

**DIVERSITY, BIOGEOGRAPHY, BODY SIZE AND FOSSIL RECORD OF PARASITIC AND SUSPECTED
PARASITIC FORAMINIFERA: A REVIEW**

SALLY E. WALKER, LEANNE G. HANCOCK AND SAMUEL S. BOWSER

Appendices for paper published in the
Journal of Foraminiferal Research v. 47(1), p. 34–55.

Available on the Cushman Foundation website in the JFR Article Data Repository:
<https://cushmanfoundation.allenpress.com/JournalofForaminiferalResearch/DataRepository>
as item number JFR_DR_2017002

APPENDICES 1–5

APPENDIX 1

PARASITIC FORAMINIFERA BY SPECIES, BEHAVIOR, TROPHIC MODES, AND ECOLOGY

Cibicides antarcticus (Saidova)

Cibicides antarcticus (formerly *Cibicides refulgens* in Antarctica, Schweizer et al. 2012) is the only foraminiferal parasite demonstrated to take nutrients from its host, the Antarctic scallop, *Adamussium colbecki* (Smith) (Alexander & DeLaca, 1987). Calcareous *C. antarcticus* etches resting scars on *Adamussium*'s shell surface (Alexander & DeLaca, 1987). Only adults bore through the thin valves and readily take up ¹⁴C-labeled amino acids that were experimentally placed within the scallop (Alexander & DeLaca, 1987). It is thought that ~ 50% of the *C. antarcticus* are parasitic, but a recent paper indicates that parasitism varies between 10 and 50% depending on Antarctic locality (Hancock et al., 2015). Over 800 *C. antarcticus* encrust *Adamussium* with densities ranging from 3.9–30.0 cm⁻² (Fig. 2; Mullineaux & DeLaca, 1984; Radford et al. 2014; Hancock et al. 2015; Bowser personal observation, 2005). *Adamussium* forms blisters on the shell interior in response to *C. antarcticus*; not all boreholes, however, produce a response from the scallop (Walker observation, 2010). *Cibicides antarcticus* is a facultative parasite and also grazes on diatoms or suspension feeds (Alexander & DeLaca, 1987). It is parasitic only on *Adamussium*, though it also attaches to sideroid spines and boulders in the Ross Sea region (David et al. 2009; Radford et al. 2014).

Fissurina marginata (Montagu)

Le Calvez (1947) cultured calcareous *F. marginata* [= *Entosolenia marginata* Montagu; *Fissurina submarginata* (Boomgart), see Gross 2015] and discovered that they only survive on *Discorbis vilardeboanus* (d'Orbigny). *Fissurina* attaches above the aperture of *D. vilardeboanus* and feeds on food particles trapped in the host's pseudopodia and ectoplasm (Le Calvez, 1947). After several experiments, Le Calvez concluded that *F. marginata* was an obligate parasite because it did not live on other foraminifera and died without the host. He did not describe where *F. marginata* lived, but presumably they occur with *D. vilardeboanus* in the North Atlantic. In Fiji, *F. marginata* presumably feeds on either the pseudopodia or food particles on the pseudopodia of *Rosalina bradyi* (Cushman) (Collen & Newell, 1999). If *F.*

marginata is likely kleptoparasitic. Future work needs to address whether *F. marginata* affects the host's growth and whether it is a common parasite of *D. vilardeboanus* and *R. bradyi*.

Floresina amphiphaga Hallock & Talge.

Floresina amphiphaga was described from populations of *Amphistegina gibbosa* d'Orbigny collected from reef rubble in the Florida Keys, U.S.A. (Hallock & Talge, 1994; Hallock et al. 1998). Although originally described as predatory, those behavioral observations are consistent with definitions of parasitism (e.g., Poulin, 2007). Trochospiral *F. amphiphaga* were shown to attack other foraminifera in laboratory conditions, such as *Amphistegina lessonii* d'Orbigny and *Amphistegina lobifera* Larsen (Hallock & Talge, 1994). *Floresina* is small (0.1–0.4 mm) and bores multiple holes through the shell of the much larger *Amphistegina* to extract diatom-enriched protoplasm (Hallock & Talge, 1994). *Floresina* appears to select pre-adults to adults and does not attack juveniles (Hallock & Talge, 1994). *Floresina* juveniles die in lab culture even in the presence of *Amphistegina*, suggesting that juveniles have other nutritional requirements (Hallock & Talge, 1994). Some *Amphistegina* are killed within seven days of a *Floresina* attack, although a few survive (Hallock & Talge, 1994).

Floresina attacks are rare, ranging from 0.4–1.2 % of *A. gibbosa* populations (Hallock & Talge, 1994). *Floresina* can selectively target partly bleached *A. gibbosa* and was more commonly recorded in spring and summer than in autumn and winter (Hallock et al., 1998). Thus, *Floresina* boreholes could be a bioindicator for bleaching in historical populations of *Amphistegina* (Hallock & Talge, 1994).

Hyrrokin carnivora (Todd)

The life cycle and ecology of the ectoparasite, *H. carnivora*, is not well known. This calcareous foraminiferan was first described by Todd (1965) as *Rosalina carnivora* Todd and transferred to *Hyrrokin* by Cedhagen (1994). Todd considered *H. carnivora* a “commensal parasite” living on deep-water limid bivalves from the Gulf of Guinea, Africa. She observed individuals attached to the umbo and lunule of the limid *Acesta angolensis* Adam & Knudsen. Cedhagen (1994), however, suggests that *H. carnivora* has a random distribution on limids. This species etches resting scars on

Acesta's surface and then bores a canal through the shell, presumably to obtain CaCO₃ (Todd, 1965) or nutrients (Cedhagen, 1994). *Acesta* forms calcareous blisters to wall off the boreholes (Todd, 1965). Cedhagen (1994) noted that 10–200 scars and from 2–50 attached *H. carnivora* occur on the valves of *A. angolensis*. *Hyrrokkin carnivora* grows up to 6 mm in diameter and a puffermasse of fine mud and organic debris surround their shells (Todd, 1965; Cedhagen, 1994). Agglutinated feeding tubes indicative of suspension feeding also occur (Cedhagen, 1994). Marche-Marchad (1979) also examined the behavior of *H. carnivora*, but Cedhagen (1994) suggested that Marche-Marchad was studying *Hyrrokkin sarcophaga* instead.

Hyrrokkin sarcophaga Cedhagen

Hyrrokkin sarcophaga is one of the best-studied foraminiferal parasites. As an ectoparasite, it attaches to deep-water corals, sponges, bivalves, and chitons the North Atlantic (Cedhagen, 1994; Freiwald & Schönfeld, 1996; Sigwart, 2009). It also attaches to stones (Cedhagen, 1994). *Hyrrokkin sarcophaga* has a trochospiral calcareous shell and grows up to 7 mm in diameter (Cedhagen, 1994; Freiwald & Schönfeld, 1996). It adds irregular chambers when growing on sponges and calcareous polychaetes (Cedhagen, 1994; Beuck et al. 2008). Compared to *H. carnivora*, *H. sarcophaga* has a thicker shell, a smooth apical surface, a rounded shell margin and umbilical sutures that are U-shaped rather than V-shaped (Cedhagen, 1994). Like *H. carnivora*, it has a brown organic layer surrounding its shell (Cedhagen, 1994).

Five to 40 individuals of *H. sarcophaga* attach to deep-sea sponges like *Stelletta*, *Isops* and *Geodia* (Cedhagen, 1994). On *Isops*, it destroys the cortex and removes the spicules, leaving round scars (Cedhagen, 1994). On *Stelletta*, *H. sarcophaga* attaches to the spicules (Cedhagen, 1994). *Hyrrokkin sarcophaga* might also eat detritus from the sponge surface, suspension feed or take food from the sponge's inhalant currents (Cedhagen, 1994).

On deep-water corals like *Lophelia pertusa* (Linneaus), *H. sarcophaga* infests the epidermis just below the tentacles (Freiwald & Schönfeld, 1996). Presumably it eats the coral's tissues. It occurs singly or in clusters of three to eight individuals, with rarely ≥ 50 individuals per coral (Cedhagen, 1994; Freiwald & Schönfeld, 1996). Single individuals reach 7 mm in diameter, while individuals in clusters are smaller, ranging from 3–4 mm. Young *H. sarcophaga* etches scars into the coral surface (Beuck et al., 2008), and adults bore a straight canal through the coral's

skeleton to invade the polyp (Cedhagen, 1994; Freiwald & Schönfeld, 1996). “Whip-shaped” bioerosion traces, presumably made by *H. sarcophaga*’s pseudopodia, penetrate the skeleton (Beuck & Freiwald, 2005; Beuck et al. 2008). Resting pits and the “whip-like” traces diagnostic for *H. sarcophaga* are given the trace fossil name *Kardopomorphos polydioryx* (Beuck et al. 2008). *Hyrrokin*’s boreholes do not cause a host-response in corals (Cedhagen, 1994; Beuck et al. 2008). This species is rare on other deep-sea corals such as *Madrepora oculata* (Linnaeus) and *Caryophyllia sarsiae* (Zibrowius) (Beuck et al. 2008).

Hyrrokin sarcophaga also infests bivalves like *Acesta excavata* (Fabricius) and *Delectopecten vitreus* (Gmelin) (Cedhagen, 1994). Ten to thirty individuals can infest the top surface of *A. excavata* (Cedhagen, 1994). Adult *H. sarcophaga* bioerode a canal through the shell of *Acesta* and extend their pseudopodia into the mantle tissue, indicative of parasitism (Cedhagen, 1994). *Acesta* repairs the canal by forming a blister of brown organic matter and nacre (Marche-Marchad, 1979; Cedhagen, 1994; Beuck et al. 2008). *Delectopecten* is rarely infested because of its small size (~3.5 mm), but canals etched by *Hyrrokin* do occur on this species (Freiwald & Schönfeld, 1996). One *Delectopecten* grew abnormally in response to a *H. sarcophaga* and was possibly killed by this parasite (Cedhagen, 1994).

Hyrrokin sarcophaga is also a predator. It feeds on a variety of tubicolous polychaetes (*Serpula*, *Spirobis*) and bryozoa (*Disporella*, *Idmidronea*; Cedhagen, 1994). *Idmidronea* exhibits a defense response by growing away from *Hyrrokin*. Cedhagen (1994) did not discuss whether *Hyrrokin* bored holes into these prey or devoured them. *Hyrrokin* also ate calcareous foraminifera, but not agglutinated foraminifera, that were in close proximity to its shell (Cedhagen, 1994, p. 77).

Hyrrokin sarcophaga has a life cycle consistent with Discorbacea, alternating between a diploid microspheric and haploid megalospheric generation (Cedhagen, 1994). The megalospheric stage was common; only one microspheric stage was observed, suggesting it is the dispersal stage (Cedhagen, 1994). Copulation between megalospheric *Hyrrokin* indicates gamontogamy, and individuals may detach from the host afterwards (Cedhagen, 1994). Marche-Marchad (1979) inferred various growth stages in *H. sarcophaga* by counting multiple calcium carbonate layers in the shell blisters of *Acesta*. The blisters stop forming when *Hyrrokin* retracts its pseudopodia from the host’s tissue during schizogamy (Marche-Marchad, 1979).

Cedhagen (1994) remarked that there are several undescribed species that could be attributed to *Hyrrokkin*. These include *Pulvinulina punctulata* (D'Orbigny) from the West Indies [cited by Brady (1884)] and *Eponides punctulata* (D'Orbigny) from the North Atlantic and Mediterranean [cited by Cushman (1931)]. We would also include *Pulvinulina punctulata* located offshore of North and South Island, New Zealand, listed by Heron-Allen & Earland (1922). Contrary to previous reports (Freiwald & Schönfeld, 1996; Beuck et al. 2008), *Hyrrokkin* (as *P. punctulata*) has not been reported from Antarctica. It is also important to re-examine the *Hyrrokkin* species studied by Marche-Marchad (1979). Cedhagen (1994) stated that Marche-Marchad's parasitic foraminiferan was *H. sarcophaga*, not *H. carnivora*. However, Marche-Marchad (1979) collected *Acesta angolensis* off the Ivory Coast, Africa, consistent with the locality for *H. carnivora*. Moreover, the behavior described by Marche-Marchad (1979) differs from that of *H. sarcophaga*. He observed juveniles (~300 um) forming canals that completely penetrated *A. angolensis* valves, whereas adult *H. sarcophaga* form the parasitic canal (Freiwald & Schönfeld, 1996). Clearly more ecological and genetic work are needed for both species of *Hyrrokkin*.

Metarotaliella tuvaluensis Collen

The calcareous foraminiferan *M. tuvaluensis* was discovered within miliolid shells from shallow lagoon sediments located on Funafuti Atoll, west-central Pacific (Collen, 1998). This very small (0.14 mm) trochospiral foraminiferan infests three miliolid species: *Triloculina barnardi* Rasheed, *Quinqueloculina laevigata* d'Orbigny and *Quinqueloculina oblonga* Montagu (Collen, 1998). Usually only one *Metarotaliella* is found within its host, but occasionally two to three individuals can occur. The association is relatively rare, with <3% infestation in host populations. It is not found on any other miliolid species or other substrate. When young, *Metarotaliella* attaches to the host and becomes trapped as the host adds chambers, which are often deformed (Collen, 1998). The aperture of *Metarotaliella* is aligned with the host's aperture, presumably for feeding. Some hosts form an extra layer to wall off the aperture of *Metarotaliella* and in others, can intergrow with the chamber wall of the parasite. *Metarotaliella* also bioerodes a round crypt. It is speculated that they may have plastogamic reproduction, similar to *Glabratella ornatissima* (Cushman) (Lipps & Erskian, 1969; Collen, 1998). Collen (1998) considers *M. tuvaluensis* an endoparasite because it lives within the host's shell. This species might

eat protoplasm or steal food from the host. Collen (1998) also suggested that *Metarotaliella* is symbiotic or might use the miliolid only as a substrate. Nevertheless, the association is more consistent with parasitism because it only occurs with three miliolids species; the aligned apertures suggest that *Metarotaliella* obtains nutrients from the host.

Planorbulinopsis parasitica Banner

Banner (1971) observed *P. parasitica* living within *Alveolinella quooii* (d'Orbigny), a large (~20 mm) fusiform foraminiferan, from reefs in Papua New Guinea. Approximately 20% of *Alveolinella* had one to two circular to subcircular boreholes stereotypically located at intercameral or apertural sutures. The robust calcareous shell of *P. parasitica* resides within the borehole, oriented with the trochospiral top exposed to the surface. Banner (1971) speculated that the young endoparasite first attaches to the outer surface of *Alveolinella* and eventually becomes embedded through its bioerosional activities. Banner (1971) suggests that *P. parasitica* eventually kills its host by feeding on its diatom-enriched protoplasm. This parasite is found only with *Alveolinella* even though other large foraminifera, like *Marginopora*, occur in the same locality. No information exists on its early life stages or how it reproduces. Future work needs to determine whether *Planorbulinopsis* affects the host's growth and reproduction.

Talpinella cunicularia Baumfalk, Fortuin & Mok

Calcareous *T. cunicularia* is commonly found within the Late Cretaceous orbitoid *Orbitoides media* (d'Archiac) that once lived in the Tethyan seaway (Baumfalk et al. 1982; Baumfalk & Van Hinte, 1985; Görmüş & Meriç, 2000). As trochospiral juveniles, *Talpinella* bored into the surface of *Orbitoides* or entered through the aperture (Baumfalk et al., 1982). Eventually it penetrated to the interior, forming tunnels and a curvilinear crypt. *Talpinella* avoided the central, embryonic region of *Orbitoides* suggesting it infested a living host (Baumfalk et al. 1982). *Talpinella* is about half the size of *Orbitoides* and could had considerable effect on its host. Infested *Orbitoides* could be smaller if *Talpinella* is feeding on its protoplasm, but size comparisons between infested and non-infested individuals need to confirm this.

Talpinella was first described as an obligate endoparasite (Baumfalk et al. 1982). However, it could also be a bioeroder (Cherchi et al. 1990; Görmüş & Nielsen, 2006). Nevertheless, there is compelling evidence that *Talpinella* is

parasitic: 1) It induces regeneration and repair in the host (Baumfalk & Nijholt, 1984); 2) it does not destroy the host's embryonic region (Baumfalk & Nijholt, 1984); and 3) it is host-specific and does not infest other large foraminifera such as *Lepidorbitoides* that co-occurs with *Orbitoides* (Baumfalk & Nijholt, 1984).

Talpinella cunicularia has the longest host-parasite relationship ever recorded: an 18-million-year history with several species of *Orbitoides*, ranging from the early Campanian to the late Maastrichtian (Baumfalk & Nijholt, 1984). During this time *Orbitoides* increased in size and its embryonic region increased in complexity (Albrich et al. 2014). This species would provide an excellent model for host-parasite evolution. Moreover, *Orbitoides* has distinct dimorphism with megalospheric and microspheric forms (Albrich et al. 2014) and it would be important to know if *Talpinella* is specific to one of these forms. Additionally, *Talpinella* infestations differ across biogeographic regions. For example, it infests up to 80% of *Orbitoides* from the Late Cretaceous of France (Baumfalk et al. 1982), but is rare in Turkey at that time (Görmüs & Nielsen, 2006). *Talpinella* has yet to be reported from Cenozoic *Orbitoides* and likely was extinct by the end of the Cretaceous.

Undescribed species

An undescribed species of parasitic foraminifera was discovered living on a parasitic eulimid gastropod, *Ophiolamia armigeri* Warén & Carney at 4000 m in the northeastern Atlantic Ocean (Warén & Carney, 1981, p. 191). It penetrated *Ophiolamia*'s shell and its pseudopodia were found within the gastropod's tissues (Warén & Carney, 1981). The gastropod, in turn, secreted epithelium around the parasitic boreholes. The foraminiferan was not illustrated, so little is known about its phylogenetic affinities, especially whether it is organic-walled, calcareous or agglutinated (Warén written communication, 2015). It may be a new species because the gastropod host is only 3.2 mm in height and lives in a specialized habitat, near the mouth of deep-sea ophioroids.

Note: All references for Appendix 1 are provided in the main paper, except for:

Lipps, J. H., and Erskian, M. S., 1969, Plastogamy in Foraminifera: *Glubratella ornatissima* (Cushman): Journal of Eukaryotic Microbiology, v. 16, p. 422–425.

APPENDIX 2

SUSPECTED PARASITIC FORAMINIFERA: BEHAVIOR, TROPHIC MODES, AND ECOLOGY

Organic-walled Species

Hospitella fulva Rhumbler.

Hospitella fulva was first described as a parasite because it lived within the shells of *Globigerina* and *Reophax* from deep-water sediments of the Northeast Atlantic (Rhumbler, 1911; Gooday et al. 2013). Alternatively, *H. fulva* could be a hermit foraminiferan living within empty globigerinacean shells or other species (Le Calvez, 1949; Loeblich & Tappan, 1988; Gooday et al. 2013). However, living planktonic foraminifera can live in deep-sea sediments (Gooday et al. 2013), and it is possible that *H. fulva* could initially feed off those species. It might settle on the host at an early stage based on recent work on *Hospitella*-like species found within radiolarian shells that have extremely small pores (Goineau & Gooday, 2015). *Hospitella fulva* has a cluster of organic pseudochambers connected by stolons that fill up the available space within the host (Gooday et al. 2013). Most perplexing is its aperture-bearing tube that apparently perforates the host's shell (Loeblich & Tappan, 1987; Gooday et al. 2013).

Incola inculta Gooday & Rothe.

Equally perplexing is the hermit foraminiferan, *Incola inculta*. It was found in globigerinacean shells from deep-sea sediments (2508 m) located in the Mid-Atlantic Ridge (Gooday et al. 2013). *Incola* has pseudochambers up to 90 μm in diameter and has agglutinated tube-like structures that perforate the host's shell (Gooday et al., 2008). In one host, *I. inculta* was found within the organic lining (Gooday et al. 2008, their fig. 6B). Unless it takes time for the organic lining to break down in a recently dead globigerinacean, this observation is suggestive of a parasitic relationship.

Thalamophaga ramosa Rhumbler.

Thalamophaga ramosa, from the North Atlantic, dissolves the shells of deep-sea foraminifera (*Pulvinulina*, *Globigerina*; Rhumbler 1911; Loeblich & Tappan, 1988). This species is similar to *I. inculta*, but has smaller chambers (2-8 μm ; Gooday et al. 2013). It is not known if it parasitizes living foraminifera.

Agglutinated Species

Bdelloidina spp.

Bdelloidina is a relatively large, agglutinated foraminiferan that attaches to carbonate substrates such as corals, molluscs, and carbonate hardgrounds (Carter, 1877; Brady, 1844; Bromley, 1970; Voigt, 1970; Voigt & Bromley, 1974; Walker et al. 2011). It is named after its shape which resembles “a group of sucking, half-filled leeches on the human skin” (Carter, 1877). *Bdelloidina* often associates with boreholes made by sponges and other invertebrates. For example, *Bdelloidina vincentownensis* Hofker encrusted boreholes in Maastrichtian hardgrounds possibly made by phoronids or callianassid shrimp (Voigt, 1970). Similarly, *B. vincentownensis* (as *Arenonina cretacea* Barnard) encircles sponge boreholes (*Entobia*) in Upper Cretaceous oysters from Sweden (Bromley, 1970) and Denmark (Bromley & Nordmann, 1971). [Voigt & Bromley (1974) suggest that *B. vincentownensis* is actually *Bdelloidina aggregata* Carter.] *Bdelloidina* is not always associated with sponge boreholes and can settle elsewhere on oyster shells (Bromley, 1970; Bromley & Nordmann, 1971; Voigt & Bromley, 1974). In the Recent, *B. aggregata* co-occur with bioeroding sponges (clionoids) associated with corals (Voigt & Bromley, 1974) and on experimentally-deployed gastropod shells in the shallow-water Caribbean (15 m; Walker et al. 2011).

Bdelloidina is speculated to take food from the sponge’s water currents (Bromley, 1970) and is likely kleptoparasitic. If *Bdelloidina* is kleptoparasitic, its aperture would be oriented toward sponge boreholes, but that is not always the case (Bromley, 1970; Bromley & Nordmann, 1971). More likely, the recruitment of *Bdelloidina* is influenced by the sponge’s water currents (Bromley, 1970). In fact, *Bdelloidina* was not common on empty gastropod shells until clionoids were abundant (Walker et al. 2011). To understand if *Bdelloidina* is a kleptoparasite of bioeroding sponges,

ecological studies need to quantify the number of *Bdelloidina* associated with bioeroding sponges compared to other settlement areas and whether *Bdelloidina* takes up nutrients from the water currents generated by the sponge.

Placopsilina spp.

Placopsilina spp., an agglutinated species, is associated with sponge boreholes in Cretaceous oysters from the Coniacian Chalk near Deal, England (Bromley, 1970). At that site, approximately 36% of the *Placopsilina* coil around sponge boreholes. *Placopsilina cenomana* d'Orbigny is also associated with boreholes in Maastrichtian hardgrounds in the Netherlands (Voigt, 1970). As in *Bdelloidina*, the sponge might influence the settlement of *Placopsilina*. For example, some *Placopsilina* coil their entire shell around sponge boreholes perhaps in response to living sponge tissue (Bromley & Nordmann, 1971). Others only have their initial chambers encircling the borehole and then grow away or settle elsewhere and grow toward the borehole (Bromley, 1970). *Placopsilina* also co-occurs with clionaid boreholes in the Recent (Voigt & Bromley, 1974), although this behavior was not observed with clionaid boreholes on experimental shells deployed in the Caribbean (Walker et al. 2011). *Placopsilina* could be kleptoparasitic, but more work is needed to determine its host-parasite relationship.

Tolypammia vagans (Brady).

Numerous agglutinated *T. vagans* inhabit siliceous sponges from the Late Jurassic Kraców-Częstochowa deposits in Poland (Kaźmierczak, 1973). This species occurs in on the surface of the sponge and in inhalant and excurrent canals. The sponge may die if heavily infested (Kaźmierczak, 1973). The shell of *T. vagans* is either a straight or bent tube that conforms to the shape of the sponge canal. Where water velocity is highest in the sponge, their shells have larger grains (~8–12 μm), and where water velocity is lowest, smaller grains (2–5 μm). *Tolypammia* does not occur in calcareous sponges presumably because the ostia are too small (Kaźmierczak, 1973).

Tolypammia's association with the sponge is interpreted in various ways, from commensal (Feifel, 1930) to inquiline or parasitic (Kaźmierczak, 1973). Some suggest that it only attaches to dead sponge spicules (Guilbaut et al. 2006). Kaźmierczak (1973) claimed the relationship was likely not parasitic because he thought that sponges and

foraminifera would not eat the same types of food, like bacteria. However, foraminifera do eat bacteria (Lee, 1980), as well as yeast, fungi, dissolved organic matter and other organisms (Goldstein, 1999). Not only could *Tolypammina* compete with the host for food, but its infestations would also restrict water flow through the sponge. The distribution of *Tolypammina* in different fossil sponge species is needed to determine whether Kaźmierczak's observations hold true.

Troglotella incrustans Wernli & Fookes.

Troglotella incrustans was first described from the Upper Jurassic of France (Wernli & Fookes, 1992). It is a common and large (~2 mm) uniserial foraminiferan associated with the crustose microfossil *Lithocodium aggregatum* Elliott (Kołodziej, 1997; Schlagintweit, 2012). Whether *Troglotella* is a parasite depends on the interpretation of its host, which has been attributed to many taxa such as a codiacean algae (Elliott, 1956; Banner et al. 1990), ulotrichalean algae (Schlagintweit et al. 2010), *Entobia* (sponge)-calcimicrobial mats (Cherchi & Schroeder, 2012; 2013) and crustose foraminifera (Schmid & Leinfelder, 1996; Kołodziej, 1997). Currently, *Lithocodium* is either a foraminiferan (Schmid & Leinfelder, 1996; Kołodziej, 1997; Flügel, 2004) or a calcimicrobe penetrated by *Entobia* (Cherchi & Schroeder, 2006; 2013; Schlagintweit, 2012). Foraminiferal characteristics include a planispiral shell, micritic wall structure with quartz grains, and alveoli similar to loftusiancean foraminifera (Schmid & Leinfelder, 1996). If *Lithocodium* is a foraminiferan, *Troglotella* is often found within its chambers suggestive of a parasitic relationship (Schmid & Leinfelder, 1996; Kołodziej, 1997). *Troglotella* could have bored into the chambers of *Lithocodium* or settled on its surface and was subsequently trapped by the host's growth; it likely fed on *Lithocodium*'s photosymbionts or their carbohydrate by products (Kołodziej, 1997).

Lithocodium is widespread in the shallow Tethys from the Late Triassic to Middle Cretaceous (Cherchi & Schroeder, 2013). Thus, there could be more than one type of *Lithocodium-Troglotella* association because of their broad geographic and temporal distribution. Cherchi & Schroeder (2013) examined Elliott's original thin sections from Lower Cretaceous deposits in southern Iraq. They interpreted *Lithocodium* as a calcimicrobe riddled with *Entobia* possessing tabulae, but *Entobia* are not known to have tabulae (Tapanilla written communication, 2015). By comparison, *Lithocodium* from the Late Jurassic of the Polish Carpathians is very different (Kołodziej, 1997). Unfortunately, neither

paper discusses the planispiral shell or agglutinated grains first described by Schmid & Leinfelder (1996). A reappraisal of *Lithocodium* and *Troglotella* from their geographic and temporal range is needed to clarify their taxonomic and paleoecological relationship.

Calcareous Species

Cymbaloporella tabellaeformis (Brady).

Cymbaloporella tabellaeformis was first discovered living in coral reef sediments off Madagascar (Brady, 1884). Heron-Allen (1915) reported its ability to bore into carbonate substrates and was the first to suggest that foraminiferal protoplasm decalcifies molluscan shells. He also suggested that these foraminifera could use the host's carbonate to make their own shells. When young, *Cymbaloporella* probably attaches to the host's surface and bores into the host. As it grows, it enlarges the borehole, which is the same size as its shell (Heron-Allen, 1915). *Cymbaloporella* eventually becomes trapped within its borehole, leaving only a small part of its shell exposed at the surface. Pseudopodia from *Cymbaloporella* presumably form canals that radiate from the main borehole into the host's interior.

Cymbaloporella occurs in mollusc shells, dead corals, calcareous algae and other skeletal debris including carbonate beach rock. Matteucci (1974) speculated that *Cymbaloporella* feeds on encrusting or bioeroding algae and fungi. Smyth (1988) reported that *Cymbaloporella* infested ~15% of 25 living gastropod species from Guam. Both Matteucci (1974) and Smyth (1988) suggest that *Cymbaloporella* is not parasitic on living tissue, but could be incorporating CaCO₃ from the host. A host response is unknown and unless it takes up CaCO₃ from living molluscs, this species is likely a bioeroding foraminiferan and not a parasite.

Hanzawaia concentrica (Cushman) var. *strattoni*.

Hanzawaia concentrica var. *strattoni* attaches to a small bivalve *Varicorbula operculata* Philippi (= *Notocorbula operculata* = *Varicorbula disparilis* d'Orbigny; see Mikkelsen & Bieler, 2001), which in turn attaches to the parchment tubes of *Chaetopterus variopedatus* (Renier) (Bock & Moore, 1968). *Hanzawaia* is widely distributed in the Gulf of

Mexico (Bandy, 1954; Culver & Buzas, 1980; Poag, 2015), but relatively little is known about its ecology. It is speculated to compete for food with *Varicorbula* (Bock & Moore, 1968), and therefore could be kleptoparasitic.

Rotaliella elatiana Pawlowski & Lee.

Rotaliella elatiana lives on and within the filaments of the intertidal alga, *Ulva* (= *Enteromorpha*) *intestinalis* Linnaeus, found in the Gulf of Elat, Israel (Pawlowski & Lee, 1992). Approximately 75% of *Rotaliella* live inside the filaments, averaging 10–20 individuals per filament. *Rotaliella* ingest chloroplasts from the host, and in laboratory cultures, will eventually kill the alga. The chloroplasts are digested immediately rather than fostered for weeks (Pawlowski & Lee, 1992). This species could be a major ecological control on *Ulva*, but little is known about its ecology and its distributions (Pawlowski & Lee, 1992).

Ramulina globulifera Brady and *Ramulina parasitica* Carter.

Ramulina globulifera and *R. parasitica* are both thought to be parasitic (Véneç-Peyré, 1996), but their taxonomic history is muddled and it is entirely possible that *R. globulifera* is not parasitic. The genus *Ramulina* was based on small, branching tubular microfossils found in the Cretaceous chalk of Ireland (Wright, 1875). These tubes were identified by T. Rupert Jones, but neither Wright (1875) nor Jones formerly described the genus. Consequently, *Ramulina* was formally described by Brady (1884, p. 587), who restricted the generic description to free-living forms. Jones & Chapman (1897) then emended *Ramulina* to include both attached and free-living species.

Ramulina globulifera is thought to be parasitic because Jones & Chapman (1897) synonymized this species with a suspected bioeroding (“parasitic”) sponge. Duncan (1880) described a “sponge” (*Möbiusispongia parasitica* Duncan) living within the chambers of the foraminiferan *Carpenteria raphidodendron* Möbius collected in waters off Mauritius. Jennings (1896) reinterpreted Duncan’s sponge as a *Ramulina* foraminiferan. Jennings noted that *Ramulina*’s stolons penetrated the wall of *Carpenteria* and that *Carpenteria* was alive because the internal chambers were still lined with “dry sarcodite” (Jennings, 1896, p. 319). He speculated that *Ramulina* took food directly from *Carpenteria*. Importantly, Jennings stated that his *Ramulina* was smaller and morphologically more complex than *R. globulifera*. Nevertheless,

Jones & Chapman (1897) synonymized this putative parasitic species with Brady's free-living *Ramulina globulifera*. Because it has parasitic and free-living members, it is likely that *R. globulifera* is a wastebasket taxon in need of taxonomic revision.

Although Jones & Chapman (1897) reviewed *Ramulina*, they missed Carter's (1889) work on *R. parasitica* that infested *Orbitoides mantelli* Morton from the Oligocene of Burma (Myanmar). *Ramulina parasitica* has a calcareous shell with a single chamber that is linked by stolons to other chambers forming a reticulated network within *Orbitoides* (Carter, 1889). He suggested it was parasitic on *Orbitoides*, but could also occur in the "free state" attached to limestone (Carter, 1889). Carter (1889) further observed that *R. parasitica* was much smaller than *R. globulifera* described by Brady (1884) and the *Ramulina* species depicted by Wright (1875). His observations indicate that *R. parasitica* is a distinct species, and there could still be other species. For instance, Heim (1908, p. 284) suggested that a *Ramulina*-like parasite caused the extinction of *Nummulites* from the Eocene of Switzerland. Since the turn of the 20th century, *R. parasitica* has not been studied, although free-living *Ramulina* species are known from the Recent (Guilbault et al. 2006).

Vasiglobulina alabamensis (Cushman & McGlamery).

Vasiglobulina alabamensis occurs in shallow marine facies from the upper Eocene to lower Miocene of the Gulf and Atlantic Coastal Plain, U.S.A. (Poag, 1969). Its pseudopodial-covered spines penetrate calcareous fragments of molluscs, crustaceans and cheilostome bryozoans (Poag, 1969, 1971). He proposed that dissolved calcite from the host could be used by *Vasiglobulina* to form the spines. He further suggested that *Vasiglobulina* settled on dead calcareous material, but latter mentioned that this species might prey on foraminifera because of its particular mode of dissolving shells (Poag, 1969). It is also conceivable that *Vasiglobulina* is parasitic, although it has yet to be found attached to once-living mollusks or bryozoa. This is a fascinating species and could be a potential parasite.

Note: All references are provided in the main paper, except for:

Lee, J. J., 1980, Nutrition and physiology of the foraminifera, *in* Levandowsky, M., and Hutner, S. H. (eds.),
Biochemistry and Physiology of Protozoa, v. 3: Academic press, New York, p. 43–66.

APPENDIX 3.

MEAN AND MEDIAN SIZE OF PARASITIC AND SUSPECTED PARASITIC FORAMINIFERA. SIZE IS BASED ON LARGEST DIAMETER OR WIDTH REPORTED FOR THE SPECIES (REFER TO TABLE 1).

Note: the maximum size of *H. sarcophaga* is 7.00 mm, but it also occurs on smaller hosts, and those sizes are also represented.

Parasites	Size (mm)	Suspected Parasites	Size (mm)
<i>Cibicides antarcticus</i>	1.24	<i>Bdelloidina aggregata</i>	0.70
<i>Fissurina marginata</i>	0.56	<i>Cymbaloporella tabellaeformis</i>	0.90
<i>Floresina amphiphaga</i>	0.37	<i>Hospitella fulva</i>	0.15
<i>Hyrrokkin carnivora</i>	6.00	<i>Incola inculta</i>	0.15
<i>Hyrrokkin sarcophaga</i>	7.00	<i>Placopsilina spp.</i>	0.50
<i>Hyrrokkin sarcophaga</i>	2.80	<i>Ramulina globulifera</i>	0.25
<i>Hyrrokkin sarcophaga</i>	0.50	<i>Ramulina parasitica</i>	0.70
<i>Metarotaliella tuvaluensis</i>	0.14	<i>Rotaliella elatiana</i>	0.12
<i>Planorbulinopsis parasitica</i>	0.14	<i>Thalamophaga ramosa</i>	0.01
<i>Talpinella cunicularia</i>	1.50	<i>Tolypammina vagans</i>	0.40
mean size	2.02	<i>Troglotella incrustans</i>	4.00
median	0.90	<i>Vasiglobulina alabamensis</i>	0.14
		mean size	0.67
		median	0.32

APPENDIX 4

SIZE IN PARASITES AND THEIR RELATIVES DEPICTED IN FIGURE 8A. SIZE WAS EITHER DIRECTLY GIVEN BY THE REFERENCE OR WAS ESTIMATED FROM THE FIGURED SPECIMENS.

Species	Size (mm)	Reference
<i>Cibicides antarcticus</i>	1.24	Schweizer et al. 2012
<i>Cibicides refulgens</i>	0.33	Schweizer et al. 2009
<i>Cibicidoides lobatulus</i>	1.00	¹ Wisshak & Rüggeberg, 2006
<i>Cibicidoides pachyderma</i>	0.50	Schweizer et al. 2009
<i>Cibicidoides wuellerstorfi</i>	0.50	Schweizer et al. 2009
<i>Floresina amphiphaga</i>	0.37	Hallock & Talge, 1994
<i>Floresina curta</i>	0.20	² Revets, 1990
<i>Floresina durrandi</i>	0.20	² Revets, 1990
<i>Floresina latissima</i>	0.27	² Revets, 1990
<i>Floresina paralleliformis</i>	0.30	² Revets, 1990
<i>Hyrrokkin carnivora</i>	6.00	Todd, 1965
<i>Hyrrokkin sarcophaga</i>	7.00	Cedhagen, 1994
<i>Rosalina globularis</i>	0.56	³ Sliter, 1971

References cited in text except for:

¹Wisshak, M., and Rüggeberg, A., 2006, Colonisation and bioerosion of experimental substrates by benthic foraminiferans from euphotic to aphotic depths (Kosterfjord, SW Sweden): *Facies*, v. 52, p. 1–17.

²Revets, S. A., 1990, The genus *Floresina*, Gen. Nov.: *Journal of Foraminiferal Research*, v. 20, p. 157–161.

³Sliter, W. V., 1971, Predation on benthic foraminifers: *Journal of Foraminiferal Research*, v. 1, p. 20–29.

APPENDIX 5

PARASITIC AND SUSPECTED PARASITIC FORAMINIFERA THAT WERE USED TO EXAMINE SIZE RELATIONSHIPS AND HARRISON'S
RULE

As depicted in Figs. 8B–9A–D; all plots and statistics were done in R at an alpha level = 0.05 (R Core Team, 2015). *Bdelloidina*, *Hanzawaia*, *Placopsilina*, *Thalamophaga*, *Tolypammina*, and *Troglotella* were not included in this analysis because it was not possible to estimate their host size. The undescribed species is also not included because size information was not available. For Fig. 9A, only ecto- and endoparasites were used in the analysis (denoted by *); for Fig. 9B, only suspected ecto- and endoparasites were used. For Fig. 9C, parasitic and suspected ectoparasites were pooled; for Fig. 9D, parasitic and suspected endoparasites were pooled. Host size was either obtained from the references or estimated based on figured specimens in the references. For *H. sarcophaga*, more size measurements were used because they were provided by the references.

Species/Host	Parasite Size (mm)	Host Size (mm)	Reference
<u>Ectoparasites</u>			
* <i>Cibicides antarcticus</i> / <i>Adamussium colbecki</i>	1.24	70.00	Schweitzer et al. 2012; host: Quaglio et al. 2010; Hancock et al. 2015
* <i>Fissurina marginata</i> / <i>Rosalina bradyi</i>	0.57	0.19	Collen & Newell, 1999
* <i>Floresina amphiphaga</i> / <i>Amphistegina gibbosa</i>	0.37	1.80	Hallock & Talge, 1994
* <i>Hyrrokkin carnivora</i> / <i>Acesta angolensis</i>	6.00	130.00	Cedhagen, 1994
* <i>Hyrrokkin sarcophaga</i> / <i>Acesta excavata</i>	7.00	130.0	Cedhagen, 1994
* <i>Hyrrokkin sarcophaga</i> /juvenile <i>Acesta excavata</i>	2.80	30.00	Beuck et al. 2008
* <i>Hyrrokkin sarcophaga</i> / <i>Delectopecten vitreus</i>	0.50	2.00	Cedhagen, 1994
<i>Vasiglobulina alabamensis</i> / <i>Pecten</i> fragment	0.14	0.50	Poag, 1969 (from Plate 2, Fig. 6, and host from pecten fragment)
<u>Endoparasites</u>			

<i>Cymbaloporella tabellaeformis</i> /largest gastropod	0.90	30.00	Brady, 1884; host: Smyth, 1988
<i>Hospitella fulva</i> / <i>Globogerina</i>	0.15	0.16	Gooday et al. 2013
<i>Incola inculta</i> / <i>Neogloboquadrina pachyderma</i>	0.15	0.17	Gooday et al. 2013
* <i>Metarotaliella tuvaluensis</i> / <i>Quinqueloculina oblonga</i>	0.14	0.47	Collen, 1998
* <i>Planorbulinopsis parasitica</i> / <i>Alveolinella quooii</i>	0.14	22.00	Banner, 1971; host: ¹ J.-P. Debenay, 2014
<i>Ramulina globulifera</i> / <i>Carpenteria raphidodendron</i>	0.25	2.00	Duncan, 1880; host: estimated from <i>C. balaniformis</i> , Loeblich & Tappen, 1988, Plate 653, Fig. 9
<i>Ramulina parasitica</i> / <i>Orbitolites</i>	0.70	5.00	Carter, 1889; host: Nielsen, 2002
<i>Rotaliella elatiana</i> / <i>Ulva</i>	0.12	10.00	Pawlowski & Lee, 1992
* <i>Talpinella cunicularia</i> / <i>Orbitoides</i>	1.50	5.00	Baumfalk et al. 1982; host: Nielsen, 2002

References cited in text except for:

¹Debenay, J.-P., 2014, A guide to 1,000 foraminifera from southwestern Pacific, New Caledonia. Institut de Recherche pour le Développement Editions: Publications Scientifiques du Muséum, Museum National d'Histoire Naturelle, Paris, 384 p.