticillated branches flatten each other as a result of their strong outward expansion. The surface of the lateral branches resembles in its mosaic-like mutually interfering outer membranes an appearance quite similar to that of recent *Neomeris*, *etc.*, only more irregular, for the placement of the branches was proverticillate. The inner structure on the other hand is very like that of the Silurian *Coelosphaeridium*, however this was spherical. Nothing is known about the sporangia.

As concerns preservation, some of the pores are filled by an especially dark colored sediment, however others also include crystalline spar calcite (see Pl. II, Fig. 2). One may conclude from the latter condition that they were closed at the outer end by a calcareous membrane. But in many cases the absence of such a membrane could be verified. The occurrence may well be explained by the circumstance that the grain of the sediments was smaller than the size of the pores, perhaps also in that the outer membrane resisted destruction longer than the rest of the plant body.



Text-Fig. 1.
Reconstruction of *Macroporella dinarica* (like Pl. VIII, Fig. 8).

Areal distribution and range: Muschelkalk, Dalmatia. Samples studied:

Muschelkalk, limestone facies, west of Lapčić (Pl. II, Figs. 1–6).

idem, between Stanišići and the Grkova voda valley.

Muschelkalk, sandy marl facies, near Ivanovići.

All locations on the Budua sheet, Dalmatia [Budva, Montenegro].

Macroporella alpina nov. sp.
(Pl. II, Figs. 13–15 [Text-Fig. 2])

This species is undoubtedly very closely related to *Macroporella dinarica*. Nevertheless, because they are so widely separated geographically I would like to maintain them as separate species as long as no intermediate transitional material is available. A comparison of the figures should make the differences in their habitus fairly obvious. But insofar as a clear concept of the characteristics that distinguish them is concerned, they in fact present some difficulties. Above all, the dimensions, to which, however, no special value should be assigned, are very different, so that the largest examples of the Dalmatian species do not reach the diameter of the smallest Alpine specimens. In absolute terms the average width of the pores in *Macroporella alpina* is appreciably larger; relatively however, especially in large specimens, they are decidedly smaller than in *Macroporella dinarica* in which the verticillated branches are only exceptionally at an angle to the main axis, which is the rule in the other species.

Often the tubules are distinctly curved. The width of the inner cavity shows very great variability, that is, the amount of calcification between the verticillated branches varies widely with respect to the main axis. In various specimens the calcareous lamellae between the branches vary much in thickness.

If we maintain the separation of both of these species of *Macroporella*, we consider them to be a beautiful example of vicarious species.

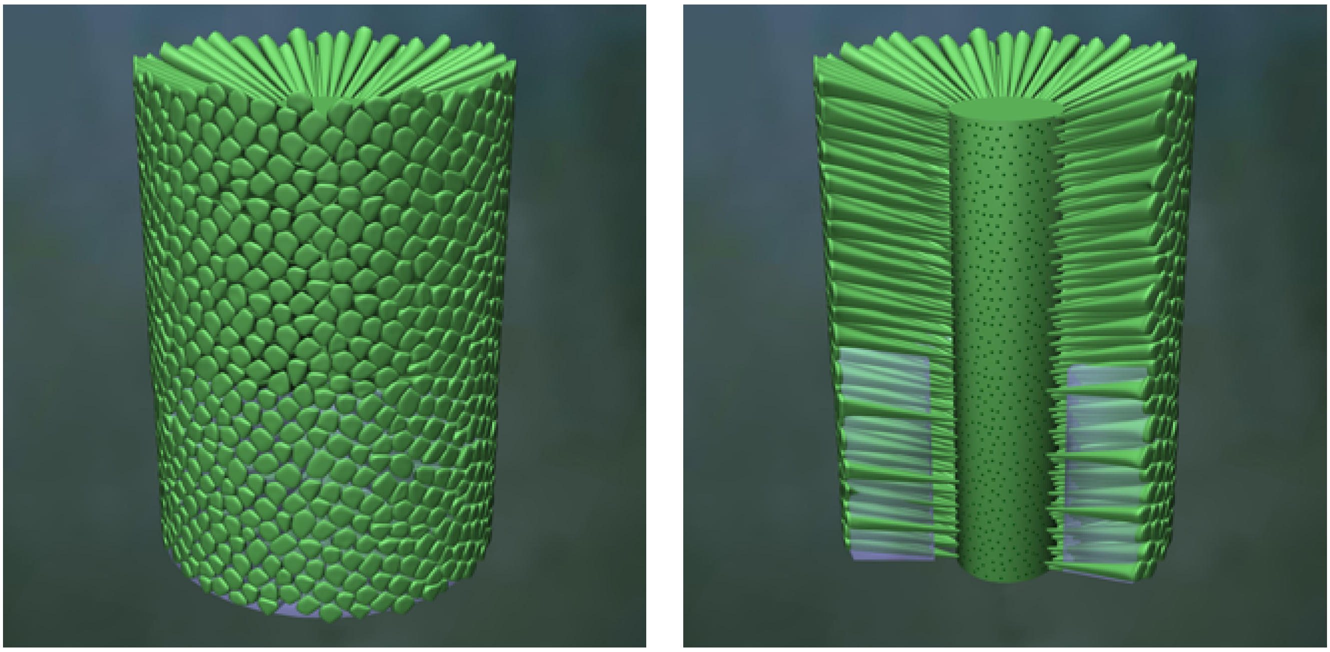
Areal distribution: So far only Fuchsriegel, south of Unter-Steinrott- (correctly Fuchsriegel-) Bauer near Schwarzenbach an der Pielach [S Schwarzenbach an der Pielach, Niederösterreich, Austria].

Macroporella Bellerophontis (ROTHPLETZ)
(Pl. II, Figs. 7–12 [Text-Fig. 3])

Gyroporella Bellerophontis ROTHPLETZ 1894-1

The illustrations show clearly that the pores of our species widen outwards and show no regularity whatsoever in their position, so that no doubt can exist concerning the validity of its assignment to my genus *Macroporella*. Most often the shape of the tubules is slightly curved and in cross section they are not circular but very irregular. The variability of this species is even greater than it is in the Mesozoic Diploporids. It shows not only in the dimensions (see the table), but also in the asymmetrical and often irregular form of the pores and in their extraordinarily variable angle in relation to the main axis. Pl. II, Fig. 12 shows a little of this, but it appears much more strongly in Pl. II, Fig. 10 which in no way represents an extreme. In general, differences in the habitus of discrete examples (compare Pl. II, Fig. 9 and Pl. II, Fig. 12) are so great that at first sight it seems hardly feasible to put them in the same species. However, after long hesitation I decided to combine the whole form group into a single species. Also, it is quite impossible to make a delimitation among the extremely numerous specimens seen (see Pl. II, Fig. 8, showing an intermediate transition). I am convinced from some of the original type slides that the author of this species too understood it in this same broad sense.

Pl. II, Fig. 12 shows an interesting occurrence, but unfortunately its interpretation is not reliable. Here we see one or perhaps a group of abnormally enlarged pores. That they open outwards is not discernible. When compared with observations on *Kantia* and *Diplopora* (see Pl. VI, Fig. 20 and Pl. VII, Fig. 9) the question arises as to whether or not we have to do here with verticillated branches transformed



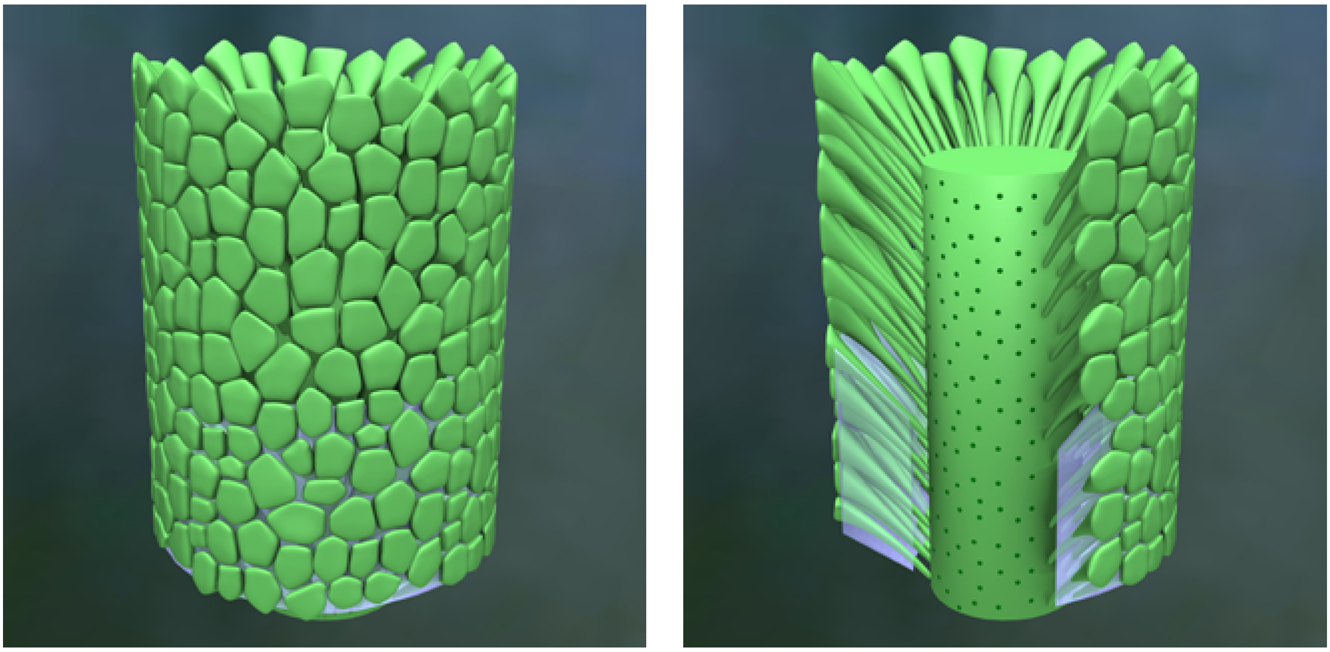
Text-Fig. 2.
Reconstruction of *Macroporella alpina* (like Pl. VIII, Fig. 8).

into sporangia. In view of the great variability of the species a single observation cannot be affirmed as a certainty.

Our species differs from *Macroporella dinarica* in that its verticillated branches are inclined at a much greater angle. They are also arranged more irregularly and are thinner so that even close together they do not flatten each other as the Triassic species does. Finally, the relative diameter of the inner cavity of the calcareous tubule in *Macroporella Bellerophontis* is greater than in *Macroporella dinarica*.

Areal distribution and range: Common in the *Bellerophon* Limestone (Permian) of the South Tyrol [Trentino-Alto Adige, Italy]. In front of me are four rock samples with the following location data:

1. mouth of the Gsellbach, south of Sexten [Sesto / Sexten], close to the edge of the woods [Pl. II, Figs. 7–9].
2. Bad Innichen [San Cándido / Innichen], eastern Paralleltal [Pl. II, Fig. 12].
3. end of the valley, south of Santa Croce [Pl. II, Figs. 10–11].
4. Sorasass am Pitschberg, northeast of St. Ulrich, Gröden [Ortisei / St. Ulrich in Gröden].
5. In addition I had the opportunity when with Prof. ROTHPLETZ to see slides from the following localities: south of Toblach [Dobbiaco / Toblach], below the Sarenkofel.
6. Plan, South Tyrol [ESE Ortisei / St. Ulrich in Gröden].



Text-Fig. 3.
Reconstruction of *Macroporella Bellerophontis* (like Pl. VIII, Fig. 8).

Macroporella (?) *helvetica* nov. sp.
(Pl. II, Figs. 16–17)

Unfortunately the state of preservation of the few available specimens of this form is extremely poor so that its generic attribution is by no means certain, especially in that it deviates from the type of the other Macroporellids. In spite of the deficiencies of the material it is possible to recognize that the pores are arranged in verticils. With the same degree of probability one may also assume that the caniculae widen outward. The endings of the caniculae, whether or not the outer ends were closed, cannot be determined. It would not be entirely impossible, but certainly it is not probable, that we have to do with a *Triploporella*, for the material is not good enough to allow secondary ramifications to be seen.

For the time being we suppose that our species is the only known euverticillate *Macroporella*. Because of the phylogenetic interest of this circumstance it is doubly regrettable that it cannot be established more securely.

Range and areal distribution: So far only in the Wetterstein Limestone. Zwecken Alp near Mythen, Canton of Schwyz. If the stratigraphic assignment is correct, then we are probably dealing here with the youngest known *Macroporella*. This would agree well with the more specialized placement of the verticillated branches.

Gyroporella GÜMBEL, emend. BENECKE
(Pl. VIII, Fig. 11)

GÜMBEL 1872-1

BENECKE 1876-1

I define this genus substantially as BENECKE did and unite in it all of the proverticillate and euverticillate Diploporids of which the pores do not penetrate the calcareous skeleton but end blindly against it and terminate outward in a more or less well-defined bubble-shaped swelling. Thus this genus belongs to the vesiculiferous subtype. The only specimen at hand shows a completely random arrangement of the verticillated branches, yet, as may be learned from the illustrations and descriptions of earlier authors, the type species, *Gyroporella vesiculifera*, may be euverticillate.

In the general anatomical section we already discussed the difficult question of the functional significance of vesiculiferous verticillated branches. In making use of this in the present case I should like to sum up my opinion as follows: The only fertile shoot of *Gyroporella* known to us was preceded by several sterile shoots, either uncalcified or only slightly so. These produced a large reserve of nourishment in a presumably large rhizoid. Then followed the development of a last particularly strong, heavily calcified shoot. Our descriptions refer to it alone. Probably it was constructed only in a vesiculiferous form, while the earlier shoots closely resembled those of *Macroporella*. To me it seems hardly doubtful that spores were produced in its verticillated branches, in their broadened distal portion. However, before this occurred these branches probably served for assimilation too. Because the calcareous coating on the outer side was ordinarily thin, this process was not hindered materially. Light could penetrate through the thin layers and the required gas exchange could also happen if we conceive of a calcareous coating with a fine, porous structure which of course is not known in fossils. As the whole calcification underwent complete recrystallization, its porous structure must necessarily have been destroyed. The calcified umbrellas of *Acetabularia* are also assimilators. As the spores developed progressively, assimilation ceased and the increased requirements for food were now met by the stored reserves.

One might also pose the question as to whether the calcareous lamellae closing the outer end of the pores are part of the actual skeleton or are only a calcified cell membrane. From my own observations I cannot decide about it, but a number of the older illustrations of *Gyroporella vesiculifera* seem to suggest the latter, which obviously is favorable to an exchange of substance through the lime (compare 1872-1, Pl. DIV, Fig. 3d and 1883-2, Pl. I, Fig. 9). Here it appears that around every cavity a sheath of lime is indicated by a dark line, and it is only this layer that might correspond to the calcified membrane that forms the outer wall of the pores.

The vertical distribution of the genus *Gyroporella* is remarkably lengthy, since on one hand it is known in the lower Muschelkalk and the Hauptdolomite and on the other in the Cretaceous. As regards the areal distribution, STEINMANN rightly pointed out (1910-2) that we do not as yet know our genus from the Triassic of the main Alpine range. Judging from the illustrations, I hold the reports of its occurrence in the Apennines as extremely doubtful (see the pertinent literature 1908-3). Also, as far as we know, in the Triassic *Gyroporella* is restricted to the Dinarides.

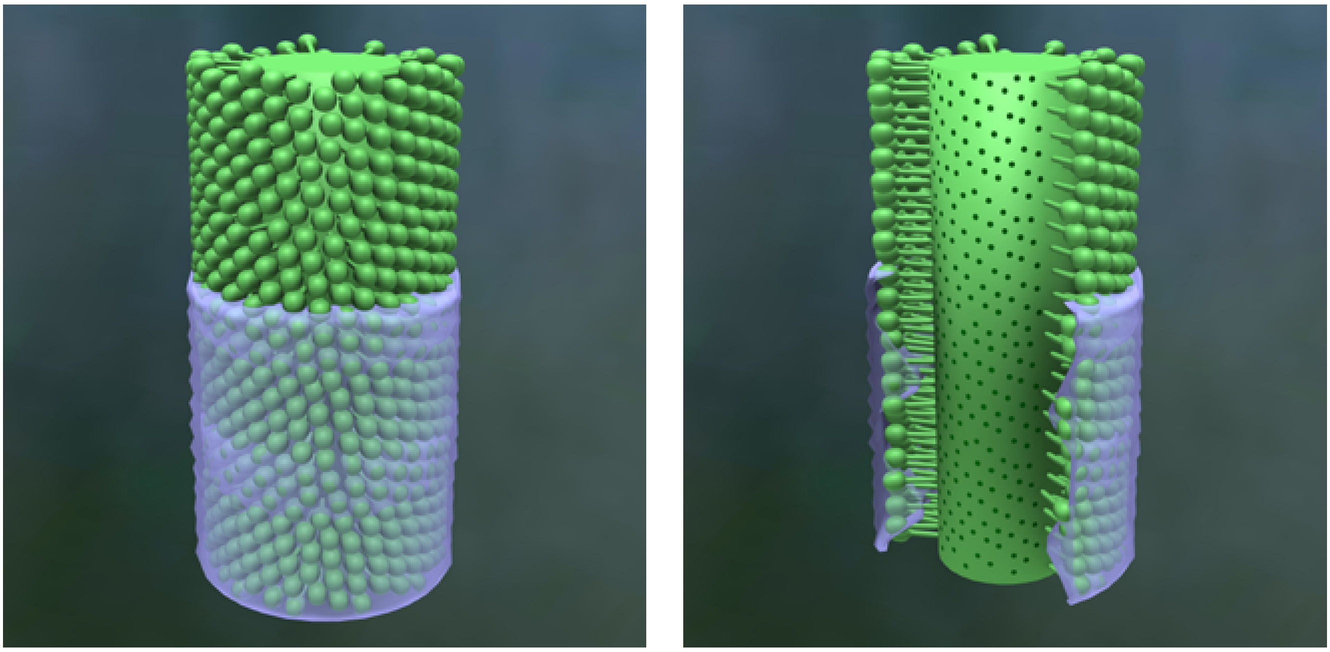
Gyroporella ampleforata GÜMBEL
(Pl. II, Figs. 18–26 [Text-Fig. 4])

Gyroporella ampleforata GÜMBEL 1872-1

Our knowledge of the soft parts of this species is as complete as at the most otherwise only in *Kantia philosophi*. This applies in particular to the main axis of which the inner membrane was so full of lime that it is commonly preserved as a fossil (Pl. II, Figs. 19–20 & 23–24). We are also reliably informed about its diameter and its purely cylindrical shape. The branches are disposed randomly. Sometimes their thickness increases evenly as they progress outward to end in a half-sphere, sometimes there is a fairly clear arrangement into a stem and a terminal bubble. Naturally, in accordance with a prescribed generic characteristic, they are always coated with a thin layer of $CaCO_3$. The calcareous skeleton, that in longer specimens mostly shows a slight curvature, offers the only example known to date of inner rings or intusannulation (see in particular Pl. II, Figs. 21 & 23).

The thickness of the calcified region increases and decreases periodically, but in such a way that the outer form always remains cylindrical while across from it on the inner surface ridges and furrows alternate in occurrence. As a rule the integrity of the calcareous skeleton is maintained even in the thinnest places. Exceptions to this are probably caused by subsequent damage. Occasionally the thickest parts of the calcareous skeleton are in direct contact with the calcified membrane of the main axis (Pl. II, Fig. 24). As one may convince oneself from a thorough study of the illustrations, it is quite obvious that these peculiar aspects in no way affect the development of the soft parts.

Range and areal distribution: All available examples of this species come from the lower Muschelkalk in the vicinity of Pontafel [Pontebba / Pontafel, Friuli - Venezia Giulia, Italy]:



Text-Fig. 4.
Reconstruction of *Gyroporella ampleforata* (like Pl. VIII, Fig. 8, but inverted, the longitudinal section is above).

1. Kar, southwesterly below the Malurch, north of Pontafel [Pl. II, Fig. 18].
2. Kar, southwesterly below the Malurch peak on the trail above the Padagozalpe (Rock type and fossil preservation are different from the previous examples) [Pl. II, Figs. 19–21].
3. Pontafel, north under the Punta Lonas on the way to the Kron-Halter hut [Pl. II, Figs. 22–25].
4. Pontafel, northeasterly below the saddle in the east of the Padagozalpe [Pl. II, Fig. 26].

Remarks: In a sample marked, «Spizze Limestone, southwesterly below the Malurch peak, Pontafel north» among numerous specimens of *Diplopora annulata* I found scattered Gyroporellae, of which a more exact determination was not possible owing to their poor preservation and small number. The identity with the above described species cannot be claimed, especially since the geologic level is higher.

Teutloporella nov. gen.
(Pl. VIII, Fig. 12)

This genus includes the largest of the Diploporids. It appears to represent a precociously independent branch that developed no farther. Many of the species belonging here are proverticillate, a smaller number euverticillate. Most of them are of a very clearly developed trichophorous type. The verticillated branches are relatively thin and very numerous. Almost always they are at quite an angle to the longitudinal axis. The basal part appears to have served as a sporangium. In the more specialized species it is rather strictly separated from a distal hair-shaped part used for assimilation. The tendency to the development of metamerization of a higher order is expressed in our genus on one hand by the development of verticils in series (*Teutloporella triasina*) and on the other by the occurrence of true annulation (*Teutloporella vicentina*). Calcification is sometimes very strong, at others very highly regressive (*Teutloporella tenuis*). As regards distinguishing characteristics that in many points resemble those of *Oligoporella*, refer to the comparisons made in the discussion of that genus.

The genus is widely distributed in the Muschelkalk of the northern Calcareous Alps and in the Dinarides. I must assume that the actual center of development was the latter.

Teutloporella herculea Stoppani
(Pl. II, Fig. 27; Pl. III, Figs. 1–2 [Text-Fig. 5])

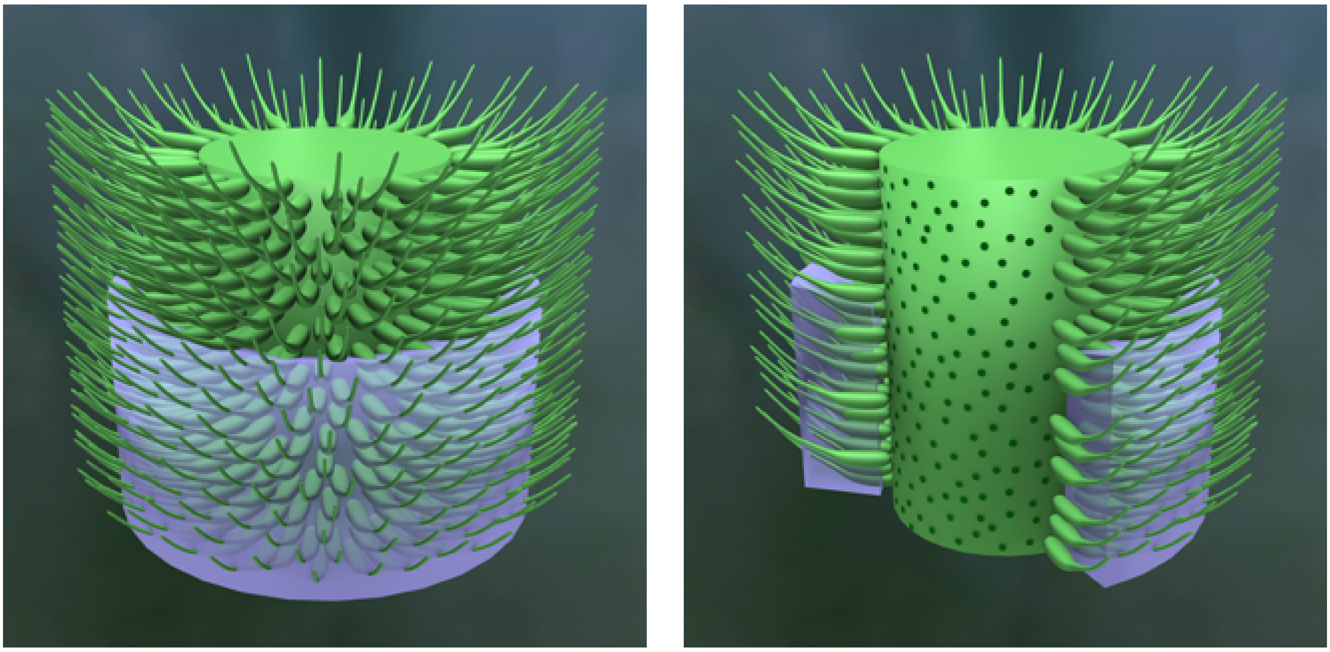
Gastrochaena herculea Stoppani 1857-1

Gyroporella aequalis Gümbel 1872-1

Diplopora herculea Salomon 1895-4

This species shows the characteristics of the genus at their purest and without further complications. The thallus appears always to be prolate and completely straight. Stoppani and after him Salomon too both indicate that the closed end of the calcareous skeleton has a thickened club shape, while Gümbel does not mention it. I too could find no such thickening in slides prepared elsewhere. By the way, Salomon has already emphasized the variability of this character. And just as infrequently have I seen a regular sculpturing of the outer surface of the calcareous skeleton (see however, what the discussion of 1895-4, p. 73 has to say). The very closely set branches that often touch each other at their thickened bases, evince no verticillate placement; on the other hand occasionally a tendency to construct vertical series aligned in the direction of the long axis was observed, as seen not only in Pl. II, Fig. 27 but also in several other specimens. The tapering of the pores outward is particularly distinct. Their development is always curved so that their inclination in relation to the main axis increases considerably from their inner ends outward. Occasionally irregular cavities occur in the calcareous skeleton (see Pl. III, Fig. 2, at the top, and Pl. III, Fig. 1) that are probably only the result of inequalities in calcification.

As regards the inner structure, we are dealing here with a very primitive representative of *Teutloporella*. Only its large



Text-Fig. 5.
Reconstruction of *Teutloporella herculea* (like Pl. VIII, Fig. 8).

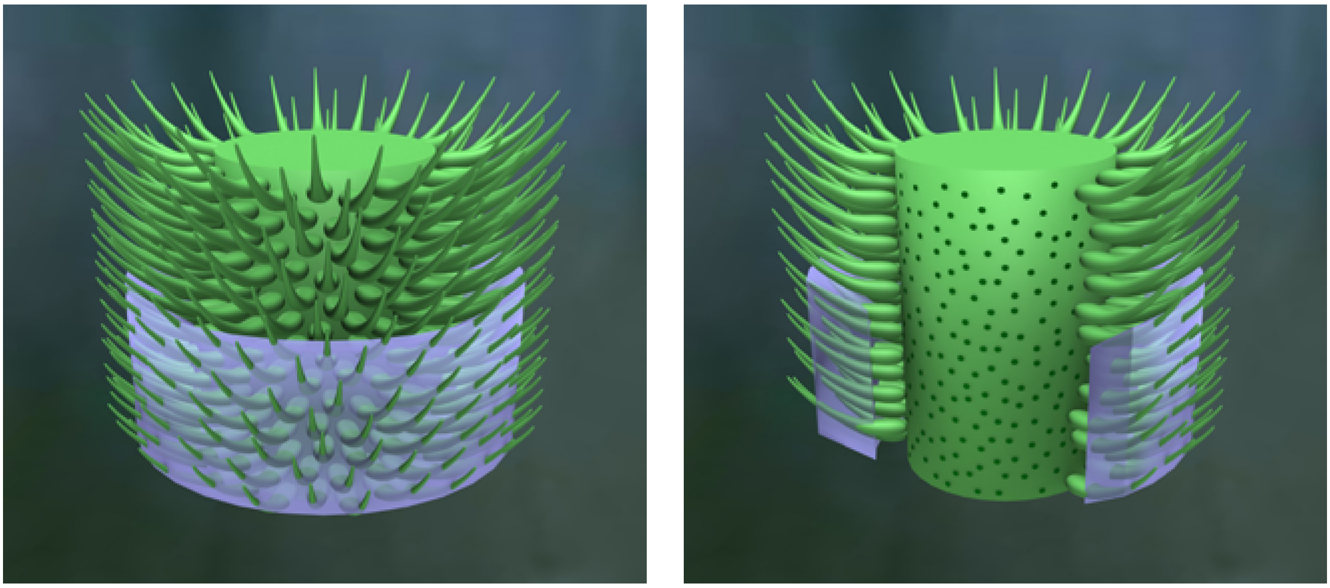
size and the linear arrangement of the caniculae indicate specialization.

Areal distribution and range: Probably a level of the Wetterstein Limestones (lower part?) in the northern and southern Calcareous Alps. Localities:

1. Rammer valley near Wegscheid [Niederösterreich, Austria], southern slopes, next to coal seam No. 3 (already Upper Limestone?) [Pl. II, Fig. 27].
2. Schiestlhaus am Hochschwab [SE Gschöder - SW Weichselboden, N Leoben, Steiermark, Austria] [Pl. III, Fig. 1].
3. Dreimarkstein, Raxalpe [NW Griesleiten, Reichenau an der Rax, Niederösterreich, Austria] [Pl. III, Fig. 2].
4. Wetterling Limestone, Rohrbach [Rohrbach in Oberösterreich, NW Linz, Austria] (from GÜMBEL'S slides).

Teutloporella gigantea nov. sp.
(Pl. III, Figs. 3–6 [Text-Fig. 6])

This species is obviously very closely related to *Teutloporella herculea*. The differences consist on one hand in a lesser thickness of the calcareous skeleton and on the other in a much decreased density of thinner and less numerous lateral branches . The greater part of these disparities is explained by the assumption that the calcification is farther from the main axis than in the former species. This hypothesis, for naturally it is no more than that, served as the basis of the reconstruction. It almost seems that we are dealing with a progressive reduction in the thickness of the calcareous skeleton from inside to outside, for the inner layer of specimens with a greater thickness of the calcareous skeleton often has a perforate structure, as shown in Pl. III, Fig. 5. In several places on this figure one can see



Text-Fig. 6.
Reconstruction of *Teutloporella gigantea* (like Pl. VIII, Fig. 8).

that calcite sheathes the verticillated branches like a tube, while the intervening spaces are interspersed with single sheets, that, however, do not appear to go from branch to branch, but rather are perpendicular to the plane linking the verticils. The irregularly placed pores taper outward quite uniformly and here too are set obliquely to the main axis and curved upward.

Areal distribution and range: Wetterstein Limestone of the northern Calcareous Alps, perhaps particularly in the lower part. Samples:

1. Hall-Bettelwurf [Hall in Tirol, E Innsbruck, Austria], Unterinn valley, Tyrol [Pl. III, Figs. 5–6].
2. on the road to the Lafatscher pass [N Hall in Tirol, E Innsbruck, Austria].
3. Wetterstein cliff.
4. several samples with no indication of provenance that probably come from the same areas as the preceding [Pl. III, Figs. 3–4].
5. (?) Waxriegel, Raxalpe [NW Griesleiten, Reichenau an der Rax, Niederösterreich, Austria].
6. Wetterstein Limestone, Pass Lueg in the Höllengebirge [Golling an der Salzach, S Salzburg, Austria].
7. darker, lower Wetterstein Limestone. Descent from Bärenkopf to Seespitz, Aachensee [Achensee, Tirol, Austria].

Teutloporella (?) *tenuis* nov. sp.
(Pl. III, Figs. 7–10)

I use this name to designate a new species, as a whole very problematic, but exceptionally easy to recognize in thin section. The extraordinary thinness of the calcareous skeleton is its most remarkable characteristic. Naturally, any judgments about its structure and systematic position will thereby be uncommonly complicated, but as appears on the only slightly oblique longitudinal sections of Pl. III, Figs. 7–8, the verticillated branches exhibit a rather clear tapering outward. The emplacement of the pores appears to be random on all of the slides. This suggests with a fair degree of probability that our species is affiliated with *Teutloporella*. The calcareous skeleton was cylindrical and sometimes strongly curved as in Pl. III, Fig. 9. That same figure shows each pore to be enclosed in a lighter (colored) layer of calcite, while the spaces between them are filled by a darker skeletal substance. It may be possible that here we are dealing with the calcified membrane of the verticillated branches. Nothing can be ascertained concerning the emplacement of the branches on which calcification took place, *i.e.* on the distance of the calcareous skeleton from the main axis.

Areal distribution and range: Up to now: Muschelkalk, limestone facies, west of Lapčić, on the Budua sheet, Dalmatia [Budva, Montenegro].

Teutloporella vicentina Tornquist
(Pl. III, Figs. 11–14 [Text-Fig. 7])

Diplopora vicentina Tornquist 1899-2

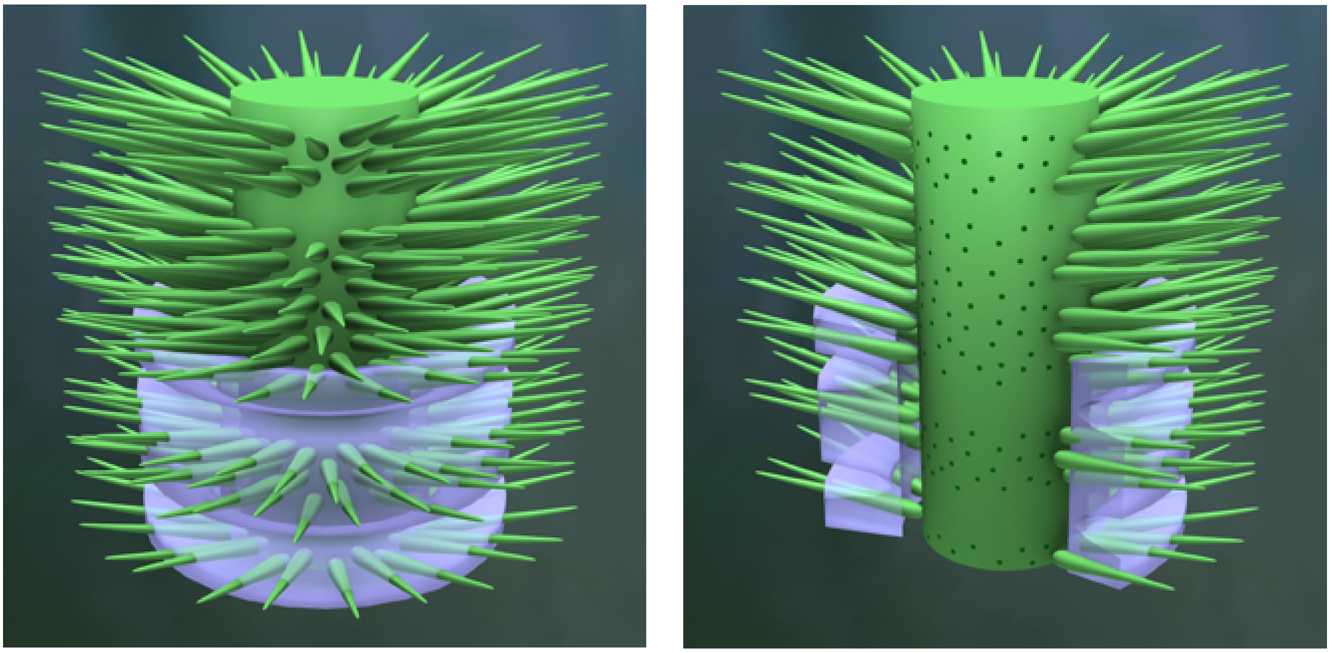
One can define this species briefly as the only annulate *Teutloporella* known to date. The pores are randomly placed. Most often they are oblique to the outer surface, some straight, some curved irregularly (occasionally downward too. See Pl. III, Fig. 13). Withal, they seem to taper uniformly and not very strongly. The annular furrows are always oblique. The height of the segments is most variable even in the same individual.

Areal distribution and range: So far this species is known only in the Spizze Limestone. Samples:

1. lower level of Spizze Limestone, Tretto [Tretto, N Schio – NW Santorso, Véneto, Italy] (Pl. III, Figs. 11–14).
2. Spizze Limestone. South slope of the upper limestone cover of Mt. Enna above Torre Belvicino [Torrebelvicino, W Schio, Véneto, Italy].

Teutloporella vicentina var. *nana* Pia
(Pl. III, Figs. 15–16 [Text-Fig. 8])

In the second of the named localities along with normal individuals of our species also occur some that differ from



Text-Fig. 7.
Reconstruction of *Teutloporella vicentina* (like Pl. VIII, Fig. 8).

them in a series of points. However, the distinguishing features are mostly of a subordinate value and as both populations also show some transitions between each other, I content myself with setting up a variety. Should it prove later that the smaller form also occurs alone, separation as a discrete species would be valid.

Our variety is distinguished primarily by its small size and its smaller number of verticillated branches The pores go through the calcareous skeleton more or less at right angles. More importantly, a truly consistent distinguishing character appears to be the relatively much smaller height of the segments. As Pl. III, Fig. 16 shows, occasionally the course of the tubules is rather strongly curved, whereby the annular segments on the inner side of the curve can exhibit a peculiar appearance of stunted growth.

Areal distribution and range: This species is known to date only from one locality, the Spizze Limestone on the south slope of the upper limestone cap of Mt. Enna, above Torre Belvicino.

Teutloporella triasina SCHAUROTH
(Pl. IV, Figs. 12–19 [Text-Figs. 9–11])

Chaetetes triasinus SCHAUROTH 1855-1

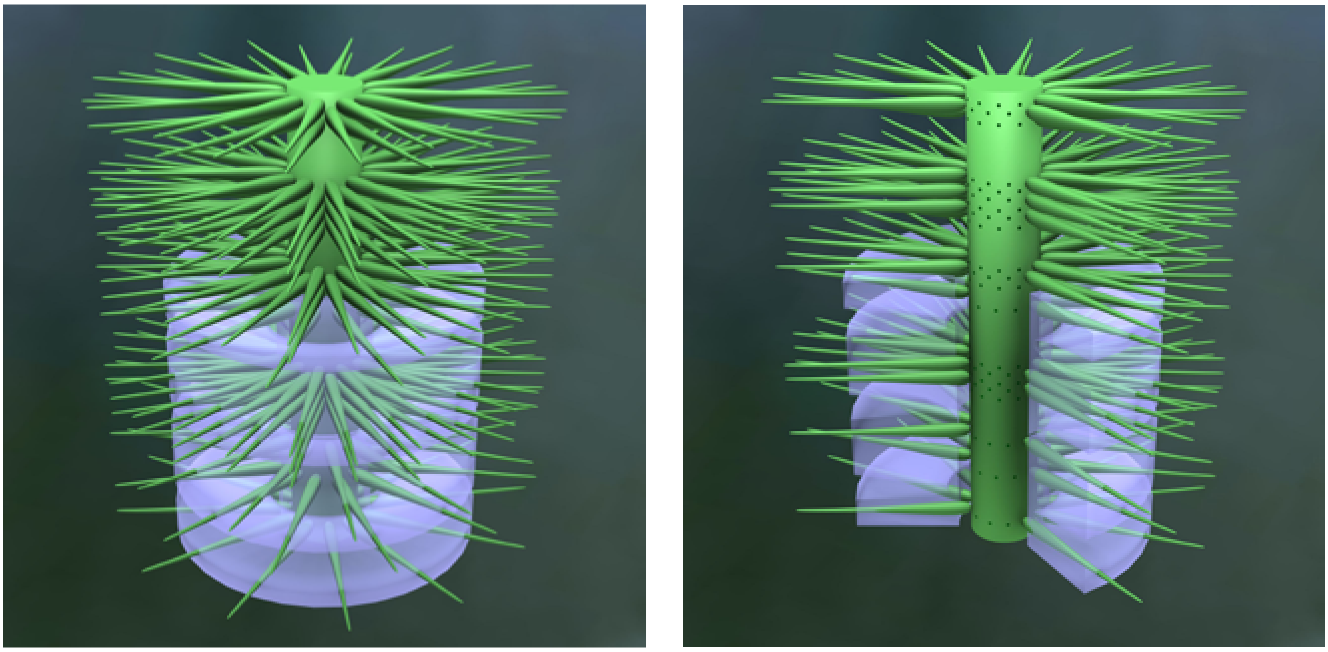
Gyroporella triasina GÜMBEL 1872-1

Diplopora triasina TORNQUIST 1900-4

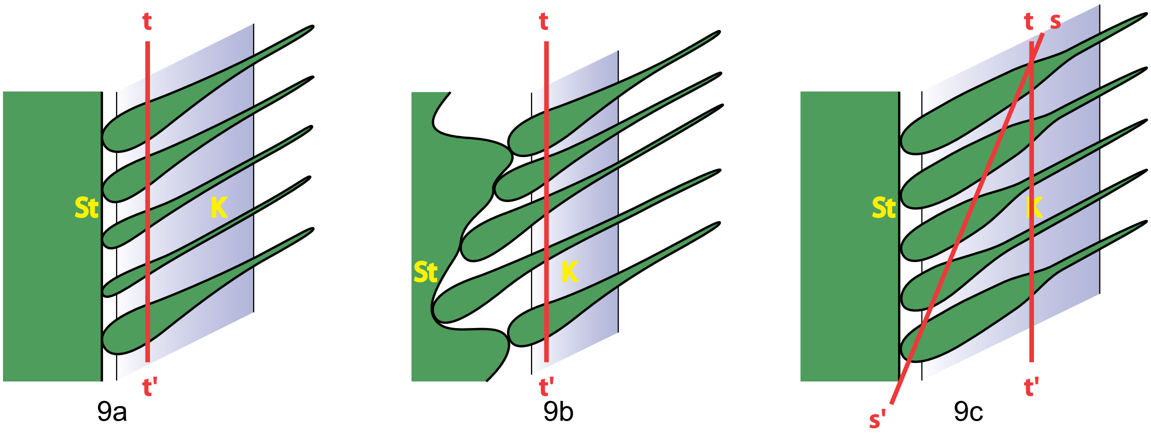
The form of the plant is straight or at most slightly curved. The branches are arranged in quite typical verticils that follow closely on one another. In most cases they are decidedly oblique to the main axis and are curved upward. The fertile part of each lateral branch is rather sharply separated from the assimilatory portion, because the tapering takes place in a rather short distance. Several places in Pl. IV, Fig. 15 show clearly that a thin part of the branch can occasionally be pushed into the thick one, as the accompanying Text-Fig. 10 shows.

A tangential axial section of the inner cavity exhibits a very conspicuous phenomenon as in Pl. IV, Fig. 12 or 16. Namely, we see here that the thickness of the sectioned pores gradually increases in size from bottom to top through several verticils, then abruptly returns to its original size. I subsume the array of pores from the thinnest to the thickest under the name «verticil series». Manifestly, the interpretation of this phenomenon is open to numerous possibilities. First, one might accept that the thickness of the verticillated branches actually varied (see Text-Fig. 9a). However, Pl. IV, Fig. 15 proves this interpretation impossible for in an appropriate diagonal placement of a section all pores of a series show the same thickness. But there are also several other interpretations still possible. One could imagine that the diameter of the main axis increases at regular intervals and then decreases again (Text-Fig. 9b), so that a tangential section approximately parallel to the axis would hit some of the branches at a more distal (thinner) place and some at a more proximal (thicker) place. I personally am not satisfied with this rather forced interpretation. It seems much more probable to me that the thickened part of the branch was wider at some times, narrower at others, *i.e.* that the fertility of the successive branches fluctuated periodically. I believe that this concept should be recommended especially because it is the nearest approach to the recent analogs of the development of verticil series mentioned at the beginning of this chapter. It was the basis for Text-Fig. 9c and the reconstruction of Text-Fig. 11. Incidentally, it seems that occasionally series may not be developed.

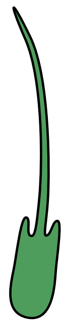
Also noteworthy is the behavior of the calcareous skeleton with respect to its segmentation. The degree to which it is developed varies greatly with the individual of which the illustrations Pl. IV, Fig. 13 and Pl. IV, Fig. 14 may represent extreme instances. As a rule we have to do only with shallow and very oblique incised furrows. The height of the rings constructed in this way coincides in general with that of the verticil series; in particular cases, however, the edge of either one diverges from the other. Because it is developed so rarely I can hardly conceive that this arrangement is functional. Taking into consideration its great variability, which, as is generally known, is taken as indicative of



Text-Fig. 8.
Reconstruction of *Teutloporella vicentina* var. *nana* (like Pl. VIII, Fig. 8).



9a 9b 9c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Text-Fig. 9. (a-c).
Three possible interpretations for the tangential section of *Teutloporella triasina*. K = calcareous skeleton St = main axis t-t' = tangential section (Pl. IV, Fig. 16) s-s' = oblique section (Pl. IV, Fig. 15).

Text-Fig. 10.
Longitudinal section through a branch of the specimen in Pl. IV, Fig. 15.

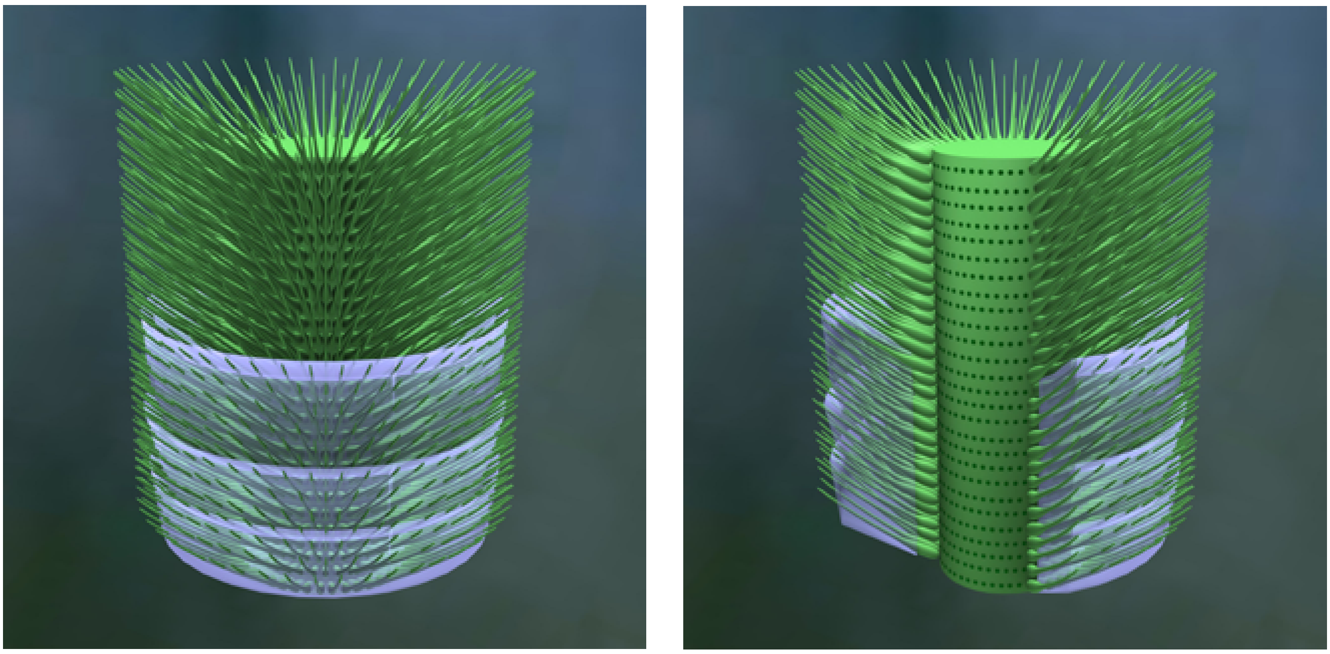
regression, it seems to me highly acceptable that we are dealing with a rudimentary annulation. It possibly derived from a state that is fully and completely represented by *Teutloporella vicentina*. We shall return to this phylogenetically important fact in the section concerned with phylogeny.

The segmentation of the calcareous skeleton visible in thin section differs from that of weathered-out specimens. In the latter it usually occurs more distinctly and in all individuals. Probably it originates primarily through great differences in resistance to weathering of the discrete parts of the calcareous skeleton that in turn might be related to the structure of the verticil series.

Areal distribution and range: This species seems to be characteristic of the lower south-Alpine Muschelkalk. Localities:

1. base of the Spizze Limestone. St. Ulderico in Tretto, northern Schio [Sant'Ulderico, N Schio, Véneto, Italy] [Pl. IV, Figs. 12–14].
2. Recoaro Limestone. Mt. San Rocco, Tretto [San Rocco, N Schio – N Santorso, Véneto, Italy] [Pl. IV, Fig. 17].
3. Dactylopore Limestone from the Mt. Spizze level. Monte Civillina, toward Val Retassone, Recoaro [Retassene, ESE Recoaro Terme, W Schio, Véneto, Italy].
4. (see 2) Virgloria Limestone. Venedig, Mt. San Rocco, Tretto [San Rocco, N Schio – N Santorso, Véneto, Italy] [Pl. IV, Figs. 15–16].
5. lower Muschelkalk. Ablitzen Ravine, northwest of the lower Bombasch valley near Pontafel [Pontebba / Pontafel, Friuli – Venezia Giulia, Italy].
6. lower levels of Mt. Spizze limestones. Loose blocks eastward below Mt. Spizze near Recoaro [Recoaro Terme, W Schio, Véneto, Italy].

Remark: The rather poorly preserved specimens reproduced on Pl. VII, Figs. 18–19 differ in some respects from typical *Teutloporella triasina* so perhaps it concerns a sepa-



Text-Fig. 11.
Reconstruction of *Teutloporella triasina* (like Pl. VIII, Fig. 8).

rate, but certainly very closely related species. The material does not warrant the introduction of a new species name. The special characteristics appear best in the tangential section of Pl. IV, Fig. 18. Here too we recognize a periodic change in the diameter of the cross sections of the pores, but the change from maximum to minimum does not occur suddenly but gradually up and down. Approximately in the middle of the figure is a verticil of which the branches are so closely packed that owing to a lack of space there is a conspicuous flattening that I have not yet observed in the typical *Teutloporella triasina*. The dimensions do not seem to be substantially different in the two forms.

Locality: Lower Muschelkalk, north Pontafel [Pontebba / Pontafel, Friuli – Venezia Giulia, Italy], westward below the Zirkel pass, on the way to the «Hole».

Oligoporella nov. gen.
(Pl. VIII, Fig. 13)

A small number of relatively thick pores taper outward more or less strongly, but this applies strictly only to the upper part of the plant. In primitive species the basal verticils could be of the phloiophorous type. To date all known species are euverticillate. Spore development probably took place in the swollen distal portion of the verticillated branches. Undoubtedly this genus has much in common with the genus *Teutloporella*. Originally I considered both of them as subgenera of a single genus. However, their habitus is so different and so easily recognizable that for practical reasons complete separation appears to be recommended. Also the importance of the distinguishing characteristics compiled in the following table must not be underestimated, so nominating two discrete genera seems fully justified at this time. During the development of the phylogenetic section I became convinced that the two genera are quite remote from each other phyletically.

Oligoporella	*Teutloporella*
Number of branches in a verticil 10–20.	Number of branches in a cross-section (in normal individuals) always over 30, up to 60.
Only euverticillate forms known.	A majority of forms is proverticillate.
Verticils separated by distinct intervals.	Verticils when present, set densely, touching each other.
Verticils commonly closely packed.	Verticils when present, always very simple.
Almost certainly derived from *Macroporella.*	Origin unknown, if derived from *Macroporella,* independent for sure.

Of all of the Diploporids *Oligoporella* resembles most the juvenile stages of *Neomeris* that we have already remarked on in the comment on the anatomy of the trichophorous type. As we shall see again, there is a certain probability that we are dealing with an interesting and in the plant kingdom a very rare case of the validity of HAECKEL'S basic law of biogenetics.

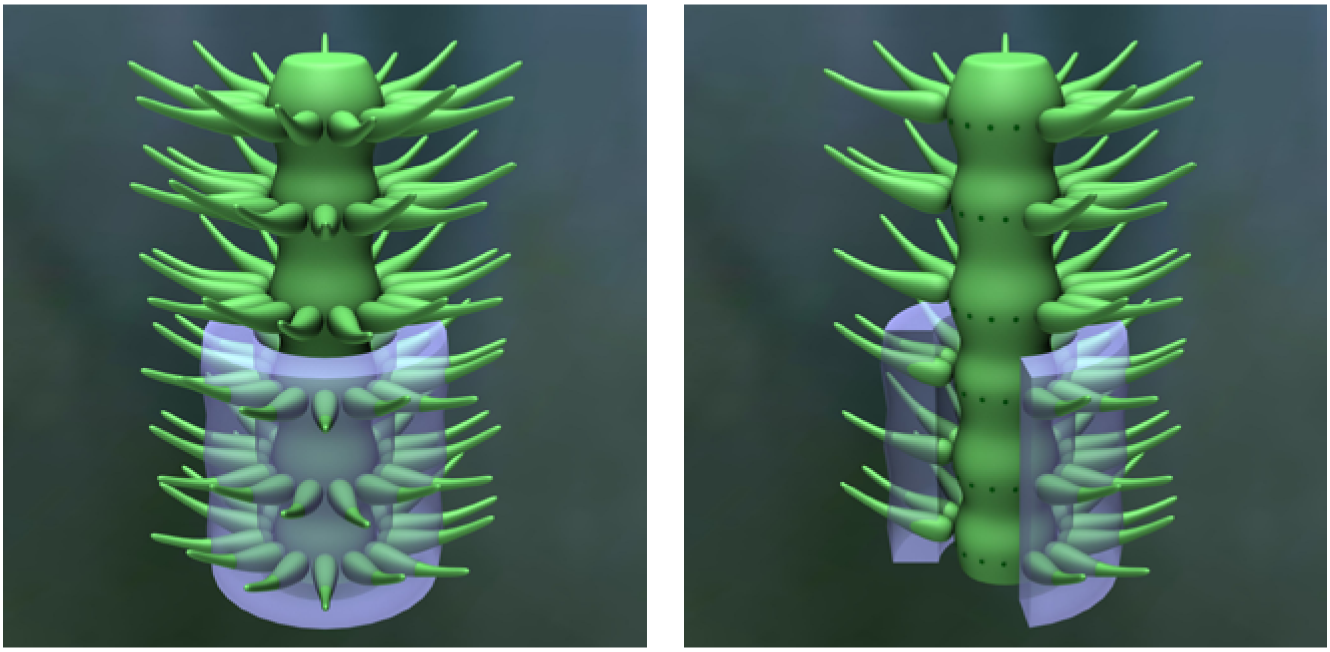
Areal distribution and range: Muschelkalk of the northern Calcareous Alps and the Dinarides.

Oligoporella pilosa nov. sp.
(Pl. IV, Figs. 1–8 [Text-Fig. 12])

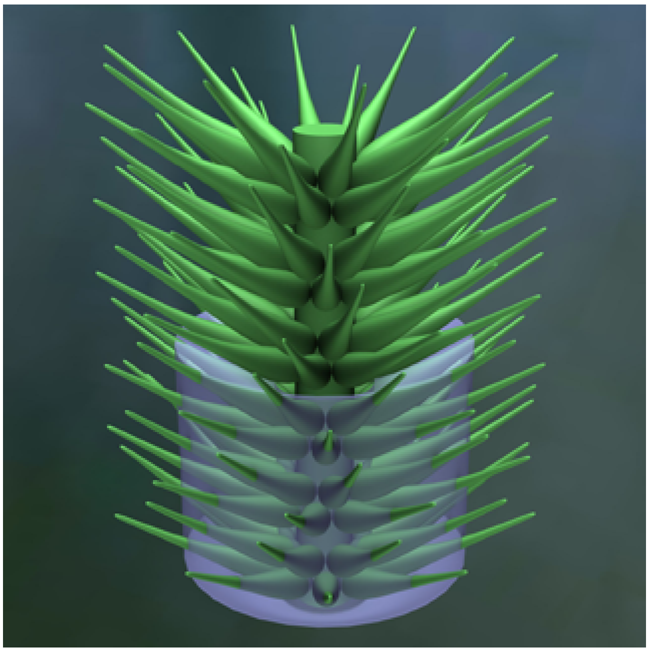
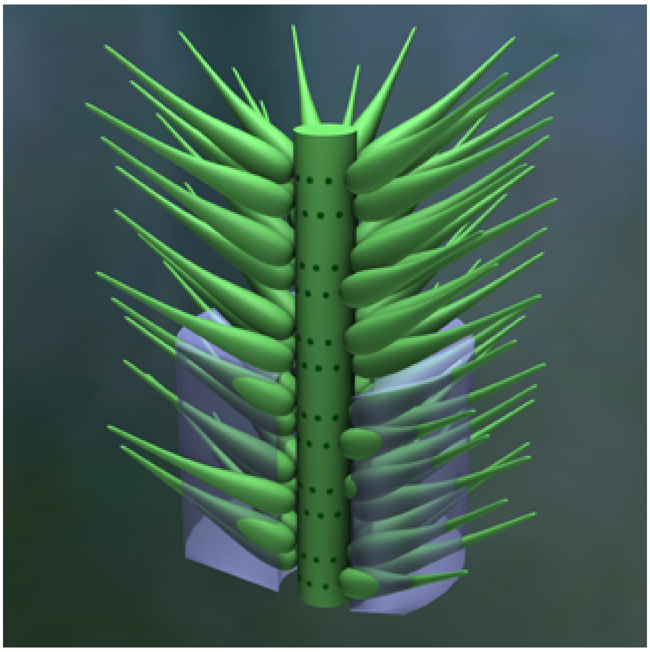
The genus *Oligoporella* is based on this species. Occasionally the calcareous skeleton shows a slight curvature. The canaliculae that occur in relatively dense verticils taper outward only moderately but for the most part very clearly. As a rule the verticils are well separated from one another by pore-free spaces, but exceptionally they are quite close together (Pl. IV, Fig. 8). The rather thin-walled calcareous skeleton is mostly unsegmented. However, it occasionally develops a well-marked bulge (Pl. IV, Fig. 6).

Areal distribution and range: To date examples of this species are known only from the Muschelkalk of Dalmatia and precisely in the vicinity of Budua [Budva, Montenegro].

1. Muschelkalk, limestone facies, west of Lapčić [Pl. IV, Figs. 1–7].
2. Muschelkalk, limestone facies, between Stanišići and Grkova voda valley [Pl. IV, Fig. 8].



Text-Fig. 12.
Reconstruction of *Oligoporella pilosa* (like Pl. VIII, Fig. 8).

Text-Fig. 13.
Reconstruction of *Oligoporella serripora* (like Pl. VIII, Fig. 8).

3. Muschelkalk, sandy marl facies. Ivanovići.

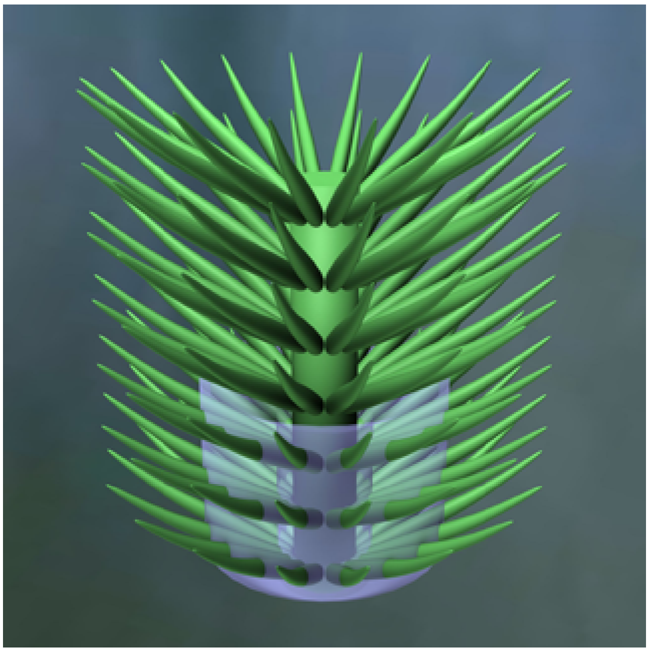
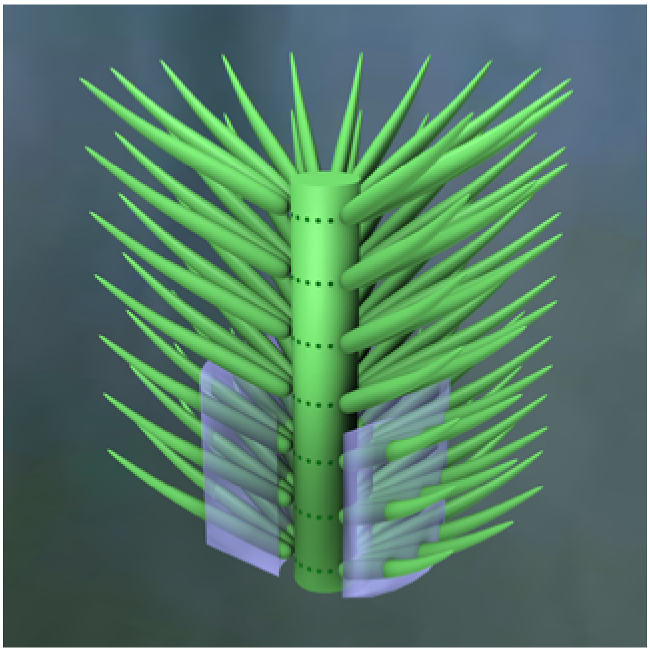
Oligoporella serripora nov. sp.
(Pl. IV, Figs. 9–11 [Text-Fig. 13])

This species is closely related to *Oligoporella pilosa*. The average size is somewhat less, the verticils are more closely spaced so that they appear to be biserial. The inclination of the branches against the main axis is rather large. But the most striking difference is that the pores taper very sharply outward. At least in part this may be related to the greater thickness of the calcification. The inner cavity (and obviously the corresponding main axis) are proportionately narrow.

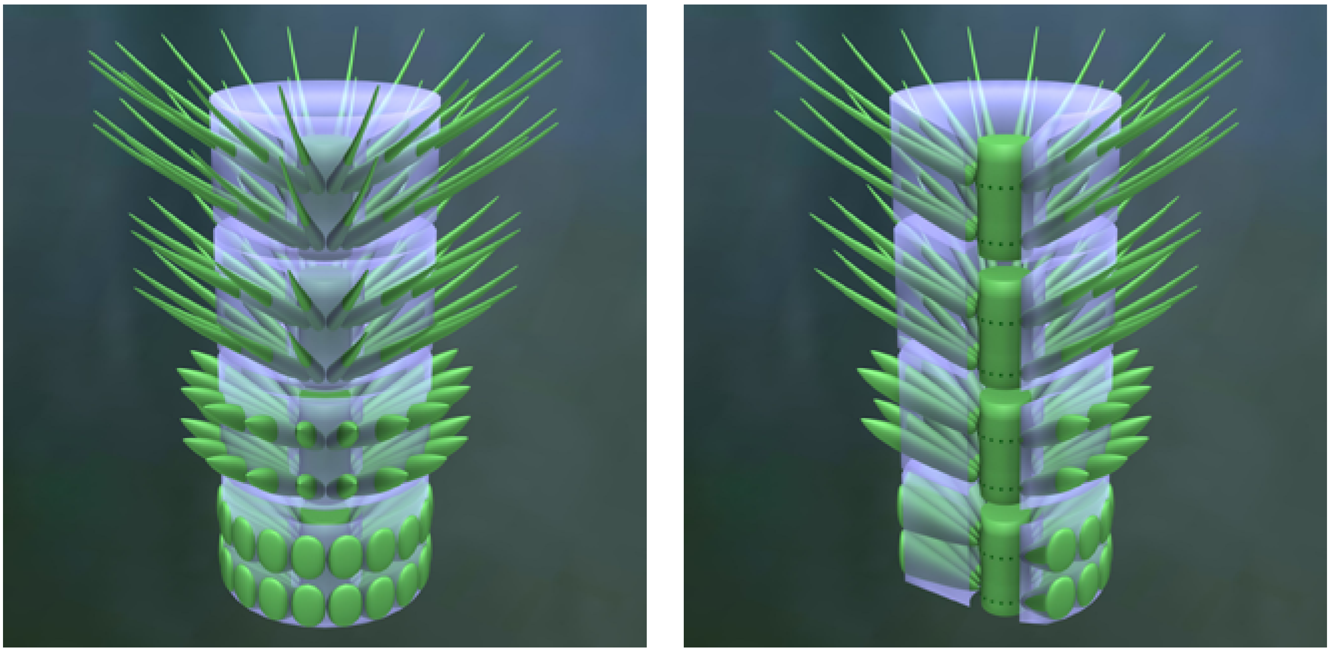
To date only one locality is known: Muschelkalk, Sarenkofel.

Oligoporella prisca nov. sp.
(Pl. V, Figs. 1–8 [Text-Figs. 14–15])

This species presents very noteworthy and phylogenetically important peculiarities. Originally I had allocated the several cross sections made from samples that had been submitted to me not just to two separate species but even to discrete genera. Looking at the figures – Pl. V, Fig. 7 and Pl. V, Fig. 8 –, one might not hesitate to assign the first to *Oligoporella* and the second to an euverticillate *Macroporella*. I might never have known the error of such a judgment, although both forms always occur together in the same

Text-Fig. 14.
Reconstruction of *Oligoporella prisca* (like Pl. VIII, Fig. 8).



Text-Fig. 15.
Four details from a longitudinal section of an example of *Oligoporella prisca*. They show the gradual change in form of the verticillated branches from bottom to top.

rock, and certain slides like Pl. V, Fig. 6 show a transition, if a lucky accident had not given me an unusually long and favorably oriented tangential section, Pl. V, Fig. 1. This slide shows at one end (the lower one judging from the angle of the branches) an unquestionable widening of the pores outward while at the other end they contract somewhat in the distal direction. So the same specimen combines the characteristics of *Macroporella* and *Oligoporella*. At first sight this appears to put in question the foundation of the entire system of our classification. Through closer examination of the relationship depicted we, however, detect a phylogenetically most informative analogy with recent Siphoneae verticillatae. We know, that is to say, *i.e.* from *Neomeris* that the lowest verticillated branches have a more primitive construction than the upper ones and represent the juvenile stages. On the other hand, as I shall have occasion to explain later, these juvenile stages recapitulate phylogenetically older stages. Too, we have good reason for the assumption that *Oligoporella* was derived from *Macroporella* (see the section on phylogeny). I feel, there also, that a completely plausible explanation of the observations is the presumption that the lower phloiophorous type verticils of *Oligoporella prisca* is a recapitulation of an ancestral form. Not only does it give a picture of the juvenile stages of this, but also of several other trichophorous species. In Text-Fig. 15 I have attempted to represent how a transition from phloiophorous and trichophorous verticils might, perhaps, be conceived. Maybe relationships similar to those of the present species exist to a lesser extent in *Oligoporella porosa* where the degree of tapering of the pores also changes.

The basal part of *Oligoporella prisca* is not easily mistaken, for up to now it is the only confirmed phloiophorous form with an euverticillate configuration of the verticillated branches. The narrowness of the inner cavities in the upper section of the plant resembles those of *Oligoporella serripora* but it is immediately distinguishable by the lesser amount of tapering in the verticillated branches that in most cases is even less than in *Oligoporella pilosa*. In contrast to the two other species of the genus the pores are arranged entirely as simple verticils. In the outer part of the calcareous skeleton this regularity is certainly blurred, as Pl. V, Fig. 1 shows, and indeed, not all of the pores originally present may be visible.

Areal distribution and range: This species seems to be confined to the Reifling Limestone of the northern Alps, as much as one can presume so far. Localities:

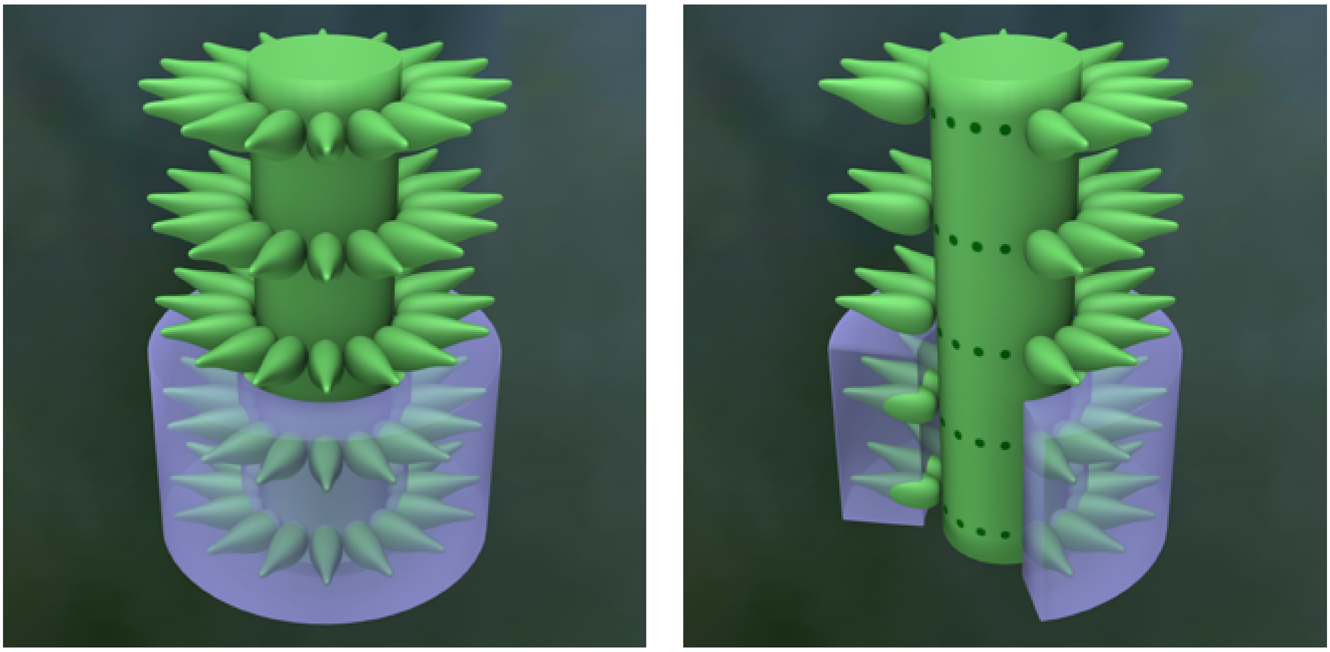
1. Schlegelberg [Sandkogel] above Vorderstaff near Schwarzenbach an der Pielach [S Schwarzenbach an der Pielach, Niederösterreich, Austria] [Pl. V, Figs. 3–7].
2. Schwarzenberg near Türnitz [S Schwarzenbach an der Pielach, Niederösterreich, Austria] [Pl. V, Fig. 8].
3. Reiflinger Limestone. East Benn Alps, SW Klein-Zell [? Kleinzell, Niederösterreich, Austria] [Pl. V, Figs. 1–2].

Physoporella Steinmann
(Pl. VIII, Fig. 14)

Steinmann 1903-1 and 1903-2

The type of verticillated branches I have defined as pyriferous is decisive in an assignment to this genus, that is the pores terminate blindly, but differ from the vesiculiferous type in that the calcareous skeleton shows no distal widening. As a rule the basal part of the branches is the thickest. All species known to date have Pore Series, and on phylogenetic grounds it is probable that this arrangement is typical of the entire genus for presumably it was derived from the already euverticillate *Oligoporella*. In our genus the occurrence of closely spaced biserial verticils is common (apparently in more specialized forms). The type of segmentation of the skeleton that we have learned to call «bulge» reaches an extreme development in some forms assigned here.

Physoporella is, as it were, a counterpart of *Gyroporella*. In the growing plant the assimilatory function of the verticillated branches quite obviously retrogresses. We must also suppose that the juvenile stages of its development are simi-



Text-Fig. 16.
Reconstruction of *Physoporella pauciforata* (like Pl. VIII, Fig. 8).

lar in structure to those of *Oligoporella*. By the way, I feel it is probable, at least in primitive species like *Physoporella pauciforata*, that the last shoot on all of the branches also had assimilatory filaments. However, before calcification was complete, these filaments dropped off. The basal part of the branches was converted into a sporangium that for better protection was completely coated with lime. In specialized forms like *Physoporella minutula* the formation of filaments on fertile shoots may already have been suppressed completely.

Areal distribution and range: So far this genus seems characteristic of the Muschelkalk of the East Alpine systems and is rather widespread in them, for it is found not only in the northern Calcareous Alps, but also in the Tauern Triassic and in certain Swiss Klippes including the East Alpine nappes.

Physoporella pauciforata GÜMBEL
(Pl. V, Figs. 9–19 [Text-Fig. 16])

Gyroporella pauciforata GÜMBEL 1872-1

Physoporella pauciforata STEINMANN 1903-2

The calcareous skeleton is cylindrical and linearly prolate without any marked segmentation. The lateral branches occur in true, simple and often very regular verticils. They are egg- or pear- shaped, more or less elongated and taper outward. Mostly they are completely enclosed in lime. Occasionally, however, a tapered pore perforates the skeleton (see Pl. V, Figs. 11 & 14). Since this occurs only exceptionally and, it appears, involves only single pores of a plant, I do not consider that much importance should be attached to it. The openings can scarcely be considered as passageways for the filaments, but only as accidental openings that would disappear if the calcareous layer were thicker. The angle of the verticillated branches and the distance between the verticils are subject to great variation.

As a whole our species displays the essential attributes of the genus *Physoporella* without specific complications. Thus it may pass for the type of the genus.

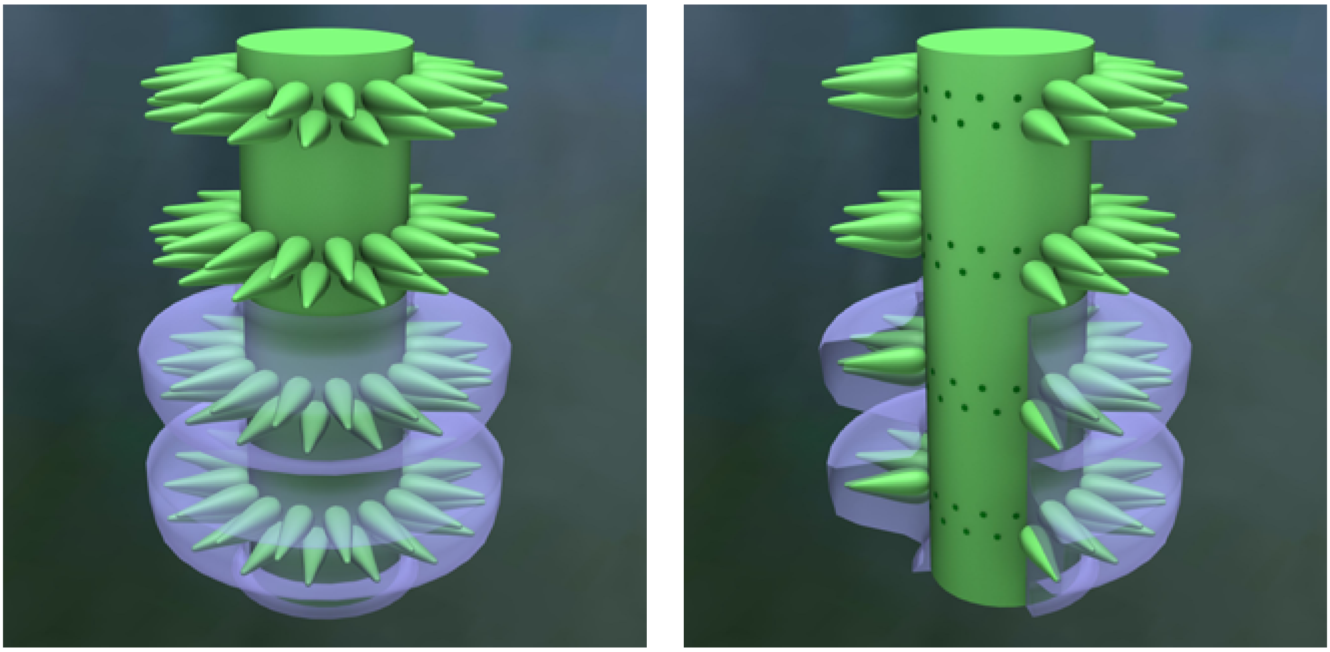
Areal distribution and range: For the present *Physoporella pauciforata* can only be strongly presumed as designating a given portion of the Muschelkalk, perhaps correlative with the Reiflinger level, while it does not appear to occur in the Wetterstein Limestone. It is worth mentioning that so far our species is the only one that has been found in the central Alps with *Diplopora debilis*. That is to say that I succeeded in assigning to it with considerable confidence a find in a gastropod-bearing limestone in the Nesslinger cliff near Krimml (Pl. V, Fig. 17. See also STEINMANN, 1910-2). This occurrence argues in favor of my view that the limestone in question is not the equivalent of the typical Tauern dolomite with *Diplopora debilis*. Localities:

1. North slope of the Brandmäuer near Puchenstuben [Pl. V, Figs. 9–12].
2. Schwarzenberg near Türnitz [Niederösterreich, Austria] [Pl. V, Figs. 13–16].
3. (?) Muschelkalk. Brenn Alps, Road to Rumpelzbauer.
4. dolomite with Gyroporellae and crinoids. Brecciated piece of the upper Muschelkalk between Süs- and Sarenkofel.
5. (?) *Gyroporella* limestone at the uppermost part of the Muschelkalk group. South slope of the Sulzberg near Fadental-Wolster, Mariazell.
6. (?) Upper Muschelkalk. Block between Badmeister and Süskofel.
7. Nesslinger cliff near Krimml [Pl. V, Fig. 17].
8. Schlegelberg [Sandkogel] above Vorderstaff near Schwarzenbach an der Pielach [S Schwarzenbach an der Pielach, Niederösterreich, Austria] [Pl. V, Fig. 18].

Physoporella dissita GÜMBEL
(Pl. VI, Figs. 1–4 [Text-Fig. 17])

Gyroporella dissita GÜMBEL 1872-1

The most conspicuous feature of this species is the segmentation of the calcareous skeleton. At first sight it appears that it is a typical annulate form. However, closer in-



Text-Fig. 17.
Reconstruction of *Physoporella dissita* (like Pl. VIII, Fig. 8).

spection shows that there is never more than one verticil to a segment. Therefore I believe we are more in accordance with the facts if we interpret the segmentation of our species as an extreme of bulge development, as an enhanced advancement of the behavior displayed in some specimens of *Oligoporella pilosa* (Pl. IV, Fig. 5) and also in the same way in *Physoporella minutula*, described below. This is even more true because true segmentation occurs neither in *Physoporella* nor in the related *Oligoporella*.

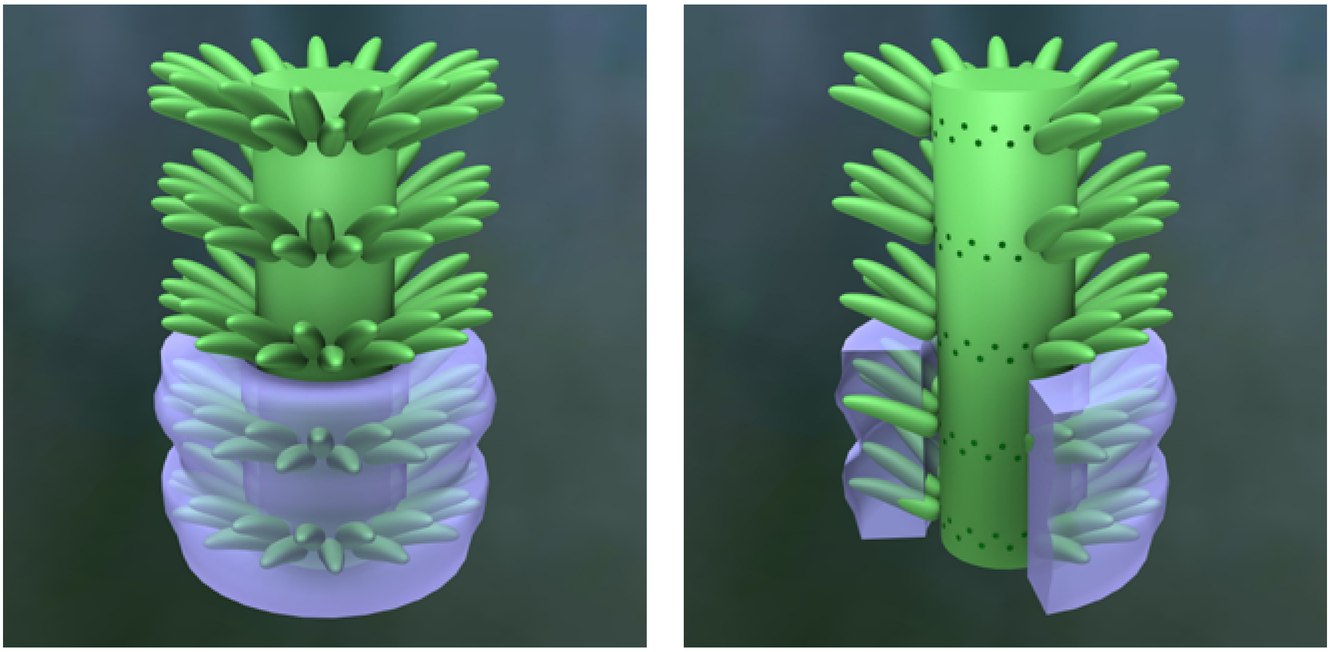
The branches, always tapered distally, are arranged in serried, tightly packed verticils most of which have a very regular biserial structure. The outer surface is always completely enclosed in calcite.

Areal distribution and range: For this species only one rock sample is available to me with the data: Light-colored massive limestone, a bed intercalated between the top of the Gutenstein Limestone and the base of the black, siliceous nodular limestones (Reiflinger Limestone). Tiefenbach graben near Saalfelden.

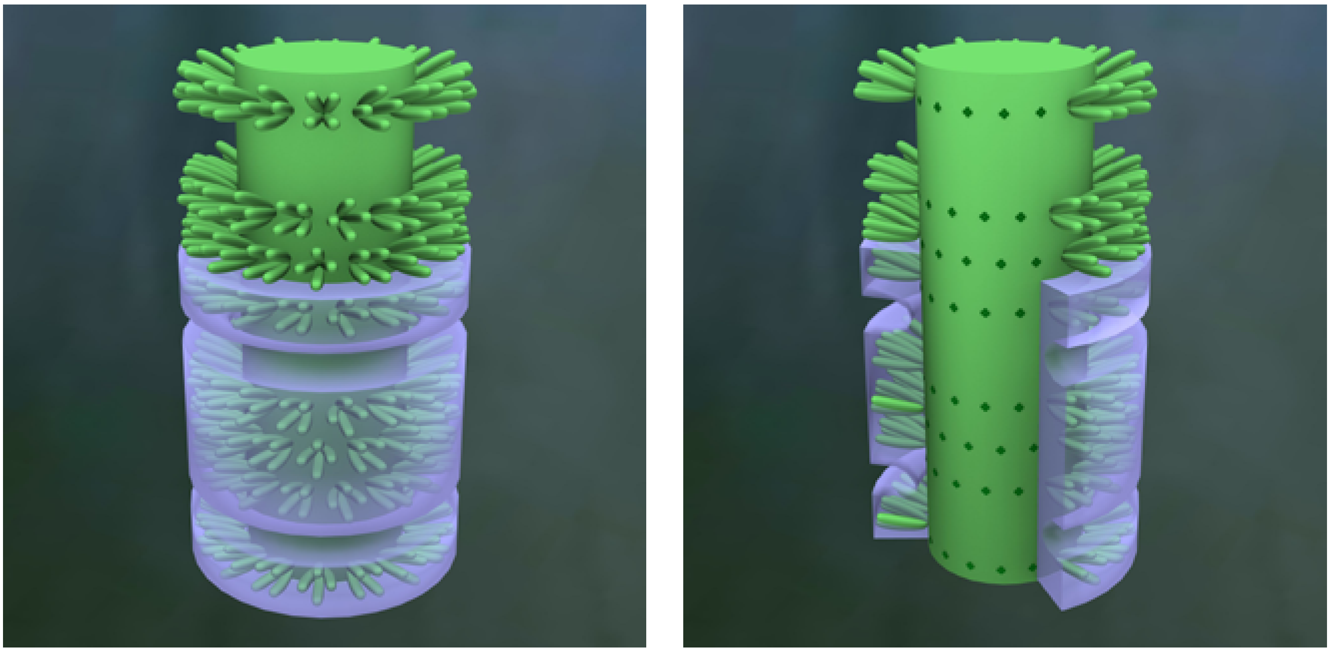
Physoporella minutula GÜMBEL
(Pl. VI, Figs. 5–12 [Text-Fig. 18])

Gyroporella minutula GÜMBEL 1872-1

The calcareous skeleton of this species shows every transition from an almost smooth outer surface to deep decisive segmentation that almost approaches the state of *Physoporella dissita*. See the transitional series on Pl. VI, Figs. 5–8. I believe it is entirely clear here that we are dealing



Text-Fig. 18.
Reconstruction of *Physoporella minutula* (like Pl. VIII, Fig. 8).



Text-Fig. 19.
Reconstruction of *Kantia philosophi* (like Pl. VIII, Fig. 8).

only with an enhanced undulation. Again the branches are arranged in closely spaced biserial verticils (see in particular the detached segment in Pl. VI, Fig. 10). However, their shapes differ from the species described previously. Their form does not taper outward, or the tapering is only scarcely perceptible. On the contrary their shape is a tube with rounded distal ends, or, if you will, sausage-like.

Areal distribution and range: Only a single rock sample with the data: Wetterstein Limestone. Zwecken Alps near Mythen, Canton of Schwyz.

Kantia nov. gen.
(Pl. VIII, Fig. 15)

This genus is characterized by being metaverticillate and phloiophorous with a tendency toward the vesiculiferous type. It seems to represent a very discrete group of forms. All currently known species are truly annulated, perfectly straightly prolate, and calcification in all of them reaches the main axis which comparatively is very thick. Probably some specialized, specifically modified branches served as sporangia. Possibly the transformation always affected an entire tuft.

As far as is known, the distribution of the genus is restricted to the Muschelkalk of the Dinarides.

Kantia philosophi nov. sp.
(Pl. VI, Figs. 17–21 [Text-Fig. 19])

The study of this species was of special importance to me, for favorable conditions permitted observation of a series of relationships that are also applicable to other forms. Above all, this species caused the concept, «metaverticillate» to be set up. As may be concluded from the almost completely smooth character of its inner surface, the calcareous tube was directly in contact with the main axis. This leads the observer to adopt two points of view: in the first place the basal part of the verticillated branches is preserved, where branches of the same tuft are closest to one another (see in particular Pl. VI, Fig. 19) and thereby that these tufts truly exist becomes distinctly unquestionable. Now it would be certainly very suggestive to compare these groups of branches with the secondary verticillated branches of *Neomeris* and its relatives. However, in the shared stem of the tufts there is no place left that corresponds to the primary verticillated branch of *Neomeris*. There can also be no doubt that the pores representing branches are not secondary but are primary verticillated branches that from a point on the main axis diverge from each other outward.

At their distal end the pores were apparently closed by a somewhat outwardly curved thin calcareous sheet, but it was obviously very delicate and in many cases was destroyed. Probably the outer membrane of the verticillated branches was not calcified to the same extent in all individuals. In any case, we have before us a phloiophorous species approaching the vesiculiferous type. I strongly doubt whether here, as (was the case) in *Gyroporella*, all lateral branches served as sporangia, for they show no trace of a bubble-like enlargement. On the other hand we see on Pl. VI, Fig. 20 on the left of the middle section two pores that in the middle of the calcareous skeleton end with conspicuous swellings. They could easily correspond to sporangia, all the more because we shall get to know a similar occurrence in the related *Diplopora annulata*. But after all this interpretation is not yet reliable.

The calcareous skeleton is divided into segments the height of which varies greatly. The furrows occasionally reach the inner cavity. Their outer edges frequently come closer together again.

The main axis, that in this case we know the shape of, was cylindrical without any constrictions. Its diameter is very large in comparison to the length of the branches.

Areal distribution and range: Up to now only one locality: Lower Muschelkalk. N Pontafel [Pontebba / Pontafel, Friuli - Venezia Giulia, Italy]. Below Punta Lonas on the trail to the Kron-Halter hut. Together with *Gyroporella ampleforata*.

Kantia hexaster nov. sp.

(Pl. VI, Fig. 13)

Unfortunately I have to hand only one example that apparently represents only one segment which is bounded above and below by natural separation surfaces. Compared to the last species it shows the following differences (see the table of dimensional relationships): There are six pores in a tuft. The diameter of the tubes should be only half as large as in a well-developed *Kantia philosophi*. Probably the number of tufts in a verticil was substantially less than 20. The systematic importance of these characteristics is not great; however, it seems to me, at least for the present, their total makes necessary a separation into two species, but it is also not impossible that the study of additional material will bring to light a complete transition between them.

Locality: Muschelkalk, west of Lapčić. Budua sheet, Dalmatia [Budva, Montenegro].

Kantia dolomitica nov. sp.
(Pl. VI, Figs. 14–16 [Text-Fig. 20])

The weathered specimens of our species have an extraordinary resemblance to *Diplopora annulata* and at first I did not doubt its affiliation with this species. However, the study of thin sections, for which, by the way, the material was not very suitable, made it appear probable to me that I was dealing with a *Kantia*, and in fact with a species with much closer connection to a vesicular type than *Kantia philosophi*. It seems to me that the best evidence for this is Pl. VI, Fig. 14 and the uppermost part of Pl. VI, Fig. 16. In particular the first section shows clearly the bulbous dilation at the end of the branches, which unquestionably are arranged into tufts. This species is distinguishable from the two preceding ones by the much thinner shape of the branches. On Pl. VI, Fig. 16 it is noticeable that the terminal widening can be seen clearly only in the upper part. Perhaps we should interpret this as indicating that only a part of the plant was fertile. An outer opening of the pores was never observed. Some of the branches are perpendicular to the main axis, some are oblique. Most are curved slightly. Too, the height of the segments is most variable again. We must have to do with a highly specialized *Kantia*, as the geologic level confirms.

Locality: Up to now: Schlern Dolomite. Val Sorda near Latemar in Fleimsvalley, South Tyrol (today: in Italy).

Diplopora SCHAFHÄUTL
(Pl. VIII, Fig. 16)

SCHAFHÄUTL 1863-1

I limit this generic name to the *Diplopora annulata* group, *i.e.* to the metaverticillate, trichophorous Diploporids. As the species just named is the only well-known representative of this type it is hard to determine additional definitive characteristics for the whole genus. In particular, it remains doubtful whether segmentation (annulation) is a general generic characteristic. However, it seems to be probable because it is a characteristic of all of the closely related Kantiae. At least in typical cases the verticillated branches are filamentous and relatively thinner than in all other Diploporids. Perhaps sporangia occurred as more or less spherical swellings on a few verticillated branches. In these cases, their lesser number would be noteworthy as permitting the presumption of extensive vegetative reproduction.

I consider this genus as the most highly specialized of the Triassic dasycladaceans known to date.

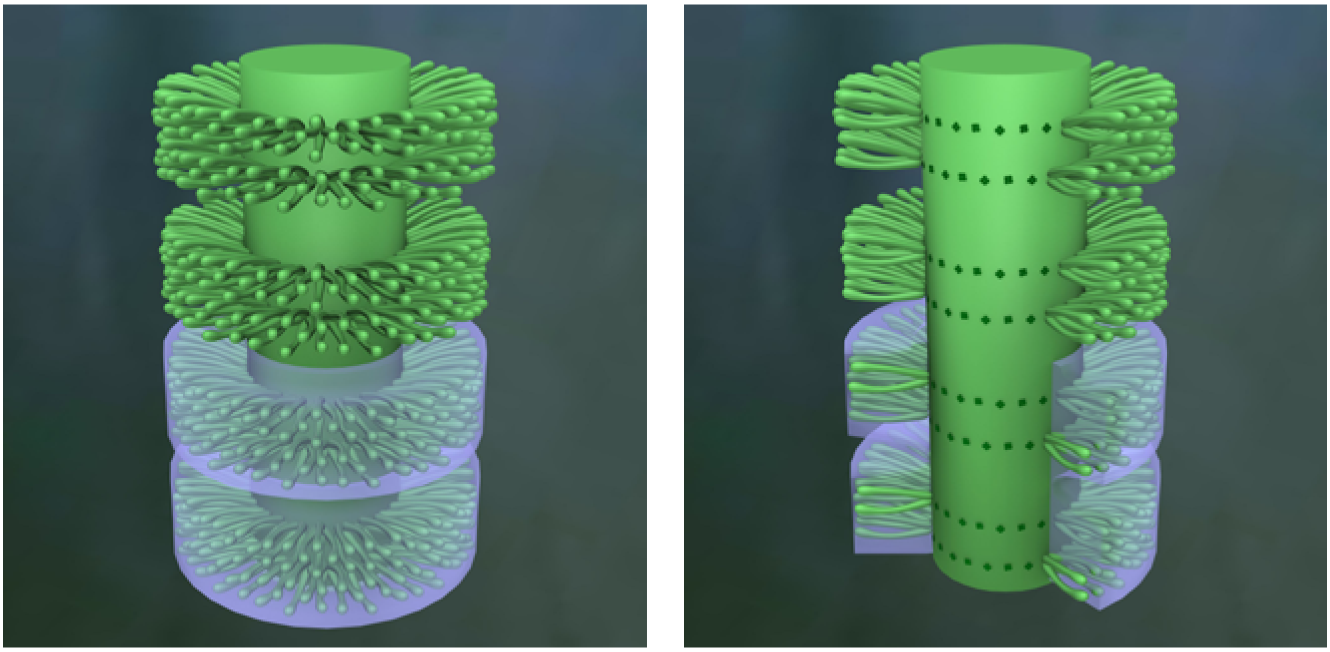
The distribution of this genus is very extensive, for it occurs as a rock builder not only in the northern Calcareous Alps, in the central Alps and in the Dinarides, but also in areas that are not Alpine, namely the Muschelkalk of Upper Silesia (Oberschlesien).

Diplopora annulata SCHAFHÄUTL
(Pl. VII, Figs. 1–17; Pl. VIII, Figs. 1–2 [Text-Figs. 21–22])

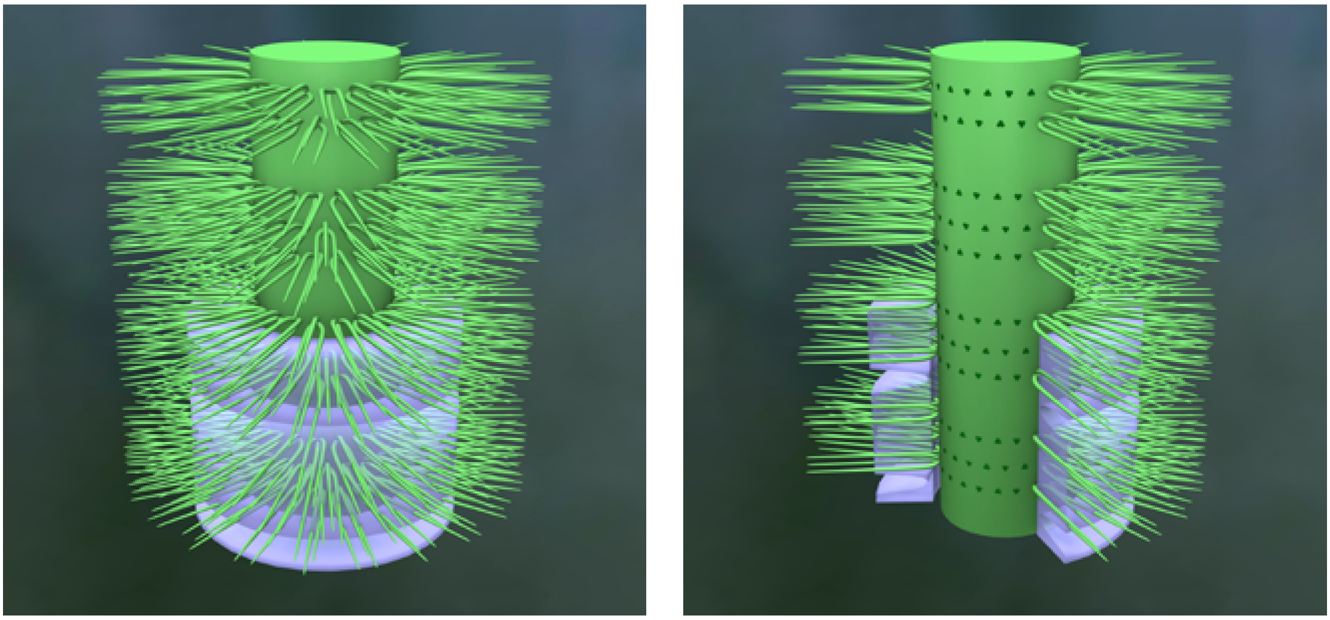
Nullipora annulata SCHAFHÄUTL 1853-1

Gastrochaena annulata STOPPANI 1857-1

Gastrochaena obtusa STOPPANI 1857-1



Text-Fig. 20.
Reconstruction of *Kantia dolomitica* (like Pl. VIII, Fig. 8, but inverted, the longitudinal section is above).



Text-Fig. 21.
Reconstruction of *Diplopora annulata* (like Pl. VIII, Fig. 8).

Chaetetes annulata GÜMBEL 1861-1

Diplopora annulata SCHAFHÄUTL 1863-1

Diplopora porosa SCHAFHÄUTL 1863-1

Diplopora articulata SCHAFHÄUTL 1863-1

Cylindrum annulatum ECK 1865-1

Dactylopora annulata REUSS 1866-2

Gyroporella annulata GÜMBEL 1872-1

Gyroporella cylindrica GÜMBEL 1872-1

Gyroporella multiserialis GÜMBEL 1872-1

All previous authors have maintained more or less decidedly that the number of Pore Series in one annular segment is an invariable specific determinant. *Diplopora annulata* was the only form described in which this number amounts to 2, while those samples with more rows were segregated under various names (see the discussions in older literature). Well apart from the fact that in a metaverticillate genus like the present one true Pore Series are never seen, through precise studies of very rich material I have now I satisfied myself with complete certainty that a classification of the diplopores into species based on the number of verticils in a segment is impossible. Segments with two pore rows (= a tuft) occur at all only with extreme rarity and always as but one example in a slide together with numerous variants; however it then seems, as far as observations go, that the number of rows remains unchanged throughout the whole individual. But in segments of greater height the number of verticils usually varies from segment to segment. Accordingly, if we eliminate completely from the definition of a species the number of verticils in a segment, then the thus more broadly subsumed *Diplopora annulata* may be described as follows:

The calcareous skeleton is perfectly cylindrical and straightly prolate. If the sample obtained is long enough it almost always shows approximately horizontal incised annular furrows that cut it into segments. Most of the furrows are not very wide and reach almost to and occasionally touch the inner cavity. Their two walls do not tend to curve gently and push into each other but meet at a sharp angle. The outer edges of the furrows often approach each other, occasionally even touching (see Pl. VII, Fig. 12). The height of the segments is not only extremely variable in different specimens but also in any one specimen.

At first sight the thin pores appear most often to be placed entirely at random. To determine their true position one must look for those specimens in which the inner cavity is especially narrow, in which calcification extends further than usual towards the main axis (see Pl. VII, Figs. 1–2 & 12; *etc.*). Then one sees how, in the innermost portion of the calcareous skeleton several pores (according to previous observations always three) converge until they finally touch. This means we have to deal with a metaverticillate form. The corresponding verticillated branches diverge very rapidly at first, then run almost parallel (see in particular Pl. VII, Fig. 1, left, where such tufts extend its full width). In most cases only this outer part is calcified.

Occasionally the calcification extends somewhat inward between discrete verticil tufts, so that the inner end of the pores come to lie in low furrows, thus indicating their correspondence with verticils (see Pl. VII, Fig. 16 as well as the weathered specimen, Pl. VII, Fig. 3). In one case (Pl. VII, Fig. 17) it was also observed that an annular furrow penetrating inward from the outer side of the calcareous skeleton has a corresponding bulge on the inner surface.

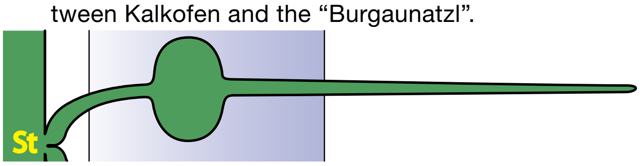
Pl. VIII, Fig. 2 shows a section that through a rare coincidence passes in an almost axial direction through the tip of a specimen. We see that the calcareous skeleton was completely closed, that manifestly growth had already ceased. The verticillated branches in this uppermost part of the plant seem to have been especially thin. According to GÜMBEL and BENECKE the placement of pores should be completely random here. Perhaps this piece of information can be explained thus: here the verticils are especially close together. The remarkably sharp and smooth inner edge of the uppermost part of the calcareous skeleton almost gives the impression that here it lays directly on the main axis, to which the markedness of the convergence of the two pores high up in the upper left would lend support.

Still there remains a remarkable occurrence to talk about, which is to be seen in the samples figured on Pl. VII, Figs. 9 & 11. We see, in particular on the first figure, about in the middle of the calcareous skeleton, that several adjacent pores obviously a part of the same verticil show a conspicuous round swelling. It seems clear that the branch continues outward on the other side of them. It is certainly very obvious that these swellings may be taken to be sporangia. However, as the observation is drawn from only two examples on the same specimen, it is not secure enough, for it may well have been a pathological alteration caused by some parasite or other. Certainly the consideration remains that preservation is rarely as good as in this case and that then similar structures might easily be interpreted as no more than dark spots.

Finally, let us refer to Pl. VIII, Fig. 1, though it was put in mainly to prevent misinterpretation. We see here two thalli of *Diplopora annulata* stuck one into the other, the outer one giving a good example for segments with only one verticil. Naturally this involves only an accidental placement of specimens in this position as by the way GÜMBEL had already recognized.

Areal distribution and range: This species seems, insofar as can be determined to date, to be essentially characteristic of the level of the Wetterstein Limestones. But it must be mentioned that I saw a specimen perhaps belonging here in a rock otherwise filled with *Oligoporella prisca* that more than likely corresponds to a deeper level of the Muschelkalk. Localities:

1. Wetterstein Limestone of the Höllengebirge, eastern Austria [Pl. VII, Figs. 3–8].
2. Esino.
3. lighter-colored Wetterstein Limestone. Foot of the Windhag, northeast of Grünau [Grünau im Almtal, S Dorf, Oberösterreich, Austria] [Pl. VIII, Figs. 1–2].
4. darker-colored Wetterstein Limestone. Southward, below Windhag mountain, northeast of Grünau [Grünau im Almtal, S Dorf, Oberösterreich, Austria] [Pl. VII, Figs. 9–11].
5. (?) Spizze Limestone, Muschelkalk. Malurch, north of Pontafel [Pontebba / Pontafel, Friuli – Venezia Giulia, Italy], slope toward the Malurch Alps.
6. Spizze Limestone, Muschelkalk. Southwest below the Malurch peak. N Pontafel [Pontebba / Pontafel, Friuli – Venezia Giulia, Italy] [Pl. VII, Figs. 12–13].
7. Schindlkogel, east of Mitterbach on the Erlaf [Mitterbach am Erlaufsee, Niederösterreich, Austria].
8. Wetterstein Limestone. Northerly below Steyersteg in the uppermost Bodinggraben [S Breitenau, Oberösterreich, Austria], Sengsen Mountains [Pl. VII, Fig. 8].
9. Wetterstein-Crag.
10. on the slope of the southern mountains on the Attersee [Attersee, Salzburg or Oberösterreich, Austria] between Kalkofen and the "Burgaunatzl".



Text-Fig. 22.
Longitudinal section through a branch of *Diplopora annulata* with a globular broadening (Sporangium?). St = main axis.

11. western foothills of the Mariahilfer Mountains, Gutenstein [Gutenstein, Niederösterreich, Austria].
12. Upper Triassic (?). Upper Ogorie, lower Muć, northern Dalmatia [N Split, Croatia].
13. (?) between Weissenhof and Durchlass, on the eastern branch of the Weißenbach near Sankt Aegyd am Neuwalde [Niederösterreich, Austria] (loose rocks).
14. Chemnizien Limestone ("oberer Alpenkalk"). Ehrwald (Gaistal) [Tirol, Austria] [Pl. VII, Fig. 17].
15. (?) Schlegelberg [Sandkogel] above Vorderstaff near Schwarzenbach an der Pielach [S Schwarzenbach an der Pielach, Niederösterreich, Austria]. A solitary example in a rock with *Oligoporella prisca*.
16. (?) Mt. Cislon near Neumarkt [Tržič, Slovenia] (from GÜMBEL's samples).
17. Gartnerkofel near Pontafel [Pontebba / Pontafel, Friuli – Venezia Giulia, Italy] (from GÜMBEL's slides).
18. Wetterstein Limestone. Brunnenstein, Karwendel.

Diplopora debilis GÜMBEL
(Pl. VIII, Figs. 3–7 [Text-Fig. 23])

Gyroporella debilis GÜMBEL, 1871-1 and 1882-2

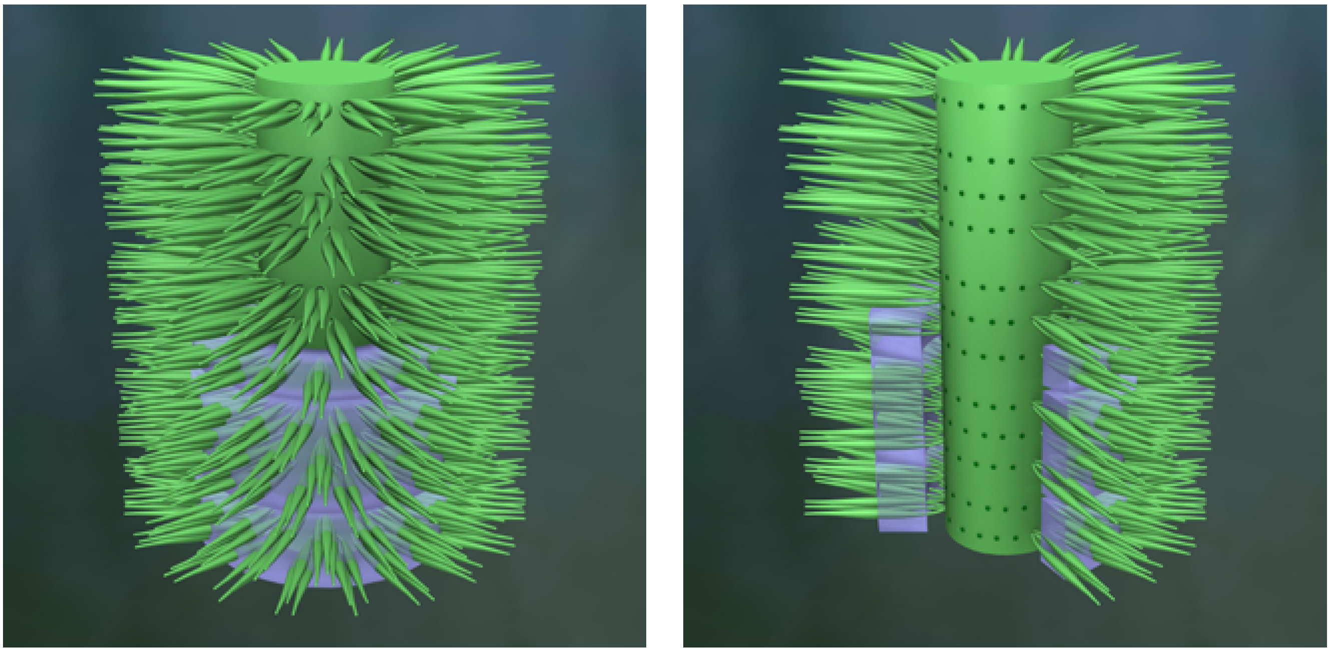
Remarkable for its distribution, unfortunately this species is in many respects poorly known. Its assignment to the genus *Diplopora* is based mainly on the type of its segmentation, which, however, as we have seen in *Teutloporella* and *Kantia* is not a proof, and by the form of the verticillated branches that in most cases are relatively thin and of the same width throughout their length. In addition, there are specimens in which the pores broaden outward very significantly (see Pl. VIII, Figs. 5 & 7). The canaliculae are placed randomly. That a metaverticillate arrangement of the branches exists cannot be proven, but that is not to be wondered at in view of the thinness of the calcareous skeleton.

If the generic assignment is correct, perhaps we are dealing with a transition between *Kantia* and *Diplopora*, from a phloiophorous to a trichophorous type, in which the verticillated branches end in filaments, but occasionally display a hereditary distal thickening, now functionless. On the basis of this assumption our reconstruction sketched an example with pores that widen outward strongly. A comparison with *Oligoporella prisca* is obvious and it would be in fact a very good concept that pores broadening outward are actually in the basal section of otherwise normally constructed individuals.

Our species is distinguished from *Diplopora annulata* in that in addition to an occasional widening of the pores outward, the calcification is significantly thinner. This statement is not to be taken to mean that every example of the first species will be thicker-shelled than those of the second. But a thickness normal for one species will be reached by the other one only exceptionally. The pores of *Diplopora debilis* are closer together than those of *D. annulata*.

Areal distribution and range: So far, this species has been proven with certitude only in the *Diplopora* Dolomite of the Tauern Triassic. Among the numerous localities I have selected the following that have provided me with the best material:

1. road from Tweng to the David Alp [Pl. VIII, Figs. 4–7].
2. road from Mittereckalm to the high bridge over the Taurach near Tweng [Pl. VIII, Fig. 3].



Text-Fig. 23.
Reconstruction of *Diplopora debilis* (like Pl. VIII, Fig. 8), specimen with strongly thickened branches.

3. just under the Pyritic Shale boundary, below the Pleislinkessels.
4. ascent to the Tappenkar, first leg.
5. north slope of the Pleislingkessel, farther westward toward the Pleisling Alp.
6. Moser Mandel.
7. in the Mauls river valley, northeast of the Mauls church. This locality seems to suggest that the so-called Mauls root was connected with the Tauern nappe, rather than the higher east Alpine nappe.

Furthermore it has to be mentioned that the poorly preserved diplopores which I have from Mt. Beletsi in Attica are perhaps better placed here than in *Diplopora annulata*.

B. Phylogenetic section

Compare this entire section to STEINMANN's 1903-1 work and my remarks about it.

Because of our inadequate knowledge of structural groupings in the Diploporidae we cannot do much more than speculate about the relationships of genera and species. Nevertheless, it is hardly possible after long-continued work with such a group that one does not surmise concerning its phylogenetic relationships. I should like the following explanations to be considered more in the sense of an account of a subjective impression rather than a strict scientific statement.

1. General principles

We can differentiate a range of types in the Diploporids on the basis of distinctive characteristics, in particular the form and placement of the verticillated branches, the structure of the sporangia, the segmentation of the calcareous skeleton. Now we must first ask ourselves in each case which type is primitive, which one is to be considered specialized, and in what way these specializations are derived from the primitive forms.

a) Form of the verticillated branches

We start here with the principle that in our family the original condition was that the verticillated branches served both for assimilation and for reproduction. I hold as derived the types in which the function of the branches is mainly or exclusively reproduction (vesiculiferous, pyriferous).

Difficult and of more substantial importance is the question whether it is the phloiophorous or the trichophorous type that is specialized. As far as the geological occurrence is concerned, in such an insufficiently known group not much weight may be attached to it, but the only Permian Diploporid known is phloiophorous. In the lower and middle Muschelkalk the phloiophores seem to stay abundant and almost equal the trichophores in number, while they have disappeared at Wetterstein Limestone time (with the exception of the very long-lived *Gyroporella* and perhaps – the level does not appear completely reliable to me – *Kantia dolomitica*). Furthermore, most of the phloiophores are proverticillate (except only Kantias). That euverticillate phloiophores occur is not at all certain according to my material. On the other hand trichophory occurs along with proverticillate positioning only in the otherwise very special genus *Teutloporella*. These grounds suggest that the phloiophorous form is primitive, the trichophore derived. However, to this view the ontogeny of *Neomeris* imposes a substantial difficulty. If we wish to apply our nomenclature to this genus we must certainly call the juvenile stage trichophorous, the adult stage, on the other hand, phloiophorous. Also we see during the development of each individual branch that at the beginning it bears a filament (which for sure – secondarily following a change in function – serves a special purpose, namely the protection of the vegetative spike), later, however, a cortical cell develops. Therefore, here the phloiophorous state clearly follows the trichophorous. I think, however, that this problem is eliminated if we but acknowledge that the cortical cells of *Neomeris* and those of the phloiophorous Diploporids are analogous but not homologous, because those are secondary but these are primary verticillated branches. In my opinion, for homologues we must point to the secondary branches of *Neomeris* and the filaments of the trichophorous Diploporids. The idea that the same organ first changes from phloiophorous to trichophorous and then reverts to phloiophorous is a most improbable conception. In reality things seem to have been conducted so that the primary verticillated branches bore filaments that (through multiplication of the filaments) became secondary branches, and these last were converted into cortical cells. By the way, we shall come back again to this point at the conclusion of this chapter.

Should my observations concerning the sporangia of the Diploporids be confirmed, I shall consider this state too as a specialization.

b) Placement of the verticillated branches

We may accept that proverticillate placement is more primitive than euverticillate and that this in turn is more primitive than metaverticillate. On the other hand, at first sight it may appear questionable whether we should consider the simple or the closely set emplacement of verticils as the more primitive. The latter may appear to be closer to the proverticillates. But we always see it in forms that judged by other characters must be considered as specialized within their genus, while the most primitive species of a genus (like *Oligoporella prisca*, *Physoporella pauciforata*) when euverticillate always have single-row verticils.

We can think of metaverticillate placement as having arisen directly from the proverticillate or from a closely packed arrangement of verticils. I am not yet in a position to decide which of these circumstances is true. To me the first seems as more probable, for no euverticillate *Macroporella* which we could trace back *Kantia* is known to date.

c) The calcareous skeleton

I think that in our family the calcareous skeleton was well developed originally and that its weak growth or complete absence is to be understood as reduction. In general we regard the occurrence of segmentation in the calcareous skeleton as specialization. But its absence can also be secondary.

2. Adaptive series

In order to obtain concrete examples of the general phylogenetic principles set forth in the preceding section we can compile a large number of adaptational series within the Diploporids, that is, we classify the forms with respect to only one feature. One such series gives us a rough picture of the evolution of that character, even though, as a rule, the forms thus assembled are not actually descended from one another. For we must be permitted to presume that evolution in parallel lines generally occurred in the same way. As the facts to be considered here have almost without exception been discussed in the special part, it suffices for the most part that the series be listed along with a few words of explanation.

a) On the form of the verticillated branches

1. *Macroporella Bellerophontis – Macroporella dinarica – Kantia philosophi – Gyroporella ampleforata – Kantia dolomitica* (– *Gyroporella vesiculifera*).

Shows us first the perfect phloiophorous type, then the transition to the vesiculiferous, which seems to have attained it highest development in *Gyroporella vesiculifera* though I know it only from literature.

2. *Macroporella Bellerophontis – Macroporella dinarica – Oligoporella prisca – Oligoporella pilosa – Oligoporella serripora – Physoporella pauciforata – Physoporella dissita – Physoporella minutula*.

We have already seen in the discussion of *Oligoporella prisca* that the construction of its basal verticils resembles that of *Macroporella* which gives us most probably direct evidence of the connection between these two genera. In an additional progression in development the pores taper outward with an ever-increasing accentuation, in other words filaments and sporangia were more distinctly separated. The transition to *Physoporella* occurred thus, in that the filaments were merely transient developments while on the adult plant only the fertile segments of the verticillated branches remained in existence. In the earlier development they still taper outward which is reminiscent of the trichophorous type. The final element of the entire series is a species in which the filaments probably were dropped very soon, perhaps were not created at all. The verticillated branches are almost of the same width, tube-shaped.

b) On the placement of the verticillated branches

Macroporella dinarica – Oligoporella prisca – Oligoporella pilosa – Oligoporella serripora.

Unfortunately there is a hiatus between the first two divisions of the series so we cannot form a clear conception of how the transition from the proverticillate to the euverticillate stages occurred. The last three members show us very clearly the evolution from a strictly unserial arrangement of verticils through moderately dense to biserial.

c) Concerning the calcareous skeleton

1. *Teutloporella herculea – Teutloporella gigantea – Teutloporella tenuis*.

As we have seen in *Teutloporella gigantea* in particular, the perforate nature of the calcareous skeleton that we noted occasionally is interpreted as a reduction process in the skeleton; if we imagine this taken a step farther, we arrive at the stage of *Teutloporella tenuis*, which I consider quite safe as a deduction.

2. *Oligoporella pilosa – Physoporella minutula – Physoporella dissita*.

This series shows us the evolution of undulation. In *Oligoporella pilosa* we remark in only a few instances a weak swelling of the calcareous skeleton over each verticil. In *Physoporella minutula* the absence of segmentation is already exceptional, but the degree to which a bulge is developed is most variable. From the most strongly swollen specimens it is only a step to the extreme formation that we know in *Physoporella dissita*.

3. *Teutloporella vicentina – Teutloporella triasina.*

We have seen that the peculiar sculpture of the calcareous skeleton of the last species can be taken with a rather good probability to be rudimentary segmentation. *Teutloporella vicentina* gives us a clear starting point for this regression.

3. Phylogenetic system of the Diploporidae

I believe that relationships in the Diploporidae are presented most correctly when I first divide the family into three subfamilies. In each of them phylogenetic relationships are discernible rather clearly, whereas the connections of the subfamilies with each other are more problematic. The allocation of genera to these three groups is as follows:

a) Macroporellinae

The most primitive Diploporid known to date is surely *Macroporella Bellerophontis*. We may very well consider it the direct ancestor of *Macroporella dinarica* and *M. alpina* if, as specified in the special section, we do not regard the thickened verticillated branches of the Permian species as sporangia. If we do, we have to regard it as a specialization that forces us to refer *Macroporella Bellerophontis* to a lateral branch, for such sporangia are not known in younger species. Both of the mentioned Triassic Macroporellae are extremely close to each other; at most one might see a greater degree of specialization in the somewhat larger size of the north Alpine species. If *Macroporella helvetica* belongs here, it would be the most highly evolved species of the genus.

Two branches arise from the genus *Macroporella*, one of which leads to *Gyroporella*, the other through *Oligoporella* to *Physoporella*.

The first succession is characterized by the development of vesiculiferous branches. In *Gyroporella ampleforata* this is not very clear, but in *Gyroporella vesiculifera* (which I do not have here) it seems to be developed typically. However, this species is not directly derived from *Gyroporella ampleforata* for it lacks the inner annulation characteristic of that species. Therefore it must be regarded as an offshoot.

Like the first one, the second lineage may have been derived from either *Macroporella dinarica* or *M. alpina*. The next stage is illustrated by *Oligoporella prisca* of which the phylogenetic significance has been pointed out repeatedly. It is questionable whether the transition from proverticillate to euverticillate already occurred in the genus *Macroporella* or if it took place only in the genus *Oligoporella*. The latter case would be possible also for it is very easily conceivable that the basal verticils of *Oligoporella prisca* remained in a primitive form while those in the upper part of the plant are related to a more evolved stage. Now evolution leads through *Oligoporella pilosa* to *Oligoporella serripora*. In that we see the trichophorous type accentuated more and more. Concurrently the placement of the verticils changes from uniserial to biserial. As we have already discussed, the next stage of development in the form of the branches is from *Oligoporella serripora* to *Physoporella pauciforata*. As this species has single-row verticils we are again confronted with a mixed specialization. Therefore we must trace back *Physoporella* to an unknown, but, owing to the placement of its branches, more primitive series that also originates in *Oligoporella prisca*. After *Physoporella pauciforata* the evolutionary line splits again. One line is characterized by an excessive development of the undulation (*Physoporella dissita*), in the other the form of the verticillated branches is comparatively more advanced (*Physoporella minutula*). Both have biserial verticils that perhaps were acquired from a common ancestor. It appears that these two specialized terminal branches soon died out without descendants.

Family Diploporidae.	
a) Subfam. Macroporellinae.	
	Macroporella,
	Gyroporella,
	Oligoporella,
	Physoporella.
b) Subfam. Teutloporellinae.	
	Teutloporella.
c) Subfam. Diploporinae.	
	Kantia,
	Diplopora.

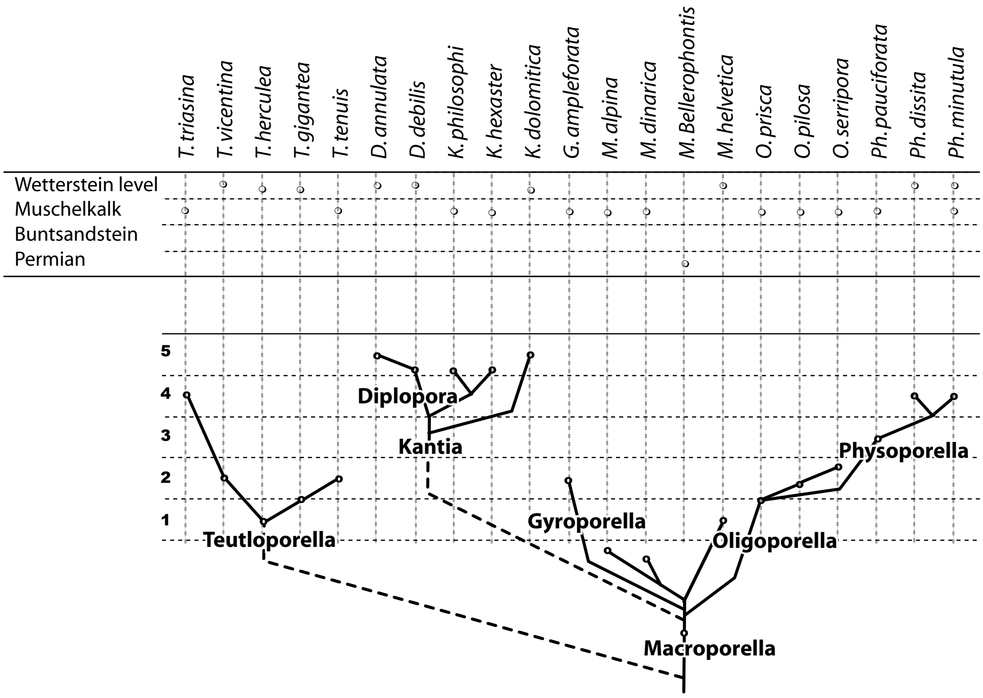
b) Teutloporellinae

This subfamily seems to occupy a very autonomous position. I consider it probable that it cannot be traced back to *Macroporella* but that the two originated together from a more primitive form in which the phloiophorous condition had not yet been fully attained. Within the only genus belonging here, *Teutloporella*, we can distinguish two groups of species. One lacks any segmentation in the calcareous skeleton. It is absolutely proverticillate. To some extent it shows a tendency toward skeletal reduction. Here belong *Teutloporella herculea*, *T. gigantea* and *T. tenuis*. The first two are very closely related but for the last no relationships can be specified, because so little of it is preserved. Their relatively small size could just as well be primitive as acquired secondarily. In the other group, incidentally with very primitive organization, true annulation appears very early: *Teutloporella vicentina*. From this species *Teutloporella triasina* was presumably derived, but we lack several intermediate elements. Placement of branches has become euverticillate, annulation has degenerated, but instead verticil series develop that originally probably appeared on every annular segment.

c) Diploporinae

The more primitive of the two genera that belong here, *Kantia*, I must trace back directly to *Macroporella*, but none of the three known species represent the original type of the genus. We think it was a true phloiophore with an uncalcified outer membrane of the cortical cells. Annulation also appeared very early here. From this archetype two methods of development evolved that apparently featured various systems of reproduction. On one hand the development of a vesiculiferous type followed (*Kantia dolomitica*). On the other hand some verticillated branches developed into special sporangia. This differentiation would make a generic separation of both groups essential, once it was determined without the possibility of error. The latter of the two lines then divided again as follows: one group retained phloiophorous verticillated branches, but the outer membrane commonly calcified, perhaps reminiscent of a temporary approach to true vesicularity (*Kantia philosophi* and *K. hexaster*), the other became trichophorous (*Diplopora*).

To conclude this section I have attempted to present in the form of a graphic phyletic tree my conception of the relationships between all of the species described here. What I have already noted in the introduction to the chapters on phylogeny applies here to an even greater degree. As regards the degree of specialization of some species, I have set up numbers for Specialization Units, as I would like to call them, from whose summation the degree of specialization of a species would result, even if the rating is only an approximation. I believe that in a relatively simple and thereby form-poor group like this one such an attempt should be dared, whereas in complicated cases it becomes practically impracticable. The characters taken into account are the following:



Text-Fig. 24.
Tentative phyletic tree of the Diploporidae.

a) Trichophory.

b) Closure of pores outward.

c) Possession of individualized sporangia.

d) The appearance of verticils.

e) The appearance of tufts.

f) Development of verticil series.

g) Segmentation of the calcareous skeleton.

h) Reduction of the calcareous skeleton.

For example, if we examine *Diplopora annulata* we find in it characteristics a, c, d, e, g. The degree of specialization of this species is expressed by the number 5. In the phyletic tree I have indicated a corresponding classification. Smaller distinctions are indicated by variation in the height of a position within any one level.

At the same time in order to give a first overview of the corresponding geological distribution, above the plot of the degrees of specialization is a second one according to geologic age. The place of each species in both of the two systems is indicated by a small circle connected to one another by a dotted line [Text-Fig. 24].

What must immediately attract attention in this overlay is the low correlation between geologic age and the degree of specialization, even within a limited group. Perhaps there are both large and numerous errors in the evaluation of heights, but I believe we should conclude that the vertical range of a given species in a limited area is due more often to migration than to its rapid development on the spot. Particularly striking in this respect is the behavior of the Teutloporellae, while in other groups, first and foremost in the Diploporids or *Physoporella*, geologic and phylogenetic sequences correlate quite well. Rather generally the principle that highly specialized forms are short-lived, while simple types stay a long time without substantial change appears to be valid. As an example of this latter case *Macroporella* is outstanding (Permian to Muschelkalk). Most probably *Teutloporella herculea* too belongs to this type, for although we know this species itself only from the Wetterstein Limestone, its occurrence at this high level, together with its primitive organization leads us very close to a conclusion that the same type is probably represented in many older beds. Amidst all this speculation we should not forget that even in a very important period in their development, namely the Lower Trias, no Siphoneae verticillatae at all are known so far. The discussion of some related questions will be found in the geologic chapter.

4. Place of the Diploporidae in the Order Siphoneae verticillatae

The position that the Diploporidae occupy within its Order will perhaps be brought out most clearly if we attempt a concise review of the evolution of the Dasycladaceans as a whole. In their phylogeny we have first to distinguish two main phases, one Paleozoic from the Silurian to the Carboniferous, the other Mesozoic-Cenozoic, from the Permian on.

A character shared by the entire siphonate flora of the first period seems to me to lie in the complete absence of fossilizable sporangia. I consider it quite probable that spores were developed in the main axis. If we regard this as a far from primitive character, then specialization in the Silurian was already scarcely less than at present. We can distinguish two well-separated structural groups in the Paleozoic. The first one is manifestly very primitive. I shall designate it as the Dasyporellidae. In the Silurian it is represented by *Dasyporella*, *Vermiporella*, *Arthroporella* and with *Stolleyella*, along with other as yet undescribed forms extends into the Carboniferous. It seem to me that the verticillated branches can be ascribed to a type intermediate between phloiophorous and trichophorous in that they certainly did not construct cortical layers but probably did project out moderately from the calcareous skeleton. Usually, the shape of the plant as a whole was irregular, oftentimes ramified, probably not upright but creeping.

The second Paleozoic group, STEINMANN's Cyclocrinidae, in many respects shows surprising analogies with recent types, as in the development of a cortical layer, the ramification of the verticillated branches (however they seem to be substantially different from those of the Neomerids and Bornetellids), the highly developed segmentation, *etc.*. The resemblance between a section through the calcareous skeleton of *Mastopora* and of *Bornetella* is just amazing (see 1896-4, p. 260, Figs. 95–97 and 1892-1, Pl. IX, Figs. 1& 5–6). The Silurian genera *Coelosphaeridium*, *Cyclocrinus* (with 25 described species), *Mastopora*, *Apidium*, *Palaeoporella* belong here. Characteristic of this group is a predominantly spherical shape and the multiple occurrences of so-called lids on the cortical cells that I take to be a partial calcification of the outer membrane of the verticillated branches. The Carboniferous *Mizzia* is closely related, the Devonian *Coelotrochium* and *Sycidium* less so. The greatest development of the whole Paleozoic group of forms fell in the Silurian.

Then a second peak of development followed in the Triassic. Here we find the Diploporids which are discussed in great detail in the present work. Spore building was shifted into the primary verticillated branches. Secondary ramification is lacking. A cylindrical form is extraordinarily predominant. Segmentation is common, but however, does not attain the same degree of development as in the Silurian-Devonian and in the Cenozoic. If we look back for the forms that we could claim as the forbears of this family, in particular for the genus *Macroporella*, the Dasyporellids come first into consideration. The transition to the Diploporids took place through the development of an upright, more or less cylindrical and straight, unramified stalks and through the alteration of the verticillated branches into reproductive organs. Potentially the development of a specialized rhizoid first occurred in this stage too. Perhaps Rhabdoporella was a lateral branch, in certain respects parallel to the Diploporids, but soon extinct.

As regards the question of the development of the Siphoneae verticillatae after the end of the Triassic, a very substantial obstacle is our inadequate knowledge of Jurassic and Cretaceous material, which in any event is quite scanty. Through the truly classic work of Steinmann we know the genera Triploporella and Tetraploporella as thoroughly as no other fossil Siphoneae. But all other forms from the younger Mesozoic like the very interesting *Petrascula*, then the remains from the upper Jurassic of the Podolic plateau in East Galicia (see 1877-1, 1878-1, 1879-1, 1882-1), *Linoporella*, *Diplopora Mühlbergi*, also *Munieria* merit a new examination. It seems to me, however, that already two groups stand out quite clearly. One proves to be of the family Diploporidae. Here I count *Diplopora Mühlbergi* (probably an *Oligoporella*) and *Munieria*. Another group is distinguished by the fact that in it too spores develop in the primary verticillated branches, but with it are several secondary branches that serve as sites for assimilation. Perhaps this group might be separated as it own family, the Triploporellidae. Here I count not only *Triploporella* and *Tetraploporella*, of which by the way the generic distinction appears questionable to me, but also *Petrascula* and the Eocene *Thyrsoporella*. The outer form is mostly club-shaped.

Now the question is from which point in the Diploporidae should this new family be derived. Perhaps one could assume that it originated from *Diplopora s.s.* because at the

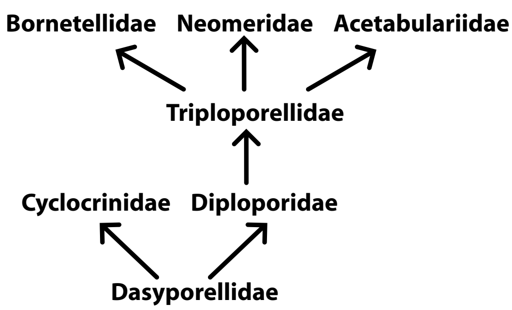
Overview of the Dasycladaceans	
Dasyporellidae	**Linoporellidae**
Dasyporella Silurian	*Linoporella* Jurassic
Vermiporella »	**Triploporellidae**
Arthroporella »	*Triploporella* (= ? *Tetraploporella*) Jurassic–Cretaceous
	Petrascula Jurassic
Stolleyella Carboniferous	*Thyrsoporella* Paleogene
(*Rhabdoporella*) Silurian	**Bornetellidae**
Cyclocrinidae	*Dactylopora p.p.* Paleogene
(*Coelosphaeridium*) Silurian	*Bornetella* Holocene
Cyclocrinus »	**Neomeridae**
Mastopora »	*Dactylopora p.p.* Paleogene–Neogene
Apidium »	*Dasycladus* Holocene
Palaeoporella »	*Botryophora* »
Mizzia Carboniferous	*Neomeris* Cretaceous–Holocene
? *Coelotrochium* Devonian	*Cymopolia* Paleogene–Holocene
? *Sycidium* »	? *Uteria* Paleogene
Diploporidae	**Acetabulariidae**
Macroporella Permian–Triassic	*Halicoryne* Holocene
Gyroporella Triassic–Cretaceous	*Chalmasia* »
Oligoporella Triassic(–Cretaceous ?)	*Acicularia* Paleogene–Holocene
Physoporella Triassic	*Acetabularia* Holocene
Teutloporella »	
Kantia »	
Diplopora »	
Munieria Cretaceous	

base of each tuft a stem, *i.e.* a primary verticillated branch, is formed, so that the branches of the tufts themselves would be secondary branches. However the characteristics of the sporangia are against this. It is far more probable that the Triploporellidae developed from *Oligoporella*, and simply by an increase in the number of filaments on each sporangium, primordially only 1.

However, in addition to the Triploporellids, the first representatives of a Cenozoic type (*Neomeris cretacea* STEINMANN) already appear in the Upper Cretaceous. This tribe, which attained its peak in the Tertiary and continues into the present, separated into 3 families. Considering that reproductive organs in the form of separate sporangia became independent of the primary verticillated branches, we may deduce that all of them were derived from Triploporellids. This development is clearest in the Bornetellidae in which the larger number of spore containers are set laterally beside the long and thin primary branches. In the Acetabulariidae we have to do only with a single fertile protuberance that in the course of ontogeny can be followed as it develops on the lower surface of a branch and then gradually migrates to a terminal position. In the specialized genera all of the sporangia of a verticil unite in a so-called umbrella. The derivation of the sporangia of the Neomeridae appears doubtful to me. One could assume that it was like that of *Bornetella*, except with the distinction that a pinching off at the end of the primary branch followed. However, in *Dasycladus* the relationship is open to a second interpretation. Namely, we could have to do with converted secondary verticillated branches.

We have seen that numerous specializations, such as the development of cortical cells, segmentation and others, occurred independently either within the several lineages or even in the same one. If we search for a feature that progressed uniformly throughout the entire phylogeny we find it only in the method of fructification. The tendency to make the organ of reproduction more and more independent prevails quite generally, and so spore forming moves from the main axis to the primary verticillated branches and from these to special sporangia adhering to the branches.

The content and names of the families are to be considered to some extent only as a provisional proposal. Naturally, this list has no pretensions of absolute completeness.



Attempt at a phyletic tree of the Dasycladaceans

III. Geology

The foreword had already pointed out the unusually great difficulties that were contended with in the stratigraphic analysis of the Diploporids. Even so, I shall try in the following to make an effort to draw preliminary and approximate conclusions from data based on my own observations on this point and from what is known to me from the literature. In doing this I shall not restrict myself to the forms that I have studied in detail, but insofar as possible take into account all of the described Triassic species that appear to me to be sufficiently valid. Where the generic assignment is not known the generic name is replaced by a star. Below I give a tabulated summary of the most important Alpine diplopore-bearing rocks with their floras, it will serve as a basis for my further remarks (see also the phyletic tree, Fig. 24).

1. Vertical distribution

In the eastern Alps, with which we are concerned primarily, four main levels of Diploporids are differentiated (see the first column of the table.) with four discrete floras that differ so greatly from one another that I have found no unquestionable case of an occurrence of the same species in two discrete levels.

In the Wetterstein horizon it may be possible later to make a subdivision so that there will be a deeper level with *Teutloporella herculea* and *T. gigantea* and a higher one with a majority of the cited species listed in the table. The species in the lower unit would then be the same as those that also occur in the Ramsau dolomite, the uppermost part of which corresponds in age to the Wetterstein Limestone. But for the moment this remains a conjecture.

2. Horizontal distribution

Understandably, *Macroporella Bellerophontis* is restricted to the southern Alps for a corresponding limestone member is lacking in the northern Alps.

On the other hand in the second of the two levels we distinguish, the Muschelkalk, there is a remarkable geographic and facies differentiation in the flora. As a glance at the table shows, the Diploporae of the northern Alps are almost all different in name from those of the southern Alps, and certainly the whole character of the two plant associations differs. The ratio of trichophorous to phloiophorous species in the northern Alps is 3:1, in the Dinarides 5:4, whereas what is more, *Macroporella* is very rare in the northern Alps. *Teutloporella triasina*, so extraordinarily abundant and characteristic in the southern Alps is completely absent in the northern Alps. Vesiculifers are generally (not only in the Muschelkalk) restricted strictly to the Dinarides, the pirifers almost entirely to the northern Alps.

Hand in hand with this differentiation in the composition of both floras also goes a contrast in the way they occur. The north Alpine Muschelkalk Diploporids occur mainly in the Reiflinger Formation, a rather clean limestone. On the contrary most of the southern Alpine species occur in a less calcareous shaly or sandy limestone. Only *Physoporella pauciforata* is an exception to this because it is present in both the Mendola Dolomite and the Muschelkalk of the Sarenkofel, along with *Oligoporella serripora* in the latter rock unit, thus significantly two trichophorous species of which one is the only species common to both areas. If we leave these two forms out, the ratio of trichophores to phloiophores in the marly limestones of the Dinarides is 3:4. It seems therefore, that while the trichophores did almost equally well in both facies, the phloiophores were the characteristic forms of the more argillaceous tracts.

Overview of Diploporid-bearing rocks and their flora			
	Northern Calcareous Alps and Carpathians	Dinaric Alps	
Permian		Bellerophon Limestone: *M. Bellerophontis*	
Muschelkalk	Reiflinger Limestone	a) pure limestone facies	
	M. alpina	Mendola Dolomite	Muschelkalk
	O. prisca	*Ph. pauciforata*	*Ph. pauciforata*
	Ph. pauciforata		*O. serripora*
	Ph. minutula	b) marly-sandy lime facies	
		Muschelkalk of Pontafel	Basal Spizze Limestone
		T. triasina	(Sturia-Limestone)
	Limestone of the Nesslinger Wall	*K. philosophi*	*T. triasina*
	Ph. pauciforata	*G. ampleforata*	*Ph. pauciforata ?*
		Dalmatian Muschelkalk	
		M. dinarica	*O. pilosa*
	Ramsau-Dolomite	*T. tenuis*	*K. hexaster*
Wettersteinkalk	*T. herculea*	Spizze Limestone	
	Wetterstein Limestone		
	T. herculea	*T. vicentina*	*D. annulata*
	T. gigantea	Marmola Limestone	Schlern-Dolomite
	Ph. dissita	*T. herculea*	*K. dolomitica*
	D. annulata	*D. annulata*	*D. annulata*
	** nodosa*	** nodosa*	** nodosa*
	Tauern Dolomite	** Gümbeli*	** macrostoma*
	D. debilis	** Beneckei*	
	Wetterling Limestone		
	T. herculea		
Upper Triassic		Hauptdolomite: *G. vesiculifera, * curvata*	

The circumstances described support the supposition that the distinction between the northern Alps and the Dinarides was brought about not so much by climatic differences or anything of the kind, but mainly by diversity in the sediments that were deposited at that time. At least this might have caused the starkly abrupt development of perhaps otherwise existing differences, especially in the Muschelkalk.

We can only be reassured concerning this opinion when we see that the flora had a more uniform character at the Wetterstein Limestones level where in both the northern and the southern Alps massive reef limestones and dolomites were deposited. Above all, *Diplopora annulata* is not only common to both areas, but also extends even farther to Dalmatia, perhaps to Greece (the examples to hand unfortunately do not permit a reliable determination). Certainly we also encounter here not a few species that are known in only one of the two areas, but only very rare forms are involved that most frequently were reported only once and consequently have no value in this assessment. It is very remarkable that in the whole area of the Tauern Triassic *Diplopora debilis* takes the place of *Diplopora annulata* and so, at least today, the two areas of distribution are separated from one another. If we accept that the true east Alpine series was shoved over the Tauern series then we can conceive through reconstruction that the original *Diplopora annulata* region was in the south and afterwards that of *Diplopora debilis* was in the north. Data concerning the occurrences of this latter species in the Piemont agrees quite well with this view too.

To my knowledge to date in strata of Norian age Diploporids are known only in the southern Alps, but their absence in the main dolomites of the northern Alps is perhaps due mainly to unfavorable conditions of preservation.

Until now reports concerning the occurrence of Diploporids outside the eastern Alps have for the most part completely escaped my criticism. Consequently, I content myself with citations from the literature, as follows:

a) Western Alps

1. *Diplopora debilis*. Wetterstein Limestone level of Villa Nuova and Saggio in the Piemontese Alps. 1882-2.
2. *Diplopora annulata*. Muschelkalk and Keuper of Canton Ticino and of the southeastern Bünden (today: Graubünden). 1890-4. If not, perhaps *Diplopora debilis* ?
3. idem. 30 m northeasterly under the Rossfluh peak in the Giswyl Klippes, Switzerland. 1908-2.
4. idem. Alpbolgenalb and circa 300 m easterly below Kringen in the Giswyl Klippes, Switzerland. 1907-2.
5. *Physoporella minutula* and *Macroporella helvetica*. Zwecken Alp near Mythen, Canton of Schwyz. Personal observation.

To my knowledge, a determination of the Diploporids occurring in the Triassic of the French Alps has not yet been attempted.

b) Hungary

1. *Diplopora annulata*. Main Dolomite of the Ofen-Kovács Mountains. 1872-3. This report must certainly be mistaken.
2. idem. Ofen peak. 1872-1.
3. idem. Csik peak, west of Bada Eors and of Hradek. 1872-1.
4. *Teutloporella herculea* = *aequalis*. Wetterling Limestone of Rohrbach. 1872-1.
5. idem. Wetterling Limestone, Vajarska area, Lower Carpathians. 1902-3.
6. idem. Wetterling Limestone, White Mountains, Lower Carpathians. 1904-1.

c) Apennines

1. *Diplopora annulata* and * *porosa* in the Triassic Limestone of the southern Basilicata. 1896-1.
2. *Gyroporella vesiculifera*. Rhaetian Limestone in the rift between Coppo del Majale and Sasso, eastern side of Mt. Malbe near Perugia. 1908-3. Determination dubious, could also be a *Macroporella*.
3. *Teutloporella triasina*. In the lower part of the light-colored Triassic Limestones, Mt. Brunito, Suavicino. 1880-2 and 3.

d) Greece

1. *Gyroporella vesiculifera*. Triassic Limestones of Mt. Parnassus. 1908-4.
2. *Diplopora annulata* or *debilis*. Top of Mt. Beletsi, Attica. Personal observation.

e) German Triassic

1. *Physoporella lotharingica* BENECKE. Dolomite below the Trochite Limestone, Gänglingen in Lorraine [Guinglan-

IV. Literature

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2. Remarks about the more important works

Without doubt the preparation of this section represents the most unpleasant and at the same time the most thankless part of my task. However, I believe that a comparative analysis of the most important of the older publications would not come amiss. My main purpose thereby is to state as precisely as possible the relationship of my observations and inferences to the older representations, and thus to facilitate the use and comparison of older literature. In addition it gave me a more precise insight into the history of the development of our knowledge regarding the Diploporids that presents some typical and not uninteresting features.

In 1872 GÜMBEL's ground-laying monograph followed earlier tentative attempts by SCHAFHÄUTL, SCHAUROTH and STOPPANI that were based on untenable systematic suppositions. It is based on the conviction that the Diploporids belong to the dactyloporids which at that time were considered to be a family of foraminifera. Its publication, that represented an extraordinary advance, resulted in a general increase in interest in our subject and thereby also an increase in the literature to follow. Besides numerous smaller works by GÜMBEL, BENECKE's excellent investigation deserves special mention here. In addition, a nomenclatural dispute on the subject «*Diplopora* or *Gyroporella*» took place. Then in 1877 appeared the short note by MUNIER-CHALMAS that brought with it a complete reversal in the systematic concepts concerning the Diploporids. The furor that this work provoked is reflected in various reports and discussions. Its influence on a broader treatment of our topics was, however, rather less than one might anticipate. The realization of the vegetal nature of our fossils was expressed for the moment more in changes in nomenclature rather than in a new way to carry out investigations. On the other hand, at this time there was some excellent detailed research, of which I should like to highlight SALOMON's work. Only STEINMANN's publications occupy a more outstanding place, of which the brilliant qualities will be referred to here as the occasion offers. In the years 1890 to 1895 an extraordinary development of our knowledge of the recent Siphoneae verticillatae took place due to the appearance of the fundamental and outstanding investigations of CRAMER and the Earl of SOLMS-LAUBACH that rendered me inestimable service at every step of my studies.

In doing the present work I started out by following in detail the methods initiated by MUNIER-CHALMAS.

SCHAFHÄUTL, 1853-1

Beiträge zur Näheren Kenntnis der Bayern'schen Voralpen.

It is hard to get an idea of what SCHAFHÄUTL actually thinks based on his decision that *Nullipora annulata* has several parts. According to him the fossil consists of the following parts:

1. A central axis with a spongier structure. It corresponds to an internal mold of the shell.
2. Around this axis a milk-white coating, delicate and thin. By this is probably meant a less transparent rock layer that in many cases coats the surface of a fossil completely. Compare Pl. VII.
3. Cone- or cup-shaped tubules. Naturally these correspond to the pores. Their walls were thought to consist of the same milk-white membrane that encloses the axis. Their placement, as SCHAFHÄUTL describes it, corresponds rather well to that of metaverticillate pores.
4. A transparent body that connects the cups to each other. This is the true calcareous skeleton of the plant.
5. A spongy mass that fills the several cells. In reality, like the central axis, it consists only of sediment.
6. A wrinkled skin is thought to overlie the whole. Obviously, here too a real part of the fossil is not involved. However, I don't understand what is meant by it.

SCHAUROTH, 1855-1

Übersicht der Geognostischen Verhältnisse der Gegend von Recoaro im Vicentinischen.

SCHAUROTH agrees with SCHAFHÄUTL on the standpoint that the Diploporids are bryozoa, believing. however, that they should rather be compared to the genus *Chaetetes*. In 1859 he named his species *Chaetetes* (?) *triasinus*. More correctly than his predecessor, this author recognizes that the space within the tubes is filled with sediment. On the other hand, the oblique positioning of the pores allowed the mistaken assumption that they were divided into several cells. Rightly recognized is the rectangular form (as a result of mutual flattening) of the inner openings of the canicules. When hemispherical swellings occur on the outer ends of the pores they are considered manifestly to be weathered out internal molds.

STOPPANI, 1857-1

Studii geologici e paleontologici sulla Lombardia.

STOPPANI's basic mistake consists in that he did not recognize the pores and considered those in SCHAFHÄUTL to be a delusion. On the other hand he correctly advocates that the inside of the tubules is filled with sediment. So he comes to consider the Diploporids as the tubes of boring clams.

1. *Gastrochaena annulata*. Strange to say, STOPPANI describes this fossil as smooth externally, but internally ringed with furrows. This relationship would correspond to our intusannulation. Probably it involved unsegmented specimens on which the badly weathered casts of some verticils suggested regularly spaced projecting bulges, as GÜMBEL described them and I myself have often observed. Nor do STOPPANI's "Sezioni od anneli" correspond to GÜMBEL's Ring-structure.

2. *Gastrochaena obtusa*.

3. *Gastrochaena gracilis*. No details of these two species are known.

4. *Gastrochaena herculea*. According to SALOMON's completely reliable report this species is identical with GÜMBEL's *Gyroporella aequalis*.

STOPPANI, 1860-1

Les pétrifications d'Esino.

STOPPANI's principal standpoint is still the same as in the «Studii». Nevertheless, noticeable progress was made in several details. The author has now recognized true annulation. The «tubercules» of which he speaks are obviously the filling of pores that project outward somewhat due to weathering. In accord with this is the comment that every projection on the outer surface of the calcareous skeleton corresponds to a groove on the inner surface. Very strange is the assertion: «Qu'ils appartiennent à des coquilles lithophages, cela va sans dire». [That they belong to lithophagous shells goes without saying] The well-known paleontologist seems to have completely forgotten at that moment that the fossils were embedded while the rocks were being laid down. Obviously STOPPANI's ideas about the mode of life of the Diploporids is hardly compatible with their occurrence in a great thickness of rock, as he himself described it.

1. *Gastrochaena obtusa*. Essentially this species may correspond to *Diplopora annulata*; but it seems to me that several other species too could be understood to fall here under.

2. *Gastrochaena herculea*. I do not understand what is meant by the two layers, of which the calcareous skeleton is said to consist.

3. *Gastrochaena gracilis*. According to STOPPANI's description one could come to the opinion that perhaps it involves my *Teutloporella gigantea*, but the small size (4.5 mm) is evidence against it.

SCHAFHÄUTL, 1863-1

Süd-Bayerns Lethaea Geognostica.

The general approach to the nature of the Diploporids is still the same as in 1853.

1. *Diplopora annulata*. I have never seen the fine surface sculpture that SCHAFHÄUTL described. The "rings" in the middle of p. 326 are not annular segments in GÜMBEL's and my sense, but are a part of the calcareous skeleton corresponding to the individual verticils, and also STOPPANI's "annelli". On the other hand, on p. 327, paragraph 2 under the term "Ringe" segments are meant. What SCHAFHÄUTL called the toes is perhaps never the natural end but always a broken surface; the orientation of the whole fossil is correct however, contrary to GÜMBEL's idea. If occasionally two tubules are really interlocked (on Pl. 65e the examples depicted seem definitely questionable to me) it is merely a coincidence, as already mentioned on

p. 49. Propagation by budding does not occur in recent dasycladaceans and also SCHAFHÄUTL's Fig. 7d cannot be interpreted in this sense. In the meantime, according to the studies of MUNIER-CHALMAS, *Vaginopora* has proved to be part of the Siphoneae verticillatae too, like *Diplopora*. SCHAFHÄUTL was right too in his conjecture regarding a relationship.

2. *Diplopora porosa*. According to SALOMON this species is identical to *Gyroporella multiserialis* GÜMBEL. In my opinion it does not differ specifically from *Diplopora annulata*. I found the surface of the skeleton in well-preserved specimens to be smooth always, (except at the pore openings), without *"ridges".*
3. *Diplopora articulata*. GÜMBEL lists this species in the synonymy of his *Gyroporella annulata*. From what I saw on SCHAFHÄUTL's original samples this judgment seems to be very reasonable. Unfortunately, it was not possible to make a thin section of it.
4. *Diplopora nodosa*. According to SALOMON, GÜMBEL's *Gyroporella infundibuliformis* belongs here.
5. *Vaginopora pustulosa*. Judging from the illustrations, it is not unthinkable that this is a weakly calcified *Gyroporella s.s.* In any case this species does not belong to *Vaginopora* which is a subgenus of *Cymopolia*.

Finally, concerning this it should be pointed out that systematically speaking the figures in Pl. 65e cannot be brought together in a species as the legend states. At least I have the impression that here very different things are called identical, and that others quite closely related are separated.

SCHAFHÄUTL, 1867-1

Weitere Beiträge zur näheren Kenntnis der bayerischen Alpen.

In this work the point of view is essentially unchanged. Consequently, we can refer to the communications of 1853-1 and 1863-1. On pages 264–265 SCHAFHÄUTL attempts, though in a less than fortunate way, to include the form of the pores in the diagnosis, as is done very extensively in our present work. In the figures, attention is invited particularly to the fine interior mold of a specimen of *Diplopora annulata* with only one verticil in each segment (Pl. I, Fig. 1k).

GÜMBEL, 1872-1

Die Nulliporen des Tierreiches.

a) The general part, p. 14 to 23, and p. 42 to 44

Without doubt GÜMBEL's work is an extraordinary advance over previous publications despite many an error that we must point out in the following. For the first time a possible correlation between the diversity in form and the geologic significance of the diplopores is referred to. The general architecture with an interior central cavity and wall-piercing caniculae was correctly represented. In any event, the new systematic position was much closer to the then current state of knowledge than assignment to the Bryozoa or even worse to the bivalves. GÜMBEL's mistakes are in large part understandable when one looks at the thin sections that he must have studied. Their poor quality obviously made it impossible for him to examine the form of single pores, to which, in my opinion, so much importance must be given.

It seems to me that GÜMBEL made two errors in the systematic arrangement of the genus *Gyroporella* that hindered further progress considerably. First of all he went too far in setting up species. Then too the grouping of species within the genus is quite unnatural, for he puts in first place as criteria segmentation and the number of rows of pores in a segment, characteristics that today we are obliged to interpret as having very little systematic importance. Indeed, it seems very doubtful to me that a natural classification of species was conceivable at all, as long as the Diploporids were considered to be foraminifera. In any event because of these circumstances GÜMBEL separates not only closely related species like *Physoporella dissita* and *Physoporella pauciforata* but also actual examples of the same species like his *Gyroporella annulata* and *multiserialis*, while forms of quite different structure like *Teutloporella herculea* (= *Gyroporella aequalis* GÜMBEL) and *Gyroporella vesiculifera* turn up in one group (the Continuae).

When I consider GÜMBEL's workmanship with respect in particular to the need for improvement, a comparison with my own observations is quite automatic. Almost everywhere the numbers given are too small. In *Diplopora s.s.* not two, but three closely spaced canicules occur together, and in such a way that any one group of canicules is always in the same segment. When there is a mention of two adjacent pore series, it is in fact a single metaverticillate verticil. Between the segments of the annulate forms there is no ring forming, outwardly closed central cavity as described on p. 15 but an open groove, the outer edges of which only very exceptionally approach close enough to be in contact with each other. I could not find that the structure of specimens with relatively high annular segments is less deep and less distinct than in shorter ones.

The small forms mentioned on p. 22 should correspond as a whole to the genus *Physoporella*. The significance of the protruding small ridges that supposedly mark a separation into segments is not clear to me. I could not find anything like them. Where they occur on the outer surface, bulge-like swellings always lie above the verticils, not between them.

b) To the special section, p. 38 to 41 and p. 44 to 54

1. *Gyroporella annulata*. To *Diplopora*.
2. *Gyroporella cylindrica*. Very probably identical to the above.
3. *Gyroporella dissita*. To *Physoporella*.
4. *Gyroporella debilis*. To *Diplopora*? I apply this name to the central Alpine species. In 1882 GÜMBEL gave a rather good description of it, although it is completely contrary to the definition of the species in the present work. Probably this circumstance can be explained by its great variability as discussed on p. 49. Whether *Diplopora debilis* also occurs in the Mendola Dolomite remains to be determined.
5. *Gyroporella macrostoma*. I do not know this species from my own observation, but according to STEINMANN (1903-1) it is assignable to *Physoporella* (?)
6. *Gyroporella pauciforata*. To *Physoporella*. As an inspection of GÜMBEL's own drawings shows, here "distinct annular rings" do not mean true annulation, nor can one speak of two pore rows in each segment. It is true that the outer surface often has protruding bulges. The pores end blindly; when the surface of the thallus

is “covered with small pits around the outer openings of the canicules” it must be that somewhat weathered specimens are involved. Incidentally, the relationship between this species name and the way I use it makes this fossil rather unreliable. It is based mainly on its location, then on Steinmann’s statement that *Gyroporella pauciforata* belongs in *Physoporella* and on older determinations by Bittner who may have known Gümbel’s conception.

7. *Gyroporella minutula*. To *Physoporella*. The description and illustration of this species are among the best, so I consider my identification of it to be rather probable. In particular, the existence of moderately dense euverticillate verticils in the description is very well expressed. Pl. D III, Fig. 4a shows clearly the strong undulation.

8. *Gyroporella silesiaca*.

9. *Gyroporella infundibuliformis*. I was not able to examine these two species. Perhaps they belong in *Teutloporella*, perhaps they comprise a discrete genus.

10. *Gyroporella triasina*. To *Teutloporella*. The description of this species is quite good, also Fig. 12a–f. On the other hand it seems to me that Fig. 13a and b do not belong here. Its occurrence in the “Mendola dolomite”, if it is understood as being identical with the Schlern dolomite of the Mendel, is most improbable on stratigraphic grounds, and until further notice I must consider it unproven. As Salomon quite rightly emphasized, the specimens in Gümbel’s hands were unusually small.

11. *Gyroporella multiserialis*. To *Diplopora*. In reality this species has no particular relationship at all to the last one. In the systematic section its identity with *Diplopora annulata* was presented in detail. It is self-evident that its occurrence is not restricted to the Mendel dolomite. As Salomon has already emphasized, *Diplopora annulata* is the main component in all localities.

12. *Gyroporella aequalis*. To *Teutloporella*. As Gümbel himself suspected and Salomon proved, this species is identical to Stoppani’s *Gastrochaena herculea*. This latter name for the species has priority.

13. *Gyroporella curvata*. I do not have it.

14. *Gyroporella vesiculifera* is the valid type of the genus *Gyroporella s.s.* ever since Benecke (1876-1). According to all of the more recent authors an opening to the exterior from the bubble-shaped central cavity does not exist.

In principle I can only agree with Gümbel’s stratigraphic interpretations. In detail there are two circumstances that caused errors: The defective state of Alpine Triassic stratigraphy in Gümbel’s time, and the unfortunate grouping of species, as shown for example by the Continuae group.

Gümbel, 1872-3

Über die daktyloporennähnlichen Fossilien der Trias.

Here Gümbel gives a summary of his genus *Gyroporella* and to this end divides it into four groups. The relationship of these groups to my genera is presented in the following table:

Gümbel	Pia
Group of ...	Genus:
Gyroporella triasina	*Teutloporella p.p.* *Oligoporella*
Gyroporella pauciforata	*Physoporella*
Gyroporella annulata and *cylindrica*	*Diplopora*
Continui	*Teutloporella p.p.* *Gyroporella*

Gümbel, 1873-2

Mikroskopische Untersuchung alpiner Triaskalke und Dolomite.

In this work I find the remark that in the Schlern Dolomite from Val Sorda at Latemar *Diplopora multiserialis* (= *annulata*) occurs. In front of me is a sample with the same locality information, that, however, does not contain this species but *Kantia dolomitica*.

Gümbel, 1874-1

Über neue Gyroporellen aus dem Gailtaler Gebirge.

This rock in which *Gyroporella ampleforata* occurs has in the meantime been proven to be Muschelkalk. To correct some failings in the description compare my analysis of the species in the descriptive section. Here I should like only to point out that among the weathered specimens I have examined there were never any that looked like funnels put together. However, as we know that *Teutloporella triasina* occurs in the same piece of rock with *Gyroporella ampleforata* (see 1898-1 and my comment on it), the assumption gets more likely that Gümbel confounded the two species with each other. That they are closely related to each other, as Gümbel believed, I naturally do not hold to be correct.

Benecke, 1876-1

Über die Umgebung von Esino in der Lombardei.

Benecke’s work is outstanding owing to its unbiased and thorough observations as well as through an in-depth and clear picture of the facts. His contributions undoubtedly are among the most reliable we have on the diplopores and it is very regrettable that his studies could not have had Munier-Chalmas’s discovery as a basis, for otherwise he would have probably contributed a significant advancement at that time. So Benecke was obliged to follow Gümbel in questions of systematics.

The distinction between *Diplopora* and *Gyroporella* that Benecke introduced was subsequently adopted generally and also serves as a basis for my nomenclature.

1. *Diplopora annulata*. The description of the pores is very good in general. The assumption of pore rows in each zone is only a construction, though. With it regularity in the behavior of the pores from the successive series is automatically omitted. Benecke also claims to have detected well-marked pore zones at the outer end of the tubules, more clearly than Gümbel depicted them. To me it appears evident that at least occasionally in the southern Alpine examples of *Diplopora annulata*, pores on the same verticil are closer together than those on the northern specimens. However, this in no way justifies a species distinction. That Benecke recognized no discrete annular segments is very remarkable in any event, since these, contrary to his surmise, also predominate in the Wetterstein Limestone. The

statement that in a longitudinal section two canicules frequently converge is entirely exact, only the occurrence is not confined to forms with oblique pores. At the same time it proves that BENECKE really had a *Diplopora* in my sense. I believe that especially in this genus the angle of the verticillated branches with the main axis has no systematic significance. For other groups, like *Teutloporella*, an oblique pore position is generally quite characteristic.

2. *Gyroporella vesiculifera*. According to BENECKE's description this form would not have been euverticillate. By the way, his drawings do not quite match with each other. Pl. XXIII, Figs. 7 & 12 show vertical pore rows (an occurrence that would be quite unique there), on the other hand on Fig. 6 they are horizontal.

GÜMBEL, 1882-2

Gyroporellen-Schichten in den Radstätter Tauern.

Obviously this time GÜMBEL had in front of him the variety of *Diplopora debilis* to which my reconstruction (Text-Fig. 23) refers. This is the probable explanation for the remarkable contradiction that in 1872-1 *Diplopora debilis* should be distinguished from all the preceding species by the greater thinness of the canicules, while now the same species is differentiated from *Diplopora annulata* through its «relatively thicker and outwardly club-shaped tubules».

DEECKE, 1883-2

Über einige neue Siphoneen.

It is not in the scope of this work to examine *Munieria* more closely, although further investigation would be very desirable. It seems to me to be impossible that the *Gyroporella*-related forms that appear with it should be considered its fertile shoots, for the following reasons: First, I consider the verticillated branches of *Munieria* to be fertile themselves and absolutely comparable to the trichophorous sporangia of *Oligoporella*. Second, it contradicts all our other experiences, if we, as DEECKE wants, assume that fertile shoots are less strongly calcified than sterile ones. Just as little do I want to be associated with the opinion that *Gyroporella* is a fertile stage of *Diplopora* aff. *aequalis*, with which it was found only once (see chapter I.2 Ontogeny).

BORNEMANN, 1885-2

Vortrag über fossile Kalkalgen.

The statement that the pores of *Teutloporella triasina* would have been closed outward is erroneous. Also the concept that the skeleton of the Siphoneae verticillatae is a calcified membrane is not correct for the forms considered here, as Solms-Laubach's investigations of recent species show.

WÖHRMANN, 1888-3

Über die untere Grenze des Keupers in den Alpen.

The form mentioned by WÖHRMANN as different from *Diplopora annulata* in the lower Wetterstein Limestone, perhaps could be *Teutloporella gigantea*.

BITTNER, 1891-1

Zur Geologie des Erlafgebietes.

The determination of the dasycladaceans from the several locations mentioned as *Physoporella pauciforata* is generally correct. Only at Schlegelberg [Sandkogel] do my observations not record this species, but *Oligoporella prisca*; however it could be very easy for the two forms to occur together.

WÖHRMANN, 1893-3

Die Raibler Schichten.

That the Diplopore-Dolomite of the Tauern is an equivalent of the Hauptdolomite is not acceptable from a phytopaleontologic standpoint. The species that occurs there is in fact *Diplopora debilis*, that we, at least tentatively, must consider a close relative of *Diplopora annulata*; this strongly indicates the Wetterstein Limestone level.

ROTHPLETZ, 1894-1

Ein geologischer Querschnitt durch die Ostalpen.

Figures and descriptions are quite good and entirely sufficient for the correct identification of the species. But I do not understand clearly what a quincunx placement of the pores means. In my opinion no doubt can exist that we are dealing with a true verticillate siphonean.

GEYER, 1895-3

Über die marinen Äquivalente der Permformation
zwischen dem Gailtal und dem Kanaltal in Kärnten.

Here the author defends an older concept of the stratigraphy of this region that consequently leads him to place the Diploporid limestone and dolomite of the Rosskofel in the Permian and leads him, citing GÜMBEL, to assume the occurrence of true Diploporids in the Carboniferous. Later (1898-1) he himself corrected this.

To date there is no evidence that the Diploporids go back as far as the Permian, and in this formation only *Macroporella* has been identified.

SALOMON, 1895-4

Geologische und paläontologische Studien
über die Marmolata.

1. *Diplopora porosa* (= *annulata*). SALOMON's arguments regarding this species undoubtedly mark considerable progress once again. Of fundamental importance is the recognition of the minor significance of segmentation in systematics, of the greatest value the evidence of the great variability of the characteristics of our plant group. Along with it though, some errors occur too. So I can affirm in absolute security that segmentation had already taken place in the living plant, and was surely not just a mere indication of a predisposition. SALOMON accepted the idea that from the beginning several plant parts had been segmented others not. He was led to this through a comparison with *Cymopolia*. Undoubtedly he overestimated quite considerably the resemblance between the segmentation of Triassic and recent forms. At least in *Cymopolia* segmentation is much more highly developed and therefore linked more intimately to the whole organism. One has only to think about the complicated way by which a single segment is terminated above and below by a verticil specifically adapted for it (see 1892-1, 1887-5, *etc.*). Furthermore, SALOMON has not freed himself completely from certain errors of his predecessors. So he searches for order in the placement of the pores that certainly does not exist in this species.
   SALOMON appears to have come close to uniting *Diplopora annulata* and *Diplopora porosa* = *Gyroporella multiserialis*. Had he not again denied GÜMBEL's assertion regarding the identity of the first two species and added his correctly determined synonymy of the above-named second and third, he would have had to come to unit-

ing all three species. His finding concerning the distribution of *Diplopora porosa* clearly supports the validity of my views for it states explicitly that it probably occurs everywhere with *Diplopora annulata* and that it is always more abundant.

2. *Diplopora nodosa*. Unfortunately not available.
3. *Diplopora herculea*. My name for this species is based on SALOMON's data given here. The specimens before me lack completely any significant swelling in the apical area. However as this behavior is similar to that of many examples from the Marmolata too, I have no doubt of their synonymy. On the other hand, some particularly thin-walled individuals that SALOMON placed here belong to a discrete species, my *Teutloporella gigantea*. I did not see a cellular structure on the surface. However, after all a question to consider would be whether it does not have a causal connection with the perforate character of the calcareous skeleton that I described in *Teutloporella gigantea*. Surely we must then contradict SALOMON's assumption that this structure first appears after weathering. On the other hand, it seems to me that an analogy with the cortical cells of *Neomeris* is precluded in view of the overall form of the pores.
4. *Diplopora Gümbeli*.
5. *Diplopora Beneckei*. A thorough investigation of the inner structure of these two species would be extremely desirable.

GEYER, 1896-2

Über die geologischen Verhältnisse im Pontafler Abschnitt der Karnischen Alpen.

The comment on this work is essentially the same as for that of 1895-3.

GEYER, 1898-1

Über neue Funde von Triasfossilien im Bereiche des Diploporidenkalk- und Dolomitzuges nördlich von Pontafel.

The author corrects his earlier concept regarding the position of the rocks named in the title and now shifts them to the level of the Schlern Dolomite. According to my observations they contain *Diplopora annulata*. The underlying beds with *Gyroporella ampleforata* (it actually is this species) fall lower into the Muschelkalk. That second diplopore that occurs in the Ablitzen gorge along with *Gyroporella ampleforata* is none other than *Teutloporella triasina*.

STEINMANN, 1899-1

Über fossile Dasykladazeen vom Cerro Escamela, Mexiko.

STEINMANN's works stand out among all of the publications on fossil Siphonea in a most gratifying way. Every line demonstrates that the author had the clearest conception not only of just the species under discussion, but also of the entire group of Dasycladaceans in general. To him the diplopores are not, as it has more or less the appearance of in some others, peculiar lime tubules, but real plants that assimilated, grew and proliferated.

The way that STEINMANN completed the secondary verticillated branches of *Triploporella* in the present work gave me the first suggestion concerning the establishment of the trichophorous type.

In this work the approach to the assignment of *Triploporella* is somewhat different from that of the closely related *Tetraporella* which will be discussed below in his next publication (1903-1). On the whole, I consider STEINMANN's later representation more correct. In the work we are currently discussing the author stresses particularly the resemblance of *Triploporella* to the Acetabularians and places the Cretaceous genus in the line of descent of this group, even close to the branching off of the Dasycladeans. To me it would be more in agreement with the sense of the mentioned later remarks that *Triploporella* be replaced into the line of descent of the Dasycladeans and shifted close to the branching off of the Acetabularians.

TORNQUIST, 1899-2 and 1900-4

Neue Beiträge zur Geologie und Paläontologie der Umgebung von Recoaro und Schio, III und IV.

I must make the following general remarks concerning this work: The constancy of characters, insofar as it can be expressed in numbers, is significantly overrated. This applies to both the diameter of tubules and the thickness of the walls, and in particular to the height of the segments and the number of verticils in them. In several places TORNQUIST speaks of partitions between the individual segments. As in reality these are open furrows filled with sediment this phrase is confusing to say the least.

Concerning the two groups that TORNQUIST set up, *infundibuliformis* and *annulata*, the first one corresponds to a part of my genus *Teutoloporella*, the latter to my *Diplopora s.s.*

1. *Diplopora vicentina*. If it happens that my identification of this species is not erroneous, I have to correct the following: According to TORNQUIST it must be accepted that the pores are arranged in verticils. We have seen that this is not the case. And so naturally there can be no alternation of pores in successive verticils. This species belongs to *Teutloporella*.
2. *Diplopora annulata*. The two verticils in each segment of which TORNQUIST speaks, probably belong, as already mentioned, to a single metaverticillate verticil.
3. *Diplopora multiserialis* is identical to the last. TORNQUIST himself mentions that both occur in the same rock. When the author asserts that the canicules in *Diplopora multiserialis* are absolutely horizontal, in *Diplopora annulata* somewhat oblique, it is to be remarked that the slope of the pores changes, but it is entirely without a relationship to the number of verticils in a segment. What TORNQUIST adduces against SALOMON is surely unsound. In fact, a specific assignment cannot be made from the number of pore rows in a segment. TORNQUIST is right though that there can be no doubt that in the living plant there was transverse segmentation. But what can be understood, however, of the inner and outer walls and the cross-walls of the segments that would all have to be preserved as a unit is quite incomprehensible given that undoubtedly the first two are both only geometrical constructions. I can think only that TORNQUIST means a more opaque layer of sediment that in a lot of cases deposited a kind of incrustation on the walls of the calcareous skeleton, with which the plant itself had nothing to do originally.
4. *Diplopora triasina*. To *Teutloporella*. The description of this species includes a number of important observations, particularly on the outward tapering of the pores. Too

the sculpture on the outer surface of the calcareous skeleton is pictured correctly and vividly.

STEINMANN, 1903-1

Tetraporella Remeši, eine neue Dasycladacea aus dem Tithon von Stramberg.

A comparison of my work with the one discussed here in itself shows how much I am indebted to STEINMANN for numerous and important suggestions and how I have to agree with him on many important points.

The distinction between my concept of the phylogenetic relationships of the Dasycladaceans and STEINMANN's is based essentially on differences regarding the systematic value of certain characteristics. STEINMANN puts great weight on the number of branches in a verticil or on the overall form of the plant. It seems to me that by so doing much too little consideration is given the great variability in these relationships as we see them in the living forms (see what SALOMON had to say in 1895-4). Too, the consistent use of his standpoint would lead to hardly acceptable conclusions, as for example, the separation of the spherical Bornetellae from the club-shaped ones, that yet conform perfectly in all other points. Withal, I never misjudge the advantages that STEINMANN's concept of numerous parallel lines of evolution would offer as an explanation of certain distinguishing characteristics that could never be interpreted as adaptations. I agree entirely with the interpretation that *Bornetella nitida* is a descendant of *Tetraploporella*; only I would not like to place this species in an exceptional category, but to derive all other *Bornetella*, *Cymopolia*, *Dactylopora*, *Neomeris*, *etc.* from *Tetraploporella* or its close vicinity. From this same point of view also I hold as not sufficiently grounded the generic distinction of *Tetraploporella* and *Triploporella*.

With certain modifications the interpretation that STEINMANN has given for the blind-ended pores of *Gyroporella* and *Physoporella* can, I believe, as has already been stated, be extended to the whole Diploporid family.

In addition, by the way, a rather disturbing error exists in the place (p. 50 [6]) regarding *Physoporella*. The sentence: «I name these forms *Physoporella*» is about a paragraph too low. I was unable to find a *Gyroporella macropora* in GÜMBEL. Perhaps they meant *G. macrostoma*, a species I do not know.

Apart from that I accept STEINMANN's views concerning the three stages in the evolution of fructification. I am not able to decide whether it is necessary, as STEINMANN would have it, for it to take place independently several times, or whether we can get along with a monophyletic development of discrete types.

That in every case rather plausible law that according to STEINMANN should be valid for the emplacement of the thickest lime deposition unfortunately is not easy to follow in Triassic species because calcification is almost always so strong that one cannot really talk about localization. Where the calcareous skeleton is reduced it appears to be a little outside of the sporangia.

The Mastoporids or, as the author later perhaps more appropriately calls them, the Cyclocrinidae, in which I also include Palaeoporella, I consider as unquestionable Siphoneae verticillatae. Their greater differences from recent forms is easily explained in that they are an early and peculiar specialization, a lateral branch already extinct in the Paleozoic. At present I lack a personal judgment about the Receptaculitidae.

STEINMANN, 1903-2

Einführung in die Paläontologie.

Lateral branches are not verticillate in all Siphoneae verticillatae.

1. Here *Diplopora* includes my genera *Diplopora*, *Kantia*, *Oligoporella*, *Teutloporella*, *Macroporella*; however the definition is suitable only for *Diplopora s.s.* and by stretching it, to *Teutloporella*. With the former, the strong possibility that the spores were actually formed in the main axis must be taken into account. It is surely hardly necessary to point out again that both of the species cited, *Diplopora annulata* and *D. porosa*, are identical. The illustration is excessively schematic as regards the course of the pores. Only extremely rarely does one see annular segments relatively so short.
2. *Physoporella*. The illustration is not in agreement with my observations in that the widest part of the sporangia lies outward here, while I always found it inward. As regards *Physoporella macropora* see the comment in 1903-1.
3. *Gyroporella*. Certain details of the generic description apply only to *Gyroporella vesiculifera*.

MERCIAI, 1908-3

Fossili dei calcari grigio-scuri del Mt. Malbe presso Perugia.

Gyroporella vesiculifera. On the pictures of the thin sections one sees unquestionably an outward closure of the caniculae. It is also mentioned that the outer surface of prepared specimens shows pores. According to the illustrations an arrangement in verticils does not seem to be present. Perhaps a new species of *Macroporella* is involved.

GEYER, 1910-1

Aus den Kalkalpen zwischen dem Steyr- und dem Almtale in Oberösterreich.

Gyroporella (correctly *Diplopora*) *porosa* has since been proved beyond doubt to be identical to *Diplopora annulata*. Also it is certain that the species in the lower, darker part of the limestones is completely congruent with the one in the upper lighter part. From a phytopaleontologic standpoint it is extremely improbable that the former is correlative to the Gutensteiner Limestone.

STEINMANN, 1910-2

Über die Stellung und das Alter des Hochstegenkalkes.

In this work the author has only a few words to say about our topic. What he says about it is true, in particular the important comment regarding the distribution of *Gyroporella*, but the genus already occurs in the lower Muschelkalk.

Continued on page 300 (Closing remarks)

Summary table of dimensions

Name of species	greatest length observed in mm	outer diameter of the thalli in mm: largest	outer diameter of the thalli in mm: smallest	outer diameter of the thalli in mm: most common	diameter of the central cavity: in mm	diameter of the central cavity: relative to outer diameter (percent of)	height of segments: in mm	height of segments: relative to outer diameter (percent of)	number of verticils in a segment
Macroporella dinarica	13.9	1.1	0.5	0.9	1. 0.3	31%			
					2. 0.34	36%			
					3. 0.4	37%			
					~0.35	~35%			
Macroporella alpina	6	2.6	1.3	2	1. 1.1	40%			
					2. 0.7	51%			
					3. 1.1	55%			
					~1	~49%			
Macroporella Bellerophontis	9	1.8	0.4	0.8	1. 0.19	50%			
					2. 1.1	65%			
					3. 0.5	63%			
					~0.8	~60%			
Macroporella helvetica	4.8	1.9	1.1	1.6	1. 0.6	37%			
					2. 0.6	40%			
					3. 0.4	24%			
					~0.5	~34%			
Gyroporella ampleforata	40	4.2	2.5	3.5		~60%	1.7 to 10.5	47%	
							2.4 to 3.7	23%	
							~1.2	~35%	
Teutloporella herculea	38	7.1	4.8	5.5	1. 3.9	63%			
					2. 3.0	55%			
					3. 2.2	52%			
					~3	~57%			
Teutloporella gigantea	46	7.2	4.6	6	1. 4.4	71%			
					2. 4.0	67%			
					3. 4.6	78%			
					~4.3	~73%			
Teutloporella tenuis	9.4	3.2	1.9	2.8	1. 2.7	83%			
					2. 1.6	84%			
					3. 2.5	89%			
					~2.3	~85%			
Teutloporella vicentina	17	5.3	3.8	4.8	1. 3.0	57%	1. 2 to 8	80%	
					2. 2.5	56%	2. 3 to 7.2	65%	
					3. 1.8	46%	~3.2	~73%	
					~2.4	~53%			
Teutloporella vicentina var. *nana*	8	2.8	2.3	2.5	1. 1.1	40%	1. 11 to 7.6	30%	
					2. 1	40%	2. 4 to 4.6	42%	
					3. 0.8	33%	3. 3 to 4.1	59%	
					~1.0	~38%	~1.1	~44%	
Teutloporella triasina	37	7.1	2.5	5.3	1. 2.8	50%	1. 7 to 10.8	29%	1. 5–6
					2. 2.4	43%	2. 5 to 6.2	24%	2. 4
					3. 2.5	48%	3. 4 to 3.8	18%	3. 3–4
					~2.6	~48%	~1.2	~26%	(3–)4–5(–6)

spacing of the verticils		number of pores in a section (verticil)	number of pores in a tuft	number of tufts in a verticil	angle of pores with the longitudinal axis	diameter of the main axis		diameter of the widest part of the pores in mm	diameter of the sporangia in mm
in mm	relative to outer diameter (percent of)					in mm	relative to outer diameter (percent of)		
		~24			90°–60°			~0.1	
		~30			~70°			>0.1	
		(12–)30			80°–30°			~0.1	>0.1
touching each other		~27			90°–60°			~0.15?	
		~32			~90°	1. 2.4 2. 1.1 ~1.7	56% 48% ~52%	~0.2	
		~60			~60°			~0.2	
		~33			<60°			~0.23	
		~30			?			>0.2	
		~38			90°–80°			~0.2	
		20?			~90°			~0.1	
touching each other at the base	~4%	~45			1. 52° 2. 60° 3. 83° ~65°			~0.2	

Summary table of dimensions

Name of species	greatest length observed in mm	outer diameter of the thalli in mm			diameter of the central cavity		height of segments		number of verticils in a segment
		largest	smallest	most common	in mm	relative to outer diameter (percent of)	in mm	relative to outer diameter (percent of)	
Oligoporella pilosa	35	2.7	1.3	2.3	1. 1.4 2. 0.8 3. 0.8	68% 54% 44%			
					~1.0	~54%			
Oligoporella serripora	29	2.4	1.4	2	1. 0.6 2. 0.9 3. 1.1	33% 48% 50%			
					~0.9	~44%			
Oligoporella prisca	20	2.3	1	1.6	1. 1.1 2. 0.6 3. 0.5	50% 36% 35%			
					~0.7	~40%			
Physoporella pauciforata	26	3	0.5	2	1. 1.6 2. 1.1 3. 0.4	53% 55% 39%			
					~1	~49%			
Physoporella dissita	12			2?	1. 1 2. 1.2 3. 0.8	50% 41% 36%	1. 7 to 5.7 2. 2 to 2.5 3. 3 to 2.7	42% 43% 38%	1
					~1	~42%	~1	~41%	
Physoporella minutula	7	2.9	1.3	2.3	1. 0.9 2. 0.5 3. 1.1 4. 2.0	59% 35% 47% 66%	1. 4 to 3.0 2. 2 to 1.8 3. 2 to 1.6	54% 59% 34%	1
					~1.1	~48%	~0.8	~49%	
Kantia philosophi	6.7	3.6	1.3	2.9	1. 2.0 2. 1.2 3. 0.6	70% 57% 50%	1. 3 to 4.2 2. 2 to 4.3 3. 1 to 6.7	50% 63% 223%	1. 2-3 2. 4-5 3. 14
					~1.3	~59%	~3.4	~112%	4. 3 5. 2 6. 5 7. 2 (2–)4–5(–14)
Kantia hexaster	1.4			1.3	0,4	31%	1,4	93%	4
Kantia dolomitica	21	4.9	2	3.4	1. 1.7 2. 1.1 3. 3.3	48% 43% 69%	1. 10 to 10.7 2. 7 to 7.0 3. 4 to 4.1	34% 32% 30%	1. 2 2. 2 3. 2
					~2.0	~53%	~1.0	~32%	2
Diplopora annulata	15	6.7	1	3.6	1. 1.9 2. 2.8 3. 2.2 4. 0.6	56% 74% 54% 55%	5. 6 to 10.3 6. 4 to 10.1 7. 1 to 12.9 8. 4 to 3.5	47% 67% 280% 18%	1–20?
					~1.9	~58%	~4.5	~137%	
Diplopora debilis	18	4.4	1.2	3.1	1. 3.4 2. 2.1 3. 1.1	79% 68% 45%	1. 3 to 2.7 2. 3 to 3.8 3. 3 to 5.0	47%	2–3?
					~2.2	~64%	~1.5	~43%?	

spacing of the verticils		number of pores in a section (verticil)	number of pores in a tuft	number of tufts in a verticil	angle of pores with the lon-gitudinal axis	diameter of the main axis		diameter of the wi-dest part of the po-res in mm	diame-ter of the sporangia in mm
in mm	relative to outer diameter (percent of)					in mm	relative to outer diameter (percent of)		
1. 4 to 2.8 2. 6 to 3.6 3. 5 to 3.5	39% 29% 33%	10–20			~90°			~0.25	
~0.7	~34%								
1. 6 to 2.9 ~0.5	~28%	~20?			>60°			~0.15	
2. 22 to 8.8 3. 9 to 2.9 4. 8 to 3.3	26% 19% 24%	~18			~55°			~0.19	
~0.4	~23%								
4. 16 to 11.4 5. 6 to 6.0 6. 10 to 5.5	25% 38%	~15			45°–90°			~0.3	
~0.8	~31%								
equal to segment height		~30?			~90°			<0.26	
equal to segment height		~30?						~0.19	
1. 0.5 3. 0.5 4. 0.5 5. 0.34 6. 0.5	18% 17% 17%	~70	(2?–)3–4	~20	<90°	equal to diameter of central cavity	~0.13	~0.2	
~0.5	~17%								
0.3	23%	96?	6	16?	<90°?			<0.1	
1. 0.4? 3. 0.5	5% 5%	60?	4	15?	90°–60°			<0.15	
~0.45	~5%								
8. 4 to 3.5 9. 9 to 5.3 10. 6 to 3.3 11. 9 to 3.9	18% 17%	75?	3	25?	~90°			0.08–0.15	0.2X0.3
~0.6	17–18%								
?	?	?	?	?	<90°			~0.19	

Plate II (I)

Figs. 1–6. *Macroporella dinarica* PIA

1. Oblique longitudinal section. [Sample I.3.] **2**. Oblique transverse section. All inner cavities are filled with spar calcite. [Sample I.3.] **3**. Oblique transverse section. [Sample I.1.] **4**. Transverse section. [Sample I.1.] **5**. Transverse section. [Sample I.3.] **6**. Tangential section. [Sample I.3.]

Figs. 7–12. *Macroporella Bellerophontis* ROTHPLETZ

7. Oblique longitudinal section. [Sample XX.1.] **8**. Oblique transverse section. [Sample XX.1.] **9**. Oblique transverse section of a particularly small specimen. [Sample XX.1.] **10**. Oblique transverse section. [Sample XXVII.1.] **11**. Oblique transverse section. [Sample XXVII.1.] **12**. Somewhat oblique transverse section of a very large specimen. Pores widening upward. [Sample XXVI.1.]

Figs. 13–15. *Macroporella alpina* PIA

13. Somewhat oblique transverse section. [Sample LVII.1.] **14**. Somewhat oblique transverse section of a specimen with few pores. [Sample LVII.1.] **15**. Oblique transverse section. [Sample LVII.2.]

Figs. 16–17. *Macroporella helvetica* PIA

16. Oblique longitudinal section. [Sample XVI.3.] **17**.Transverse section. [Sample XVI.3.]

Figs. 18–26. *Gyroporella ampleforata* GÜMBEL

18. Fragment. It shows particularly clearly the segmentation of the verticillated branches into stem and end bubble (Sporangium). [Sample VIII.1.] **19**. Slightly oblique transverse section. In the lower part of the spar-calcite-filled central cavity are the remains of the membrane of the main axis. [Sample IX.1.] **20**. Somewhat oblique transverse section through a deformed individual. In the spar calcite-filled inner central cavity are broken remnants of the membrane of the main axis. [Sample IX.1.] **21**. Slightly oblique longitudinal section. Preservation as in the two preceding examples. Very clear intusannulation. [Sample IX.2.] **22**. Transverse section. [Sample XIV.1.] **23**. Oblique transverse section. Two inner ring furrows are cut across. Membrane of the main axis torn open but completely preserved. [Sample XIV.1.] **24**. Rather oblique transverse section. In the upper part the membrane of the main axis. In the lower part, the calcareous skeleton is close to the main axis. [Sample XIV.1.] **25**. Oblique transverse section through a fragment. Two inner annular furrows. [Sample XIV.3.] **26**. Somewhat oblique transverse section. Below an inner annular furrow is cut across. [Sample XV.1.]

Fig. 27. *Teutloporella herculea* STOPPANI

Compare also Pl. III, Figs. 1–2. Oblique transverse section. [Original sample not found in the collection.]

[Statements of magnification were approximate. 1–6: scale bar 1 mm (grey bar); 7–27: scale bar 2 mm (black bar). Around each specimen a strip of the surrounding rock was left purposely.]


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Plate III (II)

Figs. 1–2. *Teutloporella herculea* STOPPANI

See also Pl. II, Fig. 27.

1. Transverse section. [Sample LXXIII.2.] **2**. Oblique transverse section. [Sample LXXIV.1.]

Figs. 3–6. *Teutloporella gigantea* PIA

3. Part of a very slightly oblique longitudinal section. [Sample LXXX.6.] **4**. Transverse section. [Sample LXXX.1.] **5**. Very oblique transverse section through a curved specimen*,. Highly perforate calcareous skeleton. [Sample LVIII.1.] **6**. Transverse section. [Sample LVIII.1.]

*In correcting the draft of the Plate I noticed that it could also be a section at the upper end of the plant (lower part in the figure).

Figs. 7–10. *Teutloporella* (?) *tenuis* PIA

7. [Sample I.6.] and **8**. [Sample I.10.] Oblique longitudinal sections. Shows the tapering of the pores outward. **9**. Section through a curved specimen. [Sample I.3.] **10**. Transverse section. [Sample I.3.]

Figs. 11–14. *Teutloporella vicentina* TORNQUIST

11. Somewhat oblique transverse section. Below an annular furrow has been cut. [Sample XLV.1.] **12**. Oblique longitudinal section. [Sample XLV.1.] **13**. Oblique longitudinal section through 3 segments of very different lengths. [Sample XLV.3.] **14**. Slightly oblique transverse section. [Sample XLI.2.]

Figs. 15–16. *Teutloporella vicentina* var. *nana* PIA

15. Somewhat oblique transverse section. [Sample XLV.1.] **16**. Oblique longitudinal section through a curved specimen. [Sample XLV.3.]

[Statements of magnification were approximate. Scale bar 2 mm (black bar). Around each specimen a strip of the surrounding rock was left purposely.]


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Plate IV (III)

Figs. 1–8. *Oligoporella pilosa* PIA

1. Oblique longitudinal section of a small specimen. [Sample I.1.] **2**. Transverse section of a small specimen. [Sample I.9.] **3**. Oblique longitudinal section. [Sample I.1.] **4**.Oblique transverse section. [Sample I.1.] **5**. Oblique transverse section. [Sample I.3.] **6**. Oblique longitudinal section of a small specimen with undulation. [Sample I.10.] **7**. Slightly oblique longitudinal section. [Sample I.6.] **8**. Oblique transverse section through a specimen with closely-spaced verticils. [Sample V.1.]

Figs. 9–11. *Oligoporella serripora* PIA

9. Slightly oblique transverse section. [Sample LIV.2.] **10**. Oblique transverse section. [Sample LIV.3.] **11**. Oblique longitudinal section. [Sample LIV.8.]

Figs. 12–17. *Teutloporella triasina* SCHAUROTH

12. Oblique longitudinal section, distinct pore series. [Sample III.1.] **13**. Oblique longitudinal section of a specimen without annual furrows. [Sample III.1.] **14**. Longitudinal section of a specimen with very well-marked annular furrows. [Sample III.1.] **15**. Oblique transverse section. Very well-marked verticil series. [Sample XXXIII.2.] **16**. Slightly oblique longitudinal section. Very well-marked verticil series. [Sample XXXIII.2.] **17**. Transverse section. [Sample VI.1.]

Figs. 18–19. *Teutloporella* aff. *triasina* SCHAUROTH

18. Tangential section. [Sample VII.2.] **19**. Oblique longitudinal section. [Sample VII.1.]

[Statements of magnification were approximate. 1–11: scale bar 2 mm (black bar); 12–19: scale bar 2 mm (red bar). Around each specimen a strip of the surrounding rock was left purposely.]

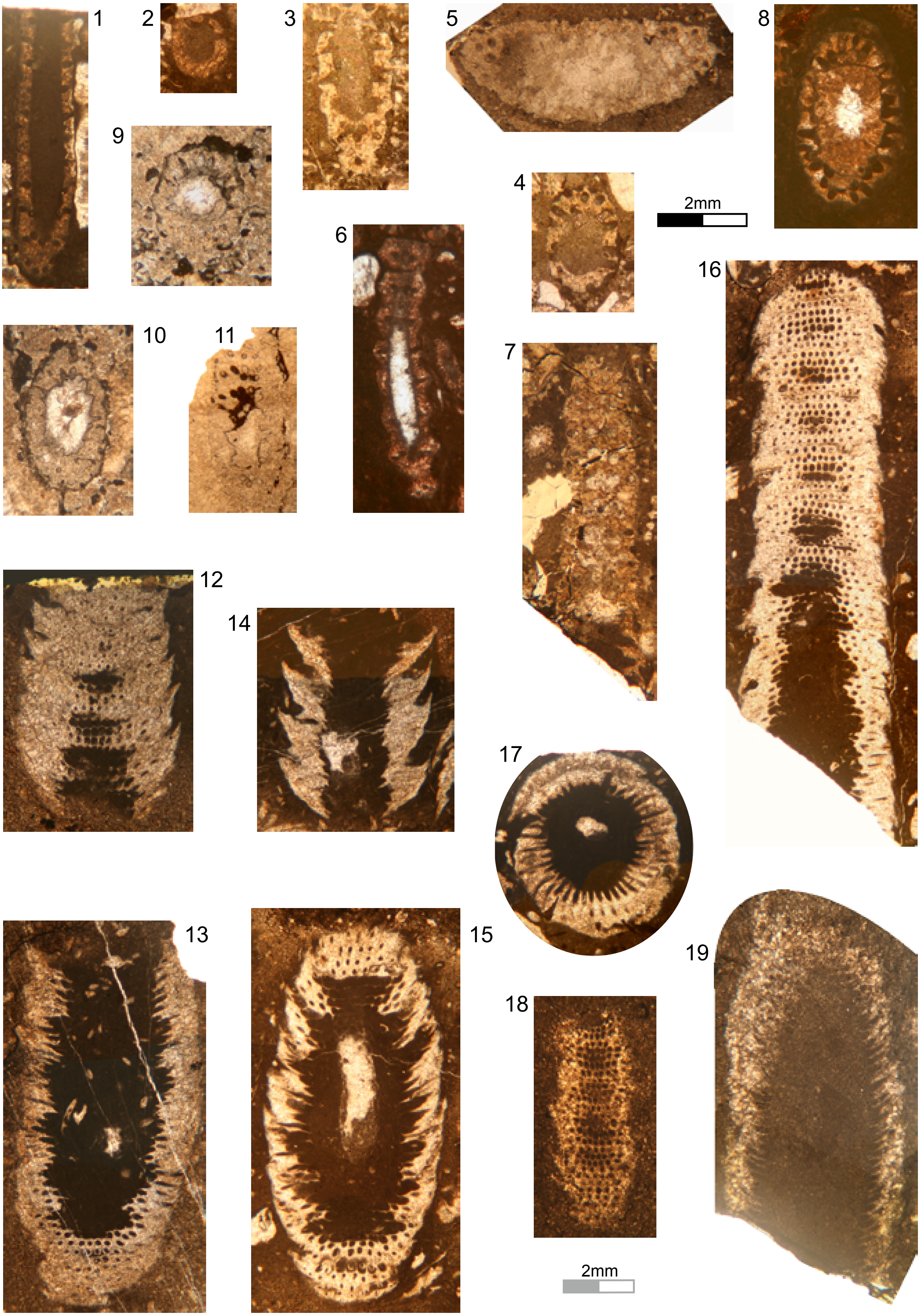
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Plate V (IV)

Figs. 1–8. *Oligoporella prisca* PIA

1. Tangential section. Below the pores widen outward, at the top they widen inward. The line in the middle of the figure is a break in the paper of the original drawing. [Sample LXXIX.1.] **2**. Transverse section of a very small specimen. [Sample LXXIX.1.] **3**. [Sample XXXIV.2.] and **4**. [Sample XXXIV.1.] Oblique longitudinal section. **5**. Oblique transverse section. [Sample XXXIV.2.] **6**. Oblique transverse section though a somewhat curved specimen*. Obvious widening of the pores outward. [Sample XXXIV.2.] **7**. Oblique transverse section. [Sample XVI.3.] **8**. Oblique transverse section. Very strong expansion of the pores outward. [Sample XXXIV.2.]

*It may also concern a section at the upper end of a specimen. If so, it would follow that not all individuals reach the trichophorous stage.

Figs. 9–19. *Physoporella pauciforata* GÜMBEL

9. Somewhat oblique transverse section of a small specimen. [Sample XXI.1.] **10**. Somewhat oblique transverse section. [Sample XXI.3.] **11**. Somewhat oblique transverse section. [Sample XXI.2.] **12**. Oblique longitudinal section. [Sample XXI.2.] **13**. Somewhat oblique transverse section. 3 verticils. [Sample XXVIII.1.] **14**. Somewhat oblique transverse section. [Sample XXVIII.2.] **15**. Oblique longitudinal section. [Sample XXVIII.2.] **16**. Slightly oblique tangential section. [Sample XXVIII.2.] **17**. Transverse section. [Sample XXII.1.] **18**. Oblique longitudinal section of a specimen with strongly inclined pores. [Sample XXXIV.1.] **19**. Oblique longitudinal section. The line in the middle of the figure is a tear in the paper of the original drawing. [Sample LIV.1.]

[Statements of magnification were approximate. Scale bar 2 mm (black bar). Around each specimen a strip of the surrounding rock was left purposely.]

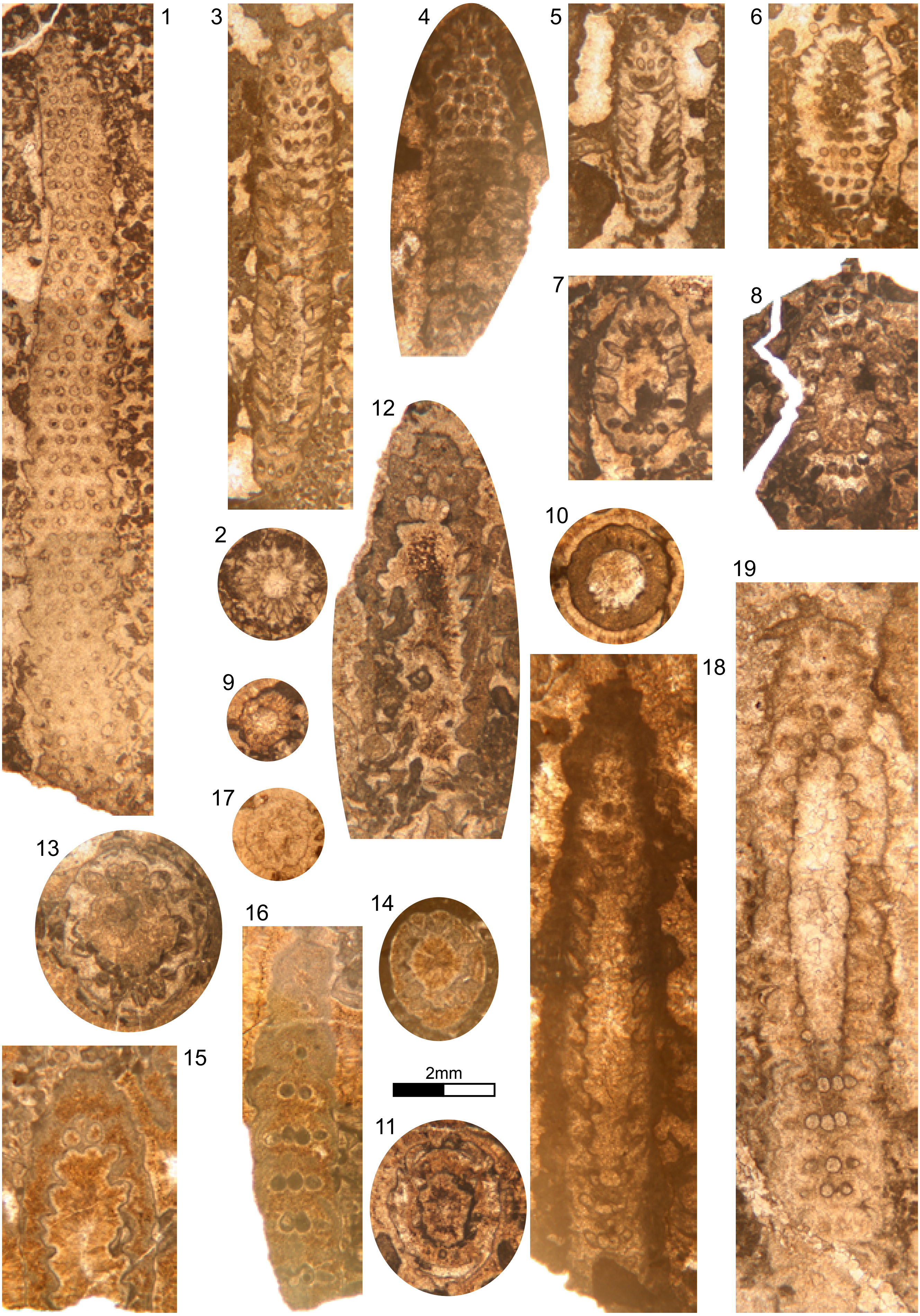
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Plate VI (V)

Figs. 1–4. *Physoporella dissita* GÜMBEL

1. Oblique longitudinal section. The specimen is broken in the thin section, the drawing is a composite of the pieces. [Sample LXII.2.] **2**. Tangential section. [Sample LXII.4.] **3**. Oblique section through a fragment. [Sample LXII.4.] **4**. Oblique transverse section. [Sample LXII.4.]

Figs. 5–12. *Physoporella minutula* GÜMBEL

5. Longitudinal section of a fragment. [Sample XVI.3.] **6**. Longitudinal section of a fragment. [Sample XVI.3.] **7**. Longitudinal section of a fragment. [Sample XVI.3.] **8**. Oblique transverse section through a fragment. [Sample XVI.3.] Figures 5–8 make up a series showing increasing segmentation of the calcareous skeleton. **9**. Oblique section through a small specimen with pores inclined steeply. [Sample XVI.1.] **10**. Eccentric longitudinal section through only one segment. [Sample XVI.1.] **11**. Oblique longitudinal section. [Sample XVI.4.] **12**. Oblique transverse section. [Sample XVI.3.]

Fig. 13. *Kantia hexaster* PIA

Oblique longitudinal section through a single segment. [Sample I.3.]

Figs. 14–16. *Kantia dolomitica* PIA

14. Fragment. Form and position of pores particularly clear. [Sample XXX.1.] **15**. Oblique longitudinal section of a broken specimen. [Sample XXX.4.] **16**. Oblique longitudinal section. [Sample XXX.4.]

Figs. 17–21. *Kantia philosophi* PIA.

17. Oblique transverse section. [Sample XIV.1.] **18**. Oblique transverse section through an extremely small specimen. [Sample XIV.1.] **19**. In the upper portion two tangential sections (the right hand one strongly oblique), below a longitudinal section of one segment. [Sample XIV.2.] **20**. Slightly oblique longitudinal section through three segments. On the left side of the middle one two broadened pores (sporangia?). [Sample XIV.3.] **21**. Transverse section. [Sample XIV.3.]

[Statements of magnification were approximate. Scale bar 2 mm (black bar). Around each specimen a strip of the surrounding rock was left purposely.]

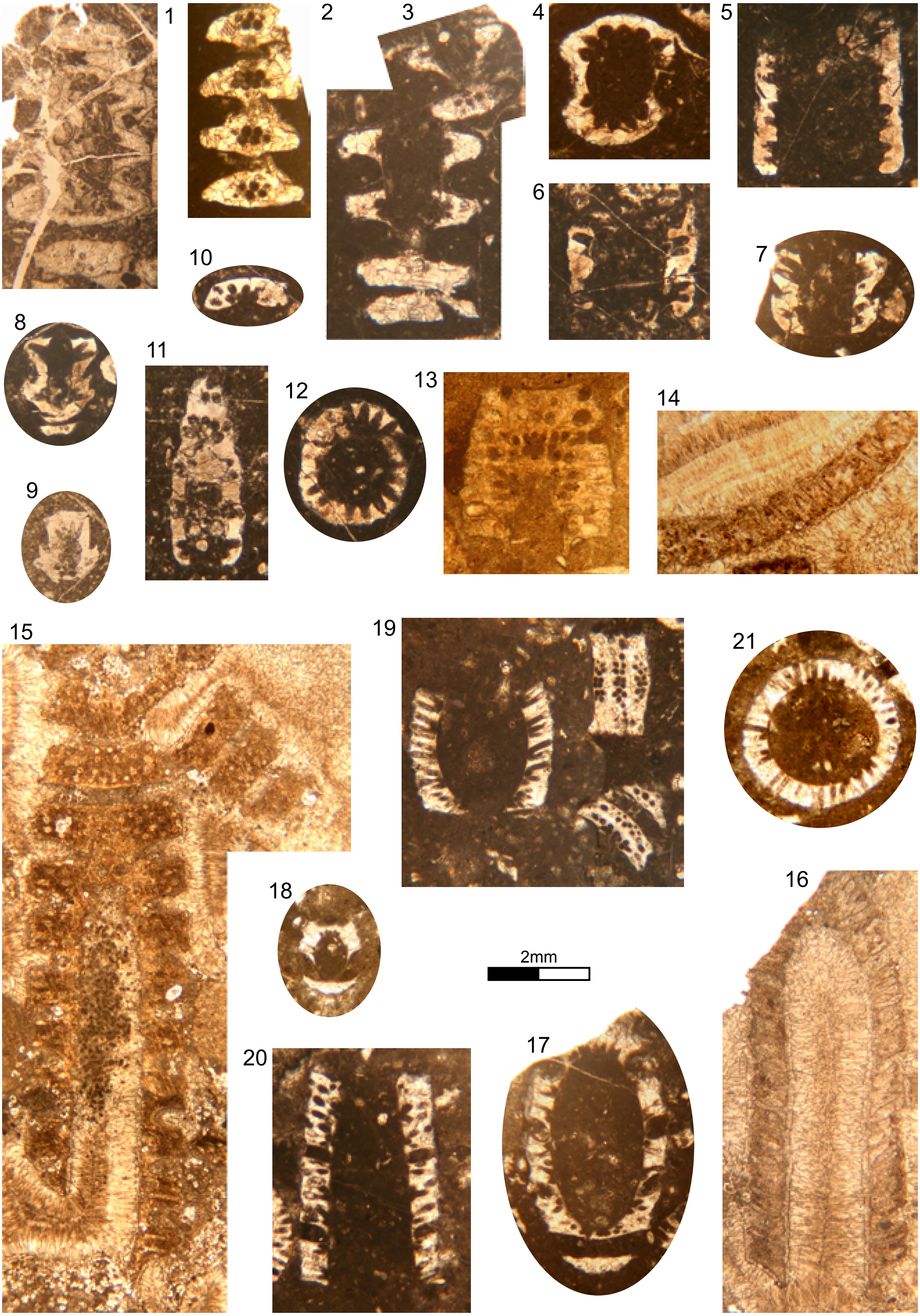
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Plate VII (VI)

Figs. 1–17. *Diplopora annulata* SCHAFHÄUTL

See also Pl. VIII, Figs. 1–2.

1. Oblique section through a very thick-walled specimen. Very clear pore tufts. [Sample XIII.1.] **2**. Oblique longitudinal section. In the middle a clearly defined grouping of three pores. The two dashed lines in the middle mark the approximate limit of the area occupied by a verticil. [Sample XIII.1.] **3**. The inner side of a weathered calcareous skeleton fragment. Between the verticils somewhat raised annular ridges. [Original sample not found in the collection.] **4**. Outside of weathered fragment. [Original sample not found in the collection.] **5**. Transverse section of a thick-walled specimen. [Sample II.5.] **6**. Oblique longitudinal section. [Sample II.2.] **7**. Oblique longitudinal section. [Sample II.2.] **8**. Oblique longitudinal section. [Sample II.5.] **9**. Oblique section through a fragment. On the left several pores with spherical enlargements (sporangia?). [Sample XXV.3.] **10**. Oblique transverse section through one segment with very inclined pores. [Sample XXV.3.] **11**. Slightly oblique transverse section. On the right a globular space (sporangium?). The corresponding pore is not in the section. [Sample XXV.1.] **12**. Oblique section through a fragment. Right and left an annular furrow almost fully closed outward. In the middle of the lower part are several distinct groups of three pores each. [Sample XL.2.] **13**. Oblique longitudinal section through three segments each with two verticils. [Sample XL.1.] **14**. Slightly oblique transverse section of a thin-walled specimen. [Sample XII.1.] **15**. Tangential section through five segments each with 1 verticil. [Sample LXIX.1.] **16**. Oblique longitudinal section of a large fragment. Between the verticils ridges extend into the inner space. [Sample L.2.] **17**. Slightly oblique longitudinal section through two segments. Corresponding to an annular furrow is a broad projection into the inner cavity. [Sample LXVVI.1.]

1–2 and 14–15: Locality unknown.

[Statements of magnification were approximate. Scale bar 2 mm (black bar). Around each specimen (except 3 and 4) a strip of the surrounding rock was left purposely.]


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Plate VIII (VII)

Figs. 1–2. *Diplopora annulata* Schafhäutl

See also Pl. VII, Figs. 1–17.

1. Oblique transverse section through two specimens accidentally nested. In the outer one only one verticil per segment. [Sample LXI.2.] **2**. Longitudinal section precisely through the apex of a specimen. On the drawing the apex is down. [Sample XXIV.1.]

Figs. 3–7. *Diplopora debilis* Gümbel

3. Slightly oblique transverse section. [Sample XXXV.1.] **4**. Oblique transverse section through a very large specimen. [Sample XLII.2.] **5**. Fragment. It clearly shows the enlargement of the pores outward. [Sample XLII.1.] **6**. Tangential section through 3 segments. [Sample XLII.1.] **7**. Oblique transverse section. The pores broaden outward. [Sample XLII.2.]

[Statements of magnification were approximate. Scale bar 2mm (black bar). Around the specimens of Figs.1–7 a strip of the surrounding rock was left purposely.]

Fig. 8. General structural plan of the Diploporids

It helps also in the explanation of the reconstruction in the text. Upper half: Lateral view, decalcified after the removal of the front verticillated branches. Lower half: Longitudinal section. A = verticillated branches, K = calcareous skeleton, M = membrane of the main axis, P = pores in the membrane, S = main axis.

Fig. 9. Young sterile shoot of *Neomeris annulata*.

From Cramer, 1891-2, Pl. 1, Fig. 2.

Figs. 10–16. Schematic generic reconstructions.

[refer to Text-Figs. 1, 4, 11–12, 16, 19 & 21 herein]

10. *Macroporella* Pia

[Refer to Text-Fig. 1 herein]

[In the original publication,] upper drawing: Section of the decalcified plant from above. Lower drawing: Lateral view of the decalcified plant. In the lower part the front verticillated branches are removed.

11. *Gyroporella* Gümbel.

[Refer to Text-Fig. 4 herein]

As in Fig. 10.

12. *Teutloporella* Pia.

[Refer to Text-Fig. 11 herein]

As in Fig. 10.

13. *Oligoporella* Pia

[Refer to Text-Fig. 12 herein]

[In the original publication,] upper drawing: Decalcified verticil from above. Lower drawing: Lateral view, decalcified. In the upper part the front verticillated branches are removed.

14. *Physoporella* Steinmann

[Refer to Text-Fig. 16 herein]

As in Text-Fig. 13. One pore of the two verticils was left out during reproduction.

15. *Kantia* Pia

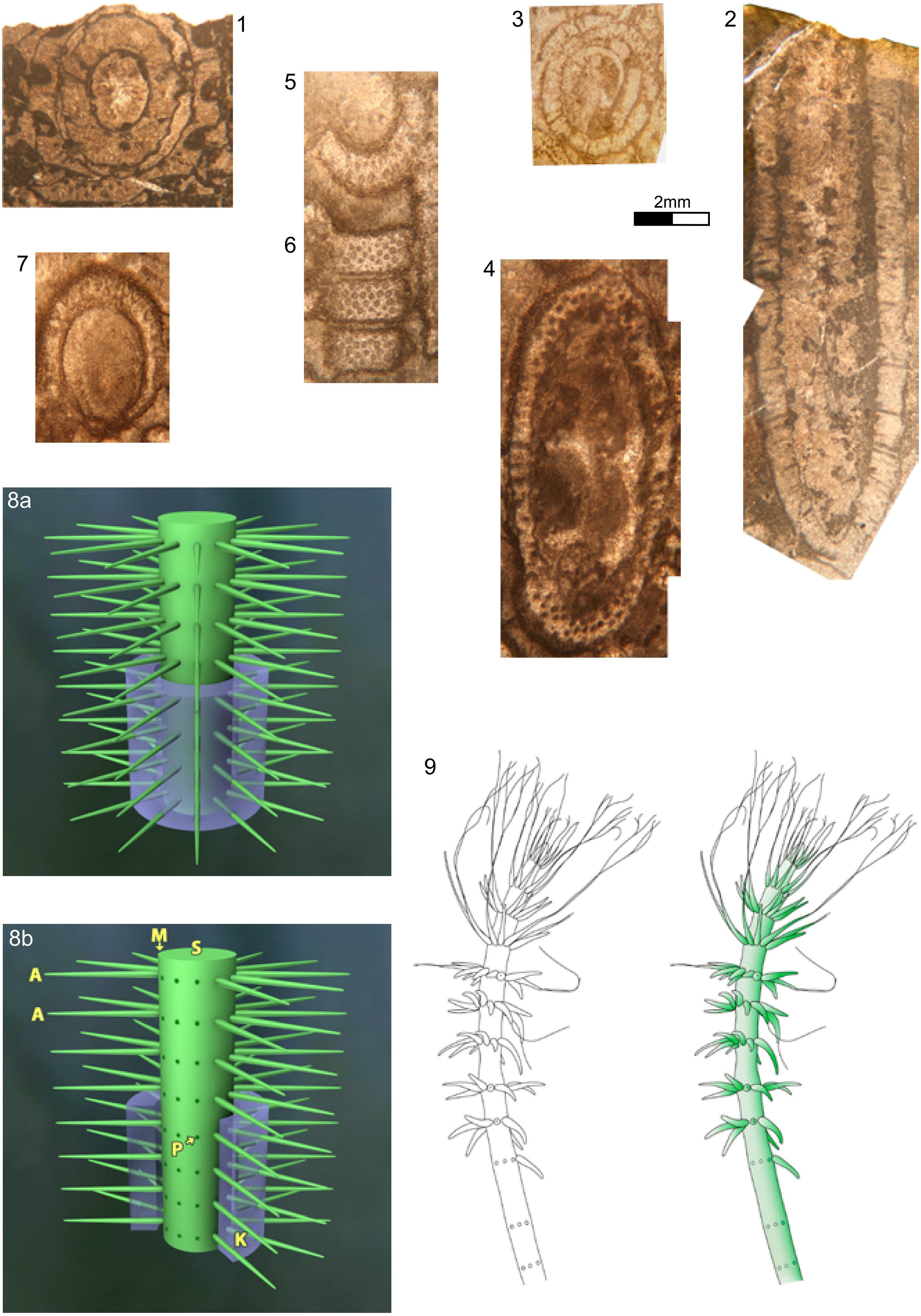
[Refer to Text-Fig. 19 herein]

[In the original publication,] upper drawing: Decalcified verticil from above. Lower drawing: Lateral View. From top to bottom: **1**. 3 verticils decalcified, frontal branches removed. **2**. 3 decalcified verticils with all branches. **3**. 5 verticils in the thallus with the calcareous skeleton.

16. *Diplopora* Schafhäutl

(Refer to Text-Fig. 21 herein)

[In the original publication,] upper drawing: Decalcified verticil from above. Lower drawing: Lateral view. From top to bottom: **1**. 2 verticils decalcified, frontal branches removed. **2**. 1 verticil decalcified, the front branches removed, the lateral ones cut off at the outer surface of the calcareous skeleton. **3**. 3 verticils decalcified. All branches cut off at the outer surface of the calcareous skeleton. **4**. 1 verticil with calcareous skeleton. Branches as in 3. **5**. 2 complete verticils with thallus.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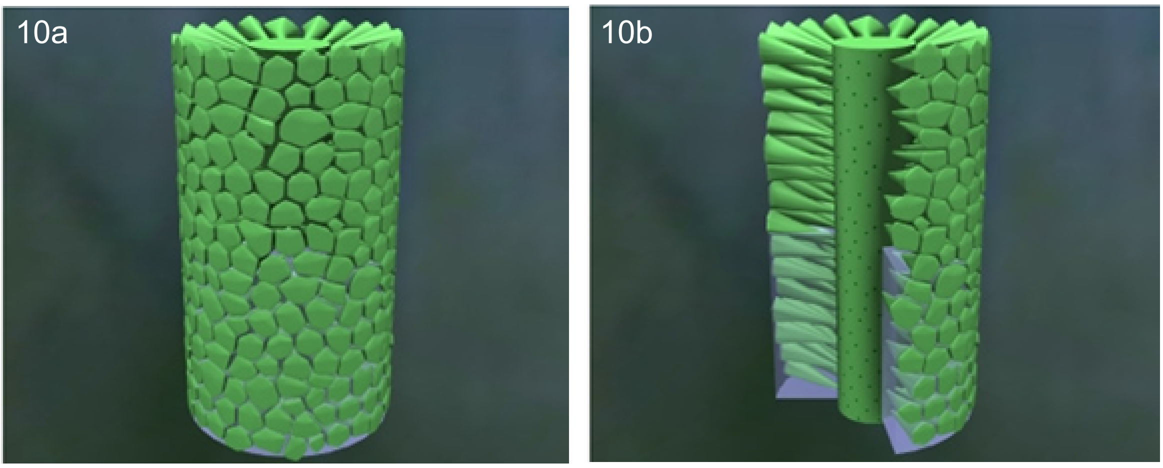
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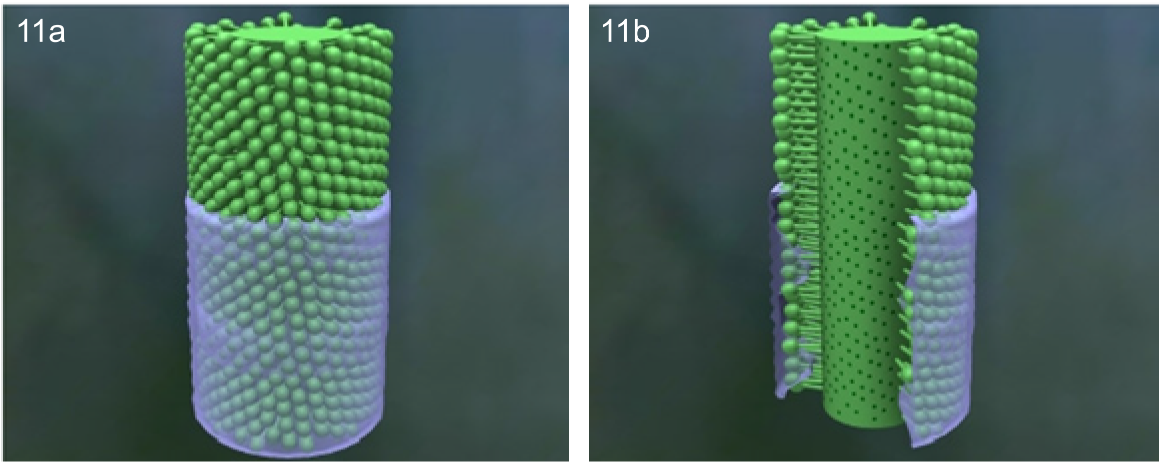
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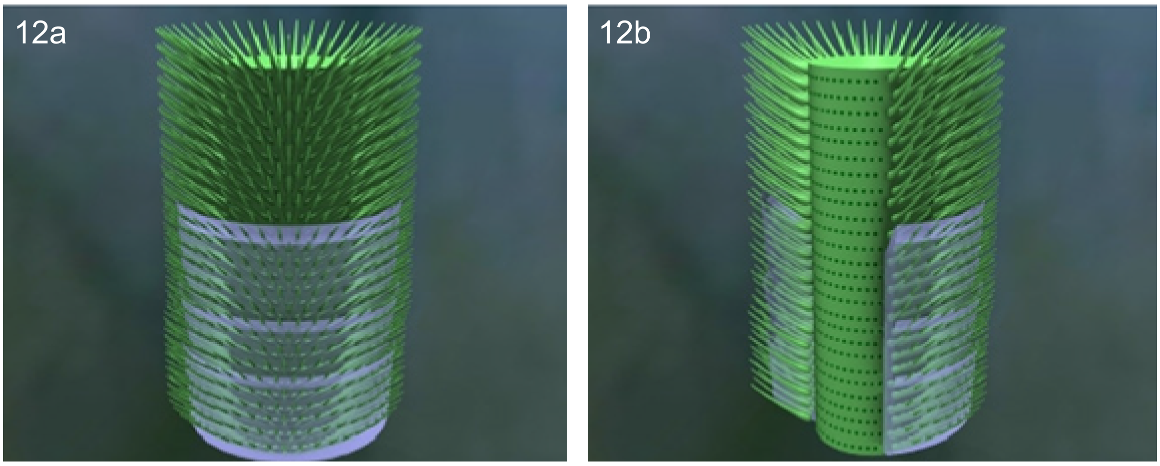
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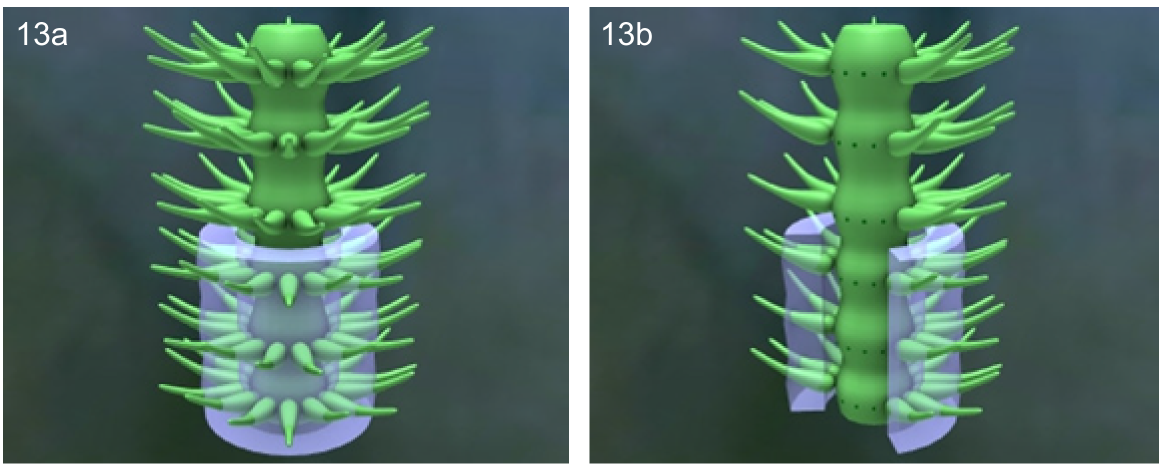
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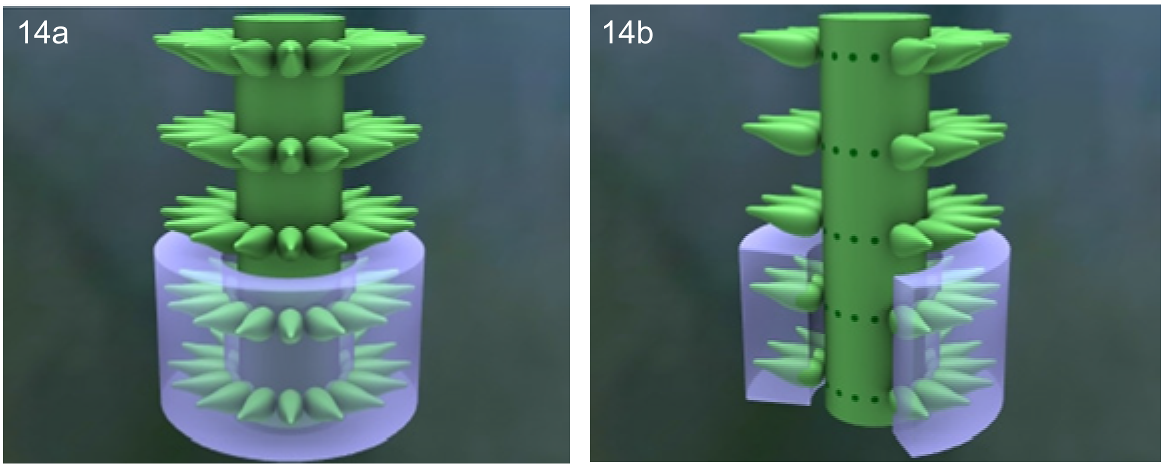
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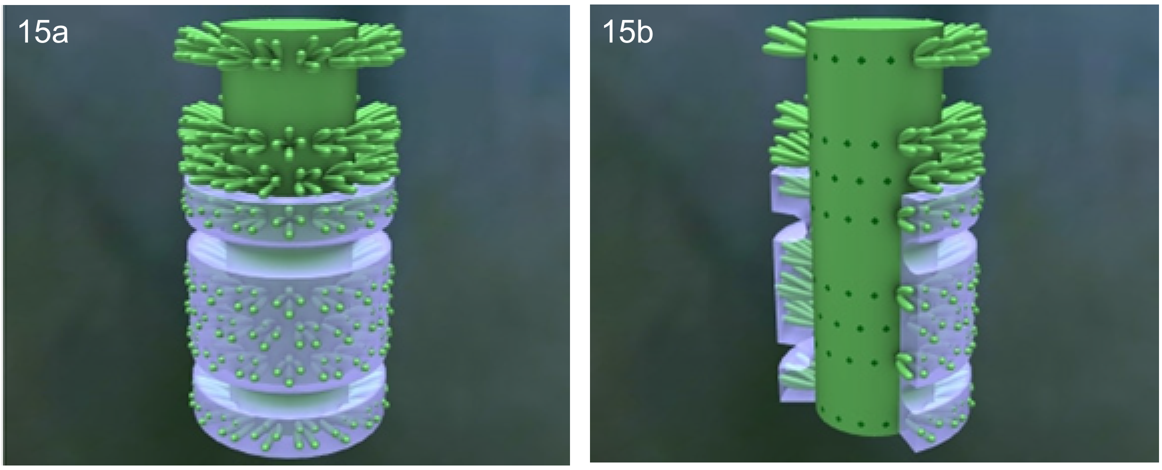
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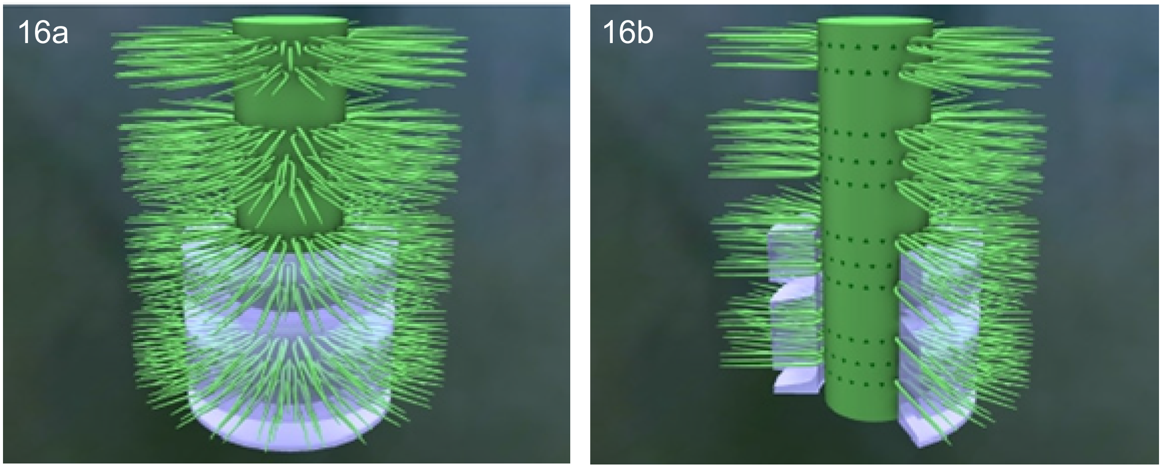
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Closing remarks

Lastly, I am allowed to list some questions that follow from those I have discussed and of which the study appears particularly desirable to me.

1. As far as my work itself is concerned, it needs most of all a more thorough study of sporangia, particularly those of the Diploporids. Furthermore, in the classification of the newer species the question should be investigated as to whether the genus *Teutloporella* should not be split, so that one genus would be comprised of *T. herculea*, *T. gigantea*, *T. tenuis*, the other, that would have a new name, of *T. vicentina* and *T. triasina*. The necessity of more comprehensive statistics for the determination the stratigraphic occurrences of the several species was already pointed out in the introduction.
2. The species that I do not have, such as *D. nodosa*, *G. macrostoma*, *G. silesiaca*, *D. Gümbeli*, *D. Beneckei*, *G. vesiculifera*, *G. curvata* should be worked on again (see 1863-1, 1872-1, 1895-4).

   Also to be undertaken:
3. An investigation of the west-Alpine Diploporids.
4. A reexamination of *Petrascula bursiformis*, *Linoporella capriotica*, in particular, however, ALTH's species *G. podolica*, *G. cyathula*, *G. subannulata*. See 1873-1, 1878-1, 1879-1, 1881-1, 1882-1, 1889-1, 1899-1.
5. A revision of *Munieria* and the forms in the Schratten Limestone of the Säntis. See 1883-2, 1902-1, 1908-1.
6. The Dasyporellids family and all Carboniferous forms seem to me to require a revision, that would perhaps lead to the suppression of one genus or another.
7. The extraordinarily rich Tertiary material should be completely revised, taking into account that in addition to the one in Paris, the collection in Bonn would probably be the main one to consider.
   These problems could be worked on anytime, for some others to be dealt with material needs to be obtained.
8. A study of the **Siphoneae verticillatae** of the Buntsandstein would be especially valuable. Here one must attempt to determine whether and how the several genera of the Muschelkalk were derived from *Macroporella*.
9. Scarcely less interesting would be a flora from the Lias or the Dogger that would probably show us the transition from the Diploporids to the Triploporellids.
10. Finally, as initiated by STEINMANN, a supplement to our knowledge of the Upper Cretaceous forms which would eventually give us a closer look at the later development of the Triploporellids, would be highly desirable.

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