AN INTRODUCTION TO THE BIOLOGY AND SYSTEMATICS OF KOMOKIACEA

(TEXTULARIINA, FORAMINIFERIDA)

By

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ABSTRACT

Komokiacea n. superfam. (Textulariina, Foraminiferida, Protozoa) comprises agglutinating foraminifers with test consisting of a complex system of fine, branching tubules of even diameter. The test wall is simple, with argillaceous particles. Stercomata accumulate within the tubules.

Eleven new species in the genera *Komokia* n. gen., *Septuma* n. gen., *Ipoa* n. gen., *Normanina* Cushman, 1928, *Lana* n. gen., *Baculella* n. gen., and *Edgertonia* n. gen. are described. Two families, Komokiidae and Baculellidae, are erected.

The group has worldwide distribution, mainly in the abyssal zone. The greatest relative abundances have been found in abyssal oligotrophic areas and in hadal trenches.

CONTENTS

I. INTRODUCTION

In the more than 100 years since deep-sea investigation began in earnest on the "Porcupine" and the "Lightning", the expeditions sent out from many nations have collected enormous quantities of material from the deep-sea floor. These investigations have employed a wide variety of gear, including cameras, dredges, trawls, grabs, corers, and submersibles. Many specialists covering a span of several generations have been involved in the working up and the publication of the results in hundreds of books, reports and papers.

The basic composition of the deep-sea fauna was revealed fairly early in this history. There are virtually no important groups that cannot be found in the "Challenger" collections. However, some major taxa have turned up from time to time in recent years. Notable were the discoveries of the Pogonophora (Johansson 1937, Ivanov 1963, Nørrevang 1970) and the monoplacophoran *Neopilina* (Lemche 1957, Lemche & Wingstrand 1959). Nevertheless, while these are major taxa, they are rarely or never dominant components in deep-sea communities. Thus, it would seem safe to maintain that it is highly unlikely that any important macrofaunal taxon is unrecognized in the literature.

Strangely enough, this prediction is wrong. There exists in the deep sea an essentially undescribed macrofaunal taxon that can be found in virtually every sample where one looks for it. Furthermore, in samples from the oligotrophic abyss, the bulk of this taxon exceeds by far that of all the metazoans put together. Not only is this group abundant, but it is diverse. Single stations contain a wide variety of species whose morphologies differ in ways that are often gross, reflecting several higher taxa. Many of these taxa are cosmopolitan in distribution.

The animals in question are small (only a few millimeters across) clusters of minute branching tubules. They are fragile and often obscure because of the sediment which covers their surfaces. We know from experience that they are often ignored or discarded from general collections during the sorting procedure because they look like lint, nondescript organic detritus, poorly-washed balls of sediment, or minor fragments from the surface of some undefined larger organism. In cases where they might be recognized as benthic organisms, they could reasonably only have been considered sponges or foraminifers. However, sponge specialists reject them as lacking any of the features of that phylum, and they are so unlike the morphologies classically regarded as belonging to the Foraminifera that specialists of that group are loath to accept them. Hessler (1974) and Hessler & Jumars (1974) have suggested that they may belong to the Xenophyophoria, but Tendal rejects this possibility. Thus, for the most part the few specimens that have been retained rest in limbo.

The only major programs in which these animals have been retained by routine are those of Hessler from his samples in the abyssal Pacific, the more recent samples of the Soviet Union's Institute of Oceanology, and the French investigations in the Bay of Biscay. The Russians call these animals "vetvistye komoktchki", which means "branching lump" (A. Kuznetsov, personal communication). This appellation seems especially appropriate, and therefore we shall continue to call them "komoki" (singular "komok") as a matter of convenience.

As a result of our investigations, we conclude that komoki are indeed foraminifers of the agglutinating type. However, except for their being members of the suborder Textulariina, they are for the most part completely unacceptable by the present taxonomic hierarchy. We therefore erect the new uperfamily Komokiacea to include them.

The problem with describing a group such as this for the first time is that it is so vast. Single samples contain dozens of species, and we suspect that the total number of species in just our few hadal, abyssal, and bathyal samples may be in the hundreds. Clearly, it will take years of laborious effort to bring the knowledge of komoki up to the level of that of other recent taxa. We therefore choose in this first treatment to confine ourselves to describing this superfamily and some of the lower taxa which typify the range of morphologies that clearly belong within it. In limiting ourselves in this way, we fully recognize that there will be many important morphologies that will need future treatment.

We will, furthermore, discuss in the light of present information the distribution of komoki and their position in deep-sea communities.

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II. MATERIALS

Our samples come from several sources. The core of the collection is part of Hessler's sampling of the abyssal oligotrophic community under the central North Pacific gyre (Hessler 1974, Hessler & Jumars 1974). We have concentrated our efforts on this material, firstly because we are familiar with the way in which it was collected and with the community from which it comes. Secondly, because we then can illustrate the range of morphologies that live together. Thirdly, because we have box core samples from this area which will ultimately allow quantification of the organisms on the bottom.

The samples used for comparative morphological study and for determination of geographic range have been selected from collections borrowed by Tendal from institutions in other countries (Table 1).

Table 1. Collections from which supplementary samples have been selected.

Expeditions	Geographical region	No. of samples	Depository of collection
"Valorous", 1875	N. Atlantic Ocean	1	British Museum of Natural History, London
"Galathea", 1950–1952	Round the world	8	Zoological Museum, Copenhagen
"Vitiaz", 1958, 1959, 1969	N. Pacific Ocean	23	Institute of Oceanology, Moscow
International Indian Ocean Expedition, "Anton Bruun", 1964	W. Indian Ocean	1	Smithsonian Institution, Washington
"Meteor" 3, 1966	Iberian Sea	3	Institut für Hydrobiologie und Fischereiwissenschaft, Hamburg
Climax II, "Argo", 1969	N. Pacific Ocean	4	Scripps Institution of Oceanography, La Jolla
"Eastward", 1972	W. Atlantic Ocean	3	Zoological Museum, Copenhagen
South Tow – leg 1, "Thomas Washington", 1972	Equatorial and South Pacific	2	Scripps Institution of Oceanography, La Jolla
Cruise 14, "Akademik Kurchatov", 1973	Caribbean	39	Institute of Oceanology, Moscow
"Thalassa", 1973	Bay of Biscay	17	Centre Océanologique, Brest
Biogas VI, "Jean Charcot", 1974	Bay of Biscay	10	Centre Océanologique, Brest
Eurydice – leg 7, "Thomas Washington", 1975	Philippine Trench	2	Scripps Institution of Oceanography, La Jolla
Wingstrand, 1975	Korsfjorden, Norway	2	Zoological Museum, Copenhagen
Wingstrand, "Dana", 1976	Skagerrak, E. North Sea	1	Zoological Museum, Copenhagen

Table 2. List of the stations from which the samples of Komokiacea used in the present investigation originate.

AB – Anton Bruun; Ar – Argo; Bi – Biogas; Eastw – Eastward; Gal – Galathea; Ku – Akademik Kurchatov; Me – Meteor; Tha – Thalassa; Va – Valorous; Vi – Vitiaz; Wash – Thomas Washington; Wing – Wingstrand.

AD – anchor dredge; BC – 0.25 m² box corer; BD – Boillot dredge; BT – beam trawl; ES – epibenthic sled; OG – okean grab; OT – otter trawl; PG – 0.2m² Petersen grab.

Atl. – Atlantic; Carib. – Caribbean; Pac. – Pacific.

eutr. – eutrophic; olig. – oligotrophic; sublitt. – sublittoral; trans. – transitional.

Ship	Stat. No.	Depth (m)	Latitude	Longitude	Location	Gear
AB	382C	4900	34°06'S	41°15'E	W. Indian eutr., abyssal	BT
Ar	H-30	6065-6079	30°05'N	156°12'W	Cent. N. Pac. olig., abyssal	ES
–	H-36	5588-5615	42°48'N	165°45'W	Cent. N. Pac. eutr., abyssal	ES
–	H-37	5532-5546	42°45'N	165°42'W	Cent. N. Pac. eutr., abyssal	ES
–	H-39	7298	50°58'N	171°38'W	N. N. Pac. eutr., hadal	BC
Bi	DS 75	3250	47°28'N	9°08'W	E. Atl. eutr., abyssal	ES
–	DS 78	4706	46°31'N	10°24'W	E. Atl. eutr., abyssal	ES
–	DS 79	4715	46°30'N	10°27'W	E. Atl. eutr., abyssal	ES
–	DS 86	1950	44°05'N	4°19'W	E. Atl. eutr., bathyal	ES
Eastw	20087	4270	32°21'N	74°54'W	W. Atl. eutr., abyssal	ES
–	20097	2400-2220	33°21'N	75°58'W	W. Atl. eutr., abyssal	ES
Gal	52	2550	1°42'N	7°51'E	E. Eq. Atl. eutr., abyssal	OT
–	65	2610	2°17'S	8°10'E	E. Eq. Atl. eutr., abyssal	PG
–	235	4810	4°47'S	46°19'E	W. Indian eutr., abyssal	OT
–	238	3960	3°23'S	44°04'E	W. Indian eutr., abyssal	OT
–	716	3570	9°23'N	89°32'W	E. eq. Pac. eutr., abyssal	OT
–	726	3670-3270	5°49'N	78°52'W	E. eq. Pac. eutr., abyssal	OT
Ku	1178-A	8150	19°33'N	68°09'W	Carib. eutr., hadal	OG
–	1181	5220-5300	19°56'N	68°20'W	Carib. eutr., abyssal	BT

Ship	Stat. No.	Depth (m)	Latitude	Longitude	Location	Gear
–	1187	5650	19°17'N	68°05'W	Carib. eutr., abyssal	OT
–	1189	7950	19°39'N	68°18'W	Carib. eutr., hadal	BT
–	1194	6650	19°49'N	68°08'W	Carib. eutr., hadal	OG
–	1201	2920	12°48'N	61°57'W	Carib. eutr., abyssal	OG
–	1209	1067	13°07'N	63°15'W	Carib. eutr., bathyal	OG
–	1238	1100-1120	16°52'N	79°34'W	Carib. eutr., bathyal	OG
Me	12-35	5300	42°N	14°W	E. Atl. eutr., abyssal	BC
Tha	410	1180	47°51'N	8°09'W	E. Atl. eutr., bathyal	BD
–	426	860	48°28'N	9°39'W	E. Atl. eutr., bathyal	BD
–	437	610	48°35'N	10°24'W	E. Atl. eutr., bathyal	BD
Va	9	3203	59°10'N	50°25'W	N. W. N. Atl. eutr., abyssal	?
Vi	4281	4360	20°02'N	122°00'W	S. E. N. Pac. trans., abyssal	?
–	6089	180	58°02'N	149°02'W	N. E. N. Pac. eutr., sublitt.	?
–	6104	2080	59°03'N	141°58'W	N. E. N. Pac. eutr., bathyal	?
–	6109	3450	52°13'N	139°44'W	N. E. N. Pac. eutr., abyssal	?
–	6118	2340	56°28'N	136°46'W	N. E. N. Pac. eutr., bathyal	?
Wash	H-29	5899	30°05'N	156°09'W	Cent. N. Pac. olig., abyssal	BC
–	H-153	5597	21°26'N	155°30'W	Cent. N. Pac. olig., abyssal	BC
–	H-170	5657	21°30'N	155°29'W	Cent. N. Pac. olig., abyssal	BC
–	H-84	4435-4438	03°02'N	125°01'W	E. Eq. Pac. eutr., abyssal	ES
–	H-99	3768-3804	21°56'S	131°08'W	Cent. S. Pac. olig., abyssal	ES
–	H-189	9600	10°36'N	126°38'E	W. Eq. Pac. eutr., hadal	BC
–	H-196	9605	10°36'N	126°38'E	W. Eq. Pac. eutr., hadal	BC
Wing	1	670	60°10'N	5°15'E	E. Atl. eutr., bathyal	ES
–	2	400	58°08'N	9°54'E	E. Atl. eutr., bathyal	ES

At this early stage in our understanding of the taxonomy we have not attempted to determine the geographic range of our species. On the other hand, the distribution of genera can be discerned with reasonable confidence. The samples used for this purpose are from the stations listed in Table 2.

The holotypes are deposited in the Zoological Museum, Copenhagen.

III. METHODS

One of the important reasons why komoki have not been recognized in the past is that the techniques used for handling deep-sea material have in large measure been inadequate. The following comments are intended to serve as a guide to handling material in the search for and investigation of this taxon.

Handling

Komoki do not have a rigid test; they are often soft and always fragile. Thus, samples must be handled with care. Preferably there should still be sediment in the sample when it reaches the sea surface; this sediment will insulate the animals from mechanical damage in the water column.

The sample should be washed gently. The elutriation technique of Sanders, Hessler & Hampson (1965) is recommended. Since komoki are often small, a fine-mesh screen should be used; a 300-500 µm mesh would be adequate.

Fixation

The washed sample must be fixed immediately in order to reduce as much as possible cytological changes after death. Hessler's samples, which are the main part of the present material, were fixed in buffered 4 % formaldehyde/sea water solution and after 2 days transferred to 80 % ethanol for storage. Although this procedure is commonly accepted as usable for small marine animals, it often poses difficulties for histological workers because of shrinkage during stages following fixation. In our samples the following features may possibly be signs of such an effect: the crooking of tubules in some species, the wavy appearance of the inner organic layer of the test in places, the extremely diffuse condition of the plasma, and the strong tendency of the stercomata to be arranged in tight clumps filling only part of the tubule lumen.

Concerning more detailed cytological and cytochemical work in future we recommend that tests be performed with fixation in Bouin's fluid, Carnoy or Clarke, Flemming's fluid, Susa and Zenker.

Because of their fragility, komoki cannot be dried without special procedures.

Staining

Rose bengal, the stain commonly used to discriminate living foraminifers, does not work well on komoki. A more promising stain seems to be the mixture of eosin B and biebrich scarlet proposed by Williams (1974). It should be used in a 1:1000 concentration of either 4-5 % formaldehyde as given by Williams, or distilled water. Alcohol does not work at all, or at best extremely faintly on protozoans. It should be noted that there are differences between genera (and species) of komoki as to the degree they are stained: *Septuma, Lana, Baculella,* and *Edgertonia* stained differently, but strongly in about 12 hours, whereas *Komokia, Ipoa,* and *Normanina* stained faintly or not at all, even when staining was prolonged to 96 hours. Destaining can be done with 96 % alcohol or 4-5 % formaldehyde. Alcohol is the most effective, removing practically all stain in 48 hours.

SEM preparation

The procedure used for preparation of specimens for scanning electron microscopy was critical point drying (Nemanic 1972). The technique was modified for use on the Komokiacea as follows: a 6 mm hole was punched in the lid of a No. 00 Beam capsule, and a 50 µm plankton netting was inserted into the cap over the hole. Solutions were injected with a hypodermic syringe via a No. 26 needle through the other end of the capsule.

From storage in 80 % ethanol, the komoki were hydrated, immersed in a 2 % solution of $AgNO_3$ for 10 minutes at room temperature and rinsed in three changes of distilled water. They were subsequently treated with Cajal's reducing solution (Luna 1968) for 5 minutes, and rinsed again in two changes of destilled water.

Dehydration was followed by two extra changes of 100 % ethanol for 15 minutes each, a 1:1 solution of ethanol and freon 113 for 15 minutes, and finally two solution changes with freon 113 for 15 minutes each. The freon 113 was drained from the capsule, which was quickly placed within the freon critical point dryer (Cohen et al. 1968) and dried using freon 13.

The specimens were affixed to an aluminum stub

with silver conducting paste and coated under vacuum with approximately 200Å of gold-palladium. They were viewed with a Cambridge S-4 Stereoscan scanning electron microscope.

Sectioning

Considerable information about morphology can be learned by examination of paraffin sections, of which we recommend 5-7 µm as a useful thickness. Schiff's PAS reaction, hematoxylin, Heidenhains Azan, and toluidine blue are general stains which highlight especially the inner organic layer of the test. Toluidine blue has the disadvantage that it may stain the outer agglutinated layer too heavily.

The terminology used is the same as for Foraminifera.

The size range given of a single species must be judged in relation to its morphology, because it is sometimes difficult to distinguish between small, entire specimens and fragments of larger ones.

One of the aims of this paper is to show the exceedingly large morphological variation found within the Komokiacea. A person unfamiliar with the group might therefore come to the conclusion that the description of species is easily done, requiring only a few discrete characters. Although it may be so in some genera, in general this will not be the case. Our experience is that a number of morphologies strongly resembling each other, when closely examined must be judged as representing separate species. This is the case both within single samples and between widely distributed samples.

It is desirable to avoid the state of affairs known from several other taxa rich in species that a great many descriptions are incomplete in important characters and inadequate for later work. Therefore, when describing a new species of Komokiacea one should always pay attention to the following features, although the elucidation of some of them may be rather time-consuming:

1. Growth form and outer dimensions.
2. Details of branching, including anastomosing versus nonanastomosing.
3. Presence or absence of beads.
4. Diameter of tubules.
5. Presence or absence of sediment filling in interstices.
6. Type of agglutinated material.
7. Structure of the tube wall, with dimensions.
8. Presence or absence of chambering (can only be reliably worked out through sectioning).
9. Presence (and structure) or absence of foramina.
10. Distribution of stercomata.
11. Appearance of plasma and nuclei.

IV. MORPHOLOGICAL PART

A. External appearance of the komoki

Komoki are visible to the naked eye, their largest dimension generally being 1-5 mm.

A tremendous number of different, characteristic body forms are to be found endowing this taxon with a degree of diversity which at least equals that seen in the other two superfamilies of the suborder Textulariina, and which is comparable to that found e. g., among hydrozoans and bryozoans.

The basic element in the morphology of komoki is a fine tubule of even diameter, containing the plasma and a large quantity of faecal material, generally in the form of pellets called stercomata. Different organizational patterns of the tubules are reflected as different body forms. The external appearance is, moreover, strongly influenced in some species by the inclusion of sediment in the interstices between tubules.

The general body form of komoki is of two sorts. There may be a center of organization as in trees or bushes; here one may speak of central and peripheral tubules or at least of a center of growth (Pls 9A-D, 10, 11A-D). In the other case there is no center of growth or organization, just as would be the case with a ball of fleece or a scouring pad (Pls 13, 14A-B, 16C).

Branching is the basic feature controlling body form. In most cases branching is dichotomous, although tri- or polychotomy also exists (Pls 10A, 14C-D). Stems and branches never comprise more than one tubule. Diameter and cross section of the branches are often constant throughout the whole tubule system. There are, however, a number of cases where they are found to be different when comparing a stem (central tubule) to its side branches, and sometimes there is stepwise reduction following each level of branching. The ends of tubules are some-

times bulbous (Pls 11E-F, 12E) but most often straight and rounded (Pls 10, 11A-B).

Two types of branching have turned out to be of constant occurrence. In the first, the tubules are of cylindrical form, with only rare constrictions, and the distance between succeeding branching points is much larger than the branch diameter (Pls 10, 14C-D). In the second type, numerous, usually close-set, very short side branches give the tubule a beadlike appearance (Pls 15B, 16E). Here, constrictions of the main tubules are often seen, and the short side branches are often constricted at the base (Pl. 16A-B, D, E). While branching of the first type generally seems to follow a simple pattern, in the second type it is quite often complicated by tightly repeated branching and partial lateral fusion.

Anastomosing is a feature found in a fairly large number of species. We limit this designation to mean that direct communication between the cavities of two tubules occurs. It does not apply to the mere fusion of the outer agglutinating layer of two tubules which have grown contact.

B. The tube wall

In the tube wall two layers can be distinguished in sections seen with the compound microscope (Pls 21B-D, 22, 23, 24). The inner layer is generally very thin, less than 0.5 μm thick. It looks smooth on the interior surface, and stains readily with toluidine blue or PAS. Scanning electron micrographs demonstrate that the inner layer is frequently laminated. On the outside this layer is sharply demarcated from an agglutinated layer of sediment into which it may in some species project long fibers.

The agglutinated layer varies considerably in thickness, but 10 μm can be given as frequent measurement. The included particles are commonly of the clay and silt fractions, although particles of sand size are found in the tests of species from comparatively shallow localities. The organic material which holds the sediment together stains with toluidine blue or PAS and in some species shows reaction for organically bound iron when treated after Pearl's or Turnbull's methods.

In some species, long flexible tubules project from the general surface of the body (Fig. 10, p.191). These tubules differ from the rest in having a very thin outer, agglutinated layer.

Several species have been found to be septate with the chambers added in a linear arrangement (Pls 21A, 24A) and sometimes with corresponding faint constrictions on the surface of the tubules (Pl. 12A). Septae are two-layered, consisting of the inner organic layers of two successive chambers (Fig. 4; Pls 21B, 24A). They never include parts of the agglutinated layer. Some sections show that the inner organic layer may be laminated and that a very thin outer lamina may follow the outer agglutinated layer, the rest taking part in the formation of the septum. Secondarily formed, simple foramina which can be provided with a circular, thickened neck exist in some species (Pls 21A, 24A).

C. Pores

Komoki are devoid of real apertures. The pseudopodia must penetrate the tube wall through minute pores, but possibly these are of only temporary character.

In the surface of some specimens very small openings can be discerned with a dissecting microscope. The SEM photos of the exterior surface of the tubules show a wide size range of small (most of them <1 μm in diameter) openings with rounded or irregular outline (Pls 16F, 19C-D). The largest of these might be identical with those seen in the dissection microscope. However, these openings may only reflect the natural porosity of the agglutinating sediment. We have not seen perforations of the inner organic layer of the tube wall, neither in SEM photographs, nor in slides. There may be two explanations for this: shrinkage during treatment of the specimens may have eliminated the pores, or they are only temporary. Scattered, temporary pores might be difficult to find, because there would be few at a given moment.

D. Colour and consistency

Komoki often show a shade of tan which varies depending on the amount and type of particles in the agglutinated layer. With a thin, agglutinated layer the dark stercomata in the interior give the tubule a grey cast, or, if the stercomata are tightly concentrated, the appearance of a dark cen-

tral mass which is round or strandlike, depending on their arrangement.

The inner organic layer and the organic cement in the agglutinated layer provide the animal with a rather high degree of flexibility. If the agglutinated particles are few or small there seems to be space enough between them to allow for a certain degree of bending. If they are numerous or of sand size, there is a corresponding loss of flexibility.

E. The interior of tubules

Plasma and stercomata are found in the tubule lumen (Pls 21B-D, 22B, 25A). Sections and close inspection with the dissection microscope reveal that in many species a large part of the tubule system is empty (Pl. 26C-D).

The plasma is difficult to stain. It may either be strongly diluted or have the character of fine threads, or it may be so filled with ingested material in vacuoles or lacunae that it is hard to see.

In a few cases plasma is encountered in the SEM photos (Pls 17B, 18A-B). Although in some areas it looks homogenous, the main impression is that it is organized in an extensive network of very fine strings. There seem to be no inclusions, but commonly plasma strings were found in intimate contact with the surface of stercomata of the rugged type mentioned below.

Bodies resembling nuclei have been found in histological sections of most species. They are spherical to ovoid, with granular interior (Pl. 21B, D). The size variation ranges over an interval of about 5 μm in any one species, being from about 4 to 10 μm in diameter for the whole group. For some reason the Feulgen reaction did not work; these bodies resemble, however, nuclei after staining with haematoxylin-eosin and Heidenhains Azan. They can be distinguished from stercomata in unstained sections. In a single species, nucleoluslike bodies with diameter about 2 μm were seen.

The most conspicuous elements in the tubules are the stercomata or faecal pellets (Pls 21B, 22B, 23B-C, 25A). They are opaque or dark brown, generally up to about 10 μm in diameter, although they have been found as large as 35 μm, and are composed of a mass of unidentifiable small particles held together by a substance of the acid mucopolysaccharide type. With the compound microscope they look smooth on the surface, in the SEM photographs some look smooth, others rugged (Pl. 19E-F).

The phases in the process of formation of stercomata are expected to start with the uptake by the pseudopodia of particles from the environment. These are accumulated inside the test as loose masses of "ingested material" (Pl. 21C). During the digestive processes they are transformed into stercomata which finally are left in the tubule system. Reasons for this retention could be either that some phase in the digestive process is dependent on the accumulation of particles in large masses which are too large to be passed back out throught the very small openings in the test wall, or that the stercomata are of some use, for instance as a weight to counteract buoyancy. Another possibility is that the stercomata after some time in the tubule lumen are recolonized by microorganisms and can be redigested by the komokiacean. There is no indication of this, but if it existed it would be of the uttermost importance. Morphological specialization and accumulations of faecal pellets in the hindgut of the abyssal *Abra profundorum* have been proposed as an arrangement allowing bacterial growth with subsequent redigestion of the faecal material (Allen & Sanders 1966). A somewhat similar nutritional pattern is possible to a certain extent for *Hydrobia* (Newell 1965) and is attributed a considerable role in some decomposer food chains (Fenchel 1972).

F. The pseudopodia

On one occasion during the scanning process, parts of a branch of *Septuma ocotillo* were seen to be covered by a formation consisting of two elements in close contact (Pl. 20A-B). One is a coherent, relatively homogenous, although heavily perforated layer (Pl. 20C-E). The other is seen as a reticulation of undivided or dichotomously divided strings which are generally of even thickness (0.1-0.2 μm in diameter) and most often straight (Pl. 20E). Some strings connect irregular lumps of various sizes (0.5–2 μm in diameter), while other strings contact a lump at one end and either seem to penetrate the underlying homogenous layer, or possibly to join it with their other end.

The whole formation may be what is left of a part of the outstretched pseudopodial system. Before capture, it may simply have covered the test surface, or it may have been extended into the surrounding mud/water.

The homogenous, perforated layer resembles the pseudopod reticulum adjacent to the test as seen in *Iridia diaphana* after freeze drying (Marszalek 1969).

One can imagine a number of interpretations of the string-lump element. It should, however, be noted that what makes the surface of some stercomata rugged, is the presence of irregular lumps of an appearance and a size variation comparable to that of the lumps found on the presumed pseudopodial system (Pl. 20C). Moreover, this type of stercomata is generally found in contact with what seems to be plasma strings (Pls 18B, 19E).

Thus, what has been described above can be interpreted as part of the pseudopodial system showing phases of transport of nutrients. The pattern of food treatment could be much as reported in *Allogromia laticollaris,* where nutritive particles are transported by the pseudopodia as "lumps" into the test lumen to be digested, not in vacuoles, but in extracellular spaces, lacunae (Lengsfeld 1969). Differences from the *Allogromia* type of food uptake would be that komoki take in a large number of very small particles (selected because of presence of microorganisms on the surface?), digest them in the tubule lumen, and then leave the indigestible parts as faecal pellets inside the test.

V. GEOGRAPHICAL DISTRIBUTION

From the present collections, comprising more than 100 samples, we have selected about 40 to elucidate the geographical range of the Komokiacea (Table 2). Not all our samples were included, because in a number of areas there were stations lying close to each other. The criteria for selection were such as to allow the greatest attainable horizontal and vertical coverage. Only taxonomic levels down to genus are considered, because only a few samples (from the area of the central North Pacific gyre, Hessler 1974, Hessler & Jumars 1974) have as yet been treated to species.

A. Horizontal distribution

The superfamily Komokiacea has been found in the three main oceans and very near to the Arctic (Table 2 and Fig. 1). This implies a cosmopolitan distribution, the obviously large gaps in the distribution being due to lack of investigation, poor methods of washing, and misidentifications.

Both families are represented in the three main oceans.

Four of the seven genera, viz., *Septuma, Ipoa, Lana,* and *Baculella,* are distributed in the Atlantic, the Pacific, and the Indian oceans, while *Komokia,*

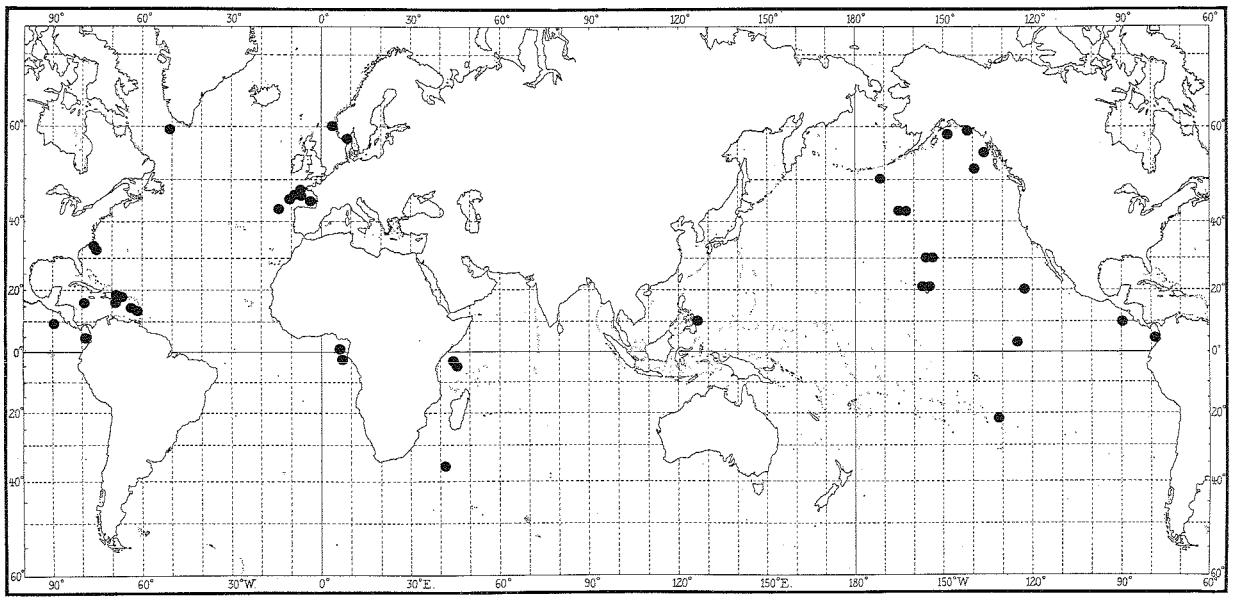


Fig. 1. Distribution of samples in which Komokiacea have been found.

Normanina, and *Edgertonia* have been found in the Atlantic and the Pacific.

B. Vertical distribution

The vertical range of the samples in which we have found Komokiacea is 400 to 9600 m, with by far the largest number of stations in the depth interval from 1000 to 7000 m (Fig. 2).

Although (as Fig. 1 shows) our samples are far from being evenly distributed over the deep-sea bottom of the world ocean (we have particularly large concentrations of stations in the North Pacific, the Caribbean area, and in the Bay of Biscay), on the basis of available information it seems reasonable to conclude that the Komokiacea is essentially a deep-sea group. Both in the Atlantic and in the Pacific we have several samples taken between 500 and 1500 m, indicating that the group has its shallowest distribution somewhere on the continental slope, perhaps the limit being physically correlated with the shift from sandy to clayey silt and with strongly diminished temperature variation.

One record is as shallow as 180 m, but this may not be reliable. There is only one specimen, and it may have been left in the gear from a previous deeper sampling.

The two families seem to have about the same depth distribution in the abyssal and hadal zones (Fig. 2). The Baculellidae has not been recorded shallower than about 2000 m.

Septuma and *Lana* are represented at true bathyal depths, while *Normanina* and *Baculella* appear between 2000 to 3000 m. *Komokia* has only been taken from the lower abyssal zone, whereas *Ipoa* and *Edgertonia* also appear in the abyssal but extend well down into the hadal zone, together with eurybathic *Lana* and *Baculella. Septuma* and *Normanina* extend down into the lower abyssal.

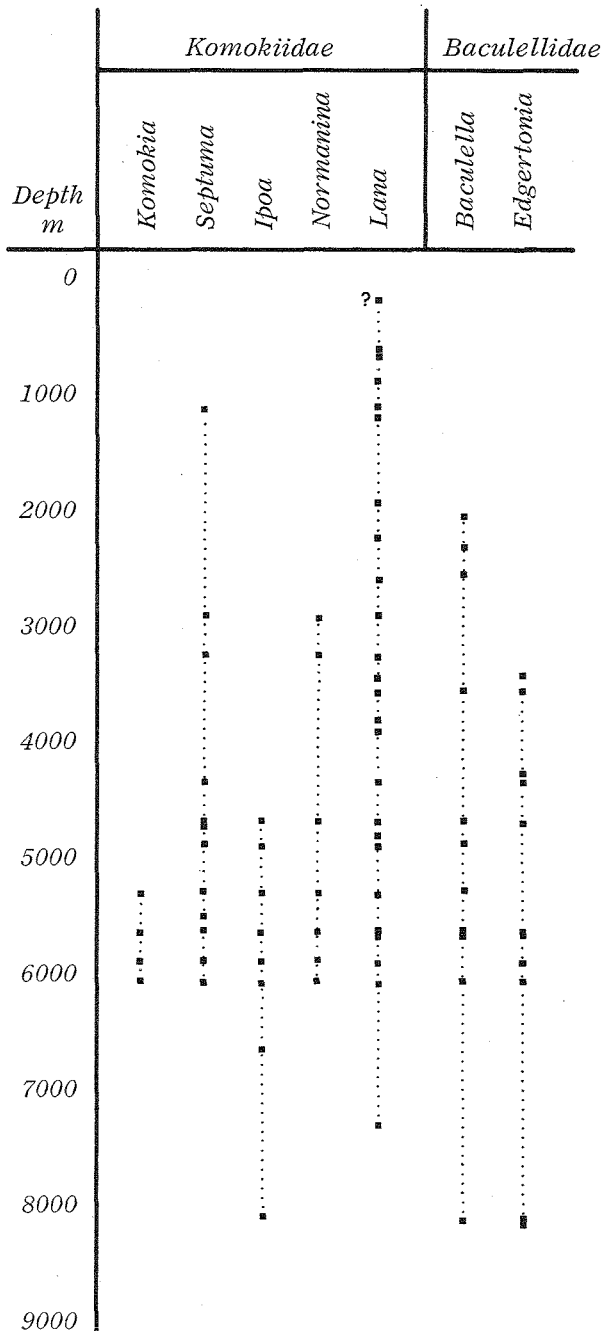


Fig. 2. The vertical distribution of families and genera of Komokiacea.

VI. POSITION IN DEEP-SEA COMMUNITIES

Because nearly all macrofaunal animals in the deep sea are very small (Sanders et al. 1965), screens with a mesh opening of 0.3–0.5 mm must be used to achieve complete retention of this faunal category. Careful sorting of samples washed through such screens reveals large numbers of komoki.

The greatest relative abundances of komoki have been seen in the oligotrophic abyss and in hadal trenches, as exemplified by samples from the central North Pacific (Hessler & Jumars 1974) and from the Philippine Trench. In such cases, their volume greatly exceeds that of all the metazoans combined and equals that of the remains of other Foraminifera. The relative abundance of komoki seems to be less in

the equatorial abyss and in the bathyal zone, as seen in the eastern equatorial Pacific and Southern California continental borderland, respectively. These data suggest that komoki are often a dominant, or at least an appreciable element in deep benthic communities.

It is difficult to quantify such relationships in terms which are meaningful for community analysis. Because komoki are so fragile, individuals are usually represented in a sample by several fragments. Thus, simple counts are insufficient to document their abundance. Obviously, at this early stage of investigation the samples are too valuable to be utilized for biomass measurements (wet weight, dry weight, organic carbon, etc.), since such techniques are more or less destructive.

Because of the test, especially in cases where it is agglutinated, it is generally difficult to determine which foraminiferan individuals in a sample are alive, unless special procedures are employed to reveal the presence of plasma. The high percentage of empty tests in shallow water samples is explained by short life span of single individuals (all plasma enters into the production of gametes and agametes), and/or high durability of the test.

In komoki the reproductive cycle is unknown. The test has a comparatively low content of organic matter, the inner organic layer being very thin and the amount of cement being small, which gives reason to believe that decomposition time may be short.

This suspicion is supported by histological studies. Ten specimens of *Septuma ocotillo,* 5 of *Lana neglecta,* and 4 of *Normanina tylota* were sectioned and inspected for evidence of having been alive at the time of sampling. The criteria used were the general condition of the body and the presence of nucleuslike bodies, especially after staining with Heidenhains Azan and haematoxylin. On these bases, all individuals were alive. These data must be viewed with caution, because no attempt was made at random sampling. However, if these observations are typical, then most komoki are alive. Even if true, such an observation must be interpreted with the understanding that only a small portion of a komokian tubule system actually contains living plasma.

To document the diversity of komoki, we analyzed 500 cm² vegematic subcores (Jumars 1975) of a 0.25 m² box core (H-153) from the type locality in the central North Pacific. Five randomly selected subcores from the same sample yielded 56 species (Table 3).

Table 3. Number of species of Komokiacea found in 500 cm² of box core sample H-153. The 56 species are roughly assigned to the morphological types represented by the known genera.

Morphological type	No. of species
Lana	20
Komokia	12
Edgertonia	6
Normanina	6
Baculella	5
Ipoa	3
Septuma	2
Others	2

General observations suggest that such high diversity is typical of abyssal samples from this area (Hessler & Jumars 1974), as is reasonable in view of the great stability of the physical regime.

These subcores were partitioned into layers and therefore allow analysis of the distribution of komoki within the bottom (Table 4). More than 80 % of the specimens were in the top 1 cm while there were only 2.5 % below 2 cm. This restriction of most individuals to the most surficial layers conforms to the pattern displayed by the rest of the fauna, and is what one would expect in a nutrient-poor, physically calm environment.

Interestingly, some species showed greatest abundance in the 1-2 cm layer, and 5 species (of *Lana* and *Baculella* morphologies) were not at all found in the 0-1 cm layer, indicating that at least some komoki live beneath the surface. This observation demonstrates that caution should be used in deducing komokian life styles from morphology and appearance alone.

Table 4: The distribution of species and specimens in the upper 10 cm of 500 cm² of box core sample H-153.

Depth (cm)	No. of species	No. of specimens
0-1	44 + ≥ 5	1637
1-2	25 + ≥ 5	297
2-4	6 + ≥ 3	46
4-7	2 + ≥ 1	3
7-10	0 + ≥ 1	1
Total	50 + ≥ 6	1984

VII. SYSTEMATIC PART

Komokiacea in the literature

Only one genus, *Normanina,* has been treated in the previous literature, commonly as a member of the family Astrorhizidae.

Poorly known organisms consisting of fine tubules can be found in "incertae sedis" positions in many different phyla. It is recommended that no such species be included in the Komokiacea without inspection of material, although merely noting the existence of these "problematica" may be useful (see e. g. p. 185).

Proposed classification of the Komokiacea

The system proposed here includes the description of eleven species, all of them new to science. These are to be regarded as a necessary formal foundation for the taxonomic pattern of the superfamily. The decisions have been made on the basis of much wider experience gained through the investigation of a large number of undescribed species.

Superfamily Komokiacea n. superfam.

1. Family Komokiidae n. fam.
   Genus *Komokia* n. gen.
   Genus *Septuma* n. gen.
   Genus *Ipoa* n. gen.
   Genus *Normanina* Cushman, 1928.
   Genus *Lana* n. gen.
2. Family Baculellidae n. fam.
   Genus *Baculella* n. gen.
   Genus *Edgertonia* n. gen.

Descriptions

The higher level classification used here is according to Honigberg et al. (1964).

Phylum Protozoa
Subphylum Sarcomastigophora
Superclass Sarcodina
Class Rhizopodea
Subclass Granuloreticulosia
Order Foraminiferida
Suborder Textulariina

Remarks: A crucial point in all diagnoses of the order Foraminiferida or the subclass Granuloreticulosia is the presence of delicate, finely granular reticulopoda. These have, however, only been described in a few species, and although there seems to be agreement on the characterization of the pseudopodial system as given above, nearly nothing is known about details of the structure and movement. The classification of a given organism as a foraminifer is generally done on test characters, and the Komokiacea is no exception to this. The features which were decisive for including the Komokiacea in the Foraminiferida were the following: an organic ("chitinoid") layer covered with a layer of foreign material held together by a secreted organic cement; the test with one to many chambers; accumulations of stercomata in the interior; pseudopodia supposed to protrude from simple wall perforations.

KOMOKIACEA n. superfam.

Diagnosis: Test consists of complex system of fine, branching tubules of even diameter. Test wall simple; agglutinated particles argillaceous. Stercomata (faecal pellets) accumulate within tubules.

Type genus: *Komokia* n. gen.

Remarks: In referring to tubules as fine, we mean that the ratio of the size of the individual to the diameter of one of its tubules is very high. Referring to ammodiscacean tubes as coarse implies the opposite of this.

When more information accumulates, other characters may turn out to be of diagnostic value also at this level, viz., the finer details of tubule wall structure, the apertures, the organization of the plasma, and the stercomata formation and arrangement.

Discussion:
The detailed knowledge of the morphology of many agglutinating foraminifers is still scarce, a fact that makes strict demarcation of subgroups difficult and complicates transferring of earlier described species from one group to another without direct examination.

In our materials from many parts of the world there is a large number of undescribed agglutinating foraminiferan species referable to several new genera, which we arrange into two new families. The step to erect a new superfamily for these within the vast array of forms of the suborder Textulariina may seem rather drastic. However, the common

morphological pattern of komoki does not satisfactorily fit either of the two existing superfamilies.

This judgment is based mainly on the classification of the Foraminifera as outlined by Loeblich and Tappan (1964, p. C184 ff.). To allow direct comparison with the definition of the Komokiacea we restate the diagnoses of the two other superfamilies in a slightly modified and rearranged form.

Ammodiscacea: Test nonseptate or only irregularly constricted, of simple form, irregular, spheroidal or tubular; tubular types branching, straight, or enrolled; tubules generally coarse, often tapering or irregular. Test wall simple or labyrinthic; agglutinated particles arenaceous or argillaceous. Apertures to external environment simple, in tubular forms generally large.

Lituolacea: Test composed of coarse chambers whose arrangement is spirally coiled, bi- or triserial, or straight; rarely branching. Test wall simple or labyrinthic; agglutinated particles arenaceous or argillaceous. Apertures single or multiple.

Lituolacea is the best defined of the two, a fact that appears not only from the diagnosis, but also when comparing the families included.

Ammodiscacea is one of those heterogeneous taxa so well known from many other parts of the animal classification, consisting of a collection of widely different groups which remain when other, well defined taxa are brought into their proper context. This is one of the reasons why the distinction between the Komokiacea and the other textulariines appears blurred. The fate of some genera hitherto included in the subfamily Dendrophryinae (family Astrorhizidae) illustrates the situation: *Syringammina* was transferred by Tendal (1972) to a family of its own within the subclass Xenophyophoria, and *Normanina* is here placed in the new family Komokiidae.

Key to the families and genera

1a. Tubules of cylindrical form; distance between succeeding branchings several times tubule diameter ..... Fam. Komokiidae 2 (p. 178)
1b. Tubules of beadlike appearance because of numerous short side branches; distance between succeeding branchings 1–3 tubule diameters ..... Fam. Baculellidae 6 (p. 187)
2a. Tubules anastomosing ..... *Lana* (p. 185)
2b. Tubules free 3
3a. Body organized into base and radially extending branches, each bearing a distal swelling ..... *Normanina* (p. 181)
3b. Body bushlike; branches without distal swelling 4
4a. Tubule diameter markedly decreasing following each branching ..... *Ipoa* (p. 180)
4b. Tubule diameter nearly similar throughout individual 5
5a. Tubules septate; branching primarily at base ..... *Septuma* (p. 179)
5b. Tubules nonseptate; branching becomes more frequent distally ..... *Komokia* (p. 178)
6a. Body stick- or club-shaped ..... *Baculella* (p. 187)
6b. Body rounded ..... *Edgertonia* (p. 190)

KOMOKIIDAE n. fam.

Diagnosis: Body variously shaped: tree- or bushlike, or tangled clump. Tubules basically cylindrical in form, infrequently constricted, and with distance between branchings generally appreciably longer than diameter.

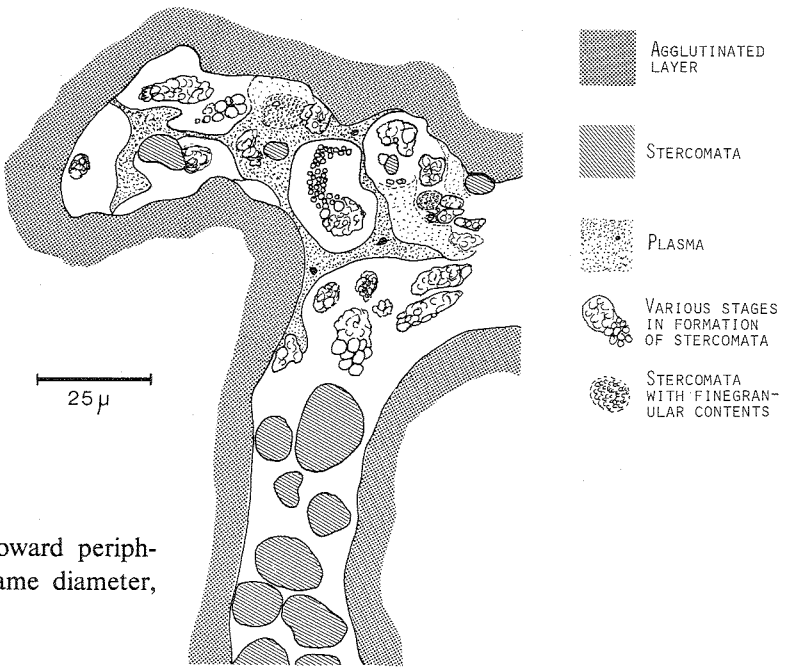
Type genus: *Komokia* n. gen.

Remarks: We prefer to put the genera in an order reflecting conditions of primary tubules and degree of complexity in overall branching pattern. At present, there is not enough general information on the Komokiidae to estimate the value of characters such as septation and presence of distal swellings, and of more special features of branching such as marked changes in diameter of tubules following divisions.

Komokia n. gen.

Diagnosis: Body bushlike, branching mostly dichotomous, nonanastomosing, occurring anyplace along

Fig. 3. Section through part of a tubule of *Komokia multiramosa* n. sp.



tubules, with increasing frequency toward periphery. All tubules of essentially the same diameter, nonseptate.

Type species: *Komokia multiramosa* n. sp.

Distribution: Cent.N.Pac.: H-29, H-30, H-36.
Carib.: Ku-1181, Ku-1187.

Komokia multiramosa n. sp.
(Fig. 3; Pls 9A-B, 11A-B, 19F)

Material: H-30.

Diagnosis: Same as that of genus.

Description: Body formed like a radial bush, but comprising only sector of sphere, usually hemisphere or less. Primary branching exposed at lower surface, at center irregular, dichotomous to multiple, with bases of branches often defined by slight constriction. Thereafter, branching occurs irregularly, although there is a tendency that each successive branching halves the distance to the tip. Commonly four to six stages of branching, but up to ten have been found. Diameter of body up to 2 mm.

Tubules near base thicker than those at tip, but not markedly so; basal thickness 35-75 μm in diameter; peripheral diameter 35-50 μm. Tubules crooked, but generally trending in single, basically radial direction. Tips rounded. Tubules flexible, but stiff.

Colour greyish owing to visible filling of tubules with stercomata. Agglutinated particles clay.

Inner organic layer of tubule wall <0.5 μm thick. Outer layer of agglutinated sediment 5-10 μm thick.

Cavity of tubules nonseptate (Fig. 3).

Remarks: Some, rather rare specimens have a very distinctive appearance because only tips of tubules are filled with stercomata, the central portion of the body being pure tan. Moreover, the tubules are less crooked and more coarse than is common for the species. In our opinion, these specimens do not represent a different species, partly because in some tubules the filling is in fact complete from base to tip, partly because the dimensions are as in *K. multiramosa,* although in the upper end of the range. These conspicuous specimens may well be the oldest in the population.

Septuma n. gen.

Diagnosis: Body bushlike; branching sparse, dichotomous, nonanastomosing, primarily at base. All tubules of nearly the same diameter, divided internally by septa with foramina.

Type species: *Septuma ocotillo* n. sp.

Distribution: Cent.N.Pac.: H-29, H-30, H-37.
SE.N.Pac.: Vi-4281.
E.Atl.: Bi-DS75, Bi-DS78, Bi-DS79, Me-12-35.
Carib.: Ku-1181, Ku-1187, Ku-1201, Ku-1209.
W.Indian: AB-382C.

Septuma ocotillo n. sp.
(Fig. 4; Pls 9C, 10A-B, 12A-B, 19A, 20A-F, 21A-D)

Material: H-30.

Diagnosis: Same as that of genus.

Description: Body formed much like a bush whose many primary branches radiate irregularly outward from a single area, whose branching may be dichotomous or multiple, but where the interbranch distances are always very short. All additional branching is dichotomous. Secondary branching may occur close to base. Tertiary and quaternary branchings are well separated by long unbranched zones. Size of body up to 3 mm across. Length from base to tip up to 2 mm.

Tubules which form branches give appearance of being of similar diameter throughout length, although they taper almost imperceptibly; near base 50-105 μm in diameter, toward tips 30-55 μm. Tubules crooked between branchings, but only modestly so, such that on the whole they appear to be straight or only gently curved. Sides of tubules straight, only faintly constricted at level of internal septa (Pls 10A-B, 12A-B). Tubule tips rounded. Tubules flexible, but stiff.

Colour tan, darker toward base, probably because of thicker accumulation of agglutinated particles there. Agglutinated particles clay, or at coarsest, silt. In distal parts of the branches are consecutive groups of stercomata, each representing one chamber; from the outside they look like a string of pearls.

Inner organic layer of tubule wall 0.5-1 μm thick. Outer layer of agglutinated sediment 5-20 μm thick, commonly around 10 μm.

Cavity of tubules subdivided into nearly equal chambers by regularly spaced, transverse septa (Pl. 21A). Chambers are 30-75 μm long and 20-50 μm across (Pl. 21B). Generally they are longer than wide, and a common size is about 50×30 μm. In short chambers the wall is often wrinkled, possibly as an artifact.

Septa are constrictions of inner organic layer, laminae of which pull away from agglutinated layer at this point (Fig. 4; Pl. 21A-B). Consequently, they are in principle double layered. In each septum is a simple, circular foramen which generally is centrally placed, although occasionally it may be acentric (Pls 19A, 21A). Edge of foramen thickened, forming ring with inner diameter of 8-12 μm, in a single case 18 μm. The ring which is 3-4 μm thick merges gradually with the rest of the septum.

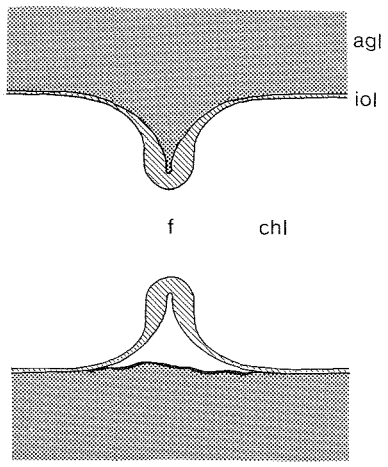


Fig. 4. Diagram of septum in *Septuma ocotillo* n. sp.; agl – agglutinated layer, iol – inner organic layer, f – foramen, chl –chamber lumen.

Chambers more or less filled with stercomata which are round or ovoid, more rarely irregular, and measure 5-10 μm in diameter.

Nuclei (Pl. 21B, D) are ovoid or spherical, measuring 5-12×6-15 μm. They look granulated in the sections, and are, at least in some cases, provided with a spherical nucleolus measuring about 2 μm in diameter. The distribution of the nuclei is difficult to elucidate because they do not stain well. Commonly only one is found in a chamber, but from time to time there may be two. In a few specimens nuclei were found in most chambers, but most often they are not seen. No particular pattern could be recognized in their distribution along the branches.

Remarks: On some specimens are rounded, light formations 100-200 μm in diameter, most often near the base and more or less entangled with the branches. These give the impression of being a basal swelling of the body of *S. ocotillo*. However, the sections reveal that these are in fact specimens of an agglutinating rhizopod, using *S. ocotillo* as substratum. It is distinguished from *S. ocotillo* by the following: no inner organic layer in the wall, no chambering, several nuclei present in the undivided plasma, plasma filled with small inclusions, devoid of stercomata, particles of the test coarser, and wall thickness generally much larger.

Ipoa n. gen.

Diagnosis: Major fragments treelike with basal stem followed by burst of tightly spaced multiple branch-

ing. Diameter of tubules decreases markedly with each branching. Tubules nonseptate.

Type species: *Ipoa fragila* n. sp.

Distribution: Cent.N.Pac.: H-29, H-30.
E.Atl.: Bi-DS78.
Carib.: Ku-1181, Ku-1187, Ku-1189, Ku-1194.
W. Indian: AB-382C.

Remarks: The branching pattern in combination with the strong decrease in tubule diameter creates an appearance much like that of segments of a head of cauliflower.

Ipoa fragila n. sp.
(Pls 9D, 11C-D)

Material: H-30.

Diagnosis: Same as that of genus.

Description: We possess only one large specimen (Pl. 9D), 3 mm long and 2 mm across, that we think is close to complete; it is characterized by having the central tubule surrounded by primary branches.

The rather vaguely defined central tubule measures 150-190 μm across and may be irregularly subdivided by constrictions. It is recumbent, as suggested by the relatively weak development of primary branches on one surface, presumably the bottom.

Few large primary branches extend radially from the stalk formed by the central tubule. Their bases are sometimes broadly connected with the central tubule, but more often constricted and therefore distinct from it. Perhaps because of the constrictions these branches are easily broken off, and therefore this species is represented almost entirely by isolated major fragments. Primary branches measure 100-125 μm across and 125-625 μm in length (from base to burst of multiple branching).

Numerous branches with rounded tips occur at the distal end of primary branches through dichotomous or multiple branching in closely spaced succession. These branches measure 25-60 μm across and up to 375 μm in total length. Some of the most distal branches are little more than knoblike processes. In combination, the distal branches give the total body a loose, lobular appearance.

Consistency stiff, although somewhat flexible. Colour of most of the body tan, but faintly greyish in distal branches owing to barely visible core of stercomata in the tubule cavity. Agglutinated particles clay.

Inner organic layer of tube wall exceedingly thin (<0.5 μm), outer layer of agglutinated particles 5-15 μm thick, with thicknesses of 5 μm restricted to distal branches.

Cavity of tubules nonseptate. In central tubule and primary branches it is nearly empty, whereas a seemingly single row of ovoid, 15-35 μm long stercomata is found in each distal branch.

Remarks: Although the species is rarely seen to be intact, its major fragments are so abundant and distinctive that its description is warranted.

Normanina Cushman, 1928, emend. herein

Normanina Cushman, 1928, p. 7; Galloway 1933, p. 80; Cushman 1948, p. 85; Loeblich & Tappan 1964, p. C192.

Diagnosis: Base or center composed of tubules tightly branching in complex, irregular pattern. Tubules radiate outward from base and terminate in globular or clublike portion.

Type species: *Normanina conferta* (Norman, 1878).

Distribution: Cent.N.Pac.: H-29, H-30, H-36.
NW.N.Atl.: Va-9.
E.Atl.: Bi-DS 78, Me-12-35.
Carib.: Ku-1187, Ku-1201.

Remarks: Starting with Cushman (1928, p. 7) the genus *Normanina* has been variously characterized by different authors. All of them, like Norman, regarded the organism as a bunch of individuals, and their definitions reflect their interpretations of two features, viz., the localization of the oldest part and the presence or absence of apertures.

In his original description of the type species (as *Haliphysema confertum*) Norman (1878, p. 279) described the tubular portion of the branches as "their bases", thereby inferring that this is the oldest part. He mentioned apertures as "mouth-opening very large", but did not say anything about the location, and his figures do not illustrate this point. Cushman (1928, 1948) interpreted the distal swelling of the

branches as the oldest part, referring to apertures at the end of the tubular portion. Galloway (1933) seems to have regarded the tubular part as the oldest, placing an aperture at the end of the tubule. Loeblich & Tappan (1964) mentioned "central mass, from which tubular portions radiate", inferring that the globular part is the youngest, and they did not observe apertures in the type specimen.

The central or basal part has been interpreted somewhat differently as "a nearly globular aggregation of pedicels", "mass", "rounded mass", and "central mass" (resp. Norman, Cushman, Galloway, Loeblich & Tappan, op. cit.). This may come from the fact that the central tubule complex is partly covered with sediment.

Although not naming or giving a closer description of the specimens concerned, Brady (1884, p. 276) seems to mention a *Normanina* sp. from 3950 m between Juan Fernandez and the South American coast as ". . . an organism . . . generally taking the form of little rosettes". The fate of the specimens is unknown (C. G. Adams, personal communication).

On the basis of his studies on a species of *Halyphysema,* the genus to which Norman ascribed *N. conferta,* Schepotieff (1912, p. 47) concluded that this species was only a growth form of the widely distributed shallow water species *H. tumanowiczii.* This point of view has not been discussed by other authors, and it is in our opinion entirely wrong.

Christiansen (1964, p. 135) reported on some specimens, which he referred to *N. conferta,* from Oslo Fiord. Although it is difficult to be sure in the absence of a detailed redescription of the type material which was not available, we doubt that he dealt with Norman's species; the swellings of the Norwegian specimens are much too regular in outline, and the basal part of the tubules were not connected with each other. The Norwegian specimens are not accessible.

Saidova (1968, p. 18; 1969, p. 133 and 134) lists three names: *Normanina fruticosa, N. ultraabyssalica,* and *N. elongata,* which are *nomina nuda* (1974, personal communication).

Two types of specimens are abundant in our material. We regard both as new species and describe them as *N. tylota* n. sp. and *N. saidovae* n. sp.

Normanina tylota n. sp.

(Figs 5-6; Pls 11E-F, 12C-D,F, 19B, 22A-B)

Material: H-30.

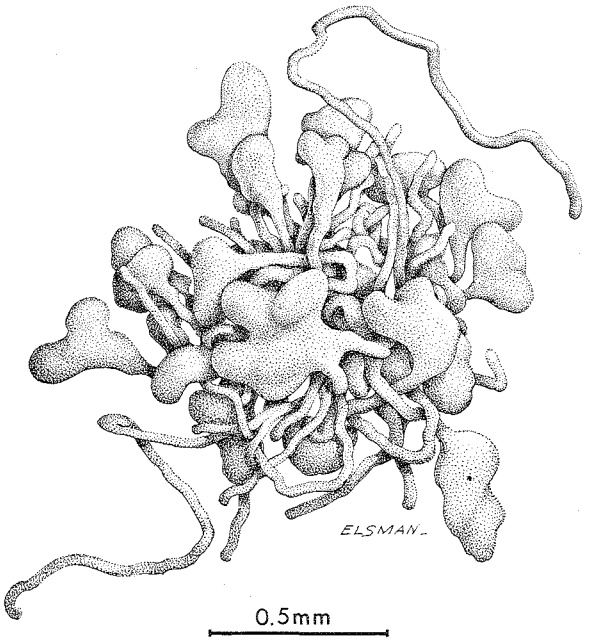


Fig. 5. *Normanina tylota* n. sp.; type specimen, slightly modified because of damages.

Diagnosis: Body 1.0-1.7 mm in diameter, roughly spherical. Up to about 60 radiating, 300-600 μm long, fragile, unbranched tubules each bearing a club-shaped to irregular swelling. Swellings internally subdivided by septae. Between swelling-bearing tubules radiate fewer, easily broken simple tubules, up to at least 1250 μm long.

Description: Diameter 1.0-1.7 mm. Specimens roughly spherical although in many cases with a somewhat flattened side, which may be the bottom, or an artifact of preservation. There is a conspicuous differentiation into a massive central or basal part, and an open, peripheral radially organized part.

The central part consists of a mass of repeatedly dichotomously dividing tubules, with sediment filling in some interstices. Anastomoses between the tubules were not seen, but their existence cannot be excluded because of the tightness of the mass.

More sediment is gradually deposited as the body grows, the central part making up 1/5-1/3 of the diameter at a given size. The branching pattern in this part of the body is, therefore, visible only in small specimens and occasionally in fragments of larger specimens. There may be a tendency of these frequently branching central tubules to have a slightly larger diameter than the unbranched peripheral tubules (in a small specimen they measured 31-38 μm against 25-31 μm).

Straight or moderately crooked, unbranched tubules of two types radiating from the central part constitute a characteristic peripheral area.

Most numerous (about 60 per specimen) are comparatively short tubules each bearing a distal swelling. They are 300-600 μm long measured from base to beginning of swelling. The diameter is even throughout the single tubule, but varies between tubules of the same individual from 25 to 50 μm, commonly about 35 μm. Branching is rarely seen, and anastomoses were not found. The distal swellings are set off from the tubules by form and darker colour. The area of transition from tubule to swelling is rather abrupt (Pl. 12C-D), although a more or less flaring part can always be distinguished. There is great variation in form and size of the swellings between individuals, and to a lesser degree within the same individual. If differences in form and dimension are expressive of different ages, the development of a swelling can be roughly outlined. The smallest swelling in our material is nicely club-shaped, measuring 150 μm in length (direction of tubule axis) and 60 μm in greatest diameter (perpendicular to tubule axis). When growth proceeds, it is at different rates in different directions. There is virtually no increase in length, whereas the diameter is considerably enlarged in two opposite directions so that a roughly biradial form is produced (Fig. 6, A-F). The growth is not always equally strong in both directions, more or less skew swellings being common (Fig. 6, G-M). In the more regular ones at this stage, the long axis (perpendicular to the tubule axis) often measures about 250 μm. During the final growth, up to a size of 350-400 μm, irregularities appear in the form of low, rounded knobs at different places on the swelling, seemingly with no relation to the former growth directions (Fig. 6, N-R). Sometimes two swellings are fused together, an event seemingly occurring only at a relatively early stage of development (Fig. 6,S).

The other, less common (10-20 per specimen) tubule type is long, up to at least 1250 μm, and bears no swelling at the distal end. The diameter is even throughout the same tubule, varying from 25 to 30 μm between tubules. The distal ends may be open, as if they were large apertures with the same diameter as the lumen of the tubule, or as if the end of the tubule was broken off. Alternatively, they taper slightly with a rounded, closed tip, representing either a growth stage of this tubule type or the unbroken condition.

Colour shades of tan; tubules light, swellings somewhat darker owing to internal accumulations of ingested material and stercomata and because of thicker layer of agglutinated material. Agglutinated particles clay and silt. Tubules fragile but nevertheless somewhat flexible.

Tubule and swelling wall in two distinct layers (Pl. 22A-B). Inner organic layer <0.5 μm thick. Outer layer of agglutinated particles about 5 μm thick in tubules, rising to about 25 μm in certain parts of

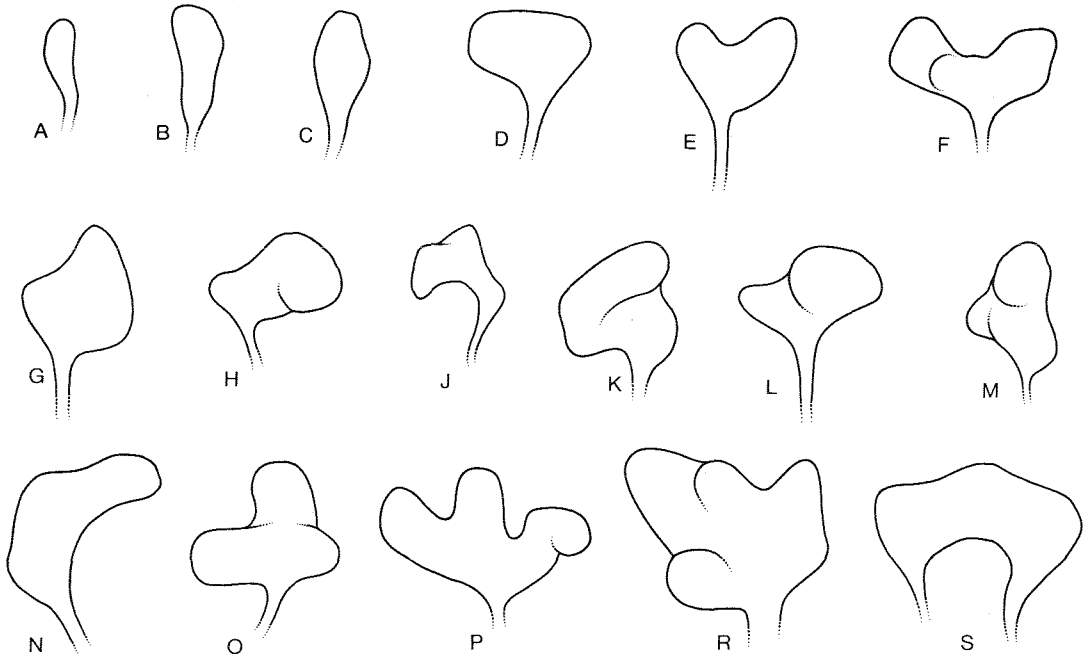


Fig. 6. *Normanina tylota* n. sp.; variation in form of swellings.

swellings. These thick parts of the swelling wall, seemingly only one per swelling, are quite often distinctly set off from the rest of the wall, and may represent accumulation sites for wall material.

Cavity of tubules without septae, most often empty, but sometimes more or less filled with stercomata or accumulated material.

Cavity of swellings subdivided by septa which are double layered (Pls 12F, 22B). In one preparation, there could be seen numerous small foramina (Pl. 19B). Fundamentally, the septa run transversely, as seen in young swellings, but with further unequal growth they are turned more or less parallel to the axis of the tubule, in some cases so much that it looks as if the septa trend toward the stalk. The chambers resulting from septation are somewhat irregular, rounded, and of different size, although they commonly measure about 20 μm across. They all share a part of the surface of the swelling.

A large mass of stercomata is found in each chamber. They are ovoid and measure 4-9 μm in length.

Nuclei may be represented by sparsely distributed, rounded or ovoid, granulated bodies 5-9 μm in diameter, seemingly one in each chamber.

Remarks: It seems possible to explain swelling form, pattern of septation, and arrangement and appearance of the demarcated stercomata masses in terms of plasma behaviour. From the beginning, in small, regular, nonseptate, club-shaped swellings, the plasma string containing accumulated food particles and stercomata is undivided. The diameter of the swelling cavity increases together with that of the plasma string, and at a certain size, when the diameter reaches about 3 times that of the stalk tubule lumen, the plasma divides, isolating the outermost part by a transverse septum. The isolated part continues to live, as indicated by the double nature of the septum, and presumably is in contact with the environment through the swelling wall. As growth proceeds new volumes of plasma become large enough and subdivide. The septa are still transversely made with respect to the growth direction of the plasma, but this no longer coincides with the long axis of the tubule which bears the swelling. The plasma string turns or bulges in the perpendicular direction after having separated the first or a few chambers, thus producing skewed and biradially swelling forms. The final irregular stage may be reached either by further growth and dividing of the original plasma string, by growth and dividing of the isolated plasma lumps in the chambers, or by a combination of the two. What makes the growth direction of the plasma change is difficult to say; it may be a question of the shortest distance to the surrounding water, or the location of the accumulation sites, or it may be an intrinsic factor related to the segregated plasma lumps.

N. tylota seems to be very near to the type species of the genus, *N. conferta,* which is known only from the type locality in the North Atlantic (Norman 1878). However, the descriptions as given by Norman and later authors are very general and devoted only to the external appearance. More detailed information on the holotype of *N. conferta* was provided by C. G. Adams (personal communication). Important differences between *N. tylota* and *N. conferta* are the presence of two types of tubules and large variation in swelling form in the former, while the latter has only one tubule type and comparatively regular swelling form. Other differences are found in the length, diameter, and number of tubules, and in the grain size of agglutinated particles.

Normanina saidovae n. sp.[1]

(Fig. 7; Pls 12E, 23A-C)

Material: H-30.

Diagnosis: Body 0.7-1.6 mm in diameter, irregularly rounded, somewhat oblong. Numerous tubules, often more than 100, flexible, radiating, up to 600 μm long, repeatedly dichotomously divided, each bearing a club-shaped, nonseptate swelling.

Description: Body 0.7-1.6 mm in diameter, irregularly rounded, often somewhat oblong. Conspicuously differentiated into a central massive part and a peripheral, radially organized part.

The central part consists of a single broad tubule or bulb. The diameter is about 100 μm and the length up to about 1 mm. In most cases, details of the central part are obscured by the numerous radiating tubules. In sections, the surface shows 3-4 deep constrictions (Pl. 23A) which together with radiating tubules branching off from the intermediate nodes are reminiscent of a short piece of backbone. In one case the tubule was seen to branch.

The peripheral part consists of radial, straight or somewhat crooked, usually dichotomously divided tubules bearing club-shaped swellings at the end of the branches (Pl. 12E). At the base, the radiating tubules

1. This honours Ch. M. Saidova for her comprehensive deep-sea foraminifer research.

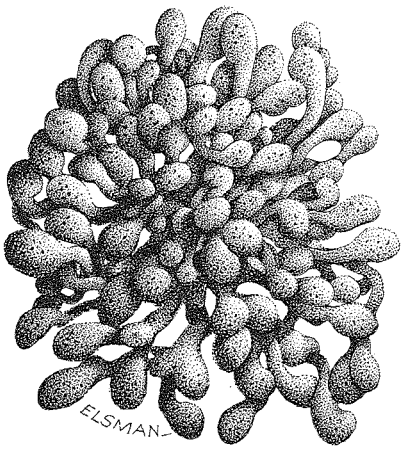


Fig. 7. *Normanina saidovae* n. sp.

originate from the central tubule in a number of 6-10 per node. Secondary and tertiary branching is very common, generally being well-spaced. Quaternary branching seems rare. The exact pattern of branching is difficult to see without destroying the specimens; only the outer one or two generations of branching are readily visible. The total length of the branched tubules, from central tubule to tip of swelling, varies greatly and may be up to 600 μm. The diameter is 25-40 μm, and it is not markedly influenced by the branching. The diameter of the swellings (measured as largest diameter) is 75-100 μm. Because they taper gradually into the tubule, their length cannot be given. Fusion of two swellings is rarely seen.

Colour tan, but stercomata usually visible as grey core. Agglutinated particles clay and silt. Tubules flexible.

In central tubule wall, inner organic layer 0.5-1.5 μm thick and outer agglutinated layer 10-20 μm thick. The cavity is incompletely subdivided by the constrictions in a short series of chambers. Both layers in the wall take part in the constrictions (Pl. 23A) which accordingly is not comparable to the septa found in other species. The cavity is nearly empty, only scattered stercomata being found.

In walls of tubules and swellings, inner organic layer <0.5 μm thick and outer agglutinated layer 5-10 μm thick. Cavity of tubules and swellings nonseptate, often filled with stercomata (Pl. 23B-C).

Stercomata are spherical or ovoid, up to 15 μm in diameter.

Remarks: *N. saidovae* is characterized by the easily visible, repeated branching which results in a larger number of radiating tubules, and by the regularity of the club-shaped swellings. In *N. tylota* and *N. conferta* branching of the radiating tubules is very rare, the number of swelling-bearing tubules is only about half of that of *N. saidovae,* and the swellings are of irregular form. From *N. tylota, N. saidovae* further differs in the organization of the central part and the lack of septation in swellings.

Lana n. gen.

Diagnosis: Loose clump of branching, anastomosing tubules; no focal point for symmetry or growth pattern. Interstices not filled with sediment. Tubules straight-sided (not constricted), nonseptate.

Type species: *Lana neglecta* n. sp.

Distribution: N.N.Pac.: H-39.
NE.N.Pac.: Vi-6089, Vi-6109.
Cent.N.Pac.: H-29, H-30, H-37.
E.eq.Pac.: Gal-716, Gal-726, H-84.
Cent.S.Pac.: H-99.
E.Atl.: Tha-410, Tha-426, Tha-437, Bi-DS78, Bi-DS79, Bi-DS86, Me-12-35,Wing-1, Wing-2.
Carib.: Ku-1187, Ku-1201, Ku-1238.
W. Atl.: Eastw-20097.
E.eq.Atl.: Gal–65.
W. Indian: AB-382C, Gal-235, Gal-238.

Remarks: In our experience the diagnosis as given by us covers an exceedingly large number of species. Later treatment of the full spectrum of our material may result in the erection of at least a number of subgenera. Characters within the genus in which some regular variation (not fully treated here) seems to be found are the form of the clump, the frequency of anastomoses, and the degree of filling of interstices with sediment.

Two previously described organisms may in formal description approximate the genus *Lana,* but we are nevertheless loath to include them. These species were members of the so-called "Deep-sea Keratosa" described by Haeckel (1889). They are only broadly characterized and cannot be referred even to phylum (Tendal 1972, p. 63). The resemblance to *Lana* is found in their reticulate tubular organization and the presence of foreign particles in the tube wall. The type specimens have been lost, and new material

has not been found. We reject their inclusion here because too few details are known, and, more important, the dimensions of body, tubules, and agglutinated particles are much larger than in Komokiacea.

Lana neglecta n. sp.
(Fig. 8; Pls 13A-B, 14D, 26B)

Material: H-30.

Diagnosis: Tubules 20-25 μm in diameter. Distance between branchings large in comparison with diameter of tubules (ratio commonly >6). Colour basically grey.

Description: Body is a loose, disorganized tangle of branching tubules forming a clump, up to 5 mm across, with rather ill-defined surface (Pl. 13A-B). Density of clumping somewhat greater toward center. Branching irregular, ranging from acute, through right-angled, to obtuse; at juncture, two branches may diverge from direction of third, or one may extend straight on from another, with the third coming off at angle (Pl. 14D). Branching generally dichotomous; successive branchings may be very close together (3 tubule diameters) but are most frequently a long distance apart (commonly 6 tubule diameters). Between branchings, tubules nearly straight, crooked, or strongly curved.

Tubules stiff, but flexible, all of same basic diameter, 20-25 μm. Larger diameters occur, but in these cases the tubules seem to be flattened and empty. Some sectors of a clump may appear grey, while others verge toward tan; in such cases grey tubules may be slightly thinner. Sides of tubules parallel, not constricted, although sometimes shriveled. Tips of tubules rounded. Agglutinated particles clay.

Tubule wall with thin inner organic layer <0.5 μm thick, and thicker agglutinated layer 1-5 μm thick. Outer layer in some parts of a specimen absent, possibly as the result of handling.

Cavity of tubules nonseptate, with stercomata varying in quantity from sparse in one area to abundant in another. Stercomata ovoid, 4-10 μm in diameter. Occasionally the tubule cavity is filled with ingested material not (yet?) formed as stercomata.

Blurred bodies resembling nuclei, spherical or ovoid, measuring 2-4 μm in diameter, were found sparsely in all specimens sectioned.

Lana reticulata n. sp.
(Pls 14A-C, 19C)

Material: H-30.

Diagnosis: Tubules 30-50 μm in diameter. Distance between branchings relatively short in comparison with diameter of tubules (ratio commonly about 4). Colour tan.

Description: We have not been able to discern what a complete individual looks like. Most of our specimens are spheroidal, 2-4 mm in diameter, but actual surficial layers may have fragmented off all of them. Distance between branchings most frequently 3-5 tubule diameters, or less. Branching dichotomous, although adjacent branchings may be so close together as to look multiple. Tubules tend to diverge at equal 60° angles, and interbranching distance rela-

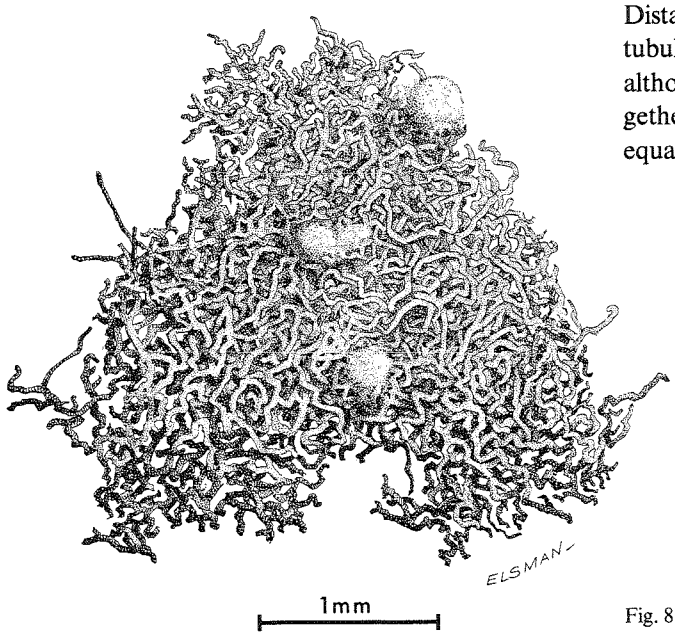


Fig. 8. *Lana neglecta* n. sp.

tively constant, so that the openings of the meshwork are fairly symmetrical in shape and constant in size (Pl. 14A-C).

Most individuals evenly tan, reflecting general paucity of stercomata within the tubule cavities. Tubules flexible, but stiff. Agglutinated particles clay.

Inner organic layer of tubule wall 0.5-1 μm thick, outer agglutinated layer 3-5 μm, occasionally up to 10 μm thick.

Cavity of tubules nonseptate, with only small but constantly occurring quantities of ingested material and spherical to ovoid stercomata which are up to 8 μm in diameter.

Nucleilike bodies spherical or faintly ovoid, 6-10 μm in diameter, with granulated interior.

Remarks: Differences separating *L. reticulata* from *L. neglecta* are that its tubule diameter is larger, its branching is more regular, and the openings of the meshwork smaller, more constant in size, and more symmetrical in shape.

Our collections contain several undescribed species whose morphology approximates that of *L. reticulata.* Station H-30 contains at least three such species. Their presence in the same sample in sufficient abundance allows recognition of the discrete, albeit subtle morphological gaps that separate them. The criteria used are tubule diameter, distance between branchings, regularity of branching, orientation of tubules, integrity of the total mass, and colour. However, the differences can be so subtle that direct comparison is advisable wherever possible.

BACULELLIDAE n. fam.

Diagnosis: Body variously shaped: straight shaft, treelike and sparsely branched, or dense clump. General fine morphology dominated by beadlike appearance which is caused by frequency of extremely short branches, often constricted at base, and by frequent constriction of main tubules at regular, short intervals.

Type genus: *Baculella* n. gen.

Remarks: The genera are presented in an order reflecting increasing complexity in primary tubule morphology.

Treelike, sparsely branched species are known to us, but not described in this report.

Baculella n. gen.

Diagnosis: Body a single, sometimes dichotomously branched shaft, formed by a single nonseptate, but sometimes constricted tubule from which arise numerous short side branches which may be simple beadlike lobes.

Type species: *Baculella globofera* n. sp.

Distribution: NE. N.Pac.: Vi-6104, Vi-6118.
Cent.N.Pac.: H-30, H-37.
E.eq.Pac.: Gal-716.
E.Atl.: Bi-DS78, Me-12-35.
Carib.: Ku-1178A, Ku-1187.
W. eq.Atl.: Gal-52.
W. Indian: AB-382C.

Remarks: The diagnosis covers a fairly large number of species, and it may be possible that the genus should in future be subdivided into at least two subgenera, one represented by *B. globofera* n. sp. and one by *B. hirsuta* n. sp.

In the diagnosis we have included the possibility that the shaft of the body may be dichotomously branched; this character is not seen in the two species described here, but it is found in other, undescribed species.

Baculella globofera n. sp.
(Pls 15A-B, 16A, 19D, 24A-B)

Material: H-30.

Diagnosis: Body straight or slightly bent, up to about 3 mm long and a little less than 0.5 mm in total diameter. Side branches relatively sparse and simply branching, with no sediment in interstices so that stalk (central tubule) is easily visible, even in large individuals. Colour tan.

Description: Body up to 2.8 mm long, always rather straight, and 250-430 μm in total diameter. The diameter is nearly constant through the whole length, although some individuals are a little thicker in the middle part, others at one end. The shaft or central tubule is 60-125 μm in diameter, the lowest numbers representing modest constrictions at intervals of 90-120 μm.

About half-way between the constrictions 2-5 primary branches arise all around the central tubule, more rarely concentrated along one side.

They measure up to 200 μm in length (generally about 125 μm) and 40-60 μm in diameter. Secondary and tertiary branching is frequent, with distance between branchings usually no more than one diameter, rarely as much as three diameters. Terminal branchlets no longer than wide, broadly rounded, and broadly based rather than constricted. Primary branches not packed together; perhaps as a result, orientation of secondary branches follows no preferred direction.

In young specimens the stalk tends to zigzag, with beadlike or short tubular side branches arising at each salient; this pattern is obscured with age.

Colour tan, with rounded masses of stercomata seen as small, dark spots inside the branches. Flexible and elastic. Agglutinated particles clay.

In central tubule the inner organic layer is about 0.5 μm thick, sometimes more, and the outer agglutinated layer is 10-20 μm thick. In the branches the two layers are <0.5 μm and 5-12 μm thick, respectively.

Cavity of central tubule nonseptate, narrowing at constrictions, most often empty, but sometimes with masses of stercomata or ingested material. Cavity of branches septate (Pl. 24A), divided into chambers 30-40 μm long and 20-45 μm wide. Septa with one simple, circular foramen, 8-12 μm in diameter when between chambers, and 12-18 μm in diameter when between central tubule and first chamber in a branch. Each branch with 3-5 chambers, each containing a mass of stercomata, or some ingested material. Stercomata ovoid, 6-10 μm in diameter.

Bodies resembling nuclei are rather common, especially in the side branches, where there generally seems to be one in each chamber. They are spherical, with granulated interior, and measure 6-10 μm in diameter. More often they are to be found with ingested, loose material than with a mass of formed stercomata. The explanation for this may either be that the chambers with stercomata are "dead", or, more likely, that these bodies are more difficult to find when together with the mass of opaque, dark stercomata.

Remarks: *B. globofera* is part of a group of species where all individuals lack sediment in the interstices between branches. Though it is possible that the sediment has been washed away, this seems unlikely. One would expect at least some material to be found in some specimens, and furthermore, there is another group of species with interstices always filled with sediment.

Baculella hirsuta n. sp.
(Fig. 9; Pls 14E-F, 19E, 24C, 25A, 26A)

Material: H-30.

Diagnosis: Body club-shaped, sometimes curved at thin end, up to 4.5 mm long and 2.5 mm in diameter at thick end, tapering to 250 μm. Side branches densely packed together and interstices filled with sediment so that central stalk (central tubule) is completely hidden. Tips of branches evident as dark spots, each tip with one or two pointed, conical, transparent projections. Thick part of body overgrown with mat of very fine fibers between which sediment is trapped, yielding fuzzy, tan cap.

Description: Outer appearance ranges from that of a faintly club-formed stick to a genuine club, sometimes strongly curved at thin end. Total length 1.8-4.5 mm. Largest part at thick end 0.5-2.5 mm in diameter, while thin end is 250-300 μm in diameter and bears a 100-200-μm-long conical tip.

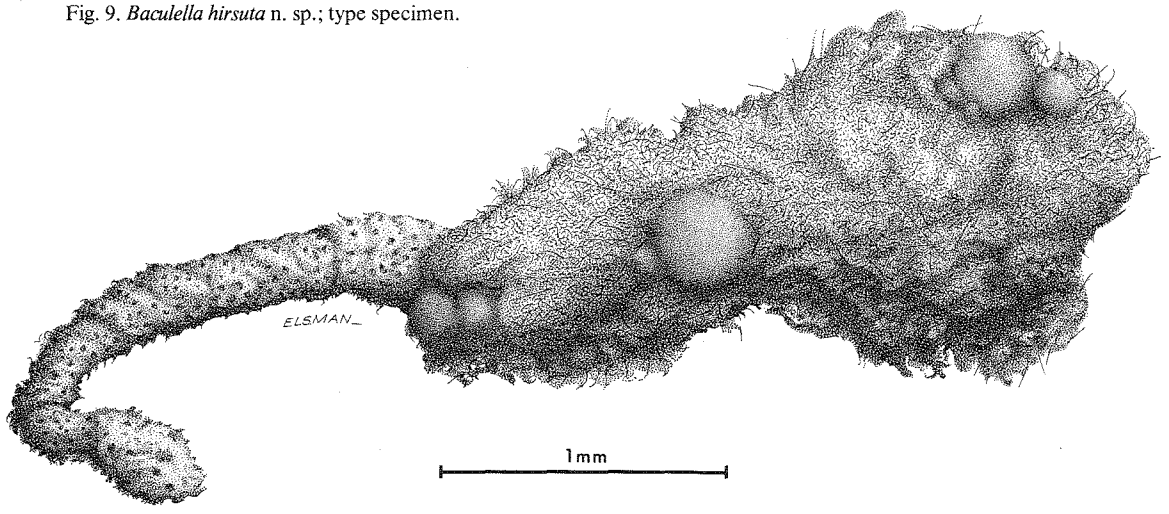
Most details of central tubule obscured by sediment filling interstices between branches. Visible parts of surface with granular appearance, the granules being the tips of beady tubules. In direct light they look rounded and appear dark because the interior filling with stercomata is seen dimly through the tubule wall. When the body is seen in silhouette, the distal ends of the beads are seen to bear one or two small, sharp protrusions which are distinctly conical and so thin that they are transparent.

The thick end is covered with a sheath of sediment which is held in place by a mass of fine fibers (Pls 14F, 26A). Usually some fibers extend free of the sediment sheath, but this may be a result of damage. The sediment layer progressively becomes thinner toward the thinner end, usually covering only half of the specimen, or less (Pl. 14E). In large specimens no fibers are seen in the sediment-free end, whereas some small specimens appear slightly shaggy from scattered fibers extending from the surface; we are, however, not sure that we are able to separate small specimens of different species from each other.

Colour tan at thick end, darker toward thin end. Body flexible and elastic. Agglutinated particles clay, but larger objects such as radiolarian tests and fragments of sponge spicules are often entangled in the fiber mass.

When the sheath of sediment is removed together with the fiber mass, it appears that the hitherto hidden part of the body is a little thicker, 300-400 μm

Fig. 9. *Baculella hirsuta* n. sp.; type specimen.



in diameter, than the free end and has fewer small protruding points. It is not possible to discern further details because of the tight spacing of the beaded tubules and the filling of interstices with sediment.

Sections reveal that the organizational pattern is a possibly meandering central tubule with branches arising all around it for its full length.

Spacing of the primary branches is exceedingly tight, only 10-25 μm, a fact that obscures the discrete existence of the central tubule. The diameter of the central tubule cavity is 15-25 μm, and the thickness of the organic layer 5-10 μm. An agglutinated layer cannot be distinguished from the sediment in the interstices. The cavity is nonseptate and seems unconstricted.

The branches are round or somewhat flattened in cross section, 35-60 μm in diameter and 100-125 μm in length. They look constricted where they leave the central tubule, but not markedly so. Each branch is provided distally with one or often two blunt or sharp projections (Pl. 24C). These projections which arise without constrictions are of widely varying length, from barely visible up to about 120 μm, and generally 5-10 μm in diameter with circular cross section. Were they to be interpreted as a set of secondary branches, the branching pattern would have to be characterized as having a very marked, stepwise decrease in diameter.

Inner organic layer 3-5 μm thick in branches and 2-3 μm in distal projections. As in the case of the central tubule, a special agglutinated layer cannot be discerned from the interstitial sediment filling. The extraordinary thickness of the organic layer seems to result from a secretion of layer upon layer of fibrous or membranous matter on the outside of the tubules (Pl. 19E). Here and there a shrinking has occurred, causing an inner lamina, <0.5 μm thick, to separate from the rest of the wall. The thickness of the organic wall decreases toward the sediment-covered end, in some places down to about 1 μm.

Cavity of branches and projections nonseptate and not constricted.

Cavity of central tubule and branches totally but loosely filled with ovoid, up to 9-μm-long stercomata, here and there with patches of loose, ingested material (Pl. 25A). There is a tendency for this material to be more common in the sediment-covered end. Stercomata are sometimes found in the projections also, but more often these are empty.

Bodies resembling nuclei are found scattered; they are spherical or ovoid with faintly granulated interior and measure 5-7 μm in diameter.

This is one of the few species in which the plasma is relatively easily seen.

The fibers in the sediment sheath arise at the surface of the body. The thickest are about 10 μm in diameter, the thinnest about 1 μm. Thickness seems to be achieved through depositing many thin fibers in a bundle. Dichotomous branching is frequent but irregular, so that parts are not equally thicks; it goes on through splitting of the bundle, not through division of the single fiber. No anastomoses were seen. The fibers appear to be of the same material as the organic layer of the wall. Sediment particles seem to stick to the fibers and are sometimes found inside the fiber bundle.

Remarks: *B. hirsuta* differs from *B. globofera* in a large number of characters. The most obvious, externally visible ones are: general body form, pres-

ence of the fibers and the sediment cap, sediment filling of interstices between branches, and presence of the small conical projections.

Because the primary tubule is of a remarkably small diameter in *B. hirsuta* and shows marked constrictions in *B. globofera,* the organization of the former might be interpreted in another way than above. What is here called central tubule and branches could, in fact, be a case of an exceedingly strong and tight constriction of a central tubule, with the distal projections representing the first and only generation of branches. The branching pattern would then be characterized by the marked decrease in diameter following the first step of branching. Only investigation of a number of other species will show if this interpretation is correct.

It appears from the description that the two ends of an individual are different, with gradual changes along the central tubule. These changes are seen in the sediment covering and fiber distribution, body diameter (without sheath of sediment), thickness of the organic layer in the test wall, and ratio of ingested, loose material to quantity of stercomata. Our interpretation is that the thick, sediment-covered end is the younger, and that the sheath is gradually cast or eroded away from the older end. Plasma and supposed nuclei are most often found in the younger end, but they are seen throughout the whole individual, and although we think that the activity is greatest in the young end, it should be taken into consideration that the more tightly packed stercomata in the old end make detection of other structures difficult.

Edgertonia n. gen.[1]

Diagnosis: Body formed as dense, rounded clump of branching tubules with numerous extremely short side branches and beads.

Type species: *Edgertonia tolerans* n. sp.

Distribution: NE.N.Pac.: Vi-6109.
SE.N.Pac.: Vi-4281.
Cent.N.Pac.: H-29, H-30, H-36.
E.eq.Pac.: Gal-716.
Carib.: Ku-1178A, Ku-1187, Ku-1189.
W. Atl.: Eastw-20087.
E.Atl.: Bi-DS78.

1. This genus is named in honour of Carol C. Edgerton, whose careful sorting led to the first appreciation of the superfamily and to our finest collection of material.

Edgertonia tolerans n. sp.
(Pls 9E, 16B-F, 26C)

Material: H-30.

Diagnosis: Body up to 4.5 mm in diameter. Tubules anastomosing. Beads usually spaced so that outline and course of single tubules can be traced. Interstices without sediment. Cavity of tubules nonseptate.

Description: Round or slightly distorted spheroid composed of tangle of closely branching, anastomosing tubules. Undamaged individuals up to 4.5 mm in diameter, and we have fragments possibly originating from even larger specimens. No sediment in interstices, giving appearance of a bath sponge. Meshwork of tubules clearly open, but moderately dense so that visibility to the interior is blocked after only 2-3 layers. Surface distinct, not frayed, except where specimen appears damaged. No visible pattern of orientation of tubules. No free tubules extending from surface.

Tubules 25-40 μm in diameter, usually dichotomously branching, but sometimes more. Short side branches protrude from surface at short, irregular intervals (from a few to 125 μm) (Pl. 16B, D-F). These side branches frequently simple spheroids ("beads"), 35-50 μm in diameter, with constricted bases, or short branches, not much longer than diameter, unconstricted at base and terminating in cluster of beads. Beads and side branches may come off singly or multiply.

Colour tan. Consistency markedly spongelike, with tubules resisting tearing off. Agglutinated particles clay.

Tubule wall with inner organic layer <0.5 μm thick. Outer agglutinated layer 2–12 μm thick, generally about 5 μm.

Cavity of tubules nonseptate, narrowing at bead constrictions. Some tubules empty, others well filled with stercomata and ingested material. Stercomata ovoid, up to 8 μm long.

Nuclei fairly numerous, spherical, and with granulated interior, 3-8 μm in diameter, generally about 5 μm.

Edgertonia argillispherula n. sp.
(Fig. 10; Pls 9F, 17A-B, 18A-B, 25B, 26D)

Material: H-30.

Diagnosis: Body up to 3.5 mm in diameter. Tubules tightly covered with beads so that outline and course of single tubule is difficult to trace. Interstices filled with sediment so that appearance is much like that of a mud ball. Cavities of body tubules infrequently septate. Long, unconstricted tubules may extend freely from body surface.

Description: Body is round, ovoid, or may look like two or more rounded bodies broadly connected to form an irregular, lobular mass. Diameter of body 1-3.5 mm.

Body surface is sharply defined and relatively smooth, but appears granular, the granules being the tips of beady tubules seen dimly through the sediment matrix (Pl. 9F). Inside the granules masses of stercomata appear as dark spots.

In specimens where the matrix has been partially washed away the appearance is that of densely packed, short tubules and spheroids 50-60 μm in diameter. The density of packing makes details of branching nearly impossible to discern.

Extending from the surface either sparsely or in moderate abundance are free tubules, somewhat crooked, up to at least 2.3 mm long and 35-50 μm in diameter. They are empty, thin-walled, and often collapsed so that the cross section is flat rather than circular, and the largest measurements of diameter may, therefore, be an artifact. Most are unbranched, but some show single dichotomous division, generally at large distance from body surface. The distal ends are broadly open, possibly as a result of breakage, or gradually tapering toward a blunt tip. Although in some specimens these tubules spring from all parts of the surface, there is in most cases a rather clear restriction to an equatorial belt.

Colour greyish tan. Rather soft, not flexible. Agglutinated particles clay.

Inner organic layer of tubule wall <0.5 μm thick, outer agglutinated layer on protruding beads 3-5 μm thick, in most of the body impossible to discern from sediment filling.

Tubule lumen 20-30 μm in diameter. Cavity of tubules irregularly septate, septa being composed of double inner layer. Partly filled with masses of stercomata (Pl. 25B). Individual stercomata spherical to ovoid, up to 20 μm in diameter.

Remarks: Tearing tubules apart is usually difficult because of something causing internal adherence. The explanation seems to be that there is a high degree of anastomosing, difficult to discern by direct handling under the dissection microscope, but highly probable as judged from the sections (Pls 17A, 26D).

The absence of the delicate tubules extending out

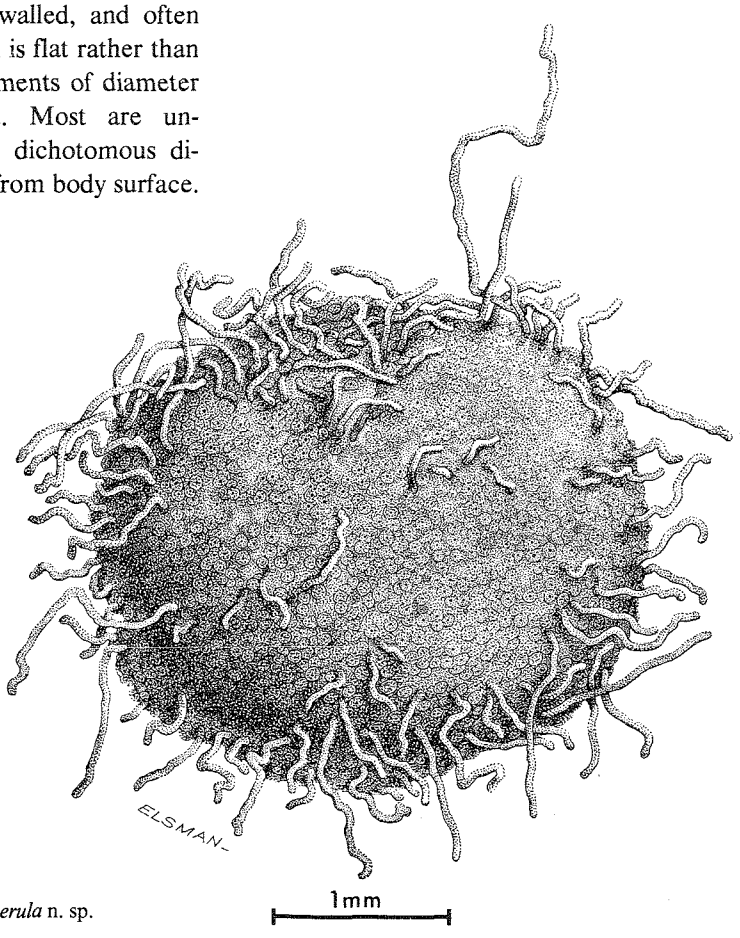


Fig. 10. *Edgertonia argillispherula* n. sp.

from the surface of many of the individuals may be an age phenomenon since it is most common in large specimens, or simply an artifact because of their fragility.

The most obvious differences between *E. tolerans* and *E. argillispherula* are the lack of sediment in the interstices, the spongy consistency, and the spaced beading of the former, as opposed to the sediment-filled interstices, the unflexibility, and the tight beading in the latter. Other differences of the latter are found in the frequent presence of long free tubules, the presence of septa in the tubule cavities, and in the the degree of adherence of the tubule latticework.

VIII. SUMMARY

The aim of this paper is to introduce and establish a hitherto overlooked group of benthic deep-sea animals, the "komoki", belonging to the Foraminiferida. Because the group has turned out to be surprisingly rich in species, this first treatment is restricted to a general characterization, the erection of a new superfamily, the Komokiacea, and the description of some lower taxa which typify the range of morphologies found in the material at disposal.

Komoki have only in recent years been secured in large numbers. The reason is that they are so fragile and small that their retention generally demands gentle washing through a fine-mesh screen. In the present work, they have been studied by use of dissection microscope, scanning electron microscope, and paraffin embedding followed by sectioning and general staining methods. The terminology used is the same as for other Foraminifera. A list of eleven points, to which attention should always be paid when describing new species of this group, is set up (p. 171).

The core of the material originates from the area under the central North Pacific gyre. The efforts were concentrated on this material because one can then see better the range of morphologies that live together than if the species are drawn from different places. Moreover, the way in which it was collected is known in technical detail, and we have a comprehensive knowledge about the community from which it comes.

After having acknowledged the reality of the group, it soon turned out that numerous, generally small, samples exist in the materials from many expeditions carried out in different parts of the world ocean. Thus the experience laid down here, especially concerning the distribution of the genera, could be drawn from more than 100 samples.

Komoki generally measure 1-5 mm in largest dimension. The basic element in their morphology is a fine tubule of even diameter, containing the plasma and a large quantity of faecal pellets (stercomata). External appearance is above all influenced by tube branching pattern and presence of sediment between the tubules in some species. Two types of branching seem to be of constant occurrence. In the first the tubes are cylindrical, rarely constricted, and with large distances between branching points. In the second type is found a rich branching, resulting in a large number of close-set, very short side branches, and the main tubules are frequently constricted.

The tube wall consists of two layers, sharply demarcated from each other. The interior layer is generally <0.5 μm thick, stains with toluidine blue and PAS, and is frequently laminated. The outer layer, which is about 10 μm thick, is agglutinated with particles commonly of clay and silt fractions. Several species were found to be septate with chambers added linearly, and with very simple septa and foramina.

Komoki have no real apertures. Pseudopodia are postulated to penetrate the tube wall through minute, possibly temporary, pores.

The colour of komoki is tan, the shade depending on the amount and type of particles in the agglutinated layer. Although very fragile, they have a rather high degree of flexibility.

Details of the cytology are poorly known. Bodies resembling nuclei, measuring 4-10 μm in diameter, have been found in most species. Stercomata, measuring generally about 10 μm in diameter, are rounded, opaque or dark brown, and consist of a mass of unidentifiable small particles.

The distribution of the group has been analyzed in detail only down to generic level, because no more than a few samples have been treated to species. Komoki are known from the three main oceans, but not yet from the arctic and antarctic seas. Four genera (*Septuma, Ipoa, Lana,* and *Baculella)* have been recorded from the Atlantic, the Pacific, and the Indian Ocean, three genera (*Komokia, Normanina,* and *Edgertonia)* only from the two former oceans.

The recorded vertical range of the group is 400 (180?)-9600 m, with by far the largest number of

samples at depths of 1000-7000 m. The conclusion is that komoki is essentially a deep-sea group, with its shallowest distribution somewhere on the continental slope, perhaps correlated with abrupt changes in temperature and sediment structure. Two genera *(Septuma* and *Lana)* are reported from bathyal depths, all seven genera have their main distribution in the abyssal, and four genera *(Ipoa, Lana, Baculella,* and *Edgertonia)* extend into true hadal depths.

The greatest relative abundances of komoki have been found in the oligotrophic abyss and in hadal trenches, where their volume exceeds that of all the metazoans combined and equals that of the remains of other Foraminifera. As a first approximation to document the diversity of komoki and their distribution in the bottom, the results of analyzing 500 cm^2 of a box core are given: about 2000 specimens were found that could be sorted into 56 species, of which 32 belong to two genera. More than 80 % of the specimens were in the top 1 cm layer, whereas only 2.5 % were below 2 cm. Some species show greatest abundance in the 1-2 cm layer, and five species were never found in the 0-1 cm layer, indicating that at least some species live well beneath the surface. One conclusion of this is that much caution should be used in deducing life style from morphology in komoki.

Within the order Foraminiferida, komoki are placed in the suborder Textulariina as a new superfamily, Komokiacea. Two new families, Komokiidae and Baculellidae are erected, respectively with five and two genera. A key is prepared for families and genera. In Komokiidae all species and genera but one are new: *Komokia* n. gen. (with *K. multiramosa* n. sp.), *Septuma* n. gen. (with *S. ocotillo* n. sp.), *Ipoa* n. gen. (with *I. fragila* n. sp.), *Normanina* Cushman, 1928 (with *N. tylota* n. sp. and *N. saidovae* n. sp.), and *Lana* n. gen. (with *L. neglecta* n. sp. and *L. reticulata* n. sp.). In Baculellidae all species and both genera are new: *Baculella* n. gen. (with *B. globofera* n. sp. and *B. hirsuta* n. sp.) and *Edgertonia* n. gen. (with *E. tolerans* n. sp. and *E. argillispherula* n. sp.).

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