AUSTRALASIAN TYPHINAE (GASTROPODA)
WITH NOTES ON THE SUBFAMILY

by PAUL VELLA

ABSTRACT. The Typhineae 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 palaeoecography, 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 species is another species of the west coast of South and Central America, Typhina and Siphonocheles both have closely related species living in Australia, New Zealand, the Indo-Pacific, the South Atlantic, and the Carribbean, 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 superspecies classification proposed by Keen (1944) is modified, her groups being redefined in terms of various types. The new genus Ragoptyphis and the new subgenus Neotyphis are described. The following genera and subgenera are recognized in Australia and New Zealand: Typhi (subgenera Typhi, Hirtotypyphis, Neotyphi), Ragoptyphis, Typhina (subgenus Typhina), Siphonocheles, Lyrotypyphis, Semityphis. A check list of Australasian 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 Typhineae were recognized in New Zealand, and all were described under the general name Typhi. Fourteen species have been described from Australia. Iredale recognized the genera Typhi, Typhina, and Siphonocheles. He erected the subgenus Chereotypyphis within Typhina but this has since been synonymized by Keen (1944) with Siphonocheles. Keen (1944, p. 56) allocated three New Zealand and six Australian species to Typhineilus. Typhineilus, however, is not recognized by the present writer, and the species placed in it by Keen are grouped below in Typhi, Typhina, and the new genus Ragoptyphis. The genera and subgenera Typhi, Hirtotypyphis, Neotyphi, Typhina, Ragoptyphis, and Siphonocheles occur in New Zealand, Typhi, Typhina, Siphonocheles, Lyrotypyphis, 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 Typhineae 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 Typhineae are used as evidence for Tertiary correlations or for faunal migrations. This is shown particularly well by the records of Hirtotypyphis from antipodal areas, but from no intermediate localities, and by the odd space-time distribution of Lyrotypyphis.

Ecology. Keen (1944, p. 51) noted that most Typhineae live in the neritic zone, almost all having been recorded from dredgings between 12 and 800 metres, averaging 50 metres.

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**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 silstones, 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 purpuris* and *Siphonocheles soles* are extremely rare and confined to the northern (Aupouriian) 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 differences from southern faunas, but they appear to be largely endemic with some relationships to New Zealand and European faunas. The Japanese fauna is essentially endemic.

*Siphonocheles* 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 *Siphonocheles* 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 *Indotrephes* 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, *Typhisoptes, Tilitrephus, Petrotyphus, Triptetriotrephus*.
2. Two tiny species from off the west coast of Africa, referred to the once widespread genus *Lutotrephes*, 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 Typhinella* and *Siphonotrephus*. *Typhina* and *Siphonotrephus* 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.

*Siphonotrephus* 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, *Siphonotrephus* has not been recorded as a fossil in America, and the Cuban species *Siphonotrephus longicornis* (Dall) must be regarded as a recent invader.

*The fossil record of Typhina* is very incomplete. *Typhina denata* (Johnson) from the Upper Eocene (Jackson) of the United States may not be a true Typhinae. The only reasonably certain fossil species are *T. laeviata* (Tate) and *T. disjuncta* (Tate) from the Lower Miocene (Bacarcan) of Australia, and *T. tetragnata* (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) eastward via the Equatorial Current in the Indian Ocean, around Cape of Good Hope, northward in the Benguela Current along the west coast of Africa, and finally north-westward in the Atlantic South Equatorial Current to Brazil (*Typhina*) and to Cuba (*Siphonotrephus*).

Fleming (1957, pp. 19-22) in a discussion of the genus *Peciea* suggested that Pleistocene cooling would prolong larval stages and account for the known Pleistocene migrations. Migrations of *Typhina* and *Siphonotrephus* 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) *Siphonochelis*, (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.
Typhonellia is represented by two living species, T. sowerbii (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. Typhonellia 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) tepangai 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.) tubifera (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 (Typhis) panperis (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) elfidensis sp. nov., T. (Hirtotyphis) aculeatus sp. nov., Rugotyphis franciscan (Finlay), and the Pliocene T. (Neotyphis) tepangai 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 elfidensis. 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 checklist 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 intervariecal 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, Siphonocheles, Laevityphis, and Tullityphis. 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. Haustiellothyphis 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. Typhinales 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 Typhis, 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 Typhinales and Typhis 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 eldredgensis in which the tubes are twisted upwards at an exceptionally high angle (c. 40°) from the horizontal. The backward deflection of the tubes is constant in Typhis s.s. and persists in the subgenus Hirtothyphis and Neothyphis. In Rougityphis, on the other hand, the tubes are nearly radial and confirm that this genus is divergent from Typhis. In Laevityphis, Siphonocheles, 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 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 Hirtityphis, Rugityphis, and Siphonocochus. 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 *Lyrotyphus* 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. *Siphonocheles* type: smooth and rounded, not crossing the shoulder to the previous whorl, but curving back at the top to coalesce with the intervaricular tube. It is misleading to describe the tubes of *Siphonocheles* 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. *Siphonocheles* has always been recognized by its distinctive varices. *Semityphis* with three growth steps per whorl, and *Lyrotyphus* with five growth steps per whorl, both have varices like those of *Siphonocheles*. As *Siphonocheles* has the fundamental 4-2 growth steps per whorl, it is considered to have evolved first, and *Lyrotyphus* and *Semityphis* are regarded as derivatives.

2. *Levityphis* type: rounded folds not crossing the shoulder, each surmounted on top by a single, vertical hollow conical spine. The intervaricular tubes are nearly vertical. In the subgenus *Indotyphus* 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 *Hiratyphus* 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 intervaricular 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 *Levityphis*. 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 *bivarcata*, and in the two living species of *Typhinellus*, part of the apertural rim is expanded to form a secondary varix. In *T. pangeris* 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 *Typhilia* the outer edge of each varix curls forward; in *Typhinellus* it curls backward.

5. *Rugotypis* type: intermediate between the *Tyrhis* type and the *Typhasis* type. It resembles the *Tyrhis* type in being broad at the base, fold-like and curved slightly but distinctly backwards. It resembles the *Typhasis* 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. *Typhasis* 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 *Typhasis* and *Tectyphila* each with 4-2 growth steps per whorl, and *Pterotypis* and *Tripterotypis* 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. *Siphonochelina* group: varices broadly rounded, fold-like, typically without spines, curving back at the top to coalesce with the tube.
   Genus *Siphonochelina*: 4-2 growth steps per whorl.
   *Lyctyphila*: 5 growth steps per whorl.
   *Sotnyphila*: 3 growth steps per whorl.

2. *Lucyphila* group: varices broadly rounded, fold-like, not crossing the shoulder, each surmounted on top by a single, nearly vertical spine.
   Genus *Lucyphila*: 4-2 growth steps per whorl.
   *Subgenus Lucyphila*: tubes nearly vertical.
   *Subgenus Induyphila*: tubes twisted forward and soldered to the base of the next varix (Keen 1944, p. 52).
   *Subgenus Pilhusyphila*: 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 spine; 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 Typhina*: outer edge of varix curling backwards; varix crossing without reduction in width from body to anterior canal; body whorl more or less regularly tapered.
4. *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; tube bent obliquely backwards, and upwards not more than 40° from horizontal.

   *Subgenus Hiratypus*: 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 tube nearly vertical; juvenile varices and tube 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. *Rosotyphis* 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 Rosotyphis*: 4-2 growth steps per whorl.

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

   *Genus Tylotyphis*: 4-2 growth steps per whorl.

*Subgenus Tylotyphis*: tubes connected to previous whorl by laminar buttresses.

*Subgenus Falsotyphis*: tubes free.

*Genus Prototyphis*: 3 growth steps per whorl.

*Subgenus Prototyphis*: tubes free.

*Subgenus Tripotyphis*: 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.

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

Genus Typhis Montfort 1810

Type species, by original designation, Pupura tubifer Bruguère 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) Bruguère’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. lebetatus 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) yatesi (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 dolatus 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, Typhinaelus, Haeastelotyphis, Talitryphis, 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,
represents the 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*, *Hirtotypus*, and *Neotypus* 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. maccovi* T.-Woods.

<table>
<thead>
<tr>
<th>Subgenera</th>
<th>HIRTOTYPUS</th>
<th>TYPHIS</th>
<th>NEOTYPHIS</th>
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<td><em>Ventricosior</em> E</td>
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**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 the new 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 *Hirtotypus horridus* (Broch) by Montanaro (1934, p. 10, pl. 1, fig. 1). On account of its greatly enlarged upper varical spine and obsolete lower spines the New Zealand Lower Miocene *Typhis* (Hirtotypus) *aceleatus* is thought to belong to the same lineage as *Hirtotypus aoteanaus* and *horridus*. *T. intermedius* also belongs to this group. These four species are grouped in *Hirtotypus* to emphasize this relationship but the earlier species *aceleatus* 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 *Hirtotypus* 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 *Neotypus*, on the other hand, has no European relatives, but it possibly has some representatives among Miocene and Pliocene American shells referred by Keen to *Laevotypus* (e.g. *L. linguisferus* (Dall)).

The double varices of the Australian Lower Miocene species *T. acanthopierus* Tate
are abnormal, but probably do not indicate a fundamental difference. A similar, though not parallel, modification is exhibited by some species of Typhinales and Typhina, particularly by Typhina (Typhina) bivariaticus (Verco).

Subgenus Hirtotyphis Jousseaume 1880
Type species, by original designation, Hirtotyphis horridus (Brocchi) = Mures 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 tepungai 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 Laevitrophyis; 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 Laevitrophyis. The neanic varices and tubes confirm this relationship.

Typhis linguisfera Dall, placed in Laevitrophyis 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. linguisfera also resembles Neotyphis and not Laevitrophyis 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. linguisfera is closer to Neotyphis than to Laevitrophyis and is tentatively included in Neotyphis.

Genus Laevitrophyis Cossmann 1903
Type species, by original designation, Typhis coronarius Deshayes 1865, Lower Eocene, France.

Laevitrophyis 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 neanie) whorls.

Laevitrophyis 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. costarcensis* was first described as a variety of *T. ligniferus* and may be a *Neotyphis*.

The East African Recent species *T. transversus* 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.

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

**Genus Rugotyphis** gen. nov.

Type species *Typhis franciscana* 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 contiguously 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 *Typhlopus*.

Two American species may belong to *Rugotyphis*, *Typhis harvisti* 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 *Typhinella*.

**Genus Typhina** Jousseaume 1880

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

*Typhina* and *Typhinella* 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) *Typhinella* 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. *Typhinella* 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 intervarical 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. bivirglicata* 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 varical 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 1833, 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. sowerbyi*. A shell from the Oligocene of Italy was described by Sacco (1904, p. 17, pl. 4, fig. 20) as *Typhis (Typhinellus) tetrapterus var. proteraster*us. 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 (Typhihs) 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 *Typhisocepis* group and probably needs a new generic name.

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

*Typhina* (*Typhina*) *becheri* (Broderip), Recent, West Africa
*Typhina* (*Typhina*) *bivirglicata* (Verco), Recent, South Australia
*Typhina* (*Typhina*) *elveri* (Patti), Recent, Brazil
*Typhina* (*Typhina*) *disjuncta* (Tate), Miocene, Australia
Typhnia (Typhnia) laciniata (Yate), Miocene, Australia
Typhnia (Typhnia) wouffordi (A. Ad.), Recent, Japan
Typhnia (Typhnia) nitens (Hinds), Recent, Straits of Macassar
Typhnia (Typhnia) pauperis (Mestayer), Recent, New Zealand
Typhnia (Typhnia) tetragonum (Cossmann), Pliocene, India
Typhnia (Typhnia) yuetsi (C. & F.), Recent, South Australia
Typhnia (Typhninella) quadrata (Hinds), Recent, Ecuador
Typhnia (Typhninella) sovayi (Broderip), Recent, Mediterranean
Typhnia (Typhninella) tetrapickest (Broth.), Pliocene, Italy
Typhnia (Typhninella) pterotyphus (Sacco), Oligocene, Italy

**Genus Typhnisops** Jousseaume 1880
Type species, by original designation, *Typhnis coronatus* Broderip 1833 = *T. granatis* A. Ad. 1855, Recent, Gulf of California.

**Subgenus Typhnisops s.s.**

**Subgenus Tali Typhnis** Jousseaume 1882
Type species, by original designation, *Typhnis 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 *Typhnisops* each tube is supported by a 'laminar remnant of former outer lip' (Keen 1944, p. 57), while in *Tali Typhnis* the tubes are free. In view of the variability in the development of the outer lip (secondary varix in *Typhninellus*, the validity of the distinction between *Typhnisops* and *Tali Typhnis* seems questionable.

Neither of these subgenera occurs in Australia or New Zealand.

**Genus Pterotyphnis** Jousseaume 1880
Type species, by original designation, *Typhnis planatus* Broderip 1833, Recent, locality unknown.

**Subgenus Pterotyphnis s.s.**

**Subgenus Tripterotyphnis** Pilch and Lowe 1932
Type species, by original designation, *Typhnis lutei Pilch* 1931, Recent, Panama.

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

*Pterotyphnis* and *Tripterotyphnis* are not known in Australia or New Zealand.

**Genus Siphonochelus** Jousseaume 1880
Type species, by original designation, *Typhnis avenatus*, misprint for *T. arenatus* 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
crosing the shoulder, more or less curved backward at the top and coalesced with the preceding tubes. Commonly an intervical axial fold is present just behind each tube.

Typical species (areatus, fistulosus, solus) have smooth, spineless varices. *Typhis parsiens* 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. parisienensis* may require a new generic or subgeneric name.

**Genus Lyrotypus** Joussseau 1880

Type species, by original designation, *Typhis cu vaculatus* Duchaté = *Murex cu vaculatus* 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 *Lyrotypus* as a subgenus of *Siphonochelus* and recognized only two species, *cu vaculatus* and *schlotheimii*, both from the Oligocene of Europe. To these must be added *Typhis* *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 intervical canal situated just behind each tube, the costules intermédiaires of Cossmann (1903, p. 62).

*Lyrotypus* 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 *cu vaculatus* 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 *Lyrotypus*.

**Genus Semityphus** Martin 1931

Type species, by monotypy, *Semityphus iuctus* Martin 1931, Upper Eocene, Java.

*Semityphus* 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*

*mucoyi* T-Woods. Oligocene (Janjukian), Australia

*advenus* sp. nov. Mid. Oligocene (Duntroonian-Waitukian), New Zealand
hebetatus Hutton. Upper Oligocene (Otaian), New Zealand
ocanthoperforatus Tate. Lower Miocene (Balkomian), Australia
plana sp. nov. Lower Miocene (Altonian), New Zealand
crassidens sp. nov. Lower Miocene (Altonian), New Zealand
n.sp. (unnamed) Mid. Miocene (Waiaitian), New Zealand
philippensis Watson. Recent, Australia
interpres Iredale. Recent, Australia
Subgenus Hirstophysis
aranilis sp. nov. Lower Miocene (Altonian), New Zealand
aoticus sp. nov. Upper Miocene (Tongaporutuan), New Zealand
Subgenus Neotyphis
teponui Fleming. Pliocene (Opoitian—Waiotaran), New Zealand
Genus Typhina
Subgenus Typhina
disjuncta (Tate). Lower Miocene (Balkomian), Australia
laevigata (Tate). Lower Miocene (Balkomian), Australia
bicornis (Verco). Recent, South Australia
vateri (C. & F.). Recent, South Australia
panoros (Mestayer). Recent, New Zealand
Genus Siphonochilus
evrgens (Tate). Lower Miocene (Balkomian), Australia
erugitatus Chapm. and Crespin. Pliocene (Kailman), Australia
generosus Iredale. Recent, New South Wales
pavlovo — pavlova Iredale. Recent, New South Wales
solus sp. nov. Recent, New Zealand
Genus Lyrotophis
syringius (Hodley). Recent, New South Wales, Tasmania
Genus Semityphsis
? Semityphsis 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 Typhina
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,
indeclined 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.


**Age.** Dunroonian to Waitakian (upper Lower to Middle Oligocene).

**Remarks.** *Typhis maccroyi* 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 maccroyi* Tenison-Woods; Suter, p. 28 (not *Typhis Maccroyi* Tenison-Woods 1878).
1924 *Typhis maccroyi* Tenison-Woods; Marwick, p. 328.
1926 *Typhis maccroyi* Tenison-Woods; Finlay, p. 427.
1944 *Typhis (Typhineolus) 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 spine varix; sutures high on spine whorls; body whorl strongly convex; surface ornamented with faint, irregular spiral ribs in line with the varicose spines, strongest on the backs of the varices.


**Repository.** Holotype, Otago Museum; Hypotypes, New Zealand Geological Survey.

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

**Age.** Otaian—Awamoaan (Upper Oligocene); Holotype: Awamoaan (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.

**Locality.** Holotype: G.S. 2945, Bed 6a (upper puri), 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 Awamoa of Riffle Butts, Oamaru, is represented by a single specimen in the collection of the Geology Department, Victoria University, Wellington.

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**Explanation of Plate 46**

Figure 7 × 3; all other figures × 2.

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

Figs. 2, 4. *Typhis (Hirtotyphis) aoteanus* sp. nov., holotype.

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

Fig. 5. *Rugotyphis franciscae* (Findlay) gen. nov., topotype.

Fig. 6. *Rugotyphis cf. franciscae* (Findlay) 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 77), Southland. 9, Holotype.

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.

Locality. G.S. 3839, Dovedale, North Canterbury.
Age. Waiaua (upper Middle Miocene).

Typhis (Typhis) maccouyi Tenison-Woods

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

1876 Typhis McCouyi Tenison-Woods, p. 22, pl. 1, fig. 5.
1888 Typhis McCouyi Tenison-Woods; Tate, p. 92.
1903 Typhis (Typhilina) maccouyi Tenison-Woods; Cossmann, p. 58, pl. 2, fig. 16.
1944 Typhis (Typhilina) maccouyi 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.
Locality. Holotype from Table Cape, Tasmania; specimens in New Zealand Geological Survey collection from Spring Creek, Torquay, Victoria.
Age. Janjuhian (Oligocene).

Remarks. The Spring Creek specimens seem stouter than Tenison-Woods’s illustration.

Several authors have regarded T. hebatus as a synonym of T. maccouyi, but T. hebatus is much stouter, with a shorter spire, smaller spines, and a more convex base. T. advenus sp. nov., closer to maccouyi, is easily distinguished by its still more elevated spire and more convex body whorl.

Subgenus HIRTOTYPHIS Jousseume

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.


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-Chilidian? (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. 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 (21½: 28; 17.


Age. Lower Tongaporutuan (base of Upper Miocene).

Remarks. An illustration by Colesmann (1903, pl. 2, fig. 24) of Hirtotyphis horridus (Broccoli), from the Pliocene of Italy, shows a smaller shell with similar low rounded varices. Colesmann notes the straightness of the spines. The shell from the Miocene of Hungary (Höners 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 tepungai* 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.


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

*Localities.* Holotype and paratype with intact protoconch, G.S. 2661, Taboraite Survey District, Southern Hawkes Bay; paratype, G.S. 2499, Taboraite Survey District; paratype, G.S. 2314, Takapau Survey District, Southern Hawkes Bay; Waitotaran (Upper Pleocene). Figured specimen (PL 47, fig. 28), G.S. 1561, Waiau River, 10 chains below Mangamone junction, Wairau Survey District, Northern Hawkes Bay, Opoitian (Lower Pleocene). Cliffs east of Whangaimoa, Palliser Bay, Southern Wairarapa, Kapite or basal Opoitian (uppermost Miocene or basal Pleocene).

*Age.* Kapitean to Waitotaran (uppermost Miocene to Upper Pleocene).

*Remarks.* The trivial name *tepungai* 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) eldisensis* 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 francisceae* (Finlay)

Plate 46, fig. 5

1924 *Typhis francisceae* Finlay, p. 465, pl. 49, figs. 6a, 6b.

1944 *Typhis (Typhinella) francisceae* 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.


*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.

*Rugotyphus 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, varicose spines extending down to the anterior canal which is shorter, very broad and flattened.


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

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

Age. Upper Altonian? to Liburnian? (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 (Typhinaeus) pauperis* Mestayer; Keen, pp. 56, 66.

Shell very small, moderately elongate, pagediform, thin and fragile, three and three-quarter 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, encrusted by three deep radial folds, each bearing a prominent trough-shaped spine curving gently inwards towards the spine and backwards; tubes straight, pointing slightly backward and upward; anterior canal narrow, slightly flattened, bent gently to right.

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

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

Localities. Holotype 38–60 fathoms off Poor Knights Island, paratype 25–30 fathoms off Hen and Chickens Islands, Hauraki Gulf. One specimen (M. 11067) 113–120 fathoms, off Myer Island, Bay of Plenty (same locality as *Siphonochelus solis*).

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)

1865 *Typhis yatesi* Crosse & Fischer, p. 54, pl. 2, fig. 3.
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. 294. 4b, 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 (Typhina) 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.


*Localities.* Holotype, Gulf of St. 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) bivariata* (Verco)

1909 *Typhis bivariata* Verco, p. 272, pl. 21, figs. 1–2.
1944 *Typhis (Typhina) bivariata* 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. bivariata* 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.

Age. Recent.

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 (Typhinae) zowerbyi (Broderip), photographs of illustrations of Reeve (1842, pl. 240), figs. 7-9, magnification not known.

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

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

Fig. 20. Typhina (Typhina) biventrica (Verco) co-type, 104 fathoms, off Neptune Islands, South Australia, ×7.

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

Fig. 22. Lyrosthyris syringiun (Hedley), Port Esperence, Tasmania, ×6.

Fig. 23. Typhus (Typhus) adventus sp. nov., holotype, ×3.

Fig. 24. Typhus (Typhus) pauperis (Meister), holotype, ×7.

Fig. 25. Typhus (Typhus) macrourus Tenison-Woods, Spring Creek, Victoria, ×3.

Fig. 26. Typhus (Typhus) eulophus sp. nov. holotype, ×3.

Figs. 27, 28. Typhus (Neothyris) tepungui Fleming subgen. nov.: 27, holotype ×3; 28, G.S. 1571 Wairoa, Northern Hawkes Bay, ×3.

Fig. 29. Typhus (Typhus) parvus (Solander), Barton, England, ×3.
PAUL VELLA: AUSTRALASIAN TYPHINAE (GASTROPODA) 389

Genus Lyrotyphys Jousseaume
Lyrotyphys syringanus (Hedley)
Plate 47, fig. 22; text-figs. 4 (3), 4 (4).

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

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

Dimensions. Hypotype: height 4.4 mm., maximum diameter 2.5 mm.


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

Age. Recent.

Acknowledgments. Specimens of Recent New Zealand shells were lent by the Dominion Museum, Wellington, the holotype of Typhis hebetatus Hatton 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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P. VELLA
Victoria University, Wellington,
New Zealand

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