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The Protists of Ernst Haeckel's *Kunstformen der Natur*

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Abstract

Haeckel's 'art book', *Kunstformen der Natur*, is likely familiar to most protistologists as it is probably Haeckel's best known work, and it prominently featured protists. No doubt many of us have used some of the images from it in our lectures. Most familiar are perhaps the often-reproduced images of nassularian radiolaria, but plates were also devoted to phaeodarians, acantharia, foraminifera, ciliates, diatoms, dinoflagellates and desmids. Despite the fame of *Kunstformen der Natur*, there are aspects of the work that have received little attention, and are of potential interest to protistologists. These include the overall importance of protists in the work, compared to other taxa, the surprisingly under appreciated role of Haeckel's collaborator, Adolph Giltsch in creating the figures, the disputed fidelity of the illustrations of protists, and Haeckel's discrete inclusion of many descriptions of new species of protists, forcing us to consider *Kunstformen* a scientific publication. Here these aspects, and the 20 plates featuring protists will be reviewed. The goal of this review is to familiarize protistologists with the most famous work featuring protists, and point out the many particular figures of protists we may wish to avoid showcasing, as the illustrations are questionable. A supplemental file is provided listing the currently accepted names of the protist taxa (for names found in a database), and the reasons for considering some illustrations as questionable.

Keywords: Scientific Illustration, Adolph Giltsch, Phaeodaria, Foraminifera, Diatoms, Radiolaria, Acantharia

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1. Introduction

Kunstformen der Natur (from hereon *Kunstformen*) was an unusual publication, unlike all of Haeckel's previous works. Although sold today as a book, it was not a book; it was a portfolio of 100 large chromolithographic plates, "suitable for framing", and each with

an explanatory pamphlet. They were sold in sets of ten plates, by subscription. At first, five sets of 10 plates each were to be issued, and then another five sets, giving a total of 100 plates, were to be published if the first five sets sold well. Publication began in 1899, when Haeckel was 65 years old and a major, even dominating, scientific figure of his time (e.g. Goldschmidt 1956). He had published lavishly illustrated monographs on a variety of taxa: radiolaria (Haeckel 1862, 1887), sponges (Haeckel 1872, 1889), medusa (Haeckel 1879, 1881, 1882), and siphonophores (Haeckel 1888). However, they were scientific works, largely concerned with taxonomy, such as the Challenger Reports on taxa found in samples from the Challenger Expedition of 1873-1876 (Haeckel 1882, 1887, 1888, 1889), and consequently directed to a scientific readership. In contrast, *Kunstformen* targeted a non-scientific audience. In the preface, included with the first set of plates, Haeckel stated that his goal was to show the beauty of organisms to "a larger circle of friends of art and nature", especially artists and artisans. This was reiterated in the publisher's description of *Kunstformen* on the back cover (Fig. 1). The last set of 10 plates and the supplementary text were published in 1904. By all accounts, the work was successful. Haeckel succeeded in reaching and influencing numerous artists, artisans, and architects. These include René Binet (of the 1900 Paris *Porte Monumentale* fame), Hendrick Petrus Berlage, August Endell, Max Ernst, Emile Gallé, Paul Klee, Gustav Klimt, Alfred Kubin, René Lalique, Gabriel von Max, Hermann Obrist, Constant Roux, Louis Tiffany and Henry Van der Velde (Bossi 2021a; Debourdeau 2016; Green 1987; Mann 1990; Williman 2019). *Kunstformen* is said to have blurred the distinctions between animal and plant, as well as that between humans and other animals (Bauman 2018). In 2021, there was a major art exhibition shown in both the Musée Orsay in Paris, and the Musée des Beaux-Arts in Montreal, "*The Origins of the World, The Invention of Nature*", and five of the plates from *Kunstformen* were exhibited, three of which were plates of protists (Bossi 2021b, annexe, 'Liste des Oeuvres'). It should be noted though that the aesthetics of *Kunstformen* are not universally appreciated. A historian of architecture, Barry Bergdoll, stated that organisms were "transformed in lurid colour" (Bergdoll 2007) and the renown ecologist Evelyn Hutchinson, described *Kunstformen* as "Biergarten Art Nouveau" (Hutchinson 1978).

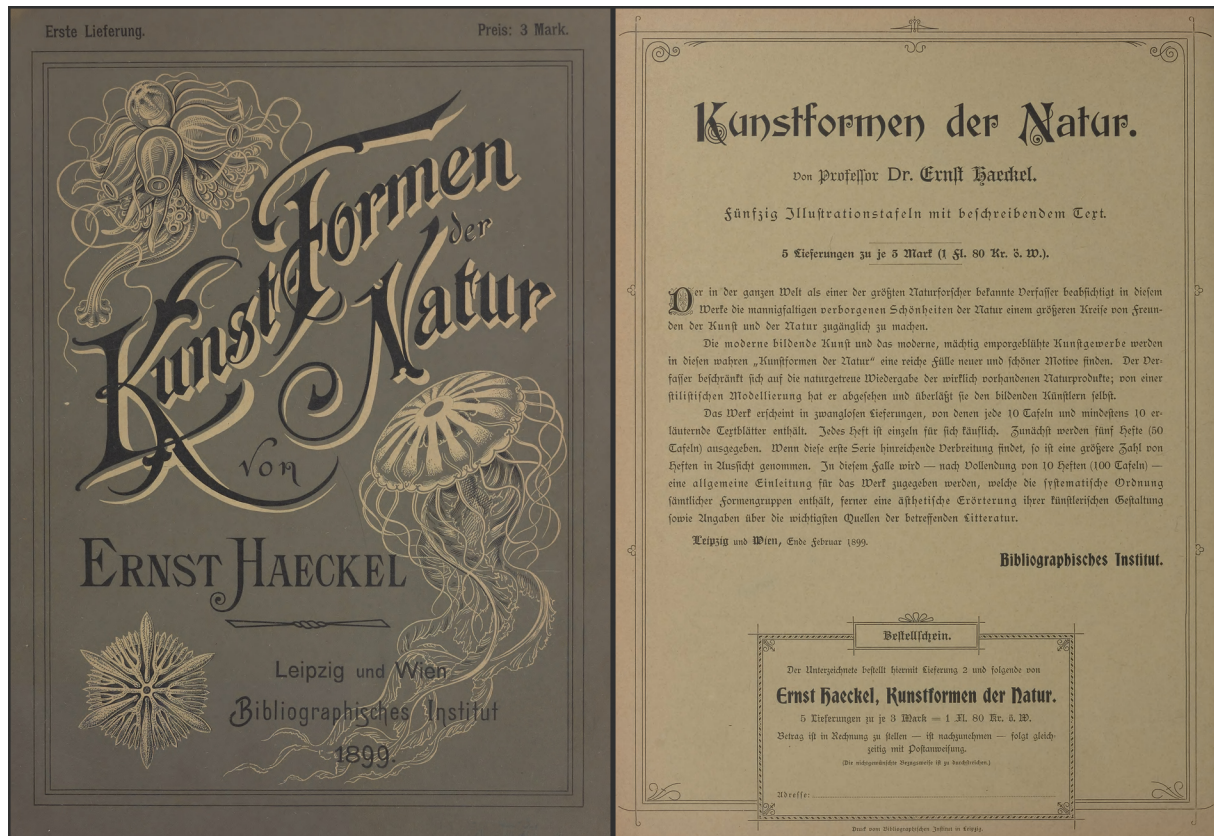


Fig. 1. The front (left panel) and back (right panel) covers of the first issue of *Kunstformen* published in early 1899. Each issue contained 10 loose plates measuring 35.4 x 26.3 cm, and 10 pamphlets, pages of explanatory text, for each plate. The front cover illustrations show a siphonophore (upper left, likely fig. 1 in plate 7), a medusa (center right, fig. 4 in plate 8), and a coral (lower left, fig. 9 in plate 9). On the back cover was the publisher's text describing the work (translation below), and a subscription form.

"The author, known throughout the world as one of the greatest natural scientists, intends in this work to make the manifold hidden beauties of nature accessible to a larger circle of friends of art and nature.

Modern fine art and the modern, powerfully flourishing arts and crafts will find a rich abundance of new and beautiful motifs in these true "art forms of nature". The author restricts himself to the true-to-life reproduction of creatures that actually exist; he has refrained from utilitarian modeling and leaves this to the visual artists themselves.

The work appears in informal volumes, each of which contains 10 plates and at least 10 explanatory text sheets. Each booklet can be purchased separately. Initially, five volumes (50 plates) will be published. A larger number of volumes is planned, if this first series is sufficiently successful. In this case, after completion of 10 volumes (100 plates), a general introduction to the work will be added, which will contain the systematic order of all form groups, an aesthetic discussion of their artistic design, and information on the most important sources of the literature."

It should be noted that the versions of *Kunstformen* sold today are usually a collection of the plates. They do not include all of the text of the pamphlets that gave the names of the species shown, and the figure legends describing the species (e.g. Haeckel 1974, 1998, 2023). In fact, some academics appear not to know that the original included a considerable amount of text (approx. 250 pages), and describe *Kunstformen* as a

collection of plates without any accompanying text (i.e., Halpern & Rogers 2013). To my knowledge, today, complete original versions of *Kunstformen* are only available online (e.g. Biodiversity Heritage Library, Gallacia,) or from rare book dealers, for a considerable sum (€ 6,000- 7,000). A complete version of *Kunstformen*, that is including all the texts, has never been published in English. For non-German speakers, the *Kunstformen* texts are not only in a foreign language, but also in a form not easily translated. The texts were printed in the old German font *Fraktur* (e.g., see the publisher's text in fig. 1), and today such texts are not easily read by non-native German speakers, nor by translation engines. Much of the information given in the following sections was found by using a cumbersome three-step process. First, the *Fraktur* texts in PDF files were converted to image files. Then, an AI-aided transcription engine (Transkribus.org) was used to convert images of the *Fraktur* text in *Kunstformen* (and other documents) into a text in a modern font. Finally, the transcribed text was then translated into English using Google Translate. The difficulty of translating the text of *Kunstformen* likely explains in part why some aspects of *Kunstformen*, such as the descriptions of new species, have received little attention.

2. The Importance of Protists in *Kunstformen*

Despite the fact that protists are curiously absent from the cover of *Kunstformen* (fig. 1), they are the most important group of organisms portrayed, both quantitatively, and qualitatively. The two dominant 'groups' of organisms in *Kunstformen* are, in common language, 'microbes' and 'jellyfish', or protists and gelatinous zooplankton. This latter category groups medusa, siphonophores, ctenophores, etc. The dominance of the two groups is not surprising given Haeckel's previous work. In quantitative terms, they together account for 48 of the 100 plates of *Kunstformen* with more plates devoted to protists, 20 plates, compared to 18 devoted to gelatinous zooplankton. A qualitatively greater importance of protists, relative to gelatinous zooplankton, is also evident considering the number of plates devoted to each group in the first five sets of plates; recall that their reception determined the continuation of *Kunstformen* to ten sets. In the first five sets of 50 plates, 15 were devoted to protists and 13 to gelatinous zooplankton. In the first two sets published, four plates depicted protists in each compared to 3 showing gelatinous zooplankton. Furthermore, throughout the ten sets of plates, a plate depicting protists was the first plate in each set. Among the protists, the radiolaria (*sensu* Haeckel) occupied ten plates, the foraminifera three plates, diatoms two plates, with a single plate each for ciliates, 'flagellates', dinoflagellates, desmids, and *Pediastrum* spp.

3. The Neglected Role of Adolph Giltch (1853-1911)

The remarkable scientific artwork of Haeckel has long been attributed to Haeckel alone (e.g. Scheffauer 1910) and has continued to be so described in more recent years (Ball 2000, 2006). While this was the case up until the 1880's, in all of Haeckel's later landmark taxonomic monographs, based on collections made during the Challenger Expedition (Haeckel 1882, 1887, 1888, 1889), all of the plates were signed "*E. Haeckel and A. Giltch, del.*" The "del." is a common abbreviation for "has drawn" (Stijnman 2012) and thus clearly indicated that the artwork used to create the lithographs was by both Ernst Haeckel and Adolph Giltch. Giltch's major role in producing the radiolarian monograph in the Challenger reports (Haeckel 1887) was specified in Haeckel's preface.

He stated that he was greatly indebted to Giltsch as both he and Giltsch drew the original sketches from the microscope, using a camera lucida. Unfortunately, which illustrations are from whose original sketches are not noted! Regardless, according to Haeckel himself, Giltsch was a close collaborator, not simply "Haeckel's lithographer" as described by some (e.g., Breidbach 2006). With regard to the plates of *Kunstformen*, Giltsch can be credited with having contributed not only to the original radiolarian images, but also to aspects of the original images of the medusa and the siphonophores in the Challenger Report according to Haeckel's prefaces (Haeckel 1882, 1888). It should be noted that although Giltsch's contributions are usually overlooked, some experts were well aware of Giltsch's important role. For example, Charles Kofoid noted it was surprising that Giltsch did not question the mis-placement of a tintinnid ciliate lorica among the radiolaria in the Challenger Report (Kofoid 1912). In more recent times, it has been recognized that Haeckel and Giltsch worked together, and were close friends (i.e., Bossi 2021a; Di Gregorio 2005, Williams et al. 2015).

Sadly, little is known about Adolph Giltsch. The only information available is from a memorial notice written by Haeckel, published in a Jena newspaper (Haeckel 1911). According to Haeckel's account, Adolph Giltsch was born into a lithography household. His father, Edward Giltsch had the only lithography firm in Jena when Haeckel was named Professor at the University of Jena. From age 14, he worked in his father's workshop. In the 1870's, the Giltsch firm started producing the plates for the journal *Jenaische Zeitschrift für Medicin und Naturwissenschaft* and produced the plates for Haeckel's Monograph on deep-sea sponges (Haeckel 1872). Adolph Giltsch started working intensively with Haeckel in 1877, at age 24, beginning with the Challenger Report on the radiolaria, and apparently worked with Haeckel continually until death in 1911. Giltsch's two sons took over the lithography firm following his death. With regard to Giltsch's contributions over the years, Haeckel stated:

"In total, during the 34 years of our joint work, Adolf Giltsch drew and lithographed over 400 folio plates for me, and numerous small plates. The execution of my drawings, which he corrected, and improved many times, was always equally careful, elegant and true to nature. Without his invaluable cooperation, without his tireless immersion in the great tasks, it would never have been possible for me to master this enormous amount of material. Likewise, without him I would not have succeeded in producing the 100 plates of my "Kunstformen der Natur", which have contributed a great deal to spreading interest and understanding of the hidden beauties of nature to wider circles."

Evidence of the high esteem Haeckel had for Giltsch is indicated by the number of taxa Haeckel named for him. Haeckel named two medusa species for him, *Carmina giltschi* (in Haeckel 1879) and *Pilema giltschi* (in *Kunstformen*), both of which were featured in *Kunstformen* plates (Fig. 2). He also named two species of radiolaria for Giltsch, *Clathrocorys giltschi* and *Lychnaspis giltschi* (in Haeckel 1887), but neither was shown in the *Kunstformen*. To put the number of species Haeckel named for Giltsch in perspective, note that he named six species for Darwin, three for his first wife, Anna Sethe (see Dolan 2019), and one for Frida von Usler-Gleichen, his late-in-life love (see Richards 2008). Haeckel also arranged for Giltsch to be appointed as "*Doctor Artis Honoris Causa*" by the Art Faculty of the University of Jena in April 1902, for Giltsch's 50th birthday (Haeckel 1902).



Fig. 2. Ernst Haeckel in 1914 (left panel), Adolph Giltsch, undated photo (right panel) and the *Kunstformen* plates showing the medusa species Haeckel named for Giltsch (central panels). In plate 26 (center left panel), *Carmaris giltschi* is shown in the center, the top right corner, and the bottom center. In plate 88 (center right panel), *Pilema giltschii* is shown in the three top figures.

4. The Disputed Fidelity of the Illustrations of Protists

The anatomical accuracy of the illustrations in *Kunstformen* is a contentious topic with a long history (e.g., Anon. 1919, Heron-Allen 1924), and many baseless opinions have been rendered (Willmann 2023). Most people would agree that reasoned judgment concerning the accuracy of an illustration can only be made in relation to the actual subject, or in comparison to an illustration taken to be authoritative; otherwise, the opinion is baseless. An example is the bald assertion by Philip Ritterbush, a historian of science, that Haeckel's drawings of radiolaria include "illusory structures" not visible to "the observer who inspects a radiolarian under the microscope today", given with no statement, or evidence, that the writer had ever examined any radiolarians (Ritterbush 1968). Similarly, the geneticist Richard Goldschmidt, stated "...Haeckel's radiolaria were too perfect all over. One had the impression that he first made a sketch from nature and then drew an ideal picture as he saw it in his mind." (Goldschmidt 1956). With the advent of scanning electron microscopy, some features of radiolarians which one might suspect were invented, were revealed to exist just as Haeckel depicted them (e.g. Emmer 2007). Note that some of Haeckel's slides are held in the Natural History Museum (London) and have been carefully catalogued for the designation of neotypes (Aita et al. 2009). Another odd opinion made is one with regard to the colors in *Kunstformen* plates. Frank Egerton, a historian of ecology, stated, in the legend of a figure showing plate 11 of *Kunstformen* (spumillarian radiolaria), that "Lithographer Adolph Giltsch transformed Haeckel's sketches into forms with somewhat exaggerated colors" (Egerton 2013). The criticism is remarkable as the forms depicted in the plate have, for the most part, never been seen by anyone other than Haeckel!

Even in the simplest case of assessing accuracy, that of comparing a figure to an illustration taken to be authoritative, unavoidably involves subjective judgment. For example, in previous publications (Dolan 2019, 2024), I have presented *Kunstformen* illustrations with the source figures, declaring the *Kunstformen* figures to be obviously stylized, compared to the figures of the original species descriptions (see fig. 3 concerning *Lagena* and *Dictyocodon*). However, with regard to the illustrations of one of my examples, the foraminifer *Lagena plumigera* (fig. 3a,b), Heron-Allen (1924) judged the *Kunstformen* image (fig. 3b), to be likely a faithful image of a 'perfect specimen' of the

species first illustrated by Brady (1884). Likewise, comparing the two figures of the radiolarian *Dictyocodon annasethe* (fig. 3c,d), one from the original species description by Haeckel in 1887 (fig. 3c), and the other (fig. 3d), from *Kunstformen* plate 31, the differences, which to me appear considerable, may appear to some as insignificant.

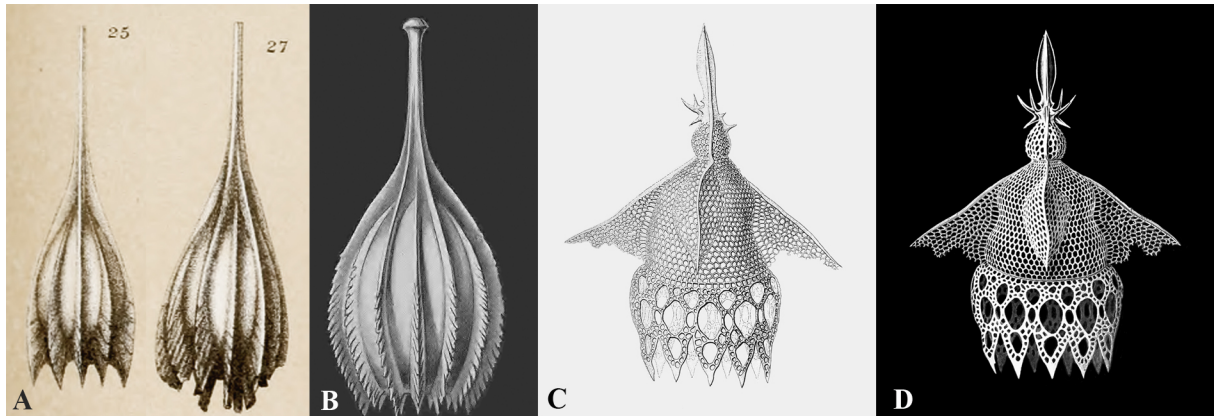


Fig. 3. Comparisons of original figures from the species descriptions, and the corresponding *Kunstformen* figures, used by Dolan (2019, 2024) to argue that *Kunstformen* figures were stylized. **A.** The figure of the foraminifer *Lagena plumigera* from Brady (1884) in which the longitudinal blades have stripes and the anterior end is bare. **B.** *L. plumigera* from *Kunstformen* plate 81, in which the blades are shown with serrations and the anterior end is topped with a knob. **C.** The figure of the radiolarian *Dictyocodon annasethe* from Haeckel 1887 with imperfect bilateral symmetry. **D.** *D. annasethe* from *Kunstformen* plate 31 showing near perfect bilateral symmetry. The anterior spine is perfectly straight, not leaning to the left, and the small spines at its base are mirror images, as are the wing-like structures extending outward in the central portion of the skeleton.

In the preface to *Kunstformen*, Haeckel stated unequivocally that the illustrations faithfully represented the organisms depicted. He reiterated the claim of the accuracy of the illustrations, in reaction to unidentified critics, in later years in one of his last publications (Haeckel 1917). Still, one might dismiss qualms concerning the accuracy of the figures as unimportant as *Kunstformen* is not a 'scientific publication', but an art book, as it has been so described by Lötsch (1998). However, *Kunstformen* must be considered a scientific publication because it contains a considerable number of original species descriptions, rendering many *Kunstformen* figures authoritative first depictions, albeit as mostly as uncertain taxa, as detailed in the following section. As a scientific publication, the accuracy of the illustrations is a matter of concern.

5. The New Species Described by Haeckel in *Kunstformen*

The new species Haeckel included in *Kunstformen* are not obvious, perhaps explaining why they have generally been overlooked. The figure legends (in the explanatory texts of the plates), give only the name of the species, credited to an individual, but without any details. For example, for plate 1, figure 1, the legend title is "Fig. 1. *Circogonia icosahedra* (Haeckel)". The taxonomic authorities for all the species depicted are incomplete (without a year), often erroneous, and no bibliography was ever included despite the claim made by the publisher (see fig. 1). All together, in the 20 protist plates, there are 278 species shown, and of these, Haeckel credited himself with 135 species. Of the 135 'Haeckel protist species', 114 are radiolarians (*sensu* Haeckel). As Haeckel was

an expert on radiolaria, these do not immediately draw attention and can be checked for appearance in the index of Haeckel's comprehensive 1887 Challenger Report radiolarian monograph. Doing so revealed that there are 5 new radiolarian species (*sensu* Haeckel) in *Kunstformen*, and two species of radiolaria that were described in the Challenger Report but without figures. The other 'Haeckel protist species' are somewhat conspicuous as they are taxa not associated with Haeckel's expertise: diatoms, foraminifera, dinoflagellates, flagellates, and freshwater green algae (desmids and species of *Pediastrum*).

Some of the new species Haeckel included were probably from his voyages. For example, his text states that the choanoflagellate *Codonocladium candelabrum* (plate 13, fig. 3) was found in Messina where Haeckel worked on radiolaria from the winter of 1859 to spring 1860. Other species were apparently found in his late travels, during the time span the *Kunstformen* was published (1899-1904). The acantharian *Lychnaspis miranda* (plate 41, fig. 3) is noted as from Ajaccio, Corsica found in September 1899. The image of this summarily described species in the *Kunstformen* was subsequently used as an example of an acantharian by Haeckel himself (Haeckel 1901) and others (Bölsche & McCabe 1906; Schmidt 1912). The foraminifer *Lagena milletti* (plate 81, fig. 6), was presumably named for the expert on foraminifera, F. W. Millett. It is noted in the figure legend as from the Malay Archipelago that Haeckel visited in his 1900-1901 voyages in Asia, the purpose of which was to gather more material for the continuation of the *Kunstformen* series (Richards 2008). Quite remarkably, Haeckel's illustration in *Kunstformen* of his *L. milletti* very closely resembles a figure published by Millett in 1901 of the species *L. striatopunctata* var. *spiralis*, in one of Millett's articles on the foraminifera of the Malay Archipelago (in Millett 1901, plate 8, fig. 7b). The very close resemblance of the two figures (discovered recently by François Le Coze, pers. comm.), suggests that Haeckel copied the 'variety' from Millett 1901 and described it as a new species dedicated to Millett. However, there are actually other organisms associated with his Asia voyage, newly described in *Kunstformen* by Haeckel: a mushroom, *Dictyophora madonna* (plate 63, fig. 1) that he found in 1900 in a botanical garden in Java, and the second meduse named for Giltsch, *Pilema giltschii* (plate 88 fig. 1-3; here fig. 2), found in Sumatra in 1901. Unfortunately, for most of the apparently new 'Haeckel protist species', the figure legends give no information as to where or when the species was found, nor even the size of the organism. Thus, they remain a mystery!

With regard to actual sizes of the sizes of the protist species shown in *Kunstformen*, it is not only Haeckel's new species that are missing size information in the legends. In all but four of the 20 plates, no sizes are given. Only for three plates, those showing foraminifera (plates 2, 12, 81) and last the protist plate showing spumellian radiolaria (plate 91), was size information given. From the sizes given in the four plates, it is obvious that the figures in a given plate are not shown to the same scale. For other protist plates, for which no size information was given, but showing species whose actual sizes were given by Haeckel in previous publications (i.e. tintinnid ciliates, radiolaria *sensu* Haeckel), it is also evident that the figures are not shown to the same scale. Thus, by default, one should assume for all of the protist plates that the figures are not shown to the same scale.

Table 1 lists the 21 protist species that Haeckel credited to himself, and whose names appeared for the first time, or only in, *Kunstformen* based on searches in multiple

databases (*i.e.*, Biodiversity Heritage Library, World Register of Marine Species which includes AlgaeBase, DiatomBase, and the World Foraminifera Database), and searches for publications containing the name (using Google Scholar). The present status of most the species is either "uncertain" or considered as a junior synonym of a previously described species. This is perhaps not surprising as Haeckel had not published on the taxa involved and was then likely somewhat unfamiliar with the literature. What is perhaps surprising, given the popularity of *Kunstformen*, is that taxonomists of the various taxa have overlooked the species depicted in *Kunstformen*. Specifically, two of the three species of Haeckel's new foraminifera were added to the World Register of Marine Species while my paper "On the curious illustration of the foraminifer *Peneroplis plantus* in Haeckel's *Kunstformen der Natur* (Dolan 2024) was in review. The third species of foraminifera was added very recently after I contacted François Le Coze (World Register of Marine Species, Taxonomic Editor for Foraminifera) of concerning the third species. Similarly, the diatom described by Haeckel has been added recently after I contacted the Chief Taxonomic Editor responsible for Bacillariophyceae in the World Register of Marine Species, Patrick Kociolek. Overall, as protistologists, we should likely avoid using any of the *Kunstformen* illustrations of the species listed in Table 1. The illustrations are questionable because most of the species are uncertain, or of currently unaccepted validity.

Table 1. Protist species first described in *Kunstformen*. Taxonomic status: A = entered in WoRMS in August 2024 as accepted as *P. muelleri*; B = entered in WoRMS in November 2023 as unaccepted junior synonym; C = name in AlgaeBase as "accepted" but without details; D = AlgaeBase as 'in quarantine'; E = name appears only in *Kunstformen*; F = AlgaeBase as "uncertain"; G accepted in AlgaeBase as Haeckel 1899; H = AlgaeBase as Haeckel 1899 "uncertain"; I= recently, August 2024, entered in WoRMS as unaccepted junior synonym.

Name	taxonomic group	plate	figure	status
<i>Pinnularia mülleri</i>	Diatom	4	19	A
<i>Vertebralina catena</i>	Foraminifera	12	13	B
<i>Vertebralina furcata</i>	Foraminifera	12	14	B
<i>Codonocladium candelabrum</i>	"Flagellate" choanoflagellate	13	3	C
<i>Pyrgidium pyriforme</i>	Dinoflagellate	14	9	D
<i>Acantholonche favosa</i>	Acantharia	21	7	E
<i>Sepalospyris pagoda</i>	Spyroidea Nassularian radiolaria	22	6	E
<i>Micrasterias trigemina</i>	Desmidea	24	7	C
<i>Euastrum agalma</i>	Desmidea	24	12	C
<i>Pediastrum octonum</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	4	F
<i>Pediastrum cruciatum</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	5	G
<i>Pediastrum elegans</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	8	G
<i>Pediastrum lunatum</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	9	H
<i>Pediastrum furcatum</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	10	H
<i>Pediastrum darwinii</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	13	H
<i>Pediastrum trochiscus</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	14	C
<i>Pediastrum solare</i>	Hydrodictyaea genus <i>Pediastrum</i>	34	15	H
<i>Lychnaspis miranda</i>	Acantharia	41	3	E
<i>Solenosphaera familiaris</i>	Spumellarian radiolaria	51	12	E
<i>Conchonia quadricornis</i>	Phaeodaria	61	14	E
<i>Lagena milletti</i>	Foraminifera	81	6	I

6. Haeckel's Protist Plates in *Kunstformen* and His Questionable Illustrations

Obviously, when *Kunstformen* illustrations are used to show a general qualitative point, for example, to show the beauty of planktonic protists (i.e., Dolan 2023), the occurrence of some questionable figures is not of much importance. However, when the figures are used in a formal setting, such as in publication, to show an example of a taxon, (e.g., the choanoflagellate shown in Larson et al. 2020, and the radiolarian shown in Burki and Keeling 2014), or in a permanent setting, such as a tattoo, it behooves us to avoid using a questionable illustration. There are, surprisingly, many "questionable illustrations" of protists in the *Kunstformen* that we may wish to avoid spotlighting in our lectures or publications, etc.. Of the 273 species of protists shown, 66 illustrations can be considered "questionable", a substantial proportion. Furthermore, each of the 20 plates contains at least one questionable illustration.

The questionable illustrations of protists fall into four categories:

- 1) Illustrations of species newly described in *Kunstformen* by Haeckel, most which are today considered problematic descriptions (see Table 1). These represent 21 illustrations.
- 2) The illustration of species previously described by Haeckel, but without figures or an incomplete figure. Consequently, the accuracy of the figures in *Kunstformen* cannot be assessed. There are five such figures.
- 3) The illustrations of a species credited to someone other than Haeckel that appear only in *Kunstformen*. There are two such figures of 'ghost species'.
- 4) Illustrations of species obviously differing in one or more aspects from the most likely source illustration, that is from the species description that appeared shortly before *Kunstformen* appeared, or a species described and illustrated by Haeckel in a previous publication. These number 38, and represent the bulk of the questionable illustrations of protists. Most of these concern *Kunstformen* illustrations of species previously described by Haeckel but shown with details not in the figure published with the original description. It should be noted that while the added detail in the *Kunstformen* figure may actually exist, the details are not in the original figure that remains the authoritative illustration.

The following section consists of an exhibition of the 20 plates of *Kunstformen* featuring protists, in sets of four plates. The Phaeodaires, foraminifera, ciliates, diatoms of plates 1, 2, 3, and 4 are shown in **fig. 4**. The Spumullarian radiolaria, foraminifera, flagellates, and dinoflagellates of plates 11, 12, 13 and 14 are shown in **fig. 5**. The Acantharia, nassularian radiolaria, desmids, and nassularian radiolaria of plates 21, 22, 24, and 31 are shown in **fig. 6**. The Hydrodictyaceae, Pediastrum species, acantharia, spumellarian radiolaria, and phaeodaria, of plates 34, 41, 51, and 61 are shown in **fig. 7**. The nassularia, foraminifera, diatoms, and spumillarian radiolaria of plates 71, 81, 84, and 91 are shown in **fig. 8**. The "questionable illustrations" of Haeckel are indicated on the plates using a magnifying glass icon, and noted in the brief figure legends. The name of the species given by Haeckel, and the details of the justification for labeling an illustration as "questionable", are given in the Supplementary File.

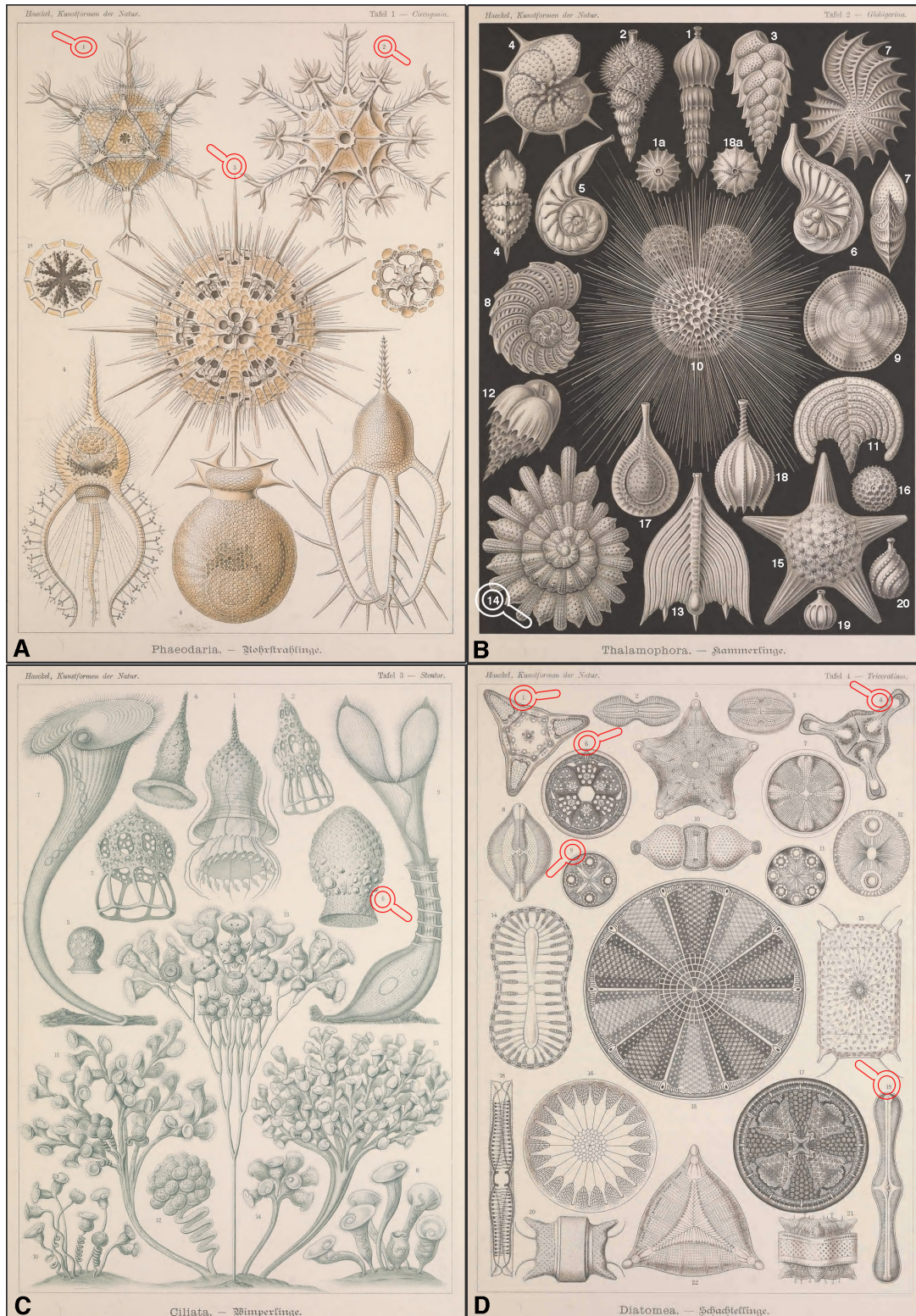


Fig. 4. A. Plate 1 phaeodaires, contains 3 figures (1, 2, 3) with details not in the original illustrations; **B.** Plate 2 foraminifera, includes the figure 14 of an unknown species; **C.** Plate 3 ciliates, fig. 3 shows details not present in the original illustration; **D.** Plate 4 diatoms, contains 3 figures showing details not present in the original illustrations (figs. 1, 4, 6), an illustration of new species Haeckel attributed to himself without any text description (fig. 19), and a species attributed a name which appears only in *Kunstformen* (fig. 9).

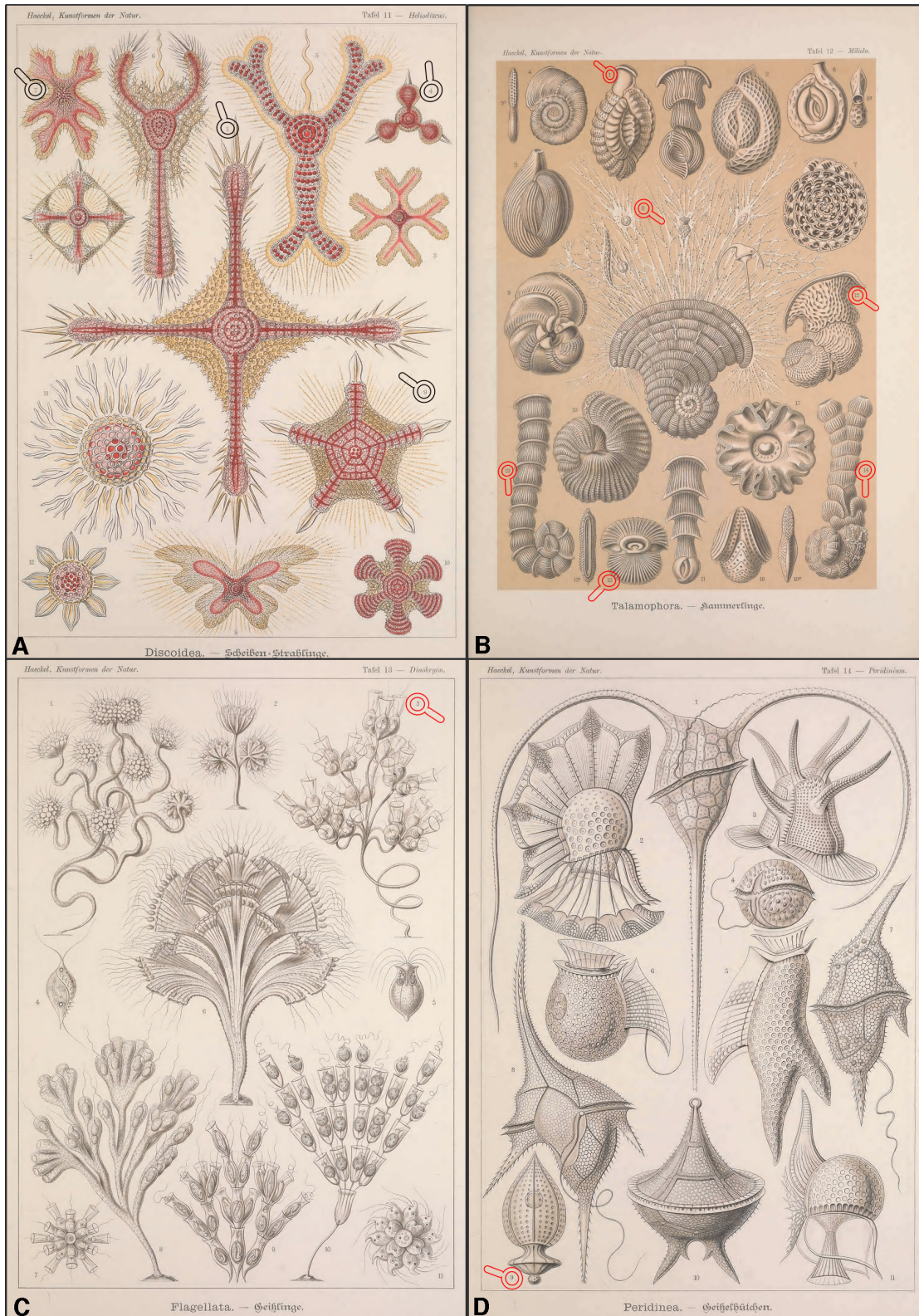


Fig. 5. **A.** Plate 11, spumullarian radiolaria, contains 4 illustrations (figs. 1, 4, 7, 9) differing from those of the original description; **B.** Plate 12, foraminifera, contains 4 figures (1, 8, 12, 15) differing from the original descriptions and 2 figures of new species (13, 14); **C.** Plate 13, flagellates, contains a new species of choanoflagellate (fig. 3); **D.** Plate 14, dinoflagellates, contains a figure of a new dinoflagellate species (fig. 9).

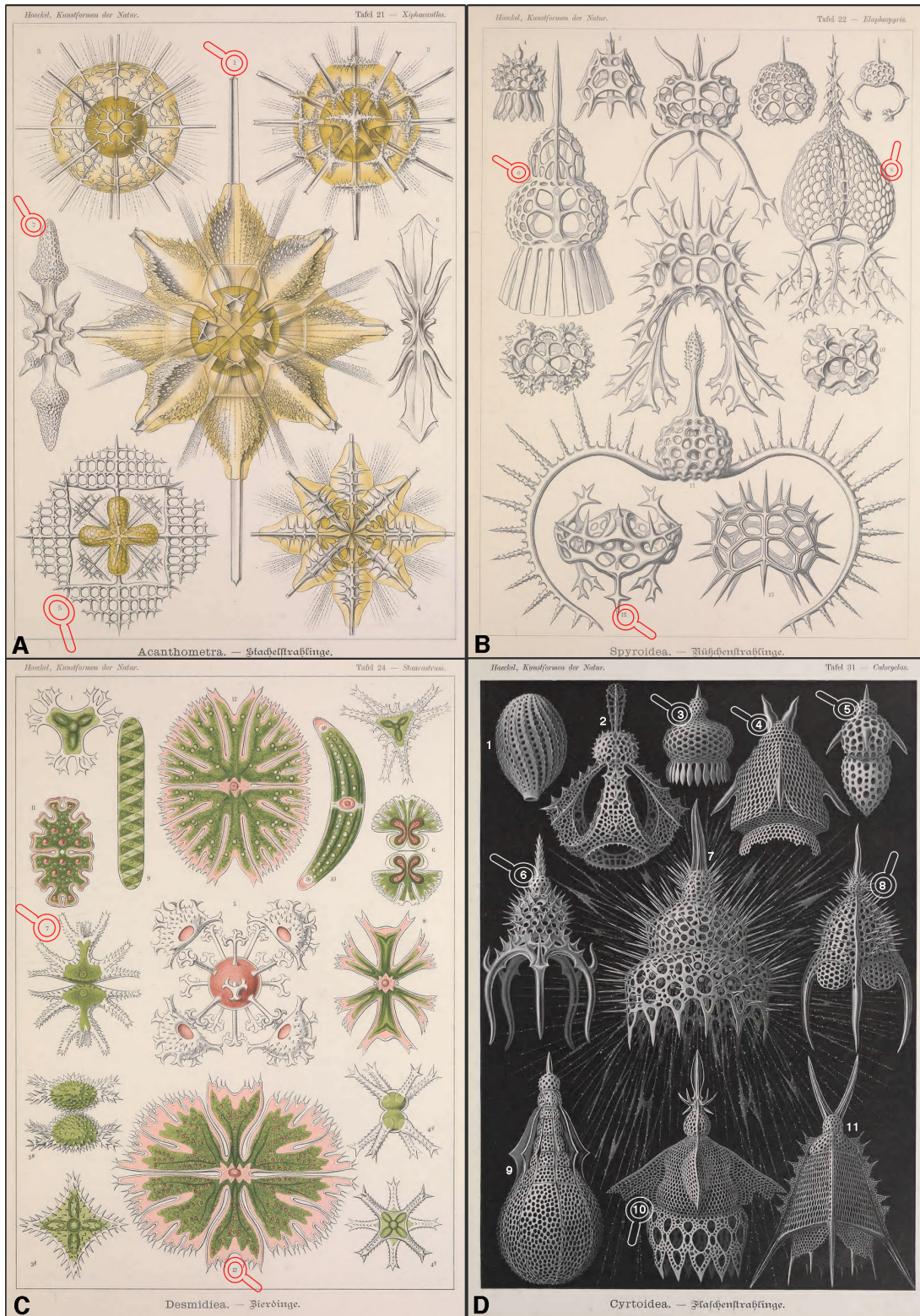


Fig. 6. **A.** Plate 21, acantharia, containing a figure differing from that of the original description (fig. 1), the first figure of a previously described species (fig. 5), and a new acantharian species (fig. 7); **B.** Plate 22, nassularian radiolaria, containing a new radiolarian species (fig. 6), a figure differing from that of the original description (fig. 8), and the first figure of a previously described species (fig. 12); **C.** Plate 24, desmids, containing 2 new desmid species (figs. 7, 12). **D.** Plate 31, nassularian radiolaria, containing figures of several species differing from those of the original descriptions (figs. 3, 4, 5, 6, 8, 10).

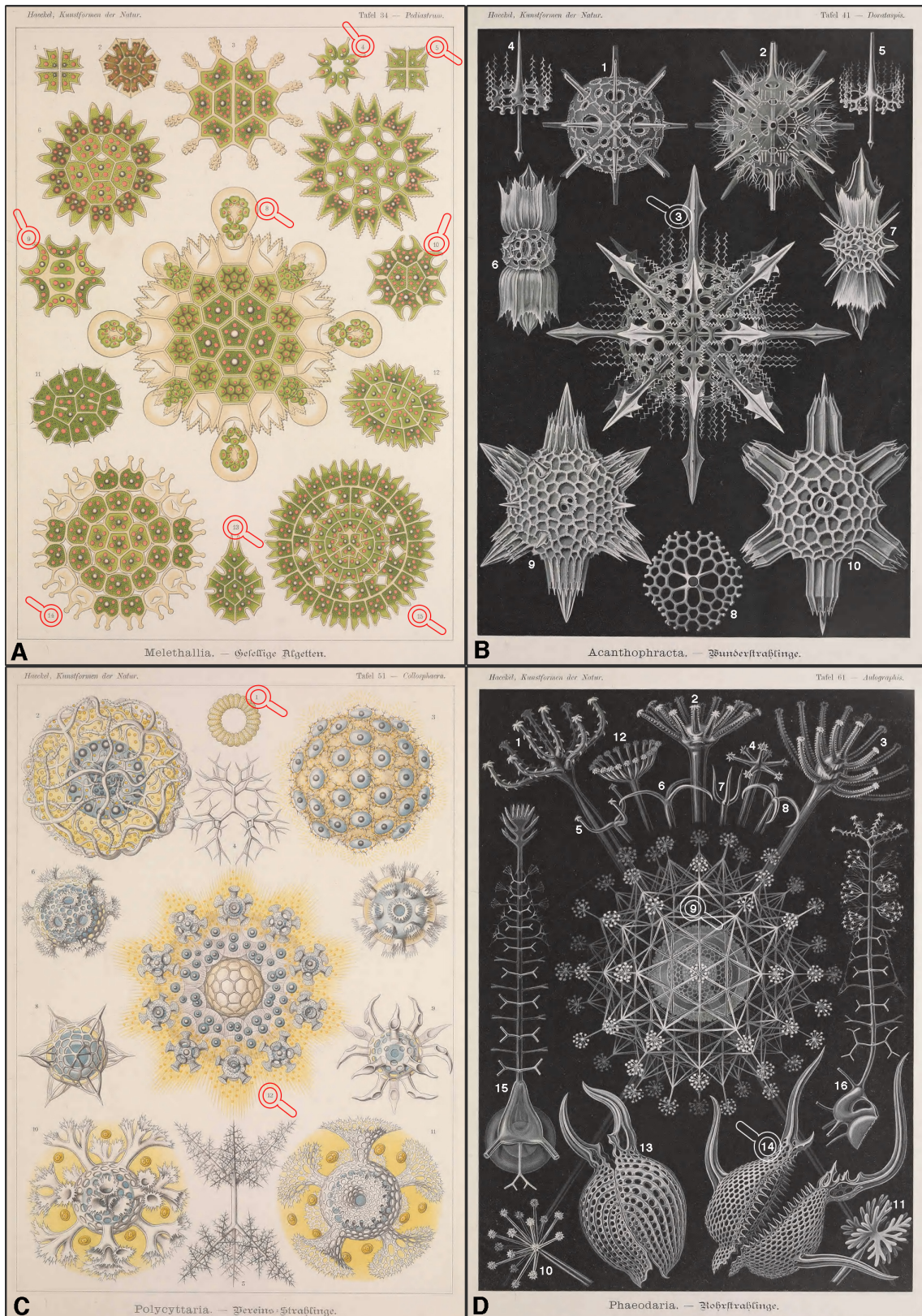


Fig. 7. A. Plate 34, Hydrodictyaceae, *Pediastrum* species, contains several new species of *Pediastrum* (Figs. 4, 5, 8, 9, 10, 13, 14, 15); **B.** Plate 41, acantharia, contains a new acantharian species (fig. 3); **C.** Plate 51, spumellarian radiolaria, contains the first figure of a previously described species (fig. 1), and a new species (fig. 12); **D.** Plate 61, phaeodaria, contains a figure differing from the original description (fig. 9) and a new species (fig. 14).

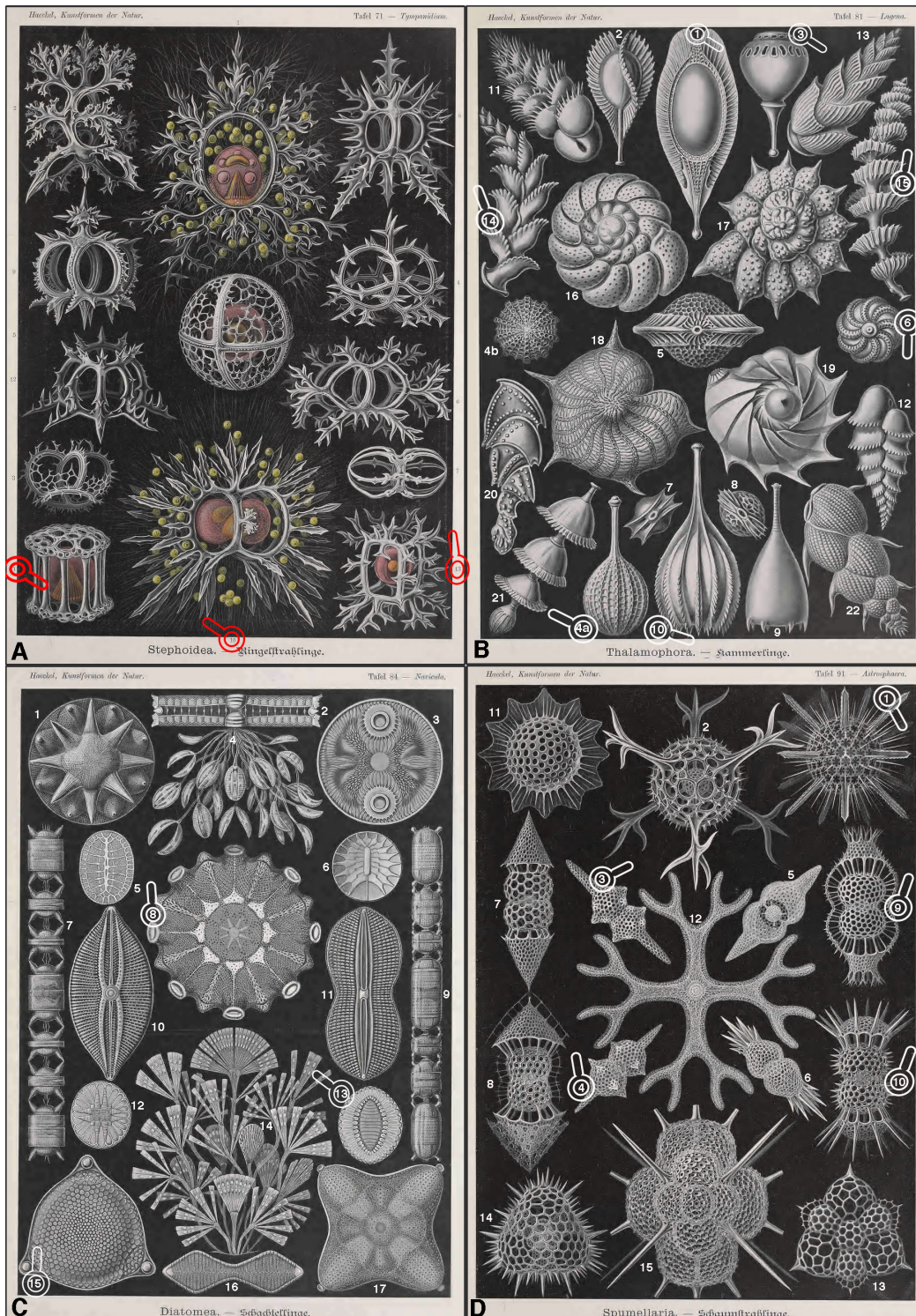


Fig. 8. A. Plate 71, nassularia, contains 3 figures differing from original descriptions (figs. 10, 11, 13). B. Plate 81, foraminifera contains 6 figures differing from original descriptions (figs. 1, 3, 4a, 10, 14, 15), and a figure of a new species (fig. 6) very curiously closely resembling an illustration by Millett (in Millett 1901, plate 8, fig. 7b) for whom Haeckel named the species! C. Plate 84, diatoms, contains 3 figures differing from the original description (fig. 8, 13, 15). D. Plate 91, spumellarian radiolaria, contains 3 figures differing from the original description (figs. 1, 3, 4) and 2 figures whose names appear to be reversed relative to the original descriptions (figs. 9, 10).

8. Concluding Remarks

Kunstformen provides us with ample evidence of the beauty of protists, and as such, it is undeniably a valuable resource. Quite naturally, the plates have therefore often been employed to show the beauty of protists (e.g. Corliss 1998, 1999, Dokulil & Teubner 2014, Dolan 2021, Glibert 2024, Hallegraeff 2024; Henstock et al. 2015; Martin 2015; O'Malley 2009; Pohnert 2016; Remick & Helmann 2023), and especially often by yours truly (Dolan 2021, 2023, Dolan & Coppola 2023). It is worth recalling that the protist plates have repeatedly graced the cover of this journal (i.e., in 1999, issue 1; in 2005, issues 1 and 4; in 2010, issue 2; in 2011, issue 3) and more recently, a chemistry journal (*Nachrichten aus der Chemie*, December, 2016). However, it is shown here that *Kunstformen* is not simply a collection of remarkable plates, as it was marketed at the time (fig. 1); it is a scientific publication. It contains many descriptions and figures of new species of a variety of taxa, and the first figures of species that Haeckel had previously described but without illustrations. Taken to be a scientific publication, in line with today's "authorship credits" policies, including Adolph Giltch as second author would likely be acceptable given his significant contributions to *Kunstformen*. The close look at the protist plates provided here revealed that many of the illustrations are questionable, showing species that may or may not exist, or showing features not apparent in the publication first describing the species shown. Consequently, caution is urged in using a *Kunstformen* illustration to portray a particular species.

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Supplementary material

A supplementary Excel file lists, for each of the protist plates the names of the species and taxonomic authorities, as given by Haeckel and as currently recognized, as well notes on each figure shown.

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