

“Pompeian” mating molluscs: sexual behaviour frozen by Paleogene submarine volcanic activity in northern Italy

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ABSTRACT - A pair of Paleogene nautilid cephalopods (*Angulithes hilarionis*) composed of dimorphed shells are interpreted as having been buried while mating. A similar behaviour was previously reported for ampullinid gastropods (Dieni, 2008), the specimens being “frozen” when covered suddenly by a mass of sediment, primarily volcanoclastics. The formation of the latter also involved acidification and consequent poisoning and/or overwarming of sea water, causing mass mortality in some cases.

As the syntypes of *Nautilus hilarionis* De Gregorio, 1880 result as being no longer available, a Lutetian neotype from the type area is proposed.

RIASSUNTO - [Molluschi “pompeiani” in accoppiamento: comportamento sessuale “congelato” dall’attività vulcanica sottomarina paleogenica nell’Italia settentrionale] - Una coppia di cefalopodi nautilidi (*Angulithes hilarionis*) paleogenici del Veneto composta da conchiglie dimorfe viene interpretata come “congelata” durante l’accoppiamento. Un simile comportamento era già stato documentato in coppie di gasteropodi ampullinidi (Dieni, 2008). L’improvviso seppellimento ad opera di materiale prevalentemente vulcanoclastico provocò anche acidificazione e conseguente avvelenamento e/o surriscaldamento dell’acqua, dando luogo in alcuni casi ad episodi di mortalità in massa.

Poiché i sintipi di *Nautilus hilarionis* De Gregorio, 1880 non sono più reperibili, è stata effettuata (in Appendice) una revisione sistematica del taxon che ha portato come risultato alla proposta di un neotipo di età luteziana proveniente dall’area tipo.

INTRODUCTION

Animal behaviour frozen in the Geological Past has long attracted the interest of zoologists and palaeontologists. Since Clarke (1908) and his exhaustive “The beginnings of dependent life”, later accounts by Dacqué (1921), Abel (1935) and Tasnádi-Kubacska (1962) have supplied much evidence of animal activities preserved in ancient sedimentary successions. However, almost all the examples recorded so far concern traces of activities left either in the substrate in which the animals lived, or in hard parts of the body (tests, shells, bones) of those organisms which the trace-producers preyed upon or parasitized.

There are very few records of casual events interrupted by sudden burial at the precise moment when an animal performed a recognisable action. These records, systematically reviewed and concisely discussed under the term “frozen behaviour” by Boucot (1990), are comparable to photographs or to the frames of a movie filming the actions of the observed animal(s).

Nevertheless, many identified cases of frozen behaviour do involve, or may involve serious discussion and yield concurrent interpretations (Boucot, 1990). Doubt often remains as to whether the “snapshot” scene really corresponds to the action of live animals or whether it illustrates post-mortem processes in dead animals or their hard parts. For instance, the pseudoscorpions attached to the legs of various insects from the Baltic and Dominican ambers of Paleogene age, which have repeatedly been credited (e.g., Boucot, 1990) as cases of phoresy, i.e., passive flight, were concurrently interpreted by Poinar (1992) in terms of commensalism or life in common,

and thus not as accidentally immortalised “hitch-hiking” when in flight.

Rapid burial is the rule rather than the exception in Baltic and Dominican ambers, for which liquid resin was an agent favouring the “freezing” of specimens often performing a recognisable behaviour. The wide range of behavioural diversity in arthropods, primarily insects, preserved in these ambers (e.g., Bachofen-Echt, 1935; Schlee & Glöckner, 1978; Boucot, 1990; Krzemińska & Krzemiński, 1992; Poinar, 1992) includes some impressive cases of what is interpreted as sexual activity. For instance, a pair of water striders (family Gerridae) in a mate-guarding position was illustrated by Poinar (1992). Even better expressed is the sex behaviour of oonopid spiders (family Oonopidae) frozen at the moment of copulation (Wunderlich, 1981, figs 25-26, and 1982, fig. 1).

We present here other candidates of sexual behaviour preserved in the fossil record, testifying this occurrence in clades other than arthropods, i.e., in marine prosobranch gastropods and nautiloids from the Paleogene of the Venetian Alps in northern Italy.

PREVIOUS STUDIES

The Eocene to Oligocene marine successions of the Venetian Alps have long been known to yield ubiquitous fossils (Fig. 1), including diverse gastropods and rarely cephalopods (e.g., Brongniart, 1823; Oppenheim, 1901; Kranz, 1911; Malaroda, 1954). Among Eocene and Oligocene gastropods, representatives of the family

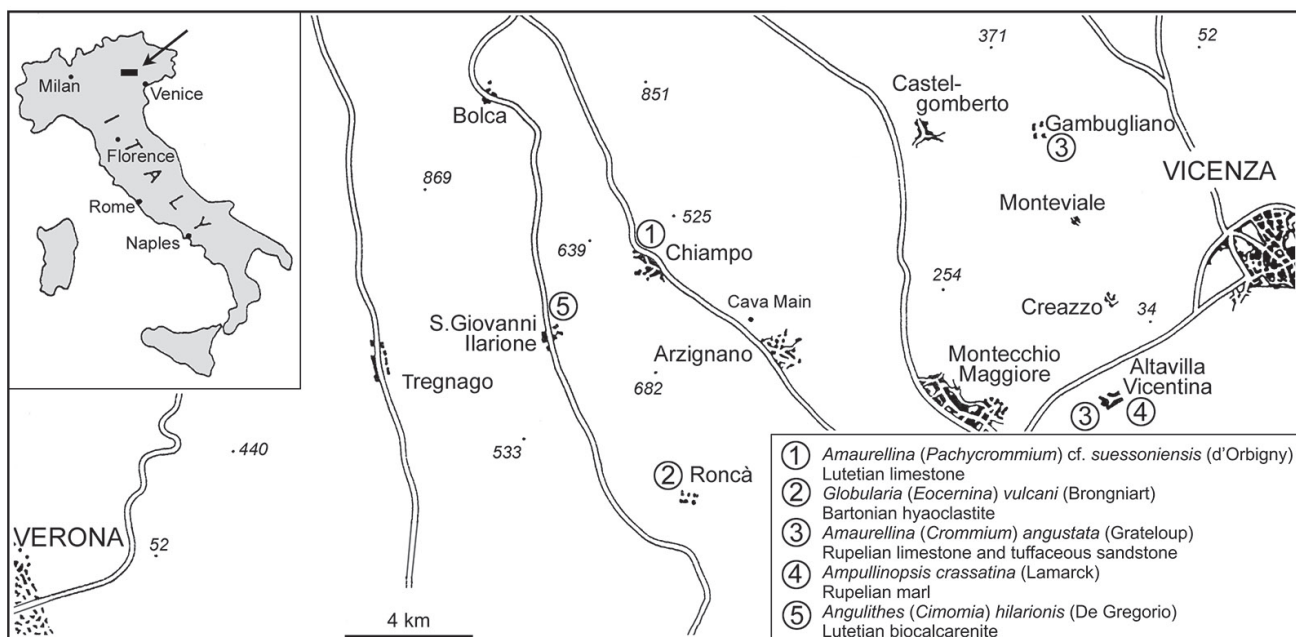


Fig. 1 - Sketch-map with some of the most important Tertiary fossiliferous localities of Verona and Vicenza provinces (northern Italy) and sites where the studied mollusc couples (1-4: gastropods; 5: nautiloids) were found. For each species, age and nature of the matrix are indicated (from Dieni, 2008, integrated).

Ampullinidae Cossmann, 1919 are particularly common at many sites. Collections in museums and in private hands comprise a number of peculiarly shaped, tightly-conjoined coupled specimens (Fig. 2; refigured after Dieni, 2008), which have sometimes been treated as oddities by amateur collectors, but also dubbed as “*gasteropodi in amore*” (gastropods in love) by others.

A comprehensive study on five occurrences from the Venetian Paleogene and interpreted as buried while mating was recently done by Dieni (2008). Such specimens are apparently easy to compare with present-day gastropod couples resting in a post-copulatory position, a behaviour which is known in marine prosobranchs and terrestrial pulmonates (Ankel, 1936; Shileyko, 1978; Fechter & Falkner, 1990). A recurrent feature of all the gastropod couples studied by Dieni (2008) is that one partner is slightly larger than the other, to an extent similar to that reported in present-day prosobranchs (see Lamy, 1937; Makowski, 1962; Sohl, 1969; Ambroise & Geysant, 1974), the protandric species (e.g., Slipper Limpet *Crepidula*) including pygmy males (Coe, 1935, 1936; Baluk & Radwanski, 1985). The larger specimens were considered to be the females and the smaller, slender ones the males (Diény, 2008; Fig. 2). Noteworthy is the ideal adjustment, as in a jigsaw puzzle, of the shell margins in the studied specimens (very clear in the couple shown in Fig. 2a). This reveals that shell morphology developed substantially to accommodate the sex activity demanded by live, mature ampullinids.

The taphonomic pathway of these gastropod couples in the fossil record is thought to be due to their rapid, unexpected burial, lethal for both partners (Diény, 2008). Identification of the causes of such burials is possibly explained by the nature of the deposits in which the couples are preserved, i.e., biocalcarenes with large amounts of basaltic products and/or hyaloclastites,

induced by submarine volcanic eruptions (for a general geological treatment of the Tertiary Venetian volcanism, see Piccoli, 1967). Such eruptions, characterised mainly by lava flows and glassy debris, regardless of the bulk of the volcanic material itself, involved acidification with consequent poisoning, increased turbidity, and/or overwarming of sea water beyond the range in which ampullinid gastropods could survive. Any physical stress, overwarming in particular, becomes lethal for part or even the whole invertebrate populations reported from present-day habitats (Higgins, 1974; Hendler, 1977; Lawrence, 1996; Heikoop et al., 1997).

COUPLED NAUTILIDS

Closely associated fossil nautilid cephalopods were collected within yellow biocalcarenes of Lutetian age cropping out in the area of Monte Serea near San Giovanni Ilarione (Verona) (Fig. 1). The two specimens, preserved in their entirety (recrystallized phragmocone and living chamber), belong to *Angulithes (Cimomia) hilarionis* (De Gregorio, 1880) (for taxonomic notes on this species see the Appendix) and were found leaning one against the other (Fig. 3). One of the specimens is larger and wider in the apertural region than the other, with maximum diameter (D_{max}) = 44.5 mm and width (W) = 32.9 mm against D_{max} = 42.6 mm and W = 28.5 mm for the smaller. On the basis of the observations previously made by Dean (1901) and Willey (1902) on sexual dimorphism in the shell of mature *Nautilus*, the relative size of the two specimens is compatible with an adult male (the larger shell) and an adult female (the smaller shell) of *Angulithes (Cimomia) hilarionis*. The aperture are facing one to the other, not in contact, with the axes of coiling forming a right angle.

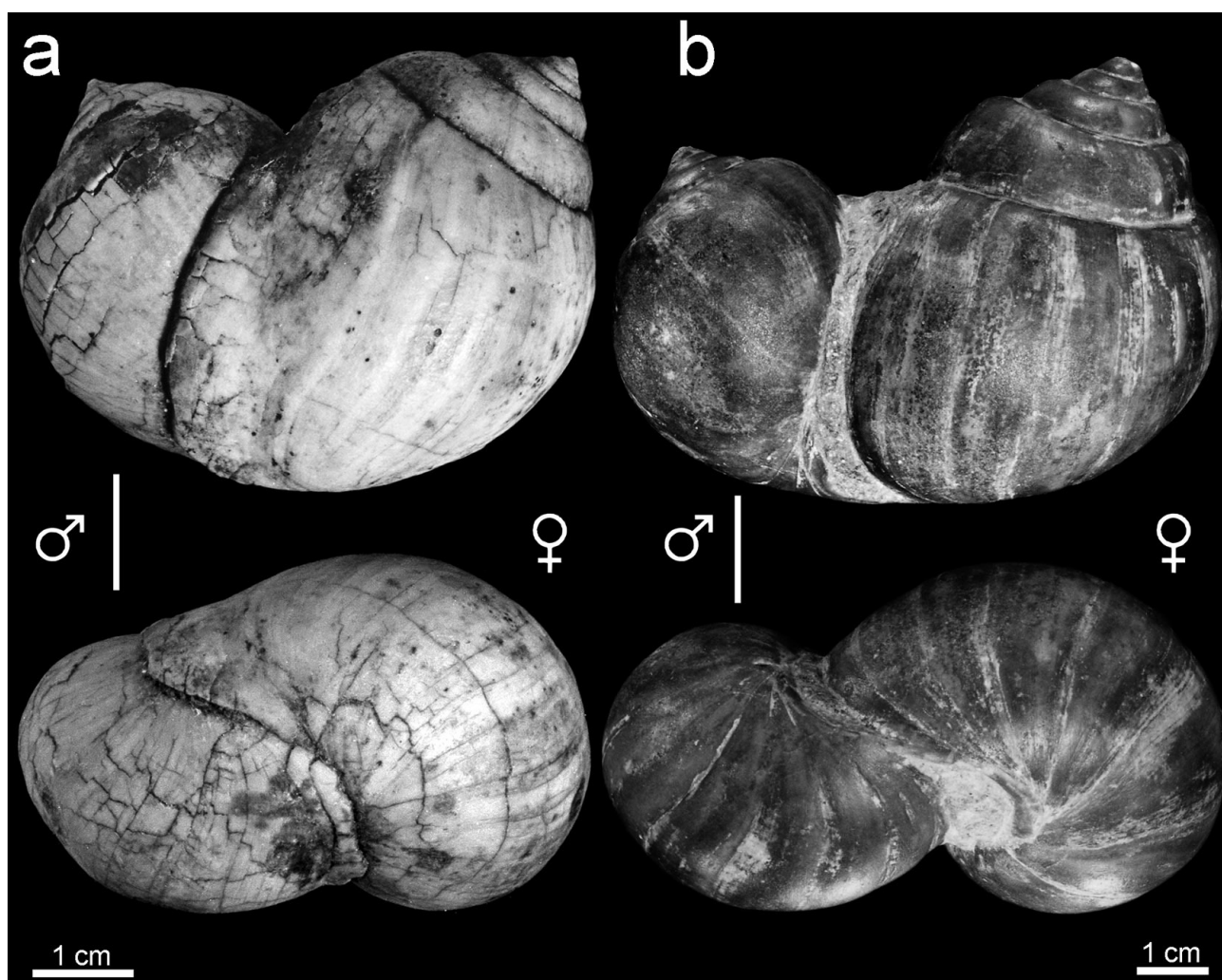


Fig. 2 - Paleogene ampullinid gastropod couples from the Venetian Alps, northern Italy, in lateral (top) and lower (bottom) views. a) Mating couple of *Globularia (Eocernina) vulcani* (Brongniart, 1823), topotypes from Bartonian basaltic hyaloclastites of Roncà (Verona). b) Mating couple of *Amaurellina (Crommium) angustata* (Grateloup, 1827) from Rupelian limestone with hyaloclastites of Gambugliano (Vicenza) (modified after Dieni, 2008).

The relative position of the two specimens can be commented in terms of mating behaviour of present day *Nautilus macromphalus* G.B. Sowerby, 1849 observed in nature and in aquarium. The best description of copulation in *N. macromphalus* was made by Mikami & Okutani (1977), who stated that it can last as long as 24 hours. A clear illustration of the position of the partners during pairing is given by Ward (1987, fig. 5.4). When mating, the two animals become enveloped in mucus and are tightly held together by their tentacles while the large copulatory organ of the male (spadix) is inserted into the female. The large size of the spadix requires an appropriate space within the male's body chamber and this is one of the main reasons why the shell of the male *Nautilus* has a wider cross section than that of the female (Saunders & Spinosa, 1978; Ward, 1987, p. 180, figs 5.10, 5.12-5.13).

Nautilids are rare in the Paleogene of the Venetian region and particularly in the San Giovanni Ilarione area, so that chance association of the two specimens is unlikely. On the other hand, nautilid shells may form at places large accumulations brought about by storms and gregarious habit (Cichowolski et al., 2012), a situation

altogether different from the occurrence of only three, closely associated specimens as here documented. We therefore propose that the two dimorphed specimens represent a male and a female of *Angulithes (Cimomia) hilarionis* and that their death occurred as a sudden event while they were mating. Some post-depositional plastic deformation of the matrix may be responsible for the slight displacement of the two specimens from the posture that mating couples display in nature.

DISCUSSION

As in the preceding case of coupled ampullinids (Dieni, 2008), and notwithstanding the different matrix in which the two nautilids were embedded, volcanism may also be invoked as a cause of death of the two nautilids. During the Middle Eocene the area around San Giovanni Ilarione was the site of intense submarine basaltic volcanism which gave rise to activities and products of various types, including lava flows, hyaloclastites, tuffs, diatremes, and dykes, distributed throughout the entire

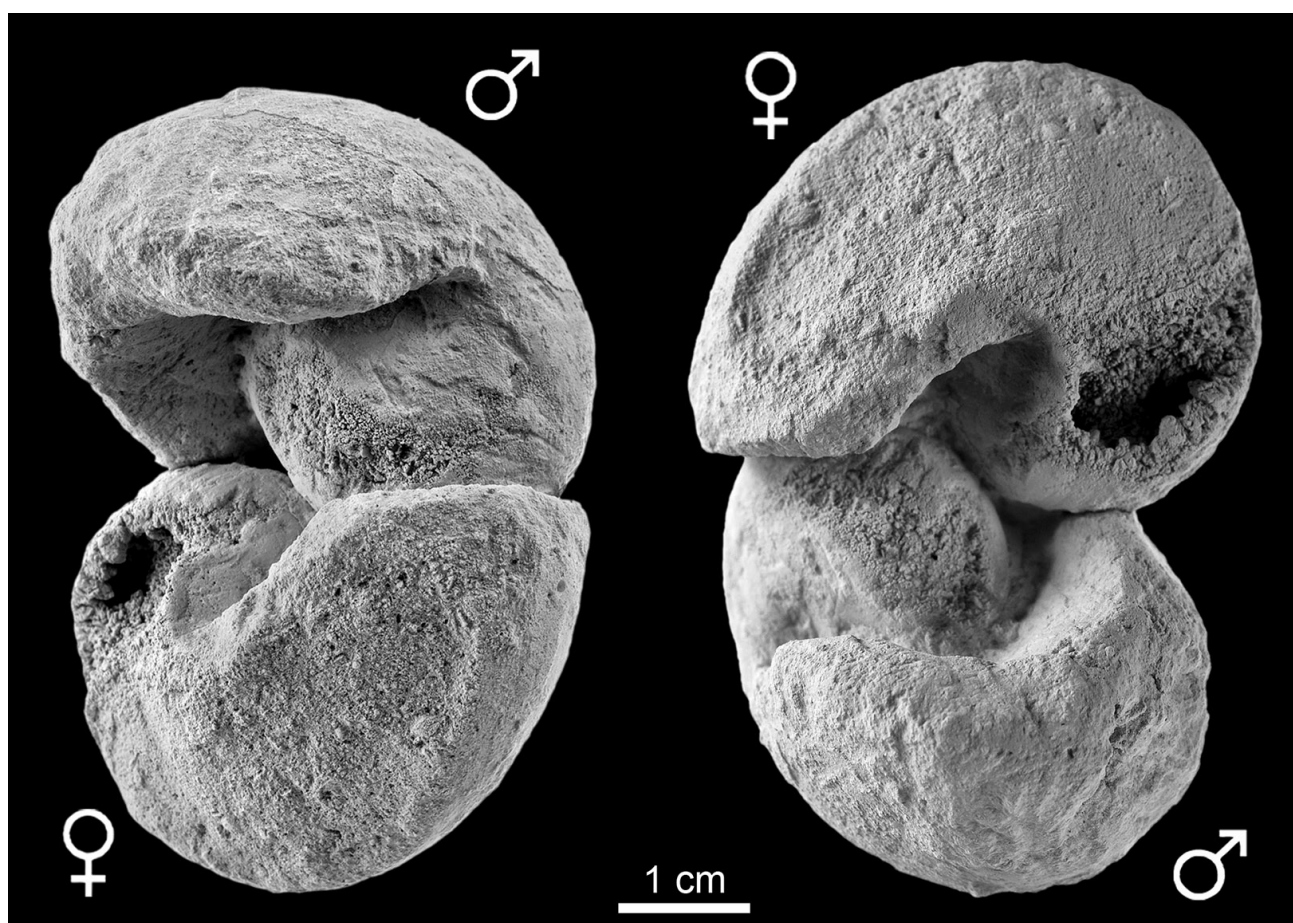


Fig. 3 - Two views of the mating couple of *Angulithes (Cimomia) hilarionis* (De Gregorio, 1880) from Lutetian biocalcarenites of Monte Serea, nearby of San Giovanni Ilarione (Verona). Neoparatypes. MGP 28717.

local sedimentary succession (Fabiani, 1911; Piccoli, 1967). In our specific case, the bed of biocalcarenite from which the nautilids were extracted lies immediately above a basaltic flow. It is therefore possible that the eruptive events were accompanied by acidification with consequent poisoning and/or overwarming of the water beyond the range within which the nautilids could survive, thus causing their death. Temperatures of 27°C or higher are lethal to living *Nautilus* in aquarium (Haven, 1977; Martin et al., 1978; Saunders, 1984). The environmental situation was comparable to that described for the ampullinid couples by Dieni (2008) and for which a similar casualty was proposed.

Living specimens of *Nautilus macromphalus* in New Caledonia and *N. pompilius* in the New Hebrides Islands have shown that these animals swim along the bottom contours (Ward & Martin, 1980; Saunders & Landman, 1988). Trapping experiments in Fiji showed that, at least there, *N. pompilius* can only be captured on the bottom (Zann, 1984). Only in the Palau Islands have observations shown *Nautilus* moving off the bottom. The latter observations, however, made utilizing remote transmitters (Ward et al., 1984), showed that movements within the water column are rare and of short duration. Adopting an uniformitarian approach to the question about the life habits of nautilids (see also Hewitt, 1989 with regards to Eocene nautilids), it is probable that our nautilid couple

would have been very close to the bottom at the moment of death. This would make it easier to maintain an eventual mating posture.

Anatomical properties of a copulating couple that would facilitate the joint burial in case of sudden death may have included: 1) the interlacement of the tentacles which kept the partners fastened to one another; 2) the mucus which, as in living *Nautilus*, very likely enveloped the partners during copulation, and 3) the anchor effect of the spadix, the large male genital organ, inserted into the female.

A parallelism with the eruption of Vesuvius in 79 A.D., when the inhabitants of Pompei were buried under pumice and their last postures “frozen” in time, allows us to regard both the ampullinid and nautilid couples from the Paleogene deposits of the Venetian Alps as having been buried, and their sexual behaviour frozen, in a “Pompeian” way. The studied gastropod and cephalopod couples are thus defined as *Pompeian fossils*, term proposed by Dieni (2008) to indicate all fossils the death of which was directly or indirectly caused by volcanic episodes.

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APPENDIX

Taxonomic notes on *Angulithes (Cimomia) hilarionis* (De Gregorio, 1880)

For the supraspecific classification the systematics proposed by Schultz (1976), largely based on the suggestions of Wiedmann (1960) in his paper on the Iberian Cretaceous nautilid faunas, is followed.

Class CEPHALOPODA Cuvier, 1797
 Order NAUTILIDA Agassiz, 1847
 Superfamily NAUTILACEAE de Blainville, 1825
 Family NAUTILIDAE de Blainville, 1825
 Subfamily NAUTILINAE d'Orbigny, 1840

Genus *Angulithes* Montfort, 1808
 Subgenus *Cimomia* Conrad, 1866

Angulithes (Cimomia) hilarionis
 (De Gregorio, 1880)

+ p 1880 *Nautilus Hilarionis* De Greg. - DE GREGORIO, p. 1, pl. 1, figs 4 a-b; non pl. B, figs 1-2 [= *Angulithes (Cimomia) imperialis* (J. de C. Sowerby, 1812)]; ? pl.1, fig. 1; ? pl. B, fig. 5).

non 1979 *Eutrophoceras hilarionis* De Gregorio - MELLINI, fig. 59.

Neotype - Specimen collected within yellow biocalcarenes cropping out at Monte Serea of San Giovanni Ilarione (Verona, northern Italy) and housed at the Museum of Geology and Palaeontology of the University of Padua under catalogue number MGP 30981 (Fig. 4).

Neoparatypes - The mating specimens collected in the same area as the neotype and deposited under catalogue number MGP 28717 (Fig. 3).

Dimensions - Neotype: D max = 32.0 mm; W = (29) mm. The dimensions of the neoparatypes are reported in the text.

Type locality - Monte Serea of San Giovanni Ilarione. For a short geological description of the area see Beschin et al., 2009, who studied the associated decapod crustaceans, erroneously dated as Ypresian.

Type area - Territory of San Giovanni Ilarione in the Province of Verona (northern Italy).

Description - The conch is medium sized and subglobular in shape. The adoral half of its outer evolution is non septate and assumed to belong to the living chamber. The cross section is more or less helmet-shaped as it is broadly rounded laterally and especially so ventrally. Dorsally it is rather deeply impressed and is considerably wider than high. The maximum width is attained at or just outside the umbilical shoulders. The umbilicus is small, closed and inconspicuous. The external suture is poorly visible and only so on the last septum of the phragmocone of the female neoparatype of the mating pair, where it seems to form a low, rather narrowly rounded ventral saddle with on either side a shallow, broadly rounded lateral lobe and a prominent narrowly rounded dorsolateral saddle centred just outside the umbilical shoulder. Although the shape of the internal suture has not been ascertained in detail, it is clear that it does not differ significantly from those of other congeneric forms. The living chamber of the neotype and of the neoparatypes is filled with sediment and as a consequence the position of the siphuncle is not determinable.

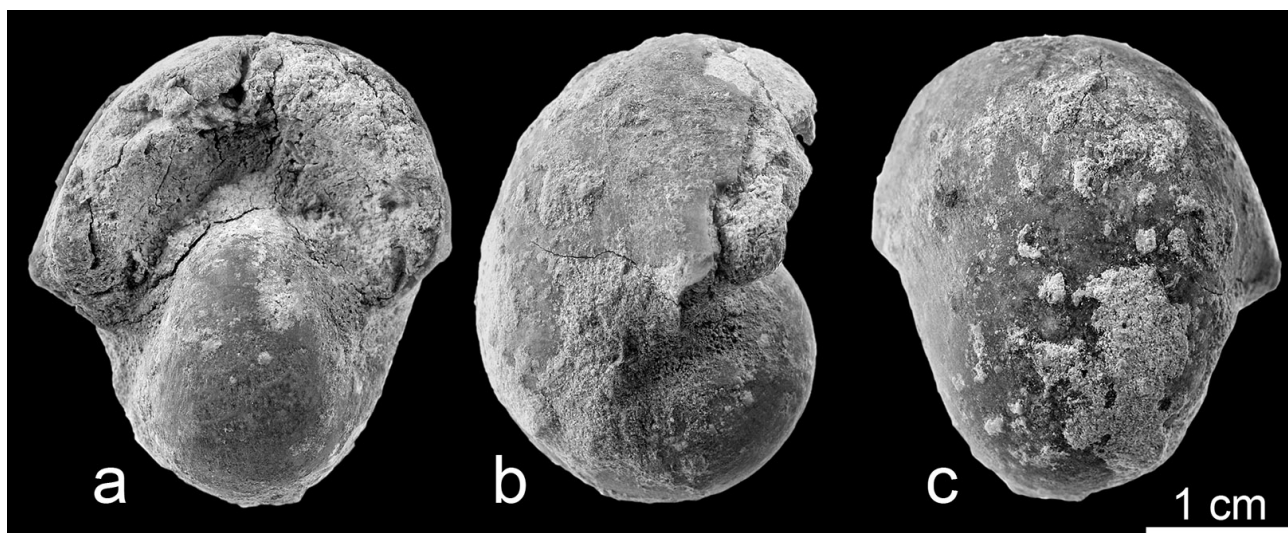


Fig. 4 - *Angulithes (Cimomia) hilarionis* (De Gregorio, 1880). Neotype. a) apertural view; b) lateral view; c) ventral view. Lutetian biocalcarenites of Monte Serea, nearby of San Giovanni Ilarione (Verona). MGP 30981.

Remarks - When De Gregorio (1880) erected his *Nautilus hilarionis* he had at disposal four specimens from the Middle Eocene of the area near San Giovanni Ilarione (Verona). Two syntypes were small and one of them [pl. 1, figs 4a-b, originally housed in the “gabinetto geologico di Palermo” (De Gregorio, pp. XIX and 1)] was incomplete, lacking at least the body chamber, but sufficiently well preserved to show the suture lines and the position of the siphuncle. The second specimen (pl. B, fig. 5, from the collection of E. Nicolis, Verona), represented only by a small fragment, was referred by the author only dubitatively to his species. The third syntype (pl. 1, fig. 1, originally deposited at Palermo), was large and deformed and ascribed by De Gregorio to his *Nautilus hilarionis* with some doubts. The best preserved specimen [lent to De Gregorio by E. Nicolis, a capable naturalist (1841-1904) from Verona, who provided a significant amount of important material, in particular fossils, to palaeontologists and geologists of his epoch] was medium sized and so well preserved that its figure (pl. B, figs 1-2, Nicolis Collection) was, according to De Gregorio, so clear in its portrayal of all the relevant characteristics of the species that he did not even need to waste his time describing it.

In 1896 Oppenheim, without even having examined the type material and therefore only on the basis of figures by De Gregorio (drawn by an artist under his supervision and not always totally accurate; e.g., De Gregorio, pp. XVIII, 2, etc.), regarded the syntypes of *Nautilus hilarionis* as a mixture of different species. The only syntype that he considered as characteristic was that figured in pl. B, figs 1-2 (see his synonymy on p. 207), which he however interpreted as a junior synonym of *Nautilus imperialis* J. de C. Sowerby, 1812. Contemporaneously (p. 208), judging the general shape, the position of the siphuncle and the “Oberflächensculptur” which “mehr an *Aturia ziczac* denken lassen”, Oppenheim suggested that the syntype of pl. 1 figs 4a-b, of De Gregorio could belong to a new species. The synonymy between *N. imperialis* and the large syntype of *N. hilarionis* of pl. B, figs 1-2,

was reaffirmed by Oppenheim in 1901 (p. 253), and was later accepted, without discussion, by the few who were concerned with Middle Eocene mollusc faunas from the Venetian region, such as Malaroda (1954, p. 72) and Abate et al. (1988, p. 152). This conspecificity seems convincing enough on the basis of many characters in common such as the general shape of the conch, the development of the internal sutures and, finally, the large dimensions [as regards *Angulithes (Cimomia) imperialis*, see the paper by Hewitt (1989, and references therein) on the nautilid cephalopods from the Eocene London Clay Formation of England].

We are convinced that, as already hypothesised by Oppenheim (1896, p. 208), the syntype of *Nautilus hilarionis* figured by De Gregorio on pl. 1, figs 4 a-b actually represents a different species from that of the syntype illustrated on pl. B, figs 1-2, referable to *A. (C.) imperialis* (J. de C. Sowerby). Unluckily the most representative syntype of *Nautilus hilarionis* (De Gregorio 1880, pl. 1, figs 4 a-b) and the other syntypes are no more available in the institutions where De Gregorio and Nicolis collections are at present housed.

We therefore establish a neotype and two neoparatypes based on the new sufficiently well preserved material from the type area, which morphological and dimensional characters are in good agreement with those of the most significant syntype mentioned above.

Age - In order to determine the age of the yellow biocalcarenites in which the new types were found, their calcareous nannoplancton content was examined. The assemblage, impoverished and moderately preserved but still useful for biostratigraphic aims, is constituted by:

Braarudosphaera spp.

Campylosphaera dela (Bramlette & Sullivan, 1961) Hay & Mohler, 1967

Chiasmolithus californicus (Sullivan, 1964) Hay & Mohler, 1967

Chiasmolithus consuetus (Bramlette & Sullivan, 1961)
Hay & Mohler, 1967
Chiasmolithus grandis (Bramlette & Riedel, 1965)
Radomski, 1968
Chiasmolithus solitus (Bramlette & Sullivan, 1961)
Locker, 1968
Chiasmolithus spp.
Coccolithus eopelagicus (Bramlette & Riedel, 1954)
Bramlette & Sullivan, 1961
Coccolithus pelagicus (Wallich, 1877) Schiller, 1930
Coccolithus spp.
Dictyococcites bisectus (Hay, Mohler & Wade, 1966)
Bukry & Percival (1971)
Dictyococcites scrippsae Bukry & Percival, 1971
Dictyococcites spp.
Discoaster barbadiensis Tan, 1927
Discoaster tanii Bramlette & Riedel, 1954
Discoaster spp.

Ericsonia spp.
Reticulofenestra umbilicus (Levin, 1965) Martini &
Ritzkowski, 1968
Reticulofenestra cf. *umbilicus* (Levin, 1965) Martini &
Ritzkowski, 1968
Reticulofenestra spp.
Sphenolithus moriformis (Brönnimann & Stradner, 1960)
Bramlette & Wilcoxon, 1967
Sphenolithus radians Deflandre in Grassé, 1952
Sphenolithus cf. *obtusius* Bukry, 1971
Sphenolithus spp.
Thoracosphaera spp.
Zygrhablithus bijugatus (Deflandre in Deflandre & Fert,
1954) Deflandre, 1959.

The simultaneous presence of *Reticulofenestra umbilicus* and *Chiasmolithus solitus* indicates that the assemblage belongs to the Biozone CP14a of Okada & Bukry (1980) and thus suggests a Lutetian age.