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ON THE CURIOUS ILLUSTRATION OF THE FORAMINIFER *PENEROPLIS PLANATUS* IN HAECKEL'S *KUNSTFORMEN DER NATUR (1899–1904)*

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ABSTRACT

In Ernst Haeckel's classic book *Kunstsformen der Natur* (Art Forms in Nature), forams are prominent; they occupy three of the 100 plates. In one plate, the centerpiece is *Peneroplis planatus*, shown with extended rhizopods, and organisms from the plankton. It is a very curious illustration as it is the only foram shown living and one of only two organisms in all of *Kunstsformen der Natur* pictured with possible prey. Here I show that the apparent planktonic prey of *P. planatus* closely resemble the prey items shown in Haeckel's earlier illustrations of his supposedly primitive life forms *Protogenes primordialis* and *Protomyxa aurantiaca* in the 1860s. These forms, now considered dubious, were described as possibly naked forams by Claus (1872), a diagnosis repeated by Brady (1884) in his *HMS Challenger* report, a source of many illustrations in Haeckel's foram plates. I speculate that Haeckel's depiction of *P. planatus*, shown much like his primitive forms, was a discrete nod of agreement with the diagnoses of Claus (1872). Examples of Haeckel's stylizations of the morphology of forams in his plates are also shown in support of the notion that Haeckel exercised artistic liberty in his depictions of forams.

INTRODUCTION

Recently, Lipps (2022) stated that foram art, while long existing in the scientific literature, "spectacularly appeared in Haeckel's *Kuntsformen der Natur*, which delighted readers with beautiful images of all sorts of organisms in both black and white, and color." *Kuntsformen der Natur* or *Art Forms in Nature* (Haeckel, 1899–1904) was indeed Haeckel's most popular book. It is said that he "aimed to introduce a broad readership to the beauty to be found in nature" (Willimann et al., 2021), and Haeckel succeeded well. Publication began in 1899, and the work was to consist of five issues with each issue consisting of ten large plates (33 × 25 cm). However, it was so successful that it was extended to ten issues of ten plates each (Willimann, 2021). Haeckel's book, from here on referred to as *Art Forms*, was not only a best seller but also had a profound effect on many artists such as Gustav Klimt and Edvard Munch, as well architects such as René Binet and Antoni Gaudi (e.g., Eibl-Eibesfeldt, 1998; Proctor & Breidbach, 2007; Debourdeau, 2016; Cardona-Rodas, 2018; Voss, 2021). The illustrations in *Art Forms* are said to have blurred the established boundaries between living and non-living, plant and animal (i.e., Schmidt, 2013; Bauman, 2018). However, not everyone admired Haeckel's illustrations. The renowned ecologist Evelyn Hutchinson described *Art Forms* as "Biergarten Art Nouveau" (Hutchinson, 1978).

Here the focus is on one particular plate in *Art Forms* with a peculiar illustration. *Peneroplis planatus*, a common, long-known, morphologically variable, and large benthic foram species (e.g., Carpenter et al., 1862) was shown by Haeckel (Fig. 1B) with pseudopods extended and contacting organisms of the plankton. It is the only foram shown alive by Haeckel. Among all the illustrations in *Art Form,* it is one of only two organisms shown with possible prey items (the other being a frog shown with a fly on its tongue in plate 68). First, a brief introduction is given to the foram plates of *Art Forms*. Then, the peculiar illustration will be dissected, so to speak, and its similarities to two of Haeckel's illustrations of supposedly primitive rhizopod forms from his publication in the 1860s will be shown. A possible explanation of Haeckel's motivation in picturing *P. planatus* with the particular prey items shown is proposed. Finally, examples are provided of original illustrations and those of Haeckel in support of the notion that he employed artistic license in his illustrations of forams in *Art Forms*.

THE FORAMS IN *ART FORMS*

In *Art Forms*, Haeckel gave special attention to protists. Out of the 100 plates, 20 were devoted to protists, reflecting Haeckel's interest and expertise in protists, especially the Radiolaria (*sensu* Haeckel). Thus, among the protists, radiolaria were represented in ten plates; three plates were devoted to forams, and diatoms were shown in two plates. Other protist groups (e.g., ciliates, dinoflagellates, etc.) were given only single plates each. The three plates devoted to forams are plate 2, plate 12, and plate 81. From these plate numbers, plate 2 was in the first issue of *Art Forms*, and its reception was, no doubt, of some consequence to the continuation of the series. Consequently, I assume that Haeckel was proud of the plate, his first plate with the organisms shown on a black background. In the entire series, 32 of the 100 plates used a black background. Plate 12, the second devoted to forams, was in the second issue of ten plates and thus among the initially planned set of 50 plates. In plate 81, forams were again represented in the second set of 50 plates.

Each plate in *Art Forms* was accompanied by a short (1–2 pg) text describing the morphology of the species shown with the species names, and the names of the taxonomic authority Haeckel credited with the first description, but without a year. No mention is given regarding the original source of illustrations, and no bibliography was included in *Art Forms*. However, in Willimann et al. (2021), the likely year of the first description is given and the authority credited with the first description. These were verified by consulting the WoRMS website linked to the World Foraminiferal Database (Hayward et al., 2023) and for the most part are in agreement. However, even with the identity of the taxonomic authority, it is difficult to uncover possible source illustrations used by Haeckel, with the difficulty in direct proportion to the age of the first description. Therefore, I abandoned an attempt to uncover the possible source of Haeckel's source illustration of *Peneroplis planatus* that was first illustrated by Fichtel & Moll

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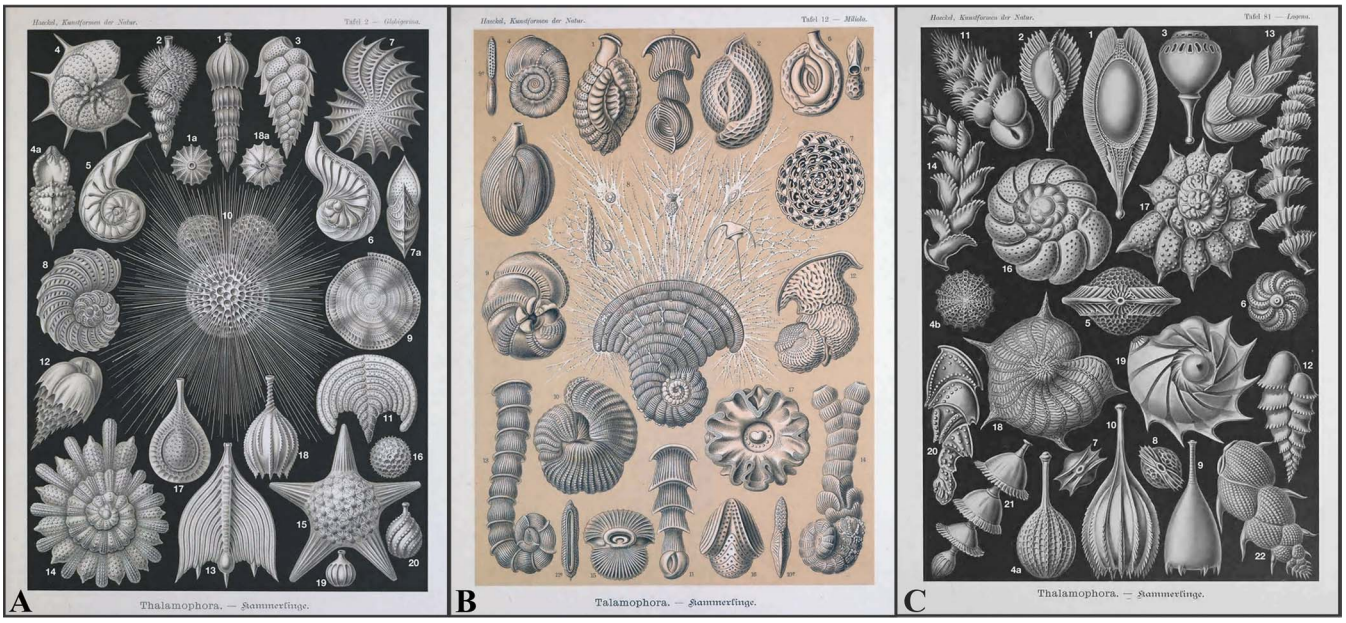

FIGURE 1. The three foram plates in Haeckel's *Art Form*s: A) plate 2, B) plate 12, and C) plate 81. The centerpiece in plate 12 (B) is a live *Peneroplis planata* (now known as *P. planatus*) with extended pseudopods under recognizable prey items of the marine plankton. Remarkably, it is the only living foram depicted in the three plates, and among all the plates in *Art Forms*, one of but two showing an organism with its prey. Figure numbers, absent from the original black background plates, have been added. The names of the species shown, by Haeckel, and as currently recognized, are given in the Appendix. The two species Haeckel presented as new species, only recently recognized in WoRMS, appear in the lower left corner (*Vertebralina catena*) and the lower right corner (*V. furcata*) of plate 12 (B).

(1798), and it is also notoriously variable in morphology (e.g., Langer et al., 2009). In contrast, the last foram plate, plate 81, was published among the last two issues in 1904, and it contains illustrations of species first described and illustrated only shortly before (i.e., Brady, 1884; Millett, 1901), thus providing examples of source illustrations to compare with those in Haeckel's plate 81.

The illustrations in the foram plates with black backgrounds (plates 2, 12) were not numbered, as in all the plates with black backgrounds. Instead, such plates were published with a key sheet—a semi-transparent sheet with numbered outlines of the figures. Unfortunately, most scanned versions, and all the modern editions, do not include the key sheets, rendering identification of the figures problematic. One digital version available includes the key sheets, the edition in the Biodiversity Library supplied by the Smithsonian Institution (https://www.biodiversitylibrary.org/item/182319#page/7/mode/1up). In Figure 1, in lieu of the key sheets, figure numbers have been added to plates 2 and 12.

The names of the 58 species shown in the foram plates, as given by Haeckel, and the current name, by plate and figure number, are provided in the Appendix. Oddly, Haeckel included two new foram species in plate 12, *Vertebralina catena* (fig. 13 in plate 12) and *V. furcata* (fig. 14 in plate 12), crediting himself. Both species apparently have been overlooked until quite recently; they were entered into World Foraminiferal Database and WoRMS while this essay was in review, at the behest of one of the reviewers. The fact that the two species apparently have been overlooked for 124 years suggests that plate 12 in *Art Forms* has received little attention from foram researchers. In contrast, Haeckel is credited with the original description of 16 species, currently accepted, of forams that he described as sponges; four species in Haeckel (1877a); and 12 species in his *Challenger* report on the deep sea sponges (Haeckel, 1889). His descriptions of some forams as sponges in 1877 was quickly challenged (Carter, 1877), as were the forms he described in his *Challenger* report on sponges (Pearcey, 1893). For an interesting summary of the studies of these odd forms, see Tendal (1972). None of the species that Haeckel first described as sponges appears in the foram plates of *Art Forms* (see Appendix).

A CLOSE LOOK AT THE PREY OF HAECKEL'S *PENEROPLIS PLANATUS*

Haeckel's legend for figure 8 in plate 12 (shown here in Fig. 1B) made scant mention of the prey items shown. It read:

> "Fig. 8. *Peneroplis planata* (Montfort). The flat shell is fan-shaped, 1 mm in diameter and marked on the surface with delicate parallel ribs. The numerous chambers, which are spirally rolled out in one plane, increase in width slowly at first, later very rapidly. Numerous branched plasma filaments emerge from the free orifice edge of the last, broadest chamber (above); they unite at the points of contact to form a transient network and take foreign bodies as food" (transcription of old German font and translation by Christophe Migon).

The identity of the 'foreign bodies' being taken as food are not specified but are distinctive and easily recognizable for the most part. Prominent among the organisms shown on the pseudopods of *P. planatus* are a *Gyrosigma* sp. diatom, the tintinnid ciliate *Dictyocysta elegans*, and the dinoflagellate, *Ceratium tripos*, all marine plankton (Fig. 2A). The organisms shown with *P. planatus* are remarkably similar to those Haeckel depicted as the food items of his supposedly primal life forms, described many years before. In Haeckel (1865), he described *Protogenes primordialis*, a

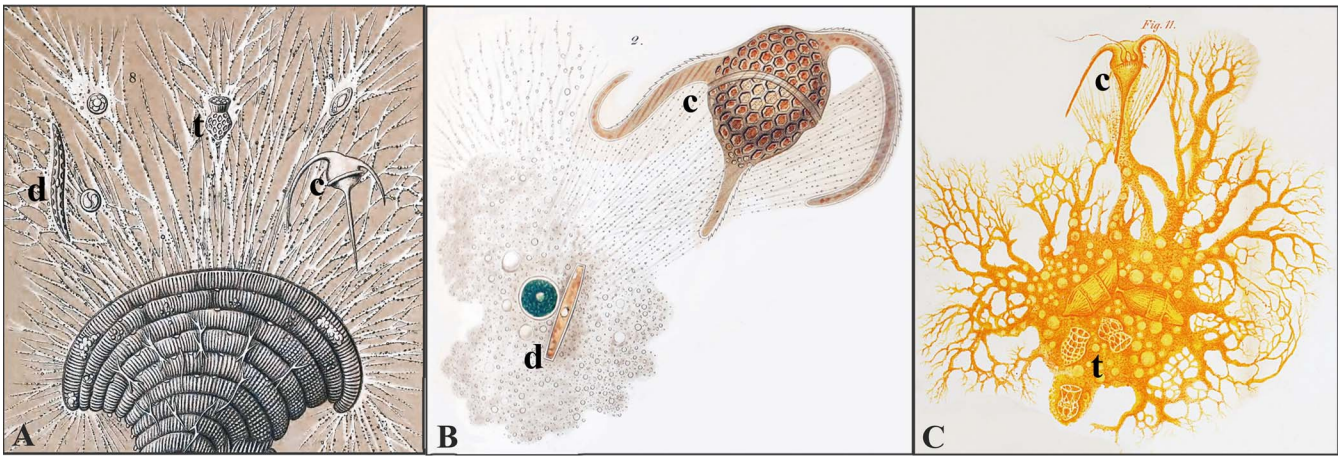

FIGURE 2. Haeckel's illustrations of A) the prey of *Peneroplis planatus* from the 1899 foram plate 12; B) the prey of the feeding stage of *Protogenes primordialis* from Haeckel (1865); C) the prey of the feeding stage of *Protomyxa aurantiaca* from Haeckel (1868). Diatoms are indicated by 'd', the dinoflagellate *Ceratium* by 'c', and tintinnid ciliates by 't'.

new form of life composed only of protoplasm, without a cell membrane nor a nucleus, and likely formed from spontaneous generation. He wrote to Charles Darwin to tell him of his discovery, a solution to the origin of life missing from Darwin's *Origin of the Species* (see Dolan, 2020). Haeckel depicted the feeding stage of *Protogenes* containing an ingested diatom and capturing a *Ceratium* sp. (Fig. 2B). The *Ceratium* was depicted lying on top of the pseudopods, similiar to the *Ceratium* shown with *P. plantus*. In his text, Haeckel states that the following day, the *Ceratium* was devoid of cytoplasm (Haeckel, 1865). A few years later, Haeckel published his monograph on Monera (Haeckel, 1868) and in it described another primitive life form, an amoeba-flagellate with a complex life cycle, *Protomyxa aurantiaca*. The feeding stage was depicted containing the remains of tintinnid ciliates, the loricas of two species of *Dicytocysta* (*D. elegans* and *D. mitra*), unidentified dinoflagellates, and, according to the text (Haeckel, 1868), capturing a live dinoflagellate (note the extended flagellum), a *Ceratium tripos* (Fig. 2C). The *Ceratium* is depicted lying on the pseudopods of *Protomyxa*, as in the illustrations of *Peneroplis* and *Protogenes*.

In all three of his foram plates, Haeckel depicted only one species living, with extended pseudopods, thus calling considerable attention to his figure of *Peneroplis planatus*. Showing the benthic foram with planktonic organisms is not unreasonable, in and of itself. Many observations exist of such feeding behavior (e.g., Culver & Lipps, 2003). The fact that he used the same presumptive prey items in his depiction of *Peneroplis planatus* as in his previous depictions of feeding primitive life forms is remarkable. It may perhaps be simple recycling of his own work with planktonic organisms added as decoration. However, if the organisms were added as decorative items, it is curious that Haeckel did not show a radiolarian, his favorite among the microplankton. Furthermore, Haeckel showed the 'foreign bodies' taken as food in the same manner as in his illustrations of primitive forms, that is lying on top of extended pseudopods. I propose the hypothesis that the illustration of *P. planatus* was a purposeful yet discrete 'callout' linking forams to his primitive life forms. Claus (1872) classified Haeckel's *Protogenes* and *Protomyxa* as likely 'naked' forams. Haeckel himself a few years later (Haeckel, 1877b) allied his primitive forms with both the infamous *Bathybius haeckeli* (Rehbock, 1975) and the supposed fossil foram *Eozoon canadense* (Dolan, 2023). Brady (1884), in his *Challenger* report on the forams, repeated Claus's proposal. Haeckel was familiar with the Claus (1872) work as he cited it in Haeckel (1873a), printed in the same journal issue as his descriptions of the tintinnid ciliates later shown as the prey of both *Protomyxa* and *Peneroplis* (Haeckel, 1873b). He was certainly familiar with Brady's *Challenger* Report. Some illustrations in Haeckel's foram plates are fairly faithful reproductions of Brady's illustrations in Brady (1884; e.g., *Miliolina parkeri* as fig. 1 in Haeckel's plate 12 from Brady's plate 7, fig. 14b, now known as *Quinqueloculina parkeri*). Haeckel's primitive life forms were later again presented as allied to forams by Rhumbler (1913) in his report on the forams of the Plankton Expedition. Today though, the place and existence of Haeckel's primitive forms are uncertain. *Protomyxa* was listed under *Incertae sedis* Cercozoa by Adl et al. (2019), and *Protogenes* was last listed under "Protista without contemporary identity: Nature uncertain" by Patterson (1999).

Rather than an invention, could Haeckel have possibly based his depiction of *Peneroplis planatus* on his own observations? It is impossible to disprove that during his many voyages Haeckel saw living *P. planatus* and perhaps one onto which some planktonic organisms had settled. However, Haeckel appears to have been rather unfamiliar with forams. As mentioned above, he misplaced many forams among the sponges in his *Challenger* report on deep-sea sponges (Haeckel, 1889). In support of the notion that the illustration of feeding in *P. planatus* was an artistic invention is the observation that Haeckel's illustrations in *Art Forms* have been repeatedly criticized as being more artistic than scientific (Richards, 2009). In this regard, compare Haeckel's illustrations of two foram species in plate 81 with the source illustrations (Fig. 3). As mentioned above, species depicted by Haeckel in plate 81 were described and illustrated by Brady (1884) and Millett (1901) not long before plate 81 of *Art Forms* was published. A comparison of Brady's and Millett's original illustrations and the figures in plate 81 show that Haeckel employed some artistic freedom in his *Art Forms* illustrations of forams, much like he did with his illustrations of radiolarians (Dolan, 2019). If Haeckel's illustrations in *Art Forms* are considered as primarily artistic representations, rather than scientific illustrations, then the pseudopods and organisms appearing in his

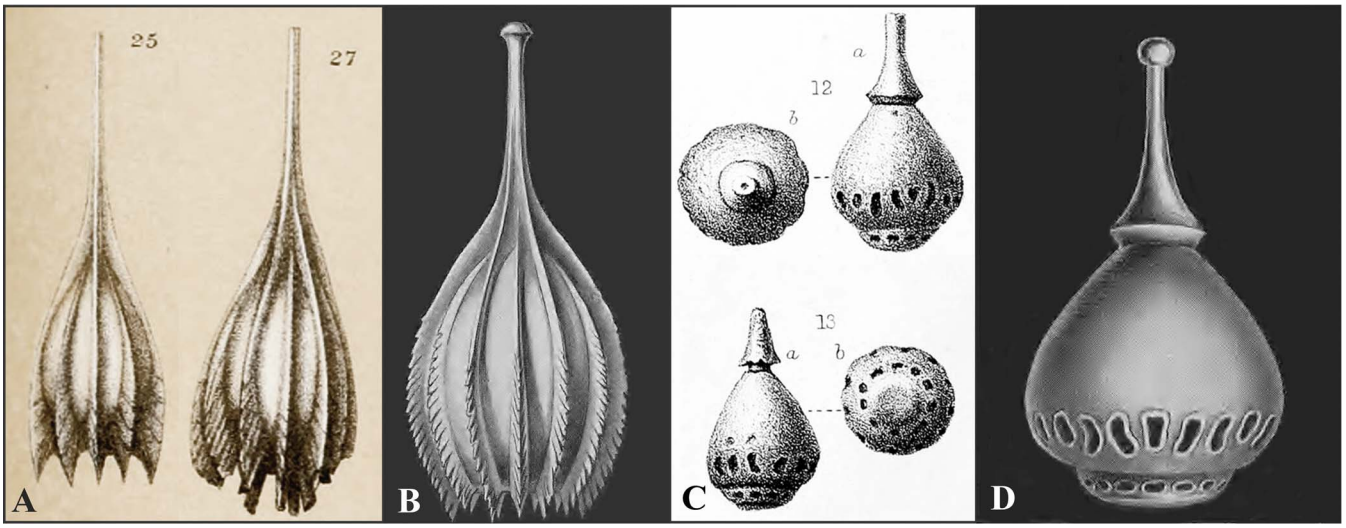

FIGURE 3. Examples of Haeckel's stylizations of forams in his plates in *Art Forms*. A) *Lagena plumigera* from the first depiction in Brady (1884). B) Haeckel's *Lagena plumigera* in Plate 81 (as fig. 10). C) *Lagena pannosa* from Millet (1901). D) Haeckel's *L. pannosa* in Plate 81 (as fig. 3). The orientations of Haeckel's illustration of *L. pannosa* are rotated to correspond with that of Millett. Note that in Haeckel's version of *L. plumigera*, the striations on the 'fins' of Brady's illustrations appear as serrations and a knob has been added to the anterior end. In Haeckel's version of *L. pannosa*, there is a knob at the anterior end, not shown in the original, the anterior end has been considerably elongated, and the surface appears smooth, not textured. While Haeckel's figure clearly resembles the original illustrations, he exercised some artistic freedom in his depictions of forams in *Art Forms*.

figure of *P. planatus* appear more likely to have been invented than observed.

CONCLUSION

Haeckel is justifiably credited with introducing the beauty and diversity of foram morphologies to a wide audience in his classic work, *Art Forms*. However, Haeckel's illustrations in *Art Forms* should likely not be considered as scientific works with exact details drawn in precise proportions. In the particular instance of his illustration of *Peneroplis planatus*, the artist Haeckel was possibly nodding in agreement with Claus's placement of *Protogenes* and *Protomyxa* within the forams.

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APPENDIX CAPTION

Appendix. The foram species in Haeckel's Art Forms. A spreadsheet file composed of three sheets listing the species shown with names given by Haeckel, and as currently recognized, by plate (plate 2, plate 12, plate 81) and two additional sheets listing species shown by Haeckel in *Art Forms* as new species (HaeckelClaimedSpp) and a sheet listing all foram species currently credited to Haeckel as author of the first description (HaeckelAuthorWoRMS). The Appendix can be found linked to the online version of this article.

Cushman Foundation for Foraminiferal Research
Est. 1950