

COUPLING AMPULLINID GASTROPODS: SEXUAL BEHAVIOUR FROZEN IN PALAEOGENE DEPOSITS OF NORTHERN ITALY

IGINIO DIENI

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Abstract. Couples of the ampullinid gastropods *Globularia (Eocernina) vulcani* (Brongniart, 1823), *Amaurellina (Crommium) angustata* (Grateloup, 1827) and *Amaurellina (Pachycrommium) cf. suesoniensis* (d'Orbigny, 1850), composed of dimorphed shells tightly conjoined at the apertures, from the Palaeogene (Eocene and Oligocene) marine successions of northern Italy, are interpreted as buried while mating, specimens being "frozen" while suddenly covered by a mass of sediment. Violent depositional events were responsible for their rapid burial, primarily by volcanoclastics, the formation of which had also involved acidification. The consequent poisoning of sea water and/or overwarming beyond the range in which the gastropods could survive, induced mass mortality. A similar set of conditional circumstances is also discussed for differently sized coupled specimens of *Ampullinopsis crassatina* (Lamarck, 1804), preserved with their shells slightly apart but with their apertures almost in contact. With reference to the catastrophic eruption of Vesuvius in A.D. 79, when Pompei was buried under tephra, it is thought that volcanic activity caused the death and burial of all these pairing gastropods in a "Pompeian" way.

Riassunto. Sono stati osservati nel Paleogene (Eocene ed Oligocene) del Veneto cinque casi di coppie di gasteropodi ampullinidi (riferibili a tre generi e quattro specie) composte da conchiglie dimorfe con le aperture combacianti. Esse vengono interpretate come individui di sesso diverso morti durante la copula a causa di eruzioni basaltiche sottomarine che avrebbero provocato, oltre al seppellimento e soffocamento ad opera di abbondante materiale ialoclastico, acidificazione (e quindi avvelenamento), intorbidamento e surriscaldamento delle acque, con conseguente mortalità in massa.

Con un evidente riferimento all'eruzione del Vesuvio del 79 d.C., nel corso della quale Pompei fu sepolta dalle pomici, viene proposta la locuzione *fossile pompeiano* per indicare tutti quei fossili la cui morte sia da collegare, direttamente o indirettamente, a fenomeni vulcanici.

Introduction

Sexual dimorphism in gastropods has long been known as an inherent characteristic of these molluscs, both ancient and living today. Among marine species, sexual dimorphism in Cretaceous aporrhoids had even been suggested by Gardner (1875, p. 398) before it was recognised in present-day buccinids by Morse (1876) who, however, followed still earlier suggestions (Adanson 1757; De Blainville 1825; *vide* Lamy 1937, p. 288). In all these cases, the sex difference was displayed by conchological attributes. As concisely argued by Sohl (1969, p. 96), shell criteria, such as size, shape, and ornamentation, represent practically the only way of identifying sexual dimorphs in fossil gastropod species, although phenotypic deviations of standards do exist in living populations.

In fossil gastropod species, of the conchological grounds upon which sexual dimorphs may be identified, size and shape are the most distinctive. They clearly indicate that females are larger and more obese than males, which are smaller and more slender (Gardner 1875; Lamy 1937; Makowski 1962, pp. 56-57, figs 7-9; Sohl 1969, p. 97; Ambroise & Geysant 1974, fig. 17). Compatible with this are the Calyptraeidae, a family of protandrous marine gastropods that includes species of the genus *Crepidula* Lamarck, 1799, both present-day and fossil, in which males attain a dwarf size, regardless of their sedentary or motile mode of life (Coe 1935, 1936; Collin 2006, and references therein). In these species, a sex change occurs during ontogeny (Coe 1935, 1936; Bałuk & Radwanski 1985; Collin 2006), in species

living in perch-like chains (stacks of two or more individuals, where a small male usually attaches to the shell of a larger female), typical of present-day *Crepidula fornicata* (Linnaeus, 1758) and some Neogene forms from the United States and New Zealand (Hoagland 1977, Grant-Mackie 1990), as well those domiciled in empty gastropod shells and exemplified by *Crepidula crepidula* (Linnaeus, 1766) from the Miocene of the Vienna Basin in Austria and the Korytnica Basin in Poland (Papp 1948; Bałuk & Radwanski 1977, 1985).

The aim of the present paper is to supplement the above few examples of sexual dimorphism in fossil gastropod species with five expressive cases of separate sexes of ampullinid specimens frozen in a post-copulatory position, and preserved uniquely in marine Palaeogene (Middle Eocene and Lower Oligocene) deposits of northern Italy. To the present author's knowledge, no such paired specimens have ever been reported in fossil gastropods, except for one uncommented illustration from the Lower Oligocene of Romania, interpreted below.

Provenance of the studied specimens

The coupling gastropod specimens were collected in the Eocene and Oligocene successions of the Venetian region in northern Italy (Fig. 1). These successions, primarily those of Eocene age (for exhaustive references, see Kranz 1911; Fabiani 1915; Malaroda 1954) have been known since the mid-16th century, due to the ubiquity of their fossils, which are both extraordinary occurrences in some peculiar facies (e.g., the world-famous Eocene localities of Bolca, Roncà, Montecchio Maggiore and Possagno; Fig. 1) and sequences classical for biostratigraphic subdivisions (Priabona). The lithologies of these sequences range from fine-grained clastics to more or less pure limestone, all commonly interbedded by basaltic products (lava flows, hyaloclastites of several types, and tephra) connected to prevalently

submarine and sporadically subaerial eruptional episodes (Piccoli 1967).

The best preserved specimens of coupling gastropods (Figs 2-6) were collected by several people, and are now in the Museum of Geology and Palaeontology, University of Padova, Italy, under catalogue numbers MGPD 28713-28717.

Taxonomy

According to the traditional systematics of gastropods proposed by Wenz (1941) and integrated and adjusted by later authors, for their morphological characters the marine species studied here should be accommodated within the order Caenogastropoda Cox, 1959, superfamily Naticoidea Forbes, 1838 (as proposed by Kabat 1991, p. 424, *pro* Naticacea Philippi, 1853, of former authors, such as Wenz 1941, p. 1017, Glibert 1963, p. 68, and Bałuk 1995, p. 194) and the extant family Naticidae Forbes, 1838. Nevertheless, for the investigated Venetian Palaeogene naticiform snails, we prefer to adopt the systematic classification of gastropod families suggested very recently by Bouchet & Rocroi (2005), which is based on the phylogenetic relationships of these molluscs. According to the hierarchical scheme of the above authors, the gastropod couples are to be ascribed to the clade Caenogastropoda, superfamily Campaniloidea Douvillé, 1904, clade Sorbeoconcha, family Ampullinidae Cossmann, 1919 (= Ampullospiridae Cox, 1930, in Kase & Ishikawa 2003). In fact, Bouchet & Rocroi (2005), in complete agreement with Kase & Ishikawa (2003) and differently from the opinion of other malacologists, such as Marinovich (1977), consider the Naticidae (Campanian to Recent, radiated at modern levels beginning in the Eocene) and Ampullinidae [Late Triassic to Recent, with extinctions of most taxa at the close of the Middle Eocene and *Cermina fluctuata* (Sowerby, 1825), of the Philippine Islands, as the sole living species] unrelated from the phylogenetic

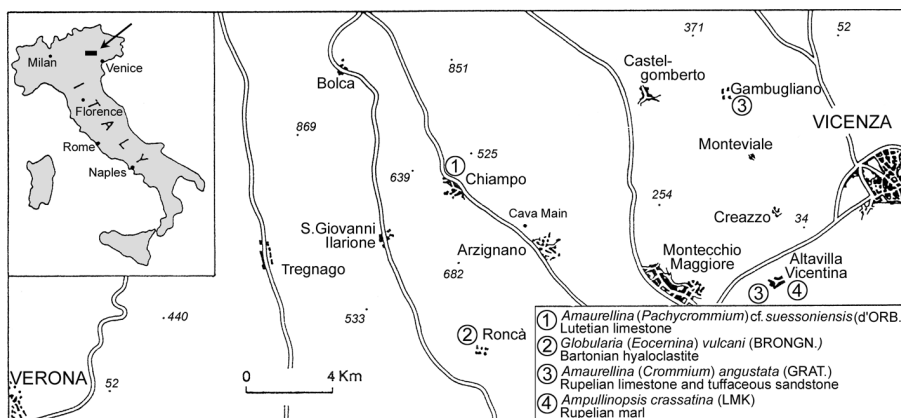
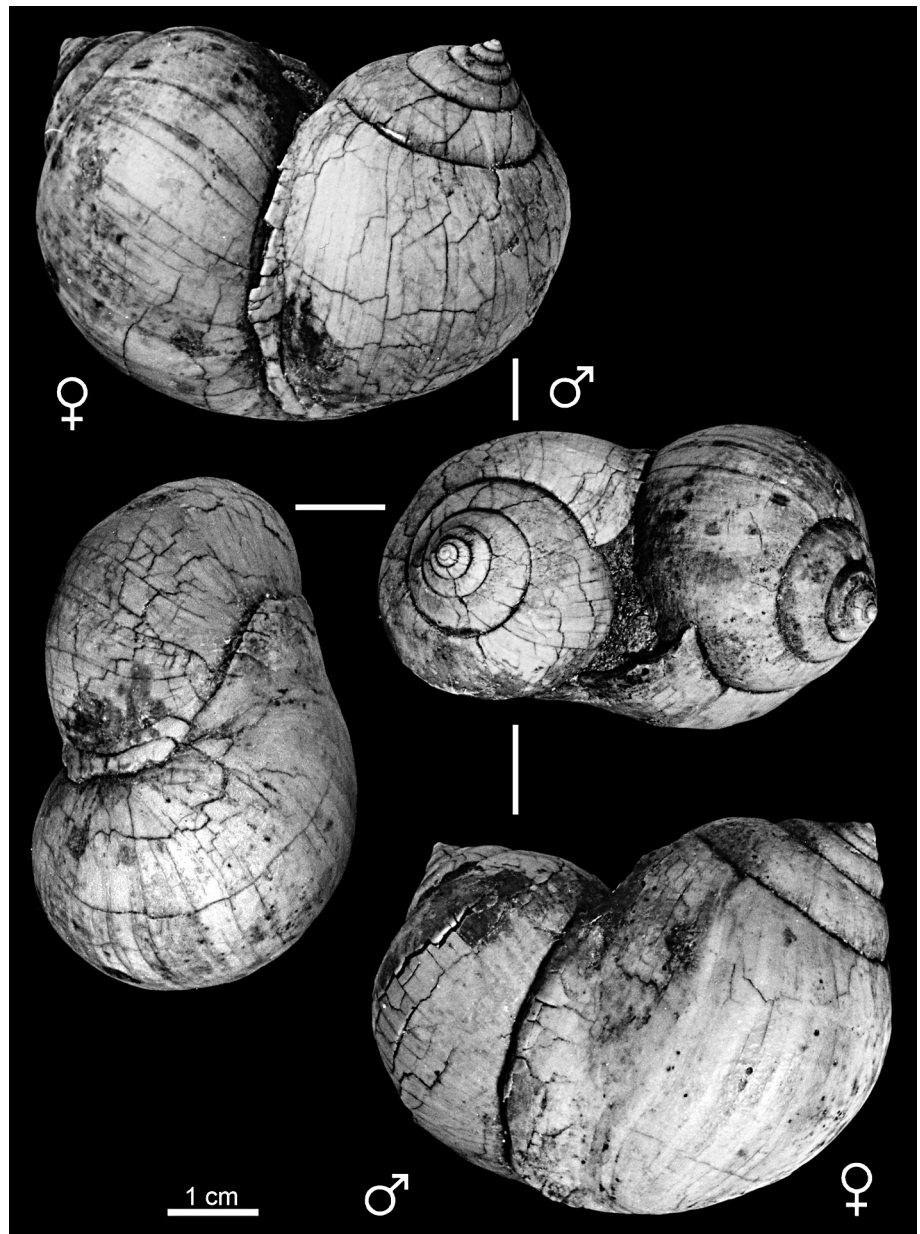


Fig. 1 - Sketch-map with some of the most important Tertiary fossiliferous localities of Verona and Vicenza provinces and sites (1-4) where the studied ampullinid couples were found. For each species, age, and nature of matrix are given.

Fig. 2 - Four views of mating couple of *Globularia (Eocernina) vulcani* (Brongniart, 1823); Bartonian basaltic hyaloclastite of Roncà (Verona); topotypes; MGDG 28713.



point of view, naticid shells representing only a case of morphological convergence with ampullinids.

It should be noted that the taxonomy of all fossil naticiform gastropods at genus/subgenus level and their relation to present-day taxa have long subjected to serious debate (e.g., Wenz 1941; Glibert 1963; Abatino & Barbera Lamagna 1972; Marincovich 1977; Martinell 1979; Kabat 1991). At species level, an even more complex jungle of taxonomy was created when parameters other than overall shell morphology, such as the shape of the operculum and/or umbilicus and the structure of the protoconch, were taken into account (see, f.i., Marincovich 1977; Solsona & Martinell 1999; Kase & Ishikawa 2003). Some definite fossil species of naticoids have also been treated as the sexes of other naticoids (see Martinell 1979, pp. 129-135).

In early and recent descriptions, the ampullinids of Palaeogene age from the Venetian region have usually been included (see, e.g., Brongniart 1823; Oppenheim 1901; Kranz 1911; Piccoli & Samburgar 1973; Siliotti 1979) in the genera *Natica*, *Ampullina*, *Ampullaria*, or *Megatylotus*. Following the systematics proposed by Wenz (1941) and also considering the integrations and adjustments of later authors particularly concerned with taxonomy of naticiform gastropods (from Glibert 1963 to Marincovich 1977 and Kabat 1991), the coupling specimens studied here were identified as belonging to four different species, best accommodated within the genera *Globularia* Swainson, 1840 (subgenus *Eocernina* Gardner & Bowles, 1934), *Amaurellina* Bayle in Fischer, 1885 (subgenera *Crommium* Cossmann, 1888, and *Pachycrommium* Woodr-

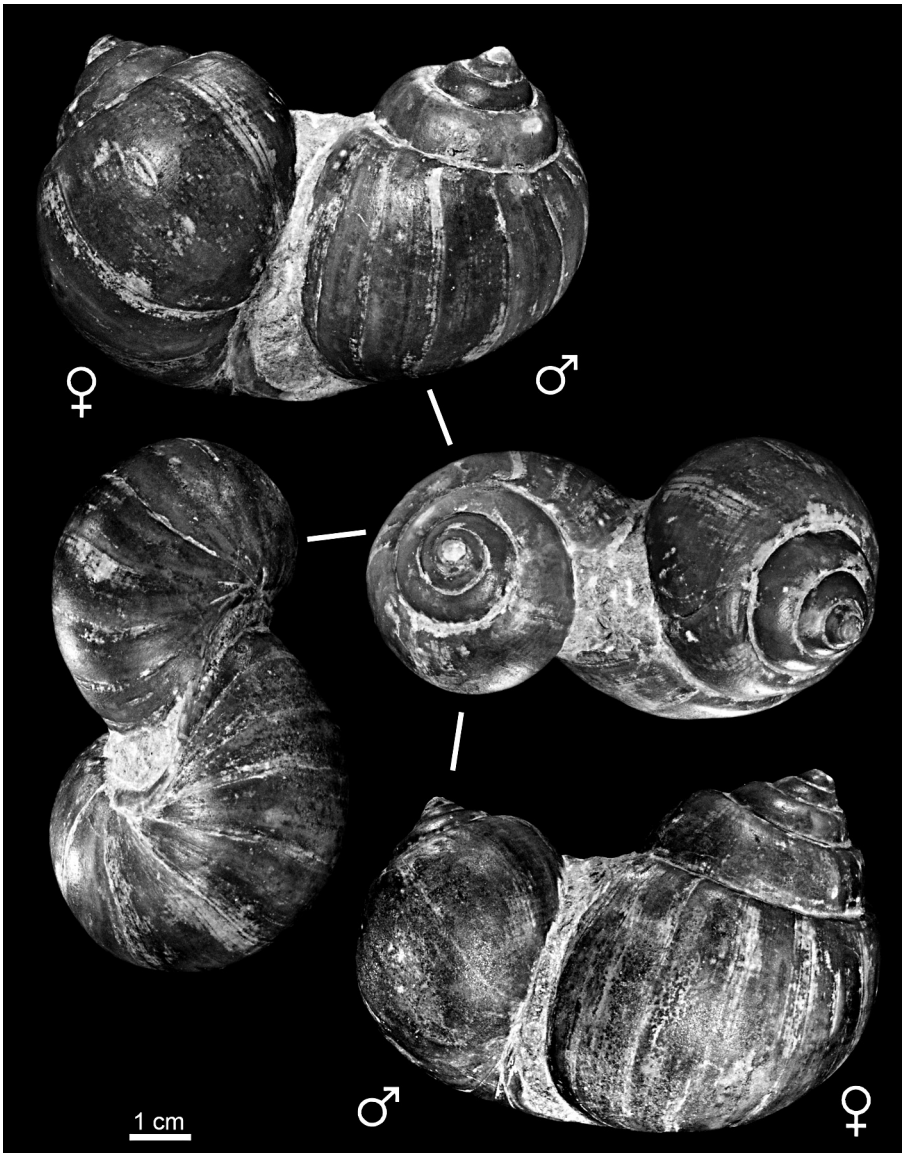


Fig. 3 - Four views of mating couple of *Amaurellina (Crommium) angustata* (Grateloup, 1827); Rupelian limestone with hyaloclastites of Gambugliano (Vicenza); MGD 28715.

ing, 1928), and *Ampullinopsis* Conrad, 1865, as follows:

couple MGD 28713 (Fig. 2) - *Globularia (Eocernina) vulcani* (Brongniart, 1823), from the Bartonian hyaloclastite of Roncà (Verona), the type locality of the species (Fig. 1);

couples MGD 28714 and MGD 28715 (Figs 3, 4) - *Amaurellina (Crommium) angustata* (Grateloup, 1827), respectively from Rupelian limestone with interbeds of volcanic products of Gambugliano (Vicenza) and calcareous sandstone with a tuffaceous matrix overlying basaltic lava of Altavilla Vicentina (Vicenza) (Fig. 1);

couple MGD 28716 (plaster cast; the original is in a private collection) (Fig. 5) - *Ampullinopsis crassatina* (Lamarck, 1804), from Rupelian marl immediately overlying basaltic lava of Altavilla Vicentina (Vicenza) (Fig. 1);

couple MGD 28717 (Fig. 6) - *Amaurellina (Pachycrommium) cf. suessoniensis* (d'Orbigny, 1850), from

Lutetian limestone with basaltic volcanites of the Chiampo valley (Vicenza) (Fig. 1).

Of these species, *vulcani* has quite perplexing synonymy (see Oppenheim 1901, p.194), like *angustata* (see Kranz 1911, p. 241). The third taxon, "*Ampullaria crassatina* Lamarck, 1804", was indicated by Fischer (1885, p. 766) as the type of his genus *Megatylotus* which, however, was considered by Wenz (1941, p. 1020) as a junior subjective synonym of *Ampullinopsis* Conrad, 1865 (see Kabat 1991, p. 432). See the Appendix for further synonyms and discussions on taxa. A taxonomic jungle among most of the Eocene-Oligocene naticiform gastropods (Glibert 1963) is not commented here – the more so, since it is certainly not lesser than among Neogene forms (Martinell 1979; Marincovich 1977; Bałuk 1995). In all fossil naticoids, it is still unclear whether any "population" collected represents one species of more or less advanced intraspecific variability,

or a group of convergent species (see Kabat 1991; Solsona & Martinell 1999).

Sexual behaviour

The four studied couples conjoined tightly at their apertures (Figs 2-4, 6) are interpreted here as preserved during copulation (Latin: *in copula*). Noteworthy is the ideal adjustment, as in a jigsaw puzzle, of the shell margins (most pronounced in the couple of *Globularia vulcani* shown in Fig. 2, where the aperture margins – see the broken edges – have clearly been crushed together somewhat after burial). This shows that shell morphology developed substantially to accommodate mating by live, mature ampullinids.

The couple with less tightly joined shells (Fig. 5) may be interpreted as preserved when relaxing after copulation, although some post-depositional plastic deformation (sediment compaction) of the marly matrix, responsible for the slight separation of the two specimens, cannot be excluded.

When taking into account that in each couple one specimen is larger and more obese than the other, then sexually controlled shell dimorphism, and consequently sex separateness, clearly occurs in the identified species of genera *Globularia* Swainson, 1840, *Amaurellina* Bayle in Fischer, 1885, and *Ampullinopsis* Conrad, 1865. As given above, the larger individuals of *Globularia* (*Eocernina*) *vulcani*, *Amaurellina* (*Crommium*) *angustata*, *Amaurellina* (*Pachycrommium*) cf. *suessoniensis* and *Ampullinopsis* *crassatina* are thus interpreted as the females, and the smaller ones as the males (Figs 2-6).

It is noteworthy that sexual organisation in gastropods is highly diversified, and contains taxa of various ranks distinguished by separate sexes, hermaphroditism, and protandry (see Coe 1935; Makowski 1962; Sohl 1969). The same concerns the act of copulation, especially in hermaphrodite forms, which may change sex when pairing, or form “copulatory chains”, as known (Geldiay 1956) in a pulmonate, the freshwater limpet *Ancylus fluviatilis* Müller, 1774. Other freshwater pulmonates display variable sex activities (Piechocki 1979, p. 33; Trigwell et al. 1997).

As regards the copulatory position of marine prosobranchs, little is found in the literature (see Ankel 1936, fig. 130). Most examples in textbooks and general monographs illustrate land pulmonates (which are all hermaphroditic), quite often the common European vineyard snail, *Helix pomatia* Linnaeus, 1758, and/or its relatives (see, e.g., Stanek 1971, p. 54; Shileiko 1978, fig. 24; Fechter & Falkner 1990, pp. 236 and 252). The attitudes of one individual towards its mate are very variable, although none of them shows couples in a post-copulatory position identical to that of the studied spe-



Fig. 4 - Mating couple of *Amaurellina* (*Crommium*) *angustata* (Grateloup, 1827) from Rupelian calcareous sandstone of Altavilla Vicentina (Vicenza); MGDGP 28714.



Fig. 5 - Mating couple of *Ampullinopsis* *crassatina* (Lamarck, 1804) from Rupelian marl of Altavilla Vicentina (Vicenza); MGDGP 28716.

cimens, and that commonly observable in *Helix pomatia*. Easy access to study of recent terrestrial pulmonates has also meant that the whole copulatory process, from courtship to final separation, is completely recognised in these gastropods, primarily in slugs (see Wiktor 1960; 1989, pp. 62-67, figs 49-51; 2000, pp. 375-379, figs 33-36). The pre-copulatory behaviour of the freshwater pulmonate *Biomphalaria glabrata* (Say, 1818) has recently been studied in detail by Trigwell et al. (1997).

Present-day naticoid gastropods (commonly called Moon Snails, Moon Shells, Shark Eyes, Sand-collar Snails, etc.) rest, move, hunt and spawn just under fine-grained bottom surfaces, as also known from British and North American nearshore habitats (Abbott 1954; Fretter & Graham 1962). However, no report has been made of the mode of their pairing, under or above the sediment surface. In the absence of any uniformitarian approach, it is suggested that pairing of the Venetian Palaeogene ampullinids took place on the bottom rather than in the underlying sediment. This hypothesis is supported, although indirectly, by the results

of researches carried out by Kase & Ishikawa (2003) on *Cernina fluctuata* (Sowerby, 1825), the sole extant species of the family Ampullinidae, and its Mesozoic and Caenozoic relatives. For all these molluscs, these authors demonstrated feeding habits as algal grazers and consequently an epifaunal mode of life.

The Palaeogene specimens, which form either tightly joined or slightly disjoined couples, were very probably buried by sediment or granulated volcanic products, and frozen just at, or immediately after copulation. Any instinctive movement at the moment of sudden burial may have had the effect of joining the mating gastropods even closer together.

Cause and conditions of burial

In order to ascertain the conditions of burial in which a copulatory act of very low preservational potential, like that shown by the Venetian Palaeogene gastropod couples, involving “freezing” them to the fossil state, some unusual events must be invoked. First, the burial itself must have been quite rapid, to be fatal to the mating animals. They may have been suddenly covered by a mass of material, caused by a violent sedimentary event, like deposition during a storm (tempestites), and/or mass movements, such as slumping caused by seismic activity accompanying eruptive episodes (possible interpretation for the Altavilla Vicentina couple preserved within tuffaceous sandstone). Second, a lethal action may have occurred just prior to or simultaneously with a violent depositional act, as may be induced from the common presence of volcanic products [basaltic lava flows, hyaloclastic materials (= hyaloclastite flows in the sense of Macdonald 1972, p. 104), etc.] within the gastropod-bearing Eocene and Oligocene successions of the Vicenza-Verona region. Submarine volcanic events, involving acidification with consequent poisoning, increase of turbidity, and/or overwarming of water beyond the range the gastropods could survive, may thus have caused the death of the mating couples, such as

those of Chiampo (Lutetian) and Gambugliano (Rupelian), preserved within limestone, and that of Altavilla Vicentina (Rupelian) preserved within marl, all associated with beds of volcanic products. For the Bartonian couple from Roncà (Fig. 2), the huge, thick, basaltic hyaloclastites, produced by abrupt flaking off of numerous, successive lava flows as a result of their sudden chilling in sea water, also became a rapid burial agent which acted in a “Pompeian” way.

Therefore, referring to the catastrophic eruption of Vesuvius (Mt. Somma) in 79 A.D., when Pompei was buried under tephra, the terms *Pompeian* or *Pompeian fossil* are introduced here to indicate all fossils the death of which was directly or indirectly caused by volcanic episodes (lava flows, tephra falls, water poisoning, seismic slumping accompanying eruptions, etc.), either subaerial (Sigurdsson et al. 1985) or subaqueous (e.g., the Cretaceous and Pleistocene cases studied by Heikoop et al. 1997). Among the numerous Palaeogene fossiliferous sites of NE Italy (for the Venetian region, see Fabiani 1915) with assemblages having this peculiarity, and of greater interest from the marine invertebrate faunal view point (Fig. 1), we mention Roncà, Sorne near Brentonico (Socin 1939), Chiampo – S. Giovanni Ilarione, Montecchio Maggiore, Castelgomberto, Cava Main at Arzignano, and S. Maria di Lugo di Vicenza (also known as Sangonini), some of which (Roncà, Sorne, Cava Main, S. Maria di Lugo) constitute good examples of fossil-Lagerstätten of the “obruption deposit” type (see Seilacher et al. 1985). As regards Cava Main, particularly impressive are the decapod crustaceans preserved in several positions, frozen by thick suffocating masses of hyaloclastites during normal life (for a concise review, see Beschin 1997, and Ungaro in Beschin et al. 1998).

Interpretation of a pair of Oligocene ampullinids from Romania

The literature on Palaeogene ampullinids contains one uncommented, but expressive, illustration of speci-

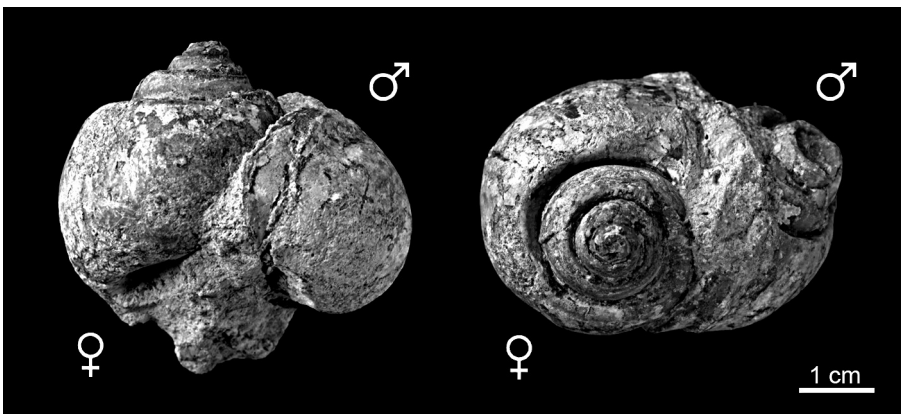


Fig. 6 - Mating couple of *Amaurellina* (*Pachycrommium*) cfr. *suessoniensis* (d'Orbigny, 1850) from Lutetian limestone of Chiampo Valley (Vicenza); internal moulds; MGD 28717.

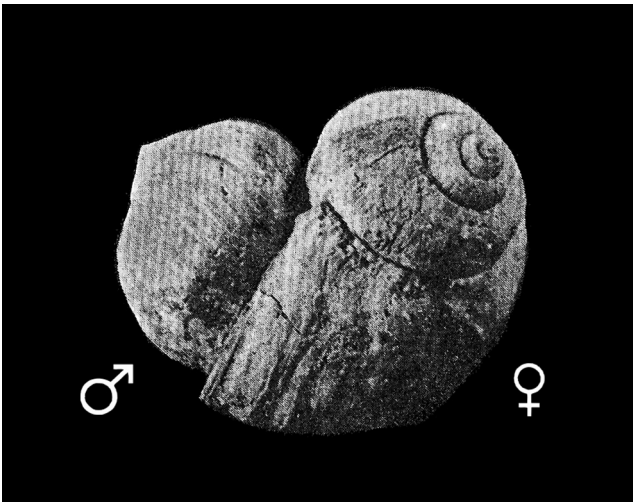


Fig. 7 - Unique case of fossil ampullinids *in copula* in literature (Rusu 1975, pl. 1, fig. 14: *Globularia porolissensis* Rusu, 1975), from Lower Oligocene of Transylvanian Basin, Romania. Sex identification by present author.

mens from the Lower Oligocene of the Transylvanian Basin in Romania. It was presented by Rusu (1975, pl. 1, fig. 14) as two paratypes of his new taxon *Globularia porolissensis* Rusu, 1975 [considered by Moisescu (1997) as a subspecies of *Globularia grossa* (Deshayes, 1864)]. The photograph (reproduced in Fig. 7) shows a pair of differently sized specimens preserved in a position identical to that of the above mating couples of Italian Eocene and Oligocene gastropods (Figs 2-6). It is thus reasonable to interpret that couple as another case of fossil ampullinids frozen *in copula*. Unfortunately, data on their depositional circumstances cannot as yet be detected in the Romanian literature (Rusu 1975; Moisescu 1989; Chira 1989).

Re-interpretation of a former report

Sex recognition in the species *Ampullinopsis crassatina* (Lamarck, 1804), as studied here (Fig. 5), is not the first record. Piccoli & Sambugar (1973) studied a collection of what they believed to contain two species, classified as “*Natica crassatina* (Lamarck)” and “*Natica cochlearia* (Brongniart)”, both coming from Lower Oligocene localities of the same areas that yielded the coupled specimens studied here (Fig. 1). Examining a collection of over 200 specimens in the Museum of Geology and Palaeontology, University of Padova, they concluded that: (i) sexual dimorphism does exist in these two species, the males being *larger* and the females *smaller* in size; (ii) the males of the latter species, due to their shell parameters, are very similar to the females of the former species; (iii) sexual dimorphism is more pro-

nounced in the latter species, typified by the more obese shell in both sexes.

Regardless of the opposite interpretation of shell size in the separate sexes given in the above report, it should be noted that differently sized specimens, considered by Piccoli & Sambugar (1973) as separate sexes, came from different localities, with different populations and habitats (Monteviale and Castelgombergo versus Montecchio Maggiore and Gambugliano; cf. Fig. 1). Moreover, neither biometric analyses nor the illustrations of Piccoli & Sambugar (1973, figs 1-9 and pls. 1-2) evidence any groups/classes which could indicate separate species, or the two sexes of one species.

In the present author's interpretation, all the material discussed by Piccoli & Sambugar (1973) regards largely conspecific forms, whose correct taxonomic assignment is beyond the scope of this paper [only as an example, the specimens presented in pl. 1, figs 4,5, and pl. 2, fig. 4, of the above authors respectively as *Natica crassatina* (Lamarck) and *Natica cochlearia* (Brongniart), must be ascribed to *Amaurellina* (*Crommium*) *angustata* (Grateloup), whereas the specimen illustrated in pl. 2, fig. 5 as *Natica cochlearia* (Brongniart) is more properly referable to *Ampullinopsis crassatina* (Lamarck)]. The variable size and/or shell ratios of these forms may be ontogenic in nature and/or due to ecophenotypic variability. In the case of the latter, factors such as fluctuations in salinity, state of health, or even diet should be taken into consideration (cf. Sohl 1969, p. 96).

Final remarks

To the present author's knowledge, the described specimens are the first record of the mating act in fossil gastropods, that is, of gastropods fossilised *in copula*. Their record supplements numerous examples of ancient invertebrates fossilised during mating, mainly Tertiary insects from the Baltic and/or Dominican amber (see review by Boucot 1990, pp. 385-389 and figs 315-321), as well as a unique pair of oonopid spiders from the Baltic amber reported by Wunderlich (1981, fig. 25, and 1982, fig. 1, re-illustrated by Boucot 1990, fig. 314, and Poinar 1992, fig. 124).

The five cases of mating ampullinids studied here were acquired after an intensive search in the stocks of private collectors, some of whom provided information about other couples, either lost/sold at some time, or damaged (separated) during preparation. In this context, significant is the oral communication kindly supplied by Massimiliano Cerato (of the historically famous family which, since 1750, has been extracting and preparing palaeontological material from Bolca and other Pa-

laeogene fossiliferous sites of the Verona and Vicenza regions), that the ampullinid gastropods *in copula*, indicated as *gasteropodi in amore* (“gastropods in love”) within the Roncà volcanoclastites have long been famous not as oddities, but as prized items for amateur collectors. It is thus hoped that some more specimens of “gastropods in love” may soon become accessible to science.

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Appendix

For a valid discussion and an exhaustive synonymic list of *Globularia* (*Eocermina*) *vulcani*, see Dainelli (1915, p. 562).

As regards *Amaurellina* (*Crommium*) *angustata*, very interesting and significant are the figures given for this taxon by Grateloup in 1840, although under many different names, here listed in their original form: *Natica ponderosa* Desh. Var. A. *major* (pl. 2, fig. 2), *Natica ponderosa* Var. B. *minor* (pl. 2, figs 3, 5), *Natica ponderosa* Var. C. *rugosa* (pl. 2, fig. 6), *Natica ferruginea* Grat. (pl. 2, fig. 4), *Natica angustata* Grat. Var. A. *ventricosa* (pl. 3, figs 1, 2), *Natica angustata* Var. B. *ovatoelongata* (pl. 3, fig. 4), *Natica angustata* Var. C. *oblonga* (pl. 3, fig. 4), *Natica angustata* Var. D. *juvenis* (pl. 3, fig. 5), unanimously considered synonymous by all authors after Bayan (1870, p. 100), who was the first to study and illustrate this species with accuracy.

For a synonymic list of *Amaurellina* (*Pachycrommium*) *suessoniensis*, see Klepač (2003, p.350).

Good illustrations of *Ampullinopsis crassatina* are provided by Grateloup 1840, pl.1, figs 1, 2 (as *Natica maxima* Grat. and *N. maxima* Var. B. *subcostata*, respectively), 3 (as *N. crassatina* Desh.), pl. 2, fig. 1 (as *N. maxima* Grat. Var. C. *subglobosa*), pl. 5, fig. 6 (as *N. crassatina* Lam. Var. B) and Cossmann 1924, pl. 3, figs 13 and 17 [as *Megatylotus crassatinus* (Lmk.)].

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