

On the foraminiferal genera *Tritaxis* Schubert and *Trochamminella* Cushman (Protozoa: Foraminiferida)

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I. On *Tritaxis* Schubert

The name *Tritaxis* was coined by Schubert (1920: 180) for triserial agglutinated post-Palaeozoic foraminifera which he considered to be the descendants of *Tetrataxis* Ehrenberg. Schubert expressed his reasoning as follows:

... die palaeontologisch primitiveren Formen *Globivalvulina* und *Tetrataxis* dagegen wandeln sich im Mesozoicum um: erstere in manche Globigerinen [*sic*] und von letzterer die einfachen Typen (z.B. die ohne extrem ausgebildete Nabelhöhlung) durch stärkere Sarkodenzunahme zunächst zu Formen, bei denen nicht vier, sondern nur drei Kammern einen Umgang aufbauen. Die letztere Verhältnis scheint nun für eine grössere Reihe von Formen konstant geworden zu sein, besonders für die postpalaeozoischen und jüngsten sogar noch lebenden Vertreter (*Fusca* Will., *conica* P. u J.) die sich durch den Mangel einer zentralen Höhlung auch nicht unwesentlich von den karbonen Valvulinen, den *Tetrataxis*arten, unterscheiden; *deshalb scheint sich auch ihre (etwa subgenerische) Abgrenzung von den karbonen etwa als Tritaxis zu empfehlen* [our italics].

Tritaxis, born therefore in the course of speculations into the evolution of agglutinated foraminifera, was formalised taxonomically by Cushman (1928) who designated as its type species *Rotalina fusca* Williamson, a trochamminid foraminifer from the Recent of the British Isles (Williamson, 1858: 55, pl. 5, figs 114, 115). Now a genus within the Trochamminidae Schwager, it was however immediately placed by Cushman (1928: 171) into synonymy with *Trochammina* Parker & Jones (type species: *Nautilus inflatus* Montagu, 1808, from the Recent of SW England). Cushman (1948: 202) subsequently did not change this opinion and listed, in the fourth edition of his *Foraminifera. Their classification and economic use*, *Tritaxis* as a synonym of *Trochammina*. This was also accepted by Bermúdez & de Rivero (1963). Glaessner (1945: 99) considered *Tritaxis* as a separate subgenus of *Trochammina* characterised by a low, conical test, and included within it Jurassic and Recent species (see discussion in Bermúdez & de Rivero, 1963: 318).

It was Loeblich & Tappan (1955: 19) who reinstated *Tritaxis* as a valid genus. They amended it to include low trochoid trochamminid tests with at first 4 chambers per whorl, then only 3 in the final whorl; free-living in early ontogeny and attached in the adult stage, with an areal ovate aperture in the free-living forms and a tubular aperture in the attached. These authors stated that ... 'the types of Williamson's species are missing from the British Museum Collections', and based their emended definition of *Tritaxis* on specimens labelled *Tritaxis fusca* (Williamson) encountered in the F.C. *Helga* haul no. SR 331 from off SW Ireland, depth 610–680 fathoms (1115–1245 m), deposited in the collections of the United States National Museum (USNM), reg. nos P 2198a, b. The two hypotypes illustrated by Loeblich & Tappan (1955: pl. 3, figs 5a–c, 6) have been examined by one of us (P.B.) who

reports that their drawings are indeed accurate representations. The non-attached individual shown in pl. 3, figs 5a–c, has spirally 4 subglobular chambers in the early, and 3 elongate crescentic chambers in the final whorl. Umbilically, the 3 final chambers are flattened and an oval areal aperture occurs close to the base of the septum of the final chamber over the first chamber of the last whorl as Loeblich & Tappan indeed state. These authors considered the attached form (1955: pl. 3, fig. 6) as conspecific. It has the same morphology as the free specimen, with 4 subglobular early chambers and 3 elongate crescentic ones in the final whorl. Around the margins, the test is surrounded by a spongy calcareous mass, with a very few agglutinated grains of irregular outline but devoid of any tunnel-like extensions as developed in *Trochamminella siphonifera* Cushman (1943: 95, pl. 16, figs 18–20). The attached and free specimens are from the same sample and in view of their morphological similarity, Loeblich & Tappan's assumption that they are conspecific, seems to us a reasonable one. In the same paper, Loeblich & Tappan illustrate (1955: pl. 3, fig. 7) the holotype of *Trochamminella siphonifera* Cushman, housed in the USNM reg. no. 39619, from Johnson-Smithsonian Expedition station 25, off Puerto Rico (depth 240–300 fathoms/440–550 m). Brönnimann has also examined this specimen and again can verify that both Cushman's original illustration (1943, pl. 16, fig. 18) and that of Loeblich & Tappan, are accurate. *Trochamminella* is however placed in synonymy with *Tritaxis* by Loeblich & Tappan (1955: 20), a conclusion they also follow in the *Treatise of Invertebrate Paleontology* (Loeblich & Tappan, 1964: C266).

Taxonomically important in Loeblich & Tappan's revision are the following two points:

- (1) They did not establish a neotype for *Tritaxis fusca* (Williamson). They based their emended definition of *Tritaxis* on hypotypic specimens considered to represent *T. fusca*, collected in deepwater off SW Ireland, not one of the localities listed by Williamson (1858).
- (2) The synonymising of *Trochamminella* with *Tritaxis* is based on the comparison of these above mentioned specimens of *T. fusca* with the holotype of *Trochamminella siphonifera*.

Hedley *et al.* (1964), in the course of a larger study of New Zealand intertidal foraminifera, re-examined the case of *Tritaxis fusca* (Williamson) on the basis of material deposited in the British Museum (Natural History). Hedley *et al.* reiterate Loeblich & Tappan's (1955) statement that the type specimen is missing from the Williamson Collection. They do however figure ... 'a specimen removed by the authors from material donated by H. B. Brady to W. C. Williamson'; it is from shore sand, Isle of Skye, and is one of the localities listed by Williamson in his original description. This specimen was illustrated by a drawing in Hedley *et al.*'s paper as their fig. 2: 1A–C and described as follows (ex tabulation, pp. 420, 421):

Test free, trochoid, concavo–convex, maximum diameter 250 μm , [axial] height 130 μm . Spirally low trochoid; umbilically excavated; outline circular. Early chambers nearly globular, later ones crescentic: 16 chambers arranged in 4 whorls with 3 chambers in the final whorl; the final chamber occupies about half of the umbilical side. Sutures distinct, slightly depressed, curved slightly backwards on spiral side and straight on umbilical side. Aperture distinct, at the inner margin of umbilical side of the last chamber, extraumbilical. Wall finely arenaceous with occasional larger grains, smoothly finished. Colour golden brown, last chamber almost white.

We have re-illustrated this specimen by Scanning Electron Microscopy (Figs 11–14). The specimen was found to be damaged prior to scanning, but nevertheless it is clear that Hedley *et al.*'s description agrees well with our photographs, except that a small portion of a fourth chamber is shown umbilically. There are, however, several differences between this specimen and that of Williamson (1858: 55, figs 114, 115) which warrant our attention. Williamson's specimen consists of 11 chambers, 3 in the final whorl, while, umbilically, the ultimate chamber makes up about half the test. In Hedley *et al.*'s specimen, on the other hand, there are 16 chambers on the spiral side, with 4 in the final whorl, and umbilically the final

chamber makes up less than half the test. Furthermore, the latter is barely half the size of the original specimen.

Nevertheless, in spite of these difficulties Hedley *et al.*'s paper (1964) contains several salient taxonomic points:

- (1) It was confirmed that the type of *Rotalina fusca* is missing from the extant part of the Williamson Collection in the BM(NH).
- (2) They did not establish a neotype.
- (3) They showed that a specimen from one of Williamson's original localities, which they considered to represent *fusca*, existed in material in the Brady Collection (BM(NH)), having been donated by Williamson himself. They demonstrated that this trochamminid was completely different in apertural features to *Tritaxis fusca sensu* Loeblich & Tappan (1955; 1964).

We now have differing concepts of *Tritaxis fusca*. One, the *fusca* of Loeblich & Tappan, based on material from off SW Ireland, with a single areal aperture, and *fusca* of Hedley *et al.* from Williamson's material, Isle of Skye, with a single interiomarginal aperture which rests with its border completely on the first chamber of the final whorl in an extraumbilical position. It will be shown that the former is referable to *Trochamminella* whereas the latter is correctly assigned to *Tritaxis*.

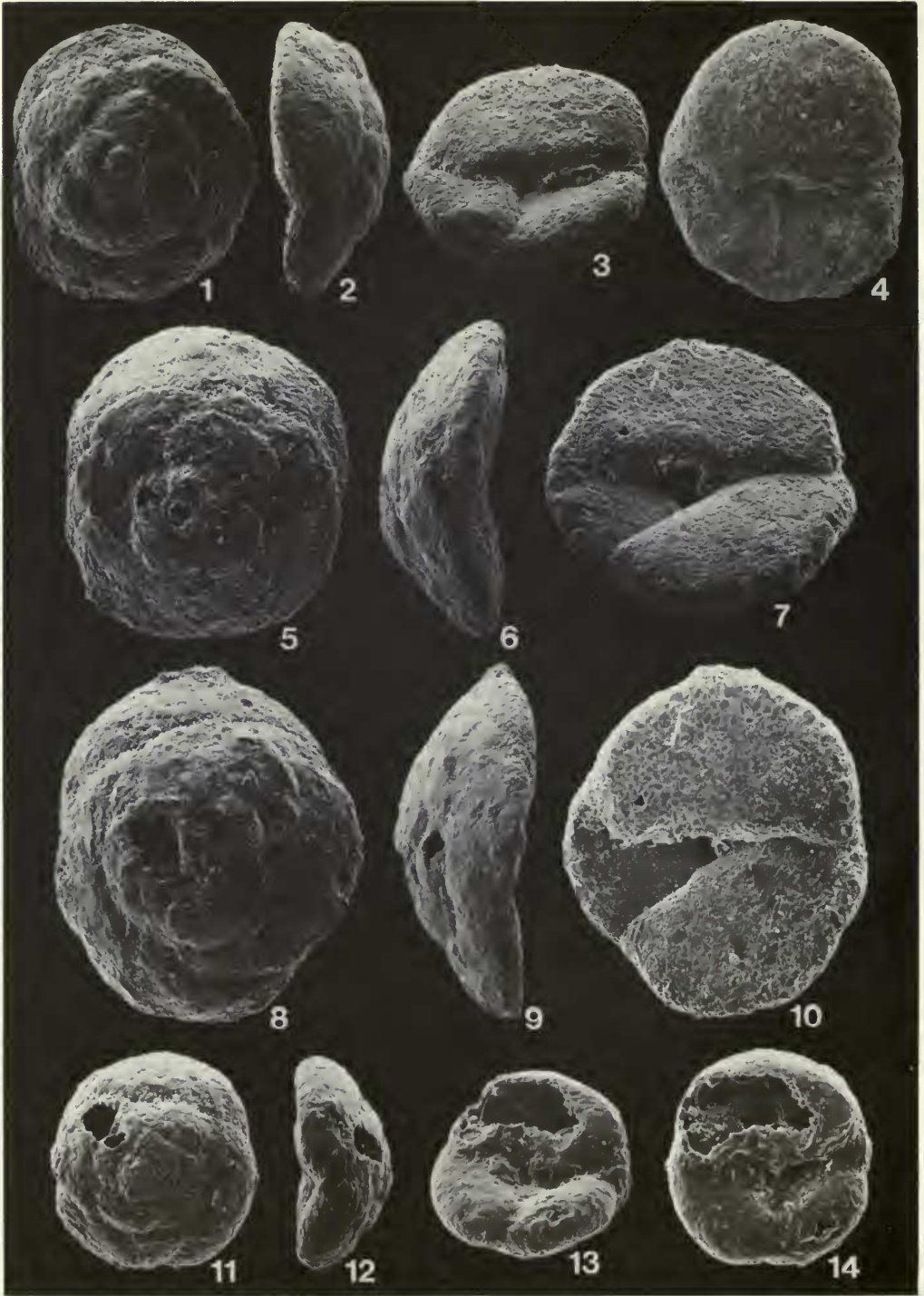
Because of our misgivings, outlined above, as to whether Hedley *et al.*'s (1964) specimen is conspecific with the true *fusca*, we initiated a further search for Williamson's type specimen. There is however a gap in the registered numbers of the Williamson Collection and it is indeed probable that the slide containing the specimen representing his figs 114, 115, was never presented in the first place; it must therefore be presumed lost. In the course of this search for the type, one of us (J.E.W.) encountered more material in the Brady Collection of the BM(NH) from 'deepwater off the Isle of Skye', donated by Williamson. This apparently belonged to the same suite of material in which Hedley *et al.* found the single specimen which they figured in 1964. Their material was however labelled 'shore sand, Skye', not 'deepwater, off the Isle of Skye', as is ours. Williamson (1858: 56) merely states under his localities . . . 'Skye (not uncommon), . . .' and therefore it is reasonable to assume that both samples were known to him when he made the description. We do not however know the locality from which his figured specimen came, while no syntypic material from the other five localities is extant. Instead of the sole specimen found by Hedley *et al.* and which they referred to *T. fusca* (we have re-picked the sample and there are no more), we have found a large suite of specimens in the latter sample which fit better Williamson's original description and figure. They all have 3 chambers in the final whorl (the last chamber being about half the size of the test), 11 or 12 chambers on the spiral side and a test diameter (400–650 μm) more in keeping with Williamson's dimensions (1/60th of an inch or c. 450 μm). The aperture is interiomarginal.

As there is obviously still confusion over what *fusca* and its genus, *Tritaxis*, really are, a neotype should now be established in order to stabilise the nomenclature. From the 'deepwater off the Isle of Skye' residue we have picked out several specimens to show the variation within the species (Figs 1–4; 5, 6; 7–10) and here select specimen ZF 4209 as neotype of *Rotalina fusca* Williamson. It is very similar to Williamson's original figures, particularly in umbilical view, and for the reasons already stated it is preferable as neotype to the specimen described by Hedley *et al.* (1964).

Tritaxis fusca (Williamson), 1858

Figs 1–10; ?11–14; 19–27

NEOTYPE. ZF 4209, from off the Isle of Skye, NW Scotland; deep water. From material donated by W. C. Williamson to H. B. Brady, ex Brady Collection, BM(NH). Figured by Scanning Electron Microscopy in Figs 1–4.



PARANEOTYPES. ZF 4208 (Figs 1–4) and ZF 4210 (Figs 5, 6), both from same sample as neotype. 5 other free specimens were picked out for comparative purposes but they are not formally designated paraneotypes. A further single attached specimen was also found in the same sample which is assumed to be conspecific; the extreme fragility of the test, however, precluded its removal for cleaning and analysis of the aperture (see p. 298, below).

OTHER SPECIMENS. 5 attached specimens from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand (long. 173°04'E, lat. 34°23'S), depth 70 fathoms (128 m), ex Heron-Allen & Earland type slide 282 (material 96D), collected 3rd August 1911. Labelled in their faunal-slide collection notes as '*Valvulina fusca* (Williamson)'. ZF 4201, 4202 (both unfigured); 4203 (Figs 25–27, attached; Figs 19–22, subsequently removed from its attachment); 4206 (unfigured); 4207 (Figs 23, 24).

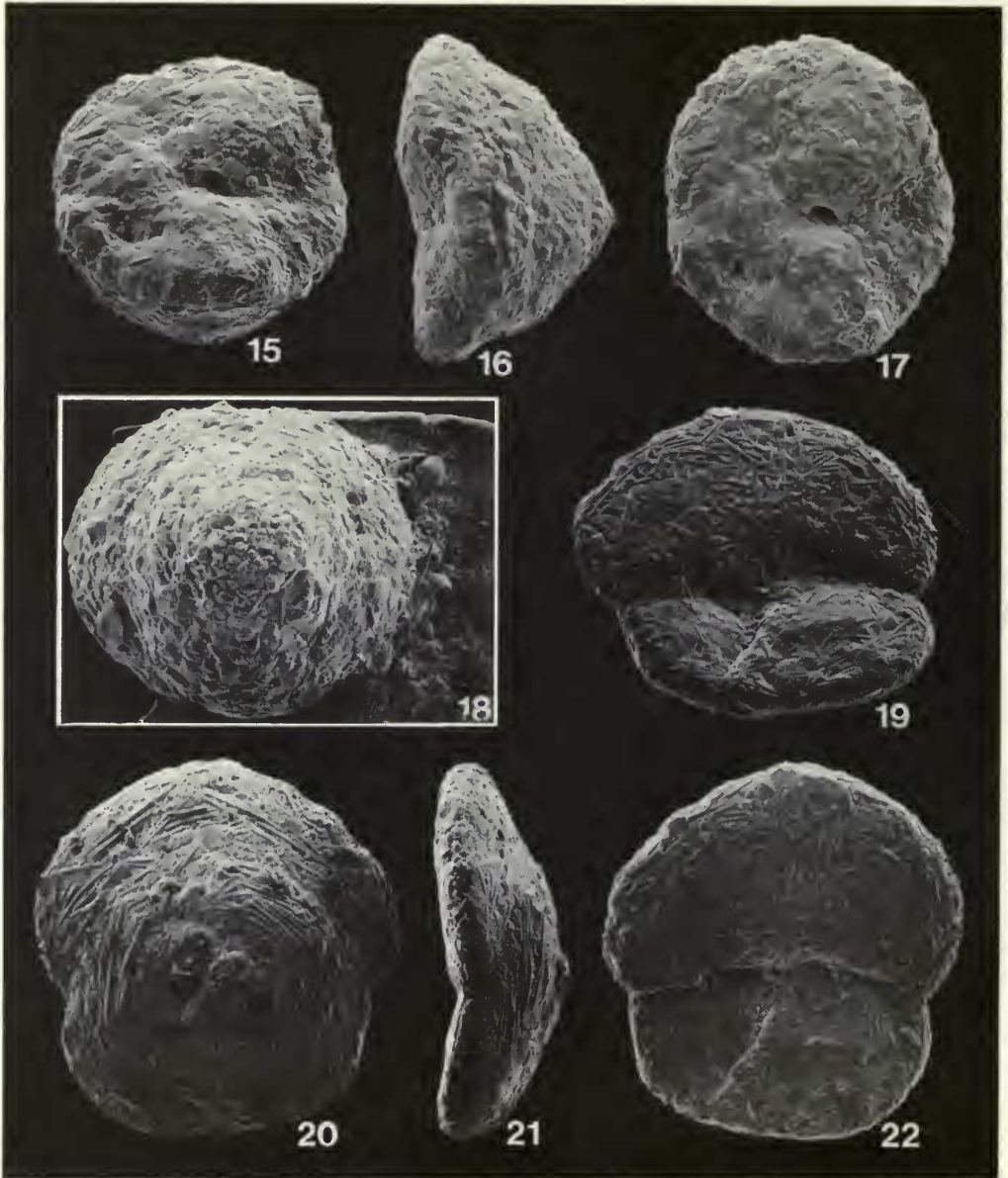
DESCRIPTION (NEOTYPE). Test free, low dextral trochospire; domed-convex spirally, shallow-concave umbilically; subcircular in outline in spiral and umbilical view; compressed-rounded periphery in edge view. Spirally with 11 chambers, including proloculus, arranged in about 2 whorls. Early chambers subglobular, those of 3-chambered final whorl strongly compressed axially, elongate-crescentic on spiral side, flattened on umbilical side; final chamber occupies about half of umbilical side, penultimate chamber, which is in part overlapped by the ultimate, occupies more than one-third, and first chamber of final whorl occupies about one-sixth. Umbilical (axial) depression small and deep, almost closed. Sutures distinct both umbilically and spirally, except over initial part of test. Aperture single, interiomarginal, a slightly obliquely arranged slit, with border resting completely on surface of first chamber of final whorl, extraumbilical and of *Trochammina*-type, with thin protruding rim. Wall agglutinated, fragile, apparently single-layered, imperforate. Agglutinant of larger scale-like rock fragments on spiral side, with smaller fragments umbilically.

DIMENSIONS (NEOTYPE). Maximum spiral and umbilical diameter 600 µm, minimum diameter 520 µm, axial height (thickness) 230 µm.

VARIATION (PARANEOTYPES). ZF 4210 is illustrated by spiral and edge views in Figs 5, 6. It is a sinistral specimen with 11 crescentic elongate chambers (including the proloculus) on the spiral side and 3 chambers, of the same proportions as found in the neotype, on the umbilical side. The umbilicus is narrow and deep and the aperture is also as seen in the neotype (the umbilical view is not shown because of a badly damaged final chamber). ZF 4208 (Figs 1–4), although a dextral specimen, has also 11 chambers in total on the spiral side. The 3 umbilical chambers, however, are of different proportions to that seen in the neotype and the aperture is a low-elongate interiomarginal slit parallel to the suture, but still of *Trochammina*-type and accompanied by a distinctly protruding lip which is discernible even in normal umbilical view (Fig. 4). Several other individuals from the type locality have an aperture of this kind, rather than the obliquely arranged aperture of the neotype and specimen ZF 4210, which cannot be readily seen without tilting the specimen and no doubt led Williamson (1858: 55) to describe the aperture as 'indistinct'.

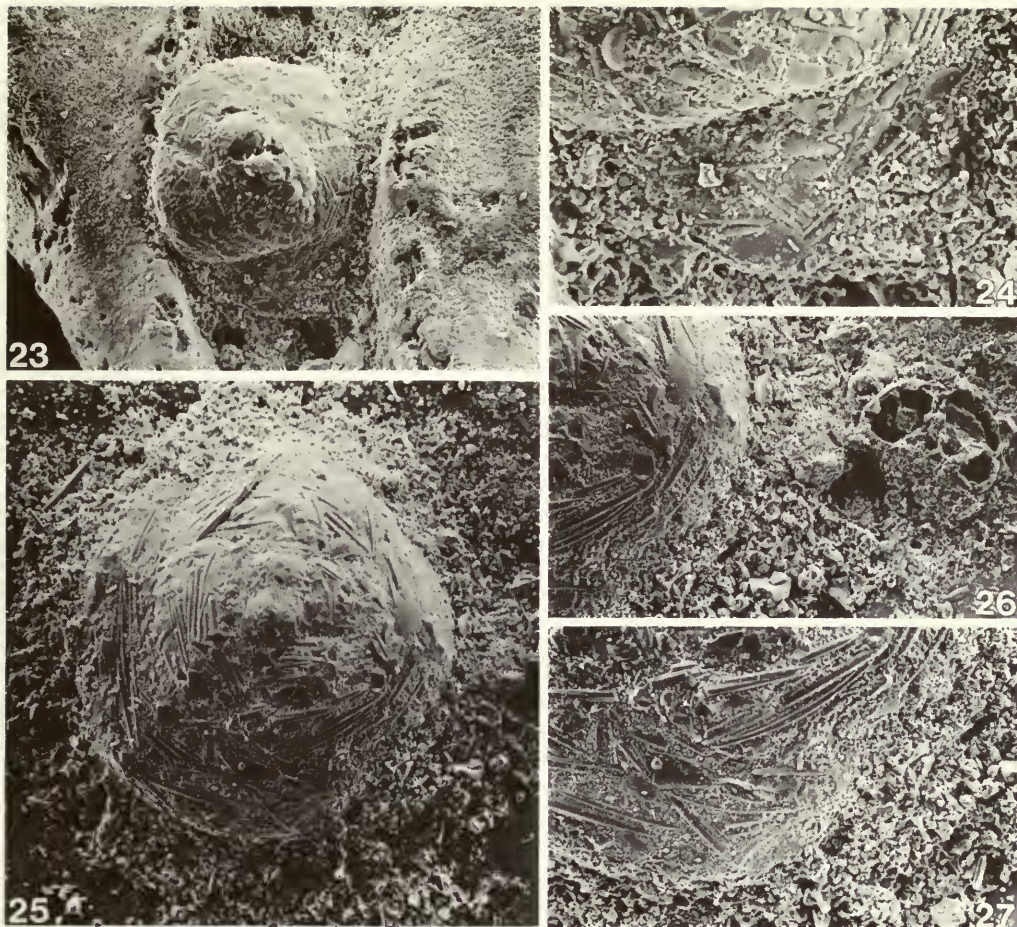
Figs 1–10 *Tritaxis fusca* (Williamson). Figs 1–4, Paraneotype (ZF 4208). Spiral, edge, oblique-umbilical and umbilical views. Figs 5, 6, Paraneotype (ZF 4210). Spiral and edge view. Figs 7–10, Neotype (ZF 4209). Oblique-umbilical, spiral, edge and umbilical views. All $\times 88$. All from Skye, NW Scotland. From material donated by Williamson to Brady; ex Brady Collection, BM(NH). Material labelled 'deep water'.

Figs 11–14 *Tritaxis* sp. 1963.2.19.17. Spiral, edge, oblique-umbilical and umbilical views. $\times 125$. Identified by Hedley *et al.* (1964) as *T. fusca* (Williamson) and figured (drawing) in figs 2: 1A–C. From Skye, NW Scotland. From material donated by Williamson to Brady; ex Brady Collection, BM(NH). Material labelled 'shore sand'.



Figs 15–18 *Tritaxis australis* Brönnimann & Whittaker sp. nov. Figs 15–17, Holotype (ZF 4204). Oblique-umbilical, edge and umbilical views. Fig. 18, Paratype (ZF 4205). Spiral view of attached specimen. Both $\times 88$. Both from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand, depth 70 fathoms (128 m), ex Heron-Allen & Earland Collection, BM(NH).

Figs 19–22 *Tritaxis fusca* (Williamson). ZF 4203. Oblique-umbilical, spiral, edge and umbilical views of formerly attached specimen (see Figs 25–27). $\times 88$. From *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand, depth 70 fathoms (128 m), ex Heron-Allen & Earland Collection, BM(NH).



Figs 23–27 *Tritaxis fusca* (Williamson). Figs 23, 24, ZF 4207. Spiral view of attached specimen; detail of wall and part of surrounding 'spongy calcareous' mass, $\times 88$ and $\times 220$, respectively. Figs 25–27, ZF 4203. Spiral view of attached specimen, since removed (see Figs 19–22); detail of wall and parts of surrounding 'spongy calcareous' mass: fig. 25, $\times 88$; figs 26, 27, $\times 115$ and $\times 130$, respectively. Both from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand, depth 70 fathoms (128 m), ex Heron-Allen & Earland Collection, BM(NH).

DIMENSIONS(PARANEOTYPES)

Specimen (Figs)	Umbilical and spiral diameter		Axial height (thickness)
	Maximum	Minimum	
ZF 4208 (Figs 1–4)	460 μm	410 μm	170 μm
ZF 4210 (Figs 5, 6)	520 μm	450 μm	210 μm

REMARKS. As the neotype of *T. fusca* is characterised by an interiomarginal *Trochammina*-type aperture, the forms described by Loeblich & Tappan (1955: 19, pl. 3, figs 5a–c, 6) with areal apertures are not conspecific and should be placed in *Trochamminella siphonifera* Cushman. *Tritaxis* is now emended to coincide with our redescription of the type-species with added observations based on attached material and a new species, previously identified as *fusca*, both from the *Terra Nova* Collection, off New Zealand.

In the Skye material there was only one attached individual and its fragility precluded its removal from its shell fragment and observation of the umbilical side. Instead, 5 attached specimens from *Terra Nova* station 96, 7 miles E of North Cape, New Zealand, which we

consider conspecific with *T. fusca*, were examined. Of these, two specimens, ZF 4203 and ZF 4207, are illustrated in Figs 19–22, 25–27, and Figs 23, 24, respectively. In its attached state (Figs 25–27), the test of the former is surrounded and glued to a bivalve fragment by a granular spongy calcareous secreted material in which some foreign elements are embedded. Subsequently removed and cleaned it is illustrated in its free state in Figs 19–22. It is a dextral low trochospire of 11 chambers (including the proloculus) and in umbilical and edge views, and in apertural characteristics is very much like the neotype. However, the agglutinant is made up primarily of sponge spicules associated with angular rock fragments and grains. The spicules are more or less aligned in direction of the elongation of the crescentic chambers and are rare or absent on the surface of the first formed chambers. The test dimensions are: Maximum and minimum diameter in spiral/umbilical views, 560 and 480 μm ; axial height (thickness) 200 μm . The specimen, ZF 4207, from the same locality, is shown only in its attached position (Figs 23, 24). It is cemented to a bivalve fragment between two ribs and the final very large, broadly crescentic chamber is partly obscured by an overhanging rib and by its own secreted surrounding spongy, calcareous material. The maximum and minimum diameter of the test are 390 and 320 μm , respectively. Again, there are a total of 11 chambers arranged in just over 2 whorls.

Most probably, therefore, this species is able to attach itself to a substrate like *Trochamminella siphonifera* or *Tritaxis australis* sp. nov. described below (p. 299, Figs 15–18), which both have free and attached individuals. Where only attached specimens are available the correct generic assignment (*Tritaxis* or *Trochamminella*) can only be made if the apertural characteristics are known and that means removing at least one specimen from its shell or rock fragment and cleaning up the umbilical side so that the aperture can be seen.

For the present the specimen described and figured by Hedley *et al.* (1964) as *Tritaxis fusca* from shore sand, Isle of Skye, is left in open nomenclature. Its small size, chamber number and appearance both in edge and umbilical view, are atypical of Williamson's species.

Genus: *TRITAXIS* Schubert, 1920, emend

EMENDED GENERIC DESCRIPTION. Test free or attached, plano-convex, trochospiral; final whorl typically with 3 spirally crescentic chambers, final chamber making up about half of umbilical side; wall agglutinated, imperforate; aperture a single interiomarginal extra-umbilical opening with borders resting on first chamber of final whorl; attached specimens surrounded and glued to substratum by spongy calcareous substance (no tunnel-like radial extensions observed).

TYPE SPECIES. *Rotalina fusca* Williamson, 1858. Neotype erected herein, Recent, N Atlantic. Distribution possibly worldwide.

REMARKS. The aperture of *Tritaxis* is fundamentally the same as that of *Trochammina* Parker & Jones, 1859 (type species: *Nautilus inflatus* Montagu, 1808). On the basis of the aperture alone, *Tritaxis* could be regarded as a junior synonym of *Trochammina* (see Cushman, 1928: 171). However, in our new classification of the Trochamminacea (Brönnimann *et al.*, 1983) the adult growth form or overall shape of the test can be of generic significance, at the same level in the classificatory framework as the apertural features. The adult growth form of *Tritaxis* is a particular arrangement within the Trochamminidae. By its plano-convex test and umbilically flattened chambers of the final whorl, the test is well adapted to attachment. The only other occurrence where we find this arrangement is in *Trochamminella*, which however differs by its areal aperture from *Tritaxis*. On the basis of apertural features and adult growth form the generic status of *Tritaxis* is retained.

During our examination of the *Terra Nova* Collections in the BM(NH) (Heron-Allen & Earland, 1922), we came across some material from off New Zealand, identified as '*Valvulina fusca* (Williamson)' (loc. cit., p. 125). There are two species involved, one is the true *Tritaxis fusca*, the other is here described as new.

Tritaxis australis sp. nov.

Figs 15–18

DIAGNOSIS. A pointed, high conical *Tritaxis* with very coarse agglutinated wall. 4 chambers on umbilical side, but sutures indistinct both spirally and umbilically. Aperture distinct.

NAME. *Australis*—southern. Referring to its occurrence in the Southern (Pacific) Ocean, off New Zealand.

MATERIAL. 2 specimens from *Terra Nova* station 96 (Heron-Allen & Earland station 6), 7 miles E of North Cape, New Zealand (long. 173°04'E, lat. 34°23'S), depth 70 fathoms (128 m), ex Heron-Allen & Earland type-slide 286 (material 96C), collected 3rd August 1911. Labelled in their faunal-slide collection notes as '*Valvulina fusca* (Williamson)'. Formally designated as holotype (ZF 4204) and paratype (ZF 4205).

HOLOTYPE. ZF 4204, illustrated in oblique-umbilical, edge and umbilical views in Figs 15–17 by Scanning Electron Microscopy.

DESCRIPTION (HOLOTYPE). Test free, sinistral trochospire, plano-convex, pointed and conical. Outline in umbilical and spiral view suboval, in edge view triangular with compressed-rounded periphery but not carinate. Umbilically very shallow-concave, with closed axial depression (umbilicus). Agglutinant coarse and sutures difficult to discern, chamber number therefore not known with certainty. Final whorl with 4 chambers, elongate-crescentic spirally, more or less flattened umbilically. First chamber of final whorl is umbilically a small wedge, followed by larger, almost equidimensional second and third chambers; final chamber occupies about one-third of umbilical side. The single aperture is an interiomarginal, small arch-like opening with a distinct but narrow rim. It rests with its border completely on the surface of the first chamber of the final whorl and is eccentric in respect to the axis of coiling. Agglutinated wall is apparently single-layered and imperforate. Coarse agglutinant consists of rock fragments and derived organic components.

DIMENSIONS (HOLOTYPE). Maximum and minimum spiral/umbilical diameter 510 and 460 μm , respectively; axial height (thickness) 330 μm . Maximum diameter of aperture 45 μm .

VARIATION (PARATYPE). ZF 4205 (Fig. 18) is attached to a bivalve fragment. It is indistinguishable from the spiral side of the holotype. Surrounding the test there is a little secreted spongy material into which are incorporated some foreign elements. There are no tunnel-like projections as normally found in the spongy mass of *Trochamminella siphonifera* Cushman. Maximum and minimum spiral/umbilical diameter, respectively 540 and 480 μm ; axial height (thickness) c. 330 μm .

REMARKS. *T. australis* differs by its pointed, high conical test and its coarse agglutinated wall from the spirally, lower, domed plano-convex test (with finer agglutinant) of *T. fusca* (Williamson). In the final whorl of *T. australis* there are 4 chambers, whereas there are typically 3 in *T. fusca*.

II. On *Trochamminella* Cushman

In 1943 Cushman proposed *Trochamminella*, a new Recent trochamminid genus. It was defined as follows:

Test trochoid, free in the early stages, sometimes attached in the later stages; wall arenaceous, aperture in the unattached forms a rounded opening near the margin of the ventral face of the last formed chamber, usually surrounded by a slightly raised ring; the attached adult surrounded by an irregular rim of material similar to that of the wall and extending out in a tabular neck with rounded aperture.

This definition is based on *Trochamminella siphonifera* Cushman (1943; 95, pl. 16, figs 18–20) which was at the same time designated type species. It is from the Johnson-Smithsonian Expedition station 25, off Puerto Rico, depth 240–300 fathoms (440–550 m), and is represented in the collections of the US National Museum, Washington, by the lectotype (reg. no. 39619), a fixed specimen, and 6 paratypes (reg. nos. 39620 and 39621), all free specimens. The two illustrated paratypes (Cushman, 1943, pl. 16, figs 19, 20) have a single, oval aperture close to the base of the final chamber above the first chamber of the final whorl. As the free and attached specimens are morphologically indistinguishable, Cushman assumed that they were conspecific. One of us (P.B.) has examined the types and concurs. His observations are given below.

The holotype is attached to a thin bivalve fragment (see also re-illustration by Loeblich & Tappan, 1955, pl. 3, fig. 7). It has a low trochospiral, plano-convex test with 3 elongate-crescentic chambers in the final whorl. The initial portion of the test is obtusely pointed and the early coiling difficult to discern; Loeblich & Tappan's illustration shows 4 subglobular chambers. The test is 'glued' to the bivalve fragment by a light coloured spongy calcareous mass. It completely surrounds, but does not cover the test and develops a radial tunnel-like extension with a fairly thick wall and a rounded terminal opening. The true aperture of the holotype is not known but it has to be assumed that it is of the same type as shown by the free paratypes. The wall of the holotype is finely agglutinated, also light coloured and some sponge spicules occur in the agglutinant. The free paratypes have all the single areal opening situated just above the suture with the first chamber of the final whorl. The opening is completely surrounded by an agglutinated rim. Spirally, all the types have 3 elongate-crescentic chambers in the final whorl. The early enrolment, where it is visible, consists of 4 subglobular chambers arranged in a coil around the subglobular proloculus.

Loeblich & Tappan's (1955: 19, pl. 3, figs 5a–c, 6; 1964: figs 177: 2a–c, 3) specimens from the F.C. *Helga* haul SR 331, off SW Ireland (see p. 291, above) and referred by them to *Tritaxis fusca* (Williamson) have the same morphology and areal aperture as Cushman's type specimens of *Trochamminella siphonifera* from Puerto Rico, and hence they clearly represent the latter taxon. Brönnimann's observations on the *Helga* specimens of the so-called *Tritaxis fusca* in the USNM (reg. nos. P 2198a, b) already discussed (p. 292), have clearly shown them to be really *siphonifera*. One unfigured specimen is attached and shows a long curved tunnel-like extension going radially out from the spongy mass by which the individual is attached to the bivalve fragment. Another attached specimen (see Loeblich & Tappan, 1955, pl. 3, fig. 6; 1964, fig. 177: 3) shows a fairly large, flattened and irregularly contoured spongy mass but no tunnel-like extensions.

In view of these facts, *Trochamminella* is clearly distinct from *Tritaxis* as emended above, and should not be suppressed as a junior synonym of the latter as proposed by Loeblich & Tappan, 1955, 1964 and by Hofker, 1976, 1979). *Trochamminella* is now also emended in the light of our re-evaluation of the situation.

Genus: **TROCHAMMINELLA** Cushman, 1943 emend

EMENDED GENERIC DESCRIPTION. Test free or attached, plano-convex, trochospiral; final whorl typically with 3 spirally crescentic chambers, final chamber making up about half of umbilical side; wall agglutinated, imperforate; aperture a single areal opening near the suture between the first and last chamber of the final whorl; attached specimens surrounded and glued to substratum by spongy calcareous substance which may develop tunnel-like radial extensions with terminal openings.

TYPE SPECIES. *Trochamminella siphonifera* Cushman, 1943. Recent, Atlantic and Caribbean.

REMARKS. *Trochamminella* is a close isomorph of *Tritaxis* but differs from that genus essentially on apertural features. Both genera have single apertures: interiomarginal, of *Trochammina*-type in *Tritaxis*, and areal in *Trochamminella*. As in the case of *Tritaxis*, also in *Trochamminella*, the adult morphology is here considered to be of generic significance: both have a plano-convex test, highly adapted for fixation to a substratum and typically with 3

chambers in the final whorl, crescentic on the spiral side, flattened on the umbilical, with the final chamber making up more or less half of the umbilical side. To be consistent, now all other trochamminids with different adult morphology, but with the same type of interio-marginal or areal aperture, will have to be placed in different genera. For species with a single areal aperture near and parallel to the base of the final chamber, but possessing a different type of adult morphology to *Trochamminella* (free, biconvex tests with inflated chambers), Frerichs (1969) introduced the Recent genus *Pseudotrochammina*, with *P. triloba* from the deep waters of the Gulf of Mexico as type species (Frerichs, 1969: 1, pl. 1, figs 3a–d; pl. 2, figs 3a, b). Pending a full evaluation of this genus, the Recent *Ammoglobigerinoides* Frerichs (1969) and the Palaeocene *Conotrochammina* Finlay (1940), now in preparation, we tentatively place the following Recent species in *Pseudotrochammina*: *Conotrochammina kennetti* Echols, 1971, Antarctic, Scotia and Weddell Seas, deep water; *Pseudotrochammina mexicana* Frerichs, 1969, Gulf of Mexico, deep water; *Pseudotrochammina triloba* Frerichs, 1969, Gulf of Mexico, deep water; *Trochamminella bullata* Höglund, 1947, Skagerrak, depth 500–700 m; *Trochamminella atlantica* Parker, 1952, North Atlantic, off Portsmouth, New Hampshire, shallow water.

Acknowledgements

The text has benefited from being read by Drs C. G. Adams and L. R. M. Cocks, British Museum (Natural History). The SEM photographs, taken by one of us (J.E.W.) were printed by the staff of the Electron Microscope Unit, BM(NH). The senior author's research was funded by the Fonds National Suisse.

References

- Bermúdez, P. J. & Rivero, C. F. de 1963. *Estudio sistematico de los foraminiferos quitinosos, microgranulares y arenaceos*. Univ. Central de Venezuela, Caracas, 398 pp.
- Brönnimann, P., Zaninetti, L. & Whittaker, J. E. 1983. On the classification of the Trochamminacea (Foraminiferida). *J. foramin. Res.*, Washington, **13**: 202–218.
- Cushman, J. A. 1928. Foraminifera. Their classification and economic use (First edition). *Spec. Publs Cushman Lab.*, Sharon, Mass., **1**: 1–401, pls 1–59.
- 1943. A new genus of the Trochamminidae. *Contr. Cushman Lab. Foramin. Res.*, Sharon, Mass., **19**: 95–96, pl. 16.
- 1948. *Foraminifera. Their classification and economic use* (Fourth edition). viii+605 pp, pls 1–55. Harvard Univ. Press, Cambridge, Mass.
- Echols, R. J. 1971. Distribution of Foraminifera in sediments of the Scotia Sea area, Antarctic waters. In Reid, J. L. (Ed.) Antarctic oceanology 1. *Antarctic Res. Ser. Washington*, **15**: 93–168, pls 1–16.
- Finlay, H. J. 1940. New Zealand Foraminifera, Key species in stratigraphy. *Trans. R. Soc. N.Z.*, Dunedin, **69**: 448–472, pls 62–67.
- Frerichs, W. E. 1969. Recent arenaceous foraminifers from Gulf of Mexico. *Palaeont. Contr. Univ. Kans.*, Lawrence, Kans., **46**: 1, 2, pls 1, 2.
- Glaessner, M. F. 1945. *Principles of Micropaleontology*. 296 pp., 14 pls. Melbourne Univ. Press.
- Hedley, R. H., Hurdle, C. M. & Burdett, I. D. J. 1964. *Trochammina squamata* Jones and Parker (Foraminifera) with observations on some closely related species. *N.Z. Jl Sci.*, Wellington, **7**: 417–426, figs 1–3.
- Heron-Allen, E. & Earland, A. 1922. Protozoa. Part 2. Foraminifera. *Nat. Hist. Rep. Br. Antarct. 'Terra Nova' Exped.*, London (Zool.) **6**: 25–268, pls 1–8.
- Hofker, J. 1976. Further studies on Caribbean Foraminifera. *Stud. Fauna Curaçao*, Utrecht, **49** (162): 1–256, figs 1–169.
- 1979. Rare and remarkable Foraminifera of the Caribbean Sea. *Stud. Fauna Curaçao*, Utrecht, **58** (181): 1–43, figs 1–26.
- Höglund, H. 1947. Foraminifera in the Gullmar Fjord and Skagerrak. *Zool. Bidr. Upps.*, **26**: 1–328, pls 1–32.
- Loeblich, A. R. Jr & Tappan, H. 1955. Revision of some Recent foraminiferal genera. *Smithson. misc. Collns*, Washington, **128** (5): 1–37, pls 1–4.

- 1964. *Protista 2. Sarcodina chiefly 'Thecamoebians' and Foraminiferida*. In Moore, R. C. (Ed.), *Treatise on Invertebrate Palaeontology, Part C. 1*: 1–510, figs 1–399. Univ. Kansas Press.
- Montagu, G. 1808. *Supplement to Testacea Britannica*. v + 183 pp., pls 17–30. Woolmer, Exeter.
- Murray, J. W. 1971. *An Atlas of British Recent Foraminiferids*. xiii + 244 pp., 96 pls. Heinemann Educ., London.
- Parker, F. 1952. Foraminifera species off Portsmouth, New Hampshire. *Bull. Mus. Comp. Zool. Harv.*, Cambridge, Mass., **106**: 391–423, pls 1–6.
- Parker, W. K. & Jones, T. R. 1859. On the nomenclature of the Foraminifera: Part 2, On the species enumerated by Walker and Montagu. *Ann. Mag. nat. Hist.*, London (ser. 3), **4**: 333–351.
- Schubert, R. 1920. Palaeontologische Daten zur Stammesgeschichte de Protozoen. *Paläont. Z.*, Berlin, **3** (2): 129–188.
- Williamson, C. W. 1858. *On the Recent Foraminifera of Great Britain*. xx + 107 pp., 7 pls. Ray Society, London.

Manuscript accepted for publication 10 August 1983