

The Cenozoic Brachiopod *Terebratula*: its type species, neotype, and other included species

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SYNOPSIS. *Terebratula terebratula* (Linnaeus, 1758) has a long and complex history. The specimen now recognised as the type was first illustrated by Colonna in 1616, and the first use of '*Terebratula*' is attributed to Lhwyd, 1699. Colonna's specimen was refigured by Klein, 1753, and the species *Anomia terebratula* was described by Linnaeus, 1758, with reference to the Colonna and Klein illustrations. The genus *Terebratula* was proposed by Müller in 1776, and *Anomia terebratula* Linnaeus designated as the type species by Lamarck in 1799, although it was not an originally included species. In spite of this history, the type of the genus was never formally ratified, the whereabouts of the type specimen was unknown, and the age and exact position of the type locality was uncertain. This paper summarises the history of *Terebratula terebratula* (Linnaeus) from 1616. *Anomia terebratula* Linnaeus is now accepted as the type species of *Terebratula* (ICZN ruling, 2000). We have collected new material from a locality near Andria, Italy, from which Colonna collected specimens of *Terebratula*, and selected a neotype from the Calcarene di Gravina Formation which is Pliocene in age. Two existing species, *Terebratula sinuosa* (Brocchi) and *T. calabra* Seguenza, are placed in synonymy with *T. terebratula*. Three species are currently recognised in *Terebratula*, ranging in age from Miocene to Early Pleistocene when the genus became extinct, probably because of ocean cooling in the Mediterranean region.

INTRODUCTION

The brachiopod genus *Terebratula* has a long and complex geological and nomenclatural history. The nominal genus *Terebratula* was proposed by Müller in 1776, and as pointed out by Muir-Wood (1955), it 'is the first valid post-Linnean brachiopod genus'. *Terebratula terebratula* (Linnaeus) is the name-bearer for the Order Terebratulida which encompasses loop-bearing brachiopods of Devonian – Recent age and includes most brachiopods living today.

The name *Terebratula* has been widely used for over 200 years: more than 850 specific names were applied to the genus between 1800–1850 alone (Sherborn, 1932). In spite of the ubiquity of the name, the genus and species on which it was originally based have, until recently, been little studied and many basic questions about *Terebratula terebratula* remained unanswered. As pointed out nearly a century ago (Buckman, 1907), not only was the type species of the genus unconfirmed, but its type locality and age were uncertain.

The present study had several aims. The first objective was to ratify the type of the genus *Terebratula* for inclusion in the revised Brachiopod *Treatise*, following the recommendation made by Muir-Wood in the 1965 *Treatise* volume on the Order Terebratulida. Secondly, we wished to summarise the complex nomenclatural history of the genus and species, *Terebratula terebratula*, since it was first illustrated and described in 1616. The third aim was to locate the type specimen and/or type locality of *T. terebratula*, or, if this proved impossible, select a neotype to act as namebearer for the order. Finally, we wished to describe the age and relationships of species currently included in *Terebratula*.

The first objective was achieved with an application to the International Commission on Zoological Nomenclature to validate the selection of *Anomia terebratula* Linnaeus as type-species of the

genus *Terebratula* as designated by Lamarck in 1799 (Lee & Brunton, 1998; Ruling of the Commission, September 2000). The remaining objectives are achieved in this paper.

DERIVATION OF THE NAME

The name *Terebratula* was first used in print by Lhwyd (1699) (Little *et al.*, 1973), and is the oldest generic name in the Phylum Brachiopoda in current use. *Terebratula* is 'so-called from the perforated beak of the ventral valve' (Little *et al.*, 1973: 2265), and is a quasi-diminutive of Latin *terebratus*, the past participle of *terebrare* 'to bore'. The brachiopods listed as *Terebratula* in Lhwyd's catalogue of shells in the collections of the Ashmolean Museum, Oxford, were 'poorly figured specimens from Witney' (Muir-Wood, 1955: 2). The name came into fairly common use in the 18th century, and some of the numerous brachiopods referred to as *Terebratula* by other pre-Linnean authors were mentioned by Muir-Wood (1955).

The species name *terebratula* was first used in a valid binomial by Linnaeus in his description of *Anomia terebratula* in *Systema Naturae* (1758: 703). Linnaeus gave no illustration, but referred to figures in Colonna (1616c), Lister (1678) and Klein (1753). The Colonna, and Colonna/Klein, illustrations are reproduced in Figs 1, 2.

THE COLONNA ILLUSTRATION OF *TEREBRATULA* (FIG. 1)

Fabio Colonna (1567–1650) (Fabius Columna) was born in Naples and was one of the first natural historians to use copper plates for engraving botanical and zoological figures. He wrote extensively on

22

Fabij Columna

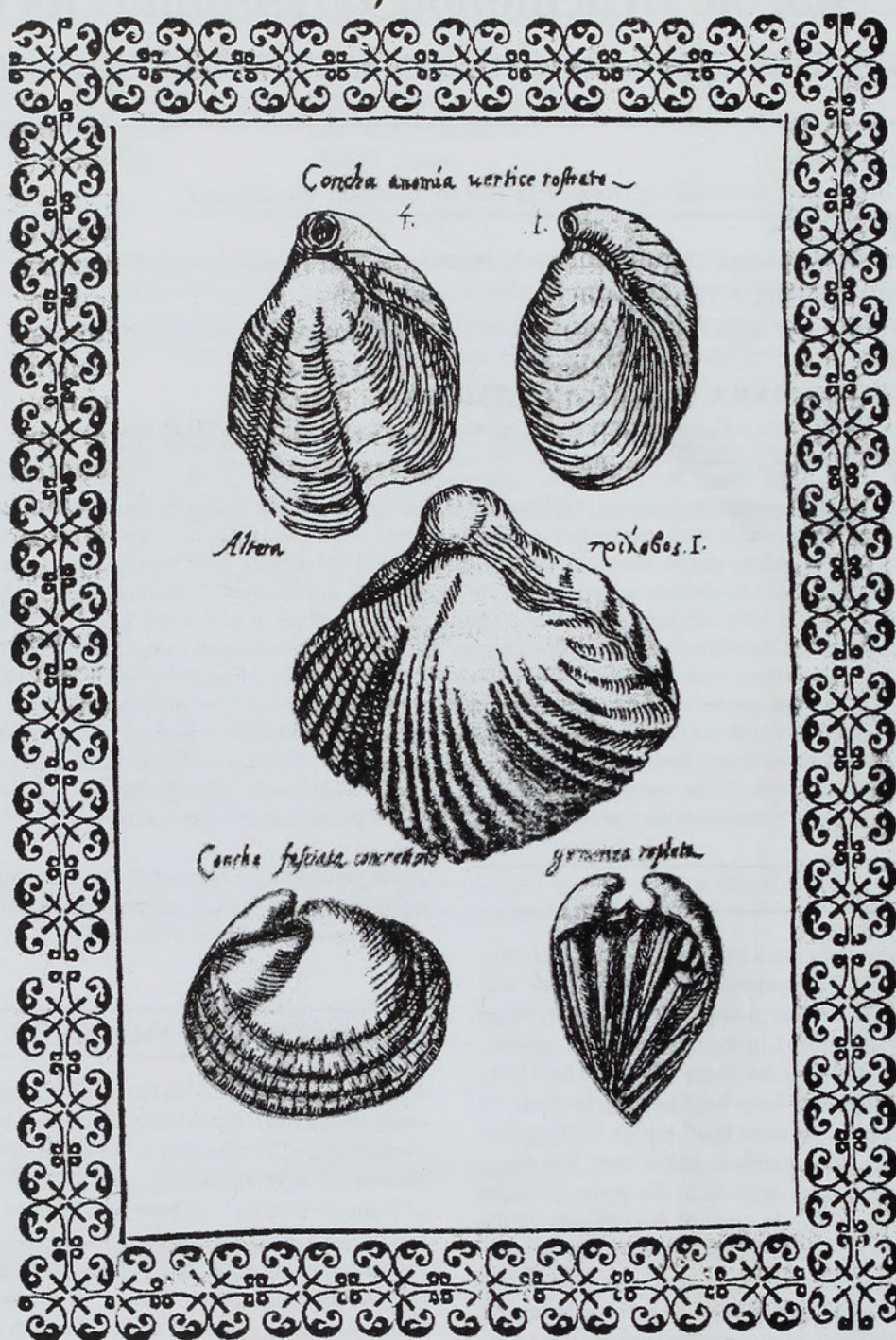


Fig. 1 Reproduction of page 22 in *Purpura* (Colonna, 1616).

fossils, and 'was one of the first to place them . . . in a primarily biological context . . . Colonna also applied the same precise nomenclature to his fossils as to his living animals, distinguishing different kinds of related fossils with more accuracy than ever before' (Rudwick, 1985: 42).

Colonna was a member of the Accademia dei Lincei (Academy of Lynxes), and in 1606, he published a work on natural history: *Minus cognitarum stirpium aliquot, ac etiam rariorum nostro coelo orientium [ecphrasis] . . . De aquatilibus, aliisque animalibus quibusdam paucis libellus [plants pp.3–340; animals I–LXXIII]*. A new edition was published in 1616 (Colonna, 1616a–c), including part III, *Purpura* (of which *De purpura, aliisque testaceis rarioribus*,

pp. 1–29, and *De glossopetris dissertatio*, pp. 31–39, are two chapters), in which he described and figured a number of shells, some fossil and some living. His illustration on page 22 (Fig. 1 herein) was a woodcut of five shells. The upper three specimens are double-valved brachiopods, while the lower specimens are internal molds of bivalves. The plate is not numbered, and the five specimens are distinguished by brief captions placed above each specimen.

Linnaeus (1758: 703) made three separate references to the illustrations of brachiopods on this plate in his discussion of species of *Anomia*. Under *Caputserpentis*. 200., he gave a brief description, and referred to Column. purp. 22. f.2, i.e. the smooth brachiopod on the upper right. Brunton & Cocks (1967) discussed in detail the

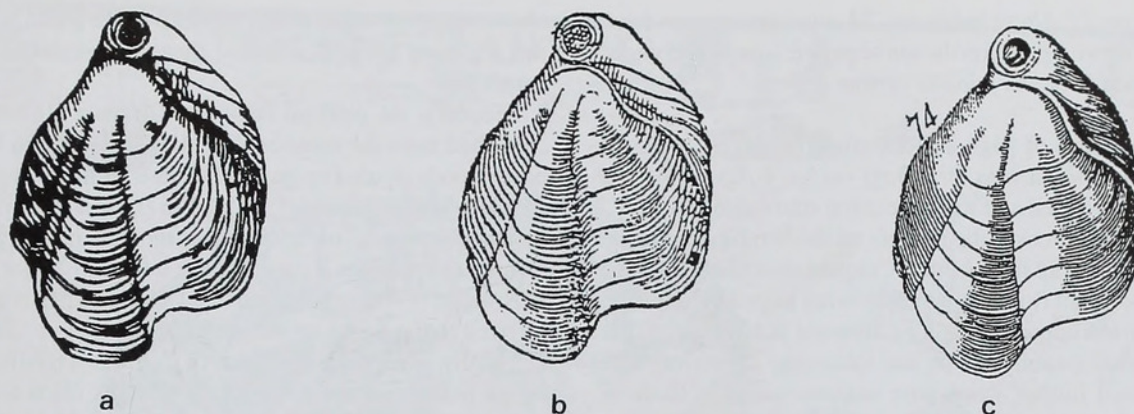


Fig. 2 Figures of *Concha anomia*, the holotype of *Anomia terebratula*. **2a**, woodcut from Colonna (1616); **2b**, woodcut from Major (1675); **2c**, engraving from Klein (1753).

ambiguities which arose when Linnaeus (1767) changed his description of *A. caputserpentis* from a smooth, fossil brachiopod to a capillate living species (now *Terebratulina retusa*), although he retained the reference to the Colonna figure. An application to the International Commission on Zoological Nomenclature to change the type species of *Terebratulina* d'Orbigny, 1847 from *Anomia caputserpentis* Linnaeus, 1758, to *Anomia retusa* Linnaeus, 1758, disposed of the ambiguity caused by Linnaeus himself when he altered his definition of *A. caputserpentis* between 1758 and 1767 (Brunton & Cocks (1967: 295); Ruling of the Commission, 1968).

Under *Terebratula*. 201., Linnaeus listed three separate illustrations. The first, 'Column. purp. 22. f. 1', refers to the upper left figure of a smooth, strongly folded brachiopod. The second refers to 'List. angl. 240. t. 8. f. 46', which is a non-plicate Jurassic shell from England (Lister, 1678). The third reference, which confirms that Linnaeus did indeed intend the upper left brachiopod to be the type of *terebratula*, is unmistakably the same (redrawn) Colonna illustration reproduced in a figure by Klein (1753) (Fig. 2 herein). Buckman (1907: 528) pointed out that Lister's figure did not match the description given by Linnaeus, and that the Colonna-Klein figure 'must be taken as the holotype, which, in fact, has been the usual practice'.

Linnaeus included the central figure in Colonna's plate in his '*Hysterita*. 203. Mus. Tess. 90. t. 5. f. 1, 2, 2. Column. purp. 22. f. 3? Trilobos.' This large, strongly ribbed and folded fossil rhynchonellid does not correspond to the Mus. Tess. illustration listed by Linnaeus, which is an internal mold of *Schizophoria* (Brunton *et al.*, 1967).

The two upper brachiopods in the Colonna figure are both smooth terebratulid brachiopods with large open foramina and strongly delineated growth bands. Across both drawings is the caption: '*Concha anomia vertice rostrato*', and beneath the left figure, although probably relating to the central brachiopod on the plate, is the word *Altera* (another). On the adjacent page 23, in *Purpura*, the chapter is headed *Concha rarior Anomia vertice rostrato*. I. Cap. XII (or 'rare *Anomia* shell with apical beak'). Although there is no scale on the illustration, the brachiopod on the upper right is at natural size (*icon magnitudinem aequat* on page 23 in *Purpura*).

CONCHA ANOMIA VERTICE ROSTRATO

Some of the problems which have made it difficult for earlier and present authors to define *Terebratula* arise from the lack of correspondence between the figures on page 22 of Colonna, and the text

on the following pages. In particular, several specimens mentioned on pages 23–24 are not illustrated at all, although they were numbered sequentially by the author.

Thus, Lee & Brunton (1998) assumed that the strongly folded figure on the upper left on page 22 was that described in the text on the facing page (Cap. XII) under the heading '*Concha rarior Anomia vertice rostrato*', and accordingly they concluded that this specimen was that collected by Colonna from Andria. More recently, we have found that this might not be correct. In five original copies of Colonna's *Purpura* (1616c) held by the University of Naples 'Federico II' (two in the Library, and three in the Department of Biologia Vegetale and the Botanical Garden) and in another original copy held in the Botany Library of the Natural History Museum, London, the two figures at the top of page 22 are marked with '4' (upper left), and 'I' (upper right). These small numbers are not shown in the two published reproductions of Colonna's plate (Dollfus & Dautzenberg, 1932; Muir-Wood, 1955), nor in the 1675 edition of Colonna's *Purpura* edited by Major.

The following section attempts to clarify the problems we have encountered.

- Colonna described four *Conchae* in the text on pages 23–24 and marked them with a Roman or Arabic notation. Of these, only the first (I) and the fourth (4) are figured on page 22. The four *Conchae* are:
 - Concha rarior Anomia vertice rostrato*. I. Cap. XII ('I' on page 22 and 'I' on page 23). The description of 'I' corresponds to figure 'I' (page 22, top right).
 - minor 2* ('2' at the edge of the margin of line 29 on page 23). This specimen is not figured by Colonna.
 - Altera Neptunia maior III. imbricata*. Cap. XIII ('III' on page 24). This specimen is not figured by Colonna.
 - Concha Anomia IV. margine undosa*. Cap. XIV. ('4' on page 22 and 'IV' of page 24). The description of 'IV' corresponds to figure '4' (page 22, top left).
- The first shell, (that is the smooth, unfolded specimen on the upper right on page 22) comes from Andria. The third comes from Nettuno (50 km south of Rome). The second and the fourth come from the Museum of Ferrante Imperato in Naples and their provenance is not given.
- Colonna thought the four *Conchae* (ie., the figured and unfigured specimens described on pp. 23–24) were similar to each other. Indeed, in the index on p. 41 three of these are included under a single name '*Concha anomia quae, rarior vertice rostrato* Plin.

descript. 23. icon. 22. *Altera imbricata*. 24. *altera margine undosa*, *ibid.* & 25'. The two figures on the top of page 22 are joined under the same caption '*Concha anomia vertice rostrato*'.

The figure in the centre of page 22, described on pages 24–25 as '*Concha altera Anomia striata [trilobos] rarior*. I. Cap. XV', is considered as another shell and its numeration starts again from 'I'.

Much of the confusion over the identity of the two figures on the top of page 22 stems from the fact that Colonna described the shell placed on the upper right first, and on a following page discussed the shell portrayed on the upper left, using a different practice from that which became well established in the following centuries. The confusion increased further when later authors assigned to these figures two numbers that Colonna had never employed. Thus Linnaeus (1758), following modern convention, designated the strongly folded specimen on the upper left as f. 1 (ie., figure 1) and that on the upper right as f. 2 (ie., figure 2). Brocchi (1814), and the present authors, until lately, have done the same.

The problem of deducing which shell description accompanied which illustration was compounded in a second edition of Colonna's work, with the associated text from the earlier edition subdivided into numbered paragraphs, which was reprinted posthumously in 1675 by J.D. Major. In this edition, the redrawn figure of the strongly folded specimen from the upper left of page 22 in the 1616 edition (i.e. *Anomia terebratula* of Linnaeus) appeared on page 32 within the text referring to the Andria locality. Similarly, in the *Dictionarium* this figure was noted by Major as that described in Cap. 12, of Colonna (1616c: 23).

A comparison of the three figures (Fig. 2 herein) shows that the Klein figure listed by Linnaeus (Klein, 1753; Tab. Nostra XI. n. 74), was redrawn from this later edition (Major, 1675) (Fab. Columnae de Purp. Cap. XII §.3. pag. 32 [Klein 1753, p. 171–2]).

Dollfus & Dautzenberg (1932) correctly interpreted the references to Major's figures, but added to the confusion, by giving the same citation for both the upper right and upper left figures: ie. 'p. 22, fig.1 (2e)'. These authors also assumed that the caption '*Altera*' pertained to the upper left figure, whereas it undoubtedly refers to the figure in the center ('*Altera [trilobos]*'), because the captions in all seven figures in Colonna's *Purpura* (pp. 13, 16, 20, 22, 27, 30, 33) are placed over, and never under, the relevant figures.

DISCUSSION AND COMMENTS

This discovery, as our manuscript was almost ready for submission and after the ICZN had approved the selection of a neotype for *Terebratula terebratula* (Linnaeus), raises some issues which need further discussion. If indeed the provenance of the specimen selected by Linnaeus as the type of *Anomia terebratula* is unknown and the specimen is lost, then the basis for the species, and consequently the genus, family and superfamily would remain uncertain.

However, since Lee & Brunton (1998) have already nominated a neotype from Colonna's locality near Andria, the neotype locality now becomes the type locality for the species, regardless of the locality of the original Colonna brachiopod (International Code of Zoological Nomenclature Article 75f).

Is it possible then to determine the provenance of the original specimen of Colonna selected by Linnaeus as the type of *Anomia terebratula*?

Firstly, it is obvious that Colonna's caption: '*Concha anomia vertice rostrato*' applies to both of the brachiopods figured on the upper right and upper left of page 22, the first of which (that on the

upper right) certainly came from Pliocene strata near Andria, and that Colonna himself regarded these specimens as similar to one another.

Secondly, six original copies of Colonna (1616c) that we have consulted have the numbers: 'I', '4' and 'I' written beside the three brachiopods figured on page 22. These numbers are not included in Major's edition. Linnaeus (1758, 1767) and Brocchi (1814), if aware of these numbers, used different, modern numbering (i.e. f.1 for Colonna's specimen 4 on the upper left), and Major (1675) and Lee & Brunton (1998) considered that Colonna's description on page 23 referred to the figure on the upper left.

Thirdly, even if the specimen of Colonna's (1616c: 22) upper left figure is from an unknown locality, it was filled with white, loose sediment (Colonna, 1616c: 24), and it is possible that it was collected from the same Pliocene calcarenites at Andria.

From a close examination of the Colonna woodcut, it seems likely that his specimen was somewhat deformed. It has a large, open foramen, and two strongly developed plicae/folds on the dorsal valve that begin at an early stage of growth, and would have resulted in a strong sulcification (*margine undosa*) of the anterior commissure. The artist (?Colonna himself) may have exaggerated the depth of the folds, although the depiction of the other brachiopods on the plate seem to be faithful to reality. No undeformed specimens collected by the authors have folds as strongly developed as those depicted in the woodcut.

From the many specimens of *Terebratula* collected by the authors from Colonna's Andria locality and from elsewhere in Italy, it is apparent that the brachiopods in any fossil assemblage/population vary considerably in the degree of folding and may be rectimarginate to biplicate or sulcificate. Thus, both specimens labelled by Colonna as *Concha anomia vertice rostrato* are species of *Terebratula* (*sensu lato*), and given the wide variation in populations of Neogene *Terebratula*, might be conspecific. Certainly, the specimens of *Terebratula terebratula* figured by us in this paper (Figs 6–9) fall somewhere in the middle of the two short-looped brachiopods illustrated in Colonna's woodcut. The specimen of Pliocene *Terebratula terebratula* from Monte Mario selected and figured by Buckman (1907) and illustrated in the 1965 *Treatise*, is crushed and deformed in a similar manner. In the Natural History Museum, London, there are several collections of *Terebratula* from this same horizon at Monte Mario, near Rome. These specimens, which are almost certainly conspecific, vary from small rectimarginate (juvenile) specimens (labelled *T. depressa*) to large rectimarginate individuals (named *T. grandis*), to examples with moderate sulcification (labelled *T. ampulla* or *T. terebratula*).

Thus, our selection of a neotype from a locality described and collected by Colonna closely follows the recommendations of the Code.

It should be noted that Muir-Wood's (1955: fig. 2) caption for her reproduction of the original Colonna figure is misleading. The caption reads 'Reproduction of early drawings of Brachiopods figured as '*Concha anomia*', and taken from Fabio Colonna's first edition of *de Purpura*, 1616, p. 22. The first figure is of a specimen from Mte. Mario, near Rome, and is probably of Tertiary (?Pliocene) age; the other two figures may represent Jurassic forms'. However, as shown here, the first figure is from an unknown locality, while the second specimen is of Pliocene age and came from near Andria, not Rome.

TYPE LOCALITY OF *TEREBRATULA* *TEREBRATULA*

Colonna (1616c: 23) described the locality from which he collected his specimen of *Terebratula* shown on the top right of his figure

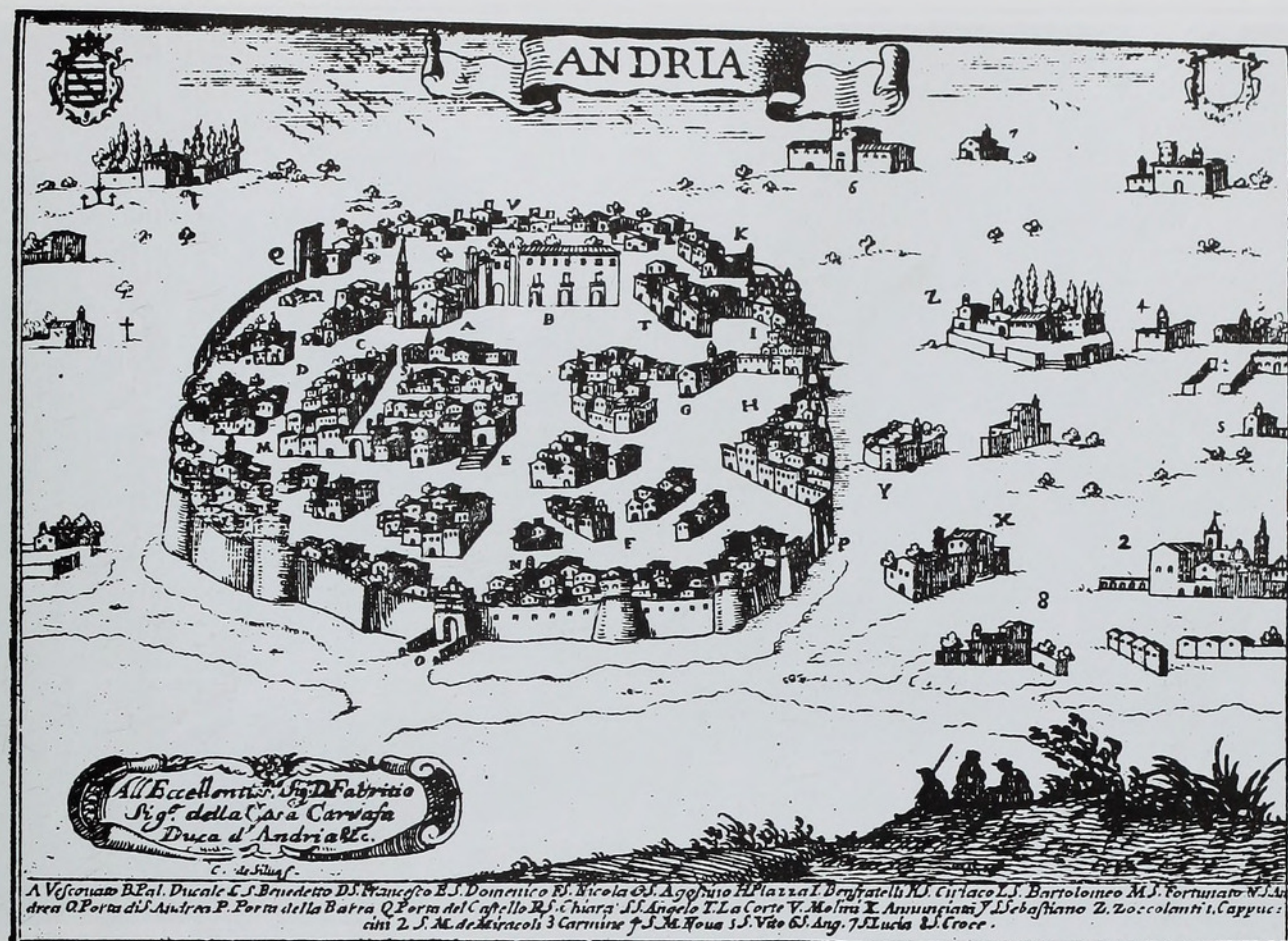


Fig. 3 Reproduction of Pacichelli's late 17th century map of Andria. North is at the bottom of the figure, and the church of Santa Maria dei Miracoli (2 in the key) is west of the city near the right hand edge of the map.

(Colonna, 1616: 22) as follows: 'We found this shell full of the white sediment [tophacea concretion] on which that whole sloping area or hill is made. This is constituted not so much of loose sediments, as of fragments of various shells and unbroken shells too. We collected this one and others in the small valley or ditch a little below the Church of D. Maria de Andria, which is situated one mile outside the city' (see the Appendix for a translation of Colonna's pp. 23 and 24).

In the modern town of Andria the names of five churches include the word 'Maria', and to find which of them was the one referred to by Colonna it was necessary to consult Pacichelli's late seventeenth century map of Andria (Fig. 3). The churches of Santa Maria Nova (4 on Fig. 3) and Santa Maria dei Miracoli (2 on Fig. 3) are both situated outside the town to the west (west is on the right hand side of Fig. 3), but only the latter church is built directly on the 'tophacea concretion' (= Calcarenite di Gravina Formation). On either side of a small natural valley (now dry) adjacent to the church of Santa Maria dei Miracoli 1–3m high cliffs of white, well-cemented calcarenite outcrop sporadically (Fig. 4), and specimens of *Terebratula* are scattered throughout the calcarenite showing that this locality is undoubtedly the one visited by Colonna. The brachiopods are not uncommon, but are often fragile and/or broken.

The basement rocks of the region around Andria are Lower Cretaceous in age. Overlying these with angular unconformity are 25 to 30m of coarse-grained highly fossiliferous marine biocalcarenes and calcirudites of the Calcarenite di Gravina Formation which is widespread in this area. In the vicinity of the Madonna d'Andria church, the sequence consists of 2m of fine, bioturbated, massive calcarenites lacking macrofossils. Above this is a coarse, bioturbated calcarenite up to 4m thick which includes

oysters, scattered pectinids, echinoids and brachiopods (Fig. 5). The upper 2m thick bed is a well-cemented, very fossiliferous calcarenite with a discontinuous oyster bed near its base. Fossils include *Ostrea*, *Chlamys*, internal moulds of bivalves such as Veneridae, echinoids, calcareous algae and brachiopods.

On macrofossil (Caldara, 1987; Caldara & Gissi, 1993) and microfossil (Taddei Ruggiero, 1996) evidence, the lower part of the Calcarenite di Gravina Formation is locally Middle to Upper Pliocene, or possibly Upper Pliocene to Lower Pleistocene in age. No trace of a cool-temperature Pleistocene macrofossil fauna was found during our visit.

Thus, the type locality for the neotype of *Terebratula terebratula* (Linnaeus) is adjacent to the church of Santa Maria dei Miracoli, about 2 km west of Andria, Puglia, Italy in the Calcarenite di Gravina Formation, of Upper Pliocene age. The specimen selected as neotype comes from beneath a small overhang about 200 m north of the church. The outcrops are difficult to access, and involve crossing private property.

SYSTEMATIC DESCRIPTIONS

Order **TEREBRATULIDA** Moore, 1952

Superfamily **TEREBRATULOIDEA** Schuchert, 1913

Family **TEREBRATULIDAE** Gray, 1840

DIAGNOSIS. Medium to large, ventribiconvex, rectimarginate to uniplicate or biplicate, rarely unisulcate or sulcificate, smooth or



Fig. 4 Outcrops of the Calcarene di Gravina Formation, from which the neotype was collected, in the small valley north of the church.

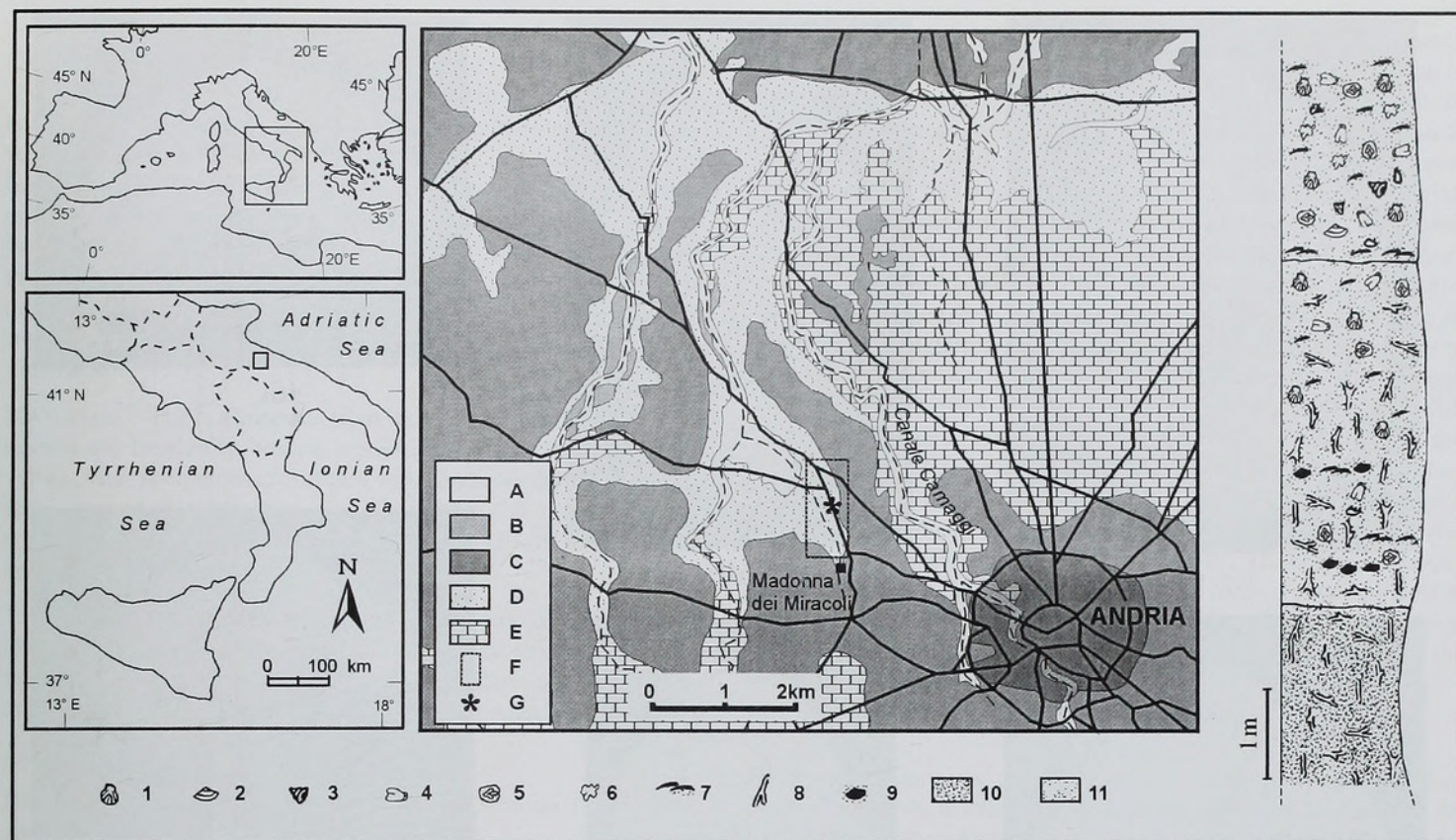


Fig. 5 Location map, geological map and stratigraphic column for the Andria region, Puglia, Italy. **A**, alluvial deposits (Holocene); **B**, terraced alluvial deposits (Pleistocene); **C**, terraced marine deposits (Pleistocene); **D**, Calcarene di Gravina Formation (Upper Pliocene); **E**, Calcare di Bari Formation (Lower Cretaceous); **F**, Colonna's locality; **G**, outcrop from which the neotype of *Terebratula* was collected (see stratigraphic column). 1, Pectinidae; 2, Veneridae; 3, gastropods; 4, brachiopods; 5, echinoids; 6, calcareous algae; 7, oysters; 8, bioturbations; 9, mud pebbles; 10, fine calcarenite; 11, coarse calcarenite.

with fine radial capillae; loop short, triangular; outer hinge plates usually concave or flat, commonly attached to dorsal edge of crural base, inner hinge plates rarely developed.

Subfamily **TEREBRATULINAE** Gray, 1840
Genus **TEREBRATULA** Müller, 1776: 249

DIAGNOSIS. Medium to large, subpentagonal to broadly oval, smooth; anterior commissure rectimarginate to uniplicate or sulcinate; beak short, erect; foramen large, symphytium partly visible. Pedicle collar short; cardinal process flat and semielliptical to a thickened boss; outer hinge plates narrow or lacking; crural processes may be long; loop short, broadly triangular; transverse band narrow, forming a low arch.

TYPE SPECIES. *Anomia terebratula* Linnaeus, 1758, by the subsequent designation of Lamarck (1799: 89).

GEOGRAPHIC RANGE. Italy, Sicily, Malta, Spain, Algeria.

STRATIGRAPHIC RANGE. Miocene – Early Pleistocene.

REMARKS. The great majority of the thousand or more specific names attributed to *Terebratula* have long been accommodated in other genera. However, although *T. terebratula* is the oldest available name for the medium to large, smooth, short-looped Miocene – Pleistocene terebratulids from Italy and the circum-Mediterranean region, it has rarely been used in the literature or in identification of specimens for the reasons outlined above. This is due mainly to the

uncertainties surrounding the identity, age and type locality of the Colonna specimen. The Colonna work is rare, and no translation has hitherto been available. Secondly, there was doubt as to the correct type species for the genus.

Gaetani & Sacca (1985), in a paper dealing with systematics and shell structure of brachiopods of Miocene – Pleistocene age from southern Italy, commented on the problem of recognising *T. terebratula*. They concluded that there were two valid species: *Terebratula sinuosa* (Brocchi) and *T. calabra* Seguenza which were restricted to the Upper Miocene and Pliocene respectively. Cooper (1983) identified large sulcinate specimens of Pliocene age from Monte Mario, Rome, as *T. ampulla*. Other authors (Taddei Ruggiero, 1986, 1990, 1994, 1996) have identified large, shellbed-forming Pleistocene specimens as *T. scillae* Seguenza. Until variation within large populations of the species placed in *Terebratula* has been studied, we are able to recognise only three valid species of *Terebratula* – *T. terebratula* (Linnaeus, 1758), *T. ampulla* (Brocchi, 1814) and *T. scillae* Seguenza, 1871.

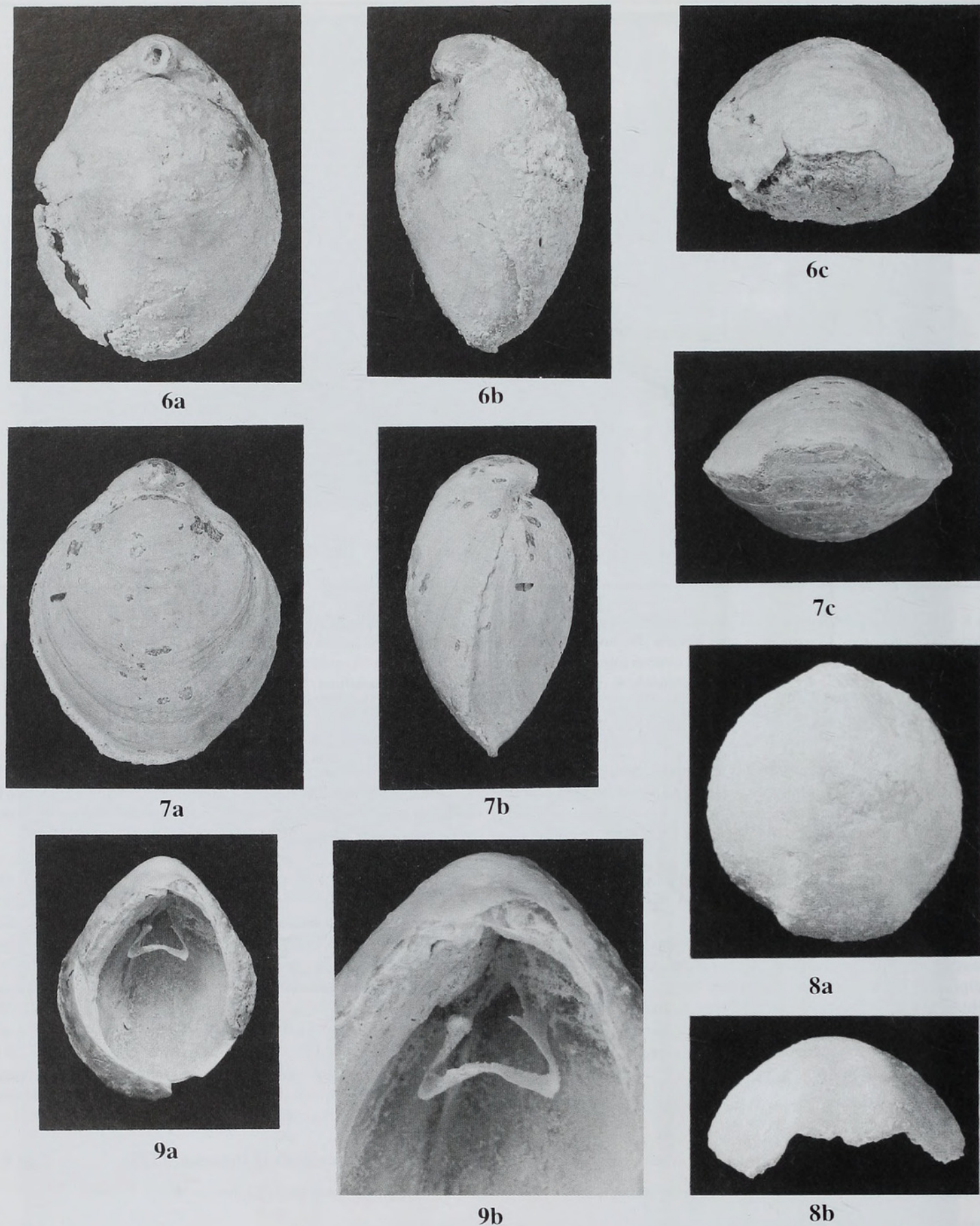
***Terebratula terebratula* (Linnaeus, 1758)**

Figs 6–9

1758 *Anomia terebratula* Linnaeus: 703.

SYNONYMS

1. *Anomia sinuosa* Brocchi, 1814: 468, is an objective synonym because Brocchi gave no figure, but referred to 'Column. 22, f.1', which is the holotype of *Anomia terebratula*.
2. *Terebratula calabra* Seguenza, 1871: 64
3. *Terebratula costae* Seguenza, 1871: 67; Taddei Ruggiero, 1994: 206.



Figs 6–9 Neotype and 3 topotypes of *Terebratulina terebratulula* (Linnaeus) from a Colonna locality at Madonna dei Miracoli, Andria, Italy. **6a–c**, dorsal, lateral and anterior views of neotype, NHM BG152 (length 55.4mm); **7a–c**, dorsal, ventral and anterior views of toptype, NHM BG194 (length 50.8mm); **8a, b**, ventral and anterior views of toptype, NHM BG195, showing M-shaped anterior commissure; **9a, b**, ventral views of loop of toptype, NHM BG196. All figures natural size, except Fig. 9b.

TYPE SPECIMENS. The holotype, the specimen figured by Colonna (1616c), is lost. We here nominate as neotype (Fig. 6a–c), an entire specimen from the Calcarene di Gravina Formation near a locality collected by Colonna, in the collection of the Natural History Museum, London (BMNH BG152), collected 22 March 1998 by M. Caldara & O. Simone. Dimensions of the neotype are: length 55.4 mm, width 43 mm, thickness 30 mm. A well-preserved complete topotype with the dimensions: length 50.8 mm, width 42 mm, thickness 28 mm, is also figured (Figs 7a–c). Two further topotypes, one with a complete loop (Figs 9a, b), and a dorsal valve with a strongly-M-shaped anterior commissure (Figs 8a, b) are also illustrated.

MATERIAL. The brachiopods from the Calcarene di Gravina Formation are frequently broken across mid-valve, or are separated valves. Most specimens are infilled with coarse, white, hard, moderately cemented calcarenite, and few have a complete anterior commissure. A number of topotypes (BG153–161, BG194–196) are held in The Natural History Museum, London.

TYPE LOCALITY. The type locality is an outcrop of Calcarene di Gravina Formation, of Pliocene age, on the east side of a small dry valley, about 200 m north of the church of Madonna dei Miracoli (41°13'52"N; 16°16'00"E), about 2 km west of Andria, Puglia, Italy.

AGE. Late Miocene (Tortonian), Pliocene.

DISTRIBUTION. Puglia, Calabria, Tuscany, Emilia (Piacentino), Abruzzi, Spain (Alicante).

DESCRIPTION. Shell of medium to large size, biconvex, anterior commissure rectimarginate, uniplicate to sulcinate, two broad plicae may be developed; beak short, massive, suberect; foramen large, mesothyrid to permesothyrid; symphytium narrow, partly concealed. Pedicle collar short; hinge teeth with moderately swollen bases. Cardinal process semielliptical, moderately protuberant; outer hinge plates narrow; no inner hinge plates; crural bases fused to socket ridges to form a deep V-shaped trough, crural processes long; loop broadly triangular, about 0.3 valve length, transverse band narrow, forming medially flattened low arch.

Terebratula ampulla (Brocchi, 1814)

1814 *Anomia ampulla* Brocchi: 466

AGE. Pliocene.

DISTRIBUTION. Italy (Emilia (Piacentino), Tuscany, from Brocchi's list), but not Calabria (see Seguenza, 1871).

COMMENTS. A medium-sized, strongly bisulcate species.

Terebratula scillae Seguenza, 1871

1871 *Terebratula scillae* Seguenza: 39

AGE. Early Pleistocene.

DISTRIBUTION. Calabria, Puglia, Sicily.

COMMENTS. The largest species of *Terebratula* (up to 95 mm in length), which formed extensive shellbeds in the Early Pleistocene.

ECOLOGY AND EXTINCTION OF *TEREBRATULA*

Terebratula grandis Blumenbach, 1803, now included in the genus *Pliothyridina* (see Cooper, 1983), may be the ancestor of *Terebratula*

sensu stricto. This large species from the Oligocene of Germany needs further study. *Pliothyridina* appears to have been widespread in northern Europe and England (see collections in the Natural History Museum, London), whereas *Terebratula* was abundant in the Mediterranean region. Both groups became extinct in the Plio-Pleistocene.

Terebratula was widely distributed in the Mediterranean region from the Miocene until the early Pleistocene. It lived in circalittoral environments on muddy, biotrital seafloors, attached to substrates which included bivalves and other brachiopods. During the Messinian, when the Mediterranean basin became too saline to support normal marine life, the brachiopod fauna disappeared from the region. With flooding of the Atlantic sea into the Mediterranean basin, the Mediterranean was recolonised by a brachiopod biota with Atlantic affinities (Logan, 1979). This does not account for the reappearance of *Terebratula*, which may have survived in refugia.

In the Pliocene, *Terebratula* was an important component of a widespread brachiopod fauna which included *Aphelesia* and *Megerlia* (Gaetani, 1986; Taddei Ruggiero, 1994, 1995). The youngest records are of very large *Terebratula scillae* which formed vast shellbeds in the Early Pleistocene (Taddei Ruggiero, 1986, 1994). The extinction of *Terebratula* by the Middle Pleistocene appears to be related to the reduction in sea temperatures as Pleistocene cooling proceeded.

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APPENDIX

Translation of Colonna, 1616c, page 23 and part of page 24, provided by Professor John Barsby, Department of Classics, University of Otago, and Professor Roberto Taddei, Dipartimento di Biologia Vegetale, Università di Napoli 'Federico II'.

Page 23, Concha rarior *Anomia vertice rostrato*. I. Cap. XII.

'Now we will discuss the one found in the city of Andria. If anyone of greater curiosity would seek them in that place, he will find many of the more rare ones, still unrecognised and unseen. And he will notice that nature has had a lot of fun in forming them. The appearance of this [shell] is smooth, depressed, a little elongated (longer than broad), differing from other shells especially in the fact that one of the two valves is longer and that it extends its umbo and the whole apex which is longer and rounder and sharper and sticks out above the apex of the other valve, so that the last apex is connected beneath the umbo of the first one. The shell is small, white, thin, and a little bit wrinkled transversely by additions [=with the surface marked by growth lines], but not for that reason rough, but smooth. We found this shell full of the white sediment on which that whole sloping area or hill is made. This is constituted not so much of loose sediments, as of fragments of various shells and unbroken shells too. We collected this one and others in the small valley or ditch a little below the Church of D. Maria de Andria, which is situated one mile outside the city. We were there to pay our thanks for favours received from most holy Mother of God, among the others who assemble there in great crowds every day to pay their vows. The church is adorned with large gifts and

signs of miracles: the church itself has a sumptuous structure, as does the monastery. We observed one shell like this at the Museum of our very learned Imperato, a rich treasure of all natural things. This shell has a little sinuous margin and the longer valve has a slight groove in the back, another in the middle, protruding in opposite way (?). All the shells have the same particular feature, i.e. an orifice in the rostrate, prominent, apex, from which they can, as a turbine, suck and eject water, in the manner of a 'sylvestre Lepas' or an 'Auris marinea'. The figure is natural size. A stony shell like this, but much greater, is figured in the first part, under the name Concha gibbosa.'

Page 24, Altera *Neptunia maior* III. *imbricata*. Cap. XIII.

'Another twice larger, with sinuous margin too, we found in tufaceous or sandy materials near Albano, in which is the ditch of Castello (Castle) or Arce. And there are many different shells never complete, but all piled-up and tangled . . . The shell is 3 inches long, 2 wide, and in the middle has like another shell built on.'

Concha anomia IV. *marginata*. Cap. XIV

'This differs from the previous similar one in the colour which is on the pale side, but was full of white, loose sediment too, for the wavy and curly margin so that it is like an 'M' letter, for the back is inflated and not hollow, because in the other valve a triple groove is recognisable, but all have a pierced apex. I had these, among the others, from the Museum of our Imperato.'

Purpura.

23

Concha rarior Anomia vertice rostrato. I. Cap. XII.

ANomias Conchas illas esse dicimus, quarum altera pars co-
hærens aliquo modo ab altera effigie, aut magnitudine, aut
vetroque modo differat *diversis*, quidem contrarium est verbi *diversis*,
quod est, *similis, par, aequalis*, scilicet, *diffimilis, impar, inequalis*: Lib. 9. c. 33
ideo inter ceteras notas à Plinio memoratas, quibus Concharum
varietates distinguit plurimas, cum inæqualitatis notam non inue-
nerimus, Anomias Conchas appellare libuit, vel Plinij more illas,
vertice rostrato, dicere; quarum etiam differentiarum sunt plures: Nunc
de hac in Ciuitate Andriæ reperta verba faciemus, in quo loco si
quis curiosior perquirere vellet, illas etiam rariores non paucas in-
ueniet adhuc incognitas, & inuisas. Naturamq; in his efforman-
dis multum luisse animaduertet. Huius igitur effigies læuis, depres-
sa, parum oblonga, ab alijs Conchis in hoc præcipue differens, quod
altera Conchæ pars oblongior est, collum, ceruicemq; totam, quæ
oblongior est, & rotundior, atque acutior, prominensq; supra cerui-
cem alterius diffundit, ut infra illius collum altera ceruix conne-
ctatur. Concha parua est, candida, tenuis, oblique parum addita-
mentis rugosa, sed non ob id aspera, sed læuis. Repletam inueni-
mus candida tophacea concretionem, qua totus ille cliuofus locus,
siue collis est editus, qui non magis terrena concretionem tophacea,
quam variarum Concharum fragmentis, & integris etiam innume-
ris est compactus: hanc & alias in vallicula illa, siue fossa quadam
parum subtus Ecclesiam D. Mariæ de Andria, extra urbem miliario
sita, exceperimus: illic enim ob gratias à Sanctissima Dei Genitrice
acceptas referendas fuimus, sicuti & alij magna cum frequentia vo-
ta soluentes concurrunt quotidie: Ecclesia quidem illa magnis do-
nis, & miraculorum signis ornatur, nec non sumptuosa structura ip-
sa Ecclesia, & Monasterium. Huius similem apud doctissimum Im-
peratorem nostrum in suo Musæo, rerum omnium naturæ satis copio-
so thesauro, obseruauimus, quæ margine erat parum vndosa, &
longiore conchæ parte canalem vix cōspicuum in dorso, altero verò
in medio, cōtrario modo extuberante, omnesque peculiari nota sūt
præditæ, quod ceruice prominente rostrata, pertusa oriuntur, qua tur-
binatorum more aquam haurire & expuere, sylvestris Lepadis, aut
Auris marinæ modo possunt: icon magnitudinem æquat. Huic simi-
lem maiorem multo lapideam depinximus in prima parte, nomine
Conchæ gibbosæ.

Altera

24

Fabij Columnæ

Altera Neptunia maior III. imbricata. Cap. XIII.

DVplō maiorem alteram Neptuni reperimus Albanen. dio-
cesis etiam vndosa margine in tophaceis, siue sabulosis illis
concretionibus, in quibus Castelli siue Arcis fossa est, & maxima
variarū testarū congeries conspicitur, nec vnā reperies integram,
sed omnes inter se congestas, & implicatas, ut non Natura, sed ma-
ris impulsu fractas, & eiectas cum sabulone, & molem illam to-
phaceā construxisse testarū fragmentis repletā sit censendum: quare
mare aliquando varijs in regionibus excreuisse & æstuasae satis cō-
stat, locaq; immutata. Mirum quidem est huiusmodi testas recentes,
& viuas hodie non reperiri, quamobrem è longè maris alluione
profectas, & aduectas censemus potius, quam Naturam desisse si-
miles parere. tres pollices longa, duos lata est testa, habetq; in me-
dio veluti alteram concham super elatam imbricis modo, ut in alijs
obseruatur, præsertim pectunculis.

Concha Anomia IV. margine vndosa. Cap. XIV.

Differt hæc à superiore congenere colore ad pallidum inclinan-
te, quæ etiam repleta erat concretionem candida terrea, &
quod margine sit vndosa in spiras contorta, M, litteram repræsen-
tante, dorsumq; habeat elatum, non cauum; altera parte triplici
canali distinguatur, sed omnes ceruicem habent perforatam, ex Im-
perati nostri Musæo habuimus inter alias.

Concha altera Anomia striata & lobis rarior. I. Cap. XV.

EX eodem genere & hæc videtur, maior Concha, & crassior; cu-
ius obesa valua minor est, atque tribus simul iunctis testis, me-
dia magis extuberante constructa videtur, & senis strijs, totidemq;
strigibus in singulis lobis, quibus margines denticulatæ fiunt, infe-
cta, præterquam pars interiecta interlobos, quæ recta linea marginē
definit. Altera parte, qua valua in caput prominet, medium habet
lobum depressiorem, & oblongiorem, reliquis à latere breuioribus,
& elatis, eodemq; modo striatis; qua parte tota concha expansis
alis auctulam incuruam repræsentare videtur Conchæ cortex ca-
stanea.

Fig. 10 Reproduction of Colonna, 1616c, pp. 23, 24.



Lee, Daphne et al. 2001. "The cenozoic brachiopod *Terebratula*: its type species, neotype, and other included species." *Bulletin of the Natural History Museum. Geology series* 57, 83–93.

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