

HETEROGENEITY AMONG JUVENILE MEGALOSPHERES IN *PENEROPLIS PERTUSUS* (FORSKÅL) FROM THE LINE ISLANDS (PACIFIC OCEAN): SIZE RANGE, MORPHOTYPES, AND TEST DEFORMATIONS

MARTIN R. LANGER^{1,*}, YAROSLAV TRUBIN^{1,2}, SKYE YUNSHU TIAN¹ AND SUSAN T. GOLDSTEIN³

ABSTRACT

Sixty fully calcified megalospheric juveniles were recovered from the brood chambers of an adult specimen of the symbiont-bearing foraminifer *Peneroplis pertusus* (Forskål) collected at Kiritimati Atoll (Line Islands, Pacific Ocean). All juvenile megalospheres consist of a proloculus and an elongated flexostyle that is one half coil in length except for one specimen consisting of only the proloculus. The juvenile specimens exhibit distinct variations in size, various forms of test deformation, and can be classified into four distinct morphotypes. The juvenile test deformations show that the calcification of the megalospheres in the brood chambers is not simultaneous but asynchronous and a key mechanism driving the test deformation in juvenile megalospheres of *Peneroplis*. Observations on more than 100 adult specimens show that the test deformities observed in juvenile specimens are not expressed in adult forms, indicating that they are either transitioning to normal growth forms or are not viable.

INTRODUCTION

Reports of juveniles, “embryonen,” or “embryonen cells” found within the tests of both modern and fossil foraminifera date from the mid-19th century (Lister, 1895) and provided a key insight during the long development of our understanding of foraminiferal life cycles. These early pioneers were nearly uniform in reporting that these tiny individuals resulted from reproduction and suggested that a foraminiferan could produce a large number of offspring via a single reproductive event. Extensive research by Schaudinn (1894, 1895) and Lister (1895), working independently on *Polystomella* (= *Elphidium*) *crispa*, ultimately provided the foundation for our current understanding of the foraminiferal life cycle. Both Lister (1895) and Schaudinn (1895) described this species as dimorphic and incorporated two distinct morphologies into a life cycle characterized by an alternation of generations: a microspheric generation in which a parent with a small initial chamber and overall large test undergoes multiple fission to produce a large number of megalospheric offspring; and a megalospheric generation in which parents with a large initial chamber and overall smaller test produce numerous flagellated “swarmer” cells, now recognized as gametes, which ultimately fuse to begin the microspheric generation. As a complication, however, both researchers reported rare multiple fission events in megalospheric individuals of this species, suggesting further complexity in the foraminiferal life cycle.

The possible occurrence of one or more intervening generations in which multiple fission occurs in a megalospheric parent was found to occur in several species of benthic foraminifera, and this led to the theory of “trimorphism,” championed by Hofker (1925, 1930). The idea was that most if not all species of foraminifera had a life cycle with three distinct generations and therefore three distinct corresponding morphologies. Hofker (1925, 1930) further insisted that all three morphologies needed to be recognized in foraminiferal species descriptions. Le Calvez (1938) rejected trimorphism and showed that intervening generations characterized by multiple fission in megalospheric individuals did indeed occur in some species, but that this did not necessarily lead to three distinct morphologies per species. Le Calvez (1938) coined the terms “holotrimorphic” and “paratrimorphic” to characterize the life cycles, but not the morphologies, of such species. The former describes a life cycle with an obligatory alternation of three generations: a megalospheric gamont, a microspheric schizont, and a megalospheric schizont. The latter pertains to species with two primary generations: a megalospheric gamont and a microspheric schizont, and occasionally one or more additional generations of an intervening megalospheric schizont, as is the case for *Polystomella* (= *Elphidium*) *crispa*. Subsequent research on foraminiferal life cycles has revealed an extensive diversity of reproductive patterns (Goldstein, 1997, 1999; Goetz et al., 2022; Timmons et al., 2024).

Currently, the life cycles of larger symbiont-bearing foraminifera are recognized as paratrimorphic, although very few such life cycles have been documented for the many unrelated members of this morphological grouping (Leutenegger, 1977; Röttger, et al., 1990; Lee et al., 1991; Harney et al., 1998). The notable exception is Winter’s (1907) exquisitely documented life cycle for *Peneroplis pertusus* (Forskål), which he described as dimorphic (in reference to morphology). Winter also showed that the offspring resulting from multiple fission of the parent initially consisted of two components: a fairly large proloculus and an accompanying elongate flexostyle. Individuals of the microspheric generation have a small proloculus and lack the flexostyle. Faber & Lee (1993) further showed that multiple fission in another species of *Peneroplis*, *P. planatus* (Fichtel & Moll, 1798), could occur in either microspheric or megalospheric individuals and that the resulting young from either type of parent were of comparable size. That is, the life cycle is paratrimorphic, but the resulting morphology is dimorphic.

In 2009, Langer et al. examined an adult specimen of *Peneroplis hoheneggeri* Förderer and Langer, 2019, from Chuuk Island (Micronesia; Langer et al., 2009) in the reproductive state ready to release megalospheric juveniles. All juveniles recovered from the brood chambers of *P. hoheneggeri* were fully calcified and composed of proloculus and tube-like flexostyle that envelops the proloculus approximately one-half coil in length. The number of megalospheric juveniles present in the parental test

¹Institut für Geowissenschaften, Paläontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany

²Micropaleontology Laboratory, Tomsk State University, Lenin Avenue 36, 634050 Tomsk, Russia

³Department of Geology, University of Georgia, Athens, GA 30602, USA

* Correspondence author. E-mail: martin.langer@uni-bonn.de

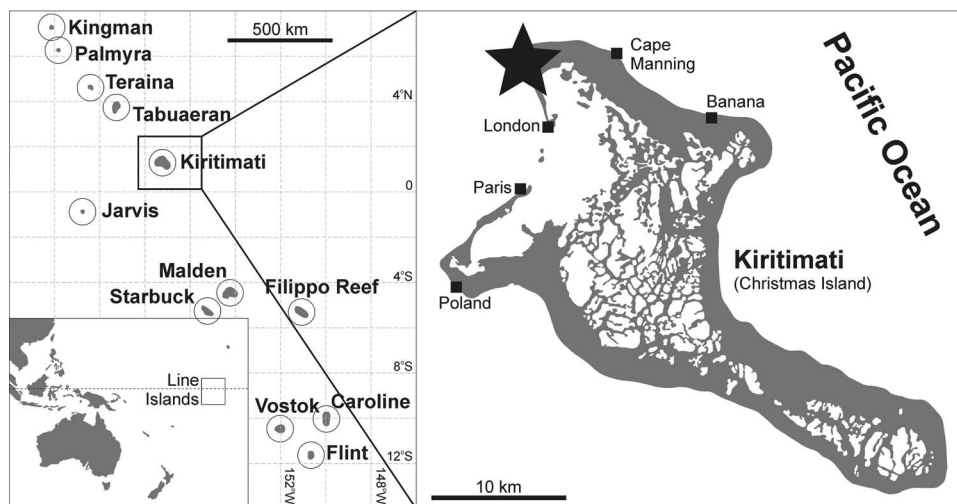


FIGURE 1. Position of Kiritimati and other atolls along the Line Island archipelago in the Central Pacific Ocean. The location of the sampling site where the reproducing adult specimen of *Pteroplis pertusus* was collected is marked with a star.

was estimated to be between 110 and 130, a number that agrees well with the observations of Winter (1907) and Schacko (1882), where ~ 100 and 118 megalospheric juvenile gamonts were reported in *Pteroplis pertusus* and *Laevipteroplis proteus* (d'Orbigny, 1839), respectively. Langer et al. (2009) also showed that the megalospheric juveniles displayed significant proloculus size variations and that more than a quarter were deformed by neighboring tests as a result of extreme space limitations. The proloculus size variations in juvenile megalospheres revealed that natural populations of *Pteroplis* produce non-uniform and highly heterogeneous offspring and the test deformations are indicative of asynchronous calcification of juveniles within the brood chamber.

Finding foraminifera during their reproductive phase is a rare occurrence in nature, but it provides valuable insights into their reproductive processes. While examining benthic foraminifera for environmental and biogeographic studies from the Line Islands atoll system, we coincidentally discovered an adult specimen of *P. pertusus* in the reproductive stage ready to release juveniles. The adult specimen was complete and contained numerous calcified megalospheric juveniles that were seen through the broken apertural face of the final chamber. We examined the parental test in detail and the megalospheric juveniles by high-resolution Scanning Electron Microscopy (SEM) to document the quantity, morphology, and size range of the juveniles and to provide novel insight into the reproductive biology and ontogenetic constraints of *P. pertusus*. We also report on morphological features in normal and deformed juvenile tests as displayed in the proloculus and the flexostyle. To test whether the juvenile test deformations are expressed in adults, an additional 101 specimens of *P. pertusus* from the Line Island Archipelago were examined.

MATERIAL AND METHODS

Sediment samples containing abundant specimens of *P. pertusus* were collected within the Kiritimati Atoll, also known as Christmas Island (Fig. 1). Kiritimati Island belongs to the Line Island atoll archipelago and belongs to the Republic of Kiribati. It is situated 232 km north of the equator, about 2000 km

south of Hawaii, and is inhabited by approximately 10,000 people (DeMartini et al., 2008; Sandin et al., 2008). The sample site containing the reproducing *Pteroplis* individual is situated in a shallow water, fore-reef setting (10.6 m) and is located at $2^{\circ}2.423'N$, $157^{\circ}29.765'W$ (Fig. 1). Divers obtained the sample via SCUBA, collecting carbonate sand in between corals from the top 2 cm, which were later carefully washed over a 63- μm mesh sieve and oven-dried at $50^{\circ}C$ (Carilli & Walsh, 2012). The material is stored in the micropaleontology collection at the University of Bonn (Germany).

The juvenile-bearing parental test of *Pteroplis* was first inspected by light microscopy and then mounted on a stub for detailed SEM examination. For complete documentation, the parental specimen was broken open in successive steps using a fine needle to record the number of juvenile specimens at each step (Figs. 2a–f). At each stage, SEM photomicrograph images were taken at different magnifications and from different angles so that all juveniles present within individual chambers of the adult foraminifer could be counted (Figs. 2, 3). During the course of the investigation, the types of deformation, unusual features, and the dimensions of the juveniles were recorded (height, width, and diameter; Figs. 4, 5). A few juvenile tests were later dissected with a razor blade to examine the inner structure (Figs. 4c,f).

RESULTS

Microscopic inspection and SEM photographs of *Pteroplis pertusus* showed the adult test to be complete (Figs. 2a,b) and to contain densely packed juveniles in the last chambers (Fig. 2). The juveniles were visible through the partly broken apertural face. Breakage of the apertural face, a common feature of *Pteroplis* specimens releasing juveniles in the final stage of the reproductive process, is induced by strong movements of the juveniles inside the adult test (Winter, 1907; Langer et al., 2009). The fracture on the apertural face of the terminal chamber formed an irregularly shaped triangle characterized by both sharp and sub-rounded edges. The fracture on the apertural face was not inflicted by the examiners and most likely occurred just prior to our collection campaign (see below).

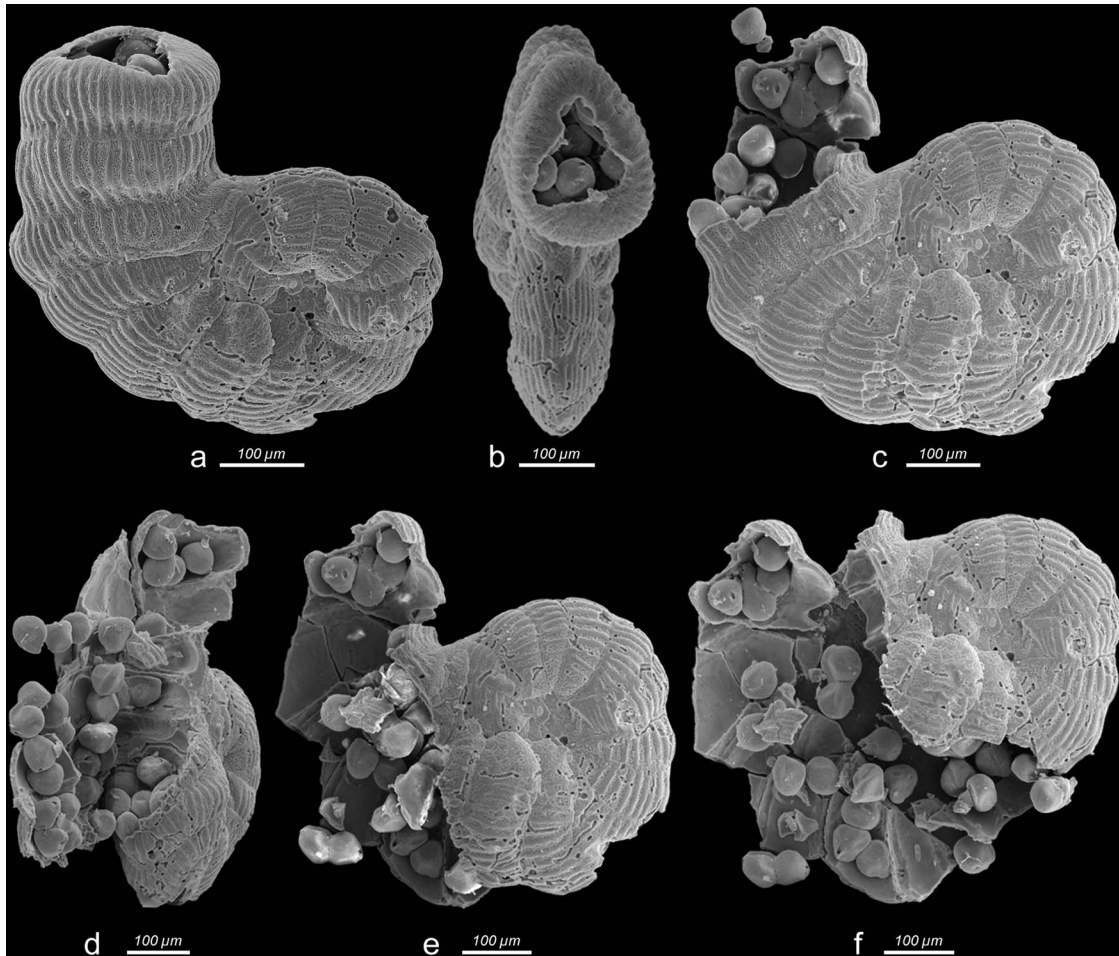


FIGURE 2. SEM photographs illustrating selected stages in breaking open the parental shell of *Peneroplis pertusus* bearing juvenile megalospheres in its brood chambers. **a–b** Complete specimen of the parental test showing densely packed juveniles through the broken apertural face on the final chamber. **c** Parental test after the last two chambers of the uniserial stage have been broken open. Note the closely packed specimens in the last chamber and the arbitrary orientation of the juveniles. **d** Oblique peripheral view of the broken test showing loosely and densely packed juveniles within individual chambers of the adult specimen. **e–f** Side views of two more fracture stages. Note that some juvenile specimens may have been displaced during the breaking open of each chamber.

Peneroplis pertusus (Forskål) is characterized by typical features of the porcelaneous miliolid genus *Peneroplis* including planispiral and initially involutely arranged chambers that rapidly increase in breadth and have a tendency to uncoil in the adult

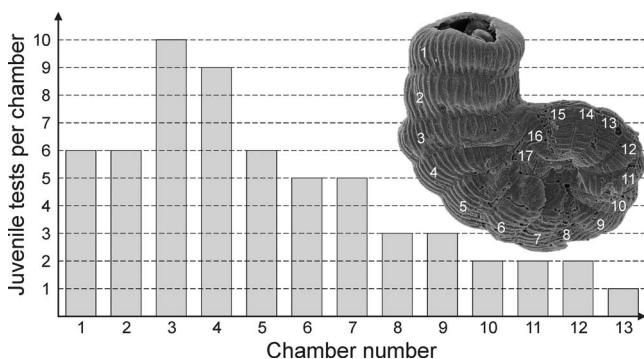


FIGURE 3. Diagram illustrating the number of megalospheric juveniles present in individual brood chambers of the parental test. Note the maximum values in chambers 3 and 4 and the continuous decrease of juvenile specimens up to chamber 13.

stage. In the uncoiled stage, the chambers are arranged uniserially and become detached from the initial coil (Figs. 2a,b). The surface of *P. pertusus* is characterized by numerous fine ribs that alternate with grooves. Fine pseudopores are present within the grooves. Ribs and grooves are aligned parallel to the test periphery (Fig. 2a). In the parental test 17 chambers were visible from the exterior (Fig. 3). Our specimens correspond well with the illustrations provided by Brady (1884), Hallock (1984), Gudmundsson (1994), and Förderer & Langer (2018), and have the characteristic multiple *Peneroplis*-like apertures arranged in a single row (for details and synonymy see Förderer & Langer, 2018).

The parental test was about 0.5 mm in diameter, and close examination showed that it was complete and did not lack any broken or partially broken chambers (Figs. 2a,b). Breaking open the chambers step by step showed that the last 13 chambers were filled with juvenile specimens. Earlier chambers were devoid of juveniles. Due to the involute chamber arrangement, the proloculus of the parental test remained hidden and could not be inspected by light microscopy or SEM.

A total of 60 densely packed juveniles were recovered from the adult specimen. After breaking open the first two chambers,

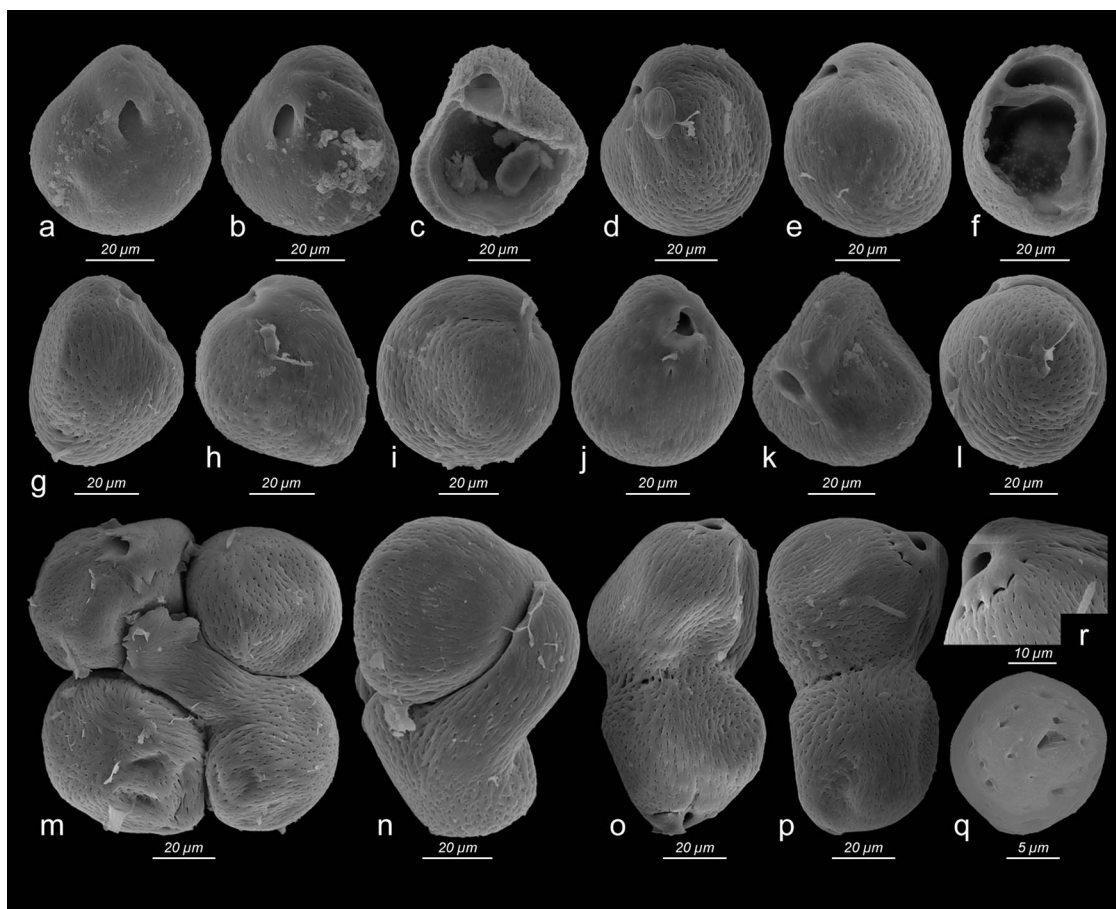


FIGURE 4. Scanning electron micrographs of juveniles recovered from brood chambers of the parental test of *P. pertusus* showing the variety of morphotypes (1–4), unusual features, and various types of test deformations observed in fully calcified megalospheric juveniles. Complete and dissected two-chambered, juvenile megalospheres of morphotype 1 (Figs. 4a–l) composed of a proloculus and tube-like flexostyle. SEM illustration of morphotype 2 (Fig. 4q) consisting of a full calcified proloculus but lacking the tube-like flexostyle. Morphotype 3 (“elephant specimens”; Figs. 4m,n) showing the partially detached flexostyle that grows laterally to the side in the form of an elephant trunk. Morphotype 4 (twins; Figs. 4o,p) consists of two tightly fused and fully calcified forms of morphotype 1.

a total of 12 juveniles were recovered, where each of the last two chambers contained 6 juveniles (Figs. 2c, 3). The juvenile specimens lay loose in the final chambers and their orientation appeared to be random. Breaking open chambers 3–5 revealed 25 more individuals. After breaking open chambers 6–8, a total of 50 juveniles were visible on the SEM stub, indicating that 15

more juveniles were present in chambers 6–8. When five more chambers were opened (chambers 9–13), another 10 juvenile specimens appeared, increasing the total number of juvenile individuals to 60. When breaking it open further, it became apparent that there were no more juvenile specimens in earlier chambers.

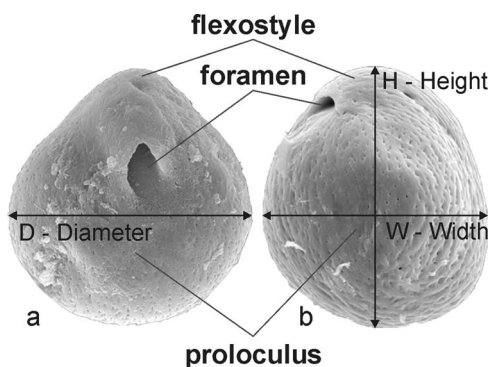


FIGURE 5. Characters used in morphometric analysis of juvenile megalospheres including diameter, width, and height. The diameter was measured in peripheral (a) and width and height in lateral view (b).

MORPHOTYPES OF JUVENILE MEGALOSPHERES

After successively breaking all brood chambers, all juveniles became clearly visible and were then examined, photographed, and measured. All juveniles recovered were fully calcified. Among the juveniles we noted four different morphotypes.

Morphotype 1 is typical of a megalospheric two-chambered juvenile composed of a proloculus and a tube-like flexostyle (Figs. 4a,d–f,i,j,l). The tube-like flexostyle is approximately one-half coil in length and provided with a sub-rounded to sub-triangular apertural opening at the end of the tube (Figs. 4a–l). Cut specimens show the proloculus to be subspherical in outline (Figs. 4c,f). The surface of the proloculus is densely and regularly pitted by pseudopores. The pseudopores on the proloculus are mostly rounded to subrounded. In contrast, the pseudopores along the peripheral margin and especially on the surface of the

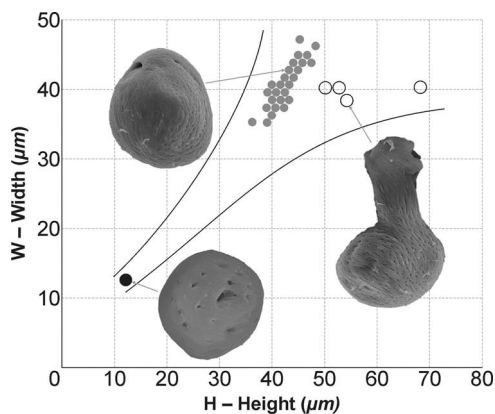


FIGURE 6. Dimensions of juvenile megalospheric morphotypes recovered from the brood chambers of *Peneroplis pertusus*: gray circles: typical two-chambered megalospheres composed of proloculus and tube-like flexostyle (morphotype 1); open circles: “elephant specimens” with laterally detached flexostyles (morphotype 3); black colored circle: juvenile megalosphere that lacks the tube-like flexostyle (Morphotype 2).

flexostyle, are elongate and arranged parallel to the periphery of the test (Figs. 4d,i,l). The size of the juvenile megalospheres of morphotype 1 ranged between 36–47 μm in height, 35–47 μm in width, and 37–43 μm in diameter (Fig. 6). With a total of 53 individuals, morphotype 1 is by far the most abundant among all juveniles.

Morphotype 2 is the smallest of these morphotypes and is represented by a single individual (Fig. 4q) that lacks the tube-like flexostyle, consisting only of a fully calcified proloculus. This proloculus has a maximum outer width and height of 12 μm , a diameter of 10 μm (Fig. 6). The proloculus is provided with a small subtriangular aperture, is subspherical in outline, subrounded in lateral (Fig. 4q) and subcarinate in peripheral view. High resolution SEM images show that the surface is pitted by a just a few pseudopores and covered by packages of mostly parallel aligned calcite needles.

Morphotype 3 is represented by four specimens and is a modified form of morphotype 1. In this form, the flexostyle does not wind semicircularly around the proloculus as in morphotype 1 but partially detaches from it and grows laterally to the side in the form of an elephant trunk (Figs. 4m,n). The laterally detached flexostyle has a length of about 30 μm and is thus of about the same size as the diameter of the proloculus. The dimensions of these “elephant specimens” range between 50–68 μm in height and 38–40 μm in both width and diameter (Figs. 5, 6).

Morphotype 4 is represented by two specimens (Figs. 4o,p), each consisting of two tightly fused forms of morphotype 1, each characterized by a proloculus and a flexostyle. In this type of twinning, both basic forms are firmly fused together and, like the other specimens, completely calcified. The surrounding rim of the apertures has no pseudopores but has short spiny extensions that are fused to the outer surface of the proloculus (Figs. 4p,r).

TEST DEFORMATIONS IN JUVENILE MEGALOSPHERES

Among all juvenile megalospheres recovered from the parental test, at least 45 out of 60 individuals showed some form of test deformation. The deformations include indentations on the

outer test surface (Figs. 4a,d,g,h,m–q) along the periphery and the flexostyle (Figs. 4h,m,o,p) and around the apertural opening (Fig. 4m). The shape and form of the indentations often resembled imprints of neighboring tests (Figs. 4m–o) or resulted from twinning (Figs. 4o–p). Another form of test abnormality that has not yet been described is seen in specimens in which the flexostyle, which normally wraps halfway around the proloculus, partially detaches off the proloculus and grows trunk-like into the available space, or clings to the shells of other megalospheres (Figs. 4m,n). In these “elephant-like” specimens, the flexostyle closely fits to the surrounding shells and its orientation depends on the available space between the closely packed individuals.

To analyze whether test deformations are carried through into adult specimens, we have picked and examined an additional 101 semi-adult and adult specimens of *P. pertusus* from the Line Island archipelago. However, none of these specimens showed shell deformation or malformed chambers.

DISCUSSION

The release of megalospheric juveniles from the parental tests in *Peneroplis* was originally described and illustrated by Winter (1907) and considered to be triggered by (i) the pseudopodia of the juveniles, which partially dissolve the parental test wall, and (ii) the vigorous movement of the densely packed juveniles in the brood chambers. The pre-dissolution and active movement of the juveniles ultimately weakens the stability of the parental test until its tensile strength is exceeded, eventually resulting in test rupture on the aperture face, along the sutures, and along the peripheral test wall (Heron-Allen, 1915; Langer & Bell, 1995; Langer et al., 2009). Given the ability of pseudopodial networks to carry out erosive activities (Winter, 1907; Bé et al., 1977; Bowser, 1985), it is very likely that pseudopodial networks are involved in breaking the parental test wall, but this requires further investigation.

In the detailed and exquisitely documented work on the reproductive cycle in *Peneroplis pertusus*, Winter (1907) clearly shows that the offspring provided with a proloculus and flexostyle results from the process of multiple fission. On the contrary, individuals of the microspheric generation have a small proloculus and no flexostyle. Winter therefore concluded that the species is dimorphic where two distinct morphologies characterize the alternation of generations: a microspheric generation with a small proloculus and large test, and a megalospheric generation with a large proloculus and an overall smaller test.

Out of the 60 juvenile specimens recovered in our study from the brood chambers of *P. pertusus*, 59 (98%) exhibit the characteristic features of proloculus and flexostyle and only one specimen did not have the flexostyle and consisted solely of the proloculus. We therefore conclude that the offspring found here resulted from the process of multiple fission, where the parent was most likely microspheric. However, we cannot exclude that the offspring resulted from multiple fission of a megalospheric parent, although this is less likely.

As pointed out by Faber & Lee (1993), the number of juveniles released from the test varies with size of the parental test in *Peneroplis*. With a total number of 60, the number of megalospheric juveniles counted here is slightly lower than those reported in other species of *Peneroplis*: Schacko (1882) reported

118 “embryos” in *P. proteus* (d’Orbigny), Winter (1907) depicted 100 juvenile megalospheres within the parental test of *P. pertusus* (Forskål), and Langer et al. (2009) estimated the total number of megalospheric juveniles in *P. hoheneggeri* (Förderer & Langer, 2018) to range between 110 and 130. Only Faber & Lee (1993) reported much higher numbers and estimated that the number of juveniles released from the parental test ranged between 500 and 1500 individuals.

The megalospheric juveniles consisting of proloculus and flexostyle and isolated from the brood chamber of the adult test display variations in size, ranging from 35–47 μm in width (w ; $n = 59$), 36–68 μm in height (h ; $n = 59$), and 38–42 μm in diameter (d ; $n = 13$). In the single individual consisting of a proloculus only, width, height, and diameter were much smaller ($w = 12 \mu\text{m}$, $h = 12 \mu\text{m}$, $d = 10 \mu\text{m}$). Both the lack of a flexostyle and the small size of the proloculus were considered to be typical for microspheric individuals of *P. pertusus* as described and measured by Winter (1907). The presence of both megalospheric and microspheric juveniles resulting from a single reproduction event, however, would certainly complicate our current understanding of the reproductive biology in foraminifera. Winter (1907), however, noted that the developing juveniles suffer from extreme space limitations within the brood chambers of the parental test, occasionally resulting in dwarfism in some of the megalospheric proloculi (see also Langer et al., 2009). The lack of a flexostyle, however, has not been reported in megalospheric juveniles of *Peneroplis* and requires further study.

TEST DEFORMATIONS

Among all juvenile megalospheres recovered from the brood chambers of *P. pertusus*, 45 out of 60 megalospheric individuals (75%) exhibit deformations of the test. The deformations included indentations on the outer test surface, dented and deformed tests, abnormal test shapes that are the result of the fusion of two connected shells (twinning), and forms with partially detached flexostyles. Previous work has described some of these test deformations (Schacko, 1882, 1883; Winter, 1907; Langer et al., 2009), but here we add two new types of deformations: a) twinning of megalospheres and b) forms with partially detached flexostyles.

The percentage of deformed megalospheres recorded here for juveniles in *P. pertusus* (75%) is higher than previously reported for juveniles in *P. hoheneggeri* (27%). As documented earlier (Langer et al., 2009), the test deformations are inflicted by the neighboring tests as a result of close packaging and asynchronous, time-shifted calcification where the developing juveniles suffer from extreme space limitations within the brood chambers of the parental test. The different percentages of deformed megalospheres in *P. pertusus* and *P. hoheneggeri* may be attributed to the available space in the parental test.

Previous studies suggested that juvenile test deformities can be carried through into the adult (Schacko, 1882, 1883; Winter, 1907; Langer et al., 2009). However, our studies on more than 100 additional adult and semi-adult specimens show that the shell deformations observed in the juvenile specimens are not expressed in the adult shells of *P. pertusus*. There are two possible explanations for this: (i) the juvenile shell deformations do not affect normal growth and do not lead to malformations in adults, or (ii) deformed juvenile specimens are not viable and do not grow into adult forms. Based on the high percentages of

deformed specimens (75%), the former explanation seems more likely. However, this requires further investigation.

The high proportion of deformed or abnormally formed juvenile megalospheres (indented, twinned, unusual flexostyles) and the observation that these morphological modifications are not expressed in the subsequent development of the peneroplids suggest that the observed deformations are a common process and part of the natural morphological development in the densely packed brood chambers of the parental test. The ability of foraminifera to repair broken or deformed shells and return to normal growth (Bé & Spero, 1981; Krüger et al., 1996; Toler & Hallock, 1998; Hohenegger, 2018; Souder et al., 2010; Hohenegger et al., 2019) clearly shows that they are highly adapted to the construction of normal or near-normal shells despite physical (mechanical breakage) or biological (predation) impacts. The detailed observations presented here suggest that these abilities are already present in the earliest phase of foraminiferal development.

CONCLUDING REMARKS

The finding of an adult *Peneroplis pertusus* parent with pre-emergent juveniles contained within the test provides a rare opportunity to examine the range of morphologic variability within a single brood of offspring resulting from multiple fission. Indeed, these 60 juveniles are nonuniform and highly heterogeneous, varying in size (from 12 to 47 μm , and “elephant” specimens ranging up to 68 μm), ornamentation (from sparsely to densely packed pseudopores), position of the flexostyle, and extent of test deformations. Such variation may reflect the space available to the juvenile at the time of calcification. Four morphotypes are documented among these juveniles, and 75% display some sort of test deformation. Test abnormalities among juveniles, however, are not expressed in adults of the broader natural population at the sampling locality, suggesting that either these deformities do not influence subsequent growth stages or that some deformed juveniles do not survive. These small juveniles ultimately become the proloculus and associated juvenile chamber(s) of adults, features that are used in the taxonomy of some larger foraminifera. Prolocular size across contemporary populations and among populations through time may also be used to infer ecological and paleoecological conditions. Results of this study inform such investigations.

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