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SHORT NOTE - NOTA BREVE

NUCINELLA ALIBRANDI (CONTI, 1864) AND *N. SEGUENZAE* (DALL, 1898), THE LAST EUROPEAN NUCINELLIDS (BIVALVIA, PROTOBRANCHIA)

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Abstract. The revision of the genus *Nucinella* Wood, 1851 from the Italian Pleistocene led to the identification of two species, *Nucinella alibrandi* (Conti, 1864) and *N. seguenzae* (Dall, 1898). The former is from the continental shelf deposit of Monte Mario (Rome), the latter from upper slope deposits in Southern Italy (Calabria and Messina). The two species are very similar to each other and differ mainly in the anterior features of hinge. The peculiar hinge of *Nucinella* is examined in detail and its ontogenetic changes are reported. The Tertiary to Quaternary palaeobiogeographic history of *Nucinella* in the European area proves the Tethyan origins of this genus. Since the closure of the seaway to the Indo-Pacific in the Early Miocene, *Nucinella* survived in the European waters as a Tethyan relict until the Plio-Pleistocene, when cooling caused its definitive disappearance. *N. alibrandi* and *N. seguenzae* are the last representatives of the genus in the European waters.

Riassunto. La revisione del genere *Nucinella* Wood, 1851 nel Pleistocene italiano ha permesso di identificare due specie, *Nucinella alibrandi* (Conti, 1864) e *N. seguenzae* (Dall, 1898). La prima proviene dai depositi di piattaforma di Monte Mario (Roma), l'altra è invece nota per depositi di scarpata superiore affioranti nell'Italia meridionale (Calabria e Sicilia). Le due specie sono molto simili tra loro e differiscono principalmente nella morfologia della parte anteriore della cerniera. La peculiare cerniera di *Nucinella* è discussa in dettaglio e ne vengono documentate le modificazioni ontogenetiche. La storia paleobiogeografica di *Nucinella* in Europa, dal Terziario al Quaternario, dimostra l'origine tetidea del genere. A partire dalla chiusura della connessione con l'Indo-Pacifico, nel Miocene inferiore, il genere *Nucinella* è sopravvissuto nell'area europea come un relitto tetideo, fino a quando il raffreddamento plio-pleistocenico ne ha causato la scomparsa definitiva. *N. alibrandi* e *N. seguenzae* sono le ultime rappresentanti del genere nell'area europea.

Introduction

The family Nucinellidae Vokes, 1956 includes unusual bivalves, whose taxonomic position was only understood in relatively recent times by Allen & Sanders (1969), who recognised protobranch traits and close affinities to solemyoids. In shell shape and dentition, nucinellids resemble nuculids or limopsids, but they are the sole monomyarian bivalves in which the posterior adductor is lost, while the anterior one is preserved in its typical position. Actually, nucinellids range from a truly monomyarian condition to an extreme heteromyarian one (Boss 1982). Two genera are assigned to this family, *Nucinella* Wood, 1851 (monomyarian, ligament pit fully external) and *Huxleyia* Adams, 1860 (dimyarian, ligament pit chiefly internal) (Vokes 1956; Keen & Newell 1969; Allen & Sanders 1969; Pojeta 1988; Coan et al. 2000). *Nucinella* has a Jurassic to Recent distribution, while *Huxleyia* is only known as a living genus. The depth distribution ranges from shelf to slope.

The family is represented by only 15 modern species, which might "represent the high point in known nucinellid diversity" according to Pojeta (1988, p. 201). As in the modern seas, nucinellids must have been rare and with a scattered distribution in the past and this makes the study of this group particularly difficult.

No living species is known from the European waters or from other areas in the Northeast Atlantic, while there are several records of *Nucinella* from the Tertiary and Pleistocene of Europe (Vokes 1956). The youngest known *Nucinella* reported from Europe is from the Pleistocene of Italy, but there is a confused history of descriptions and identifications, preventing one from drawing any conclusion about *Nucinella* in the Mediterranean Pleistocene, other than the mere occurrence. The aim of the present work is to check these records and identify the taxa involved. This work is also an occasion to provide new observations on the nucinellid shell and to attempt an outline of the Tertiary to Quaternary palaeobiogeography of the European nucinellids.

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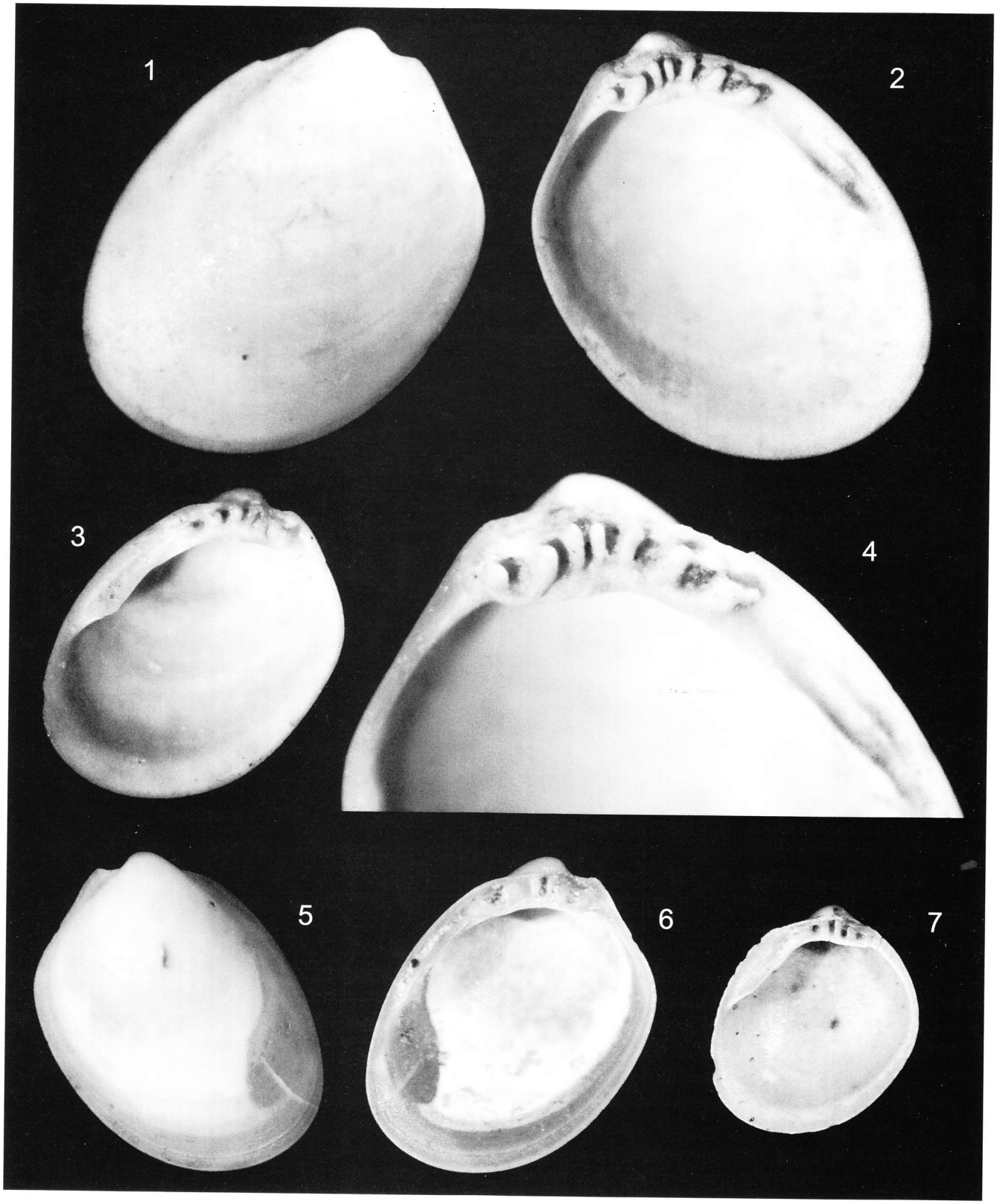

PLATE 1

Figs 1-4 - *Nucinella alibrandi* (Conti, 1864), Monte Mario (Rome), Pleistocene (Cerulli-Irelli collection). 1, 2. left valve, 3.28 mm; 3. right valve, 2.35 mm (illustrated by Cerulli-Irelli 1909, pl. 23, figs 15a, b); 4. hinge detail of fig. 2.

Figs 5-7 - *Nucinella seguenzae* (Dall, 1898), Bovalino Superiore (Southern Calabria), Pleistocene. 5, 6. right valve, 2.46 mm; 7. right valve, 1.77 mm.

Systematic palaeontology

Class **Bivalvia** Linné, 1758

Subclass **Protobranchia** Pelseneer, 1889

Order **Solemyoida** Dall, 1889

Family Nucinellidae Vokes, 1956

Genus *Nucinella* Wood, 1851

Type species: *Pleurodon ovalis* Wood 1840

Nucinella alibrandi (Conti, 1864)

Pl. 1, figs 1-4

1864 *Nuculina alibrandi* Conti, pp. 23, 47.

1907 *Nucinella ovalis* (Wood) – Cerulli-Irelli, p. 123.

1909 *Nucinella ovalis* (Wood) – Cerulli-Irelli, p. 195, pl. 23, figs. 15a, b.

1956 *Nucinella alibrandi* – Vokes, p. 668.

Type material. Probably lost. The Conti collection is in Ferrara (Museo di Storia Naturale) and a minor part in Vienna (Naturhistorisches Museum), but no material of *Nucinella* is present in either museum (E. Trevisani pers. comm.).

Examined material. Cerulli-Irelli collection, Museo Paleontologico dell'Università di Roma, 2 valves, Monte Mario (Rome), Pleistocene.

Description. Shell small, obliquely ovate, strongly inequilateral, thin-walled, moderately convex. Umbo small. Dorsal margin narrow, almost straight. Anterior margin as a long smooth curve. Ventral margin well rounded. Postero-ventral margin barely convex, narrowly curving to an almost straight postero-dorsal margin. Hinge plate moderately thick, wider posteriorly and extending to antero-dorsal margin. Largest valve 3.28 mm in height, with seven subumbonal teeth in a single arched series, and a long lamellar antero-dorsal tooth. Subumbonal teeth more-or-less perpendicular to shell margin, ranging in shape from rather flattened (central teeth) to square (anterior and posterior teeth). Last posterior tooth smaller and roundish. Lateral tooth prominent, blade-like, separated from shell margin by a wide socket with a small internal tooth forming an ill defined low ridge. Tooth-like structures, close and parallel to dorsal margin, are present between anterior and posterior subumbonal teeth. Ligament insertion external, ovate, immediately posterior to beak. Pallial line indistinct, no sinus. Anterior adductor muscle scar large, ovate; no posterior adductor scar. Outer shell surface smooth, except for weak growth striae. Prodissoconch not seen.

Distribution. Only known from the Pleistocene shelf deposits of Monte Mario, Rome.

Remarks. See under the following species.

Nucinella seguenzae (Dall, 1898)

Pl. 1, figs 5-7; Fig. 1

1877 *Nucinella ovalis* (Wood) - Seguenza, p. 10, pl. 2, figs. 8a-c.

1898 *Pleurodon seguenzae* Dall, p. 601.

1956 *Nucinella seguenzai* - Vokes, p. 664 (unjustified emendedation).

Type material. Probably lost. No type material of *N. seguenzae* is present in the Dall collection of the United Nations National Museum, Washington D.C. (W. Blow pers. comm.).

Examined material. Bovalino Superiore (southern Calabria, Jonian side, author's collection), Pleistocene, 4 valves (two partly broken).

Description. Shell small, obliquely ovate, strongly inequilateral, thin-walled, moderately convex. Umbo small. Dorsal margin narrow, almost straight. Anterior margin a long smooth curve. Ventral margin well rounded. Postero-ventral margin moderately convex, narrowly curving to a straight to slightly concave postero-dorsal margin. Hinge plate moderately thick, posteriorly and anteriorly a little wider than centrally, extending to antero-dorsal margin. Largest valve 2.46 mm in height, with six subumbonal teeth as a single arched series, and a long lamellar antero-dorsal tooth. Subumbonal teeth more-or-less perpendicular to shell margin, ranging in shape from rather flattened (central teeth) to square (anterior and posterior teeth). Lateral tooth prominent, blade-like, separated from shell margin by a narrow socket. Tooth-like structures, close and parallel to dorsal margin, are present between anterior and posterior subumbonal teeth. Ligament insertion external, ovate, immediately posterior to beak. Pallial line distinct, no sinus. Anterior adductor muscle scar large, ovate; no posterior adductor scar. Outer shell surface smooth, except for weak growth striae. Prodissoconch roundish, about 260 μm in diameter.

Distribution. Only known from the Pleistocene of Southern Italy (Calabria and Messina). The present material is from upper slope silty beds.

Remarks. The confused history of descriptions and records of Italian Pleistocene nucinellids can be summarised as follows:

1) Seguenza (1877) reported *Nucinella ovalis* (Wood 1840) from Calatabiano, a locality of "Astian" age near Messina, Sicily. The size scale indicates a shell height of a little less than 4 mm. This species was again reported (Seguenza 1880) from another "Astian" locality (Gallina) on the Calabrian side of Messina Strait, with brief remarks about the larger size of the new specimen(s). Most of the "Astian" (Late Pliocene) localities reported by Seguenza have proven to be Pleistocene in age (Di Geronimo & La Perna 1997) and the mollusc fauna reported by Seguenza from Calatabiano and Gallina points to a Pleistocene age, rather than Pliocene, and to a deep shelf-upper bathyal deposition.

2) Conti (1864) described *Nuculina alibrandi* from Monte Mario, near Rome. The species was not illustrated and most of the description deals with the hinge features: "Hinge wide, a little curving, below two auricles like in

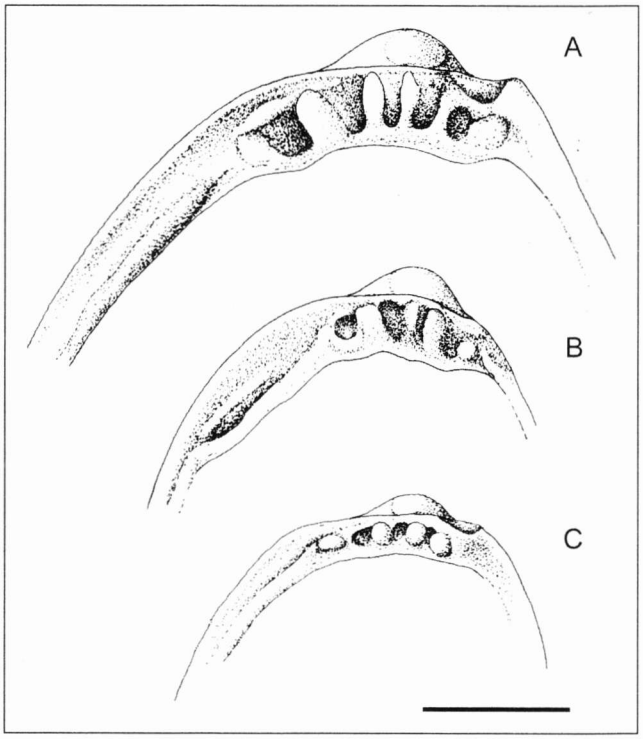

Fig. 1 - Hinge growth series of *N. seguenzae*. Size (height) of valves: A. 2.46 mm (same as Pl. 1, figs. 5, 6); B. 1.60 mm; C. 1.30 mm. Scale bar = 0.5 mm.

Limopsis, with an uninterrupted series of seven unequal conical teeth; a large elongated lateral tooth triangular in shape in its posterior part [= anterior, because, previously, the single muscle scar of *Nucinella* was thought to be posterior]". Size was reported as "2 mm in length and 3 mm in width". In the same work and from the same locality, Conti described *Nuculina riccioli*, but this species was most probably based on juvenile broken valves of *Nucula*, as also thought by Cerulli-Irelli (1909) and Vokes (1956). Monte Mario is a classical Pleistocene locality, with a rich shallow-water mollusc fauna.

3) Dall (1898), described *Pleurodon seguenzae* on "Pliocene" material from Calabria which "was sent to Dr. Jeffreys [by Seguenza] under the name of *P. ovalis*". This species was supposed to be the same as that reported by Seguenza (1880) and described as being "much larger even than *P. miliaris*", as having eight "crowded" teeth, of which five are posterior [= anterior], an anteriorly [= posteriorly] excavated inner edge of the hinge plate, and a cardinal border at the lateral teeth narrower than in other species. *P. seguenzae* was not illustrated and size was said to be 5 mm in height and 4 mm in width.

4) Cerulli-Irelli (1907) reported *Nuculina ovalis* (Wood 1840) from Monte Mario, synonymising it with *Nuculina alibrandi* Conti 1864. He wrote to have seen only two valves in the Conti collection. The species was again reported by Cerulli-Irelli (1909), who illustrated one valve from Monte Mario.

5) Vokes (1956) made an annotated list of all the fossil and living nucinellids. As far as *Nucinella seguenzae* is concerned, he emended the name to *seguenzai*, but this is an unjustified emendation (ICZN, Art. 33). Also, he noted a certain disagreement between Seguenza's illustration (of *Nucinella ovalis*) and the description given by Dall (of *Pleurodon seguenzae*), since the former reported a smaller size, five cardinal teeth instead of eight, and a straight edge of hinge plate. He thus hypothesised that at least two distinct species might occur in the Italian "Pliocene". Concerning the valve illustrated by Cerulli-Irelli (1909), Vokes noted an "unusual arrangement of the cardinal teeth with what appear to be interdigitating elements" and thus, he left in doubt the status of *N. alibrandi*. However, there is no unusual hinge feature on this valve, as seen in the present illustration (Pl. 1, fig. 3) of the same valve.

The present data allow us to believe that two distinct species occurred in the Pleistocene of Italy, namely *N. alibrandi* and *N. seguenzae*. No species of *Nucinella* has a hinge plate edge so straight as illustrated by Seguenza (his illustration seems to be diagrammatic, as also suggested by the cardinal teeth, mostly of similar size and shape). The inner edge of the hinge plate appears anteriorly "excavated" in both species and this feature is more and more evident with growth (Fig. 1). In *N. seguenzae* the "cardinal border at the lateral tooth" is narrow, as described by Dall, while it is markedly larger in *N. alibrandi*. Further, *N. alibrandi* has a "large triangular elongated" lateral tooth, as originally described, larger than the lateral tooth of *N. seguenzae* in valves of similar size (Pl. 1, figs. 3, 6). The distinctive features between *N. seguenzae* and *N. alibrandi* are thus mainly represented by the lateral dentition: smaller lateral tooth and narrower marginal socket in *N. seguenzae*, larger tooth and wider socket in *N. alibrandi*. The number of subumbonal teeth can not be considered as a distinctive feature, because they increase in number with growth (Fig. 1) and this may explain the differences between Seguenza's and Dall's description of *N. seguenzae*. It is difficult to find other differences between *N. seguenzae* and *N. alibrandi*. The former most probably attained a larger size (up to 5 mm) but, at a similar size, the shell of *N. seguenzae* is more delicate and with a thinner wall than *N. alibrandi*. The antero-dorsal margin of *N. alibrandi* is almost straight, whereas it is seems slightly concave in *N. seguenzae*. Further, the different ecologic distribution of *N. alibrandi* (shelf) and *N. seguenzae* (upper slope), supports the hypothesis of two distinct species.

Nucinella ovalis is the most frequent name among the records of living and fossil nucinellids (e.g. Vokes 1956, Lauriat-Rage 1981, Marquet 2002), but almost none of its records, ranging from Oligocene to Recent and from Europe (fossil) to South Africa and even to Indo-Pacific (living), can be uncritically accepted. *N. ovalis* was described from the Coralline Crag Formation (Ear-

ly Pliocene), Southeastern England (Wood 1840, 1851). Unfortunately, no type material is present in the Wood collections at the British Museum of Natural History (P. Jeffery pers. comm.), the Ipswich Museum (D.J. Lampard pers. comm.), the Norfolk Museum (T. Irwin pers. comm.) and also the search at the British Geological Service (P. Taylor pers. comm.) has been unsuccessful yet. *N. ovalis* was recently reported by Marquet (2002) from the Early Pliocene of Belgium and this record actually is the best candidate on which to base the concept of *N. ovalis*, because of its geographic location (close to the type locality) and its stratigraphic position. *N. ovalis* is large up to 2.0 mm in height, much more elongated and narrower than *N. alibrandi* and *N. seguenzae* and with a narrow lateral socket.

The two Pleistocene species are notably similar to *N. calabra*, described by Seguenza (1877) from the Late Miocene of southern Calabria. It was reported by Moroni & Ruggieri (1983) from the Late Miocene of Sicily, but the illustrated specimens (a closed shells and two hinge fragments) prevent making a full comparison with other species. However, *N. calabra* has a slightly more oblique shell shape and the hinge plate has a straighter inner margin.

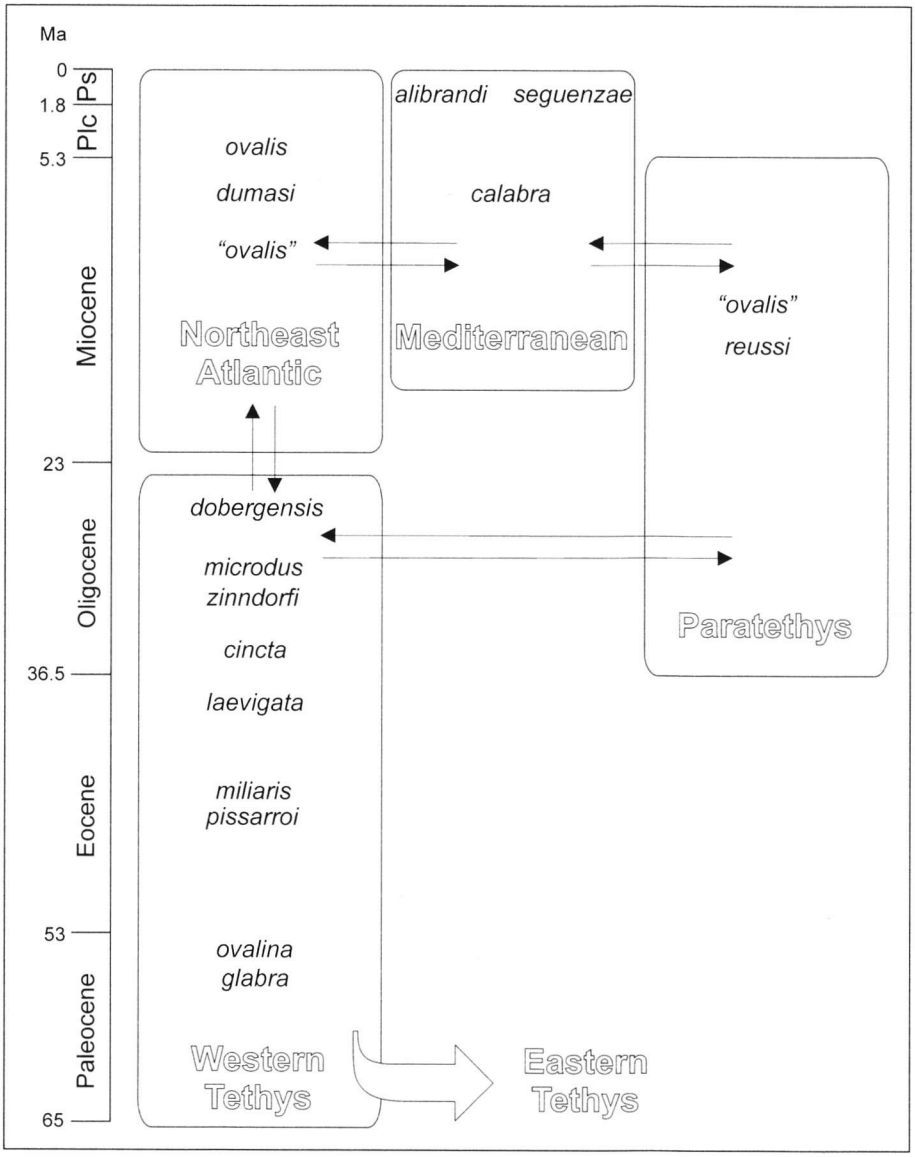

Fig. 2 - Palaeobiogeographic scheme of *Nucinella* in Europe. Rectangular areas represent distinct palaeogeographic-biogeographic units and arrows indicate connections among them. The stratigraphic ranges of species follow Vokes (1956), with additional data from Janssen (1979), Lauriat-Rage (1981), Moroni & Ruggieri (1983), Studencka et al. (1998) and Marquet (2002). *N. glabra* (Ravn, 1939), Paleocene, Denmark; *N. ovalina* Cossmann, 1887, Upper Paleocene, Paris Basin; *N. pissarroi* Cossmann, 1904, Middle Eocene, Loire Basin; *N. miliaris* (Deshayes, 1829), Middle Eocene, Paris Basin; *N. laevigata* (Vincent, 1897), Upper Eocene, Belgium; *N. cincta* von Koenen, 1893; Early Oligocene, North Germany; *N. microdus* (Boettger, 1869), Middle Oligocene, Germany; *N. zinndorfi* (Zilch, 1937), Middle Oligocene, Germany; *N. dobergensis* (Lienenklaus, 1890), Upper Oligocene, Germany; *N. dumasi* (Cossmann & Peyrot, 1914), Late Miocene, Atlantic France; *N. calabra* Seguenza, 1877, Late Miocene, southern Italy; *N. reussi* Deshayes, 1860, Miocene, Austria; *N. ovalis* (Wood, 1840), Early Pliocene, South England and Belgium (brackets indicate probable misidentifications); *N. alibrandi* (Conti, 1864), Pleistocene, central Italy; *N. seguenzae* (Dall, 1898), Pleistocene, southern Italy.

The hinge of *Nucinella*

As stated by Campbell et al. (2001), the odd hinge of *Nucinella* is a mixture of "peg, blade and chevron teeth", which "does not fit into any existing category of dentition". This pseudo-taxodont hinge may support the hypothesis of Pojeta (1988, p. 210) about a new evolution of teeth in nucinellaceans from the edentulous solemyoids, but Cope (2000) believes that the Nucinelloidea and the Solemyoidea are derived from a common dentate ancestor. The hinge of *Nucinella* consists of few subumbonal teeth (two to nine, according to Pojeta 1988) and one or two lateral anterior teeth, all developing on a rather wide hinge plate. The subumbonal teeth usually have different shape, size and orientation, with the central ones being thinner than the more distal ones. There is no separation between posterior and anterior teeth, whereas the lateral teeth are widely separated from the subumbonal ones. The

lateral teeth are definitely lamellar, and when two teeth are present, only one is well developed and prominent. In this case the second tooth is placed within the socket and parallel to the larger one.

There is another unusual hinge feature, i.e. some "pseudo-teeth" margining the dorsal side of sockets, better seen between the last anterior and posterior tooth couples. They are elliptic-elongated or somewhat arched and Campbell et al. (2001) referred to them as "hinge spurs". These tooth-like structures were noted for the first time by Vokes (1966) on an Eocene species of *Nucinella*. They can be also seen in various illustrations of *Nucinella* (e.g. Moroni & Ruggieri 1983; Matsukuma et al. 1982; Pojeta 1988). The tooth-like structure margining the last posterior socket is located below the ligament pit and is coalescent with the penultimate tooth, making it appear like a chevron. The meaning of the hinge-spurs is unclear, since they do not correspond to sockets in the opposite valve.

The hinge growth series of *N. seguenzae* (Fig. 1) matches the nucinellid ontogenetic pattern reported by Bernard (1897). The subumbonal teeth are roundish and of similar size in the early stages, becoming more and more different with growth. The growth pattern gives the impression that new teeth are added in the central part of the series, below the beak, with the older ones giving space to the new ones. Other changes comprise the development of hinge spurs and the appearance of an edentulous gap between the lateral tooth and the subumbonal teeth. A second smaller lateral tooth may develop in the intermediate stages (Fig. 1b). The presence of a smaller lateral tooth seems to be also an intraspecifically variable feature, as reported by Matsukuma et al. (1982) on a Japanese living species.

Palaeobiogeographic history of the European nucinellids

In the Early Pliocene *Nucinella* was present at relatively high latitudes in the Northeast Atlantic, from Southern England (Wood 1840, 1851) and Belgium (Marquet 2002), south to France and Portugal (Lauriat-Rage 1981). There are no records from the Mediterranean Pliocene, but the occurrence of *Nucinella* is to be expected, because it was present both in the Late Miocene of Southern Italy (see above) and in the Pleistocene (present work). *Nucinella* was also present in the Middle Miocene Paratethys (Studencka et al. 1998), and in the Atlantic Miocene (Glibert 1945). As far as we know, *N. alibrandi* and *N. seguenzae* were the last nucinellids in the European area.

According to present knowledge, nucinellids have a temperate to tropical distribution, ranging from ca 50°N to 45°S, but the genus *Nucinella* seems to have a narrower and lower latitudinal distribution than *Huxleya*. It is important to note that many living nucinellids are from deep waters, while all the fossil records from Europe are probably from shelf deposits, except for *N. seguenzae*, found in upper slope sediments. *Nucinella* thus appears as a group with warm to temperate biogeographic affinities, but with a tendency to migrate into deeper waters. The biogeographic character of *Nucinella* is related to its Tethyan origin, as testified by the oldest record of this genus, from the Early Jurassic of Europe (Vokes 1956), and by its history in the European area (Fig. 2). There are several records from the European Tertiary, belonging to the Western Tethys Region as biogeographically defined by Harzhauser et al. (2002). With the closure of the northern seaway (around the Oligocene-Miocene boundary), a new biogeographic area in the Northeast Atlantic became established. In this area, *Nucinella* is present up to the Early Pliocene. The closure of the southeastern seaway to the Indo-Pacific in the late Early Miocene (Rögl 1998; Harzhauser et al. 2002) led to the definitive disconnection of the European nucinellid stock from the Indo-Pacific one and, from then on, *Nucinella* represents a "Tethyan relict" in the European waters (Northeast Atlantic, Mediterranean and Paratethys) and even in the tropical Western Atlantic, where two living species are known (Campbell et al. 2001). Finally, the Plio-Pleistocene cooling played an important role in the extinction of *Nucinella*, first in the Northeast Atlantic (Middle Pliocene) and then in the Mediterranean (Pleistocene).

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