Zoological Journal of the Linnean Society, 2008, **153**, 399–423. With 16 figures

New organic-walled Foraminifera (Protista) from the ocean's deepest point, the Challenger Deep (western Pacific Ocean)

A. J. GOODAY[1]*, Y. TODO[2], K. UEMATSU[3] and H. KITAZATO[2]

[1]*National Oceanography Centre, Southampton, Empress Dock, European Way, Southampton SO14 3ZH, UK*
[2]*Institute for Research on Earth Evolution, and* [3]*Marine Technology Center, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka 237-0061, Japan*

Received 20 April 2007; accepted for publication 31 July 2007

We describe four new species and a new genus of very small (< 500 μm) Foraminifera from the Challenger Deep, the deepest point in the world's oceans (10 896 m water depth). All have transparent, mainly organic test walls that incorporate some minute agglutinated mineral particles of various shapes and compositions. ***Nodellum aculeata* sp. nov.** has an elongate proloculus with a pointed proximal end followed by a long, tubular section. The genus *Resigella* is represented by two species: in ***R. laevis* sp. nov.**, the test comprises 3–4 elongate, oval to cylindrical chambers while ***R. bilocularis* sp. nov.** has an oval proloculus followed by a second, larger globular chamber. The fourth species, ***Conicotheca nigrans* gen. et sp. nov.**, is characterized by a tiny, elongate, conical test filled with dark stercomata. Except in *C. nigrans,* the test wall has a brownish tinge; energy-dispersive spectroscopy (EDS) suggests the presence of organically bound Fe in all species including *C. nigrans*. Scanning electron microscopy (SEM) combined with EDS reveals distinctive wall structures. In *N. aculeata*, the proloculus is strewn with tiny (< 0.7 μm), elongate grains. In this species and in *R. laevis*, the test surface (except for the proloculus) is covered with a carpet of minute (~0.1 μm) finger-like projections, rather similar to the organic cement of agglutinated Foraminifera. In *R. bilocularis*, the larger second chamber often has a partial veneer of fine mineral grains of varying composition, as well as organic areas consisting of meshed strands. SEM images of these three species reveal flat, plate-like features that we interpret as clay particles. In *C. nigrans*, the wall is relatively featureless except where the surface is raised into hummocky mounds and scale-like features, again probably clay particles. We suggest that these species represent a distinctive group of 'agglutinated' Foraminifera in which the test is predominately organic.

ADDITIONAL KEYWORDS: agglutinated Foraminifera – allogromiid – deep-sea trench – hadal – inner organic lining – KAIKO – organic cement – wall structure.

INTRODUCTION

Benthic Foraminifera are represented in deep-sea trenches by more species than any other taxon apart from crustaceans (Belyaev, 1989). The Challenger Expedition collected the first hadal Foraminifera in the 1870s from the Japan Trench (water depth 7224 m) (Brady, 1884). Most of the 14 species identified by Brady in this sample were known from shallower sites. However, it was Russian scientists, in particular Kh. M. Saidova, T. A. Khusid and I.A. Basov, who pioneered the study of Foraminifera from depths > 6000 m. The extensive body of literature published between the 1950s and late 1980s on hadal faunas was reviewed by Belyaev (1989). In appendix 2, table 1 of this publication, Belyaev lists 103 foraminiferal species collected at depths between 6000 and 10 687 m. These species included two with organic-walled tests: *Nodellum membranacea* found

*Corresponding author. E-mail: ang@noc.soton.ac.uk

in the above-mentioned sample from 7224 m (Brady, 1884), and *Xenothekella elongata* Saidova, described from > 9000 m depth in the Kurile–Kamchatka Trench (Saidova, 1970). Six of the remaining species were calcareous, six were ammodiscaceans, 49 were multilocular agglutinated species and 46 (including three komokiaceans) belonged to monothalamous (single-chambered) agglutinated taxa. Tendal & Hessler (1977) and Kamenskaya (1989, 2006) reported a variety of komokiaceans, a distinctive group of large protists currently placed in the Foraminifera, from the Pacific Ocean, including eight trenches. The deepest trawl sample examined by Kamenskaya was recovered from a reported depth of 10 915 m in the Tonga Trench and yielded komokiaceans belonging to the genus *Edgertonia*.

These earlier studies revealed a predominance of larger agglutinated Foraminifera amongst trench faunas (Saidova, 1970). Apart from the two species listed by Belyaev (1989), however, there are few records of organic-walled Foraminifera ('allogromiids') from these extreme depths. Undescribed 'allogromiids' accounted for 41% of organisms belonging to meiofaunal taxa in the > 300-μm residue of a box core from 7298 m water depth in the Aleutian Trench (Jumars & Hessler, 1976), but it was unclear whether they had organic or agglutinated test walls. Only Sabbatini *et al*. (2002) provide reliable reports of organic-walled Foraminifera from a hadal setting. These taxa accounted for 82% of 'live' (rose Bengal stained) individuals in a core sample collected at 7800 m in the Atacama Trench. Species resembling members of the genera *Chitinosiphon*, *Nodellum* and *Resigella* were particularly abundant.

Here, we describe a new genus and four new species of Foraminifera with test walls composed mainly of organic material. They were collected in the Challenger Deep, the deepest part of the world's oceans, using the Remote Operated Vehicle *KAIKO*, belonging to the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). Unlike most previously described hadal Foraminifera, the species are all of diminutive size. Their discovery was announced in an earlier note (Todo *et al*., 2005). The only previous record of Foraminifera from the Challenger Deep was that of Akimoto *et al*. (1996, 2001) who illustrated several agglutinated species in samples that were dried before sorting.

MATERIAL AND METHODS

Study site

The Challenger Deep, discovered in 1951 by the British survey vessel *Challenger VIII*, is situated in the south-west part of the Izu–Bonin–Mariana-Arc trench system. Geologically, it is of relatively recent origin and may have developed to its present depth during the past 6–9 Myr (Fujioka *et al*., 2002). As part of a Japan–USA–Korea cooperative research programme, a series of dives to study the diversity and distribution of organisms in the western depression of the Challenger Deep was carried out in 2002 using JAMSTEC's Remote Operated Vehicle *KAIKO* (Hashimoto, 2002). The bottom-water oxygen concentration in the study area was 3.4 ml L^{-1} and the sediment was well oxygenated. Video recordings of coring operations taken by the ROV show the sediment to be very soft and easily penetrated by the coring tube. A variety of larger animals, particularly holothurians and polychaetes, were observed during the *KAIKO* dives.

Sampling

Sampling was carried out in the Challenger Deep (11°20.093′N, 142°11.803′E; 10 896 m) by members of the *KAIKO* operation team (Dive 275, *Kaiko/Kairei* Cruise no. KR02-13, 23 October 2002). Pushcore samples (7 cm internal diameter) collected by *KAIKO* were cut, immediately after recovery, into layers 0.25 cm thick to a depth of 1 cm, in 0.5-cm layers to 3 cm, and then 1-cm layers to 10 cm depth. Each layer was fixed in buffered formalin. In the laboratory, the sediment was sieved on 32-μm and 63-μm mesh screens and stained with rose Bengal solution, which permits the recognition of individuals that were alive when collected. All stained and unstained specimens from the 32–63-μm and > 63-μm residues were handsorted under a binocular microscope and stored in glycerol on glass cavity slides. Only the top 1 cm of sediment was included in this study.

Imaging and chemical analyses

Images of the tests were obtained using a JEOL JSM-6700F scanning electron microscope (SEM). The elemental composition of test surfaces was analysed by means of an energy-dispersive spectroscopy (EDS) system (JED-2300) attached to the SEM. An acceleration voltage of 5 kV was used for imaging and 15 kV for the EDS analyses. Different counting times mean that the EDS data are not entirely comparable between specimens. We therefore interpreted them qualitatively.

SYSTEMATIC DESCRIPTIONS

We follow Adl *et al*. (2005) in placing the Foraminifera in the supergroup Rhizaria. For reasons explained by Gooday, Kamenskaya & Kitazato (2008), we recognize only two taxa between the levels of genus and supergroup and we do not assign a rank to one of them, the Foraminifera. Our placement of the species that we describe in the subclass Textulariia reflects the belief, discussed below, that they are related to agglutinated Foraminifera.

Holotypes and paratypes are stored in the Micropalaeontology Collection, National Museum of Nature and Science, Tokyo (registration numbers prefixed by MPC). Additional paratypes are stored in the Palaeontology Department, Natural History Museum, London (registration numbers prefixed by ZF).

PROTISTA
SUPERGROUP RHIZARIA CAVALIER-SMITH, 2002
FORAMINIFERA D'ORBIGNY, 1826
SUBCLASS TEXTULARIIA MIKHALEVICH, 1980
GENUS *NODELLUM* RHUMBLER, 1913

Nodellum Rhumbler, 1913, pp. 442–443, 473–474
Chitinosiphon Thalmann & Bermudez, 1954, pp. 53–54
Nodellum Rhumbler. Loeblich & Tappan, 1964, C179–182 (in part), 1987, p. 17.

Type species: Reophax membranacea Brady, 1879

Diagnosis: Test elongate, ranging in length from < 0.5 to 2 mm or more. Initial part (proloculus) either oval in shape, sometimes with deep, pocket-like invagination at base, or spindle-shaped with pointed proximal end. Main part of test gently arcuate; either tubular or with series of distinct, fairly regularly spaced constrictions dividing it into more or less clearly defined segments that tend to become shorter towards proloculus. One or two internal partitions may be present. Aperture terminal, round, constricted, sometimes with delicate, tubular extension. Test wall rigid, fairly brittle, orange or yellowish-brown in colour, mainly organic but with some minute, adhering or embedded mineral particles. (After Gooday *et al*., 2008.).

Remarks: In some earlier publications (e.g. Gooday *et al*., 2004), the senior author and others considered *Chitinosiphon* to be distinct from *Nodellum*. Loeblich & Tappan (1964, 1987), however, regarded *C. rufescens* and *N. membranacea*, the types species of their respective genera, to be conspecific and the two genera therefore to be synonymous. Gooday *et al*. (2008) examined the type specimens and additional material of both species and concluded that they are distinct. In *N. membranacea*, the test comprises a series of segments; the initial segment (proloculus) has a blunt, truncated base with a distinctive, pocket-like invagination. In *C. rufescens*, the test is basically tubular, not subdivided into 'segments', and has a pointed proloculus which lacks a basal invagination, although a small opening is often present at the pointed end. However, the proloculus in *Chitinosiphon*-like morphotypes is sometimes oval (see below) and an invagination is present at the base of the proloculus in some larger *Chitinosiphon*-like tubes from the abyssal Pacific. These features blur the distinction between the two genera and Gooday *et al*. (2008) therefore followed Loeblich & Tappan (1964, 1987) in combining them.

Saidova (1970) described *Xenothekella* from 9170 to 9335 m in the Kurile–Kamchatka Trench. The test in this genus comprises a proloculus with a rounded proximal end, followed by an undivided tubular section ending in a simple terminal aperture. All these features are included in the diagnosis of *Nodellum* given above, suggesting that the two genera are possibly synonymous. However, Saidova's (1970: pl. II, fig. 3) illustration shows a test that is much less slender and less clearly curved than either the type specimens of *Nodellum rufescens* figured by Thalmann & Bermudez (1954), or the new species from the Challenger Deep described below. We have examined two fragments of *Xenothekella*, both lacking a proloculus, in the collection of Dr Kh. Saidova (Shirshov Institute, Moscow). They are wider than *N. rufescens* and much larger than the new species described below.

***NODELLUM ACULEATA* SP. NOV.** FIGS 1–7

'Needle-shaped, organic-walled allogromiid resembling *Chitinosiphon*'. Todo, Kitazato, Hashimoto, Gooday, 2005, fig. 1A

Derivation of name: Latin *aculeolus*, a small needle, referring to the needle-like test morphology.

Diagnosis: Small, delicate species of *Nodellum*, < 500 µm in length with maximum width 5–9% of length. Test wall mainly organic, usually yellowish and several micrometres thick. Proloculus with closed proximal (basal) end that is usually pointed. Surface of proloculus strewn with minute rod-shaped particles, typically 0.4–0.7 µm long and ~0.1 µm wide. Main part of test tubular, usually gently curved. At submicrometre scale most areas covered in short, branching, finger-like projections of organic wall, in some areas interrupted by flake-like patches (probably clay particles).

Types: The type specimens are deposited in Tokyo and London under reg. nos MPC-02705 (holotype), MPC-02706-02709 (four paratypes) and ZF 5169 (six paratypes)

Other material examined: 42 specimens.

Description
Test morphology: The test is 230–426 µm long (Table 1) and forms a very narrow tube that follows a slightly to gently curved, occasionally almost straight

course (Fig. 1). The proximal part consists of an elongate proloculus, 27–44 μm long and 11.0–15.5 μm wide and occupying 7.9–17.3% (usually 9–14%) of the total length of the test. The end is usually pointed (Figs 1, 2A) but in a few cases narrowly rounded (Figs 1K, 3B). The proloculus gives rise to a long, tubular section that gradually increases in width from around 10 μm just in front of the proloculus to

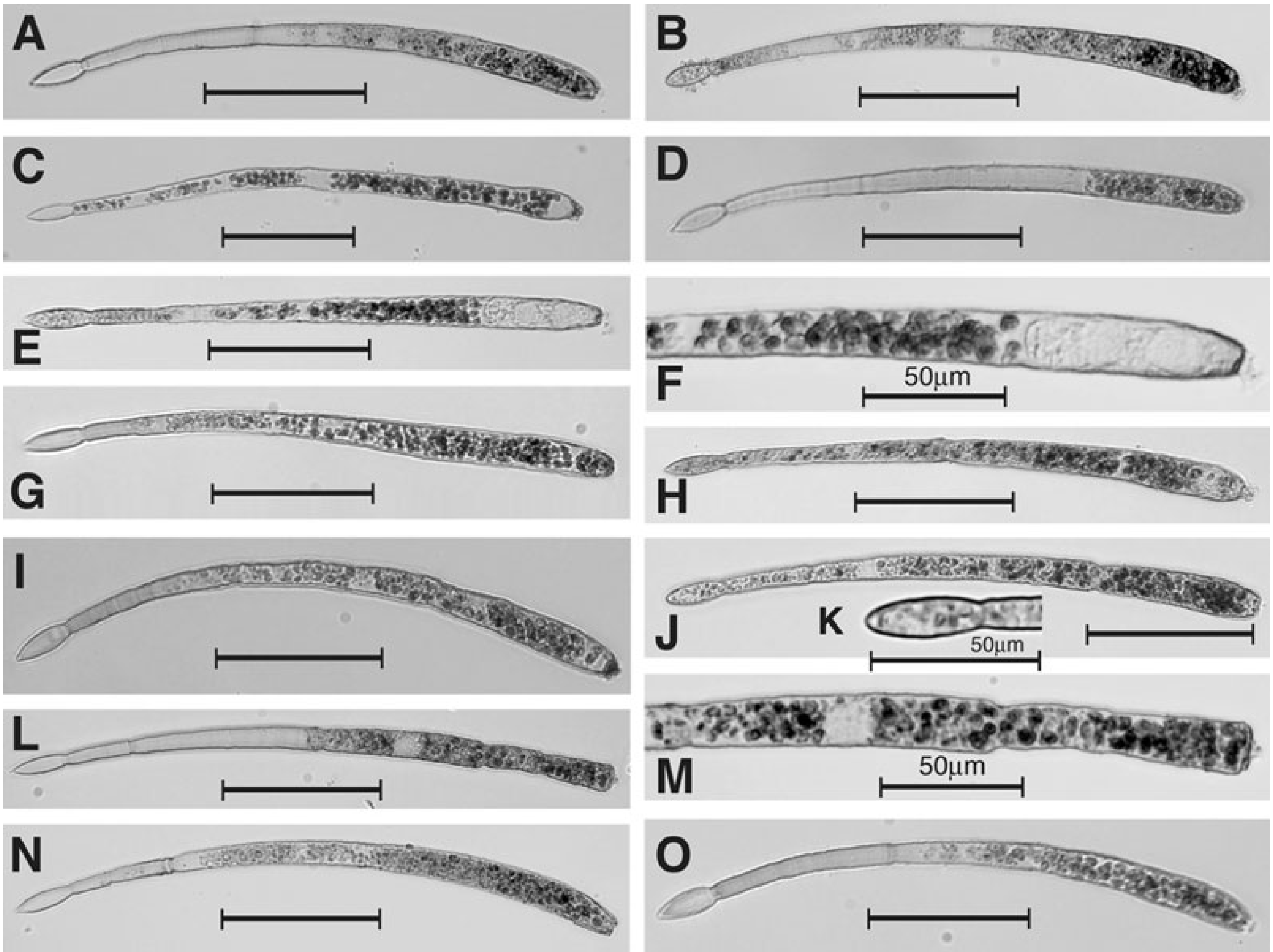

Figure 1. ***Nodellum aculeata*** **sp. nov.** Transmission light micrographs of type specimens, on open slides in glycerol. A, holotype, reg. no. MPC-02705. B–H, paratypes, reg. nos. ZF 5169; F, detail of distal end showing mass of cytoplasm. I–O, paratypes, reg. nos. MPC-02706-02709; K, detail of proloculus with rounded end; M, detail of distal part of specimen showing abrupt decrease in width and truncated end. All scales bars = 100 μm except where indicated otherwise.

Table 1. ***Nodellum aculeata*** **sp. nov.:** dimensions of the test and proloculus (μm)

	Range	Mean ± SE	*N*
Length	230–426	346 ± 48.7	53
Minimum width	8.6–12.4	10.3 ± 1.05	53
Maximum width	15.1–24.7 (32.3)	21.3 ± 3.41	53
W_{max} as percentage of L	4.9–9.6	6.4 ± 1.1	53
Proloculus length	27–44	36.7 ± 4.05	53
P_{length}/T_{length} (%)	7.9–17.3	11.2 ± 2.2	53
Proloculus width	11.0–15.5	12.9 ± 1.0	53

The figure in parentheses is an outlier.
SE = standard error, *N* = number of specimens.

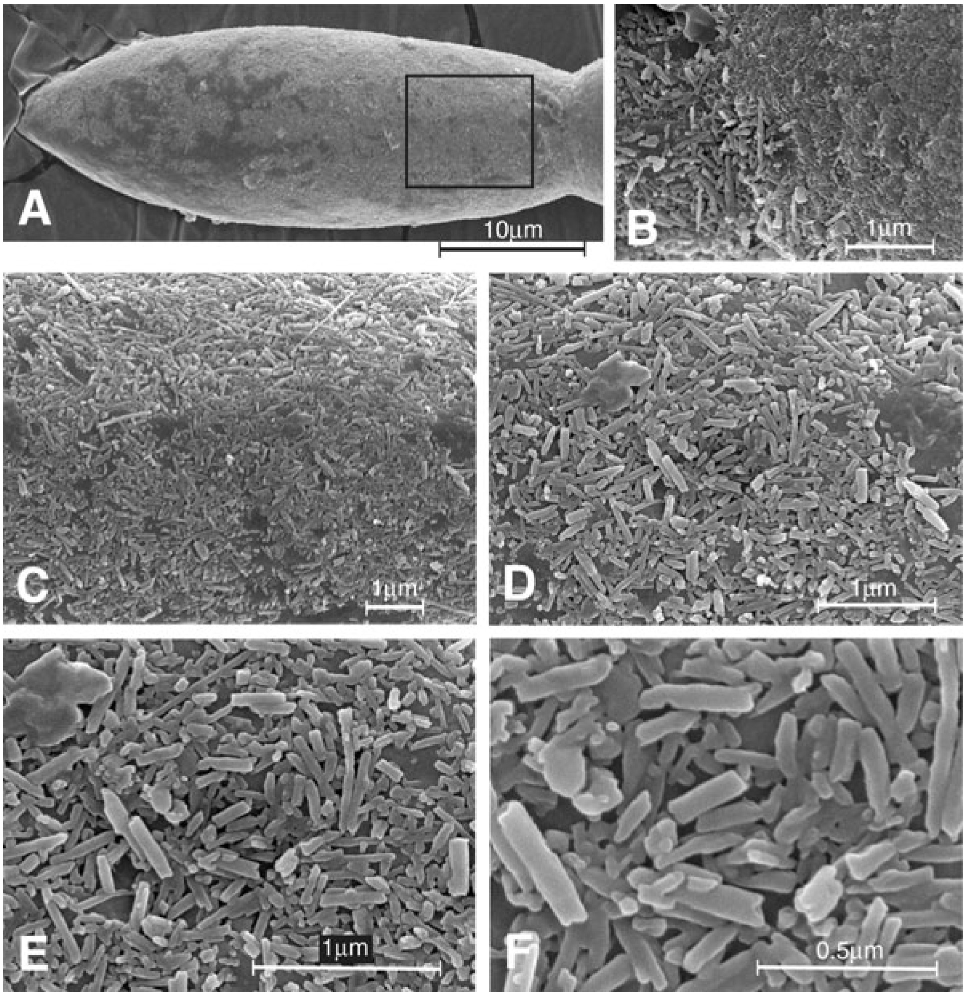

Figure 2. ***Nodellum aculeata* sp. nov.** Scanning electron micrographs. A, proloculus; box indicates area shown in C. B, transition between surface of proloculus with obvious agglutinated particles (to left) and predominately organic surface of the main tubular part of the test. C–F, progressively closer views showing rod-like agglutinated particles strewn across the surface of the proloculus.

about 20 μm near the distal end. The final section of the tube usually tapers towards the aperture. The outline of the test is fairly smooth but there are sometimes slight irregularities and discontinuities in width (Figs 3F, 4A). Occasional specimens exhibit an abrupt decrease in width (Fig. 1M), possibly reflecting a growth interruption.

Aperture: The aperture is a simple opening, 6–8 μm in diameter, usually with a somewhat puckered rim (Figs 3E, 5C, D). Occasionally, the apertural end is sharply truncated (Figs 1M, 3F, 5B). An aperture is never developed at the proximal end.

Wall structure and composition: The test wall is transparent, smooth, with a slight brownish tinge and composed mainly of organic material. Viewed in the SEM, the surface of the proloculus is strewn with submicrometre-sized particles, many of which are more or less rod shaped, typically 0.30–0.70 μm long and 0.08–0.10 μm wide (Figs 2B–F, 3C, D). Some more equidimensional grains, 0.10–0.15 μm in diameter, occur between these elongate particles.

The tubular part of the test beyond the proloculus is devoid of rod-shaped agglutinated particles. The surface has a complex appearance in the SEM. At magnifications of ~15 000×, it often appears lumpy (Figs 4E, 6B, D). At higher magnifications, the lumps resolve into a complex mass of short, branching, finger-like projections (Figs 4F, 6C, E) that appear to be elaborations of the underlying organic wall. Flat, scale-like patches with free edges around a part of their circumference (Fig. 7F, G) are interpreted as clay particles (see below). Along the border between

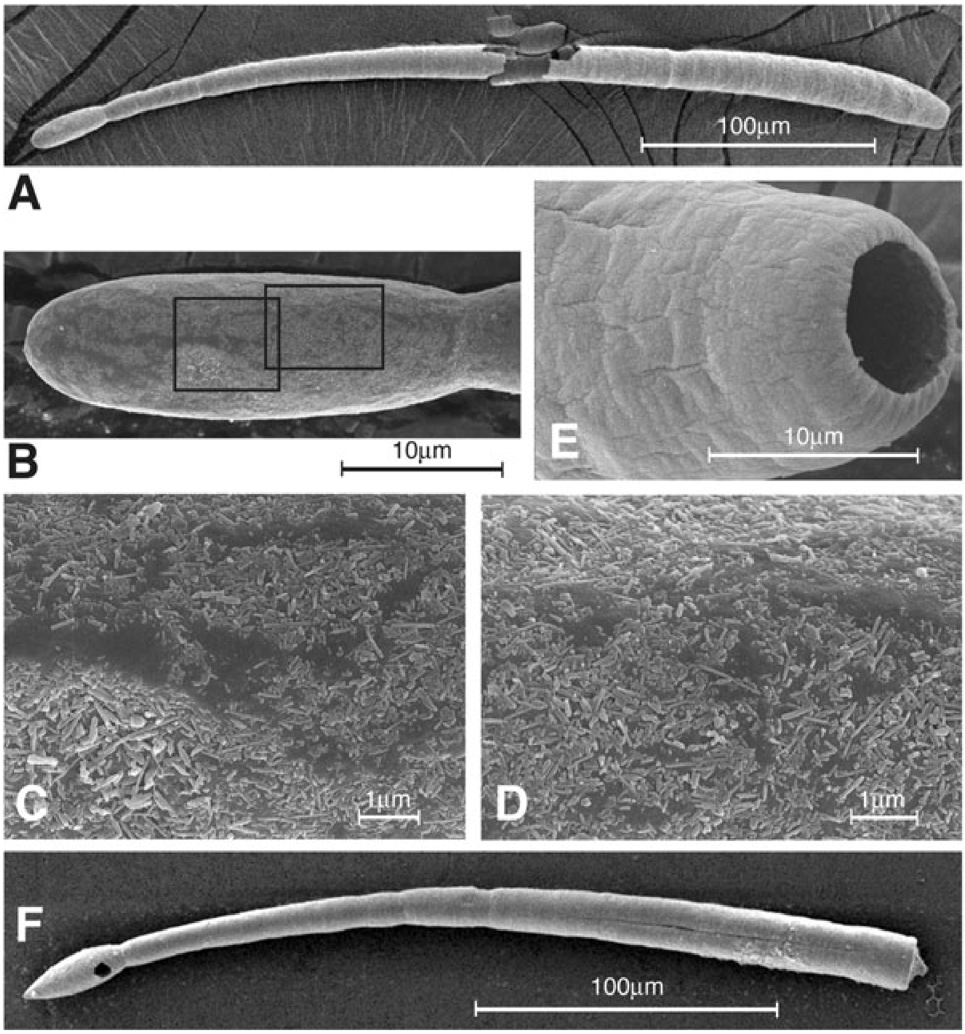

Figure 3. ***Nodellum aculeata*** **sp. nov.** Scanning electron micrographs. A, general view of entire specimen. B, proloculus with rounded end; boxes indicate areas shown in detail in C and D. C–D, details of proloculus; most of the surface is strewn with rod-like particles but the organic wall is exposed in irregular patches. E, oblique view of aperture. F, general view of entire specimen with pointed proloculus and abruptly truncated distal end.

the proloculus and the tubular part of the test, the two types of surfaces tend to interdigitate, with V-shaped, agglutinated areas penetrating into areas devoid of obvious grains (Fig. 4B, D).

When damaged mechanically, the test wall shatters into fragments, sometimes with curved edges (Fig. 7B), indicating that the wall is brittle rather than soft. Broken sections viewed by SEM are ~0.10–0.12 µm thick. The complex surface structure is visible on the outer margin of these sections, but the wall exhibits no obvious internal structure (Fig. 7C, D).

EDS analyses of the grains covering the proloculus reveal strong peaks for Fe and Si with secondary peaks for Mg and Al. Areas of test beyond the proloculus devoid of rod-like particles show a strong Fe peak and secondary peaks for Al and Si. These analyses suggest that the rod-like particles on the proloculus are composed of clay minerals, that other kinds of clay particles (presumably the flake-like patches referred to above) are also present on the tubular part of the test, and that the organic wall contains iron.

Test interior: The inner surface of the test is smooth. At very high magnifications (100 000×), however, it resolves into closely packed lumps, 0.02–0.05 µm in diameter, which impart a granular appearance at a submicrometre scale (Fig. 7E). The lumen of the tube is usually uninterrupted, but occasionally is divided by a transverse partition. It contains brownish stercomata that occupy a greater or lesser proportion of the cavity. Sometimes, most of the interior is filled

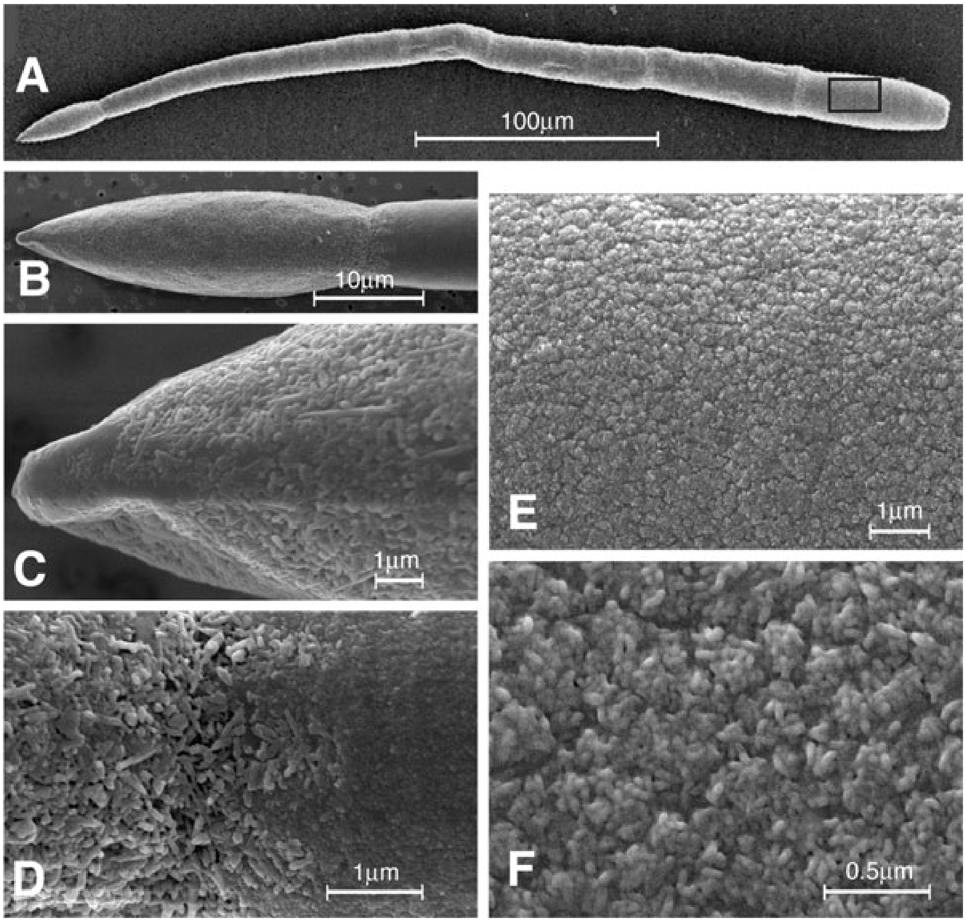

Figure 4. ***Nodellum aculeata*** **sp. nov.** Scanning electron micrographs. A, general view of entire specimen with somewhat crooked shape; box indicates area shown in detail in E. B, proloculus. C, pointed end of proloculus showing tip devoid of agglutinated particles. D, transition between surface of proloculus with agglutinated particles (to left) and predominately organic surface of the main tubular part of the test; note the interdigitation of the two areas. E, detail of surface. F, higher magnification showing tiny, finger-like projections covering test surface.

with stercomata while in other cases only part of the test, usually towards the distal end, is occupied (Fig. 1). Sometimes there are empty gaps, possibly artifactual, between stercomata-filled sections. In specimens that appear to be dead, the stercomata have lost their identity and decayed into a greyish powder. Distinct areas of cytoplasm are occasionally observed adjacent to the aperture (Fig. 1F).

Remarks: This '*Chitinosiphon*-like' species resembles *Nodellum rufescens* in the general shape of the test, but is much smaller (maximum test length ~500 μm), and more delicately constructed. The wall is also considerably thinner and only slightly tinged with brown rather than being deep, brownish-red in colour, as in the type specimens of *N. rufescens*. Another difference is the frequent presence of a small aperture at the pointed end of the proloculus in *N. rufescens*. A similar structure is never present in *N. aculeata*. The new species is much smaller and more slender than *Xenothekella elongata*.

Needle-like, organic-walled Foraminifera resembling *Nodellum aculeata* are fairly widespread across a considerable bathymetric range in the Pacific and Atlantic oceans. There are published records of these '*Chitinosiphon*-like' forms from 1345 m water depth in the Porcupine Seabight (north-east Atlantic) and at abyssal depths on the Porcupine Abyssal Plain (north-east Atlantic, 4850 m), the central Weddell Sea (4975 m), the North Pacific (4263–5289 m), the western Equatorial Pacific (5300–5570 m), the eastern Equatorial Pacific (4032–4089 m) and 7800 m in the Atacama Trench, south-east Pacific (Gooday, 1986; Gooday *et al*., 2001, 2004; Sabbatini *et al*., 2002; Cornelius & Gooday, 2004; Nozawa, 2005). Slight differences in the shape of the proloculus and the relative width of the tubular part of the test suggest that several species are represented amongst this

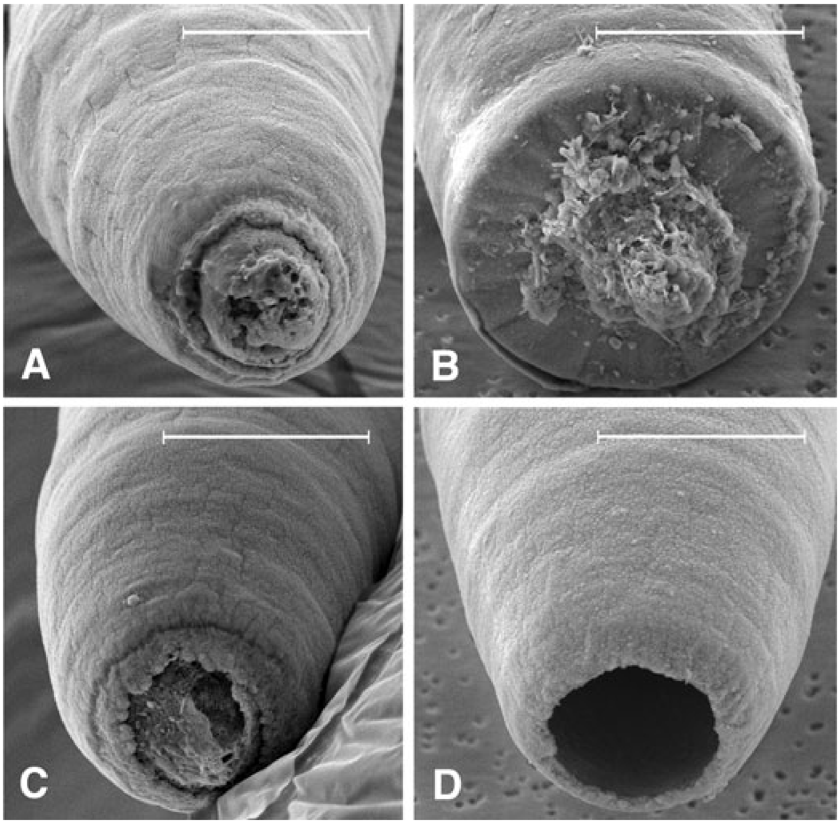

Figure 5. ***Nodellum aculeata* sp. nov.** Scanning electron micrographs of test apertures. A, C, D, specimens in which test tapers gently towards circular aperture. B, specimen with abruptly truncated apertural end (entire test shown in Fig. 3E). The specimen shown in D is probable dead (empty); those shown in A–C probably contain cytoplasm. All scale bars = 10 μm.

material. The Challenger Deep specimens are smaller than any of those previously illustrated (length < 500 μm compared with > 700 μm). They resemble most closely specimens from the Atacama Trench (Sabbatini *et al*., 2002: pl. 1, fig. 4) in having a rather inflated proloculus and in the relative width of the tubular part of the test.

RESIGELLA LOEBLICH & TAPPAN, 1984

Resigella Loeblich & Tappan, 1984, p. 1158

Type species: Nodellum moniliforme Resig, 1982.

Diagnosis: Test < 1 mm in length, consisting of symmetrically oval proloculus followed by 1–6 approximately droplet-shaped to subcylindrical chambers separated by distinct, regular constrictions or short stolons. Chambers arranged in linear sequence along straight, gently arcuate or occasionally slightly sinuous axis. Proximal end (base) of initial chamber (proloculus) either smoothly rounded or interrupted by pocket-like invagination. Test wall rigid, fairly brittle, orange or yellowish-brown in colour and more or less transparent. Wall mainly organic but incorporating some fine, adhering particles, in some species concentrated in constrictions between segments. Some or all chambers contain stercomata. (Slightly modified after Gooday *et al*., 2008).

Remarks: In the type species, *Resigella moniliforme*, the base of the proloculus has a pocket-like invagination (Gooday *et al*., 2008) that is not present in the two Challenger Deep species described below. The taxonomic significance of this feature is unclear and it is possible that *Resigella* should be split into two genera based on its presence or absence. However, because of their general morphological similarity, we prefer to retain the three species in one genus for the present.

***RESIGELLA LAEVIS* SP. NOV.**
FIGS 8–10

Resigella-like form 1. Todo, 2003, pl. 6, fig. 5
'Multichambered organic-walled allogromiid similar to *Resigella*'. Todo, Kitazato, Hashimoto, Gooday, 2005, fig. 1B.

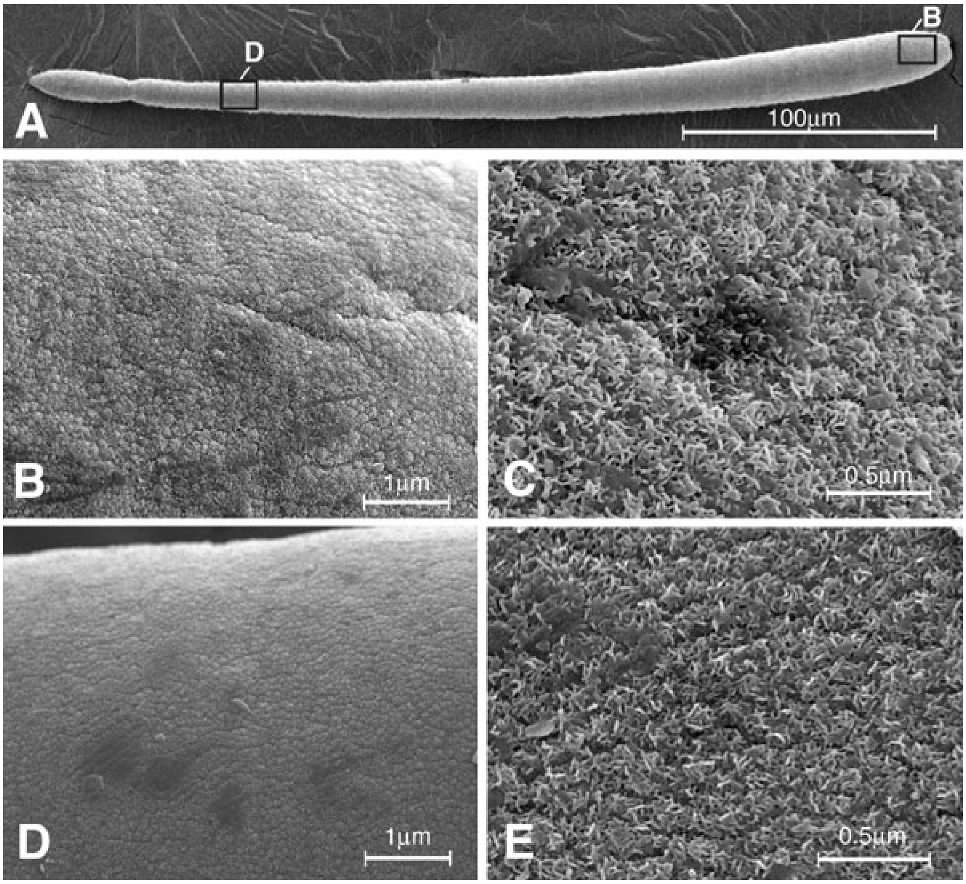

Figure 6. ***Nodellum aculeata*** **sp. nov.** Scanning electron micrographs. A, general view of entire specimen; boxes indicate areas shown in detail in other images. B, C, progressively closer views of test surface near the aperture. D, E, progressively closer views of test surface near proloculus. Note the finger-like projections covering the surface of the wall in both areas.

Diagnosis: Species of *Resigella* with test comprising gently curved series of 3–4 (occasionally five) elongate, droplet-shaped to subcylindrical chambers, separated by distinct constrictions. Initial chamber (proloculus) with smoothly rounded proximal end lacking basal invagination. Final chamber somewhat asymmetrical with round terminal aperture. Test wall transparent, pale yellowish in colour, mainly organic but incorporating some clay particles. Surface of proloculus smooth at submicrometre scale. Surfaces of later chambers covered in mass of short, branching, finger-like projections up to 0.1 µm long, visible only by SEM.

Types: The type specimens are deposited in Tokyo and London under reg. nos. MPC-02710 (holotype), MPC-02711-02715 (five paratypes) and ZF 5170 (two paratypes)

Other material examined: 78 specimens.

Derivation of name: Latin *laevis*, smooth, referring to the appearance of the test surface under the light microscope

Description

Test morphology: The test usually consists of 3–4 elongate chambers (two out of 86 specimens have five chambers) joined in a gently curved, linear series and separated by distinct necks (Fig. 8). The final chamber is elongate and has a slightly asymmetrical shape with one side being more or less straight and the other side gently curved. The first one or two chambers (including the proloculus) are usually approximately symmetrical and oval to fusiform in shape with curved sides. Occasional specimens have an additional swelling between two of the main chambers (Fig. 8D). Detailed dimensions are given in Table 2. The test ranges from 120 to 266 µm in length. The chambers generally increase in length from the proximal to the distal end of the test. The proloculus

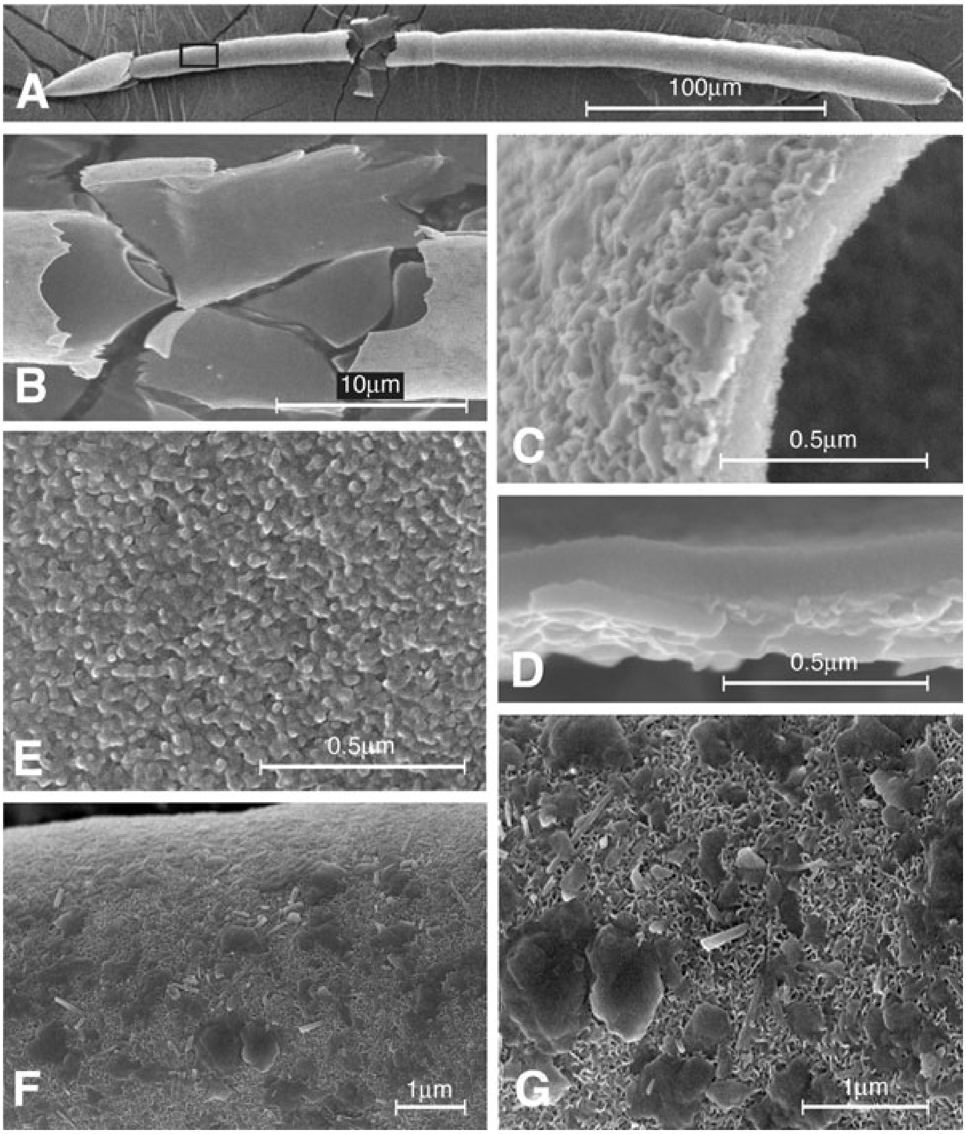

Figure 7. *Nodellum aculeata* sp. nov. Scanning electron micrographs. A, general view of test; area indicated by box is shown in detail in F. B, damaged region showing curved lines of fracture. C, D, broken sections of the wall showing probable agglutinated grain and lack of internal structure. E, inner surface of wall. F, G, surface of wall showing scale-like patches (probably clay particles) surrounded by masses of tiny, finger-like projections.

and the adjacent chamber (numbers 1 and 2 from the proximal end) are similar in size, 13–49 μm long and 11–24 μm wide, chamber 3 is 28–76 μm long and 15–35 μm wide, and chamber 4, which is always the longest, is 46–111 μm long and 20–38 μm wide.

Aperture: The aperture is located at the bluntly pointed end of the final chamber (Fig. 9A). In specimens examined by SEM, it is a simple opening, 5–7 μm across, with a slightly puckered rim (Fig. 10A, B, F). The aperture sometimes extends into a flimsy, organic, tubular structure.

Wall structure and composition: The wall is mainly organic and transparent with a distinct brownish tinge and completely smooth with a shiny surface when viewed by light microscopy. When examined by SEM, the surface of the proloculus has a slightly crumpled appearance but is otherwise smooth at magnifications up to 10 000× (Fig. 9B, F, G). The surfaces of subsequent chambers, however, resolve at magnification of 10–15 000× into a mass of short, branching, finger-like projections similar to those observed in *Nodellum aculeata*. They clearly arise from the underlying test wall. Individual branches are up to

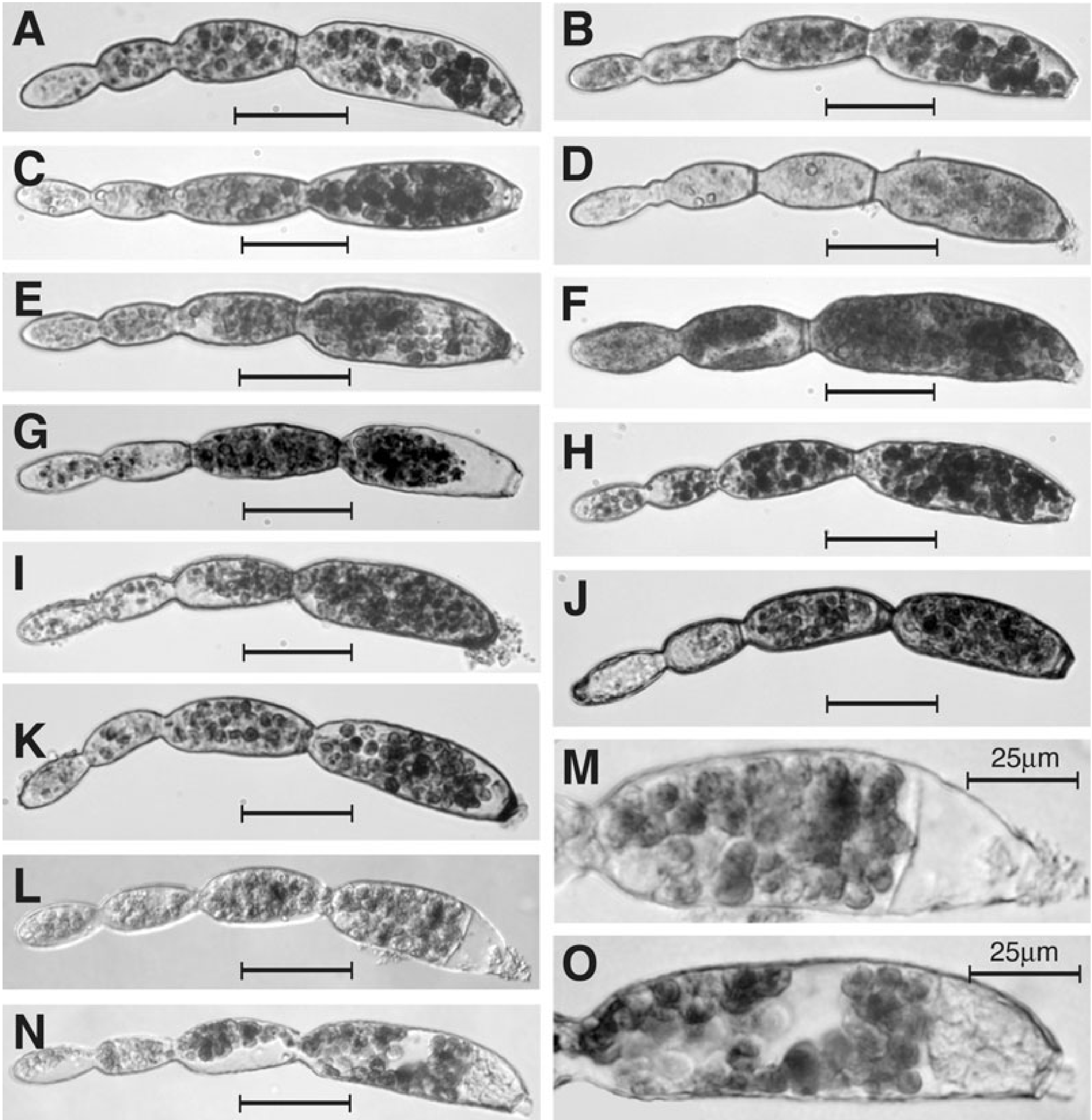

Figure 8. ***Resigella laevis*** **sp. nov.** Transmission light micrographs of specimens on open slides in glycerol. A, holotype, reg. no. MPC-02710. B–G, paratypes, reg. nos. MPC-02711-02715. H, I, paratypes, reg. nos. ZF 5170. J–O, other specimens; M shows detail of final chamber with partition in front of stercomata; O shows detail of final chamber with mass of cytoplasm in front of stercomata. All scale bars = 50 µm except where indicated otherwise.

about 0.10 µm (100 nm) long and no more than 0.015 µm (15 nm) wide. The density of these projections is not uniform across along the test. They are fairly sparsely developed near the terminal aperture of at least one specimen (Fig. 10C, D). Where the proloculus joins the second chamber, there is a regular, zig-zag interdigitation of the two types of surface (Fig. 9B, C). Flat plate-like features that often merge with the projections (Fig. 9E), and scale-like structures around the aperture (Fig. 10B), are interpreted as clay particles (see below). The wall appears fairly rigid and tends to crack or split when damaged

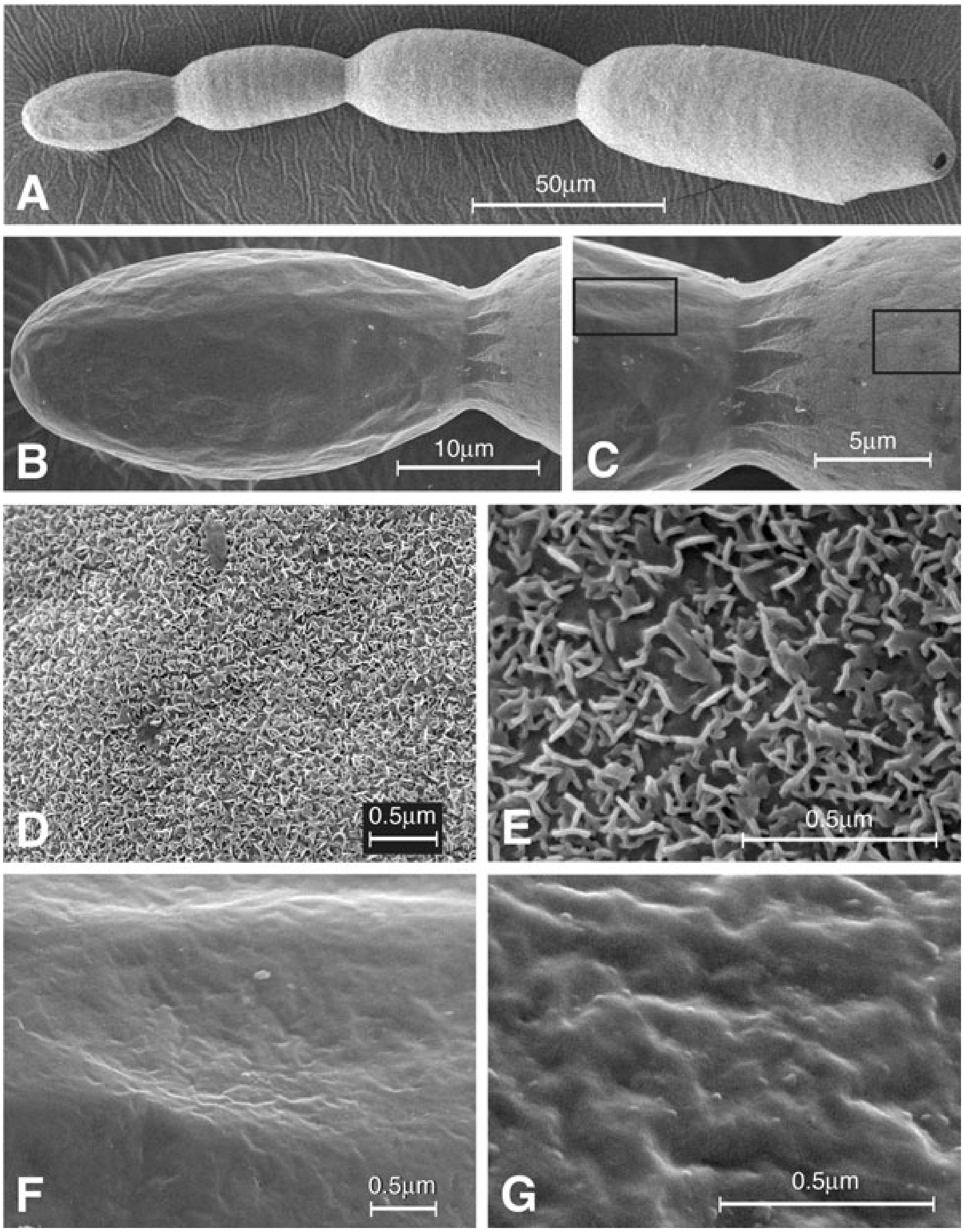

Figure 9. ***Resigella laevis*** **sp. nov.** Scanning electron micrographs. A, general view of test. B, proloculus. C, detail of interdigitated border between smooth organic surface of proloculus and highly ornamented organic surface of later chambers; boxes indicate areas shown in detail in D and F. D, E, surface of chamber immediately in front of proloculus showing mass of finger-like projections; the flat features are probably clay particles. F, G, surface of proloculus.

mechanically (Fig. 10F). It is ~0.25–0.55 μm thick, becoming thicker near the aperture. Broken sections display no obvious internal structure (Fig. 10G).

EDS analyses of the proloculus and later chambers reveal the presence of Fe, Mg, Al, Si and Ca. Peak sizes are variable, but those for Mg, Al, Si and Ca tend to be higher on later chambers whereas Fe peaks tend to be higher on the proloculus. These analyses suggest that clay particles are present on later chambers, and probably also on the proloculus, and that the organic wall contains iron.

Test interior: In live individuals, all or some of the chambers are filled, or partially filled, with brownish stercomata (Fig. 8). Occasionally, an obvious cytoplasmic mass is located just inside the aperture of the final chamber (Fig. 8O). It is sometimes separated from the stercomata by a thin organic partition (Fig. 8M). In

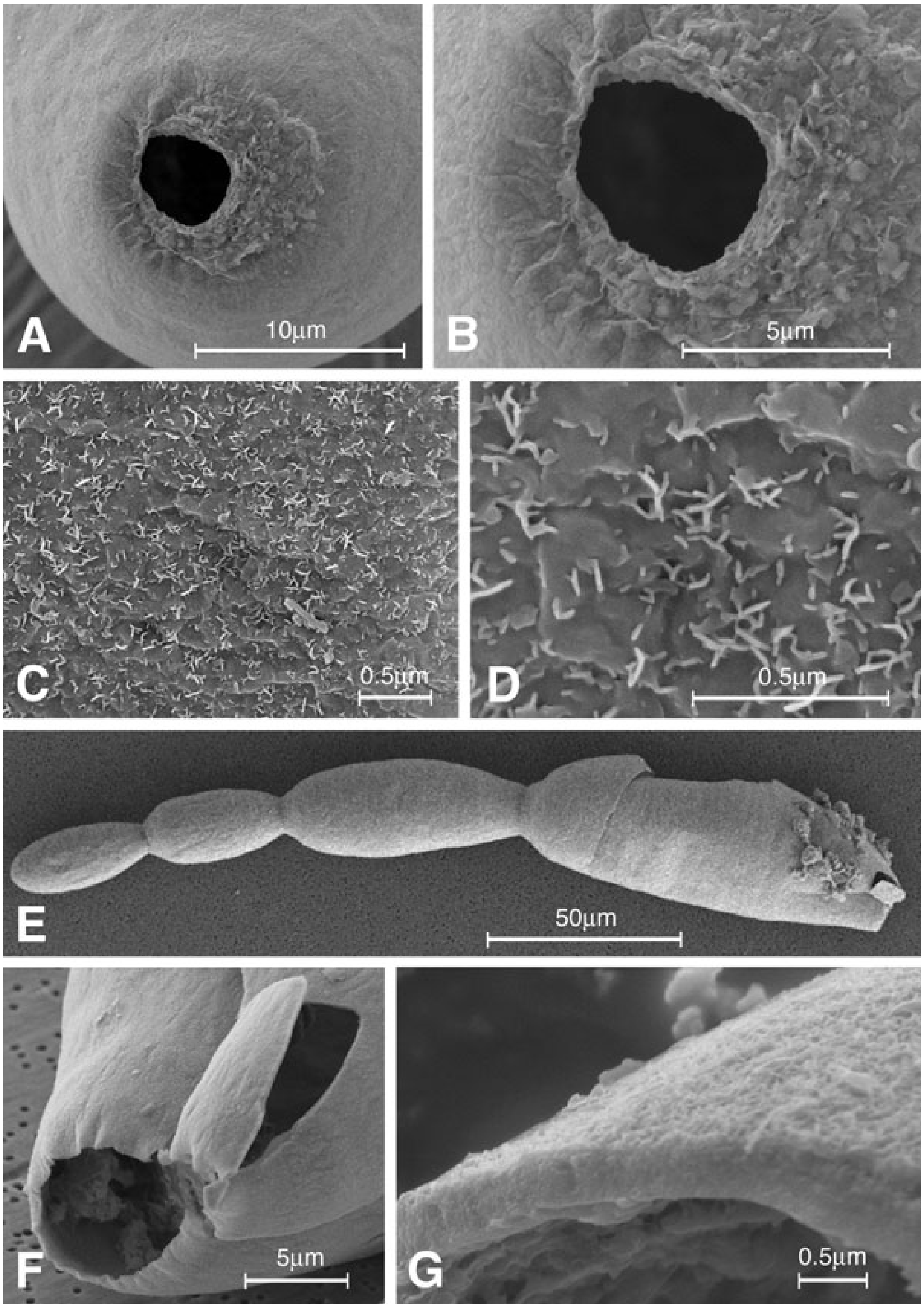

Figure 10. ***Resigella laevis* sp. nov.** Scanning electron micrographs. A, B, aperture. C, D, surface of test near aperture showing relatively sparse development of finger-like projections. E, general view of test. F, aperture. G, broken section of wall.

dead individuals, the stercomata become greyish in colour and break down into finely granular material.

Remarks: Resigella laevis lacks the pocket-like invagination at the base of the proloculus that is always present in *R. moniliforme*, the type species of *Resigella*. It is also smaller than the type species (usually < 250 μm in length compared with 280–670 μm) and the chambers are much more elongate, sometimes subcylindrical, rather than droplet-shaped. Another difference is that the new species lacks the accumulations of agglutinated particles that

Table 2. *Resigella laevis* sp. nov.: dimensions of the test and its component chambers (μm)

	Length			Width		
	Range	Mean ± SE	*N*	Range	Mean ± SE	*N*
Test (5 chrs)	195–257		2			
Test (4 chrs)	164–266	233 ± 24.5	62			
Test (3 chrs)	120–186	161 ± 17.5	23			
Chamber 4	46–111 (151)	89 ± 15.8	86	20–38 (53)	30 ± 4.8	86
Chamber 3	28–76	53 ± 10.5	86	15–35	24 ± 3.6	86
Chamber 2	13–49	38 ± 7	86	11–24	19 ± 2.6	86
Proloculus	18–46 (56)	36 ± 6.4	62	(7) 13–22	18 ± 2.3	62

The figures in parentheses are outliers.
SE = standard error.

are developed in the constrictions between the chambers in *R. moniliforme*.

Resigella-like form 1 of Todo (2003: pl. 6, fig. 5) from Stn NK-3 in the Japan Trench (7761 m water depth) may be conspecific with *R. laevis*. The only difference is that the constrictions between the chambers are somewhat less prominent than in the Challenger Deep specimens. *Resigella*-like form 2 of Nozawa (2005: pl. 6, fig. C) from the abyssal Kaplan East site in the Equatorial Pacific (4100 m depth) also resembles the new species, but has a much more pronounced constriction between the two chambers (the specimen may be incomplete). A similar, three-chambered, organic-walled *Resigella*-like form from 7800 m in the Atacama Trench is illustrated by Sabbatini *et al*. (2002: pl. 1, fig. 2) and Gooday *et al*. (2004: fig. 5D). However, the final chamber has a more symmetrically oval shape, and the proloculus is more inflated than in *R. laevis*. It probably represents a distinct species.

RESIGELLA BILOCULARIS SP. NOV.
FIGS 11–13

Diagnosis: Species of *Resigella* with test comprising two oval to droplet-shaped chambers arranged on a linear axis and separated by short neck. Initial chamber (proloculus) with rounded or somewhat pointed proximal end which lacks basal invagination. Test wall basically organic and transparent; second chamber distinctly brownish-yellow in colour. Surface of proloculus smooth at submicrometre scale, sometimes with partial veneer of plate-like clay particles. Second chamber with variable number of small, irregularly arranged mineral grains concentrated in proximal part; other parts of wall with flat, scale-like features (probably clay particles) merging into meshwork of bar-like elements, visible only by SEM.

Types: The type specimens are deposited in Tokyo and London under reg. nos. MPC-02697 (holotype), MPC-02696 (one paratype) and ZF 5171 (four paratypes)

Other material examined: 15 specimens.

Derivation of name: The name refers to the consistently bilocular nature of the test.

Description
Test morphology: The test consists of two globular chambers, the initial chamber (proloculus) being about half the size of the second chamber (Fig. 11). The initial chamber is more or less symmetrically oval, often with a somewhat pointed proximal end. The second chamber is droplet-shaped, widest behind the mid point, and tapers towards the slightly truncated apertural end. The initial chamber is joined to the second chamber by a very short, narrow neck. The overall length of the test is 107–190 μm (usually 164–190 μm; mean 167 μm, SE 25.0 μm). The first chamber measures 50–85 μm (mean 65 μm, SE 11.7 μm) long and 28–53 μm (mean 43 μm, SE 6.6 μm) wide. The second chamber measures 70–133 μm (usually 106–133 μm; mean 112 μm, SE 18.2 μm) long and 38–93 μm (usually 54–93 μm; mean 67 μm, SE 18 μm) wide.

Aperture: The aperture is located at the distal end of the second chamber (Fig. 11D, G). In some specimens examined by light microscopy, it is a simple, circular opening; in others it is produced slightly into a very short, delicate neck composed of transparent organic material. One specimen examined by SEM has a circular opening, ~15 μm diameter, enclosing a rather complex organic structure (Fig. 13A). The inner part of this structure (~10–11 μm diameter) has vague,

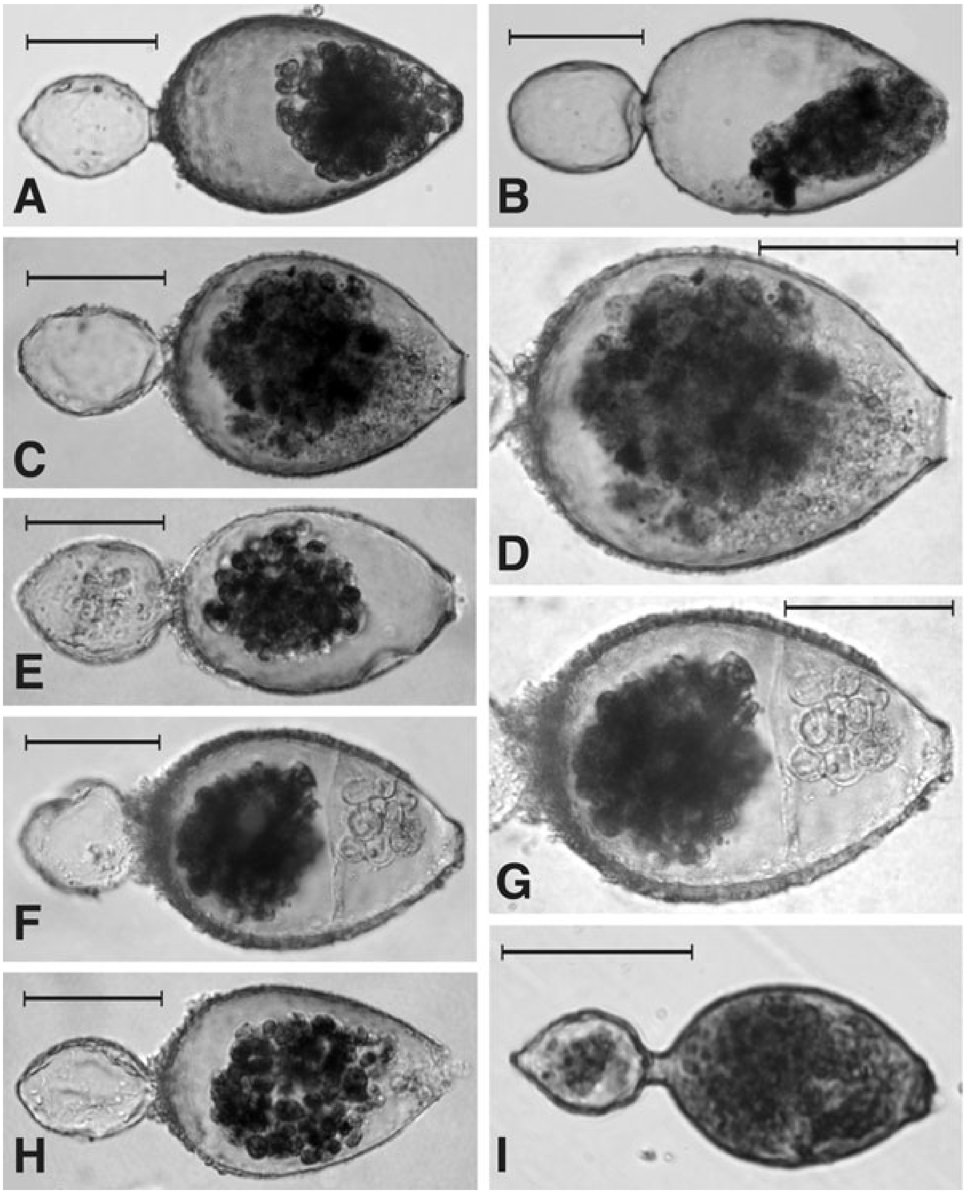

Figure 11. ***Resigella bilocularis* sp. nov.** Transmission light micrographs of specimens on open slides in glycerol. A, holotype, reg. no. MPC-02697. B, paratype, reg. no. MPC-02696. C, D, general view and detail of specimen illustrated by SEM in Figure 12A–B. E, general view of specimen illustrated by SEM in Figure 13E–F. G, specimen with delicate partition in front of stercomata. H, paratype, reg. no. ZF 5171. I, small specimen with clearly developed neck between the two chambers. All scale bars = 50 μm.

linear features radiating from a central cluster of raised lips within which the aperture presumably lies. This probably corresponds to the delicate neck sometimes visible by light microscopy

Wall structure and composition: The test wall is basically organic, transparent, with a distinct, brownish-yellow colour in transmitted light. The colour is usually more evident in the second chamber, which has a thicker wall than the first chamber. A deposit of finely agglutinated material, visible by light microscopy, is often loosely attached to part of the wall of the second chamber (Fig. 11D, G), but is variably developed and in some specimens seems to be entirely absent. Where present, it typically becomes thicker away from the aperture, particularly in front of the join between the first and second chambers. Viewed in the SEM, the agglutinated layer is composed of a mixture of mostly angular mineral grains, the largest of which are 1.0–1.5 μm in size (Fig. 12E).

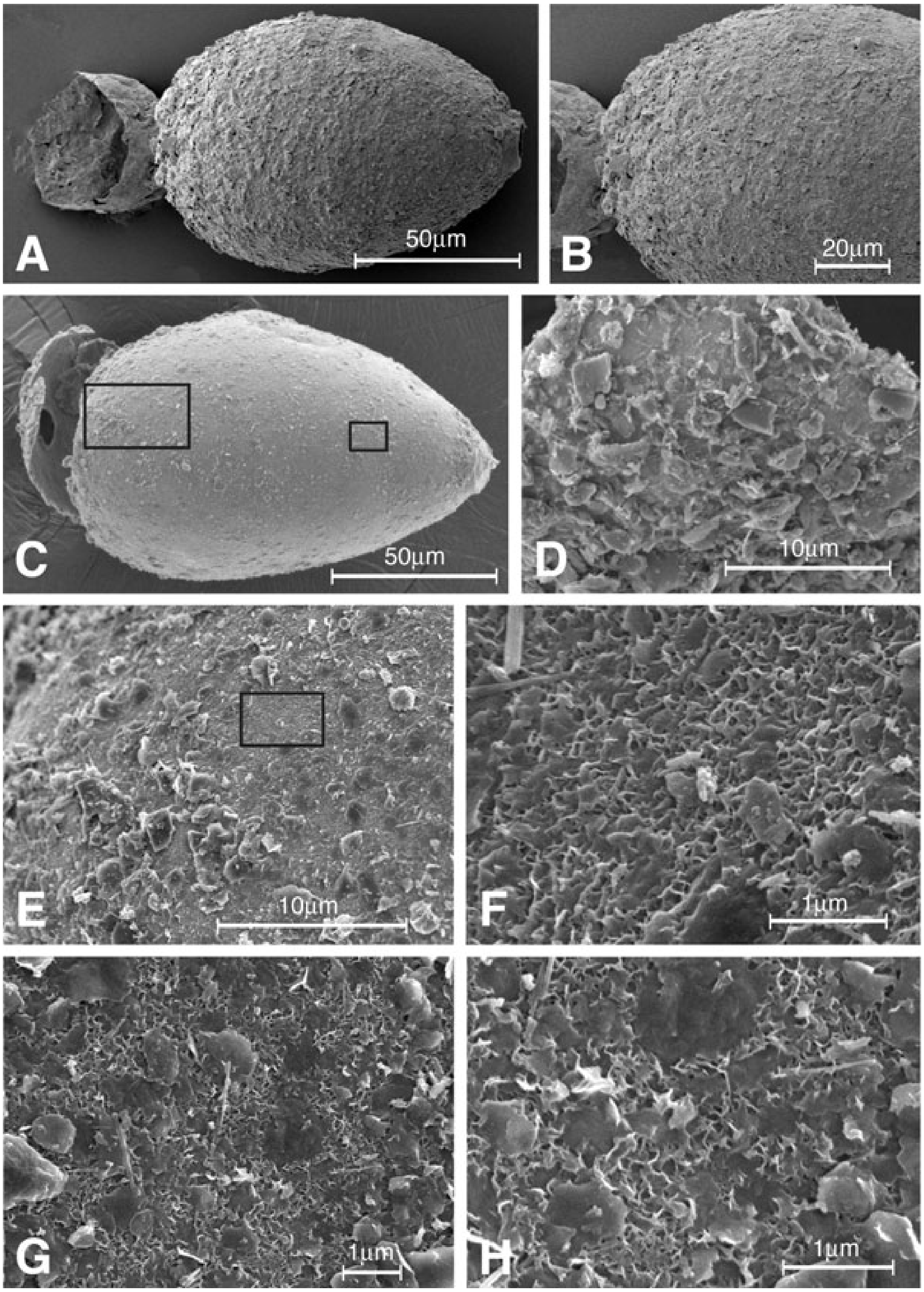

Figure 12. ***Resigella bilocularis*** **sp. nov.** Scanning electron micrographs. A, general view; note collapsed initial chamber. B, detail of same specimen showing agglutinated coating of organic wall; note that the grains become more prominent towards proximal part of chamber. C–H, damaged specimen; the initial chamber has been lost. C, general view; areas within boxes are shown in more detail in E–H. D, surface of proximal part of chamber showing agglutinated grains. E, surface towards posterior end of chamber showing agglutinated grains and smoother, intervening areas; box indicates area shown in detail in F. F, detail of organic wall with mesh-like structures and a few flat areas. G, H, surface towards distal part of chamber showing smooth, flake-like features separated by areas with a fine, mesh-like structure. The flake-like features in F–H are probably clay particles.

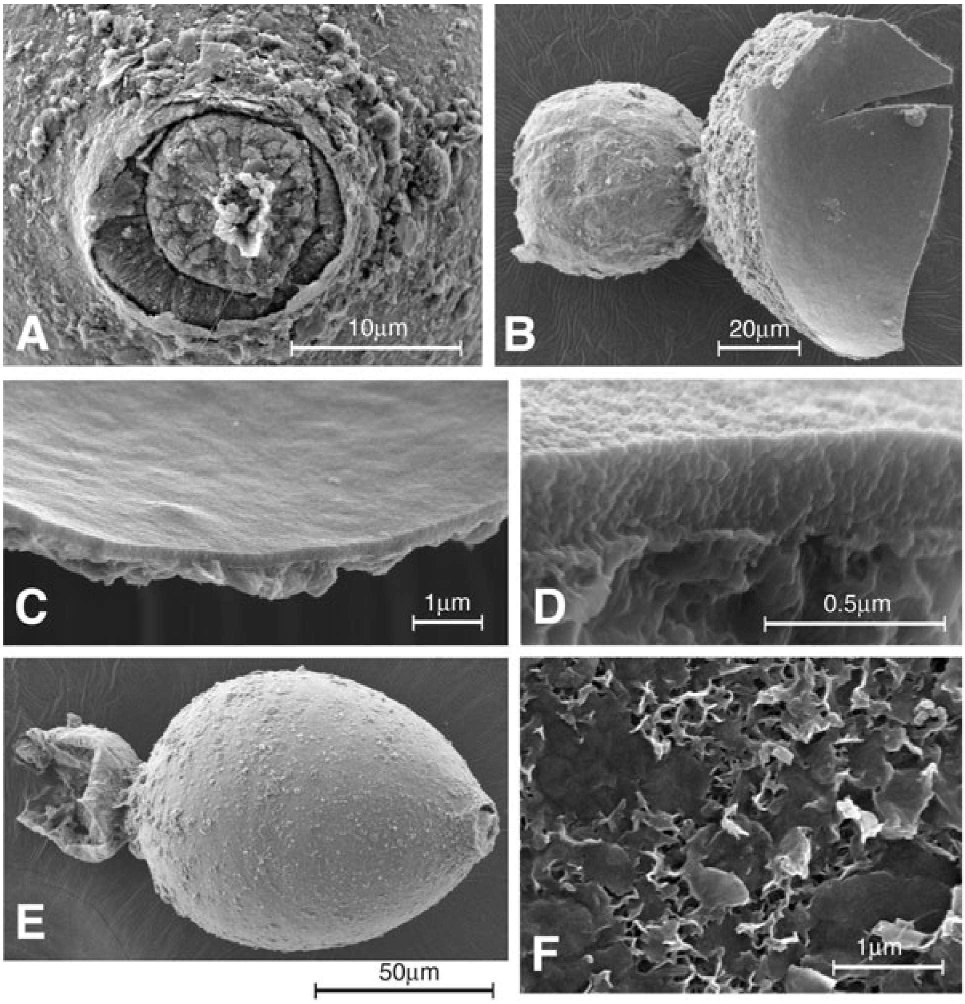

Figure 13. ***Resigella bilocularis*** **sp. nov.** Scanning electron micrographs. A, aperture of specimen shown in Figure 12C. B, general view of specimen with intact intial chamber and broken second chamber. C, D, broken cross-section of test wall showing organic layer overlain by agglutinated grains. E, F, general view of test and detail of organic surface with flake-like features (probably clay particles) separated by mesh-like structures.

The surface of the larger second chamber has a complex appearance when viewed by SEM (Figs 12F–H, 13F). It includes flat areas of varying sizes (up to ~1 μm but usually smaller), some of them scale-like. These features may be clay particles (see below). They merge at their edges into a tangled meshwork of bar-like elements, the individual bars being 0.01–0.02 μm (10–20 nm) in width. The smaller first chamber has a smooth surface, sometimes with a partial coating of plate-like grains a few micrometres in diameter and some flake-like features at submicrometre scale. Broken cross-sections of the organic part of the wall are ~0.20–0.35 μm (200–350 nm) thick and appear featureless, apart from irregularities probably related to fracturing (Fig. 13D).

EDS analyses of the proloculus reveal strong Al and Si peaks suggesting that the plate-like grains are clay minerals. Analyses of more equidimensional grains on the second chamber indicate a variety of compositions. A strong peak for Si with additional peaks for Mg and Al suggest that some grains are clay minerals. Other particles have high concentrations of Ca and S. The organic part of the wall of both chambers yields a strong Fe peak, a weaker Si peak and small peaks for Mg and Al.

Test interior: The initial chamber is usually empty. In live individuals, the second chamber contains stercomata and protoplasm. The protoplasm forms a distinct mass just inside the aperture and behind this is an area occupied by stercomata. In one of the specimens, there is a thin partition between the two parts of the chamber (Fig. 11G).

Remarks: The droplet-like second chamber of *Resigella bilocularis* is remarkably similar in shape to the later chambers of *R. moniliforme* (illustrated by Gooday *et al*., 2008: fig. 9). The test surface of both species is often characterized by an irregularly developed sprinkling of agglutinated particles that becomes thicker towards the proximal end of the later chambers. However, the two-chambered test of *R. bilocularis* distinguishes it from both *R. moniliforme* (up to six chambers) and *R. laevis* (3–4 chambers). The chambers are also much more globular than in *R. laevis*, and there is no trace of the basal invagination of the proloculus, which is a consistent feature of *R. moniliforme*.

Brownish, bilocular, organic-walled tests resembling *Resigella bilocularis* are an occasional but widespread component of abyssal foraminiferal assemblages, having been reported in the North and Equatorial Pacific (Gooday *et al*., 2004; Nozawa, 2005), the Weddell Sea (Cornelius & Gooday, 2004) and north-east Atlantic (Gooday, Carstens & Thiel, 1995). These abyssal specimens are generally rather smaller (120–155 μm) than those from the Challenger Deep but in other respects are similar. However, in the absence of molecular data, we hesitate to regard them as conspecific. Bilocular morphotypes of *Resigella* are not represented in the Atacama Trench (Sabbatini *et al*., 2002).

CONICOTHECA GEN. NOV.

Type species: Conicotheca nigrans gen. et sp. nov.

Derivation of name: Refers to the shape of the organic theca (test).

Diagnosis: Test tiny (usually < 120 μm long), elongate, more or less conical in shape, tapering towards proximal end from widest point in distal third to quarter. Proximal end often slightly bulbous; distal end truncated or bluntly pointed with single terminal aperture that is round to elongated in shape. There are no internal subdivisions. Test wall mainly organic, transparent and colourless. Some areas smooth on submicrometre scale; other areas with scale-like surface pattern, probably due to presence of clay minerals. Test interior contains large, dark-coloured stercomata.

Remarks: The much smaller test size, the more compact, streamlined shape and the lack of a well-defined proloculus distinguish *Conicotheca* from *Nodellum*. The new genus differs from *Resigella* in the absence of chamber-like subdivisions. The tapered shape of the test is most similar to that of *Micrometula*, a monothalamous, organic-walled genus that occurs on the continental margins of north-west Europe and Svalbard (Nyholm, 1952; Gooday *et al*., 2005; Majewski, Pawlowski & Zajczkowski, 2005). However, *Conicotheca* has a relatively shorter test and lacks the short apertural neck present in *Micrometula*. Another important difference is that the test of *Coniotheca* is filled with stercomata whereas that of *Micrometula* contains only cytoplasm.

In addition to the type species from the Challenger Deep, at least one species that can be assigned to this genus occurs at the abyssal Kaplan East site in the eastern Equatorial Pacific (Nozawa *et al*., 2006).

CONICOTHECA NIGRANS GEN. ET SP. NOV.
FIGS 14–16

Diagnosis: As for genus.

Types: The type specimens are deposited in Tokyo and London under reg. nos. MPC-02704 (holotype), MPC-02699-02703 (five paratypes) and ZF 5168 (six paratypes).

Other material examined: 62 specimens

Derivation of name: Latin *nigrans* (black or dark) alluding to the dark appearance of this species due to the presence of stercomata within the transparent test.

Description

Test morphology: The test resembles an elongate cone with either a bluntly rounded or truncated distal (apertural) end (Figs 14, 15A, B, F, G). It typically measures 80–120 μm long and tapers from 23 to 35 μm at the widest point in the anterior third to quarter to 9–13 μm just in front of the rounded proximal end (Table 3), which is often slightly bulbous. Occasionally, there is a rather abrupt decrease in width at some point along the length of the test (Fig. 14D), possibly reflecting a growth discontinuity. A few specimens are larger, up to 156 μm long and 52 μm wide. The length/width ratio varies from 2.7 to 5.2 but is usually between 3 and 4. The position of the widest point varies from 16% to 42% of the length from the distal end; in more than three-quarters of specimens it is situated between one-fifth and one-third (25–33%) of the length from the distal end. In dried specimens viewed by SEM, the proximal end maintains a rounded shape whereas adjoining parts of the test tend to collapse (Figs 15D, 16D). It may represent a poorly defined proloculus.

Aperture: The aperture is difficult to see clearly by light microscopy. Some specimens have a rounded

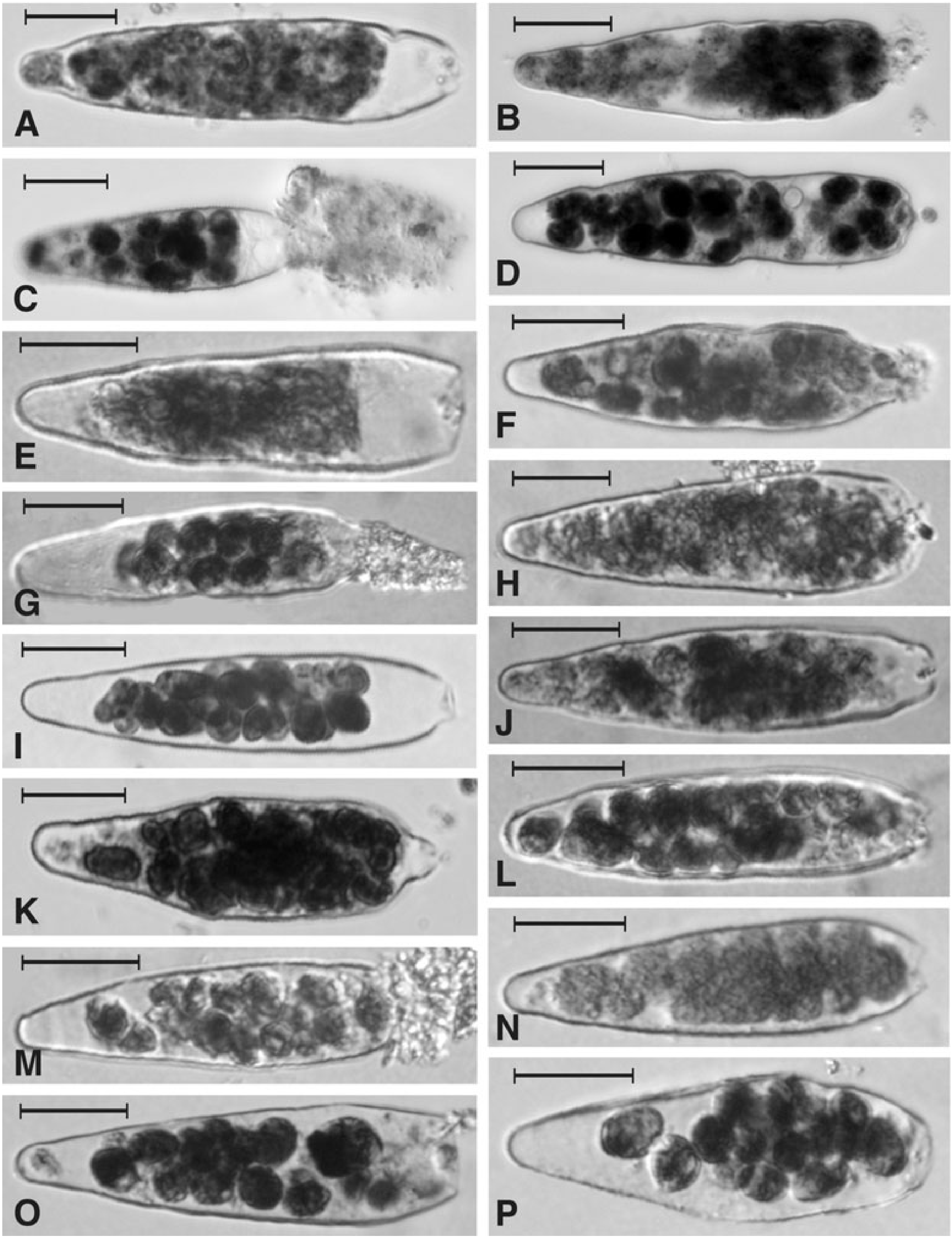

Figure 14. ***Conicotheca nigrans*** **gen. et sp. nov.** Transmission light micrographs of specimens on open slides in glycerol. A, holotype, reg. no. MPC-02704. B–D, paratypes, reg. nos. MPC-02699-02701. E–I, paratypes, reg. nos. ZF 5168. J–P, additional specimens. All scale bars = 25 µm.

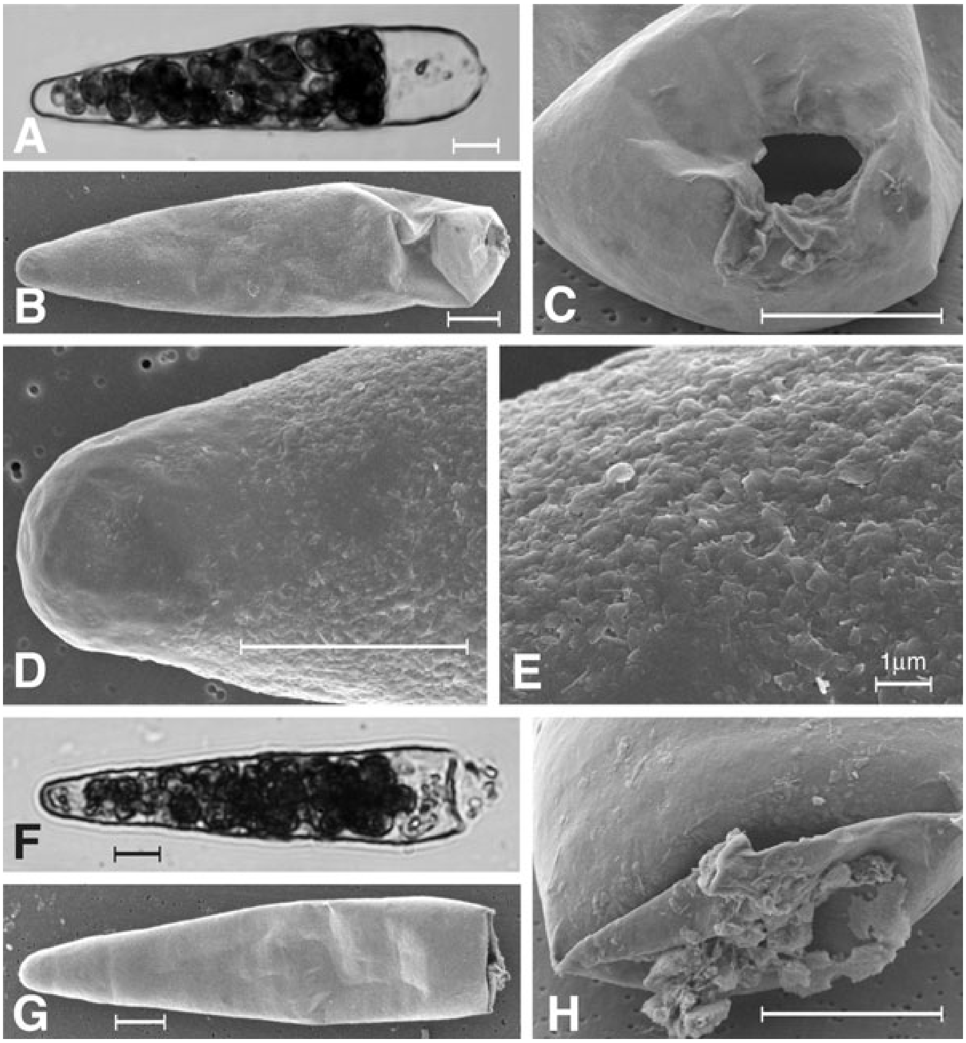

Figure 15. ***Conicotheca nigrans* gen. et sp. nov.** A–E, transmission light and scanning electron micrographs of same specimen. A, B, general views. C, aperture. D, proximal part of test ('proloculus') showing smooth surface. E, part of test with rougher surface covered in scale-like features, probably clay particles. F–H, transmission light and scanning electron micrographs of same specimen. F, G, general views. H, distal (apertural) end.

distal end and a relatively small aperture (e.g. Fig. 14I, J), but in many cases, the end of the test is truncated and the aperture appears to be more elongated (e.g. Fig. 14E, O, P). Examination of four specimens by SEM confirms the impression gained from light microscopy. In one individual (Fig. 15A–C), the end of the test is rounded and the aperture forms a simple, oval opening measuring 5.5 by 3.0 µm. In another (Fig. 15F–H), the end is truncated and the aperture, although obscured by detritus, seems to be slit-like. The third specimen (Fig. 16A, B) also has a truncated end, with a relatively large, elongate oval aperture, measuring 14 by 7 µm. The aperture of a fourth specimen (not illustrated) forms a circular opening ~6 µm across.

Wall structure and composition: The wall is mainly organic, transparent and colourless. A variable proportion of the test surface is rough and lumpy on a submicrometre scale. In places, the surface irregularities merge into irregularly shaped, scale-like features, < 1 µm in size, which form an imbricated pattern on the surface (Fig. 16F). These rough surfaces are more extensively developed in some specimens than in others. The remaining areas of the test, and particularly the rounded, proximal end, are smooth on a submicrometre scale (Figs 15D, 16D), except for occasional, tiny, finger-like projections of the organic wall (Fig. 16E).

EDS analyses of test areas covered by scale-like formations reveal strong peaks for Al and Si with

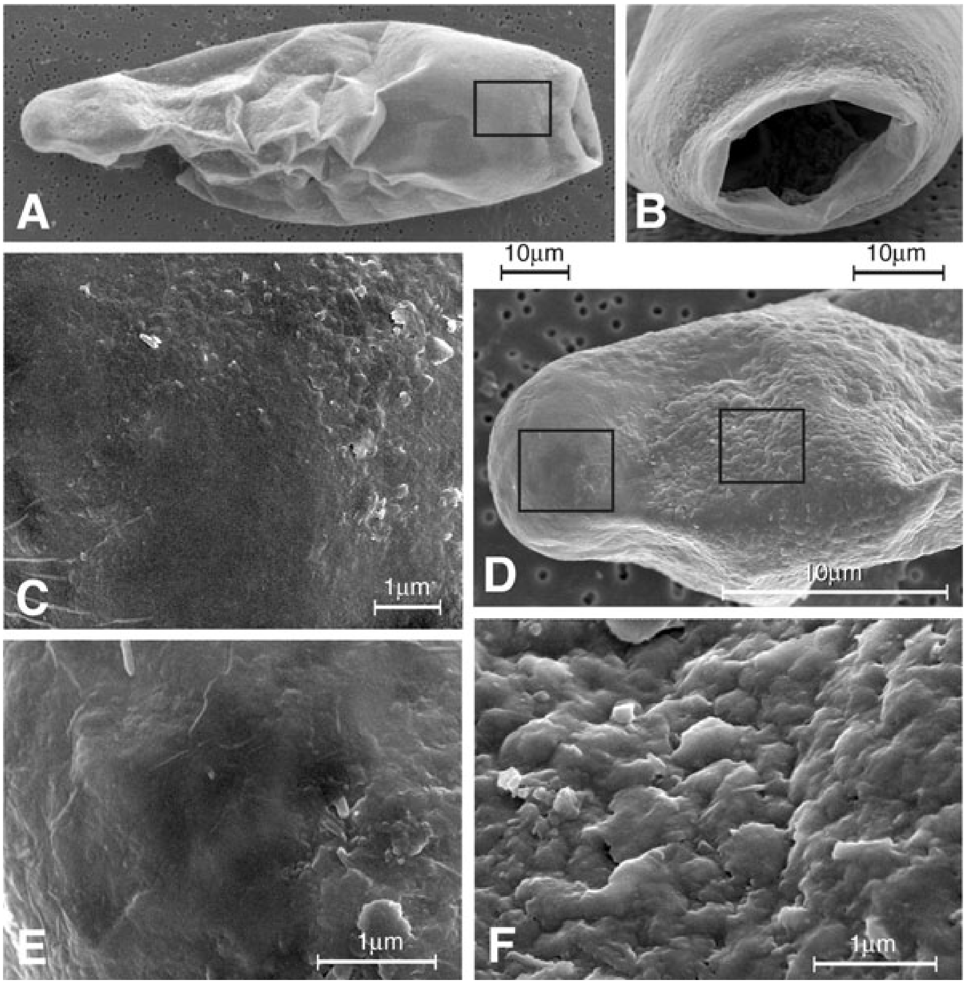

Figure 16. ***Conicotheca nigrans*** **gen. et sp. nov.** Scanning electron micrographs of same specimen. A, general view; area indicated by box is shown in detail in C. B, aperture. C, detail of surface. D, proximal part of test with swollen 'proloculus'; areas indicated by boxes are shown in detail in E and F. E, smooth area on 'proloculus'. F, rough area with scale-like features, probably clay particles.

Table 3. ***Conicotheca nigrans*** **gen. et sp. nov.** Test dimensions (μm); the minimum width is measured just in front of the narrowly rounded proximal end

	Range	Mean ± SE	*N*
Length	74.1–155.6	103.1 ± 15.9	74
Width maximum	19.8–51.9	29.5 ± 5.34	74
Width minimum	8.6–13.0	11.0 ± 1.22	35
L : W_{max}	2.7–5.2	3.57 ± 0.52	74

SE = standard error.

additional peaks for Mg, K and Ca. The smooth, proloculus-like part has much lower peaks for these elements. These analyses indicate that the scale-like features are clay minerals. Fe concentrations are similar in the initial and later parts of the test, suggesting that the colourless organic wall incorporates iron.

Test interior: The test interior is undivided. It contains relatively large stercomata, typically 8–12 μm in diameter (Fig. 14). In some cases, these appear fresh with clearly defined outlines. In specimens that are obviously dead, the stercomata appear in various stages of decomposition, the final product being a fine powder containing large inclusions. Obvious cytoplasm has not been observed.

Remarks: Some similar organic-walled Foraminifera occur in other parts of the Pacific Ocean. They include *Nodellum*-like form 7 of Todo (2003: pl. 5, fig. 2) from a 7123-m-deep site (Stn 40) close to the Challenger Deep. This form resembles *Conicotheca nigrans* in shape but is considerably larger (~360 μm long). Two other *Nodellum*-like forms (Todo, 2003: pl. 4, figs 4, 5) from a shallower site in the western Equatorial Pacific (Stn 64, 5507 m depth) are similar to the new species in size (lengths = 105 and 160 μm) as well as shape. They differ in other respects, however, notably the test contents that comprise a mixture of stercomata and material that stains red with rose Bengal. *Nodellum*-like form 5 of Nozawa *et al*. (2006: fig. 2B) from the Kaplan East site in the Equatorial Pacific (~4100 m depth) has a conical, organic-walled test truncated at the distal end. This specimen resembles *C. nigrans* but is relatively wider with a more strongly flared test and a length/width ratio of 2.8. These forms require further study in order to clarify their relationship to the new species.

Another similar but clearly distinct species, informally designated *Nodellum*-like form 3, is well known from the Pacific, Indian, Atlantic and Southern oceans (Cornelius & Gooday, 2004; Gooday *et al*., 2004, and references therein). The proximal two-thirds of the test is more or less conical, as in *C. nigrans*, and contains relatively large stercomata. However, the distal part tapers towards the aperture. Other important differences between the two species are the presence of a tubular extension of the aperture, a small mass of cytoplasm just inside the aperture, and a canopy of fine sediment over the distal part of the test (Gooday *et al*., 2004: fig. 4F–J).

DISCUSSION

Comparison with previous studies

Akimoto *et al*. (1996, 2001) reported several agglutinated foraminiferal species, identified as *Lagenammina difflugiformis*, *Hormosina globulifera*, *Reophax guttifera* and *Rhabdammina abyssorum*, from the Challenger Deep. Most specimens were dead but a few individuals of *L. difflugiformis* contained rose-Bengal-stained cytoplasm. Their core sample was washed on a 125-μm sieve and specimens picked from the dried residue (Akimoto *et al*., 2001). The Foraminifera illustrated by Akimoto *et al*. (2001) were between 230 and 480 μm in maximum dimension. Our material, which was washed on a finer (32-μm) sieve, yielded occasional coarsely agglutinated specimens of *Reophax* and *Lagenammina*, and *Rhabdammina*-like tubes (probably *R. abyssorum* of Akimoto *et al*., 2001) up to 1 mm in size, as well as some much smaller hormosinaceans, textulariinids and trochamminaceans (Todo, 2003; Todo *et al*., 2005). However, the sample was overwhelmingly dominated by the tiny, organic-walled species described here. The differences between our results and those of Akimoto *et al*. (1996, 2001) reflect the different methods used to analyse the samples. Many of our tiny, elongate morphotypes would have passed through a 125-μm mesh sieve. Also, our samples were wet sorted, whereas Akimoto *et al*. examined dried residues in which delicate, organic-walled Foraminifera would have been destroyed or unrecognizable.

Previous studies of hadal Foraminifera by Russian scientists (Saidova, 1970, 1975) were based either on grab samples (usually 0.2 m^2 surface area) that were much larger than our small core (38.5 cm^2), or on trawl samples collected from an extensive area of seafloor. In particular, komokiaceans were recovered at a number of hadal sites, including one located in the Tonga Trench at depths approaching those in the Challenger Deep (Kamenskaya, 1989, 2006). These relatively large samples were sieved on a 1-mm and 0.4-mm mesh screen (O. E. Kamenskaya, pers. comm.). Although our core contained a few fragments of delicate, flexible, agglutinated tubules that were probably derived from komokiaceans, it was too small to sample these relatively large organisms adequately.

Influences on assemblage composition

Similar species to those described here are known from bathyal and abyssal sites in the Pacific and Atlantic oceans (Gooday *et al*., 1995, 2001, 2004; Todo, 2003; Todo *et al*., 2005, supplementary material; Nozawa, 2005; Nozawa *et al*., 2006), but they are never a dominant faunal component. As far as we are aware, the only other site where organic-walled Foraminifera of this type are abundant is located at 7800 m depth in the Atacama Trench where species resembling *Nodellum aculeata* and *Resigella laevis* are both common (Sabbatini *et al*., 2002). An association characterized by *Placopsilinella aurantiaca*, a stercomata-bearing species with a brownish, organic wall similar to that of *Nodellum* and *Resigella*, occurs in the central Arctic Ocean (Wollenburg & Mackensen, 1998). This species was abundant at 573-m depth on the slope of the Nansen Basin, north-east of Svalbard, where it was accompanied by species assigned to *Nodellum* and *Resigella* (Wollenburg, 1992).

The composition of the Challenger Deep foraminiferal assemblage probably reflects the oligotrophic nature of the overlying water column, as well as the location of the sampling site well below the Carbonate Compensation Depth. In the species that we describe, the test is filled with stercomata. This kind of organization is typical of Foraminifera living in oligotrophic regions and may be linked to a feeding strategy that involves the ingestion of sediment particles (Nozawa *et al*., 2006; Gooday *et al*., 2008). The above-mentioned Arctic assemblages dominated by stercomata-bearing Foraminifera were found at highly oligotrophic, permanently ice-covered sites (Wollenburg & Mackensen, 1998).

Test wall and taxonomic affinities

The test wall in *Nodellum aculeata*, *Resigella laevis* and *R. bilocularis* is yellow-brown in colour. Three related species, *Nodellum membranacea*, *N. rufescens* and *R. moniliforme*, have a similar coloration, although it is more intense (dark reddish-brown), particularly in *N. membranacea* and *N. rufescens*, which are much larger (> 1 mm) than the Challenger Deep species (Gooday *et al*., 2008). Hedley (1963) demonstrated the presence of organically bound iron in the tests of various agglutinated Foraminifera. He further observed that white chambers gave positive results as well as brown chambers, indicating that the colour of the agglutinated test was not a guide to the presence of iron. Our EDS analyses are consistent with these observations. Iron is present in the walls of the three yellow-brown species, as well as in *Conicotheca nigrans*, which has a colourless test wall. The sometimes colourless proloculus of *R. bilocularis* also exhibits a prominent iron peak.

Parts of the test surface have a complex structure at a submicrometre scale in three of our species. The surface comprises a dense mass of minute, branched, finger-like projections in *N. aculeata* (Fig. 6C, E) and *R. laevis* (Fig. 9D, E), and meshed strands and flat, scale-like areas in *R. bilocularis* (Fig. 12F–H). The finger-like projections in *N. aculeata* and *R. laevis* are similar morphologically to the organic cement that binds the grains of many agglutinated Foraminifera (Bender & Hemleben, 1988; Bender, 1989, 1995). They particularly resemble the cement in *Miliammina fusca* (Bender, 1989: pl. 2, figs 4, 5). SEM images of the test surface of our fourth species, *Conicotheca nigrans*, reveal occasional, finger-like projections (Fig. 16E), but not the masses of closely spaced projections seen in *N. aculeata* or of the meshed strands in *R. bilocularis*.

The organic test in our new species resembles the inner organic lining present in all agglutinated Foraminifera (Bender, 1989, 1995). This structure is sometimes very thin and obscure (Bender, 1995) but in other cases it forms a distinct 'organic sheath' (Hedley, 1958; Bowser & Bernhard, 1993). Buchanan & Hedley (1960) described experiments in which part of the wall of a large agglutinated species, *Astrorhiza limicola*, was removed. The organism secreted an organic 'membrane' to replace the damaged section of wall, usually within 12 h, and after a few days it became brown and translucent. The test in *Conicotheca*, *Nodellum* and *Resigella* may be homologous to the inner organic lining of agglutinated Foraminifera or to the organic membrane secreted by *A. limicola*. Gooday *et al*. (2008) came to a similar conclusion in the case of *N. membranacea*, *N. rufescens* and *R. moniliforme*. They drew attention to examples of basically agglutinated tests resembling the genus *Bathysiphon* in which the initial part forms a tapered organic tube with a closed proximal end. Similarly, some species of the agglutinated genus *Hyperammina* have an organic proloculus. The early, organic parts of these tubular tests may be equivalent to the largely organic tests of the Challenger Deep species.

Although the test wall is predominantly organic, all four species incorporate some mineral grains, strengthening the case that they are related to agglutinated foraminifera. *Resigella bilocularis* has a variably developed veneer of equidimensional, often angular grains, some of which are visible by light microscopy. Several grains yield strong peaks for Ca and S when analysed by EDS. The presence of these elements suggests the possibility that the grains are composed of gypsum (hydrated $CaSO_4$). However, we are not aware of any records in hadal sediments of this mineral, which is normally associated with evaporite deposits. EDS indicates that clay minerals are also present in *R. bilocularis*, as well as in the other three species. Plate-like grains are probably responsible for the flat patches and scale-like features seen in SEM images (Figs 7G, 12H, 13F, 16F). Distinctive, rod-like mineral grains were observed only in *N. aculeata* where they are strewn randomly across the proloculus. Gooday *et al*. (2008) described similar particles in *Nodellum rufescens*. However, in *N. rufescens* they are present across much of the test surface rather than being confined to the proloculus. Gooday *et al*. (2008) drew attention to the similarity between the particles in *N. rufescens* and the needle-like mineral grains incorporated into the walls of some species of *Bathysiphon* and related genera (Geslin, Heinz & Hemleben, 2004; Cole & Valentine, 2006). The presence of rod-like agglutinated grains in a second *Nodellum* species supports the idea that these tubular forms are related to *Bathysiphon*.

Whether the similar wall structure in *Conicotheca*, *Nodellum* and *Resigella* is the result of convergence, or whether it reflects a close phylogenetic relationship between these genera, is not clear. The basically tubular test characteristic of *Nodellum* species seems rather distinct from the subdivided ('chambered') tests of *Resigella* species, although undescribed, morphologically intermediate forms are known (Gooday *et al*., 2008). Molecular approaches may help to clarify this point.

ACKNOWLEDGEMENTS

Drs Jun Hashimoto, Shinji Tsuchida and Dongsung Kim kindly collected an MBARI core sample for us during the *Kaiko/Kairei* KR02-13 cruise to the Challenger Deep. Dr Takashi Toyofuku helped to conduct EDS analyses of the elemental constituents of the foraminiferal tests. Dr Olga Kamenskaya provided information about Russian trench samples and access to specimens of *Xenothekella*. Mrs Kate Davis provided valuable help with the figures, and two anonymous reviewers provided helpful comments on an earlier draft of the manuscript. This study was partly supported by a Grant-in Aid for Scientific Research (A) from the Japan Society for the Promotion of Science (JSPS) (no. 17204046) to H.K. and by the BICEP core strategic programme funded by the UK Natural Environment Research Council (A.J.G.).

REFERENCES

Adl SM, Simpson AGB, Farmer MA, Andersen RA, Anderson OR, Barta JR, Bowser SS, Brugerolle G, Fensome RA, Fredericq S, James TY, Karpov S, Kugrens P, Krug J, Lane CE, Lewis LA, Lodge J, Lynn DH, Mann DG, McCourt RM, Mendoza L, Moestrup O, Mozley-Standridge SE, Nerad TA, Shearer CA, Smirnov AV, Spiegel FW, Taylor MFJR. 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *Journal of Eukaryotic Microbiology* **52:** 399–451.

Akimoto K, Hattori M, Uematsu K, Kato C. 2001. The deepest living foraminifera, Challenger Deep, Mariana Trench. *Marine Micropaleontology* **42:** 95–97.

Akimoto K, Uematsu K, Hattori M, Kato C. 1996. Recent benthic foraminiferal assemblage discovered from the Hadal Zone of Mariana Trench, Northwest Pacific Ocean. *JAMSTEC Journal of Deep Sea Research* **12:** 263–273.

Belyaev GM. 1989. *Deep-sea ocean trenches and their fauna*. Moscow: Nauka.

Bender H. 1989. Gehäuseaufbau, Gehäusegenese und Biologie agglutinierter Foraminiferen (Sarcodina: Textulariina). *Jahrbuch Geologische Bundesanstalt* **132:** 259–347.

Bender H. 1995. Test structure and classification in agglutinated foraminifera. In: Kaminski MA, Geroch S, Gasiñski MA, eds. *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera.Grzybowski Foundation Special Publication* **3:** 27–90.

Bender H, Hemleben C. 1988. Cement structures in some agglutinated foraminifera. In: Gradstein MF, Rögl F, eds. Second workshop on agglutinated foraminifera. *Abhandlungen Geologische Bundesanstalt* **41**: 13–21.

Bowser SS, Bernhard JM. 1993. Structure, bioadhesive distribution and elastic properties of the agglutinated test of *Astrammina rara* (Protozoa: Foraminiferida). *Journal of Eukaryotic Microbiology* **40:** 121–131.

Brady HB. 1884. Report on the Foraminifera dredged by H.M.S. Challenger during the years 1873–1876. *Reports on the Scientific Results of the Voyage of the H.M.S. Challenger During the Years 1873–1876, Zoology* **9:** 1–814.

Buchanan JB, Hedley RH. 1960. A contribution to the biology of *Astrorhiza limicola* (Foraminifera). *Journal of the Marine Biological Association of the United Kingdom* **39:** 549–560.

Cole KE, Valentine AM. 2006. Titanium biomaterials: titania needles in the test of the foraminiferan *Bathysiphon argenteus*. *Dalton Transactions* **2006:** 430–432.

Cornelius N, Gooday AJ. 2004. 'Live' (stained) deep-sea benthic foraminifera in the western Weddell Sea: trends in abundance, diversity and taxonomic composition in relation to water depth. *Deep-Sea Research II* **51:** 1571–1602.

Fujioka K, Okino K, Kanamatsu T, Ohara Y. 2002. Morphology and origin of the Challenger Deep in the Southern Mariana Trench. *Geophysical Research Letters* **29:** 10-11 to 10-4.

Geslin E, Heinz P, Hemleben C. 2004. Behaviour of *Bathysiphon* sp. and *Siphonammina bertholdii* under controlled oxygen conditions in laboratory: implications for bioturbation phenomenon. In: Bubik M, Kaminski MA, eds. *Proceedings of the Sixth International Workshop on Agglutinated Foraminifera.Grzybowski Foundation Special Publication* **8:** 105–118.

Gooday AJ. 1986. Soft-shelled Foraminifera in meiofaunal samples from the bathyal northeast Atlantic. *Sarsia* **71:** 275–287.

Gooday AJ, Bowser SS, Cedhagen T, Cornelius N, Hald M, Korsun S, Pawlowski J. 2005. Monothalamous foraminiferans and gromiids (Protista) from western Svalbard: a preliminary survey. *Marine Biology Research* **1:** 290–312.

Gooday AJ, Carstens M, Thiel H. 1995. Micro- and nanoforaminifera from abyssal northeast Atlantic sediments: a preliminary report. *Internationale Revue Gesamten Hydrobiologie* **80:** 361–383.

Gooday AJ, Hori S, Todo Y, Okamoto T, Kitazato H, Sabbatini A. 2004. Soft-walled, monothalamous benthic foraminiferans in the Pacific, Indian and Atlantic Oceans: aspects of biodiversity and biogeography. *Deep-Sea Research I* **51:** 33–53.

Gooday AJ, Kamenskaya OE, Kitazato H. 2008. The enigmatic, deep-sea, organic-walled genera *Chitinosiphon, Nodellum and Resigella* (Protista, Foraminifera): a taxonomic re-evaluation. *Systematics and Biodiversity*.

Gooday AJ, Kitazato H, Hori S, Okamoto T. 2001. Monothalamous soft-shelled foraminifera at an abyssal site in the North Pacific: a preliminary report. *Journal of Oceanography* **57:** 377–384.

Hashimoto J. 2002. *KR02-13 Kaiko/Kairei Cruise in the Challenger Deep.* Onboard Report. International Cooperative Program Japan–USA–Korea.

Hedley RH. 1958. A contribution to the biology and cytology of *Haliphysema* (Foraminifera). *Proceedings of the Zoological Society of London* **130:** 569–576.

Hedley RH. 1963. Cement and iron in the arenaceous foraminifera. *Micropaleontology* **9:** 433–441.

Jumars PA, Hessler RR. 1976. Hadal community structure: implications from the Aleutian Trench. *Journal of Marine Research* **34:** 547–560.

Kamenskaya OE. 1989. Peculiarities of the vertical distribution of komokiaceans in the Pacific Ocean. *Transactions of the P.P. Shirshov Institute of Oceanology* **123:** 55–58.

Kamenskaya OE. 2006. Komokiaceans (Foraminifera, Komokioidea) from the hadal trenches of the West Pacific. In: Thatje S, Tyler P, Talbot P, Horton T, Maclaran L, Murty S, Rothe N, Billett D, eds. *11th International Deep-Sea Biology Symposium.* Book of Abstracts, 127.

Loeblich AJR, Tappan H. 1964. Sarcodina, chiefly 'Thecamoebians' and Foraminifera. In: Moore RC, ed. *Treatise on Invertebrate Palaeontology Part C, Protista 2*, Vols 1–2. Geological Society of America and Kansas University Press, C1–900.

Loeblich AR, Tappan H. 1987. *Foraminiferal genera and their classification*. Vol. 1-2. New York: Van Nostrand Reinhold.

Majewski W, Pawlowski J, Zajczkowski M. 2005. Monothalamous foraminifera from West Spitsbergen fjords, Svalbard: a brief overview. *Journal of Foraminiferal Research* **26:** 269–285.

Nozawa F. 2005. Deep-sea benthic foraminifera in the equatorial Pacific Ocean. Master's Dissertation, Graduate School of Natural Sciences, Chiba University (in Japanese).

Nozawa F, Kitazato H, Tsuchiya M, Gooday AJ. 2006. 'Live' benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: abundance, diversity and taxonomic composition. *Deep-Sea Research I* **53:** 1406–1422.

Nyholm K-G. 1952. Studies on Recent Allogromiidae: 1. *Micrometula hyalinostriata* n. gen., n. sp., from the Gullmar Fjord, Sweden. *Contributions from the Cushman Foundation for Foraminiferal Research* **3:** 14–17.

Resig JM. 1982. *Nodellum moniliforme, Ammomarginulina hadalensis and Favocassidulina subfavus,* three new species of recent deep water benthic foraminifera. *Journal of Paleontology* **56:** 977–982.

Rhumbler L. 1913. Die Foraminiferen (Thalamophoren) der Plankton-Expedition; Teil II – Systematik: Arrhabdammidia, Arammodisclidia und Arnodosammidia. *Ergebnisse der Plankton-Expeditie der Humboldt-Stiftung* 332–476.

Sabbatini A, Morigi C, Negri A, Gooday AJ. 2002. Soft-shelled foraminifera from a hadal site (7800m water depth) in the Atacama Trench (SE Pacific): preliminary observations. *Journal of Micropalaeontology* **21:** 131–135.

Saidova Kh M. 1970. Benthic foraminifers of the Kurile-Kamchatka Trench area. In: Bogorov VG, ed. Fauna of the Kurile-Kamchatka trench and its environment. Academy of Sciences of the USSR. *Proceedings of the Shirshov Institute of Oceanology* 86: 144–173.

Saidova Kh M. 1975. *Benthonic foraminifera of the Pacific Ocean*. Moscow: Academy of Sciences of the USSR, P.P. Shirshov Institute of Oceanology.

Tendal OS, Hessler RR. 1977. An introduction to the biology and systematics of Komokiacea. *Galathea Report* **14:** 165–194, pls 9–26.

Thalmann H, Bermudez PJ. 1954. *Chitinosiphon,* a new genus of the Rhizamminidae. *Contributions from the Cushman Foundation for Foraminiferal Research* **5:** 53–54.

Todo Y. 2003. Deep-sea benthic foraminiferal fauna that dwell at abyssal depths in the Pacific Ocean. Dissertation, Shizuoka University, in Japanese.

Todo Y, Kitazato H, Hashimoto J, Gooday AJ. 2005. Simple foraminifera flourish at the ocean's deepest point. *Science* **307:** 689.

Wollenburg JE. 1992. Zur Taxonomie von rezenten benthischen Foraminiferen aus dem Nansen Becken, Arktischer Ozean. *Berichte zur Polarforschung* **112:** 1–137.

Wollenburg JE, Mackensen A. 1998. Living benthic foraminifers from the central Arctic Ocean: faunal composition, standing stock and diversity. *Marine Micropaleontology* **34:** 153–185.