AUSTRALASIAN TYPHINAE (GASTROPODA) WITH NOTES ON THE SUBFAMILY

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Abstract. The Typhinae are a rare but widely distributed Muricid group. Because of their rarity they are of little value for local geological correlation, but are useful for regional correlation and palaeogeography, and as facies indicators.

Tertiary distributions indicate distinct American and Australo-European provinces and probably a third, Javanese province. The modern American fauna remains distinct. The single living European species is related to a living species on the west coast of South and Central America. *Typhina* and *Siphonochelus* each have closely related species living in Australia, New Zealand, the Indo-Pacific, the South Atlantic, and the Carribean, showing a remarkable parallelism in their distribution, and are believed to have radiated simultaneously from Australia.

Two New Zealand species are members of a Tertiary endemic lineage. The remaining ten are not closely related to one another. Four are certainly related to distant overseas groups of similar age; five are possibly related to overseas groups of similar age; one is not closely related to any other known species.

The superspecific classification proposed by Keen (1944) is modified, her groups being redefined in terms of varix types. The new genus Rugotyphis and the new subgenus Neotyphis are described. The following genera and subgenera are recognized in Australia and New Zealand: Typhis (subgenera Typhis, Hirtotyphis, Neotyphis), Rugotyphis, Typhina (subgenus Typhina), Siphonochelus, Lyrotyphis, Semityphis. A check list of Australiaian species with revised generic groupings is given. Twelve New Zealand species (eight new) and four Australian species are described.

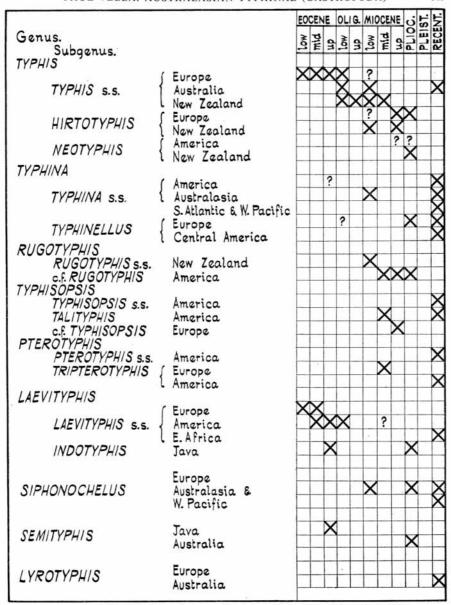
INTRODUCTION

PREVIOUSLY only four species of Typhinae were recognized in New Zealand, and all were described under the general name *Typhis*. Fourteen species have been described from Australia. Iredale recognized the genera *Typhis*, *Typhina*, and *Siphonochelus*. He erected the subgenus *Choreotyphis* within *Typhina* but this has since been synonymized by Keen (1944) with *Siphonochelus*. Keen (1944, p. 56) allocated three New Zealand and six Australian species to *Typhinellus*. *Typhinellus*, however, is not recognized by the present writer, and the species placed in it by Keen are grouped below in *Typhis*, *Typhina*, and the new genus *Rugotyphis*. The genera and subgenera *Typhis*, *Hirtotyphis*, *Neotyphis*, *Typhina*, *Rugotyphis*, and *Siphonochelus* occur in New Zealand; *Typhis*, *Typhina*, *Siphonochelus*, *Lyrotyphis*, and possibly *Semityphis* occur in Australia.

Eight Tertiary and Recent new species from New Zealand are described below, bringing the New Zealand total to twelve. These with the Australian species make up a large proportion (about 30%) of all the species ascribed to the subfamily, and provide significant information relevant to phylogeny and classification.

Living and fossil Typhinae are rare. It must be assumed that present known ranges are generally less than true ranges and this must be taken into account when occurrences of Typhinae are used as evidence for Tertiary correlations or for faunal migrations. This is shown particularly well by the records of *Hirtotyphis* from antipodal areas, but from no intermediate localities, and by the odd space-time distribution of *Lyrotyphis*.

Ecology. Keen (1944, p. 51) noted that most Typhinae live in the neritic zone, almost all having been recorded from dredgings between 12 and 800 metres, averaging 50 metres. [Palaeontology, Vol. 4, Part 3, 1961, pp. 362–91, pls. 46–47.]



TEXT-FIG. 1. Stratigraphic and geographic distributions of the genera of Typhinae.

New Zealand Tertiary occurrences are all in very similar rocks-massive to poorly bedded, blue-grey calcareous siltstones, with rich molluscan faunas. These sediments were probably deposited in moderately deep to deep water (50–200 metres) on the continental shelf.

Modern Typhinae occur only in tropical or warm temperate seas. The New Zealand Recent species *Typhina pauperis* and *Siphonochelus solus* are extremely rare and confined to the northern (Aupourian) faunal province. Hence New Zealand's warmest waters must be close to the lower temperature limit.

DISTRIBUTION

Typhinae have been described from Tertiary rocks in southern and central Europe, the United States, the West Indies, Panama, Peru, Australia, New Zealand, Java, and India (a single Pliocene species). Australasian faunas more closely resemble European faunas than those of America or Java. The American faunas are difficult to interpret from literature, because of their difference from southern faunas, but they appear to be largely endemic with some relationships to New Zealand and European faunas. The Javanese fauna is essentially endemic.

Siphonochelus and Typhina are the only widely distributed living genera of the subfamily and are particularly interesting because they have the same distribution. Other living genera, even Typhis which was widespread in the Tertiary, are now restricted to small areas.

Many Typhine genera seem to have been able to disperse rapidly and to cross deep oceanic basins relatively freely. The mechanism by which they accomplished this is not known. Neither the larva nor the mode of life of the adults has been studied. The protoconch is paucispiral with a large nucleus and suggests that the larval stage has a short life. The relationship of present distributions of *Siphonochelus* and *Typhina* to existing ocean currents, however, shows that these genera almost certainly migrated in the currents. This implies, in spite of the protoconch, that the larval stage has a relatively long life.

The stratigraphic and geographic distribution of all the genera are summarized in the accompanying chart, text-fig. 1.

Tertiary distributions. Distributions and inferred migration directions of Eocene to Miocene Typhinae are summarized in text-figs. 3a and 3b.

During the Eocene (3b) distinct faunas occurred in Europe, America, and Java. The American fauna extended into Europe, but the European fauna did not reach America. The Java fauna of two essentially endemic genera remained distinct through most of the Tertiary and was probably confined to tropical water.

During the Oligocene and Miocene (3a) European genera spread to Australia and New Zealand. Most American genera were endemic, but some were related to New Zealand genera. Two European Miocene forms belong to a predominantly American group.

The persistence of a distinct fauna in Java and the lack of Typhinae in the Tertiary of Japan make it reasonably certain that migrations between New Zealand and America took place not around the Pacific margin, but directly across the central Pacific. Migration routes between America and Europe necessarily include many thousands of miles of deep ocean. It is assumed that most migrations of Typhinae resulted from the transport of larval stages in ocean currents.

From the order of appearance of groups in different areas, and from phylogenetic relationships, all migrations appear to have been eastward as shown in text-fig. 2, except for that of *Indotyphis* which is thought to have migrated to Java from America. Main migrations are believed to have taken place: (1) across the Atlantic from America to Europe; (2) through a Tethyan route, i.e. through the Mediterranean and northern Indian Ocean from Europe to Australia and New Zealand; (3) across the Pacific from New Zealand to America.

Distribution of living genera. Recent distributions are better known than those of the past and can be related directly to existing currents. Since Typhinae are confined to relatively warm waters, only warm ocean currents need be considered as possible aids to migration.

Restricted groups are:

1. The American group of related genera with wide flange-like varices extending across the shoulder, Typhisopsis, Talityphis, Pterotyphis, Tripterotyphis.

Typhisopsis, Talityphis, Pterotyphis, Tripterotyphis.

2. Two tiny species from off the west coast of Africa, referred to the once widespread genus Laevityphis, but possibly requiring a new generic name.

3. Two species of Typhis s.s. now confined to the New South Wales coast.

Three forms are widespread: *Typhina*, its subgenus *Typhinellus*, and *Siphonochelus*. *Typhina* and *Siphonochelus* have remarkably similar distribution, both occurring in Australia, New Zealand, the north-west Pacific, and the south Atlantic (text-figs. 2a, 2b). The living species of each are more closely related to one another than to any Tertiary forerunners.

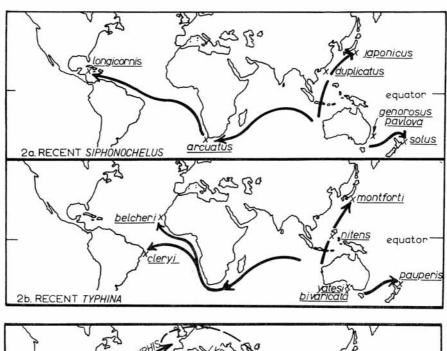
Siphonochelus became extinct in Europe after the Pliocene. It occurs in the Miocene and Pliocene of Australia, and now lives in New Zealand, Australia (two species), Japan, China Seas, South Africa, and Cuba. Though several Typhinae occur in the richly fossiliferous Tertiary rocks of Panama, the West Indies, and the United States, Siphonochelus has not been recorded as a fossil in America, and the Cuban species Siphonochelus longicornis (Dall) must be regarded as a recent invader.

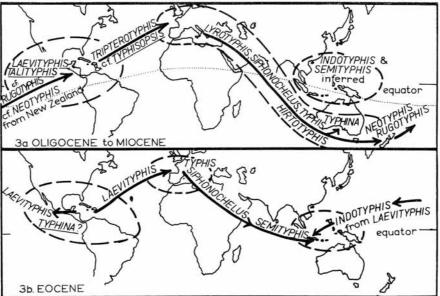
The fossil record of *Typhina* is very incomplete. *Typhina dentata* (Johnson) from the Upper Eocene (Jackson) of the United States may not be a true Typhinae. The only reasonably certain fossil species are *T. laciniata* (Tate) and *T. disjuncta* (Tate) from the Lower Miocene (Balcomian) of Australia, and *T. tetragoniatus* (Cossmann) from the Pliocene of India. Living species have been reported from New Zealand, Australia (two species), Straits of Macassar (Borneo), Japan, Brazil, and north-west Africa. Australia was probably the source from which other areas were colonized (text-figs. 2a and 2b).

Each genus appears to have migrated along three routes, two of which correspond to existing ocean currents: (1) northward along the western Pacific margin, (2) eastward via the Tasman Current to New Zealand, (3) westward via the Equatorial Current in the Indian Ocean, around Cape of Good Hope, northward in the Benguella Current along the west coast of Africa, and finally north-westward in the Atlantic South Equatorial Current to Brazil (*Typhina*) and to Cuba (*Siphonochelus*).

Fleming (1957, pp. 19–22) in a discussion of the genus *Pecten* suggested that Pleistocene cooling would prolong larval stages and account for the known Pleistocene migrations. Migrations of *Typhina* and *Siphonochelus* probably also took place during the Pleistocene and could be explained in this way.

Tertiary migrations were on a smaller scale, but might similarly have depended on geologically more or less brief periods of favourable conditions.





TEXT-FIGS. 2, 3. 2, Distributions and inferred migration routes of (2a) Siphonochelus, (2b) Typhina; migration routes correspond to existing warm ocean currents. 3, Distribution and inferred migration routes of typhine genera during (3a) Oligocene to Miocene, (3b) Eocene; dashed lines delineate fossils; square brackets indicate geographic restriction. Dotted line in 3a indicates possible Miocene equator, after Koppen and Wegener 1924.

Typhinellus is represented by two living species, T. sowerbyi (Broderip) in the Mediterranean and T. quadratus (Hinds) on the Ecuador and Panama coasts. It is known as a fossil in the Pliocene of Italy, is possibly present in the Oligocene, and probably originated in Europe. Typhinellus must have migrated across the Atlantic before the emergence of the Isthmus of Panama near the end of the Pliocene (Dunbar 1949, pp. 491–2).

STRATIGRAPHIC USE

Local correlation. New Zealand Tertiary Typhinae are rare and have little value for internal correlation. Of the ten species known, nine are from single localities or local districts, and one, Typhis (Neotyphis) tepungai Fleming, from several localities in the south of the North Island.

Regional correlation. New Zealand species from at least three stratigraphic levels are more closely related to overseas species of similar age than to earlier New Zealand species.

- (1) Lower-Middle Oligocene: *Typhis (Typhis) adventus* sp. nov. is closely related to the Australian Oligocene *T. (Typhis) maccoyi* Tenison-Woods, and to the European lower Tertiary type species, *T. (T.) tubifer* (Brug.).
- (2) Upper Miocene: Typhis (Hirtotyphis) aoteanus sp. nov. is related to T. (H.) horridus (Brocchi), widely distributed in the upper Miocene and Pliocene of Europe.
- (3) Recent: the genera *Typhina* and *Siphonochelus* have no known Tertiary representatives in New Zealand. The Recent species *Typhina* (*Typhina*) pauperis (Mestayer) and *Siphonochelus solus* sp. nov. have affinities with Recent species in Australia and elsewhere, as explained above.

Several less definite overseas correlations are suggested by Typhinae. The Lower Miocene Typhis (Typhis) clifdenensis sp. nov., T. (Hirtotyphis) aculeatus sp. nov., Rugotyphis francescae (Finlay), and the Pliocene T. (Neotyphis) tepungai Fleming, have no known closely related ancestors in New Zealand. Rugotyphis and Neotyphis are possibly represented by species in the Miocene of Central and North America. No known overseas species of Typhis is close to clifdenensis. A possible relative of T. (Hirtotyphis) aculeatus in the Miocene of Italy is discussed in the systematic section below.

Stratigraphic ranges of New Zealand and Australian species are given in the check list on p. 379.

CLASSIFICATION

In 1880 Jousseaume subdivided the genus *Typhis* by introducing twelve new generic names. Of these nine are now in use, though some are reduced to subgeneric rank. For more than sixty years, however, most of Jousseaume's names were neglected and the remainder were largely misapplied. Authors dealing with local faunas usually described species under one of the group names *Typhis*, *Siphonochelus*, and *Typhina*, and both Cossmann (1903) and Thiele (1931) synonymized many of Jousseaume's valid groups. Jousseaume's work received due credit for the first time in the revision by Keen (1944).

Keen's catalogue of species and bibliography greatly facilitate study. Her generic revision, though a great step forward, was yet too conservative. Keen's phylogenetic account and subgeneric groupings are based mainly on the number of varices per whorl, and the position of the intervariceal tubes relative to the varices. Other important features are neglected.

The number of growth steps per whorl, the position and inclination of the intervariceal tubes, and the form of the varices, protoconch, aperture, and anterior canal are useful conservative shell features that are discussed below.

Growth steps. Each varix (sometimes paired) terminates a growth step. Of nine genera of Typhinae, six have 4·2 growth steps per whorl, and these include such distinct groups as Typhis, Siphonochelus, Laevityphis, and Talityphis. The number of growth steps per whorl is constant from juvenile to adult. It follows that 4·2 growth steps per whorl is a fundamental character of the subfamily, presumably inherited from a pre-Eocene common ancestor. Various groups with 4·2 growth steps per whorl, distinguishable mainly by variceal characters, evolved, in most cases prior to the Eocene, and some of these subsequently gave rise to the divergent groups with three or five growth steps. Two genera have three growth steps per whorl and one has five, and these can be related by the forms of their varices to groups with the standard 4·2 growth steps.

Aperture and anterior canal. The aperture and anterior canal are so conservative that they are only exceptionally of use for generic classification. Typically the aperture is entire, broadly ovate or circular, surrounded by a thin, raised rim which rarely is in part expanded to form a secondary varix; the lower border may be rounded, or faintly angled in accordance with the angle at which the outer and inner walls of the final growth stage are united. The only exception is the aperture of *Lyrotyphis*.

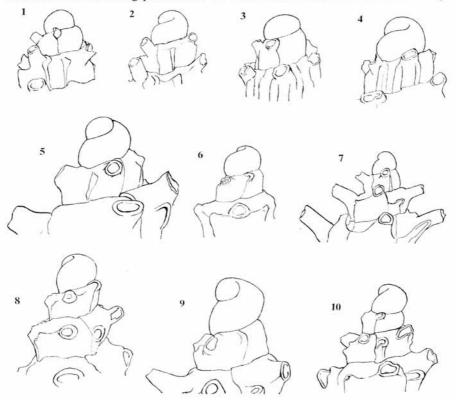
The anterior canal is always closed, typically broad and flattened, carrying the lower part of the varix, and bent more or less sharply to the right, tapering in well-preserved specimens to a delicate subcylindrical tube. Canals of the previous growth steps forming the body whorl are visible, and distinct from the final canal and from one another. *Haustellotyphis* is exceptional in having a straight canal without distinct earlier canals.

Intervariceal tubes. In all specimens examined the intervariceal tubes have approximately the same position on the growth steps. All the shells have linear ridges or scars indicating the positions of former apertures, and the tubes arise on the shoulder directly in front of these. The tubes are usually about mid-way between the varices, but their position relative to the varices depends on the position of the varices on the growth steps. Typhinellus sowerbyi has secondary varices developed on the apertural rim, and consequently Keen was correct in stating that the tubes are 'nearer to preceding than to succeeding varices'. Some species of Typhina, however, which are supposed to have tubes mid-way between the varices, also have secondary varices on the apertural rim, and just behind the tubes on earlier growth steps. In both Typhinellus and Typhina the tubes are mid-way between the primary varices, and other characters must be used to distinguish these forms. The position of the intervariceal tubes seems to have no value except for distinguishing a few overseas groups.

In some groups the inclination of the intervariceal tubes is significant. In $Typhis\ s.s.$ the tubes consistently point obliquely backwards and usually only slightly above the horizontal. The most divergent species is $Typhis\ clifdenensis$ in which the tubes are twisted upwards at an exceptionally high angle $(c\ 40^\circ)$ from the horizontal. The backward deflection of the tubes is constant in $Typhis\ s.s.$ and persists in the subgenera Hirtotyphis and Neotyphis. In Rugotyphis, on the other hand, the tubes are nearly radial and confirm that this genus is divergent from Typhis. In Laevityphis, Siphonochelus, and

Lyrotyphis the tubes point almost vertically upward, sometimes a little backward. The adult shell of *Neotyphis* is convergent to *Laevityphis* in the characters of the tubes and varices, but the juvenile characters show it to be related to *Typhis*.

Protoconch. In describing protoconchs the term nucleus is used as recommended by



TEXT-FIG. 4. Apices of Typhinae: 1, 2, Typhina (Typhina) bivaricata (Verco); 3, 4, Lyrotyphis syringianus (Hedley). 5, Typhina (Typhina) yatesi (C. & F.). 6, Typhis (Typhis) hebetatus Hutton. 7, Typhina (Typhina) pauperis (Mest.). 8, Typhis (Typhis) adventus sp. nov. 9, Typhis (Neotyphis) tepungai Fleming. 10, Typhis (Typhis) maccoyi Ten.-Woods.

Marwick (1957, p. 14) for the 'semiglobular initial part' consisting of about half a whorl. Protoconch whorls were counted as proposed by Burnett Smith (1945).

Protoconchs are lacking from most New Zealand specimens and are not known for *Hirtotyphis*, *Rugotyphis*, and *Siphonochelus*. Protoconchs have been available on *Neotyphis tepungai*, *Lyrotyphis syringianus*, and three species each of *Typhis s.s.* and *Typhina s.s.*, all of which are illustrated in text-fig. 4.

In both Typhis and Typhina the protoconchs have a consistent form, and between

each group are consistent differences. *Typhis* has a tall protoconch of one and a half to one and three-quarter whorls, commencing with a large rounded eccentric nucleus. From the nucleus the initial whorl rapidly expands to full diameter so that the protoconch is subcylindrical. *Typhina* has a protoconch of about one and a quarter whorls, with an eccentric nucleus similar to that of *Typhis*, but expanding more gradually so that the lower part is considerably broader than the top.

Only one slightly worn protoconch of *Neotyphis* is known. Except that it seems to have an incipient peripheral angle, it is similar to that of *Typhis*. The protoconch of *Lyrotyphis* differs from that of *Typhina* only in having a more depressed initial whorl. Protoconchs have systematic value but few useful descriptions have been published.

Types of varices. Six varix types are recognized. At least three have existed since the Eocene. Varix types are regarded as more fundamental to classification than the number of growth steps per whorl, and in the classification proposed below each varix type distinguishes a genus or a group of related genera. Forms with more or less than the standard 4·2 growth steps per whorl are given generic rank within their varix type group. Most subdivisions based on other characters are given subgeneric rank.

For convenience, each varix type is referred to by the name of the genus or most important genus of which it is characteristic. The six varix types are described below:

- 1. Siphonochelus type: smooth and rounded, not crossing the shoulder to the previous whorl, but curving back at the top to coalesce with the intervariceal tube. It is misleading to describe the tubes of Siphonochelus as immediately preceding the varices, because the tubes are situated just ahead of the scars of former apertures, and occupy the same relative position on the growth steps as in other genera. Siphonochelus has always been recognized by its distinctive varices. Semityphis with three growth steps per whorl, and Lyrotyphis with five growth steps per whorl, both have varices like those of Siphonochelus. As Siphonochelus has the fundamental 4·2 growth steps per whorl, it is considered to have evolved first, and Lyrotyphis and Semityphis are regarded as derivatives.
- 2. Laevityphis type: rounded folds not crossing the shoulder, each surmounted on top by a single, vertical hollow conical spine. The intervariceal tubes are nearly vertical. In the subgenus *Indotyphis* the tubes are differently disposed, and relationship is inferred solely from variceal characters.
- 3. Typhis type: broad, rounded folds not crossing the shoulder, each with hollow conical spines arranged in a linear series along the crest and diminishing downwards. In Typhis s.s. the varices and variceal spines curve backwards. In Hirtotyphis the spines become grotesquely enlarged, straight or nearly straight and radial. In Neotyphis all but the uppermost spine on each varix are obsolete and the uppermost spine points nearly vertically upward.

Typhis s.s., with typical varices, has persisted from the Lower Eocene to the Recent. The consistent backward deflexion of the intervariceal tubes, and the similarity of protoconchs, discussed above, are confirming evidence of the relationship of the forms grouped in Typhis.

4. *Typhina* type: thin, frilled flanges, with open trough-shaped spines contrasting with the closed, hollow, conical spines of *Typhis* and *Laevityphis*. The main varix does not cross the shoulder vertically, but runs forward along the peripheral angle of the whorl as a low flange, then curves upward to join the apertural rim at a tangent. In *T. belcheri*

and bivaricata, and in the two living species of Typhinellus, part of the apertural rim is expanded to form a secondary varix. In T. pauperis and yatesi the apertural lip is not expanded.

At the top of each primary varix a large trough-like spine curves upward and in toward the spire, usually with a slight twist either backward or forward. The outer edge of each varix may be produced to small trough-shaped spines at intervals below the upper spine, or may be simply frilled. In *Typhina* the outer edge of each varix curls forward; in *Typhinellus* it curls backward.

- 5. Rugotyphis type: intermediate between the Typhis type and the Typhisopsis type. It resembles the Typhis type in being broad at the base, fold-like and curved slightly but distinctly backwards. It resembles the Typhisopsis type in extending across the shoulder and having an acute foliated crest. Other distinctive features are an ornament of irregular, more or less radial ribs on the front face only, and tiny trough-shaped spines on the crest of the varix below the shoulder. The part of the varix crossing the shoulder is lower and narrower than the part below the peripheral angle, bears no spines, and runs obliquely forward toward the suture, abutting against the corresponding varix on the previous whorl. The varices thus form four continuous ridges ascending in steep sinistral spirals to the apex of the shell.
- 6. Typhisopsis type: elevated, flange-like, frilled, crossing the shoulder, extending with little change in elevation from the anterior canal to the previous whorl, characteristic of an American group which appeared in the Miocene and persists at the present day, comprising Typhisopsis and Talityphis each with 4·2 growth steps per whorl, and Pterotyphis and Tripterotyphis each with 3 growth steps per whorl.

Summary of classification based primarily on varix types.

The suggested reclassification of the Typhinae is set out in tabular form below. The asterisk (*) indicates subgenera not known in Australasia.

1. Siphonochelus group: varices broadly rounded, fold-like, typically without spines, curving back at the top to coalesce with the tubes.

Genera Siphonochelus: 4.2 growth steps per whorl.

Lyrotyphis: 5 growth steps per whorl. Semityphis: 3 growth steps per whorl.

2. Laevityphis group: varices broadly rounded, fold-like, not crossing the shoulder, each surmounted on top by a single, nearly vertical spine.

Genus Laevityphis: 4-2 growth steps per whorl.

*Subgenus Laevityphis: tubes nearly vertical.

*Subgenus *Indotyphis*: 'tubes twisted forward and soldered to the back of the next varix' (Keen 1944, p. 52).

*Subgenus Pilsbrytyphis: irregular axial sculpture.

3. Typhina group: primary varices flange-like, excavated in front, inclined forward, each with a large, trough-like spine at the top, curving up and in toward the spire; not crossing the shoulder vertically, but running forward along the periphery as a low lamellar flap, then curving up to join the apertural rim. Secondary varices developed in some species by extension of the apertural rim.

Genus Typhina: 4.2 growth steps per whorl.

Subgenus *Typhina*: outer edge of varix curling forward; varix retracted at the top of the anterior canal, in some species represented on the canal by flattened, fin-like spines; body whorl more or less convex.

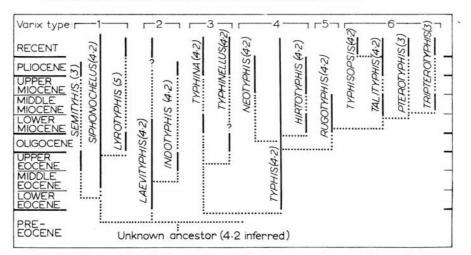
*Subgenus Typhinellus: outer edge of varix curling backwards; varix crossing without reduction in width from body to anterior canal; body whorl more or less regularly tapered.

 Typhis group: varices broad, rounded, fold-like, not crossing the shoulder, each bearing on the crest a row of hollow conical spines.

Genus Typhis: 4.2 growth steps per whorl.

Subgenus *Typhis*: varices of body whorl each with three to eight backward curving spines of moderate size; tubes bent obliquely backwards, and upwards not more than 40° from horizontal. Subgenus *Hirtotyphis*: varices of body whorl each with three to six large, nearly straight, radial spines.

Subgenus *Neotyphis*: adult varices each with one nearly vertical spine on top, obsolete spines below; adult tubes nearly vertical; juvenile varices and tubes as in *Typhis*.



TEXT-FIG. 5. Phylogeny of the Typhinae; where possible names are written opposite epoch at which genera or subgenera make their first definite appearance; query (?) indicates species doubtfully referred to a genus or subgenus; dotted lines show where lineages are not represented by fossils; varices per whorl given by number in brackets above each name.

5. Rugotyphis group: varices extending across shoulder to previous whorl, ornamented on the front faces with irregular, more or less radial ribs, broad based, but with acute foliated crests serrated by tiny trough-shaped obsolete spines.

Genus Rugotyphis: 4·2 growth steps per whorl.

6. Typhisopsis group: varices elevated, flange-like, frilled, extending with little change in width from anterior canal to previous whorl.

Genus Typhisopsis: 4-2 growth steps per whorl.

*Subgenus Typhisopsis: tubes connected to previous whorls by laminar buttresses.

*Subgenus Talityphis: tubes free.

Genus Pterotyphis: 3 growth steps per whorl.

*Subgenus Pterotyphis: tubes free.

*Subgenus Tripterotyphis: tubes coalesced with succeeding varices.

PHYLOGENY

The relationships of the genera and subgenera are summarized in the phylogenetic table, text-fig. 5, and are discussed in the systematic descriptions below.

SYSTEMATIC DESCRIPTIONS OF THE GENERA

Descriptive terminology. 'Preceding varix' and 'succeeding varix', Keen (1944), mean previously formed varix and later formed varix.

The shell is considered to be oriented with the axis of coiling vertical, the apex pointing up and the aperture facing the observer. Top and bottom and similar words are applied in their absolute sense to the shell as oriented. Forward and backward mean toward and away from the aperture in the direction of coiling.

Synonymies. Full synonymies of the genera were given by Keen (1944) and are not repeated.

Genus TYPHIS Montfort 1810

Type species, by original designation, Purpura tubifer Bruguière 1792 (Eocene, Grignon, France).

Cossmann's figure (1903, pl. 2, fig. 23) of *Typhis tubifer* shows rather narrow, but rounded variceal folds, each bearing on the crest a linear series of tubular spines. The varices do not cross the shoulder, and the final one extends, gradually diminishing downwards, on to the anterior canal. According to Keen (1944, p. 53) Bruguière's original figure shows *tubifer* to have about twice as many variceal spines as *T. pungens* (Solander) (here figured Pl. 47, fig. 29), a British Eocene species which has three spines per varix. New Zealand species of *Typhis s.s.* invariably have six spines on each varix of the body whorl.

Each variceal spine bears on its front face a longitudinal, linear, sutural groove, extending from the tip on to the front surface of the varix. On well-preserved specimens the varix between each pair of sutural grooves is covered by arcuate growth-lines which are convex towards the aperture and meet the sutural grooves almost tangentially. A specimen of *T. hebetatus* Hutton from Awamoa (Pl. 46, fig. 13) has an incompletely formed final growth step on which the spines are trough-shaped, lamellar structures still open towards the front. It is clear that the sutural groove of the complete spine is the seam along which the two sides of the originally open trough-shaped spine are joined. On neanic whorls of all species of *Typhis* that have been examined the variceal spines are open trough-shaped structures.

On adult whorls of *Typhina* the single large variceal spine on each varix is typically a lamellar trough-shaped structure. The only known exception is the Australian *Typhina* (*Typhina*) vatesi (C. & F.) in which the spine is closed for part of its length, the sides of the trough having curled far enough around to meet and become soldered together. The neanic variceal spines of *Typhis* apparently recapitulate a stage in evolution comparable with the adult spines of *Typhina*. The latter was probably represented in the Eocene by *Typhis dentatus* Johnson (Jackson, Mississippi), referred to *Typhina* by Keen (1944, p. 66), and it is inferred that *Typhis* and *Typhina* evolved, as shown in text-fig. 3, from a hypothetical pre-Eocene ancestor close to *Typhina*.

Typhina, Typhinellus, Haustellotyphus, Talityphis, and Typhisopsis, all having 4.2 growth steps per whorl, and regarded by Keen as subgenera of Typhis, are here grouped in different genera. Three subgenera of Typhis are recognized:

Typhis sensu stricto

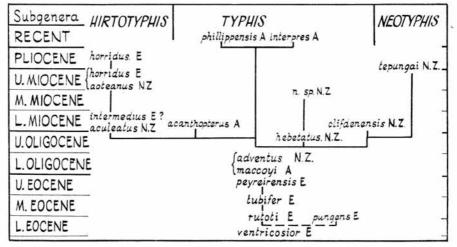
Hirtotyphis (regarded by Keen as synonymous with Typhis)

Neotyphis new subgenus.

Hirtotyphis and Neotyphis are Miocene-Pliocene short-lived derivatives of Typhis,

represented by few species. The subgenus *Typhis* is a conservative group including six European, five New Zealand, and four Australian species, ranging in age from lower Eocene to Recent. The stratigraphic and geographic occurrences and probable phylogenetic relationships of species of *Typhis*, *Hirtotyphis*, and *Neotyphis* are summarized in text-fig. 6.

A description of the French Eocene *T. peyreirensis* Cossmann and Peyrot has not been seen. The Australian and New Zealand Oligocene species *T. maccoyi* T.-Woods.



TEXT-FIG. 6. Phylogeny of Genus *Typhis*. Subgenera shown in upper-case italics, species in lower-case italics. E, Europe, A, Australia, NZ, New Zealand, indicate where species occur.

and *T. australis* sp. nov. are close to the European upper Eocene *T. tubifer* (type species of *Typhis*). Relationship of these three species to the European Oligocene *T. peyreirensis* is inferred but has not been confirmed. According to Keen (1944, p. 65) the Italian Lower Miocene *T. intermedius* was confused with *Hirtotyphis horridus* (Brocchi) by Montanaro (1934, p. 10, pl. 1, fig. 1). On account of its greatly enlarged upper variceal spines and obsolete lower spines the New Zealand Lower Miocene *Typhis* (*Hirtotyphis*) aculeatus is thought to belong to the same lineage as *Hirtotyphis aoteanus* and *horridus*. *T. intermedius* also belongs to this group. These four species are grouped in *Hirtotyphis* to emphasize this relationship but the earlier species *aculeatus* and probably the Italian form are less distinct from *Typhis s.s.* than are the later species.

The genetic relationships between species of *Typhis* and of *Hirtotyphis* suggested in text-fig. 6 imply communication between Europe and Australasia (or at least New Zealand) from about Middle Oligocene to Upper Miocene time. The Pliocene *Neotyphis*, on the other hand, has no European relatives, but it possibly has some representatives among Miocene and Pliocene American shells referred by Keen to *Laevityphis* (e.g. *L. linguiferous* (Dall)).

The double varices of the Australian Lower Miocene species T. acanthopterus Tate

are abnormal, but probably do not indicate a fundamental difference. A similar, though not parallel, modification is exhibited by some species of *Typhinellus* and *Typhina*, particularly by *Typhina* (*Typhina*) bivaricatus (Verco).

Subgenus HIRTOTYPHIS Jousseaume 1880

Type species, by original designation, *Hirtotyphis horridus* (Brocchi) = *Murex horridus* Brocchi 1814, Upper Miocene-Pliocene, Europe.

Hirtotyphis horridus is distinguished by three very large, nearly straight, radially directed spines on each varix of the body whorl. The discovery of related species in Miocene rocks of New Zealand lends greater significance to the form which is widely divergent from the New Zealand Miocene and Australian Recent species of Typhis s.s.

Subgenus NEOTYPHIS subgen. nov.

Type species Typhis tepunga Fleming 1943, Pliocene, New Zealand.

Shell of moderate size with 4·2 growth steps per whorl, varices rounded folds, not crossing the shoulder, nearly smooth except for a single vertical spine on top of each—simulating *Laevityphis*; tubes midway between varices, directed obliquely backwards, steeply upwards on adult whorls but almost horizontally on the first post-nuclear whorl; neanic varices as in *Typhis s.s.*; protoconch large, differing from that of *Typhis s.s.* in having an incipient peripheral keel.

Remarks. Each varix of the body whorl of Neotyphis tepungai has two nodules on the crest at intervals below the vertical spine. On the holotype the upper nodule of the terminal varix is produced to a tiny hollow conical backward curving spine. The nodules are vestigial spines with sutural grooves. The growth-lines of the varices have the same relation to these as in Typhis s.s. Neotyphis is thus closely related to Typhis, not to the superficially similar Laevityphis. The neanic varices and tubes confirm this relationship.

Typhis linguiferus Dall, placed in Laevityphis by Keen, may be a Neotyphis. According to Dall (1890, p. 152, pl. 12, fig. 7) the protoconch has 'two laxly coiled, polished, peripherally-keeled nuclear whorls'. Judged from Dall's figure (Gardner 1947, p. 53, fig. 17) the peripheral keel is not obvious, and the protoconch is very like that of Neotyphis tepungai. T. linguiferus also resembles Neotyphis and not Laevityphis in the position of the varices relative to the tubes and in the nature of the neanic varices and tubes. On the other hand, Dall's figure shows no trace of vestigial spines on the varices. T. linguiferus is closer to Neotyphis than to Laevityphis and is tentatively included in Neotyphis.

Genus LAEVITYPHIS Cossmann 1903

Type species, by original designation, Typhis coronarius Deshayes 1865, Lower Eocene, France.

Laevityphis coronarius is a small, elongate shell with narrow, but rounded, smooth varices each with a single almost vertical spine on top. The terminal varix is well behind the aperture and earlier varices are closer to the preceding than to the succeeding tubes. Cossmann's illustration (1903, pl. 2, fig. 18) shows both tubes and spines nearly vertical on all (including neanic) whorls.

Laevityphis is mainly an Eocene-Oligocene group. Of the American Miocene species referred here, Typhis cercadicus Maury (from Santa Domingo) seems to be the only true

Laevityphis. Typhis sawkinsi Mansfield has varices extending across the shoulder and may be generically distinct. T. costaricensis was first described as a variety of T. linguiferus and may be a Neotyphis.

The East African Recent species *T. transcurrens* von Martens and *T. tubuliger* Thiele, referred to *Laevityphis* by Keen, are much smaller than Tertiary species and may be a distinct genus or subgenus.

Pilsbrytyphis Woodring 1959 is regarded as a subgenus of Laevityphis, differing in having irregular ornament.

Genus RUGOTYPHIS gen. nov.

Type species Typhis francescae Finlay 1924, Lower Miocene, New Zealand.

Shell large for the subfamily, solid, with 4·2 growth steps per whorl; tubes directed radially or only slightly backwards, nearly horizontal; varices about midway between tubes, broad, elevated, with acute, foliated, crenulated crests, inclined away from the aperture, continued across the shoulder and contiguous with varices of previous whorl, forming four steep, sinistral spiral ridges from body to apex; apertural sides of varices ornamented with irregular, more or less radial ribs; reverse sides of varices and remainder of shell smooth except for growth-lines; protoconch not seen.

Remarks. Superficially Rugotyphis secundus sp. nov. resembles Typhis hebetatus Hutt. but Rugotyphis differs from Typhis in the nearly radial tubes, the continuation of the varices over the shoulder, and the lack of conical spines on the varices. The part of the varix crossing the shoulder is narrower and less elevated than the portion below the peripheral angle and is not crenulated. The crenulations of the lower parts of the varices are formed by tiny lamellar spines which curl forward at the edges to become shallowly trough-shaped.

The size and shape of the shell and the solidness and backward inclination of the varices suggest that *Rugotyphis* is intermediate between *Typhis* and *Typhisopsis*.

Two American species may belong to *Rugotyphis*, *Typhis harrisi* Olsson (Florida, Miocene), and *T. floridanus* Dall (Florida, Pliocene). *T. floridanus* has varices extending across the shoulder, with oddly twisted spines on the peripheral angle. Dall (1889, p. 216) described the ornament on the front surface of the varix as follows: 'spiral sculpture of a few low ridges extending from the vicinity of the aperture to the summit of the varix, where they appear as serrations or abortive spines'. This description fits *Rugotyphis* much better than *Typhina* or *Typhinellus*.

Genus TYPHINA Jousseaume 1880

Type species, by original designation, Typhis belcheri Broderip 1833, Recent, off Cape Blanco, West Africa.

Typhina and Typhinellus are here grouped together as subgenera of the genus Typhina. Both names were first published in Jousseaume's summary list of the Muricidae (1880, p. 335). According to Iredale (1924, p. 272) Typhinellus appears ahead of Typhina in the list, and therefore has page precedence for generic status. The International Rules recommend that page precedence should be observed in the event of 'other things being equal'. Typhina is given generic status because it is the larger, more important, more widespread and apparently older group. Typhinellus is considered to be a specialized

derivative of Typhina and therefore is more appropriately regarded as a subgenus of Typhina.

Reeve's illustrations of T. belcheri (1842, pl. 240, figs. 5, 6) show clearly the structure of the varices. Photographs of Reeve's illustrations are reproduced below (Pl. 47, figs. 17, 18). Both primary and secondary varices are present. The outer edges of the primary varices are crenulated and curled forward. The secondary varices are simple low outgrowths of the apertural rim, extending from the previous whorl to opposite the peripheral angle. The intervariceal tubes are situated midway between the primary varices and are bent obliquely backwards and upwards at a moderate angle from the horizontal.

In the indisputable species of Typhina, yatesi and pauperis, secondary varices are not developed. In T. bivaricata the secondary varices are almost as large as the primary varices, the whole of the outer semicircle of the apertural rim being expanded to form a prominent variceal flange. In Typhina, therefore, the secondary varix is quite variable, and has no generic significance.

Subgenus TYPHINELLUS Jousseaume 1880

Type species, by original designation, Typhis sowerbyi Broderip 1883, Recent, Mediterranean.

That Knudsen (1956, pp. 20, 21) regarded T. belcheri as a synonym of T. tetrapterus of Kobelt 1887 (= T. sowerbyi) emphasizes the similarity between Typhinellus and Typhina. Separation of the two subgenera, however, is supported by their different space-time distributions.

T. sowerbyi is well illustrated by Reeve (1842, pl. 240, figs. 7, 8, 9), and his figures are reproduced (Pl. 47, figs. 14, 15, 19).

Three main characters distinguish Typhinellus from Typhina: (1) The outer edges of the primary varices of Typhinellus curve backward instead of forward as in Typhina. (2) The primary varices of Typhinellus continue without constriction on to the anterior canal, whereas those of Typhina are constricted at the top of the canal and in most species are absent from the canal or are represented by flat fin-like spines. (3) The body whorl of Typhinellus tapers almost regularly from the peripheral angle to the anterior canal; that of Typhina is generally strongly convex.

Typhinellus appears to have originated in Europe. The only undoubted fossil record is T. tetrapterus (Brown) from the Pliocene of Europe, regarded by Keen as a synonym of T. sowerbi. A shell from the Oligocene of Italy was described by Sacco (1904, p. 17, pl. 4, fig. 20) as Typhis (Typhinellus) tetrapterus var. protetrapterus. The writer has not seen Sacco's description. If a true Typhinellus, this shell would show that Typhinellus has been distinct from Typhina for a much longer time than would seem likely from their relatively small differences.

The shell from the Miocene of Hungary, illustrated as Murex (Typhis) tetrapterus by Hoernes (1856, pl. 26, fig. 10), has varices continuing directly across the shoulder and lacking even the single spines of Typhinellus. It is not a Typhinellus, but seems to belong to the American Typhisopsis group and probably needs a new generic name.

A revised list of species of Typhina and Typhinellus is given below:

Typhina (Typhina) belcheri (Broderip), Recent, West Africa Typhina (Typhina) bivaricata (Verco), Recent, South Australia Typhina (Typhina) cleryi (Petit), Recent, Brazil

Typhina (Typhina) disjuncta (Tate), Miocene, Australia

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Typhina (Typhina) laciniata (Tate), Miocene, Australia Typhina (Typhina) montforti (A. Ad.), Recent, Japan Typhina (Typhina) nitens (Hinds), Recent, Straits of Macassar Typhina (Typhina) pauperis (Mestayer), Recent, New Zealand Typhina (Typhina) tetragoniatus (Cossmann), Pliocene, India Typhina (Typhina) yatesi (C. & F.), Recent, South Australia Typhina (Typhinellus) quadratus (Hinds), Recent, Ecuador Typhina (Typhinellus) sowerbyi (Broderip), Recent, Mediterranean Typhina (Typhinellus) tetrapterus (Bronn), Pliocene, Italy Typhina (Typhinellus)? protetrapterus (Sacco), Oligocene, Italy

Genus TYPHISOPSIS Jousseaume 1880

Type species, by original designation, *Typhis coronatus* Broderip 1833 = *T. grandis* A. Ad. 1855, Recent, Gulf of California.

Subgenus TYPHISOPSIS s.s. Subgenus TALITYPHIS Jousseaume 1882

Type species, by original designation, *Typhis expansus* Sowerby 1874, Recent, probably Caribbean (Keen 1944, p. 56).

The varices are close behind the aperture or apertural scars and continue across the shoulder without break or decrease in size.

In *Typhisopsis* each tube is supported by a 'laminar remnant of former outer lip' (Keen 1944, p. 57), while in *Talityphis* the tubes are free. In view of the variability in the development of the outer lip (secondary varix) in *Typhinellus*, the validity of the distinction between *Typhisopsis* and *Talityphis* seems questionable.

Neither of these subgenera occurs in Australia or New Zealand.

Genus PTEROTYPHIS Jousseaume 1880

Type species, by original designation, Typhis pinnatus Broderip 1833, Recent, locality unknown.

Subgenus PTEROTYPHIS s.s. Subgenus TRIPTEROTYPHIS Pilsbry and Lowe 1932

Type species, by original designation, Typhis lowei Pilsbry 1931, Recent, Panama.

Pterotyphis has three growth steps per whorl and very elevated flange-like varices continuous from low on the anterior canal to the previous whorl. In Pterotyphis s.s. the tubes are close to but not joined to the succeeding varices; in Tripterotyphis the tubes are coalesced with the succeeding varices. The varices are similar to those of Typhisopsis and for this reason Pterotyphis is thought to have evolved, in the late Oligocene or Miocene, from Talityphis by reduction of the number of growth steps in each whorl. The anomalous position of the intervariceal tubes may indicate that Pterotyphis is of greater antiquity, convergent with Typhisopsis in variceal characters.

Pterotyphis and Tripterotyphis are not known in Australia or New Zealand.

Genus SIPHONOCHELUS Jousseaume 1880

Type species, by original designation, *Typhis avenatus*, misprint for *T. arcuatus* Hinds 1843 (corrected by Jousseaume 1882, p. 337), Recent, South Africa.

Siphonochelus has 4.2 growth steps per whorl and rounded, fold-like varices, not

crossing the shoulder, more or less curved backward at the top and coalesced with the preceding tubes. Commonly an intervariceal axial fold is present just behind each tube.

Typical species (arcuatus, fistulosus, solus) have smooth, spineless varices. Typhis parisiensis d'Orbigny was illustrated by Cossmann (1903, pl. 2, fig. 19) as Typhina, and by Wrigley (1930, pl. 10, fig. 40) as Typhis, but was placed in Siphonochelus by Keen (1944, p. 66). Specimens from Barton, England (Eocene), in the New Zealand Geological Survey collection have sharp-crested varices with obsolete trough-shaped spines or crenulations on the varices. It is probably a primitive form intermediate between Siphonochelus and a hypothetical pre-Eocene ancestor common to Typhis or Typhina. S. parisiensis may require a new generic or subgeneric name.

Genus LYROTYPHIS Jousseaume 1880

Type species, by original designation, *Typhis cuniculosus* Duchatel = *Murex cuniculosus* Nyst 1836, Oligocene, Belgium.

Varices as in *Siphonochelus*; five growth steps per whorl; aperture acutely angled at the bottom, encroaching on to the anterior canal. Cossmann (1903, pl. 3, figs. 4, 5) and Keen (1944, p. 54, fig. 5) show a straight anterior canal, though Cossmann stated that it is slightly bent.

Keen regarded *Lyrotyphis* as a subgenus of *Siphonochelus* and recognized only two species, *cuniculosus* and *schlotheimi*, both from the Oligocene of Europe. To these must be added *T. syringianus* Hedley, Recent, New South Wales.

Hedley (1903, p. 381) states *syringianus* has four post-nuclear whorls with twenty 'double-varices', implying five varices per whorl. A specimen from Tasmania, in the New Zealand Geological Survey collection, agrees well with Hedley's figure and description. As well as five growth steps per whorl, it has a less constricted aperture than is usual in Typhinae, with an acutely angled lower border encroaching on the anterior canal, as in the type species. The apertural rim is lower than in the other Typhinae examined, and becomes indistinct about the basal angle. Hedley's 'double-varices' consist of the varices and smaller intervariceal folds situated just behind each tube, the *costules intermédiaires* of Cossmann (1903, p. 62).

Lyrotyphis is very similar to Siphonochelus in all except the number of growth steps per whorl and the atypical aperture. Cossmann (1903, pp. 62–63) noted in cuniculosus a weak posterior channel, no more than a slight angle in the apertural border, and the extension of the aperture downward on to the anterior canal. He considered these features important, and gave full generic status to Lyrotyphis.

Genus SEMITYPHIS Martin 1931

Type species, by monotypy, Semityphis incisus Martin 1931, Upper Eocene, Java.

Semityphis has three growth steps per whorl. The smooth varices suggest closer relationship to Siphonochelus than to other genera.

CHECK LIST OF AUSTRALASIAN SPECIES OF TYPHINAE

Genus Typhis
Subgenus (Typhis)
maccoyi T.-Woods. Oligocene (Janjukian), Australia
adventus sp. nov. Mid. Oligocene (Duntroonian-Waitakian), New Zealand

hebetatus Hutton. Upper Oligocene (Otaian), New Zealand acanthopterus Tate. Lower Miocene (Balcomian), Australia planus sp. nov. Lower Miocene (Altonian), New Zealand clifdenensis sp. nov. Lower Miocene (Altonian), New Zealand n.sp. (unnamed) Mid. Miocene (Waiauan), New Zealand philippensis Watson. Recent, Australia interpres Iredale. Recent, Australia Subgenus Hirtotyphis

aculeatus sp. nov. Lower Miocene (Altonian), New Zealand aoteanus sp. nov. Upper Miocene (Tongaporutuan), New Zealand Subgenus Neotyphis

tepungai Fleming. Pliocene (Opoitian-Waitotaran), New Zealand

Genus Typhina

Subgenus Typhina

disjuncta (Tate). Lower Miocene (Balcomian), Australia laciniata (Tate). Lower Miocene (Balcomian), Australia bivaricata (Verco). Recent, South Australia yatesi (C. & F.). Recent, South Australia pauperis (Mestayer). Recent, New Zealand

Genus Siphonochelus

evaricosus (Tate). Lower Miocene (Balcomian), Australia rugicostatus Chapm. and Crespin. Pliocene (Kalimnan), Australia generosus Iredale. Recent, New South Wales pavlovae = pavlova Iredale. Recent, New South Wales solus sp. nov. Recent, New Zealand

Genus Lyrotyphis

syringianus (Hedley). Recent, New South Wales, Tasmania

Genus Semityphis

? Semityphis sp. = Typhis tripterus Tate, 1888 (homonym of T. Tripterus Grateloup 1833). ? Pliocene, Adelaide bore, Australia

DESCRIPTION OF SPECIES

All New Zealand species are illustrated and described below, together with four Australian species from the New Zealand Geological Survey collection.

Measurements. For most species three dimensions are given in the following order: (a) height; (b) maximum diameter, i.e. including the varices, and spines if present, measured when possible between the terminal and antepenultimate varices; (c) the diameter excluding the varices and spines, measured immediately behind the terminal and antepenultimate varices. All dimensions are in millimetres. Estimated dimensions of broken specimens are given in brackets.

Genus TYPHIS Montfort Subgenus TYPHIS Typhis (Typhis) adventus sp. nov.

Plate 47, fig. 23; text-figs. 4, 8

Shell of moderate size, delicate, elongate, with elevated spire; peripheral angle high, shoulder narrow, base convex; varices narrow, raised folds, each with two spines visible on spire whorls, six on body whorl, the uppermost of which are of moderate size with strong backward curvature, decreasing downwards, the lowest two very small, situated on the anterior canal; tubes situated on the shoulder, higher than the tops of the varices,

inclined obliquely backwards and slightly upwards; surface of shell smooth except for growth-lines and scars of former apertures.

Dimensions. Holotype: 21 (24); 14; 11. Paratype: 21; 12.5; 10.

Repository. Holotype and paratype, New Zealand Geological Survey.

Localities. Holotype: G.S. 1473—Otiake Trig. Z, North Otago, Waitakian (Mid. Oligocene). Paratype: G.S. 1281—Wharekuri Greensand, Waitaki Valley, North Otago, Duntroonian (upper Lower Oligocene).

Age: Duntroonian to Waitakian (upper Lower to Middle Oligocene).

Remarks. Typhis maccoyi Tenison-Woods is close but has more acutely angled whorls, less convex base and shorter spire with suture higher on whorls, so that usually only one spine on each spire varix remains uncovered.

Typhis (Typhis) hebetatus Hutton

Plate 46, figs. 10-13; text-fig. 4 (6)

- 1877 Typhis hebetatus Hutton, p. 594, pl. 16, fig. 1.
- 1915 Typhis maccoyi Tenison-Woods; Suter, p. 28 (not Typhis M'Coyi Tenison-Woods 1876).
- 1924 Typhis maccoyi Tenison-Woods; Marwick, p. 328.
- 1926 Typhis maccoyi Tenison-Woods; Finlay, p. 427.
- 1944 Typhis (Typhinellus) hebetatus Hutton; Keen, pp. 56, 65.

Shell broad, biconic, solid, of moderate size, with short spire; whorls sharply angled with a carina connecting each tube to succeeding varix; varices narrowly rounded raised folds with relatively small spines, six on each body varix, one only visible on each spire varix; sutures high on spire whorls; body whorl strongly convex; surface ornamented with faint, irregular spiral ribs in line with the variceal spines, strongest on the backs of the varices.

Dimensions. Holotype: 28·9; 20·6; 14·9. Topotype (small but with protoconch): 20·1; 13·3; 9·6. Hypotype from Bluecliffs (Pl. 46, fig. 10): 25·4; 19·8; 14·3. Hypotype from Ardgowan (Pl. 46, fig. 11): 23·3; 17·5; 13·1. Hypotype from Awamoa (Pl. 46, fig. 13): 22·6; 16; 12·3. Extra large specimen from Ardgowan: 31·5; 24·7; 17·8.

Repositories. Holotype, Otago Museum; Hypotypes, New Zealand Geological Survey.

Localities. Holotype and two topotypes, Mount Harris, South Canterbury; Ardgowan, Awamoa, Target Gully, Devil's Bridge, all near Oamaru, North Otago; Suter Coll. 159 Bluecliffs, Otaio River, South Canterbury; G.S. 162, Pareora River, South Canterbury; Otaian (upper Oligocene).

Age. Otaian-Awamoan (Upper Oligocene); Holotype: Awamoan (uppermost Oligocene)

Remarks. Specimens from the Otaian localities, Bluecliffs and Pareora River, though somewhat older than the holotype, agree closely in the development of the spines and the elevation of the spire. Specimens from the Oamaru localities Ardgowan, Awamoa, Target Gully, and Devil's Bridge have the spire consistently more depressed, with sutures reaching almost up to the peripheral angle, and generally smaller spines. The Oamaru specimens are about the same age as the type and the differences are probably attributable to varying ecological conditions.

Typhis (Typhis) planus sp. nov.

Plate 46, fig. 7

Shell small, elongate, biconic, consisting of typical protoconch and five post-nuclear whorls; peripheral angle sharp; varices narrowly rounded with only slight backward

inclination, each with six spines, the uppermost long and narrow, curving backwards and upwards, the next below prominent, lower ones tiny, diminishing progressively downwards; body whorl contracted regularly from immediately below the peripheral angle, with flattened intervariceal spaces; tubes set low, just above the peripheral angle, inclined obliquely backwards, only very slightly upwards (3°-4° from horizontal) on adult whorls, more strongly upwards (30° from horizontal) on early whorls.

Dimensions. Holotype: 15; 10; 6.5. Paratype (protoconch missing): 19; 12; 8.

Repository. Holotype and paratype, New Zealand Geological Survey.

Localities. Holotype: G.S. 2945, Bed 6a (upper part), Clifden, Southland. Paratype: G.S. 2948, Bed 4, Clifden; Lower Altonian.

Age. Lower Altonian (Lower Miocene).

Remarks. Distinguished by small elongate form, slight backward inclination of varices, nearly horizontal tubes set low on shoulder, sharp peripheral angle and flattened variceal interspaces on the base.

Typhis (Typhis) clifdenensis sp. nov.

Plate 47, fig. 26

Shell small, elongate, biconic, with elevated spire; periphery broadly rounded; body whorl strongly convex and ventricose; varices narrowly rounded, with six spines, the lower five rudimentary, the highest one somewhat larger with only slight curvature, directed slightly upwards; tubes slightly closer to succeeding than to preceding varices, set high on the shoulder, inclined obliquely backwards and relatively steeply upwards (35° to 40° from horizontal on adult whorls, about 45° on the earliest whorl).

Dimensions. 16 (C. 18); 10-5; 7.

Repository. New Zealand Geological Survey.

Age and locality. Holotype (the only specimen), G.S. 2937, 'Long Beach', Clifden, Southland, upper Altonian (Lower Miocene).

Remarks. The tubes are more steeply inclined than in any other species of *Typhis s.s.* A related, but probably distinct, form with less steep tubes, from the Awamoan of Rifle Butts, Oamaru, is represented by a single specimen in the collection of the Geology Department, Victoria University, Wellington.

EXPLANATION OF PLATE 46

Figure 7×3 ; all other figures $\times 2$.

Figs. 1, 3. Typhis (Hirtotyphis) aculeatus sp. nov., 1, Holotype, 3, Paratype G.S. 2155.

Fig. 2. Typhis (Hirtotyphis) aoteanus sp. nov., holotype.

Fig. 4. Typhis (Typhis) sp. nov. G.S. 3839, Dovedale.

Fig. 5. Rugotyphis francescae (Finlay) gen. nov., topotype.

Fig. 6. Rugotyphis cf. francescae (Finlay) gen. nov. G.S. 2937, 'Long Beach', Clifden.

Fig. 7. Typhis (Typhis) planus sp. nov., holotype.

Figs. 8, 9. Rugotyphis secundus gen. et sp. nov. 8, Apical view of paratype, V.79, Clifden (bed 7?), Southland. 9, Holotype.

Figs. 10–13. Typhis (Typhis) hebetatus Hutton. 10, Suter Coll. 159, Bluecliffs, S. Canterbury. 11, Ardgowan, Oamaru. 12, Holotype. 13, Showing incomplete terminal varix, Awamoa, Oamaru.

Typhis (Typhis) sp. nov.

Plate 46, fig. 4

This species is represented by a single, apparently badly worn specimen. Of moderate size, broadly biconic, with short, but acuminate spire; tubes set only slightly above the tops of the varices, inclined obliquely backward and slightly above horizontal; varices seem rather broad and rounded, convex in front, deeply excavated behind, and have borne six or seven spines which are worn quite away; differs from all other species in the profile of the body whorl and its varices which descend vertically from the poorly defined peripheral angle, then turn very rapidly under to join the anterior canal.

Dimensions. 24-5; 19; 14.

Repository. New Zealand Geological Survey.

Locality. G.S. 3839, Dovedale, North Canterbury.

Age. Waiauan (upper Middle Miocene).

Typhis (Typhis) maccoyi Tenison-Woods

Plate 47, fig. 25; text-fig. 4 (10)

1876 Typhis M'Coyi Tenison-Woods, p. 22, pl. 1, fig. 5.

1888 Typhis M'Coyi Tenison-Woods; Tate, p. 92.

1903 Typhis (Typhina) maccoyi Tenison-Woods; Cossmann, p. 58, pl. 2, fig. 16.

1944 Typhis (Typhinellus) maccoyi Tenison-Woods; Keen, pp. 56, 66.

The following description is based on eight specimens from Spring Creek, Torquay, Victoria.

Shell of moderate size, moderately elongate, biconic, with elevated spire; peripheral carina prominent; base gently convex, contracting sharply from the periphery; usually only one spine showing on spire varices, sometimes the second not covered by the following whorl; body varices with six moderately large backward-curving spines; tubes inclined obliquely backward and only slightly upward.

Dimensions. Hypotype: 22.0; 14.4; 11.2.

Localities. Holotype from Table Cape, Tasmania; specimens in New Zealand Geological Survey collection from Spring Creek, Torquay, Victoria.

Age. Janjukian (Oligocene).

Remarks. The Spring Creek specimens seem stouter than Tenison-Woods's illustration. Several authors have regarded *T. hebetatus* as a synonym of *T. maccoyi*, but *T. hebetatus* is much stouter, with a shorter spire, smaller spines, and a more convex base. *T. adventus* sp. nov., closer to *maccoyi*, is easily distinguished by its still more elevated spire and more convex body whorl.

Subgenus HIRTOTYPHIS Jousseaume Typhis (Hirtotyphis) aculeatus sp. nov.

Plate 46, figs. 1, 3

Shell of moderate size, solid, broadly biconic with somewhat depressed spire; shoulder broad and sloping, peripheral angle distinct, but not sharp, almost reached

by sutures on spire whorls; base strongly convex; varices prominent, rounded folds with slight backward inclination, each surmounted by five spines with very slight backward curvature, diminishing downwards, the second lowest situated at the point of maximum concavity between the body and the anterior canal, lowest on the upper part of the canal; below it, and slightly behind the crest of the varix, an oblique ridge, which in some paratypes is produced to form an obsolete spine offset slightly backwards from the higher spines; upper three spines grotesquely large; tubes set low on the shoulder, bent obliquely backwards and upwards at 10° from horizontal; three or four faint spiral ribs on the base of some specimens, some in line with variceal spines, others not.

Dimensions. Holotype: 24; not determinable; 11·5. Paratype (Pl. 46, fig. 3): 21; 17; 10. Topotype-paratype: 18; 14; 9.

Repository. Holotype and four paratypes, New Zealand Geological Survey.

Localities. Holotype and three paratypes, G.S. 2957, North Bank, Waiau River, Clifden, Southland; one paratype, G.S. 2155, North Bank, Clifden; Altonian. A doubtful worn specimen, G.S. 2946, Bed 6a, Clifden, Lower Altonian.

Age. Altonian-Clifdenian? (Lower Miocene). Holotype: Altonian?

Remarks. This species is undoubtedly intermediate between the later *Hirtotyphis* with three spines on each varix (horridus, aoteanus) and the more conservative typical *Typhis* with spines of moderate to small size. *T. planus* sp. nov. may be related, but has much smaller spines and is retained in *Typhis s.s.*

Although morphologically close to *Typhis s.s.*, *T. aculeatus* is more appropriately classed as *Hirtotyphis*.

Typhis (Hirtotyphis) aoteanus sp. nov.

Plate 46, fig. 2

Shell large for the genus, broadly biconic, squat, solid, spire depressed; periphery broadly rounded; sutures immediately below uppermost variceal spines on spire whorls; base convex, but shape distorted by crushing; varices low, broadly rounded, surmounted by three straight, radial spines, the uppermost grotesquely large, the next intermediate in size, the lowest, on the base, quite small; tubes set high on the shoulder with narrow interspace to the variceal spine on the preceding whorl, inclined obliquely backward and upward at 30° from horizontal.

Dimensions. 27 (31+); 28; 17.

Repository. Holotype, New Zealand Geological Survey.

Locality. Holotype G.S. 5349, Hurupi Formation, Pahaoa River, East Wairarapa. A juvenile from a nearby locality in the Hurupi Formation.

Age. Lower Tongaporutuan (base of Upper Miocene).

Remarks. An illustration by Cossmann (1903, pl. 2, fig. 24) of *Hirtotyphis horridus* (Brocchi), from the Pliocene of Italy, shows a smaller shell with similar low rounded varices. Cossmann notes the straightness of the spines. The shell from the Miocene of Hungary (Hoernes 1856, pl. 26, fig. 9) has the spines curved slightly backward.

The remarkable similarity of the European and New Zealand species is attributed to close genetic affinity and not to convergent evolution.

Subgenus NEOTYPHIS nov. Typhis (Neotyphis) tepungai Fleming

Plate 47, figs. 27, 28; text-fig. 4 (9)

1943 Typhis tepunga Fleming, p. 205, pl. 30, fig. 21.

Shell of moderate size, elongate, fusiform, with elevated spire; peripheral angle at the middle of spire whorls, becoming ill-defined on the adult whorls; base convex; varices broadly rounded, moderate folds, convex in front, a little excavated behind.

For other details see description of the subgenus, above.

Dimensions. Holotype (lacking protoconch): 21.5; 13; 10.5. Paratype (G.S. 2499): 21; 11; 9.

Repository. Holotype and three paratypes, New Zealand Geological Survey.

Localities. Holotype and paratype with intact protoconch, G.S. 2661, Tahoraite Survey District, Southern Hawkes Bay; paratype, G.S. 2499, Tahoraite Survey District; paratype, G.S. 2314, Takapau Survey District, Southern Hawkes Bay; Waitotoran (Upper Pliocene). Figured specimen (Pl. 47, fig. 28), G.S. 1561, Waiau River, 10 chains below Mangaone junction, Wairoa Survey District, Northern Hawkes Bay, Opoitian (Lower Pliocene). Cliffs east of Whangaimoana, Palliser Bay, Southern Wairarapa, Kapitean or basal Opoitian (uppermost Miocene or basal Pliocene).

Age. Kapitean to Waitotaran (uppermost Miocene to Upper Pliocene).

Remarks. The trivial name tepunga is formed from a patronymic, and, at the request of Dr. C. A. Fleming, is changed to tepungai to conform with the International Rules.

The varices of *Neotyphis tepungai* differ from those of all other New Zealand species. *Typhis* (*Typhis*) clifdenensis sp. nov., with its elongate form, reduced variceal spines and steeply inclined adult tubes is probably close to the ancestor of *Neotyphis*.

Genus RUGOTYPHIS nov. Rugotyphis francescae (Finlay)

Plate 46, fig. 5

1924 Typhis francescae Finlay, p. 465, pl. 49, figs. 6a, 6b. 1944 Typhis (Typhinellus) francescae Finlay; Keen, pp. 56, 65.

Shell large for the subfamily, solid, with rhomboidal outline; periphery sharply angled below the middle of spire whorls; shoulder broad, sloping, flattened; front of each body varix with one rib at the peripheral angle larger than the remainder, between this and the base of the aperture six or seven parallel, irregular ribs sloping gently downward from the apertural rim; no ribs on the varix below the level of the base of the aperture; on the section of varix crossing the shoulder three or four weak parallel ribs sloping steeply upwards from the apertural rim; five or six tiny trough-shaped spines on the crest of each varix not all in line with the variceal ribs, the uppermost at the peripheral angle, a little larger than the remainder; tubes situated just above the peripheral angle, inclined very slightly backwards and upwards; surface between varices smooth except for growth-lines.

Dimensions. (After Finlay) height 34 mm.; diameter 23 mm.

Repository. Holotype, Auckland Institute and Museum. Hypotype, New Zealand Geological Survey.

Localities. Holotype and hypotype, Bed 6a, Clifden, Southland; a fragment from Bed 4, Clifden;

Lower Altonian (Lower Miocene). A small and non-typical specimen (Pl. 46, fig. 6) from G.S. 2937, 'Long Beach', Clifden, Upper Altonian (Lower Miocene).

Age, Altonian (Lower Miocene).

Remarks. The hypotype, though broken, is nearly as large as, and agrees well with, the type. The fragment from Clifden bed 4 is an anterior canal with a portion of varix attached. The upper Altonian specimen illustrated is a less adult shell than the type with about five post-nuclear whorls (apex missing); it is considerably smaller than the lower Altonian specimens would be at the same stage of development, and differs further in having four lamellar spines on the varices below the lowest rib, two being situated on the canal.

Rugotyphis secundus sp. nov.

Plate 46, figs. 8, 9

Shell of moderate size, solid, broadly biconic, differing from *francescae* in having a more depressed spire with sutures higher on the whorls, almost reaching the peripheral carina, body whorl contracting more sharply from the periphery, tubes quite radial, variceal spines extending down to the anterior canal which is shorter, very broad and flattened.

Dimensions. Holotype: 25; 20.5; 15. Paratype: 24; 18; 13.

Repositories. Holotype, New Zealand Geological Survey. Paratype, Geology Department, Victoria University of Wellington.

Localities. Holotype G.S. 2155, left bank, Waiau River, Clifden, Southland, upper Altonian (Lower Miocene). Paratype V. 79, ? bed 7, Clifden, Lilburnian (Middle Miocene).

Age. Upper Altonian? to Lilburnian? (Lower to Middle Miocene?).

Genus TYPHINA Jousseaume Subgenus TYPHINA s.s. Typhina (Typhina) pauperis (Mestayer)

Plate 47, fig. 24; text-fig. 4 (7)

1916 Typhis pauperis M. K. Mestayer, p. 127, pl. 12, figs. 9, 9a. 1944 Typhis (Typhinellus) pauperis Mestayer; Keen, pp. 56, 66.

Shell very small, moderately elongate, pagodiform, thin and fragile, three and threequarter post-nuclear whorls with carinate periphery high on spire whorls; base tapering from the periphery, lightly convex; no secondary varices; primary varices not extending on to the anterior canal, crenulated by three deep radial folds, each bearing a prominent trough-shaped spine curving gently inwards towards the spire and backwards; tubes straight, pointing slightly backward and upward; anterior canal narrow, slightly flattened, bent gently to right.

Dimensions. Holotype: 8; 5; 3-2.

Repository. Holotype (M. 1749) and paratype (M. 779) Dominion Museum, Wellington.

Localities. Holotype 58-60 fathoms off Poor Knights Island, paratype 25-30 fathoms off Hen and Chickens Islands, Hauraki Gulf. One specimen (M. 11067) 113-120 fathoms, off Mayor Island, Bay of Plenty (same locality as Siphonochelus solus).

Age. Recent.

Remarks. Typhina pauperis is distinguished from other species mainly by its small size, regularly tapering body whorl, and lack of secondary varices.

Typhina (Typhina) yatesi (Crosse & Fischer)

Plate 47, fig. 16; text-fig. 4 (5)

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1865 Typhis yatesi Crosse & Fischer, p. 54, pl. 2, fig. 3.
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1866 Typhis yatesi C. & F.; Sowerby, p. 319, pl. 284, figs. 20, 21.

1874 *Typhis yatesi* Angas; Sowerby, pl. 3, fig. 14. 1880 *Typhis yatesi* Angas; Sowerby, pl. 284 *bis*, figs. 22, 23.

1880 Typhis yatesi C. & F.; Tryon, pl. 30, fig. 294. 1939 Typhis yatesi C. & F.; Smith, p. 19, pl. 14, fig. 8. 1944 Typhis (Typhinellus) yatesi C. & F.; Keen, pp. 56, 68.

Shell of moderate size, rather broad, with moderately elevated spire; peripheral angle poorly defined, high on whorls; base strongly convex, subquadrate in profile; no secondary varices; primary varices stopped above the anterior canals, but represented on each anterior canal of the body whorl by a large, flat, triangular, fin-like spine; adult variceal spines partly trough-shaped, partly tubular, the sides having curled around far enough to meet and become soldered together for about half the length of each spine.

Dimensions. Hypotype: 16.5; 9.6; 7.6.

Repository. Hypotype, New Zealand Geological Survey.

Localities. Holotype, Gulf of Saint Vincent, South Australia; hypotype, South Australia (no other details available).

Age. Recent.

Remarks. Though smaller than many Typhinae T. yatesi is extraordinarily large for Typhina. It is distinguished by its size, convex body, partly tubular variceal spines, and fin-like development of the varices on the anterior canal.

Typhina (Typhina) bivaricata (Verco)

Plate 47, fig. 20; text-figs. 4 (1), 4 (2)

1909 Typhis bivaricata Verco, p. 272, pl. 21, figs. 1-2.

1944 Typhis (Typhina) bivaricatus Verco; Keen, pp. 55, 63.

Shell very small, biconic, compact, with moderately elevated spire; peripheral angle high on whorls; base moderately convex; secondary varices nearly as large as the primary varices, extending from top to bottom of the outer edge of the aperture; primary varices decreasing downwards, not reaching the anterior canals.

Dimensions. Hypotype height 4.8, maximum diameter 3.0 mm.

Repository. Hypotype (cotype), New Zealand Geological Survey.

Locality. 104 fathoms, 35 miles south-west of Neptune Islands, South Australia.

Age. Recent.

Remarks. T. bivaricata is distinguished from all other species by the extraordinary development of its secondary varices.

Genus SIPHONOCHELUS Jousseaume Siphonochelus solus sp. nov.

Plate 47, fig. 21

Shell small, elongate, fusiform, solid, apex worn, final two growth steps mostly broken off, four and a half whorls intact; peripheral angle high, shoulder narrow and deeply channelled behind tubes and varices; spire whorls contracting slightly below periphery; base gently convex, contracting gradually to the anterior canal; varices rounded oblique folds raised above the shoulder and curved back to join the preceding tubes; in front of each varix a deep sulcus about one-third of a growth stage in width, containing apertural scars slightly in front of the middle; sulcus followed by a broad rounded fold initiating the next growth step, decreasing downwards and dying before reaching the anterior canal; tubes all worn down to stumps, directed steeply upwards and obliquely backwards, flattened, broadened in the spiral direction extending from the initial fold to somewhat behind the varix to which it is united; below the tube, between the initial fold and the varix, a broad shallow concavity about two-thirds the width of the total growth step; surface of shell smooth except for growth-lines; aperture not seen.

Dimensions. Height 8 mm.; maximum diameter 4 mm.

Repository. Holotype (the only specimen) (M. 11067), Dominion Museum, Wellington.

Locality. 113-130 fathoms off Mayor Island, Bay of Plenty.

Remarks. Siphonochelus solus seems close to the South African species S. arcuatus judged by the figures of Tryon (1880, pl. 30, fig. 293) and Keen (1944, p. 54, fig. 11). S. solus is distinguished by its broad, flattened intervariceal tubes.

The holotype of S. solus and a specimen of Typhina pauperis were dredged from the same locality. Both are chalky, broken shells, and these species may not be living there now.

EXPLANATION OF PLATE 47

Figs. 14, 15, 19. Typhina (Typhinellus) sowerbyi (Broderip), photographs of illustrations of Reeve (1842, pl. 240, figs. 7-9), magnification not known.

Fig. 16. Typhina (Typhina) yatesi (Crosse and Fischer), Recent, South Australia, ×3.

Figs. 17, 18. Typhina (Typhina) belcheri (Broderip), photographs of illustrations of Reeve (1842, pl. 240, figs, 5, 6), magnification not known.

Fig. 20. Typhina (Typhina) bivaricata (Verco) co-type, 104 fathoms, off Neptune Islands, South Australia, \times 7.

Fig. 21. Siphonochelus solus sp. nov., holotype, ×4.

Fig. 22. Lyrotyphis syringianus (Hedley), Port Esperance, Tasmania, ×6.

Fig. 23. Typhis (Typhis) adventus sp. nov., holotype, ×3.
Fig. 24. Typhina (Typhina) pauperis (Mestayer), holotype, ×7.
Fig. 25. Typhis (Typhis) maccoyi Tenison-Woods, Spring Creek, Victoria, ×3.

Fig. 26. Typhis (Typhis) clifdenensis sp. nov. holotype, ×3.

Figs. 27, 28. Typhis (Neotyphis) tepungai Fleming subgen. nov.; 27, holotype ×3; 28, G.S. 1561 Wairoa, Northern Hawkes Bay, ×3.

Fig. 29. Typhis (Typhis) pungens (Solander), Barton, England, ×3.

Genus Lyrotyphis Jousseaume Lyrotyphis syringianus (Hedley)

Plate 47, fig. 22; text-figs. 4 (3), 4 (4)

1903 Typhis syringianus Hedley, p. 381, text-fig. 94. 1944 Siphonochelus (Siphonochelus) syringianus (Hedley); Keen, pp. 58, 67.

Shell tiny, broadly biconic, solid; whorls rounded, without perceptible peripheral angle; base moderately convex; tubes ovate, slightly elongated in the spiral direction, inclined steeply upward, very slightly backwards; varices curved back at the top to join the tubes; broad rounded intervariceal folds just behind tubes; apertural scars in the sulcus behind the intervariceal folds; surface smooth except for growth-lines; for other details see generic description.

Dimensions. Hypotype: height 4·4 mm., maximum diameter 2·5 mm.

Repository. Hypotype, New Zealand Geological Survey.

Localities. Holotype, 41-50 fathoms, Cape Three Points, New South Wales, Australia; hypotype, Port Esperance, Tasmania.

Age. Recent.

Acknowledgements, Specimens of Recent New Zealand shells were lent by the Dominion Museum, Wellington, the holotype of Typhis hebetatus Hutton by the Otago Museum, and most of the fossil specimens by the New Zealand Geological Survey. Also available from the Geological Survey, and of particular value, were several overseas specimens. The University of New Zealand Research Grants Committee gave financial assistance.

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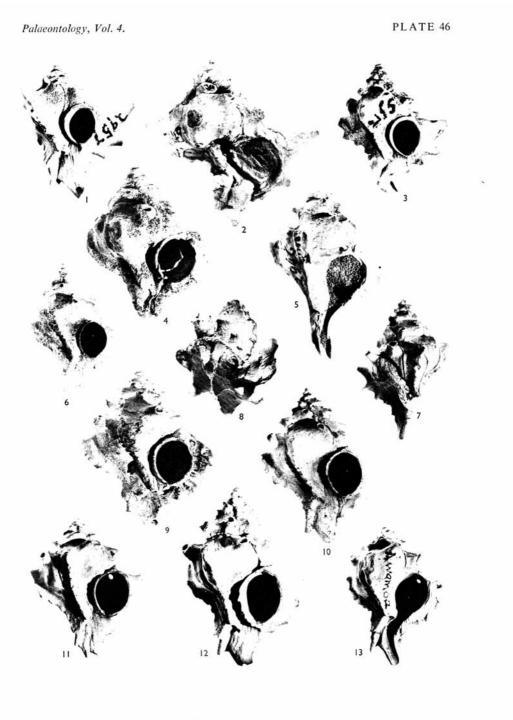
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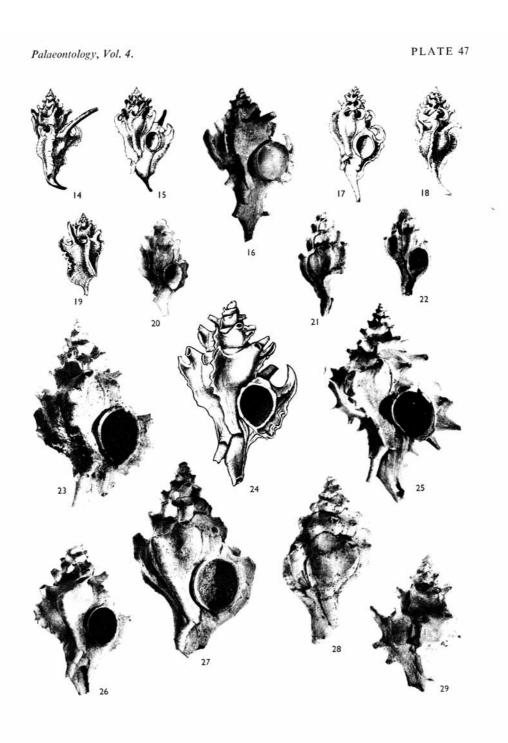
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Manuscript received 8 August 1960



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