MODERN FORAMINIFERA ATTACHED TO HEXACTINELLID SPONGE MESHWORK ON THE WEST CANADIAN SHELF: COMPARISON WITH JURASSIC COUNTERPARTS FROM EUROPE

Jean-Pierre Guilbault, Manfred Krautter, Kim W. Conway, and J. Vaughn Barrie

ABSTRACT

A foraminiferal fauna from siliceous sponge remains, collected in modern sponge bioherms on the continental shelf off British Columbia, Canada, are compared with assemblages reported from Late Jurassic sponge reefs in central and southern Europe. Forty arenaceous and 53 calcareous taxa were found either loose in, attached to, trapped within or engulfing parts of the meshwork. Specimens found loose belong to the same species as present in the surrounding mud or nearby on the shelf. The most common attached, trapped or engulfing genera are *Crithionina*, *Gaudryina*, *Karreriella*, *Placopsilina*, cf. *Tritaxis*, *Trochammina*, *Islandiella*, *Lobatula* and *Ramulina*. Two new taxa are described and illustrated: *Placopsilina spongiphila* n. sp. and *Ramulina siphonifera* n. sp. The main genera attached or closely associated with Jurassic reefal sponges are *Vinelloidea*, *Thurammina*, *Tolypammina*, *Tritaxis*, *Subbdelloidina* and *Bullopora*. Comparison of Recent and Jurassic sponge reef foraminiferal assemblages indicate that there are no taxa in common at the species level and few at the genus level. However, foraminifera from both the Recent and the Jurassic seem to have interacted with the sponge meshwork in a way that taxa are attached to, trapped in, laced-in and to a certain extent engulf the meshwork. Many ecological niches seem to have remained essentially unchanged since the Jurassic in the dead sponge meshwork environment with new taxa substituting themselves into niche spaces to replace taxa that went extinct.

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INTRODUCTION

Hexactinellid sponges appeared with the Order Lyssacinosida in the Late Proterozoic. Although the Order Hexactinosida appeared in the Late Devonian, their representatives did not begin to form reefs until the Late Triassic. The maximum extent of reef distribution was in the Late Jurassic, when they spread without discontinuity over hundreds of kilometers and discontinuously for 7000 km on the North side of the Tethys and the early North Atlantic. This reef type declined rapidly during the Cretaceous and was thought to have completely vanished during the Tertiary, at least until Conway et al. (1991) reported siliceous sponge bioherms living and growing on the continental shelf off western Canada, at depths of 150-250 m in Queen Charlotte Sound and Hecate Strait (Figure 1). Because of the potential for interpreting the widespread but little understood Late Jurassic sponge reefs and of the need for protecting this heretofore unique biotope, the University of Stuttgart, Germany, and the Geological Survey of Canada have undertaken a joint study of these modern sponge reefs. Continued reconnaissance of the western Canadian seafloor has revealed the existence of additional sponge reefs in the Strait of Georgia, between Vancouver Island and the city of Vancouver (Conway et al. 2004).

The investigation techniques included various methods of echo-sounding (sidescan sonar, Huntec Deeptow Seismic, and swath multibeam bathymetry), close-up observation with remote controlled vehicles and manned mini-submersibles, and seafloor sampling both by bottom grabs and direct sampling using submersibles. About 200 foraminiferal species have been identified from the sponge reef complexes. This includes species found attached or trapped in dead sponge fragments lying in or on the sediment. The foraminifera from the mud (that is, not attached to any sponge fragment) are abundant and representative of the modern Canadian west coast. These taxa will be discussed in a subsequent publication. This paper reports on the foraminifera found attached to sponge fragments recovered by various sampling techniques, both for their affinity and for their mode of occurrence. Late Jurassic sponge reefs are primarily constituted of sponges cemented together by microbially induced carbonates (automicrites) and were colonized by various organisms, including foraminifera. Modern sponge fragments were analyzed with the aim of comparing their foraminiferal content with that of the Jurassic sponge fragments, with the understanding that automicrites are not a reef-cementing agent for the modern reefs.

SETTING

There are four reef complexes spread over 1000 km^2 of shelf from Queen Charlotte Sound to Hecate Strait (map, Figure 1). The physiography and oceanography of this region are described in Thomson (1981) and in Whitney et al. (2005). This part of the western Canadian continental shelf consists of banks that are separated by seaward trending troughs of glacial origin. The shallowest and least dissected part is northern Hecate Strait, mostly at less than 100 m. Elsewhere, the main troughs (Moresby, Mitchell's and Goose Island troughs) commonly extend to depths greater than 200 m, at times to 300 m, and their deep ends open on the edge of the shelf. The banks may be at any depth less than 150 m, locally less than 50 m.

The sponge reefs are all located in the troughs, at depths of between 150 and 250 m. They consist of bioherms of up to 21 m high with steep flanks, and of biostromes of 2-10 m thickness that may stretch for kilometers in all directions (Figures 2-3). Individual sponges are commonly more than 1 m high. The sponge population is composed of only eight species of Hexactinellida (three of Hexactinosida, five of Lyssacinosida) and eight species of Demosponges (see Conway et al. 2005, and Lehnert et al., in press, for a list of species). Taxonomic work on the demosponge fauna is ongoing so this list must be considered incomplete.

During late glacial times, drifting icebergs ploughed the glacial and glaciomarine deposits covering the continental shelf, thus bringing to the surface coarse clastic material such as boulders and cobbles from the underlying glacial till. After winnowing, these exposed hard surfaces served as anchor points for the first sponges to settle (Conway et al. 1991). Other sponges developed on the top of these first sponges and then spread laterally. In Hecate Strait, the relationship between iceberg furrows and reef distribution is still evident (Figure 3). The earliest sponge reefs probably began to grow around 9000 years BP based on an extrapolated radiocarbon date of 5700±60 years BP (TO-1338) obtained from the lower middle part of a bioherm sampled by a piston core in Moresby Trough (Conway et al. 1991).

In contrast to the situation in the Jurassic where sponge reef organisms were held together to a great extent by microbially-induced precipitation of carbonate, modern sponges are held in place by a dense envelope of tendrils, which cover the dead sponge substrate and are attached to the reefal buildup by deposits of silica secreted by the

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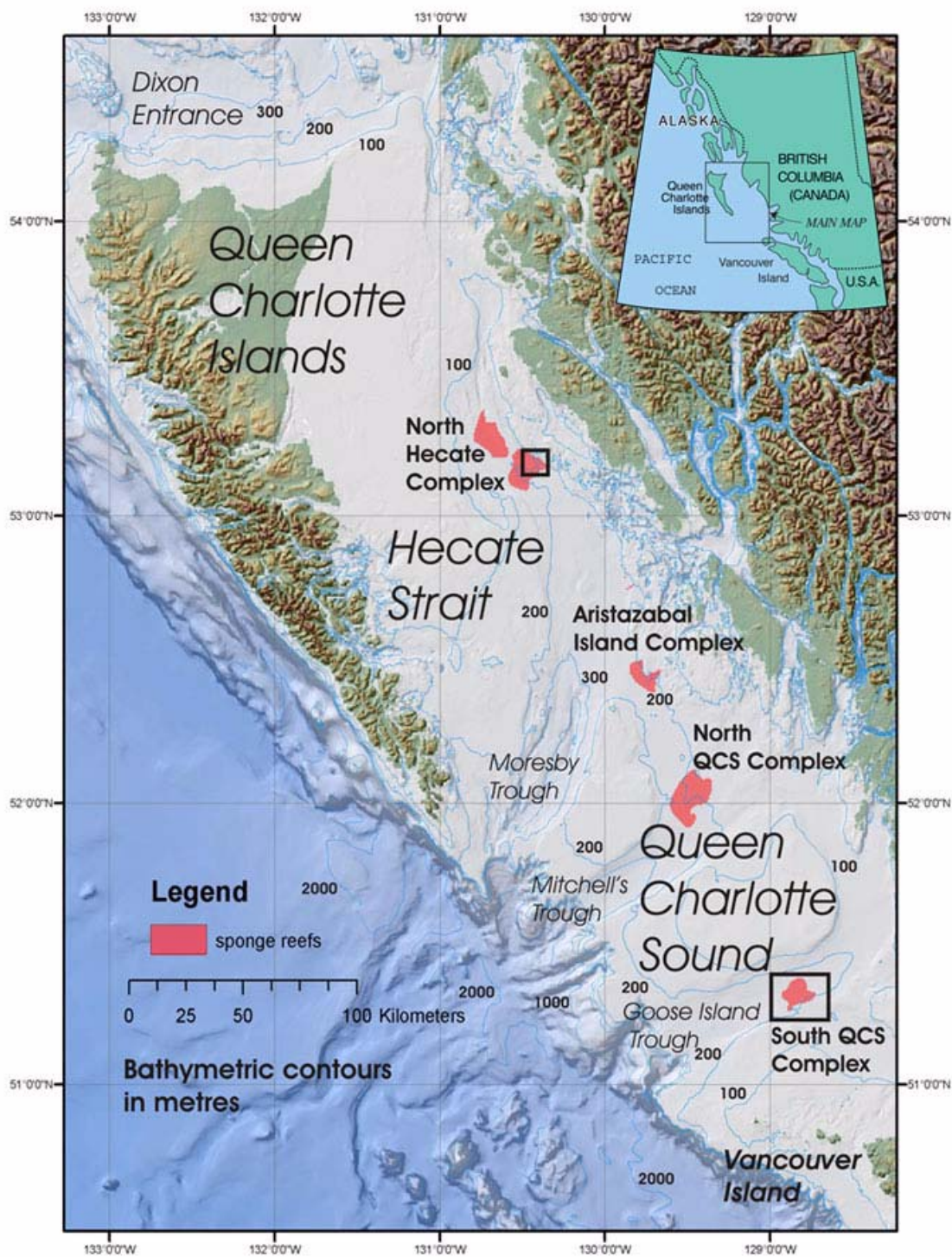
Figure 1. Map of Hecate Strait and Queen Charlotte Sound showing sponge reef complexes. Boxes indicate areas covered by figures 2 and 3. QCS = Queen Charlotte Sound.

young sponge (Krautter et al. 2001; Krautter et al. 2006).

The sponges act as baffles, trapping sediments in suspension, which quickly fill up any spaces between individual sponges, and thus stim-ulate the growth of the bioherm. In contrast, the areas immediately surrounding the bioherms have no sedimentation occurring as the velocity of the currents is too high. The support provided by the trapped sediment prevents the sponge skeleton
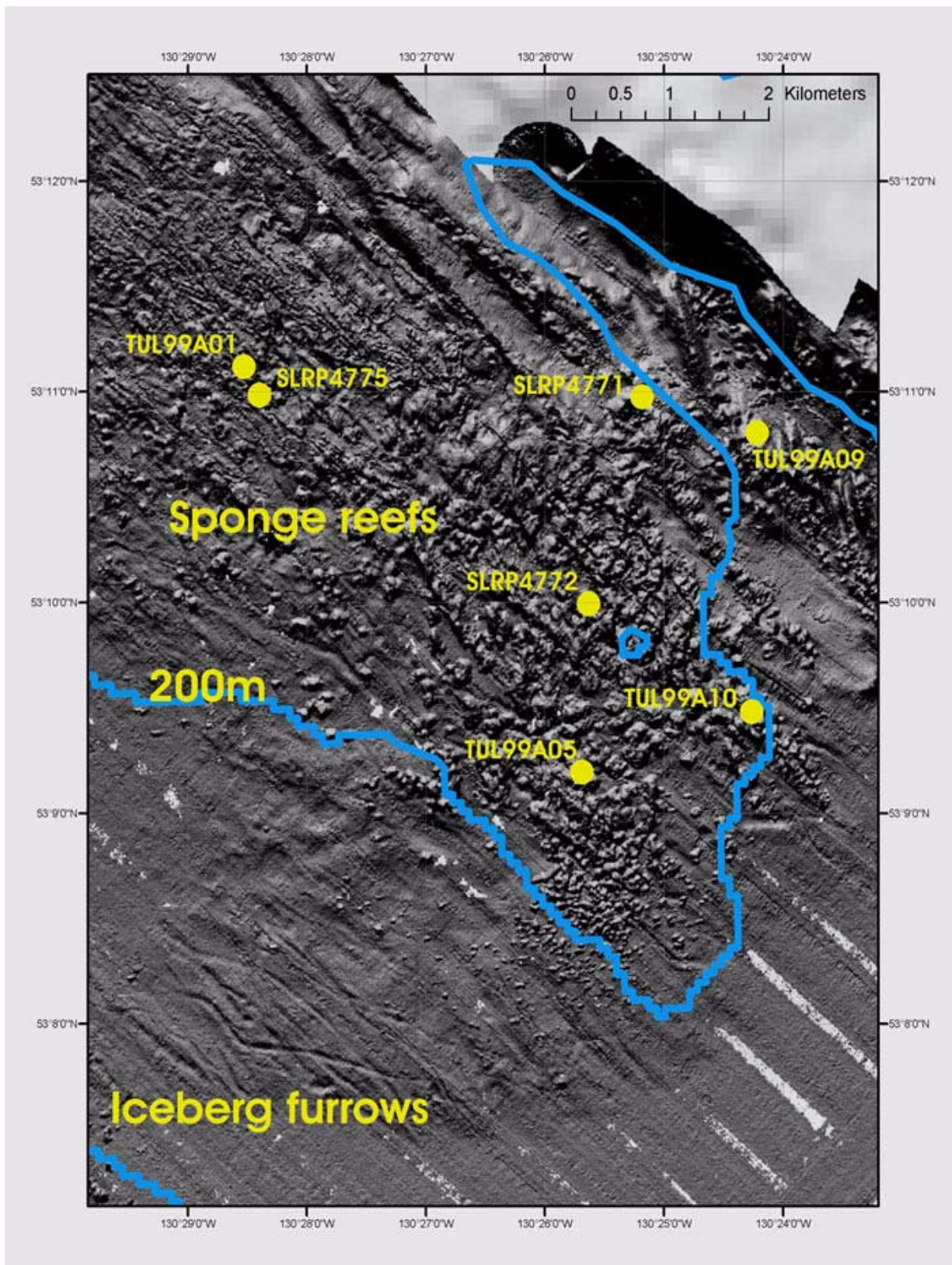
Figure 2. Multibeam bathymetric image of southern part of Hecate Strait reef complex showing sample locations. The blue line is the 200 m isobath (N of the blue line is >200 m) and the mottled area indicates sponge reef mounds. The picture shows how sponge mounds are related to iceberg furrows.
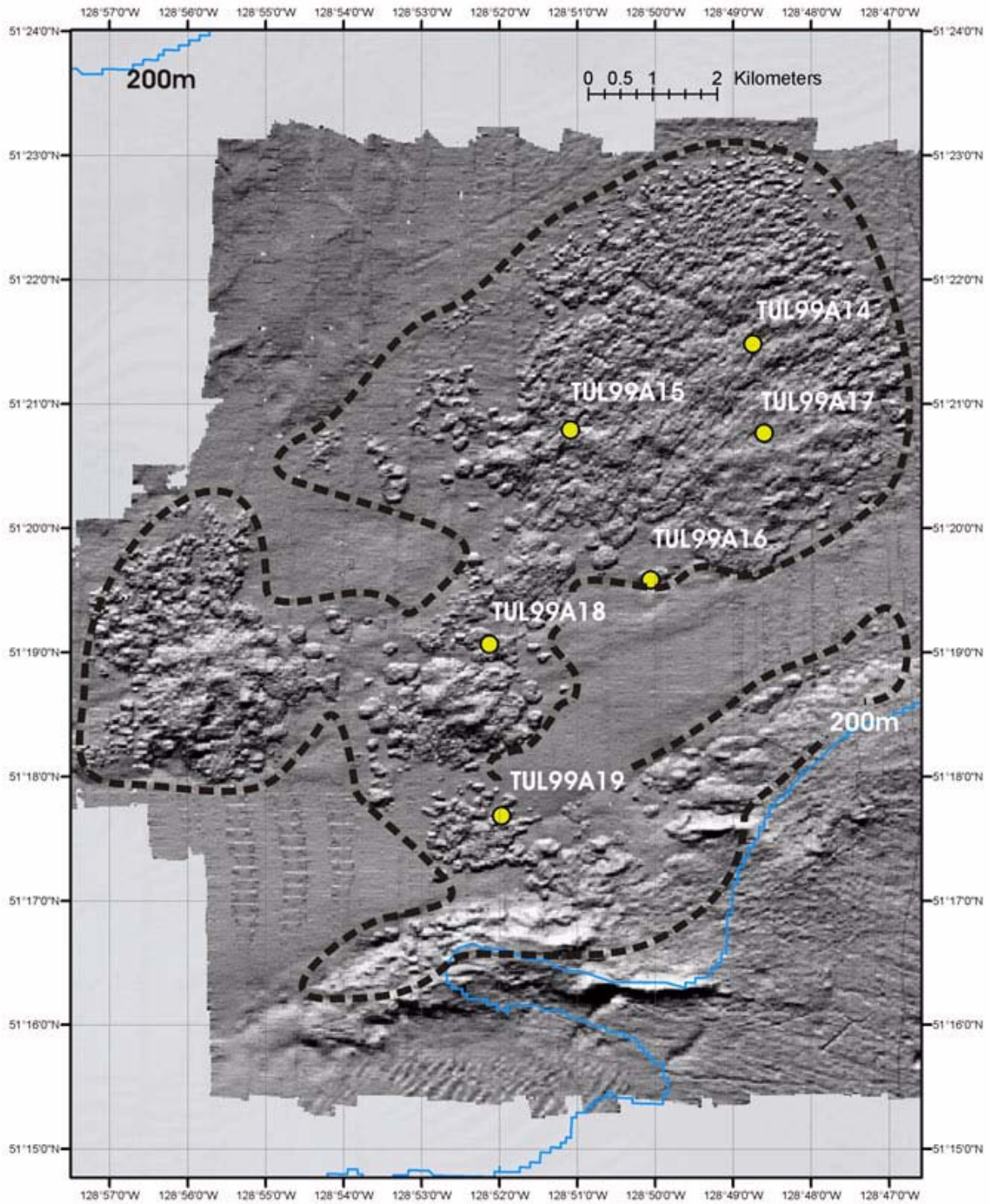
Figure 3. Multibeam image of the Southern Queen Charlotte Strait sponge reef complex showing sample locations. The blue line is the 200 m isobath. The black stippled lines delineate the reef area. The reefs are in the >200 m depth area.

framework from collapsing under its own increasing weight. No trace of induration or cementation of the sediment has been observed at any level in the modern reefs.

PREVIOUS WORK ON FORAMINIFERA

Modern Foraminifera from the West Coast of Canada

Cushman (1925) reported on a few samples collected near the Queen Charlotte Islands. This is the earliest report on modern foraminifera from this region. The work of Cockbain (1963) bears on the Strait of Georgia (between Vancouver Island and the mainland) where oceanographic conditions are restricted, not open marine. Saidova's (1975) extensive study on the benthic foraminifera of the Pacific Ocean includes many samples from off the Canadian coast. The same author (Saidova 2000) later reported on benthic foraminiferal communities off western North America. Studies by Bergen and O'Neil (1979) and Echols and Armentrout (1980) are more localized and situated off the Alaska Panhandle; despite the distance to our sampling sites, the assemblages are very similar to those we see in scattered grab samples from Queen Charlotte Sound and those reported in the Holocene part of piston cores from the same region (Patterson 1993; Patterson et al. 1995; Guilbault et al. 1997).

Jurassic Sponge Reef Foraminifera

Quantitative studies of foraminifera from Jurassic sponge reefs are difficult because they often cannot be extracted from the sediment and fossil matrix. Even though forms such as *Vinelloidea*, *Bullopora*, *Placopsilina, Tolypammina* and *Thurammina* have been widely observed in association with the reef sponges in central and southern Europe, only a few authors have made a quantitative estimate of the species present by etching silicified foraminifera out of the limestone (Haeusler 1890; Feifel 1930; Frentzen 1944; Seibold and Seibold 1960a and b; Oesterle 1968; Wagenplast 1972; Schmalzriedt 1991; Munk 1994). Some typical calcareous taxa of these sponge reef dwellers (*Vinelloidea*, *Bullopora*) probably did not silicify since they are never reported in the etched fraction; they are known to be associated with sponges only from thin sections and from unprocessed rock samples. Other important studies are by Gaillard (1983) and Schmid (1996). Gaillard (1983) made a synthetic study of all aspects of life in and around the Upper Jurassic sponge reefs of the French Jura, while Schmid (1996) carried out an in-depth thin-section study of the encrusting organisms found in and on Upper Jurassic reefs in central and southern Europe, including foraminifera.

METHODS

Three types of bottom samplers were used in this study: slurp gun, Shipek and IKU grab sampler. The slurp gun is a vacuum cleaner-like device that sucks in the uppermost layer (ca. 1 mm) of the seafloor and thus samples only what is present at the surface or very close to it. The Shipek grab sampler, a spring loaded "clam shell" type sampler, obtains samples of surficial seafloor sediments. The samples collected cover an area 20 cm x 20 cm to a maximum depth of about 10 cm. The IKU grab sampler is a large volume (0.5 cubic metre) grab sampler developed by IKU (Institutt for Kontinentalsokkelundersøkelse - Norway) specifically for sampling continental shelf seabed sediments. The sampler penetrates to a depth of 50 cm into the substrate as the sample is obtained and retains the stratigraphic relationships of the surficial materials sampled. The grab sampler operates much like a construction excavator, employing large and widespread spring-loaded jaws that close as the sampler is retrieved from seafloor. The closing force of the jaws is generated through a system of pulleys attached to the retrieval cable. For pictures of the Shipek grab sampler, see: http://www.porifera.org/a/cipixgrab.html; for the IKU grab sampler, see: http://www.porifera.org/a/cipix-iku.html.

All samples other than piston core samples were stained in Rose Bengal and preserved in a mixture of water and methanol. All samples were sieved with a 63 µm sieve, and in most cases an additional 1 mm sieve was used to retain coarser material. A separate count was made of both residue sizes after residues had been split into countable aliquots. Wet samples were split with a wet sample splitter (Scott and Hermelin 1993), and dry samples were split with an ordinary desk sample splitter. Larger sponge fragments found in the 1 mm sieve were set aside, and a separate count was made of the specimens attached or clinging to them. This constitutes the "sponge fraction" referred to herein. Smaller fragments were left in the >1 mm fraction and except for those foraminifera conveniently positioned at the outer surface of sponge fragments, most specimens had to be extracted manually. This procedure was achieved by holding a fragment with the fingers (when large enough) or a needle and by breaking away the individual sponge lattice silica rods surrounding a foraminiferal specimen until it could be removed with a wet brush. Because this process was time

Table 1. Sampling stations. Piston cores were collected with 6 m barrel assembly using a 1000 kg head weight.

Station	Area	Latitude	Longitude	Water Depth (m)	Sampling Device
TUL99A01	Hecate Strait	53° 11.121'	130° 28.528'	180	IKU grab
TUL99A05	Hecate Strait	53° 09.194'	130° 25.689'	193	IKU grab
TUL99A06	Aristazabal Island	52° 25.978'	129° 41.703'	215	IKU grab
TUL99A07	Aristazabal Island	52° 26.889'	129° 40.941'	204	IKU grab
TUL99A09	Hecate Strait	53° 10.807'	130° 24.218'	194	Piston core + Gravity core
TUL99A10	Hecate Strait	53° 09.481'	130° 24.264'	193	Piston core + Gravity core
SLRP4771	Hecate Strait	53° 10.977'	130° 25.204'	182	Slurp gun
SLRP4772	Hecate Strait	53° 09.939'	130° 25.631'	172	Slurp gun
SLRP4775	Hecate Strait	53° 10.985'	130° 28.398'	169	Slurp gun
TUL99A14	Goose Island Trough	51° 21.482'	128° 48.75'	221	Shipek grab
TUL99A15	Goose Island Trough	51° 20.792'	128° 51.085'	229	Shipek grab
TUL99A16	Goose Island Trough	51° 19.586'	128° 50.058'	229	Shipek grab
TUL99A17	Goose Island Trough	51° 20.766'	128° 48.603'	218	Shipek grab
TUL99A18	Goose Island Trough	51° 19.069'	128° 52.128'	230	Shipek grab
TUL99A19	Goose Island Trough	51° 17.689'	128° 51.973'	229	Shipek grab
TUL02A20	Strait of Georgia	49° 09.32'	123° 23.36'	185.4	Piston core + Gravity core

consuming, the exploration of the sponge fragments was not comprehensive. The examination of the surface of large fragments was often more complete than that of the deep interior, and the counts are therefore not perfectly representative. As this paper is primarily dedicated to the non-quantitative aspects of the foraminifera found in the sponge ecosystems, an additional qualitative examination of the >1 mm fraction as well as of the sponge fractions, was carried out to find specimens attached to sponge fragments that would provide valuable information on sponge-foraminifer relationships.

MATERIAL

The material presented here is modern. The Jurassic part of the discussion is based mostly on published literature. We illustrate some specimens from our large collection of thin sections from Jurassic sponge reefs in Europe. However, only silicified material extracted by etching can provide the three-dimensional specimens needed for direct comparison with the Recent. To accomplish this goal, we have re-illustrated some of the material of Schmalzriedt (1991), which was loaned to us by the University of Tübingen.

Modern samples were obtained from the North Hecate Strait, the Aristazabal Island and the South Queen Charlotte Sound (Goose Island Trough) reef complexes (Tables 1 and 2). All sam-ples were collected inside the reefs. For the Hecate Strait complex (Figure 2), two IKU grab samples were collected. In each of these, one subcore, 9 cm in length, was split into three segments at 0-3, 3-6 and 6-9 cm depth (Table 2). In addition, sponge fragments were collected from the surface of one of the IKU grab samples (TUL99A01 "forams" sample in Table 2). Two piston cores, with associated triggerweight cores, were also obtained from the Hecate Strait complex. Both piston cores cross the mixture of sponges and trapped mud that constitute the sponge reef and reach into the underlying glaciomarine sediment. Still in the Hecate Strait reef complex, three slurp gun samples were collected by a manned mini-submersible.

In the Aristazabal Island reef, two IKU grab samples were collected, each with one 9cm subcore (no multibeam imagery is available for this location). Dead sponge fragments from the surface of one of the IKU grabs have also been investigated (TUL99A07 "forams" sample in Table 2). Six Shipek grab samples were obtained from the South Queen Charlotte Sound complex (Figure 3) while in the Strait of Georgia, one piston core and its associated triggerweight core were collected from the seafloor. The Strait of Georgia (not on Figure 1) is situated between Vancouver Island and the Canadian mainland; the core was taken at the latitude of the city of Vancouver.

Table 2. Summary of samples (continued next page)..

Sample number	Location	63-1000 µm	>1 mm	sponge fragments
IKU scoops:				
loose sponge frags.:				
TUL99A01 "forams"	Hecate Strait	OK (>63 µm)		pres/abs
TUL99A07 "forams"	Aristazabal I.	OK (>63 µm)		pres/abs
subcores:				
TUL99A01	Hecate Strait			
(0-3 cm)		OK	barren	barren
(3-6 cm)		OK	OK	
(6-9 cm)		OK	barren	small number
TUL99A05	Hecate Strait			
(0-3 cm)		OK	small number	
(3-6 cm)		OK	barren	
(6-9 cm)		OK	barren	small number
TUL99A06	Aristazabal I.			
(0-3 cm)		OK	OK	small number
(3-6 cm)		OK	barren	small number
(6-9 cm)		OK	small number	
TUL99A07	Aristazabal I.			
(0-3 cm)		OK	small number	barren
(3-6 cm)		OK	small number	barren
(6-9 cm)		OK	barren	small number
Shipek grabs:				
TUL99A014	Goose I. Trough	OK	OK	OK
TUL99A015	Goose I. Trough	OK	OK	OK
TUL99A016	Goose I. Trough	OK	OK	OK
TUL99A017	Goose I. Trough	OK	OK	OK
TUL99A018	Goose I. Trough	OK	OK	OK
TUL99A019	Goose I. Trough	OK	pres/abs	OK
Slurp gun:				
SLRP 4771	Hecate Strait	OK (0.5-1mm)	OK	OK
SLRP4772	Hecate Strait	OK (0.5-1mm)	OK	OK
SLRP4775	Hecate Strait	OK (0.5-1mm)	OK	OK
Gravity core:				
TUL99A010	Hecate Strait			
85-88 cm		OK	small number	OK
TUL02A-20	Strait of Georgia			
0-3 cm		OK	small number	
80-83 cm		OK	barren	

RESULTS

General Results

A total of 40 arenaceous and 53 calcareous taxa were recorded from the sponge fragment fraction. Two of the foraminiferal species are new: *Placopsilina spongiphila* n. sp. and *Ramulina siphonifera* n. sp.; they are described in the Appendix. The specimens of the "sponge fraction" fall into three broad categories: loose, trapped and attached. The loose specimens are those that fall off when sponge fragments are tapped on, or that can be picked out with a wet brush. Such individuals may be there accidentally (postmortem transport, sample processing) or may have crawled in. They are small compared to the meshwork cells.

Table 2 (continued)..

| Sample number | Location | Fraction | | |
		63-1000 µm	>1 mm	sponge fragments
Piston cores:				
TUL99A09	Hecate Strait			
367-370 cm		OK	small number	no meshwork
302-305 cm		OK (>63 µm)		no meshwork
247-250 cm		OK (>63 µm)		no meshwork
167-170 cm		OK		small number
92-95 cm		OK	small number	small number
TUL02A-20	Strait of Georgia			
0-3 cm		OK		barren
50-53 cm		OK		barren
100-103 cm		OK		small number
153-158 cm		OK		barren
200-203 cm		OK		barren
250-253 cm		OK		barren
300-303 cm		OK		barren
350-353 cm		OK		small number
400-403 cm		OK		small number
450-453 cm		OK		barren

Notes. "OK": 50 specimens or more counted. "Small number": less than 50 specimens counted. "Pres/abs": present/absent results only. Merged cells designate fractions that were counted together.

The trapped specimens became caught in the sponge meshwork after crawling into it and then growing to the point of being tightly trapped between sponge spicules, occasionally overflowing their silica prison. Many specimens are slightly loose but still cannot be extracted from the meshwork. The determination of whether a specimen is trapped or loose is subjective, because the distinction is not always sharp, particularly for specimens situated deep inside the meshwork and impossible to reach without breaking through many sponge rods.

Among the specimens that are attached to the silica mesh, some are typically attached forms (*Lobatula*, *Tritaxis*) that happen to have settled on or in the sponge meshwork. These specimens are often contorted due to adaptation to the surface of the meshwork. There are also forms that are normally free-living but that here managed to weakly attach themselves, particularly the trochamminids. Others form a category all by themselves: they visually appear to have been impaled on sponge spicules, actually growing as if the meshwork was not there and engulfing it while deviating only slightly from their normal growth pattern (ex.: Figure 4.4-4.5 and 4.14-4.15). Both attached and impaled individuals may occur within a given species. Many impaled forms are normally free-living forms which at some point in their development engulfed the meshwork and are therefore attached to it by their late chambers (ex.: Figure 5.14-5.15).

Table 3 gives the list of the species encountered while doing the counts; species found separately in non-quantitative searches are not included. The mode of occurrence, loose, attached, etc., is also given. Despite the limited representation of the counts, the table gives the reader an idea of the frequency with which a given species was encountered, and its most common mode of occurrence.

Species not accompanied by a heavy checkmark in Table 3—i.e., which are represented mostly by loose specimens—are numerous but represented by only a few specimens each. The only common forms among these are *Trochammina* sp. 5 and *Chilostomella oolina*. The loose fauna resembles the <1 mm fraction and the trapped mud fauna, being dominated by the same calcareous species: *Epistominella vitrea*, *Bolivina decussata, Eponides pusillus, Seabrookia earlandi, Angulogerina* spp*., Lobatula* spp*., Cassidulina reniforme* and *Astrononion gallowayi.*

Attached, Trapped and Impaled Species

The attached-trapped-impaled assemblage of the sponge fraction contains a greater abundance and diversity of arenaceous foraminifera than the assemblages of the surrounding sediment (i.e.,
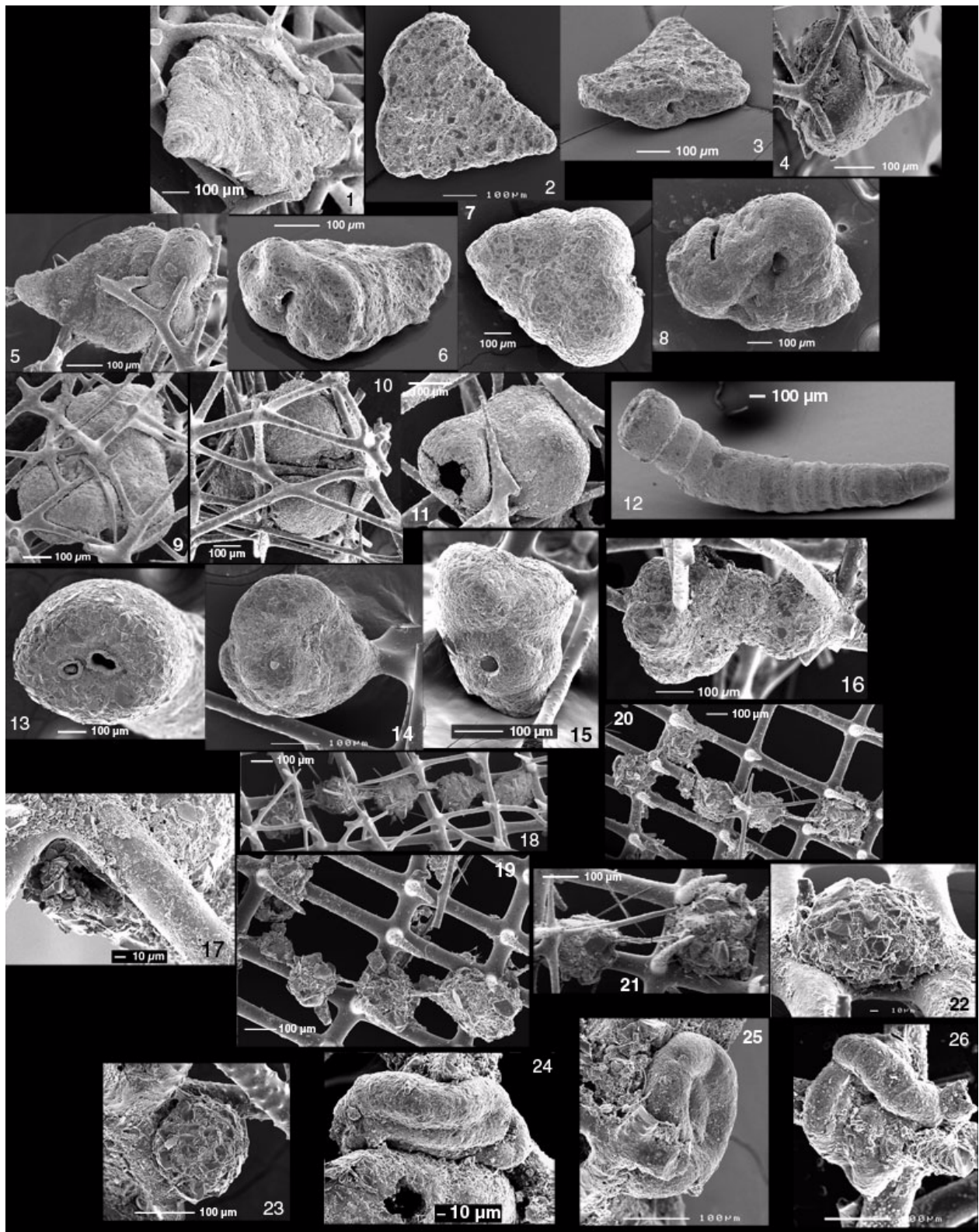
Figure 4 (caption on next page).

Figure 4 (figure on previous page) 4.1-4.26. 1: *Gaudryina accelerata* Natland. Trapped specimen. Shipek grab TUL99A015, sponge fraction. **2-3:** *Gaudryina accelerata*. Loose specimen. 2: side view. 3: oblique view showing aperture. Surface of IKU sample TUL99A07 ("forams"), sponge fraction. **4-5:** *Gaudryina subglabrata* Cushman and McCulloch. Trapped and impaled specimen. 4: oblique view showing apertural end. 5: side view. Shipek grab TUL99A018 sponge. **6:** *Gaudryina subglabrata*. General view of loose specimen. Shipek grab TUL99A018, <1 mm. **7:** *Karreriella bradyi* (Cushman). Side view, loose specimen. Slurp gun sample SLRP4775, <1 mm. **8:** *Karreriella bradyi*. General view of specimen removed from meshwork showing scars due to the presence of spicules. Triggerweight core TUL99A010, 85-88 cm depth, >1 mm. **9-10:** *Karreriella bradyi*. Trapped and impaled specimen. 9: side view (aperture at bottom). 10: oblique view showing aperture just above a spicule. Shipek grab TUL99A016 sponge fraction. **11:** *Karreriella bradyi*. Trapped specimen. Aperture is hidden behind the vertical spicule at the front. Shipek grab TUL99A017 sponge fraction. **12-13:** *Martinottiella pallida* (Cushman). 12: side view of loose specimen. 13: close-up of aperture. Slurp gun sample SLRP4772 <1 mm. **14-15:** *Martinottiella pallida*, impaled on sponge spicules. 14: apertural (or foraminal) view. 15: side view. The two dark circles on the sides of the specimen of Figure 4.15 are the broken ends of spicules crossing the test. Shipek grab TUL99A018, sponge fraction. **16-17:** *Placopsilina* sp., growing attached to sponge meshwork. 16: side view; the aperture is at the right end and faces to the right. 17: close-up of aperture. Triggerweight core TUL02A20, sample 0-3 cm, >1 mm. **18:** *Telammina fragilis* Gooday and Haynes. Five chambers attached to sponge meshwork. Shipek grab TUL99A015, sponge fraction. **19:** *Telammina fragilis*. Four chambers with stolon-like connections between chambers. Triggerweight core TUL99A010, 85-88 cm depth, >1 mm. **20-21:** *Telammina fragilis*. Five chambers on sponge meshwork. 20: general view. 21: close-up of broken stolon between the last 2 chambers of Figure 4.20. Triggerweight core TUL99A010, 85-88 cm depth, >1 mm. **22:** Indeterminate arenaceous ball. Foraminifer? Isolated chamber of *T. fragilis*? Slurp gun sample SLRP4771, sponge fraction. **23:** Indeterminate arenaceous ball. Foraminifer? Slurp gun sample SLRP4771, <1 mm. **24:** ?*Tolypammina* sp. (possibly *Tolypammina schaudinni* Rhumbler) attached to meshwork (behind) and on a trochamminid (below). Shipek grab TUL99A017, sponge fraction. **25:** ?*Tolypammina* sp. (possibly *T. schaudinni*) attached to meshwork. Shipek grab TUL99A015, sponge fraction. **26:** ?*Tolypammina* sp. (possibly *T. schaudinni*) attached on meshwork. Shipek grab TUL99A017, sponge fraction.

trapped by the sponges). The grab samples we examined elsewhere on the British Columbia shelf show a strong dominance of calcareous species.

Among the attached forms (including impaled forms), the most common are *Crithionina* sp., *Placopsilina spongiphila*, *Karreriella bradyi*, cf. *Tritaxis fusca*, *Trochammina* spp., *Lobatula lobatula*, *Lobatula mckannai* and *Ramulina siphonifera*. The most frequent trapped forms are *Gaudryina* spp., *Karreriella bradyi*, *Trochammina* spp., *Chilostomella oolina* and *Islandiella californica*. This also includes *Martinottiella pallida*, *Ammobaculinus recurvus*, *Dorothia* aff. *bradyana* and *Reophax scorpiurus*, which are few in number but proportionately more frequent than in the surrounding mud. *Rhabdammina* is absent while *Ammodiscus arenaceus*, *Psammosphaera* and *Saccammina atlantica* are few; however, these forms are common in the >1 mm fraction elsewhere in the material. Species most commonly impaled are *Crithionina*, *Karreriella bradyi*, *Tritaxis fusca*, *Lobatula* spp. and *Ramulina siphonifera*.

Foraminifera can attach themselves to various sponge species. Many of the illustrated specimens are attached to *Farrea occa* giving the impression they prefer that sponge. Because of its rectangular skeleton and of the fact it tends to break into thin chips, *F. occa* is an ideal substrate on which to find attached foraminiferal tests that can be easily photographed. On other sponges, foraminifera are often situated deep inside the chip where it is difficult to extract them without damage—unless a considerable amount of time is spent doing so.

Some "trapped" specimens may have become so accidentally. This interpretation is implied by the rare presence in the meshwork of trapped sand grains (Figure 6.16-6.17). However, the existence of many specimens that grew to the point of bulging beyond their lattice cage, demonstrates the existence of this type of growth. So does the fact that many trapped, normally vagile calcareous species (*Islandiella californica* for example) commonly have their surface etched, the most clearly trapped being usually the most etched (Figure 7.18-7.22). This suggests that they underwent a distinct mode of postmortem preservation in comparison with well-preserved, loose specimens.

Sponge fragments vary in preservation from clean and pristine, to slightly stained, to heavily encrusted with oxides. The surfaces of exposed biogenic silica (e.g., siliceous sponge skeletons) are quickly coated and enriched in Fe and Al (Dixit and van Capellen 2002; Michalopoulos and Aller 2004). The present sponge material has been analyzed by inductively coupled plasma spectroscopy and X-ray fluorescence and the crusts found to consist of a mixture of oxides, iron oxide being the most abundant. The coating with oxide crusts gives a "dirty" appearance to the skeletons. In general, a clean sponge meshwork holds fewer attached, trapped or impaled foraminifera than a "dirty" sponge. On a clean meshwork, one will commonly
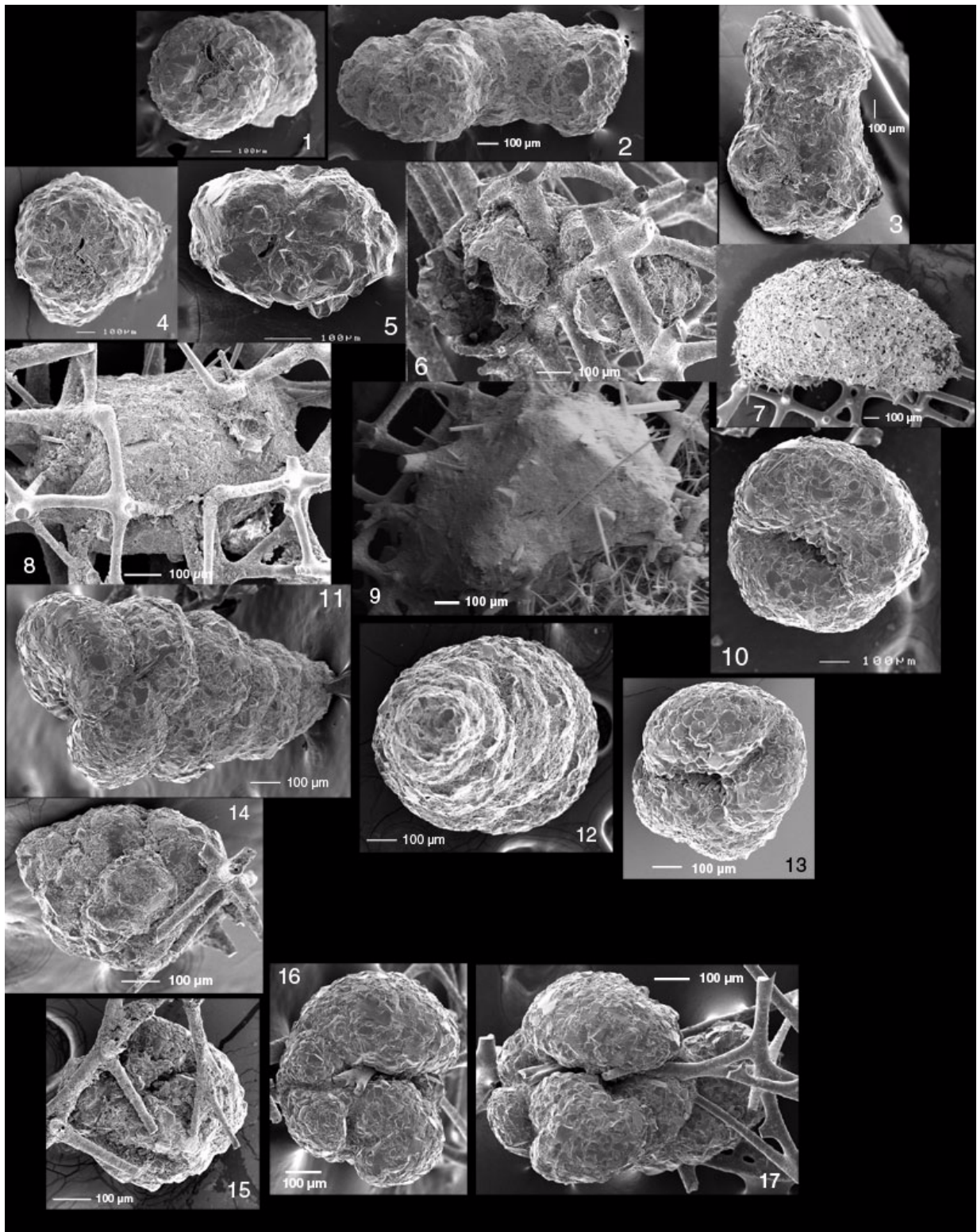
Figure 5 (caption on next page).

Figure 5 (figure on previous page). 5.1-5.17. 1-2: *Ammobaculinus recurvus* Saidova. Specimen with double aperture. 1: apertural view. 2: side view. Slurp gun sample SLRP4775, <1 mm. **3-4:** *Ammobaculinus recurvus*. Specimen with single aperture. 3: side view. 4: apertural view. Shipek grab TUL99A017, >1 mm. **5:** *Ammobaculinus recurvus*. Small specimen that has not reached the uncoiling stage. Note aperture in the form of a crescent pointing outwards, in conformity with Saidova's type description. Slurp gun sample SLRP4775, sponge fraction. **6:** Probable *Ammobaculinus recurvus*, trapped and impaled in the meshwork. Aperture not obvious, probably along the sponge spicule. Slurp gun sample SLRP4775, sponge fraction. **7:** *Crithionina* sp., attached on meshwork. Slurp gun sample SLRP4772, >1 mm. **8:** *Crithionina* sp., attached and impaled in meshwork. Slurp gun sample SLRP4775, >1 mm. **9:** *Crithionina* sp., attached and impaled on meshwork. Small spicules at lower right are rossellid sponges, probably posterior to the death of the supporting sponge. Shipek grab TUL99A015, sponge fraction. **10-12:** *Dorothia* cf. *bradyana* Cushman in Todd and Low (1967). Loose and undeformed specimen. 10: apertural view. 11: side view. 12: basal view. Slurp gun sample SLRP4775, <1 mm. **13:** *Dorothia* cf. *bradyana*. Apertural view; the straight feature pointing at ca. 2 o'clock is not a cameral suture but a scar left by the presence of the sponge meshwork to which the specimen was attached. Slurp gun sample SLRP4771 <1 mm. **14-15:** *Dorothia* cf. *bradyana*. Oblique view of specimen attached to the meshwork by the apertural end. 14: side view. 15: apertural view, partly obscured by dirt. Slurp gun sample SLRP4771, sponge fraction. **16-17:** *Dorothia* cf. *bradyana*. Specimen trapped and impaled within the meshwork, extreme entanglement. 16: apertural face, with trace of broken-off spicules. 17: general view. Slurp gun sample SLRP4771, <1 mm.

find calcareous forms, mostly *Lobatula* spp. and *Ramulina siphonifera*. On dirty meshwork, arenaceous forms are more common, the dominant taxon being *Placopsilina spongiphila*.

Stained Foraminifera

In the sponge meshwork fractions, only a very small number of specimens were stained with Rose Bengal, and they were found in only five of the samples. One was a Shipek sample, one was a sponge fragment lying at the surface of an IKU scoop and the rest were the three slurp gun samples. The stained sponge fragment foraminifera (and stained foraminifera from other fraction too) were thus collected preferentially at or near the very surface of the sediment, which is normal in an area of low sedimentation rate. A total of 18 taxa were found stained in the sponge fractions (Table 4). They tend to belong to the more commonly occurring taxa in the fraction. The only form that is present in larger proportions is *Crithionina*; its stained/unstained ratio is also quite high, probably because it disintegrates rapidly after its death.

Close Examination of Pertinent Species

Modern foraminiferal taxa are examined here, either because of their abundance, because their relationship to the sponge meshwork is unusual, or because similar forms are known from Jurassic sponge reefs. Trapped specimens are often deformed and difficult to photograph. Because of this difficulty, for many species, representative pictures of specimens picked outside of the meshwork (<1 mm and >1 mm fractions) have been added so the reader may have an idea of their undeformed appearance.

***Ammobaculinus* cf. *recurvus* (Figure 5.1-5.6).** Until now, this taxon has been reported only by Saidova (1975) at three stations, two off southern Alaska and one off the Strait of Juan de Fuca. The only illustration available to our knowledge is the original of Saidova (1975), which does not show the aperture. We sent pictures of our material to Khadija Saidova (personal commun. 2003) who confirmed the generic identification; however, she could not confirm the species on the basis of only a few pictures. Our specimens range gradually from morphologies close to the type illustration of *A. recurvus* to extreme variants with multiple apertures, which Saidova (personal commun. 2003) does not recall having seen. Because of the intergradation between all our specimens, we believe they all belong to a single species. *Ammobaculinus* cf. *recurvus* is a rather large arenaceous form. It is rarely found inside sponges, where it is mostly trapped (Figure 5.6); it is more common outside, particularly in slurp gun samples.

***Crithionina* sp. (Figure 5.7-5.9).** *Crithionina* occurs either as a ball attached to the exterior of a sponge fragment (Figure 5.7) or to other objects, such as sand grains or tubes of *Rhabdammina abyssorum*. Free specimens are observed as well. It can also be found impaled inside the sponge framework (Figure 5.8-5.9). *Crithionina granum* from Sweden is known to be a predator attacking prey larger than itself (Cedhagen 1992, and personal commun., 2003) while *Crithionina delacai* from Antarctica seems to prefer a diet of diatoms and possibly bacteria and detritus (Gooday et al. 1995). It is not clear why a predator would settle on the interior of a sponge fragment. Other foraminifera do not seem affected by its presence though, which suggests that foraminifera are not part of its diet. However, most of the *Crithionina* we observed were attached on the outside of sponge fragments, to *Rhabdammina* tubes or to sand grains which is a

Table 3. Species observed in the dead sponge fragments. Taxa are listed in alphabetic order, the arenaceous coming first, then the calcareous. Taxa that are neither attached, nor trapped, nor impaled (ex.: *Adercotryma glomerata*) were found only as "loose". Taxa that are mostly trapped or attached are indicated by a heavy checkmark to increase visibility.

species	may be attached	mostly attached	may be trapped	mostly trapped	may be impaled	counted
Ammobaculinus cf. *recurvus* Saidova (1975)	✓		✓	✓		9
Adercotryma glomerata (Brady 1878)						1
Ammodiscus arenaceus (Williamson 1858)	✓		✓			2
Cribrostomoides jeffreysi (Williamson 1858)	✓		✓		✓	16
Cribrostomoides scitulus (Brady 1881a)			✓	✓		3
Crithionina sp.	✓	✓			✓	104
Dorothia aff. *bradyana* Cushman *in* Todd and Low (1967)	✓	✓	✓		✓	3
Gaudryina arenaria Galloway and Wissler (1927)			✓	✓		3
Gaudryina subglabrata Cushman and McCulloch (1939)			✓	✓		30
Gaudryina accelerata Natland (1938)	✓		✓	✓		10
Haplophragmoides canariensis (d'Orbigny 1939a)						2
Haplophragmoides ringens (Brady 1879)					✓	2
Haplophragmoides sphaeriloculus Cushman (1910)						3
Haplophragmoides sp.						1
Hemisphaerammina sp.	✓	✓				2
Hyperammina sp.						1
Karreriella bradyi (Cushman 1911)			✓	✓	✓	138
Martinottiella pallida (Cushman 1927)	✓		✓		✓	20
Pelosina sp.	✓					2
Placopsilina spongiphila n. sp.	✓	✓				341
Placopsilina spp.	✓	✓			✓	1
Polystomammina nitida (Brady 1881a)	✓		✓			4
Proteonina difflugiformis (Brady 1879)						2
Psammatodendron arborescens Norman in Brady (1881b)	✓	✓				4
Psammosphaera fusca Schultze (1875)	✓					5
Recurvoides cf. *turbinatus* (Brady 1881a)			✓	✓		1
Reophax cf. *guttifer* Brady (1881)						2
Reophax scorpiurus Montfort (1808)	✓		✓	✓		5
Reophax subfusiformis Earland (1933)	✓	✓	✓		✓	3
Reophax cf. *enormis* Hada (1929)			✓	✓		3
Saccammina atlantica (Cushman 1944)			✓			5
Saccammina sp. 2	✓					5
Spiroplectammina biformis (Parker and Jones 1865)						2
Telammina fragilis Gooday and Haynes (1983)	✓	✓	✓			13
?*Tolypammina* sp.	✓	✓				9
cf. *Tritaxis fusca* Williamson (1858)	✓	✓	✓		✓	<79
Trochammina sp. 2	✓		✓	✓		6
Trochammina sp. 3¶	✓		✓	✓	✓	15
Trochammina sp. 5	✓		✓			36
Indet. attached *Trochammina*-like form		✓				<79
Angulogerina angulosa (Williamson 1858)			✓			11
Angulogerina fluens Todd in Cushman and McCulloch (1948)						3
Astrononion gallowayi Loeblich and Tappan (1953)						4
Bolivina (*Euloxostomum*) *alata* (Seguenza 1862)			✓			5

Table 3 (continued).

species	may be attached	mostly attached	may be trapped	mostly trapped	may be impaled	counted
Bolivina (*Euloxostomum*) *bradyi* Asano (1938)			✓	✓		1
Bolivina argentea Cushman (1926)			✓			5
Bolivina decussata Brady (1881a)						5
Bolivinellina pacifica (Cushman and McCulloch 1942)						7
Buccella frigida (Cushman 1922a)			✓	✓		2
Cassidulina reniforme Nørvang (1945)						7
Chilostomella oolina Schwager (1878)			✓			44
Cibicidoides sp. 1						7
Cyclogyra involvens (Reuss 1850)			✓	✓		1
Dyocibicides biserialis Cushman and Valentine (1930)	✓	✓				1
Elphidium hallandense Brotzen (1943)						1
Epistominella vitrea Parker in Parker, Phleger, and Peirson (1953)						3
Eponides pusillus Parr (1950)						7
Euuvigerina juncea (Cushman and Todd 1941)						3
Euuvigerina aculeata (d'Orbigny 1846)			✓		✓	3
Fissurina marginata (Walker and Boys 1803)						1
Globobulimina auriculata (Bailey 1851)			✓	✓		19
Globocassidulina bradshawi (Uchio 1960)						2
Globocassidulina subglobosa (Brady 1881a)			✓	✓	✓	14
Gordiospira sp. 1			✓	✓		1
Gyroidinoides altiformis Stewart and Stewart (1930)						1
Homalohedra guntheri (Earland 1934)						1
Hyalinonetrion dentaliforme (Bagg 1912)			✓	✓		1
Islandiella californica (Cushman and Hughes 1925)	✓		✓	✓	✓	88
Islandiella limbata (Cushman and Hughes 1925)			✓	✓		16
Islandiella norcrossi (Cushman 1933)						1
Lagena clavata (d'Orbigny 1846)			✓	✓		1
cf. *Lamarckina haliotidea* (Heron-Allen and Earland 1911)						1
Lobatula fletcheri (Galloway and Wissler) + *lobatula* (Walker and Jacobs 1798)	✓	✓	✓		✓	82
Lobatula mckannai (Galloway and Wissler 1927)	✓	✓	✓		✓	159
Lobatula pseudoungeriana (Cushman 1922b)			✓	✓		1
Neoconorbina parkerae (Natland 1950)						1
Nonionella auricula Heron-Allen and Earland (1930)						1
Nonionella digitata Nørvang (1945)			✓	✓		2
Nonionella stella Cushman and Moyer (1930)						1
Nonionellina labradorica (Dawson 1860)						4
Aff. *Oolina caudigera* (Wiesner 1931)			✓	✓	✓	19
Oolina lineata (Williamson 1848)			✓			4
Oolina melo d'Orbigny (1939b)			✓			2
Polymorphina kincaidi Cushman and Todd (1947)						1
Procerolagena gracilis (Williamson)						1
Pseudononion basispinatum (Cushman and Moyer 1930)			✓			3
Pullenia salisburyi Stewart and Stewart (1930)			✓			13
Pyrgo rotalaria Loeblich and Tappan (1953)						1
Ramulina siphonifera n. sp.	✓	✓	✓		✓	312
Rosalina sp. 1			✓			4
Seabrookia earlandi (Wright 1891)						7
Stainforthia feylingi Knudsen and Seidenkrantz (1994)						3

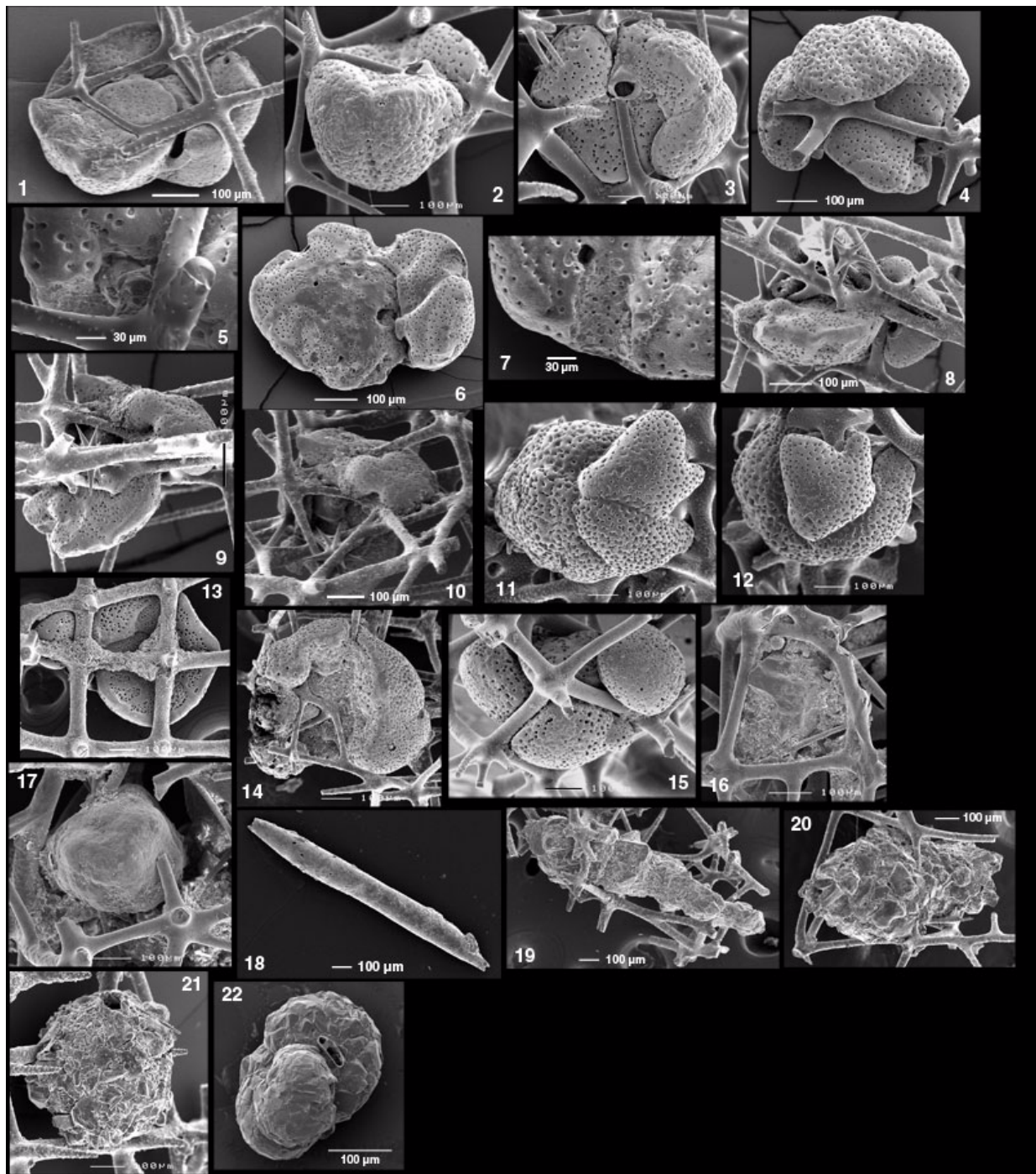Note. Includes a few *Portatrochammina bipolaris* (Brönniman and Whittaker).

Figure 6 (caption on next page).

behaviour more suggestive of a predator looking for the best spot to catch prey. It is possible that we have two species of *Crithionina* in our material, each with its own diet. Analysis of gene sequencing (Pawlowski et al. 2002; Cedhagen, personal commun., 2003) has shown that what is commonly reported as *Crithionina* may include different genotypes that are distinct enough to include not only different species but different genera.

The agglutinated grains in *Crithionina granum* and *C. delacai* are held in place by fine reticulopodia and not by secreted adhesives; they can therefore change shape by moving agglutinated grains around their test (Cedhagen 1992, and personal commun., 2003; Gooday et al. 1995) to adapt

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Figure 6 (figure on previous page). 6.1-6.19. 1: *Lobatula lobatula* (Walker and Jacob). Attached and impaled, growing planispirally; does not tend to wrap itself on the meshwork. Shipek grab TUL99A016, sponge fraction. **2-3:** *Lobatula mckannai* (Galloway and Wissler). Attached and impaled. Slight tendency to wrap itself on the meshwork. 2: side view. 3: spiral side. Shipek grab TUL99A014, sponge fraction. **4-5:** *Lobatula mckannai* (Galloway and Wissler). Attached and impaled, wrapping itself over the meshwork. 4: general view. 5: close-up of spicule "piercing" spiral side wall (at lower right on Figure 6.4). IKU subcore TUL99A06, 6-9 cm, 63-1000 µm. **6-7:** *Lobatula lobatula* (Walker and Jacob). Originally attached, shows notches in test due to presence of spicules. 1: general view. 2: close-up of a notch. Shipek grab 99A014, sponge fraction. **8-10:** *Lobatula lobatula*. Various angles on a specimen that grows impaled on (or through) meshwork with minimal disturbance of its planispiral growth form. Shipek grab 99A016, sponge fraction. **11-12:** *Lobatula mckannai*. Umbilical (11) and side (12) views on a specimen that grows on meshwork. Its attached face wraps itself over the substrate. IKU grab sample TUL99A07, surface subsample (99A07 "forams"), sponge fraction. **13:** *Lobatula lobatula*. Attached to meshwork, but with a flat spiral face. Shipek grab TUL99A015, sponge fraction. **14:** *Lobatula* cf. *lobatula*. Attached and impaled, with a tendency to wrap itself over the meshwork. Shipek grab TUL99A016, sponge fraction. **15:** cf. *Lobatula lobatula*. Attached, trapped and contorted. Grab sample TUL99A015, sponge fraction. **16-17:** Two sand grains trapped in lattice. Grain in 16 is partly covered by mud leftover from incomplete washing. Both grains are on the same sponge fragment. Slurp gun sample SLRP4772, sponge fraction. **18:** *Hyalinonetrion dentaliforme* (Bagg). Somewhat etched and dirty specimen found inserted in a succession of cells in the rectangular meshwork of a *Farrea occa*. Was removed with a wet brush but is considered trapped. Slurp gun sample SLRP4771, sponge fraction. **19:** *Reophax scorpiurus* Montfort, trapped in meshwork. Slurp gun sample SLRP4775, sponge fraction. **20:** *Reophax* sp., trapped and impaled. Grab sample TUL99A019, sponge fraction. **21:** *Saccammina* sp. 2. Attached on meshwork. Grab sample TUL99A016, sponge fraction. **22:** *Recurvoides* cf. *turbinatus* (Brady). Apertural view. Slurp gun sample SLRP4772, <1 mm.

themselves to their prey or to the substrate. A consequence of this is that the test is fragile and ephemeral. If our *Crithionina* is related to these two species, this would explain how it can wrap itself on the meshwork. This may be the case, as the test wall of our specimens disaggregates easily when repeatedly wetted and dried.

***Dorothia* aff. *bradyana* (Figure 5.10-5.17).** This is probably the same as *Dorothia* aff. *bradyana* in Todd and Low (1967). According to these authors, it differs from the type material in that the chambers are lower and more bulging between the incised sutures, and in a more nearly circular cross-section. It is an uncommon dweller of sponge fragments. It is often found loose but with an indentation on the last chamber that gives the impression it is triserial (Figure 5.13). However, we found a few specimens attached by engulfing some of the meshwork in the adult part of their test (Figures 5.14-5.15). The indentation of Figure 5.13 thus appears to be the trace of the sponge meshwork from which the specimen fell off. On the completely entangled specimen of Figures 5.16-5.17 it is possible to see, on the apertural face, the scars left by two broken off spicules. A roughly similar mode of attachment can be seen in *Gaudryina* and *Martinottiella*.

***Gaudryina* spp. (Figure 4.1-4.6).** *Gaudryina* is a common genus in the sponge fragments. Three species are found: *Gaudryina subglabrata*, *Gaudryina arenaria* and *Gaudryina accelerata*. *Gaudryina arenaria* is a minor occurrence and is observed more often outside the sponge fragments. *Gaudryina accelerata* (Figure 4.1-4.3) may be loose or trapped. Some specimens have grown so that their test fits the surrounding sponge spicules. These are tightly trapped and can be considered as attached, although the overall shape of the test is not affected. Specimens grow in a single plane and do not bend around the rods (Figure 4.1). It seems to attach itself in later life, i.e., by its adult chambers. Some specimens have sponge spicules that penetrate them, but are not impaled throughout. *Gaudryina subglabrata* may be loose, trapped or impaled (Figure 4.4-4.6). It is the most common *Gaudryina* species inside sponge fragments. Even if not quite completely trapped, it may have notches due to the presence of the spicules. Its overall test shape may be more or less twisted in order to adapt to the meshwork around it.

***Karreriella bradyi* (Figure 4.7-4.11).** This is one of the most commonly trapped species in the material, and it tends to bulge beyond the bars of its silica trap more often than any other. Outside of the sponge reefs, *K. bradyi* is common in the bank areas where it constitutes, along with *Islandiella californica*, *Islandiella limbata* and some attached forms, the major portion of the very rich, mostly epifaunal assemblages that occurs there. These bank faunas can be found in Queen Charlotte Sound and further north, off southern Alaska (Bergen and O'Neil 1979). *Karreriella bradyi* is a rather large form, often exceeding 1 mm in length, and consequently it tends to become trapped when it grows.
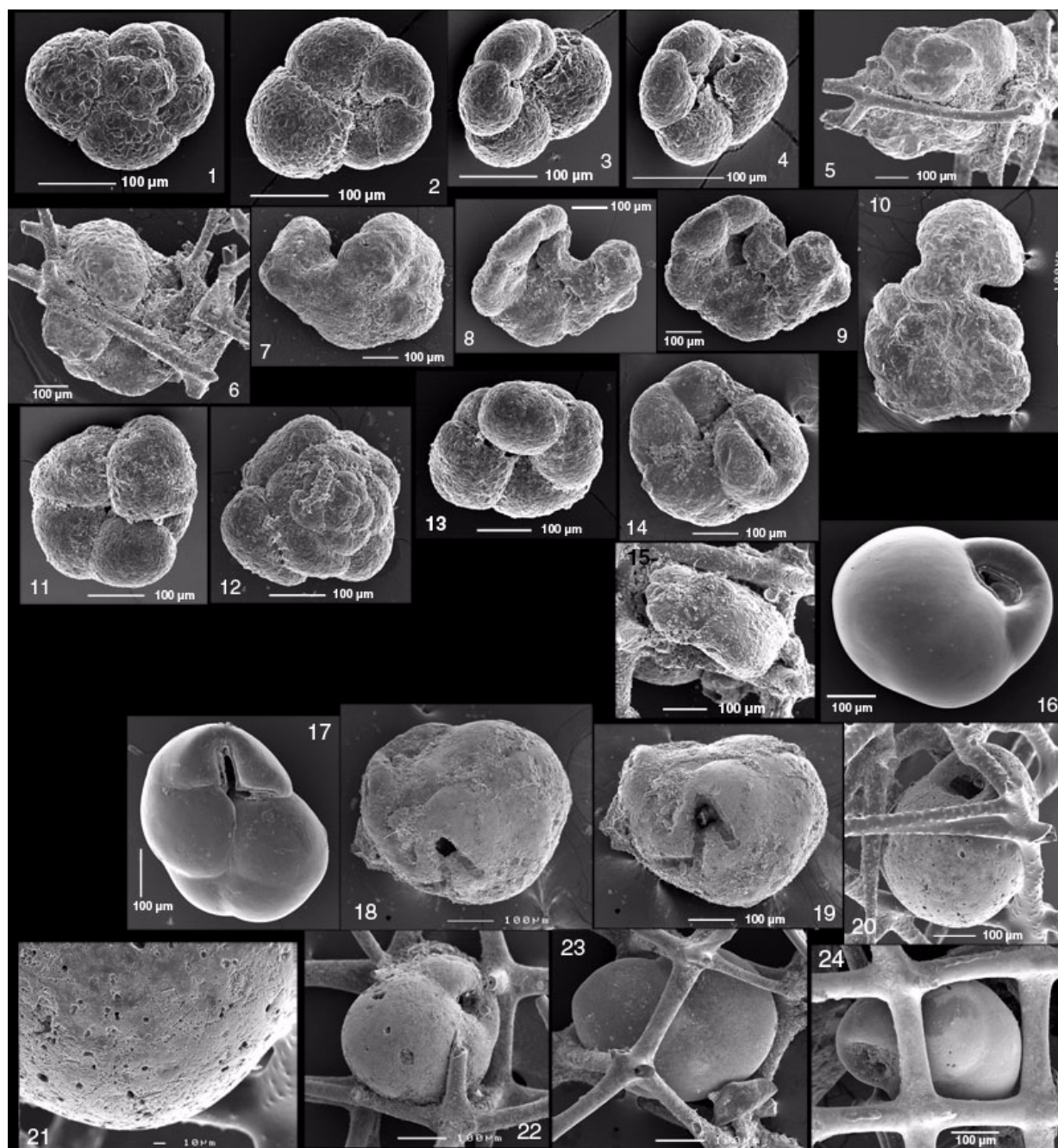
Figure 7 (caption on next page).

***Martinottiella pallida* (Figure 4.12-4.15).** Like the preceding species, *M. pallida* is a fairly large arenaceous form. It is rare in the bank fauna but more common in and around sponges. However, it is much less common in the sponge fauna than *K. bradyi*. It is not usually trapped in the meshwork but rather impaled on it. Large and long specimens (Figure 4.12-4.13) are not found inside sponge fragments. Instead we find short specimens (Figure 4.14-4.15) that attach or impale themselves by the side or by the distal chambers of their test,

implying that they started their life free and attached themselves later. Small specimens like this one have often not reached their uniserial stage and are differentiated from *Dorothia*, etc., by the fact they agglutinate almost only fine, pure white grains (essentially quartz according to electron microprobe analysis).

***Placopsilina spongiphila* (Figures 8 and 9.1-9.12).** This new species (Appendix) is the most frequent taxon associated with sponge fragments. *Placopsilina spongiphila* grows attached to rods of

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Figure 7 (figure on previous page). 7.1-7.19. 1-3: *Trochammina* sp. 3. 1: spiral side. 2: umbilical side. 3: oblique view showing aperture. Slurp gun sample SLRP4772, <1 mm. **4:** *Portatrochammina bipolaris* (Brönniman and Whittaker). Oblique view showing aperture and flaps. Slurp gun sample SLRP4772, <1 mm. **5-6:** Attached trochamminid, growing deformed inside the meshwork. Two views of the same specimen. Slurp gun sample SLRP4771, sponge fraction. **7-9:** *Trochammina* sp. 2. Three views of the same specimen detached by wet brush from the meshwork on which it had grown. Shipek grab TUL99A017, >1 mm. **10:** *Trochammina* sp. 2. Spiral side view of specimen that has grown and trapped itself into the meshwork. Slurp gun sample SLRP4771, sponge fraction. **11-13:** *Trochammina* sp. 5. 11: Umbilical view. 12: Spiral view. 13: Oblique view showing aperture. Shipek grab TUL99A017, sponge fraction. **14:** *Trochammina* sp. 5, umbilical view of attached (impaled) specimen with scar due to meshwork. Shipek grab TUL99A018, sponge fraction. **15:** *Trochammina* sp. in meshwork. It is not clear whether it is attached or trapped or even loose. Shipek grab TUL99A017, sponge meshwork. **16:** *Islandiella californica* (Cushman and Hughes). Small (young) specimen, well-preserved, not from a sponge. Piston core sample TUL99A09, 167-170 cm, <1 mm. **17:** *Globocassidulina subglobosa* (Brady). Aperture partly obstructed by glue. Piston core sample TUL99A09, 167-170 cm, <1 mm. **18-19:** Two views of a deeply etched cassidulinid (*I. californica*?), showing deep scar due to presence of meshwork. Specimen formerly impaled. Triggerweight core sample TUL99A010, 85-88 cm, >1 mm. **20-21:** Deeply etched cassidulinid (*I. californica*?), trapped but probably not impaled. 20: general view. 21: close-up of etch marks. Slurp gun sample SLRP4771, sponge fraction. **22:** Indeterminate (*Islandiella californica*?) etched and trapped juvenile cassidulinid. Some spicules have been broken away to show foraminifer. Shipek grab TUL99A014, sponge fraction. **23-24:** *Islandiella californica*, trapped and well preserved. 23: aboral side. 24: oral side. Slurp gun sample SLRP4775, >1 mm.

the meshwork, most commonly on oxide-covered sponge fragments, implying that the sponge had already decayed and the skeleton had been exposed to seawater for a while before the *Placopsilina* settled. Its diameter being small in comparison to the size of the meshwork's cells, it may grow without ever having to squeeze between silica rods. Its earliest chambers, however, may wind around a spicule.

The genus *Placopsilina* is known to grow on hard surfaces such as hardgrounds or shell surfaces. It has been found in abundance on indurated sediment near hydrothermal vents on the Juan de Fuca Ridge, off British Columbia, by Jonasson and Schröder-Adams (1996) along with other attached arenaceous forms, mostly *Tolypammina*, *Tumidotubus* and *Subreophax*. Resig and Glenn (1997) report *Placopsilina* from phosphatic hardgrounds in the oxygen minimum zone off Peru where its main companions are *Ammodiscellites* and *Tholosina*. They interpret the fact that *Placopsilina* never becomes erect as suggesting that it finds its food on the surface. Gooday and Haynes (1983) have found it attached to empty *Bathysiphon* tubes in the abyssal Atlantic, where the main attached forms were *Crithionina*, ?*Psammosphaera*, *Tumidotubus* and *Telammina* and where dense populations coincide with iron and manganese coatings (Jonasson and Schröder-Adams, 1996, and Resig and Glenn, 1997, also report this phenomenon). There were also abundant attached calcareous microforaminifers, juvenile miliolids and indeterminate small hemispherical forms.

***Placopsilina* spp. (Figures 4.16-4.17 and 9.13-9.15).** Some *Placopsilina* specimens could not be identified as *P. spongiphila*. Only a few were recorded, all in open nomenclature, one of which was attached to a sponge fragment from the Strait of Georgia (Figure 4.16-4.17), another attached to the test of an *Ammobaculinus recurvus* (Figure 9.13-9.15) and the rest, detached from their support.

***Telammina fragilis* (Figure 4.18-4.21).** We found *T. fragilis* on a few sponge fragments only. It is characterized by a very thin and fragile stolon connecting the chambers. Andrew Gooday, co-author of *T. fragilis*, confirmed our identification. This genus would not be recognizable if it was not still attached to its substrate because the stolon would break apart immediately. Therefore, it is possible that some of the small arenaceous balls that we see elsewhere in our material are isolated *T. fragilis* chambers (Figure 4.22-4.23). *Telammina fragilis* is a deep-sea dweller, and this could be its shallowest record ever. The surface of the sediment around the sponges (slurp gun samples in particular) contains abundant *Rhabdammina* and large *Ammodiscus*, often stained. This, along with *T. fragilis*, gives a definitely deep-water, if not deep-sea, appearance to the assemblage as if the conditions, locally, mimicked those of the deep-sea. Gooday and Haynes (1983) discovered *T. fragilis* in the abyssal North Atlantic growing inside the dead tests of *Bathysiphon* in assemblages that show some similarities with our own material (Table 5).

?*Tolypammina* sp. (Figure 4.24-4.26). We found only two sponge fragments holding a total of nine very small specimens of this unchambered and loosely tubular form. We are not sure of the generic determination because we could not observe the typical ovoid proloculus of *Tolypammina*. The diameter of the tubes is only 40-50 μm, and it is proba-

Table 4. Occurrences of Rose Bengal-stained specimens in the sponge fraction. Only 5 samples contained stained specimens. Only stained species are listed.

TUL99A01 (forams) present/absent data	stained	unstained
Crithionina sp.	✓	✓
Haplophragmoides canariensis	✓	✓
Psammosphaera fusca	✓	
Trochammina sp. 3	✓	
TUL99A018 (Shipek)		
Counted 102 specimens		
Crithionina sp.	5	15
SLRP4771 (slurp gun)		
Counted 155 specimens		
Cribrostomoides jeffreysii	2	4
Crithionina sp.	8	23
Gaudryina subglabrata	1	2
Indeterminate attached *Trochammina*-like form	1	11
Ramulina siphonifera	1	29
aff. *Oolina caudigera*	1	3
SLRP4772 (slurp gun)		
Counted 62 specimens		
Crithionina sp.	4	7
Psammosphaera fusca	1	0
Trochammina sp. 3	1	3
cf. *Tritaxis fusca*	1	7
SLRP4775 (slurp gun)		
Counted 169 specimens		
Cribrostomoides jeffreysii	1	2
Crithionina sp.	1	7
Gaudryina accelerata	1	1
Ammobaculinus cf. *recurvus*	1	1
Indet. tubular arenaceous	1	0
Placopsilina spongiphila	1	20
Bolivina decussata	1	0
Islandiella californica	1	22
Lobatula mckannai	1	10
Pullenia salisburyi	1	3

bly not *Tolypammina vagans* (Brady, 1879), whose tube usually has a diameter of 100 μm or more. *Tolypammina schaudinni* Rhumbler (1904) may be closer to our material.

cf. *Tritaxis fusca* (Figure 10.1-10.12)*.* This species is frequent and commonly attached by a cyst to sponge meshwork as well as to other hard substrate including *Rhabdammina* or *Hyperammina* tubes, other arenaceous foraminifera and sand grains. It can be both attached and impaled at the same time. The specimens in the sponge fraction, whether loose or attached, are often deformed or have an attachment cyst hiding apertural characteristics, therefore a few loose and undeformed specimens from other fractions are also illustrated (Figure 10.1-10.5). We leave cf. *T. fusca* in open nomenclature because 1) it usually has 3½ chambers in the last whorl, at times more, compared to *T. fusca*'s less than 3 (typically 2½), and 2) the sutures on the umbilical side curve slightly backwards whereas in *T. fusca* they are straight. Our specimens are not quite like *Trochamminella siphonifera* either, because they have a deep umbilicus not found in this last species; it is even larger/ deeper than that found on *T. fusca*. The distinction between *Trochamminella* and *Tritaxis* is made on whether the aperture is interio-areal (in *Trochamminella*) or interiomarginal (Brönniman and Whittaker 1984; Loeblich and Tappan 1988). In our material, this is often not clear though the specimen of Figure 10.1-10.3 seems closer to *Tritaxis*. Also, *Trochamminella* may show, in its attachment cyst, radial tunnels that open terminally; this feature is absent from our material.

We find some trochospiral arenaceous forms with approximately five chambers in the last whorl whose later chambers, contrary to cf. *T. fusca*, overlap the preceding ones on the spiral side (Figure 10.13-10.14). With the data we have, it is not possible to say whether there is an intergradation between ?*T. fusca* and cf. *T. fusca*. Because of the attachment cyst, ?*T. fusca* is closer to *Tritaxis* than to *Trochammina*. Both forms add up to a total of 79 specimens; since we recognized this distinction late in the study, a complete recount would be necessary to find out how many of each are present (hence the count of "<79" for both forms in Table 3).

Trochamminids (Figure 7.1-7.15). We find various morphotypes of trochamminids in and around the sponges. We leave all of them in open nomenclature. Those from inside the sponges are harder to identify because of damage that occurs when trying to remove them from the meshwork to see their umbilical side. *Trochammina* sp. 2 is rather flat with five to seven chambers in the last whorl (Figure 7.7-7.10, specimens deformed by the presence of spicules). *Trochammina* sp. 5 (Figure 7.11-7.14) is thick and its chambers are inflated; it has about four chambers in the last whorl. *Trochammina* sp. 3 (Figure 7.1-7.3) is intermediate between the other two but clearly different. A few *Portatrochammina bipolaris* (Brönniman and Whittaker 1984) (Figure 7.4) are included under "*Trochammina* sp. 3" in Table 3.

Trochamminids are mostly loose or trapped. Often they are too contorted to be identified even
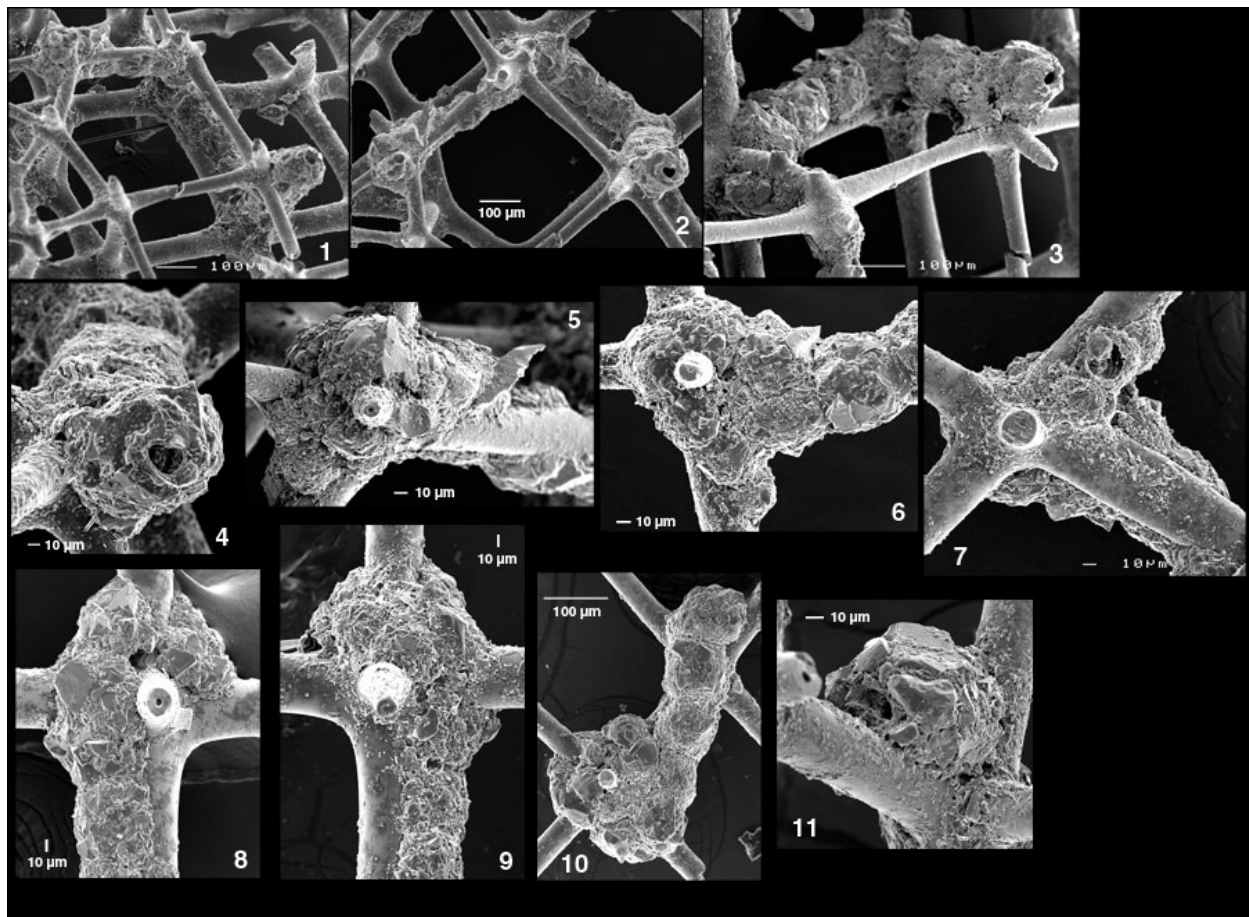
Figure 8.1-8.11. 1-5: GSC127649 (holotype) *Placopsilina spongiphila* n. sp. 1-3: Oblique views on specimen growing on 3 different axes of a *F. occa* meshwork. 4: Close-up of aperture. 5: Close-up of initial part. Shipek grab TUL99A015, sponge fraction. **6-7:** GSC127650. *Placopsilina spongiphila* growing on the meshwork of *Farrea occa*. Opposite sides of the initial part of the same specimen in close-up view. Proloculus is on Figure 8.7. Chambers increase gradually in size. Shipek grab TUL99A015, sponge fraction. **8-9:** GSC127651. *Placopsilina spongiphila*. Opposite sides of the initial part of a specimen growing on *F. occa*. Proloculus is on Figure 8.8. Shipek grab TUL99A014, >1 mm. **10-11:** GSC127652. *Placopsilina spongiphila*. Short specimen with complex coiled initial part. 10: General view. 11: Apertural face. Shipek grab TUL99A015, sponge fraction.

at the informal morphotype level (Figure 7.5-7.6). Some, like the *Trochammina* sp. 2 of Figure 7.7-7.9, wrap themselves around sponge spicules but do not get impaled. Trochamminids at times may adhere only because of residual dry mud in which case we do not consider them attached. Attached trochamminids are not as firmly attached as *Lobatula*.

***Chilostomella oolina, Globobulimina auriculata and Nonionella digitata* (Figure 10.18-10.20).** Streamlined, ovoid species are not rare in the meshwork. Their distribution is irregular, and one single sample accounts for most of the *C. oolina* reported in Table 3. It is difficult to decide whether they are trapped or loose. Only once did we find a *C. oolina* with perforations possibly corresponding to sponge spicules. The *N. digitata* of Figure 10.18-

10.20, with its reaction boss is most likely trapped, but it is the only one of its kind. Specimens are commonly easy to dislodge but become damaged in the process because of the thinness of their test. These are typical deep sediment infaunal species and could have crawled easily into the meshwork especially if the sponge fragment was buried in the mud.

***Hyrrokkin* cf. *sarcophaga* Cedhagen (1994) (Figure 10.15-10.17).** We found only a few of these large (>1 mm) Rosalinidae. None of them were in or on the dead sponge fragments and thus the species is not listed in Table 3. It is a parasite known to attack marine invertebrates, in particular sponges (Cedhagen 1994), and therefore it is logical to think that our specimens were living as parasites on the reef's sponges. It is probably not a
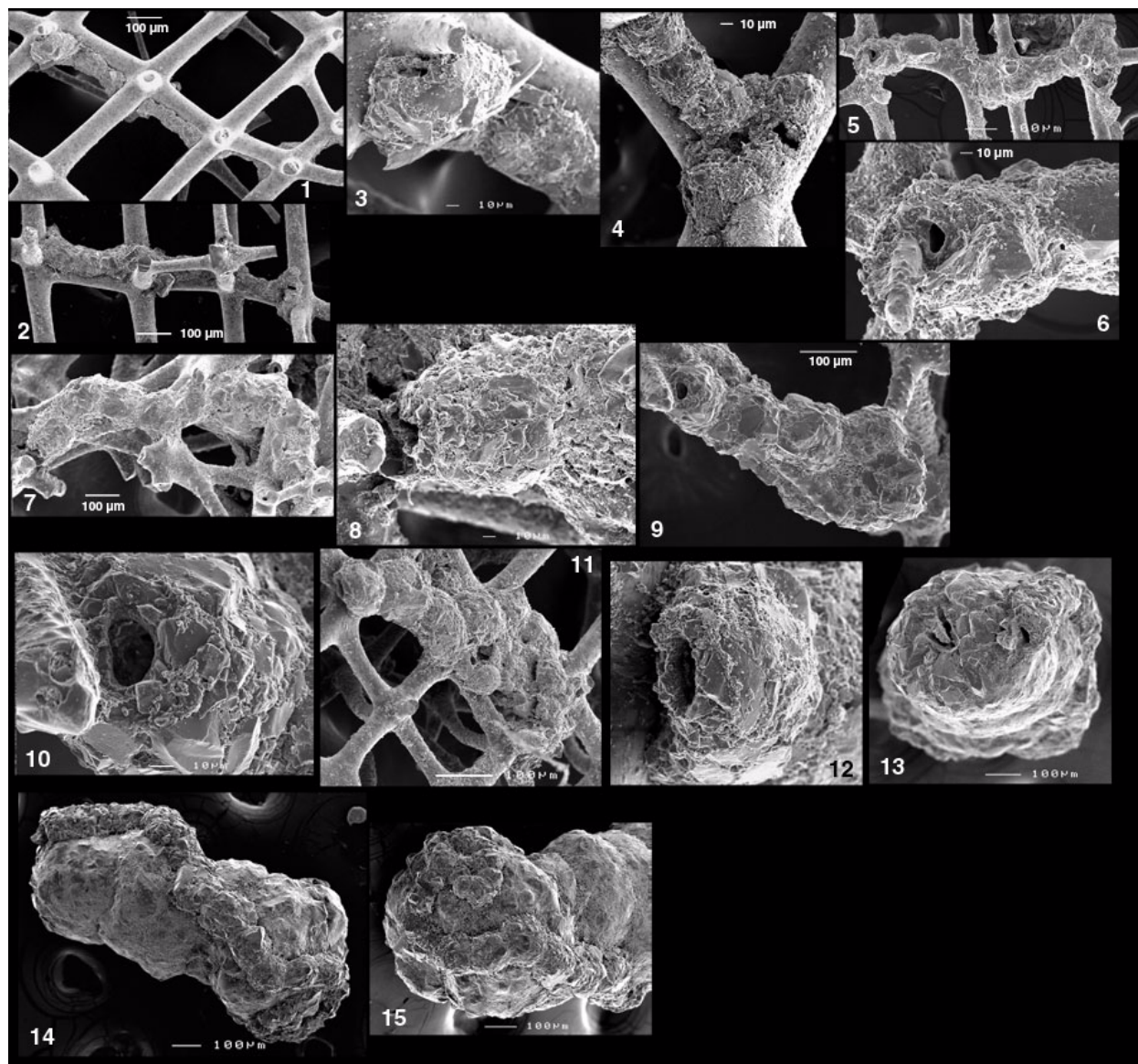
Figure 9.1-9.15. 1-4: GSC127653. *Placopsilina spongiphila*. 1 and 2: general views from opposite sides. In both pictures, the initial end is at right. 3: close-up of aperture. 4: close-up of initial part. Shipek grab TUL99A015, sponge fraction. **5-6:** GSC127654. *Placopsilina spongiphila*. 5: general view. 6: close-up of foramen. Shipek grab TUL99A015, sponge fraction. **7-8:** GSC127655. *Placopsilina spongiphila*. 7: general view. 8: close-up of aperture. Slurp gun sample SLRP4771, sponge fraction. **9-10:** GSC127656. *Placopsilina spongiphila*. 9: general view. 10: close-up of foramen. Slurp gun sample SLRP4775, sponge fraction. **11-12:** GSC127657. *Placopsilina spongiphila* with distinct, globular and somewhat flattened chambers. 11: general view. 12: close-up of aperture. Shipek grab TUL99A015, sponge fraction. **13-15:** *Placopsilina* sp. (*bradyi* Cushman and McCulloch or *spongiphila*) growing on *Ammobaculinus recurvus*. 13: view of the apertures of both specimens. 14: view from the side of the *A. recurvus*. 15: view of the early parts. Slurp gun sample SLRP4772 <1 mm.

coincidence that it occurs here but has been reported nowhere else on the west coast of North America (except for the similar form *Vonkleinsmidia elizabethae* reported by McCulloch 1977, from off California). Tomas Cedhagen (personal commun., 2003) examined our specimens and found them to be not quite like *Hyrrokkin sarcoph-*

aga and preferred to leave them in open nomenclature.

***Islandiella californica*, *Islandiella limbata* and *Globocassidulina subglobosa* (Figure 7.16-7.24).** These three large cassidulinid species are the most important constituents of the bank fauna on the British Columbia shelf and southern Alaska but are rare or absent in the sediment infauna (Ber-

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Table 5. Foraminifer content of sponge fragments, modern and Jurassic, compared with that of some modern deep-sea environments characterized by slow non-clastic sedimentation (precipitates) and absence of clastic sedimentation.

Modern BC sponge fragment dwellers, loose forms excluded (this paper)	Jurassic sponge dwellers (German authors + Gaillard 1983)	*Bathysiphon* tubes (Gooday and Haynes 1983) Oxides	Phosphate crusts (Resig and Glenn 1997) Phosphates	Deep-sea volcanic vents (Jonasson and Schröder-Adams 1996) Sulphides	Manganese nodules (Mullineaux 1987)* Oxides
Typically encrusting: *Crithionina* sp. *Hemisphaerammina* *Placopsilina spongiphila* *Psammatodendron arborescens* *Telammina fragilis* ?*Tolypammina* cf. *Tritaxis fusca* Indeterminate attached trochamminid Indeterminate agglutinated subspherical tests *Lobatula lobatula* *Lobatula mckannai* *Ramulina siphonifera* Aff. *Oolina caudigera* **Parasitic:** Hyrrokkin sarcophaga **Trapped and impaled:** *Ammobaculinus recurvus* *Cribrostomoides* spp. *Dorothia* aff. *bradyana* *Gaudryina* spp. *Karreriella bradyi* *Martinottiella pallida* *Reophax* spp. *Saccammina atlantica* *Trochammina* spp. *Bolivina alata* *Bolivina aregentea* *Chilostomella oolina* *Globobulimina auriculata* *Globocassidulina subglobosa* *Islandiella californica* *Islandiella limbata* *Pullenia salisburyi*	**Silicified (typically encrusting, including *Einschnürungen*):** *Thurammina papillata* *Tolypammina* sp. *"Thomasinella" pauperata* *Tritaxis lobata* *Placopsilina* spp. *Subbdelloidina haeusleri* **Encrusting, non-silicified:** *Lithocodium aggregatum* *Troglotella incrustans* "*Tubiphytes*" *morronensis* *Vinelloidea crussolensis* *Nodophthalmidium* sp. *Bullopora laevis* *Bullopora rostrata* *Bullopora tuberculata* **Not typically encrusting, silicified:** *Glomospira* sp.+*Usbekistania* sp. *Textularia* spp. *Bigenerina* spp. *Reophax* spp. *Haplophragmoides* spp. *Ammobaculites* spp. *Miliammmina jurassica* *Trochammina* spp. *Gaudryina uvigerinoides* *Gaudryinella deceptoria* *Spirillina* spp. *Paalzowella* spp. Nodosariids **Non-silicified:** *Ramulina fusiformis*	?*Psammosphaera* sp. *Crithionina mamilla* ?*Crithionina* Small hemispherical and dome-shaped tests *Thurammina* spp. *Tumidotubus albus* *Telammina fragilis* *Tolypammina* aff. *schaudinni* *Placopsilina bradyi* ?*Bullopora* *Glomospira gordialis* *Ammodiscus* sp. *Saccodendron* ?*Psammosphaera* ?*Haplophragmium* sp. *Trochammina* sp. Calcareous microforaminifers (2 forms) Juvenile miliolids	**Encrusting species:** *Ammodiscellites prolixus* *Hemisphaerammina celata* *Hemisphaerammina depressa* *Placopsilina bradyi* *Placopsilina* sp. *Tholosina bulla* **Adherent species:** Trochamminids *Cancris carmenensis* *Planulina ornata* Textularids	**Typically attached:** *Tolypammina vagans* *Tumidotubus albus* *Crithionina?* sp. *Placopsilina bradyi* *Placopsilina* sp. *Ropostrum amuletum* **Attached but elsewhere free-living:** *Subreophax adunca* *Saccodendron heronalleni* *Reticulum reticulatum* *Lana spissa* *Trochammina globulosa*	Indeterminate mats Indeterminate tunnels Indeterminate crusts Indeterminate chambers Indeterminate tubes Chamber, sphere with stercomes Allogromiina *Tumidotubus* *Telammina* *Reophax* *Marsipella* *Rhizammina* *Saccorhiza* *Protobotellina* *Ammodiscus* *Tolypammina* *Rhabdammina* *Ammolagena* *Dendrionina* saccamminid, soft dome *Saccammina* *Hemisphaerammina* *Pseudowebbinella* *Crithionina* *Tholosina* *Placopsilina* *Ammotrochoides* *Hormosina* *Trochammina* *Normanina* *Cibicides* *Pyrgo* *Bulimina* *Quinqueloculina* *Patellina*

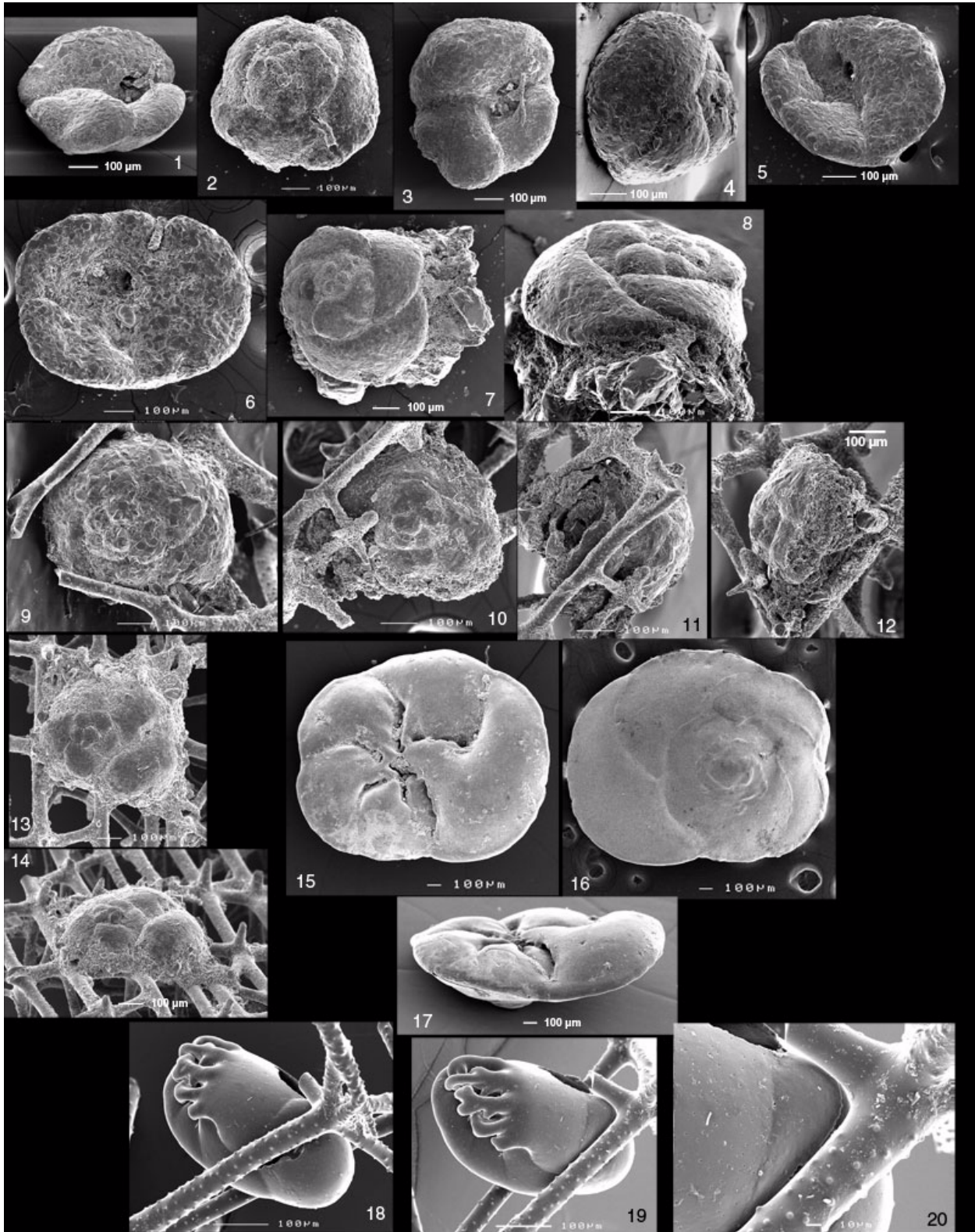Note. * To limit the size of the table, taxa are given only to the genus level only for this reference.

Figure 10 (caption on next page).

Figure 10 (figure on previous page) 10.1-10.25. 1-3: cf. *Tritaxis fusca* Williamson. 1: Oblique-lateral view showing aperture. 2: Spiral side view (with small foreign tube attached). 3: Apertural side. Slurp gun sample SLRP4771, sponge fraction. **4-5:** cf. *Tritaxis fusca*. 4: Oblique view of spiral side. 5: Oblique umbilical view showing aperture. Umbilicus filled with mud. Slurp gun sample SLRP4771, <1 mm. **6:** cf. *Tritaxis fusca*. Apertural side of specimen still holding a spicule. There is some leftover material of the attachment cyst in the umbilical area. Slurp gun sample SLRP4771, <1 mm. **7-8:** cf. *Tritaxis fusca* attached to fragment of *Rhabdammina*. 7: Spiral view. 8: Oblique view showing attachment cyst. Slurp gun sample SLRP4771, <1 mm. **9:** cf. *Tritaxis fusca* attached to meshwork, spiral view. Slurp gun sample SLRP4771, <1 mm. **10-12:** cf. *Tritaxis fusca* attached to meshwork. Stained attachment cyst. 10: Spiral view. 11: Side view from the left on Figure 10.10. 12: Side view from the right on Figure 10.10. Slurp gun sample SLRP4772, sponge fraction. **13-14:** ?*Tritaxis fusca* attached to meshwork, with cyst. 13: Spiral view. 14: Oblique view. Shipek grab TUL99A017, sponge fraction. **15-17:** *Hyrrokkin* cf. *sarcophaga* Cedhagen. 15: umbilical side. 16: spiral side. 17: edge view showing aperture. Shipek grab TUL99A015, >1 mm. **18-20:** *Nonionella digitata* Nørvang. Trapped specimen. 18: the crack in the test along the spicule results from trying to remove the specimen with a brush. 19: different angle. 20: close-up of a boss that possibly developed in reaction to the presence of the spicule and seems to effectively hold the foraminifer in place. Piston core sample TUL99A09, 92-95 cm, >1 mm.

gen and O'Neil 1979; Echols and Armentrout 1980). In the sponge reef samples, they are frequently very close to the surface (particularly in slurp gun samples) where many are stained. Although many are large, they are often small enough to tread into the sponge meshwork. *Islandiella californica* may grow until it becomes tightly trapped inside the meshwork but will not tend to bulge as *Karreriella bradyi* does. The mark of the meshwork may remain imprinted in the test, which may be impaled, though this is rare (Figure 7.18-7.19). Specimens of subglobular cassidulinids, either *I. californica* or *G. subglobosa*, which are found trapped or somewhat loose, are often deeply etched (Figure 7.18-7.22), whereas loose individuals are well preserved and fresh. It could be that the trapped specimen died in their trap and then remained exposed to seawater above the sediment/water interface. The most etched specimens tend indeed to occur on the most oxide-covered sponge fragments, which have probably been the longest exposed to seawater (see above about *P. spongiphila*). Even though the British Columbia shelf lies far above the CCD, seawater is still undersaturated with respect to $CaCO_3$ and slow dissolution remains possible. Specimens that are not associated with sponge fragments instead probably become quickly buried and escape dissolution.

***Lobatula* spp. (Figure 6.1-6.15).** Four forms of *Lobatula* were found: *Lobatula lobatula*, *Lobatula fletcheri*, *Lobatula mckannai* and *Lobatula pseudoungeriana*. Intergradations between *L. lobatula* and *L. fletcheri* can be seen, here and at other localities on the British Columbia shelf. Some specimens may be *L. fletcheri*-like in the first half of their last whorl and *L. lobatula*-like in the last half. As a consequence both are lumped as "*Lobatula fletcheri + lobatula*" in Table 3. The *L. fletcheri* type may be observed in the loose fauna and in the 63-

1000 µm fraction but only the *L. lobatula* type is present among the attached, trapped and impaled.

Lobatula is a widespread genus in the sponge lattice where it can be attached but also impaled. Some are trapped (Table 3), being attached but at the same time bulging beyond the exiguous mesh cells. They are often considerably deformed having to grow in such a setting (Figure 6.8-6.10, 6-15). On the other hand, they may grow as if spicules were not there, engulfing them and (or) at times having their spiral face, normally attached to a continuous substrate, facing empty space (Figure 6.1, 6.8-6.10, 6.13). This suggests that when the individual was living, the attached face was actually lying on the surface of something which is not there anymore. That could have been sponge tissue. Jenö Nagy of Oslo University (personal comm. 2003) once observed off Spitsbergen abundant *Lobatula lobatula* living attached to the surface of an ascidian. This is not sponge tissue, but it is nevertheless a soft substrate. Our *Lobatula* may thus have grown on living sponges, but as they are firmly attached to the meshwork, we believe that they settled after the death of the sponge.

Lobatula, a suspension feeder, is usually found at of near the surface of sponge fragments. Infaunal forms on the other hand, may be seen deeper. It may be that the *Lobatula* in their larval stage, if they originate from outside the sponge fragment, find it easier to settle at the most immediately accessible place, but it may be also that the exterior of a fragment is a better place to catch drifting particles. Contrary to *Islandiella* spp., *Lobatula* spp. rarely if ever show traces of dissolution or etching. This does not agree with the notion that $CaCO_3$ tests will etch more if exposed to seawater for a longer period of time.

***Ramulina siphonifera* (Figures 11 and 12).** This attached *Ramulina* is a new species (Appendix) and is the most distinctive taxon in the sponge

fauna. It is widespread in our material and can be found wherever there are foraminifera in or on the sponge fragments. Even the Strait of Georgia sponge fragments, nearly devoid of foraminifera, have yielded four specimens. The genus has never been reported from the west coast of North America between Alaska to Oregon (Culver and Buzas 1985; other authors quoted in the present paper) but none of the workers in the region have specifically searched the content of sponge fragments. The presence of this species seems therefore linked to the existence of a particular habitat: dead sponge fragments. The fragility of the apertural siphon is such that it must live attached in a protected habitat. Sponge fragments supply this habitat but a specimen found attached to a sand grain (Figure 11.16), shows that this is not an absolute necessity. However, this is one of only two specimens of its kind. The sponge fragment may offer a base from which to catch drifting food although Polymorphinidae are not usually recognized as suspension feeders.

We have a few specimens which, like some *Lobatula*, are flat and non-spinose on one side as if they had been growing on "something" that is not there anymore (Figure 12.20-12.22). Even more than in *Islandiella*, it is common to find specimens of *R. siphonifera* that have been etched, possibly due to exposure to seawater for a long time postmortem.

Two modern *Ramulina* species are described as attached: *Ramulina grimaldii* Schlumberger (1891a) and *Ramulina vanandeli* Loeblich and Tappan (1994); they have rarely been reported after their original publications. Modern reports of *Ramulina* are few, and almost nothing is known of its ecology. Hugh Grenfell and Brian Hayward (University of Auckland, personal commun., 2005) record *Ramulina* occasionally from deeper waters, as broken fragments and very rarely as whole specimens, with no evidence of attachment.

Ramulina siphonifera engulfs silica rods by wrapping them completely and tightly with its wall so that the content of the lumen is completely insulated from the meshwork. An individual may thus appear completely pierced by the meshwork and still the protoplasm would have no contact with it (Figure 12.10-12.14). Thus, *R. siphonifera* may have two growth modes: it may creep between the rods of the meshwork, or it may engulf them.

Aff. *Oolina caudigera*. Only 19 specimens of this form have been observed from the sponge meshwork. The free specimen of Figure 13.22-13.23 is from the >1000 µm fraction. This taxon resembles

O. caudigera except that most specimens were found attached to the meshwork, usually by the aboral end (Figure 13.1-13.2). The test tends to be symmetrical relative to an axis passing through the aperture, but among the attached specimens, it may be laterally compressed or deformed depending on its relationship to the meshwork. The basal spine or tube may be placed sideways depending on the deformation of the test (Figure 13.11-13.12, 13.21). The very finely porous, optically radial calcareous wall is deformed or completely interrupted at the contact with the sponge spicules to which the specimen is attached, leaving open scars in detached specimens (Figure 13.6). It is not possible to know whether or not the wall wraps completely around the silica rods as in *Ramulina siphonifera* because of the limited availability of material. The aperture is radiate (Figure 13.8, 13.14 and 13.23) contrary to *Oolina* where it is rounded; hence it cannot be included in that genus. The only entosolenian tube we found was short but broken (Figure 13.16). Overgrowths or frills develop at the contact between wall and substrate as in *Ramulina siphonifera* (Figure 13.10).

Oolina and other unilocular lagenids are never attached. For this reason, a new genus ought to be erected for these specimens. However, the existence of essentially identical, unattached and undeformed specimens shows that this is not a fixed feature of this form. The attachment may be seen as an adaptation to suspension feeding; however, this is unexpected in unilocular lagenids. Also, one may wonder why some specimens are not attached. The attachment in aff. *O. caudigera* is more of the impaled type, the specimen engulfing parts of the meshwork. There are other taxa in this material that become attached in this way, often late in their development (ex.: *Gaudryina*, *Dorothia*). A more plausible explanation would be that these specimens have grown inside the meshwork to the point of being trapped and that one reaction to this stress consists in engulfing part of the meshwork, because nothing else is possible (this explanation could be applied to most other taxa observed in an impaled position). Many specimens appear attached with their aperture pointing away from the meshwork, but this could be an illusion. Since all these are broken sponge fragments, one has to imagine what the position of the specimen was before fragmentation of the sponge. Figure 13.18 shows a specimen whose aperture is resting against an already broken segment of meshwork; clearly, it was trapped in a very restricted space.
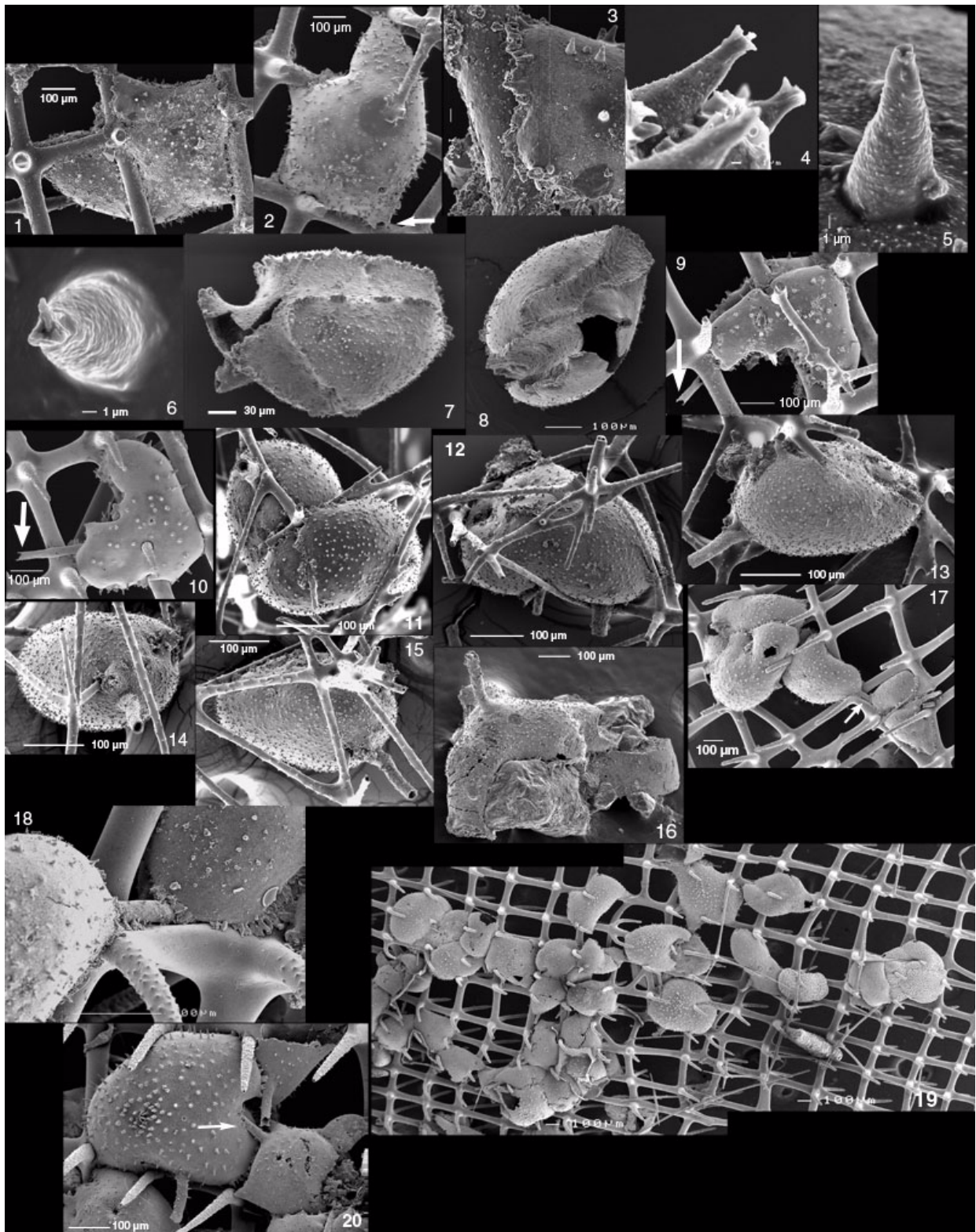
Figure 11 (caption on next page).

Figure 11 (figure on previous page). 11.1-11.20. 1-6: GSC127659. *Ramulina siphonifera* n. sp. Attached (impaled) on *Farrea occa* meshwork. 1-2: opposite views, whole specimen. Arrow: aperture with exceptionally short siphon. 3: close-up of attachment to spicules, showing barbs or frills. 4: close-up of spines with bifurcating overgrowths at their tip. 5: close-up of spine without bifurcations. 6: close-up of spine with bifurcations. Shipek grab TUL99A014, sponge fraction. **7:** GSC127660. *Ramulina siphonifera* fallen off its substrate, showing imprint of meshwork and frills at the limit between the outer wall and the spicule. The wall is spinose except for the part wrapping around the spicules. Shipek grab TUL99A015, sponge fraction. **8:** GSC127661. *Ramulina siphonifera* showing imprint of sponge spicules. Piston core TUL99A09, sample 167-170 cm, <1 mm. **9-10:** GSC127662. *Ramulina siphonifera*. Opposite sides of a specimen growing on *F. occa*. Arrow points at aperture. IKU grab TUL99A06 subcore, 6-9 cm depth, >1 mm including sponge fraction. **11-12:** GSC127663. *Ramulina siphonifera*. Opposite views on specimen twisting inside the meshwork of *Heterochone calyx*. Piston sore TUL99A09, sample 167-170 cm depth, <1 mm. **13-15:** GSC127658 (holotype) *Ramulina siphonifera*. Three different views. Piston core TUL99A09, sample 167-170 cm depth, <1 mm. **16:** GSC127664. *Ramulina siphonifera* attached to sand grain. IKU grab TUL99A01, surface subsample ("forams" sample), sponge fraction. **17-18:** GSC127665. *Ramulina siphonifera*. 17: Five specimens on *F. occa*. Arrow points at tube apparently joining two successive chambers. 18: Close-up of tube: frills around tube suggest that specimen at right came later and overlapped tube belonging to specimen at left. These are not successive chambers of the same specimen. IKU grab TUL99A01 subcore, 3-6 cm depth, >1 mm and sponge fraction combined. **19-20:** GSC127666. *Ramulina siphonifera*. 19: Two-image composite showing *R. siphonifera* specimens clustering on *F. occa* meshwork. This view includes two specimens of *Lobatula mckannai* and one of *Gaudryina accelerata* (in the right hand part of the picture). 20: Close-up of a few specimens at extreme left of Figure 11.19. One apertural siphon is engulfed by a later specimen (arrow). IKU grab TUL99A01 subcore, 3-6 cm depth, >1 mm and sponge fraction combined.

COMPARISON WITH DEEP-SEA ENCRUSTING ASSEMBLAGES

Save for a few specimens that seem to have grown on substrates that no longer exist, the material as a whole suggests colonization following the death and decomposition of the sponges. The living sponges we examined did not bear any attached, clinging or otherwise trapped foraminifera, in contrast to previous reports to the contrary (Lutze and Thiel 1989; Klitgaard 1995) of deep-sea living sponges bearing many species of attached foraminifera. Postmortem colonization is suggested also by the fact that foraminifera are more abundant on meshwork that is stained by oxides. Staining by oxides takes place in open water and implies that the dead sponge fragments stood for a while above the sediment; the foraminifera probably colonized them during that time, the suspension feeders almost certainly did.

There is a definite resemblance with the deep-sea encrusting, mostly arenaceous assemblages mentioned above (Jonasson and Schröder-Adams1996; Resig and Glenn 1997; Gooday and Haynes1983) and also with the faunas observed by Dugolinsky et al. (1977) and Mullineaux (1987) on manganese nodules, which include *Cibicides*, *Placopsilina*, *Crithionina*, *Tolypammina, Telammina,* and *Thurammina*, as well as many simple tubular forms such as *Saccorhiza* and *Rhabdammina* (Table 5). The faunal composition may vary from paper to paper depending on the kind of stress exerted locally, for example changing temperatures and low pH around hydrothermal vents, and low dissolved oxygen in the case of phosphatic hardgrounds. In environments where physical and chemical stress is high, diversities are less and calcareous taxa are few or absent - perhaps suggesting dissolution occurred. In all cases, the substrate is always hard and stable and free of clastic sedimentation. Assemblages closest to our own and, to a certain extent, to Jurassic sponge fragments, are found at sites where stress is least. The most abundant species in our material, *Placopsilina spongiphila*, grows on sponge fragments (hard substrate) that most probably stood above the sediment and often have been stained or even encrusted with oxides. There is no particular chemical stress. Species otherwise known as free are observed as attached (example: *K. bradyi*, *G. subglabrata*, *Reophax* sp., etc.) though this is often achieved by engulfing part of the meshwork.

Hughes and Gooday (2004) reported on foraminifer assemblages living on dead xenophyophores in the deep North Atlantic. As a habitat, this can be compared with dead sponge fragments: a meshwork lying above the sediment/water interface. However, the rods of the xenophyophore meshwork are actually tubes that contain a characteristic assemblage of Allogromiids and *Chilostomella*, which we do not see in sponges. In addition, the authors report an attached fauna and a fauna from the mud trapped between the branches. The attached fauna is quite different from ours, in part because of the presence of *Cibicides wuellerstorfi*, a typical deep-sea species absent on the British Columbia shelf. Also, Hughes and Gooday (2004) do not mention trapped or impaled foraminifera. As to the assemblage from
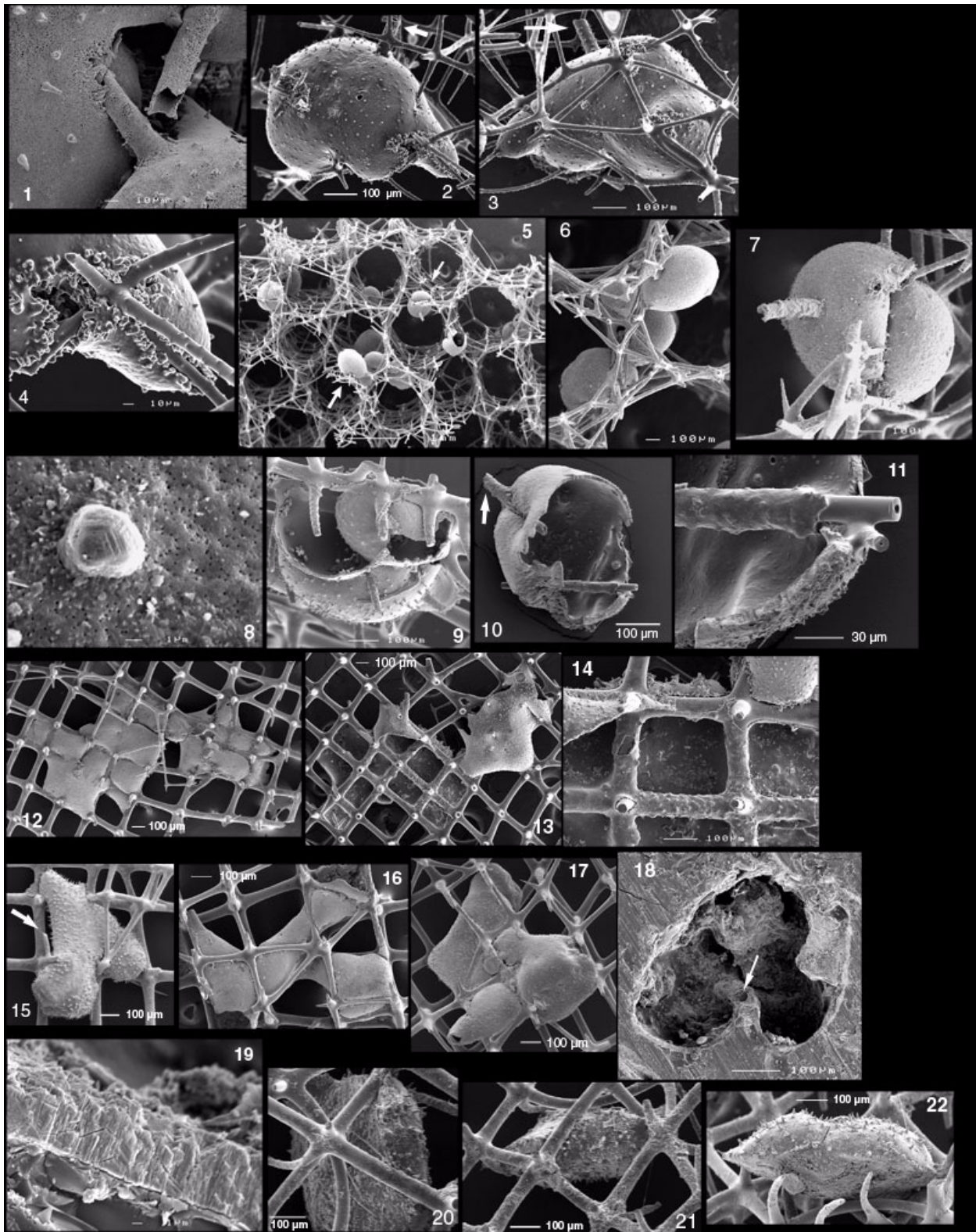
Figure 12(caption on next page).

Figure 12 (figure previous page). 12.1-12.22. 1: GSC127666. *Ramulina siphonifera* n. sp. Same specimen as Figure 11.20, close-up of apertural siphon engulfed by later specimen. IKU grab TUL99A01 subcore, sample 3-6 cm, sponge fraction. **2-4:** GSC127667. *Ramulina siphonifera*. Attached (impaled) inside *Aphrocallistes vastus*. 2-3: opposite sides, arrow points at aperture. 4: frills around sponge spicules: close-up of Figure 12.2. Piston core TUL99A09, sample 167-170 cm depth, >1 mm. **5-8:** GSC127668. Many specimens of *Ramulina siphonifera* attached (impaled) on *Aphrocallistes vastus*. 5: low magnification view of specimens dispersed in meshwork. 6: group of specimens marked by lower arrow on Figure 12.5. 7: specimen marked by upper arrow on Figure 12.5. Where there is little constraining meshwork, *R. siphonifera* tends to assume a more or less spherical shape. 8: High magnification of the wall of the specimen of Figure 12.7. The large feature is the beginning of a spine. Some etching has taken place postmortem, hence the crystalline marks on the "spine." The pores may have been enlarged by dissolution. Shipek grab TUL99A019, sponge fraction. **9:** GSC127669. *Ramulina siphonifera*. This species may be considered unilocular and this picture probably represents specimens engulfing each other, with broken-in walls. IKU grab TUL99A01 subcore, sample 3-6 cm, >1 mm. **10-11:** GSC127670. *Ramulina siphonifera*. Broken in specimen, engulfing spicules. 10: general view, arrow points at apertural siphon, not to be confused with the spicule besides. 11: close-up of lower right part showing how the foraminifer wraps the engulfed spicules by a calcite wall. Shipek grab TUL99A017, sponge fraction. **12-14:** GSC127671. *Ramulina siphonifera*. 12-13: opposite sides of one or more specimens growing on *F. occa*. All of the left part is just one chamber. On Figure 12.13, a large part of the wall of the left side is broken off, showing the interior of the opposite wall and the calcite layer wrapping the meshwork and insulating it from the protoplasm. 14: close-up of the meshwork and of the insulating calcite layer. A similar growth mode is reported in *Thurammina* from Jurassic sponge reefs. Shipek grab TUL99A014, sponge fraction. **15:** GSC127672. *Ramulina siphonifera* on *F. occa*. Arrow points at aperture. Shipek grab TUL99A014, sponge fraction. **16:** GSC127673. *Ramulina siphonifera* spreading through *F. occa*. Triggerweight core TUL99A010, sample 85-88, >1 mm. **17:** GSC127674. *Ramulina siphonifera* spreading through *F. occa*. Triggerweight core TUL99A010, sample 85-88, >1 mm. **18-19:** *Ramulina siphonifera*. 18: section through specimen embedded in Lakeside 70. Arrow points at a sponge spicule more or less normal to image plane. Note how wall wraps around the spicule. Compare with Figure 99 in Gaillard (1983). 19: close-up of wall showing radial structure. Interior of the test is up. Shipek grab TUL99A019, sponge fraction. **20-22:** GSC127675. *Ramulina siphonifera*. Three specimens flattened on one side. All three attached to the same sponge fragment. The approximately flat side is non-spinose whereas the opposite side is spinose. These specimens may have grown on a soft substrate (sponge tissue?) which has not been preserved. Shipek grab TUL99A014, sponge fraction.

the trapped mud, it consists, like our own "loose" fauna, of the same species as found in the surrounding sediment. In addition to suggesting that xenophyophores can provide habitat for suspension feeders and deposit feeders, they propose that they serve as refuge from predators. The presence of some species inside the sponge meshwork, in particular *Ramulina siphonifera*, which occurs nowhere else, might be explained in the same way.

King et al. (1998) found evidence that fine pore space within deep-sea laminated diatom mats was limiting the size of the endobenthic population and favouring small taxa. The assemblage they report is the equivalent to our loose fauna. With sponge fragments, mesh size is not a limitation, at least for some taxa, as they will grow to the point of engulfing the mesh rods.

COMPARISON WITH JURASSIC SPECIES ATTACHED TO SPONGES

In this section, modern taxa examined above are compared with Jurassic sponge facies foraminifera to find possible "equivalents." By "equivalent" we mean either having a close taxonomic relationship, a similarity in external morphology or a similarity in the habitat they colonize. Jurassic sponge

species that are absent or rare in the Recent will be discussed at the end of the section.

Arenaceous/Calcareous Ratio

Both in the Jurassic and in the Recent, the percentage of arenaceous taxa is higher among the sponge fragment dwellers than in the surrounding mud. The modern reefs, however, contain a larger proportion of calcareous taxa than the Jurassic reefs. After subtracting the always-loose taxa (Table 3), the calcareous individuals in our material are nearly as numerous as the arenaceous (810 against 880). Calcareous forms are abundant in modern reefs despite the fact that 1) the waters off British Columbia are certainly colder than the subtropical northern Tethys and 2) in the carbonate-laying environment in which the sponge reefs developed, postmortem dissolution of $CaCO_3$ is likely to have been slower than on the modern British Columbia shelf. It is possible that silicification of Jurassic calcareous foraminifera was poor—this would have affected the quantitative results of etched sponge studies though it is impossible to say how much. Bias in the representative value of Table 3 should not have affected the arenaceous/calcareous ratio. An obvious factor is that some of the very common modern taxa, *Lobatula* and
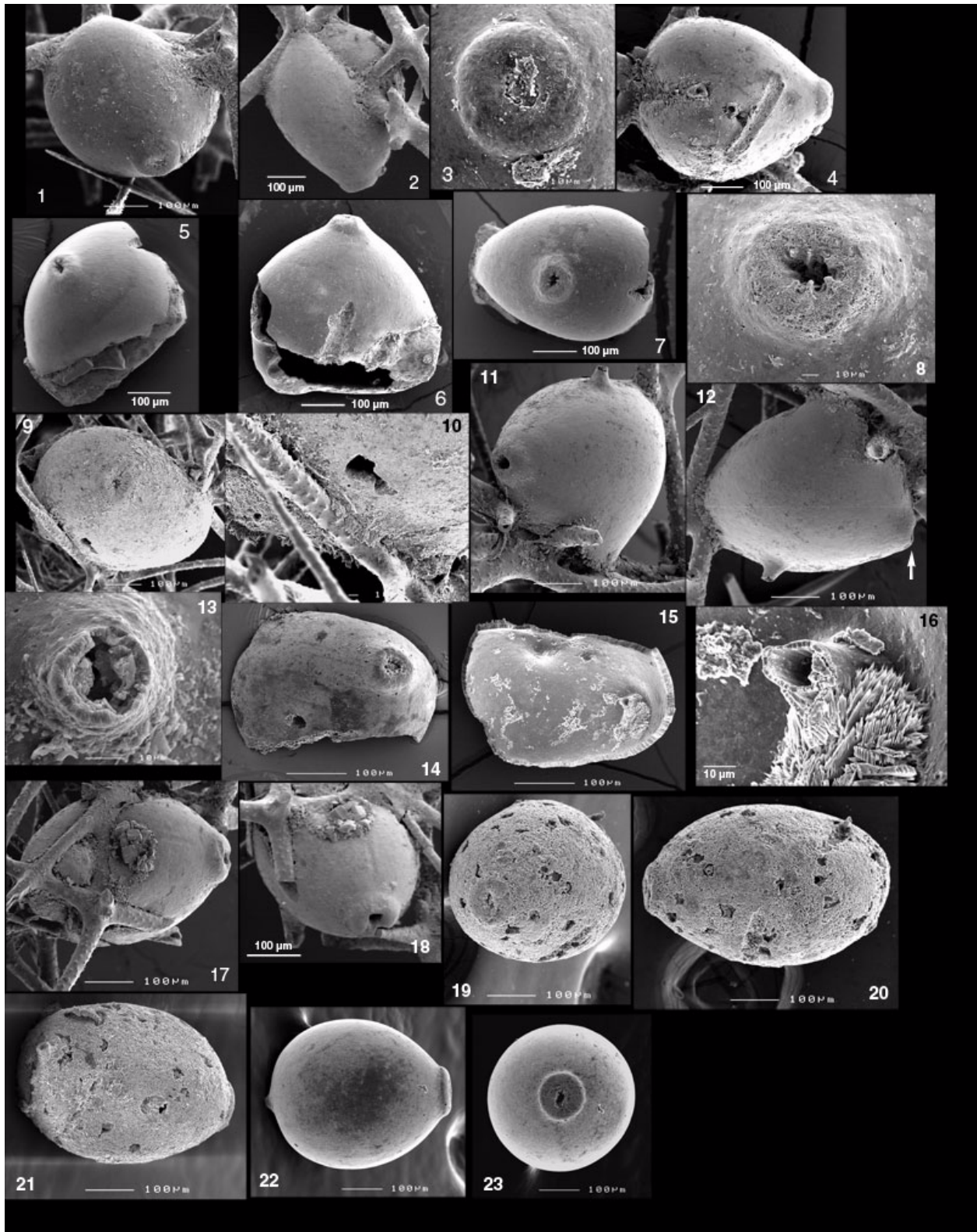
Figure 13 (caption on next page).

Figure 13 (figure on previous page). 13. 1-13.25. 1-4: Aff. *Oolina caudigera*. 1: oblique view showing aperture. 2: side view. 3: close-up of aperture. 4: side view, trace of contact with sponge spicule and tips of spicules poking out of test wall. Shipek grab TUL99A017, >1 mm. **5-8:** Aff. *Oolina caudigera* detached from its sponge substrate. 5: oblique view; the lower part of the specimen looks like substrate material but is actually a rough-looking part of the test wall. There are only two small extraneous fragments attached to the test. 6: lateral view (opposite side of Figure 13.6) showing gap at the place where the meshwork was. 7: apertural view. 8: close-up of aperture showing radial structure. IKU grab TUL99A07, surface subsample ("forams"), sponge fraction. **9-10:** Aff. *Oolina caudigera*. Apertural view of etched specimen. This preservation is typical of most individuals. 9: apertural view. 10: close-up of contact between test and spicule showing attachment frills. Shipek grab TUL99A019, sponge fraction. **11-13:** Aff. *Oolina caudigera* attached to meshwork, with small secondary aperture ("basal spine" in free *Oolina*?). 11: oblique view; main aperture is at left, secondary aperture is at top. 12: side view; main aperture is at right (arrow), secondary aperture at bottom. 13: close-up of secondary aperture. Shipek grab TUL99A017, >1 mm. **14-16:** Aff. *Oolina caudigera*. 14: External view of broken off fragment of apertural region. The radiate aperture indicates it is an aff. *O. caudigera*. 15: Same, showing interior; entosolenian tube is broken but visible. 16: close-up of entosolenian tube; the calcite crystal are probably secondary. IKU grab TUL99A07, surface subsample ("forams"). **17-18:** Aff. *Oolina caudigera*. Specimen attached to meshwork. 17: side view. 18: oblique view. The aperture rests against a spicule that had fallen off at the time Figure 13.17 was taken. Shipek grab TUL99A017, >1 mm. **19-21:** Aff. *Oolina caudigera*. This deeply etched specimen was found trapped inside the meshwork. 19: oblique view of oral end. 20: side view showing an indeterminate prominence by which it may have been attached. 21: oblique aboral view showing skewed basal "spine" or tube. Slurp gun sample SLRP4775, sponge fraction. **22-23:** Aff. *Oolina caudigera*. This specimen was found loose. 22: side view. 23: apertural view. Slurp gun sample SLRP4771, <1 mm.

Islandiella, did not exist in the Jurassic and may have since moved into niches formerly occupied by arenaceous forms.

Arenaceous Species

By its growth form and wall characteristics, *Ammobaculinus recurvus* resembles the widespread Jurassic genus *Haplophragmium*. *Ammobaculinus* differs from this last taxon only by its aperture. *Haplophragmium*-like forms are uncommon in the Recent: the only other genus is *Acupeina* Brönniman and Zaninetti (1984) (multiple aperture) from shallow, brackish tropical waters. Among the authors that extracted silicified foraminifera from Jurassic sponges, none reported *Haplophragmium*.

Crithionina is not reported from Jurassic reefs. This may be due to the tendency of some of its species to disaggregate postmortem.

The phenomenon of trapped foraminifera in the Jurassic is observed mostly among the genera *Thurammina*, *Tolypammina* and *Subbdelloidina.* Silicified foraminifera extracted from the limestone by etching show marks left on the tests by the presence of the spicules. Such specimens are described by German authors as *eingeschnürt*, or "laced in" (Seibold and Seibold 1960a, 1960b; Schmalzriedt 1991; Munk 1994).

Subbdelloidina haeusleri Frentzen (1944) is a close Jurassic equivalent of *Placopsilina spongiphila*. Both grow attached to rods of the meshwork. The specimens illustrated by Frentzen (1944) and by Seibold and Seibold (1960a) differ from *P. spongiphila* by their generally larger diameter, more depressed sutures and primarily, their tendency to branch (see Appendix). The illustrations seem to indicate that they are "pseudoattached" (*sensu* Hofker 1972, quoted by Gooday and Haynes 1983) whereas *P. spongiphila* is generally "attached." We re-photographed the specimens of Schmalzriedt (1991) and illustrate them on Figure 14.15-14.19.

Schmalzriedt (1991) synonymizes *Subbdelloidina* with *Placopsilina*. He reports two species of *Placopsilina* but since he sees all intermediates between both, we believe they should be considered as morphotypes of the same species. Whether this species should be included under *Placopsilina* or *Subbdelloidina* should wait for a review of *Placopsilina*. In the meantime, we will go on using the name *Subbdelloidina haeusleri*.

Schmalzriedt's smallest specimens of *Subbdelloidina* have about the same diameter as *P. spongiphila* (~100 µm) and fill only a part of the space inside the meshwork; more commonly, they are 200 µm or more and fill most of the mesh space, depending on the sponge species they were colonizing. As a result, *Subbdelloidina* is contorted and shows obvious traces of the presence of the sponge meshwork. As *P. spongiphila*, it does not show any tendency to lift its test from the substrate, which suggests it fed on the substrate. The *S. haeusleri* illustrated by Munk (1994) are fairly large, often with a tangled (*knäuelig*) initial part, and may be attached to other foraminifera. The initial part of *P. spongiphila* is often a sort of tangle but it is wound around an intersection of the meshwork, something not usually seen in *S. haeusleri*.

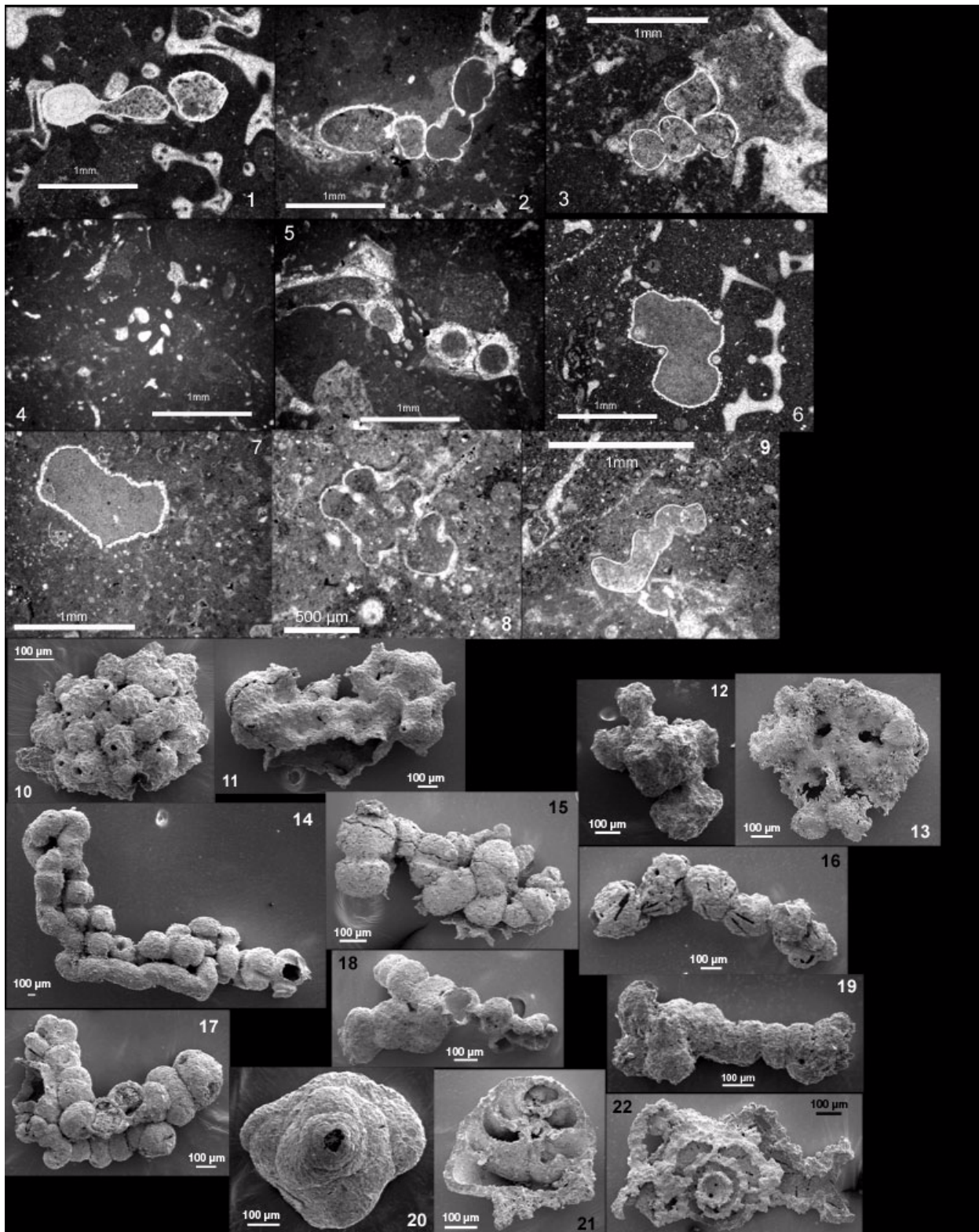In Jurassic sponge reefs, the genus *Placopsilina* (not *Subbdelloidina*) occurs as large specimens

Figure 14 (caption on next page).

Figure 14 (figure on previous page). 14.1-14.22. 1: *Bullopora tuberculata* (Sollas). Foraminifer laced-in within relatively coarse sponge meshwork. Tuejar near Chelva, Province Valencia, Spain, Oxfordian. **2:** *Bullopora tuberculata* (Sollas). The lower and right edges of the picture are filled with sponge meshwork on which the *Bullopora* grows. See foramen. Hanner Steige, Urach, Swabian Alb, Germany, Uppermost Kimmeridgian. **3:** *Bullopora tuberculata* (Sollas). Note foramina and central canal within spines. Closely associated with serpulids (on the right) and to microbial crust (left). Jabaloyas, Province Teruel, Spain, Oxfordian. **4:** *Vinelloidea crussolensis* growing on sponge meshwork. Büchelberg near Urach, Swabian Alb, Germany, Uppermost Kimmeridgian. **5:** *Vinelloidea crussolensis* (dark) grows around a serpulid (clear). Willmandingen, Swabian Alb, Germany, Early Kimmeridgian. **6:** *Thurammina papillata*. Foraminifer is laced-in within coarse sponge meshwork. Jabaloyas, Province Teruel, Spain, Oxfordian.**7:** *Thurammina papillata*. The whole SE half of this picture is sponge meshwork to which the foraminifer is attached. Calatorao near La Almunia de Doña Godina, Province Zaragoza, Spain, Oxfordian. **8:** *Thurammina papillata*. Foraminifer grows within sponge meshwork and is pierced and impaled by it. Spicule alignments cross the picture diagonally, at right angle to one another. Calatorao near La Almunia de Doña Godina, Province Zaragoza, Spain, Oxfordian. **9:** *Tolypammina vagans*. Calatorao near La Almunia de Doña Godina, Province Zaragoza, Spain, Oxfordian. 10-22 are reillustrations of specimens figured in Schmalzriedt (1991). Specimens were loaned by the University of Tübingen and photographed with the SEM at Geological Institute in Stuttgart. **10-13:** *Thurammina papillata*. 10: Specimen of Plate 1, fig. 7 in Schmalzriedt. 11: Plate 1, fig. 5. 12: Plate 1, fig. 6. 13: Plate 1, fig. 9. 10-11: apertures visible, not much evidence of meshwork presence. 12-13: imprint of meshwork clearly visible. **14:** *Tolypammina vagans.* Plate 3, fig. 9 in Schmalzriedt. This specimen was growing through a now-dissolved meshwork whose presence left marks at many places. **15-19:** *Subbdelloidina hauesleri* Frentzen. Schmalzriedt calls uniserial forms *Placopsilina cenomana* d'Orbigny and forms with irregular pile-ups of chambers (*traubig*), *P. hauesleri* (Frentzen). He names 15, 16 and 18, *P. cenomana*; 17, *P. hauesleri*, and 19: *P. cenomana/haeusleri* transitional form. 15: Plate 5, fig. 10 in Schmalzriedt; imprint of spicules is visible. 16: Plate 5, fig. 8; rectilinear marks are left by spicules agglutinated by test and subsequently dissolved. 17: Plate 5, fig. 12, few spicule marks. 18: Plate 5, fig. 9; branching specimen. 19: Plate 5, fig. 14; partly uniserial and partly *traubig*. **20-22:** *Tritaxis lobata* (Seibold and Seibold). 20: Plate 6, fig.10 in Schmalzriedt; spiral side. 21: Plate 6, fig.11; specimen broken along the vertical axis. 22: Plate 6, fig.22; horizontal cross-section including attachment cyst.

encrusting the exterior of sponge fragments. This form and habit is absent from our material with the possible exception of the single above-mentioned specimen from the Strait of Georgia (Figure 4.16-4.17).

If *Telammina*-like forms ever inhabited Jurassic sponge fragments, it is likely that attempts at extracting them by etching would have destroyed the delicate stolons (assuming these were preserved) and left only indeterminable agglutinated balls.

Valvulina lobata, a species very close to ?*Tritaxis fusca* was described from the Jurassic sponge reefs by Seibold and Seibold (1960a) and later transferred to *Tritaxis* by Oesterle (1968). *Tritaxis lobata* is common and is one of the few attached species inside Jurassic sponge fragments. Wagenplast (1972) reports it as *Valvulina* sp. from the material etched out of the sponges, but does not find it in the surrounding marl (*Schwammmergel*). Schmalzriedt (1991) reports it (as *Tritaxis*) as abundant inside the sponges themselves, as single specimens elsewhere in the reef, and as absent off-reef. *Tritaxis lobata* occasionally shows a large attachment cyst with one or more apertures (Schmalzriedt 1991; Munk 1994) which we do not find in our modern specimens. Such a structure would be typical of *Trochamminella*. Gaillard (1983) reports it (as *Valvulina*) as exclusive to the sponge facies (equivalent to the reef-facies of Schmalzriedt) where it is fairly common. Munk

(1994) illustrates the apertural side of *T. lobata* and shows a specimen attached to a *Thurammina*, itself contorted, having grown inside the meshwork. The main difference between *T. lobata* and our modern specimens is that the periphery of the former is lobate and irregular; moreover, *T. lobata* has 2 1/2 chambers in the last whorl, like *T. fusca* (Seibold and Seibold 1960a). These differences are minor: these are two closely related taxa living attached in and on sponge meshwork, 150 Ma apart.

Trochamminids have been widely reported from Jurassic etched sponge faunas. They show approximately the same range of thickness-to-diameter ratio, sharpness of periphery, chamber inflatedness, and number of chambers in the last whorl as the morphotypes from modern sponges. The Jurassic species illustrated in the literature show no trace of attachment or entrapment as we see in our modern specimens.

Calcareous Species

Chilostomella oolina, Globobulimina auriculata and *Nonionella digitata* had not appeared yet in the Jurassic, but other streamlined forms were present, *Guttulina*, *Eoguttulina*, *Dentalina* and *Nodosaria*. They have been found both in the reef facies and off-reef but only Schmalzriedt (1991) reported them from etched sponges, as "occasional."

Cassidulinidae appeared only in the Tertiary and are thus absent in Jurassic sponge reefs. Other mid-sized calcareous species are reported but those from inside the sponges are few in numbers; this could be explained by postmortem dissolution as is the case with *Islandiella* in our material. The specimens illustrated (in particular by Schmalzriedt 1991) appear poorly preserved, but this is more likely the result of incomplete silicification than of etching of the $CaCO_3$.

The genus *Lobatula* did not exist in the Jurassic. Calcareous attached forms were probably *Trocholina* and *Paalzowella* (*Patellina*? in Schmalzriedt 1991*)*, but their test wall is quite different from that of *Lobatula* and the preservation/dissolution may have differed too. These genera are occasional (Schmalzriedt 1991), or locally frequent (Seibold and Seibold 1960a) in the etched sponges, and are often totally absent. The clinging (i.e., epifaunal) genus *Spirillina* is very abundant around Jurassic sponges but less so inside, and its presence there could be accidental (loose fauna). The suspension feeder niche in the dead Jurassic sponges appears mostly occupied by *Tritaxis* and *Tolypammina*.

Kazmierczak (1973) and Gaillard (1983) have discussed the question of whether foraminifera on Jurassic reefs are commensal organisms or postmortem settlers. Our specimens of *Lobatula*, even when they suggest the former presence of soft parts, are firmly attached to the meshwork and nothing in their position suggests that they were inside a canal of the living sponge benefiting of the food particles carried by the currents produced by the sponge, as Kazmierczak (1973) believed for *Tolypammina*.

Ramulina siphonifera must be compared with the pictures of Schmalzriedt (1991, plate 1, figure 9 re-illustrated in the present Figure 14.13) which show a Jurassic *Thurammina* similarly punched with holes, and with the original illustrations of *Thurammina canaliculata* Haeusler (1883). *Thurammina* is the only Jurassic taxon to fit our concept of "impaled."

Some species of *Ramulina* and *Bullopora* are associated with Upper Jurassic sponge reefs. *Ramulina fusiformis* Khan (1950), and *Ramulina spandeli* Paalzow (1917) have been found in the sponge reef facies and the bank facies but not in the sponges themselves (Seibold and Seibold 1960a; Gaillard 1983). These do not have the contorted aspect of *R. siphonifera* nor its very thin siphon and are quite different. *Bullopora rostrata* Quenstedt (1857) grows attached on the exterior of sponges; its closest equivalent in modern sponge reefs would be *Lobatula* sp. rather than *R.*

siphonifera. By contrast, *Bullopora tuberculata* (Sollas 1877), another attached form, is quite close to *R. siphonifera*. Both grow intertwined with the meshwork. The modern form is rarely found anywhere else, whereas the Jurassic species may also be present away from the sponge reefs, at various water depths (Septfontaine 1977; Gaillard 1983; Schmid 1996). Both have an irregular shape consisting of a succession of constrictions and widenings (see illustrations in Gaillard 1983 and Schmid 1996). In *R. siphonifera*, this results mostly from the presence of the meshwork through which it creeps and does not represent a true succession of chambers. No connection between successive chambers has been found in *R. siphonifera*, contrary to *B. tuberculata* (Figure 14.2-14.3). Both have remarkably similar conical spines—which are more representative of *Ramulina* than of *Bullopora*—though we have not been able to check whether the spines of *R. siphonifera* have a central canal like those of *B. tuberculata*. Our modern specimens have a rather thin wall, less calcification being normal in cool waters with predominantly clastic sedimentation, compared with the subtropical Jurassic sea in which carbonate sediments were deposited. The most obvious difference is the thin apertural tube; such a structure has not been reported from the Jurassic *Bullopora*. The overall exterior outlook of *B. tuberculata* can be only reconstructed from thin sections as it has never been extracted from the sponge fragments; however, something as characteristic as a thin protruding tube would undoubtedly have been reported by some of the authors working on Jurassic faunas.

Bullopora tuberculata is common in thin sections but absent in the silicified residues. It is possible that lenticulinids became silicified while *B. tuberculata* did not, but it is not clear why it would be so as both have a similar wall structure and composition. It is possible both are silicified but that researchers working with thin sections have sampled different levels than investigators of silicified foraminifera because of differences in working methods and in sampling goals, and that the latter sampled essentially beds without *Bullopora*.

We would not pretend that *R. siphonifera* and *B. tuberculata* are synonyms; there are clear morphologic differences. We would not even argue that the first descends directly from the second. Despite the obvious taxonomic changes since the Jurassic, it is remarkable that, after 150 Ma, dead sponges continue to offer the same habitat and that different organisms adapt to it in the same way, generating similar morphologies that are found nowhere else.

In the Jurassic sponge reef facies, *Bullopora rostrata* may seem to be the closest equivalent to

aff. *Oolina caudigera*. Both belong to the Nodosari-aceae, are subspherical and attach to dead sponges. However, *B. rostrata* is plurilocular and limited to the outside of sponge fragments (never found in the etched assemblage) and it is a true attached form, like *Lobatula*. On the contrary, the attachment of aff. *Oolina caudigera* is accidental; it is more impaled than attached, and on this point resembles many other forms in this material that are not normally known to attach (*Gaudryina*, *Dorothia*, etc.). Its closest Jurassic equivalent would thus be the genus *Thurammina*.

Jurassic "Sponge Foraminifera" Rare or Absent in Modern Reefs

A certain number of taxa commonly reported from sponge reefs by Jurassic authors (Table 6) are not discussed above. They are either totally absent or rare in the modern sponge fragments, or they are important enough in the Jurassic to deserve a separate discussion. The species discussed below were selected on the basis of our experience in the Jurassic as well as a review of the literature.

***Vinelloidea crussolensis* Canu (1913) (Figure 14.4-14.5).** Often reported as *Nubeculinella bigoti* Cushman (1930) (for taxonomy see Voigt 1973; Loeblich and Tappan 1988), this is probably the most abundant foraminiferal species to attach to Jurassic sponges. It is found on the outer surface of sponges along with abundant serpulid worms and comparatively rare *Placopsilina*. It is not observed intertwined in the meshwork. It may encrust hard surfaces on the Jurassic seafloor far from any sponge reef, as long as sedimentation rate is low (Gaillard 1983).

Members of the subfamily Nubeculinellinae are widespread in the Recent but their distribution is limited to warm temperate to tropical waters. Queen Charlotte Sound, with its temperatures not exceeding 7°C, is not the kind of habitat where one would expect Nubeculinellinae.

Vinelloidea is closely associated with stroma-tolitic layers that encrust the upward facing side of sponges; nothing else but a few pelecypods can be found in these crusts. Hiller (1964), Hiller and Kull (1967) and later Gaillard (1983) suggested a possible symbiotic relationship within the crust, which they consider to be built by photosynthetic algae, and *Vinelloidea*. In more recent literature (Neuweiler and Reitner 1993; Leinfelder et al. 2002) these crusts are interpreted as microbially induced carbonate precipitations (automicrites) for which light is not necessary. Even though stromatolitic crusts still exist today, for example in Shark Bay, Australia, the deep water, stromatolite-reinforced

sponge mound biotope disappeared gradually after the end of the Jurassic. This may have been the cause for the extinction of *V. crussolensis*, which was adapted to this very specific ecological niche.

As a group, miliolids are rare in our modern sponge reefs. Of the 17,000 foraminiferal specimens identified in the sponge reefs, only 36 were miliolids. Of these, only three were found in the sponge fragments, one of which was a deep-water *Pyrgo*. This cold and deep environment is probably not the kind that will attract a rich and varied miliolid assemblage, except for species that prefer it (ex.: *Pyrgo vespertilio* [Schlumberger, 1891b]) and for a few cosmopolitan forms (ex.: *Cyclogyra*). However, some miliolids can be found in the Arctic, and cool temperatures alone cannot explain their quasi-absence on the British Columbia shelf.

The assemblages obtained by etching are not reported to contain *Vinelloidea* or any other miliolid test, as if they did not become silicified postmortem. It is possible also that the *Vinelloidea*-rich stromatolitic layers encrusting the sponges were not sampled by authors who studied etching residues.

***"Tubiphytes" morronensis* Crescenti (1969).** This form, reported by Schmid (1996) as attached (even impaled: Schmid's figure 116) to siliceous sponges, has never been reported in strata younger than Mesozoic. Its wall is characterized by a thick, porcellaneous, "micropeloidal" outer layer probably resulting from the action of algal symbionts. Although Schmid (1996) speculates that it could have lived at depths in excess of 70 m in the tropical Jurassic sea, it is improbable that light penetration on the modern British Columbia shelf could allow algae to develop at 200 m or even at much shallower depths. Thus it is not surprising to find no light-dependent microencrusters in our modern sponge fragment fauna.

***Thurammina* sp. (Figure 14.6-14.8).** *Thurammina* sp. is another common species in Jurassic sponge reefs. *Thurammina papillata* Brady (1879) and variants are the only Jurassic sponge-reef foraminifera to be impaled (illustrations in Schmalzriedt 1991) with rare exceptions (above-mentioned "*Tubiphytes*"). *Thurammina* was recognized as pierced with holes by Hauesler (1883), but he thought these holes were canals. Seibold and Seibold (1960a, 1960b) recognized these holes as the trace of sponge spicules. This is due to the test being so large as to engulf a few cells of the meshwork and even to bulge beyond that, the same way *Ramulina siphonifera* does in the Recent. Note that the originally siliceous sponge meshwork was transformed to $CaCO_3$ early in diagenesis, and that

Table 6. Foraminifer taxa reported inside and on the surface of sponges in Jurassic sponge reefs. The data are from etched material, not etched sieved samples, and from thin sections. Rare occurrences are excluded (continued on next page).

Authors	Seibold and Seibold (1960)	Oesterle (1968)		Wagenplast (1972)*¶	Gaillard (1983)	Schmalzriedt (1991)	Munk (1994)		Schmid (1996)
Sampling	etched sponges	only in etched sponges	not only in etched sponges	etched sponges	etched, not etched, and thin sections	etched sponges	etched sponges	etched sponge reef material	thin sections
Thurammina sp. (various morphotypes)	✓	✓	✓	✓	✓	✓	✓		✓
Miliammmina jurassica				✓		✓			
Glomospira + *Uzbekistania*	✓		✓	✓		✓			
Tolypammina vagans or *Tolypammina* sp.	✓		✓	✓	✓	✓	✓		✓
Reophax spp.	✓	✓		✓		✓		✓	
Haplophragmoides spp.	✓	✓		✓		✓		✓	
Ammobaculites spp.						✓		✓	
Placopsilina spp.	✓	✓	✓	✓					✓
Subbdelloidina haeusleri	✓	✓		✓	✓	✓ (as *Placopsilina*)	✓		
Thomasinella? *pauperata*						✓			
Coscinophragma sp. (unclear affinity)									✓
Lithocodium aggregatum									✓
Troglotella incrustans Wernli and Fookes (1992)									✓
Textularia spp.	✓	✓		✓		✓		✓	
Bigenerina spp.	✓	✓		✓		✓		✓	
Gaudryina spp.	✓			✓					
Gaudryinella	✓			✓					
Tritaxis lobata	✓		✓	✓	✓	✓		✓	
Trochammina spp.	✓		✓	✓		✓		✓	
"*Tubiphytes*" *morronensis*									✓

sample etching yielded only silicified foraminiferal tests bearing scars or holes left by the former presence of spicules.

Thurammina papillata lives in the Recent but we found none in the sponge reefs, despite looking carefully for it. This niche seems to be occupied now by many different species, *R. siphonifera*, *K. bradyi* and *Lobatula* spp. being the most common. *Ramulina siphonifera* is the only one for which we positively know that it wraps every silica rod it

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Table 6 (continued from previous page).

Authors / Sampling	Seibold and Seibold (1960) etched sponges	Oesterle (1968) only in etched sponges	Oesterle (1968) not only in etched sponges	Wagenplast (1972)¶ etched sponges	Gaillard (1983) etched, not etched, and thin sections	Schmalzriedt (1991) etched sponges	Munk (1994) etched sponges	Munk (1994) etched sponge reef material	Schmid (1996) thin sections
Nodophthalmidium sp.				✓					✓
Vinelloidea crussolensis					✓				✓
Spirillina spp.	✓			✓					
Paalzowella feifeli Paalzow (1932)	✓					✓ (as *Patellina*)			
Lenticulina spp.						✓			
Bullopora rostrata				✓					
Bullopora tuberculata					✓				✓
Ramulina spp.				✓					
Koskinobullina socialis Cherchi and Schroeder (1979)									✓

*Note. This author gives identifications only to the genus level.

engulfs with its test wall. Some other species possibly do, but determining this will require careful dissection.

***Tolypammina vagans* (Brady 1879) (Figure 14.9).** This is one of the most common species in the Jurassic sponge reefs (Table 6). It is also one of the rare Jurassic foraminiferal species still present in modern oceans, but it is absent from sponge reefs. Seibold and Seibold (1960a) believe that their *Tolypammina* is not the same as the modern *T. vagans* and therefore report *Tolypammina* spp. Wagenplast (1972) does not determine his foraminifera beyond genus level. Kazmierczak (1973) reports *T. vagans* from inside sponges where he thinks they were collecting food carried by the currents circulating through the sponges' pores.

This is the second main trapped Jurassic species. It grows by winding its way through the meshwork. The Jurassic sponge meshwork commonly reported by the above-mentioned authors has often smaller cells than our modern sponges, and given the rather large diameter of its tubes, *T. vagans* is often tightly trapped within the meshwork (illustrations in Schmalzriedt 1991 and the "*Hyperammina contorta*" of Haeusler 1890). The few slender ?*Tolypammina* sp. we report in our modern

material have a quite different growth habit from the Jurassic *T. vagans* due to their smaller diameter (40-50 μm). *Placopsilina spongiphila* creeps through the meshwork, but it is attached to the meshwork, not trapped. The fact its aperture never lifts from the substrate may be an indication that it collects food lying around on the meshwork and is not a suspension feeder as *T. vagans*. We occasionally observe large agglutinated tubes, probably Polychaete worms, meandering through the lattice in a way that reminds us?? of the Jurassic *T. vagans*. However, polychaete worms are probably too different from foraminifera to be considered as ecological equivalents.

?*Nodophthalmidium* sp. Schmid (1996) reports this *Ophthalmidium*-related form from Upper Jurassic sponge reefs (Table 6). We find it quite commonly, in thin sections, in the Jurassic sponge facies of the Swabian Alb. It is not far from "*Tubiphytes*" nor from *Nodobacularia* or *Vinelloidea*, but it is not a form that is known to be attached. We did not find any related form on the modern British Columbia shelf, but this is not surprising as conditions there are not favourable for miliolids except for a few taxa.

***Textularia* spp., *Bigenerina* spp., *Ammobaculites* spp., *Gaudryinella* sp. and *Reophax* spp.**

These taxa are common in the Jurassic sponge facies and reported by most of the authors of Table 6. They are all arenaceous, elongate, uniserial or biserial (at least in the later parts), and their length is in the 400-1000 µm range approximately. *Gaudryina uvigeriniformis* Seibold and Seibold (1960a) should be included in this group. This constitutes a group that is crudely comparable to the "moderately large arenaceous" taxa of our modern material: *Gaudryina*, *Martinottiella*, *Karreriella*, *Dorothia*, *Ammobaculinus* and *Reophax*. The modern specimens are commonly trapped or impaled. By contrast, the Jurassic specimens illustrated in the literature do not show evidence of having been laced-in (*eingeschnürt*). They may have been slender enough to fit within the meshwork without pressing against it, provided the mesh is large enough. This however corresponds to the definition of "loose fauna." A large collection of Jurassic sponge foraminifera would have to be examined looking specifically for scars due to the meshwork.

***Thomasinella*? *pauperata* (Haeusler) emend. Oesterle (1968).** This taxon of uncertain affinity was first described as *Reophax pauperata* by Haeusler (1885). It is reported as "*Thomasinella*" *pauperata* by Schmalzriedt (1991). It resembles *Placopsilina spongiphila* by its growth habit but it is nearly three times the diameter; also, it is vertically flattened and laterally "keeled." It was probably not creeping inside the lattice but instead grew attached to the surface of sponge fragments. No trace, scar or hole due to the presence of the lattice is mentioned nor shown. This taxon is known mostly from fragments, which makes any inference about its mode of life difficult. We found no comparable form in our modern material.

***Cribrostomoides* spp. + *Recurvoides* spp.** We would place many of the specimens illustrated by Oesterle (1968) and Schmalzriedt (1991) under the name *Haplophragmoides* in the genus *Cribrostomoides* (because of the aperture's position) or even *Recurvoides* (because of bent coiling plane: Figure 6.22). These genera are present in small numbers in our material and in larger numbers in the Jurassic etched sponges. The species are not the same as in the Recent. Our most common form is *Cribrostomoides jeffreysi*, and it is not quite like any of the reported Jurassic species. Many of Jurassic forms are small and could be part of the Jurassic "loose" fraction though Schmalzriedt (1991) reports none from the "normal" (i.e., bedded or bank) facies.

***Spirillina* spp. and *Lenticulina* spp.** These are common open shelf genera in the Upper Jurassic and are reported as part of the sponge fauna (Table 6). *Spirillina* in particular has been reported by all workers as being particularly abundant in the immediate surroundings of sponge reefs. Collectively, these forms occur in percentages that are comparable to those of the most common species in the mud retained by modern sponges: *Epistominella vitrea, Bolivina decussata, Eponides pusillus, Seabrookia earlandi* and *Angulogerina* spp. Whenever they are small enough, they may be found "loose" inside the meshwork (Table 3). It is impossible to say whether they crept in by themselves or were brought in accidentally, but their presence is not surprising considering their abundance in the mud. Contrary to what happens with modern samples, the sieving process cannot be held responsible for the introduction of *Spirillina* and the smaller lenticulinids into the meshwork of Jurassic sponges. These two genera could be part of the Jurassic "loose" fauna. The larger lenticulinids could be like some of the moderately large modern specimens whose situation cannot be definitely assigned to the "loose" or "trapped" category. We think the report of "globigerinids" in the Jurassic etched sponge facies (Wagenplast 1972) can be explained in the same way; we also find occasional planktonics in our modern sponge fragments.

SUMMARY

Dead sponge fragments in modern sponge reefs on the British Columbia shelf contain an assemblage of foraminifera that differs entirely from that found in Jurassic sponge reefs at the species level. At the genus level, there is a slight resemblance among some long-ranging taxa. There is on the contrary a strong resemblance when the foraminifera's relationship to the sponge meshwork is considered. In both periods, there are taxa that tend to get trapped and laced into the meshwork, others that attach to it and some that engulf it as they grow. In the Jurassic, there are essentially four laced-in taxa: *Thurammina* sp., *Tolypammina* sp., *S. haeusleri* and *B. tuberculata*. However, *Thurammina* is the only taxon to be impaled. In the modern oceans, *Thurammina papillata* is still common but totally absent from our sponge reefs. A number of modern species get trapped, impaled or attached, some arenaceous (*Gaudryina, Karreriella*) and some calcareous (*Lobatula, Ramulina*). *Lobatula* did not exist back in the Jurassic but *Ramulina* did. The species of *Ramulina* reported from the Jurassic are not found inside sponge fragments, but *Bullopora tuberculata*, another irregular polymorphinid, is common and can be considered trapped or laced in.

Crithionina is abundant in the modern attached fauna; it is a primitive genus that probably existed in Jurassic times but did not fossilize. The genus *Tritaxis*, except for some differences at the species level, seems to be the same and live in the same way, then and now. *Tolypammina* is virtually absent from modern sponge fragments: the few thin tubes we find probably do not occupy the same niche. The Jurassic *Subbdelloidina haeusleri* is quite close morphologically to the modern *Placopsilina spongiphila* and grows approximately in the same way; it probably fed in the same way too, from the substrate.

One of the most striking differences between modern and Jurassic reefs is the absence of attached miliolids such as the Jurassic *Vinelloidea*, "*Tubiphytes*" and *Nodophthalmidium*. The cool and dark waters off British Columbia are probably the main factor explaining the near-absence of miliolids. The disappearance, after the end of the Jurassic, of sponge mounds cemented by stromatolitic microbial crusts may have caused the extinction of *Vinelloidea*, which was narrowly adapted to this environment.

The arenaceous/calcareous ratio is higher among the assemblages closely associated with dead sponge meshwork than in the surrounding mud. This is true in the Recent and even more so in the Jurassic. There are many biases that may affect quantitative estimates however: counting bias (see Methods), postmortem etching, irregular silicification of Jurassic assemblages and the fact that paleontologists working on the Jurassic may have different sampling methods or targets depending on the goal of their research.

Modern foraminiferal assemblages of the "loose" type consist mostly of smaller specimens of calcareous species that are found in large numbers in the region: *Epistominella vitrea*, *Bolivina decussata, Eponides pusillus, Seabrookia earlandi* and *Angulogerina* spp. Their presence may be in part accidental and should be distinguished from the typical sponge fragment dwellers. The *Spirillina* and *Lenticulina* found in the assemblage extracted by etching probably represent the Jurassic "loose" fauna.

The most characteristic species in our material is *Ramulina siphonifera*. The genus *Ramulina* is rare but widespread in the Recent, but has never been reported growing in a similar trapped or impaled fashion. In the Jurassic, the closely related *Bullopora tuberculata* does grow attached or intertwined with the meshwork. *Ramulina siphonifera* may completely engulf sponge meshes and tightly wrap silica rods with its wall in the same way *Thurammina* does in the Jurassic. This is a clear case of convergent evolution implying that at least some niches inside the sponge reef environment have not changed, even though the setting of our modern reefs, with its cool temperate waters, clastic sedimentation, food chain based on diatoms, and absence of bacterial mats is quite different from that of the Jurassic sponge reefs.

Modern dead sponge assemblages as a whole show definite resemblance with some assemblages reported from the deep-sea and characterized by attached-encrusting species, mostly arenaceous, growing on hard substrate, away from clastic sedimentation but surrounded by precipitation of dissolved minerals. These can be observed on hydrothermal vents, phosphatic hardgrounds, manganese nodules and dead tests of large foraminifera. The similarity is greatest with settings where chemical/physical stress is least and where oxides are being deposited , such as settings characterized by manganese nodules and dead foraminiferal tests.

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APPENDIX: NEW TAXA

All figured holotypes and paratypes are deposited in the National type collection of invertebrate and plant fossils, Geological Survey of Canada, 601 Booth Street, Ottawa ON, Canada K1A 0E8.

SYSTEMATIC DESCRIPTIONS

Order FORAMINIFERIDA Eichwald, 1830
Suborder TEXTULARIINA Delage and Hérouard, 1896
Superfamily LITUOLACEA de Blainville, 1827
Family PLACOPSILINIDAE Rhumbler, 1913
Subfamily PLACOPSILININAE Rhumbler, 1913

Genus *Placopsilina* d'Orbigny, 1850
Placopsilina spongiphila new species
Figure 8.1-8.11; Figure 9.1-9.12.

Holotype: Specimen GSC127649 in Geological Survey of Canada collections, Ottawa. Figure 8.1-8.5.

Paratypes: GSC127650 to 127657 in Geological Survey of Canada collections.

Type locality: Sponge reefs in Queen Charlotte Sound and Hecate Strait, continental shelf off British Columbia (west coast of Canada). The holotype was collected at: lat. 51° 20.792'N, long. 128° 51.085'W. Station TUL99A015, Shipek grab sample, water depth 229 m, southern Queen Charlotte Sound.

Type level and range: Modern seafloor.

Description: Test attached to dead siliceous sponge meshwork. Generally linear uniserial, though may form a pileup of chambers. Never biserial and never branching. Grows straight along sponge rods, but may change direction at any intersection of the meshwork. Test diameter is 60 to 120 µm, usually about 80 µm. Chambers vary from cylindrical to slightly inflated, as long as wide but with some variation. Sutures vary from nearly indistinct to clearly depressed. Initial part winds (rarely more than one whorl) around a sponge spicule or an intersection in the meshwork; may be slightly irregular or entangled. Proloculus and early chambers generally smaller (around 40 µm) than later chambers but increasing quickly in size; chamber diameter thereafter remaining approximately constant. Aperture at the tip of the last chamber, more or less flattened oval in shape. It may be located at the base of the apertural face, against the substrate or up in the apertural face. It is bordered by a thin lip of agglutinated material.

Wall coarsely arenaceous relative to the diameter of the test, contributing into making the sutures indistinct. In most parts of the test except near the aperture, *P. spongiphila* is not floored, and the lumen lies against the substrate. It is "attached" in the sense of Hofker (1972, quoted by Gooday and Haynes 1983).

Dimensions: Holotype ca. 1 mm in length. Diameter of tube: 100-120 µm in adult part. Earliest chambers: ca. 40 µm. We do not have complete specimens of more than 1 mm. Longer specimens exist but segments are broken off or are concealed in dried mud.

Remarks: Modern species of *Placopsilina* are *Placopsilina bradyi* Cushman and McCulloch (1939), *Placopsilina confusa* Cushman (1920), *Placopsilina kingsleyi* Siddall (1886), and *Placopsilina vesicularis* Brady (1879). Only the first two are close to *P. spongiphila*. *Placopsilina confusa* differs from *P. spongiphila* by having more distinct chambers (depressed sutures) and a much more irregular and entangled growth. The closest modern species is *P. bradyi*. It differs from the present species by its larger diameter, chambers that are much shorter than broad, more inflated or else as broad as wide but then more or less hemispherical. The sutures are well-marked and deeply depressed whereas in many specimens of *P. spongiphila,* they are nearly invisible. *Placopsilina bradyi* often has a spiral initial part, or else no spiral part at all; it has no tangled early part nor does it start by wrapping itself around a prominence of the substratum—such as a sponge spicule. Cushman and McCulloch (1939) also report "a very few specimens attached to echinoid spines or to sponge spicules, one of which is figured. These are very slender perhaps due to the small amount of surface and may represent another species." The illustrated specimen of their figure 15 might have been *P. spongiphila*, but this single picture is not enough to judge.

The Jurassic sponge dweller *Subbdelloidina haeusleri* is larger than *P. spongiphila* (twice the diameter or more), has more inflated chambers and more depressed sutures. More characteristically, it may branch whereas *P. spongiphila* never does. Its growth is more irregular, and it more often tends to grow biserially, make tangles or pileups of chambers. The early part of *S. haeusleri* is typically entangled ("*knäuelig*" of German authors), but it does not wind around meshwork intersections in the way *P. spongiphila* does. In *S. haeusleri*, the whole test may be strongly contorted (Figure 14.15), in part because of the geometry of the

sponges in which the specimens grew. This has no taxonomic value. The aperture is often not mentioned. Seibold and Seibold (1960a) mention a single round aperture. The aperture of the specimen of our Figure 14.16 is more probably a broken end of chamber; that of Figure 14.17 is slit-like. The multiple apertures reported by Frentzen (1944) have been shown later to be only artefacts of the etching process (Seibold and Seibold 1960a; Oesterle 1968).

Many species that have been referred to *Placopsilina* in the literature do not show one fundamental characteristic of the genus, which is having an initial spiral part. Others exhibit branching although the generic description does not mention it. A review of *Placopsilina* and of *Subbdelloidina* would be needed to find out the importance of these features.

Types and Occurrence: The nine types come from sponge reefs on the floor of Queen Charlotte Sound and Hecate Strait, off British Columbia, Canada. All specimens were growing attached to the dead meshwork of reef sponges. We counted 341 specimens, most of which consist of fragments.

Suborder LAGENINA Delage and Hérouard, 1896
Superfamily NODOSARIACEA Ehrenberg, 1838
Family POLYMORPHINIDAE d'Orbigny, 1839c
Subfamily RAMULININAE Brady, 1884

Genus *Ramulina* T.R. Jones, 1875
Ramulina siphonifera new species
Figure 11.1-11.20; Figure 12.1-12.22.

Holotype: Specimen GSC127658 in Geological Survey of Canada collections, Ottawa. Figure 11.13-11.15.

Paratypes: GSC127659 to GSC127675 in Geological Survey of Canada collections.

Type locality: Sponge reefs in Queen Charlotte Sound and Hecate Strait, continental shelf off British Columbia (west coast of Canada). The holotype was collected at: lat. 53° 10.807'N, long. 130° 24.218'W. Station TUL99A09, piston core sample, depth in core: 167-170 cm, water depth 194 m, Hecate Strait.

Type level and range: Holocene deposits and modern seafloor.

Description: Test unilocular, with no definite shape, stretching in the space within the sponge meshwork and embracing it in such a way as to be attached. Engulfs silica rods by wrapping them completely and tightly with its wall so that the content of the lumen is completely insulated from the meshwork ("pseudoattached" according to the terminology of Hofker 1972). Shape of larger specimens depends on shape of meshwork cells in which they grow; that of smaller specimens not constrained by meshwork tends to be oval or even spherical. Wall calcareous, optically radial, pores visible only at high magnification (X15,000) on a slightly etched surface. Wall may be covered with conical spines that may be abundant or rare, low and blunt or high and sharp, and in some cases grow triple bifurcations at their tip. Suggestion but no clear evidence of a central canal inside the spines. The part of the wall that wraps around sponge spicules is not spinose; its junction with the rest of the wall is angular and bears barbs or overgrowths (frills) that further embrace the sponge spicules (Figures 11.3, 11.7-11.8, 12.1, 12.4). These may be the result of a healing process. Single aperture at the open end of a delicate siphon which may be spinose. Siphon never connects two successive chambers even though one specimen may grow over and engulf the siphon of another specimen. Therefore, the species may be considered unilocular.

Dimensions: Specimens are commonly 400 μm or more in their greatest dimension, with some up to 1100 μm.

Remarks: In many *Ramulina* species, both Mesozoic and Cenozoic, the chambers look like gradual enlargements of a tube. In other species, the tube is sharply distinct from the chamber but often there are many tubes emerging from each chamber. When preservation is good, *Ramulina* specimens are commonly multi-chambered. Of the six modern *Ramulina* species illustrated by Loeblich and Tappan (1994) from the Sahul Shelf, two show some resemblance to *R. siphonifera*: *Ramulina vanandeli* and *Ramulina confossa*, both described as new. *Ramulina siphonifera* resembles *R. vanandeli* by being attached to the substrate, but the latter is plurilocular, the connection between chambers is gradational and the wall is more coarsely porous. *Ramulina confossa* resembles our species in being unilocular, but its wall is much more porous and the aperture is not on a siphon.

The *Ramulina* species reported from the Upper Jurassic, *Ramulina spandeli* Paalzow (1917), *Ramulina fusiformis* Khan (1950) and *Ramulina nodosarioides* Dayn (1958) are all quite different from *R. siphonifera*. On the other hand, there is a definite resemblance between *Bullopora tuberculata* and our material in the way both grow through the sponge meshwork, in the coarse prismatic nature of the wall (Figure 12.19) and in the spines. We have not been able to make a section through

a spine to compare it with *B. tuberculata*'s characteristic canaliferous spines. If there is a central canal in the spines of our specimens, it must be no more than 1 µm in diameter, compared with ca. 4 µm for the Jurassic species. The latter tends to have larger (~double) overall dimensions than *R. siphonifera*, which may be reflected in the pore canal size. *Bullopora tuberculata* is plurilocular (Figure 14.2-14.3); there are few published pictures clearly showing the foramen.

Types and Occurrence: The types (18 individually figured specimens plus three sponge fragments with many uncounted specimens attached to them) come from sponge reefs on the floor of Queen Charlotte Sound, Hecate Strait and Strait of Georgia, off British Columbia, Canada. Many specimens were attached to the dead meshwork of reef sponges while some had obviously been torn off their substrate; only two specimens in one sample were growing attached to a sand grain. We counted 312 fairly complete specimens, many of which were damaged either for having been torn off the meshwork or because of dissolution. There are also many uncounted specimens in the material.