

Neogene *Macoma* (Bivalvia, Tellinidae) migration from the Pacific to the Atlantic through the Bering Strait: taxonomic and biogeographic remarks

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ABSTRACT – Modern North Pacific shells traditionally ascribed to *Macoma obliqua* (Sowerby, 1817) from European Neogene belong to a distinct, although related species, *M. golikovi* Scarlato & Kafanov, 1988. The latter may be considered the ancestor of *M. obliqua*. It is likely that the migration of *Macoma golikovi* - *M. obliqua* species-complex from the Pacific to the Atlantic through the Bering Strait occurred in the Late Miocene or in the earliest Pliocene.

RIASSUNTO – [Migrazione della neogenica *Macoma* (Bivalvia, Tellinidae) dal Pacifico all'Atlantico attraverso lo Stretto di Bering: osservazioni tassonomiche e biogeografiche] – Le conchiglie attuali del Nord Pacifico, tradizionalmente attribuite a *Macoma obliqua* (Sowerby, 1817) specie del Neogene europeo, appartengono a una specie distinta, seppure correlata a questa, *M. golikovi* Scarlato & Kafanov, 1988. Quest'ultima può essere considerata come l'antenato di *M. obliqua*.

È probabile che la migrazione della specie-gruppo *Macoma golikovi* dall'Oceano Pacifico all'Atlantico, attraverso lo Stretto di Bering, sia avvenuto nel tardo Miocene o all'inizio del Pliocene.

INTRODUCTION

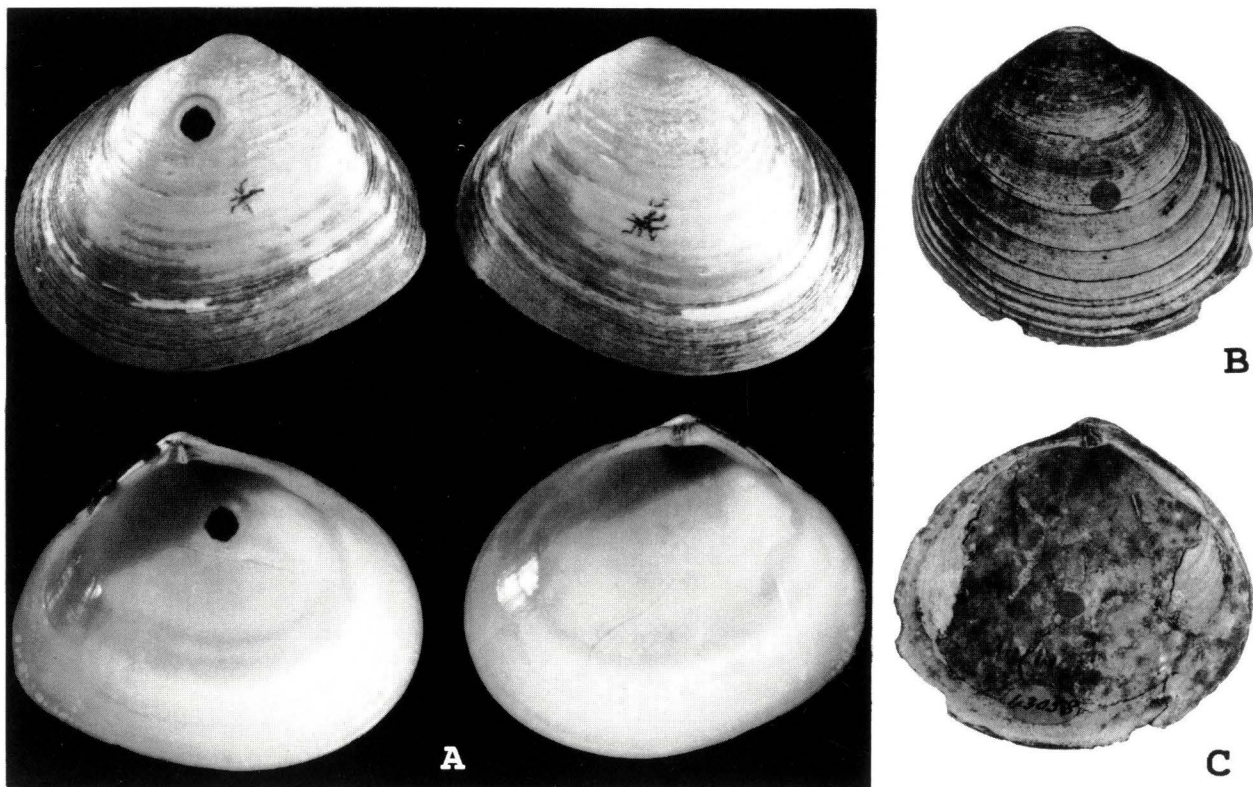
The taxonomic status of a widely distributed and abundant species of Recent North Pacific *Macoma* has so far remained unclear. Up to 1960s, this species was identified as *Macoma incongrua* (von Martens, 1865) (for synonyms see Coan, 1971; p. 26) (Text-fig. 1A).

According to Golikov & Scarlato (1967) and Coan (1969, 1970) *M. incongrua* is geographically restricted only to the Asian warm-temperate zone (Sea of Japan, Pacific coast of Japan) and was not found elsewhere in the northwestern Pacific. Related American specimens were identified (Coan, 1969) as *M. obliqua* (Sowerby, 1817) [non W. Wood, 1815, nor Soot-Ryen, 1932], a species originally described from the Red Crag of England and commonly occurring in the Pliocene-Pleistocene of western Europe and Mediterranean (Heering, 1950; Anon., 1963; Gladenkov *et al.*, 1980; Raffi, 1986; Malatesta & Zarlenga, 1988; Bellomo & Raffi, 1991). The overall shape of pallial line and pallial sinus in Recent Pacific and Neogene European shells seemed to support this identification. However, Kafanov *et al.* (1997) investigated statistically the variability of the external and internal shell features in the North Pacific *Macoma balthica* Linnaeus, 1758 and *M. calcarea* Gmelin, 1791 and showed that the patterns of the pallial line and pallial sinus, as well as the extent of their development were adaptive characters (Evseev, 1975) and should not be overestimated in identification at species-level.

Thus, there are some doubts that the North Atlantic *Macoma obliqua* (Sowerby, 1817) and the North Pacific *M. obliqua* auctt. are identical. This implies that the migration of *M. obliqua* from the Pacific to the Atlantic through the Bering Strait during the Late Miocene, as suggested by Coan (1969), should be reinvestigated. Moreover, Coan (1969, 1971) based his reconstruction only on the Pleistocene records of "*M. obliqua*" from the North Pacific. The presence of relatives of *M. obliqua* in the Early Pliocene deposits from the Atlantic Coast of North America could equally suggest a possible opposite migration from the North Atlantic to the North Pacific.

MATERIAL

The collections of Recent American "*M. obliqua*" of authors in the Los Angeles County Museum of Natural History (LACM), California Academy of Sciences (CAS) and Santa Barbara Museum of Natural History (SBMNH) were studied and compared with the allied Asian species from the collections of the Zoological Institute (ZISP), Russian Academy of Sciences, St.-Petersburg, the Geological Institute (GIN), Russian Academy of Sciences, Moscow, the Zoological Museum of the Far East State University (ZMFESU), Vladivostok, and the Institute Museum, Institute of Marine Biology (IMIBM), Far East Branch of the Russian Academy of Sciences, Vladivostok, Russia. The total material



Text-fig. 1 - A) *Macoma incongrua* (von Martens, 1865), lectotype (designated by Coan, 1971, p. 26) of *Tellina incongrua* von Martens, 1865, Yokohama, Japan, Zoologisches Museum, Humboldt Universität, Berlin, no. 7624, shell length 24.4mm; B, C) *Macoma obliqua* (Sowerby, 1817), lectotype (designated by Coan, 1971, p. 26) of *Tellina obliqua* Sowerby, 1817, Red Crag, Suffolk, England, BMNH Fossil Mollusca Section no. 43058, shell length 45.6mm, left valve exterior (B) and interior (C).

examined belongs to 253 sets (more than 1,000 specimens). Shells of Neogene European *Macoma obliqua* (Sowerby, 1817) were studied in the Museum of Paleontology (UCMP), University of California, Berkeley, U.S.A. (8 sets, 12 specimens).

Symbols are: L = valve length, H = valve height, B = valve convexity, A = the length of the anterior part of valve. The ratios are given for adult specimens only. Abbreviation for other collections consulted: BMNH = The Natural History Museum (former British Museum (Natural History)), London, England; LACM = Los Angeles County Museum of Natural History, Los Angeles, CA, U.S.A.; USNM = United States National Museum, Smithsonian Institution, Washington, DC, U.S.A., PIN = Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

TAXONOMY

MACOMA (MACOMA) GOLIKOVI Scarlato & Kafanov, 1988

Text-figs. 2A-F

Macoma incongrua VON MARTENS, auctt., non von Martens, 1865: MERKLIN *et al.*, 1962, p. 42, pl. 8, figs. 2-3; PETROV, 1966, p. 229, pl. 19, figs. 12-16; GOLIKOV & SCARLATO, 1967, p. 124 (part.), not pl. 14, fig. 3.

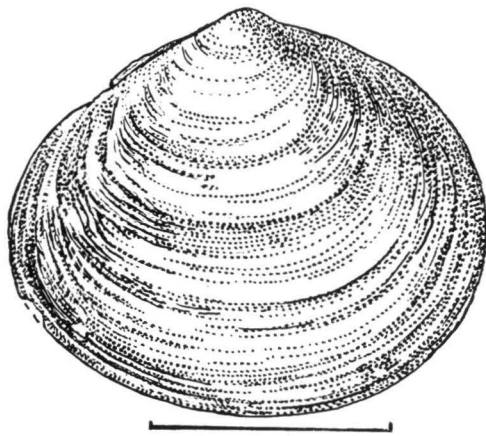
Macoma obliqua J. SOWERBY, auctt., non J. Sowerby, 1817: COAN, 1969, p. 277 (part.); COAN, 1971, p. 26 (part.), pl. 7, fig. 33, text-fig. 14, not pl. 6, fig. 31; PETROV, 1982, p. 111, pl. 20, figs. 7-11.

Macoma orbiculata SCARLATO, 1981, p. 361, photo 359; GLADENKOV *et al.*, 1984, p. 219, pl. 53, figs. 9, 14, 16.

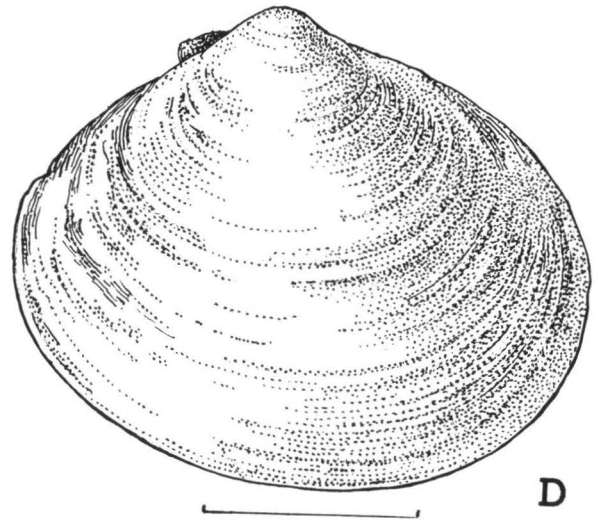
Macoma (Macoma) golikovi SCARLATO & KAFANOV, 1988, p. 939, as *nom. subst.* for *Macoma orbiculata* Scarlato, 1981, non

Text-fig. 2 - *Macoma golikovi* Scarlato & Kafanov, 1988; A-C) paratype of *Macoma orbiculata* Scarlato, 1981, PIN no. 173/3962, Sea of Japan, off Uspeniya Cape, 48°25.5'N 141°58.8'E, depth 35m, sand and stones, coll. r/v "Toporok", sta. 26, August 19, 1949, shell length 31.7mm, right valve exterior (A), left valve interior (B) and right valve interior (C); D-F) ZMFESU no. 12151/Bv-1562 (former LACM 75-67), Lituya Bay, Glacier Bay Nat Mon, Skagway-Yukutat Co., Alaska, 58°37.2'N 137°38'W, depth 15m, greenish gray mud, coll. L. Marinovich, Jr., 7 Jun 1975, shell length 28.5mm, right valve exterior (D), left valve interior (E) and right valve interior (F). All figures (A-F) were drawn from Hewlett Packard ScanJet 3p scanner pictures (x 1.5).

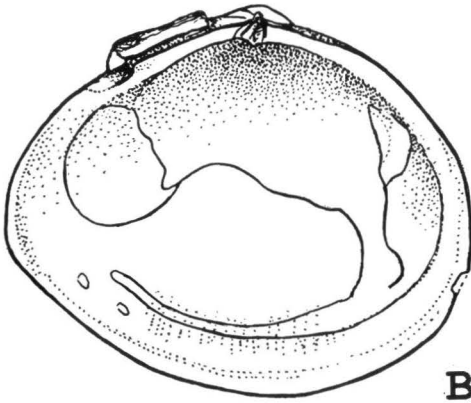




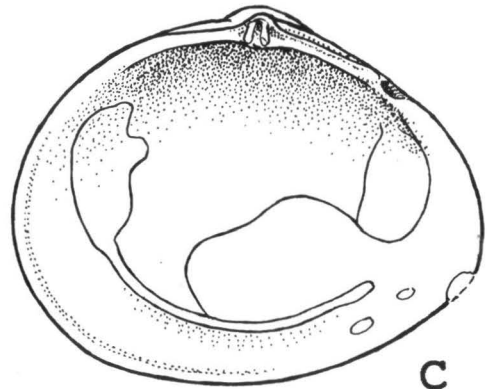
A



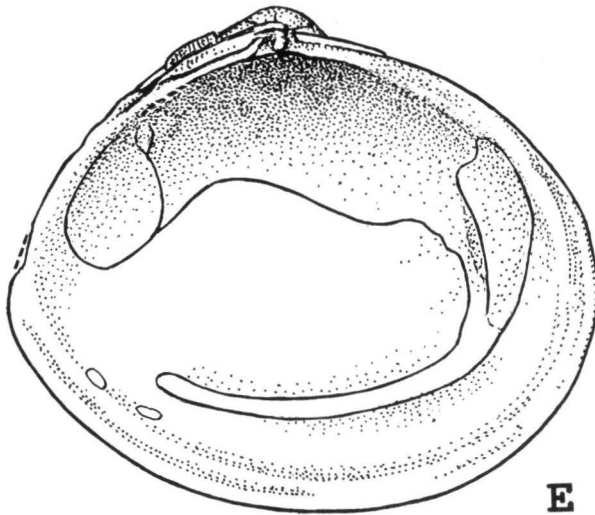
D



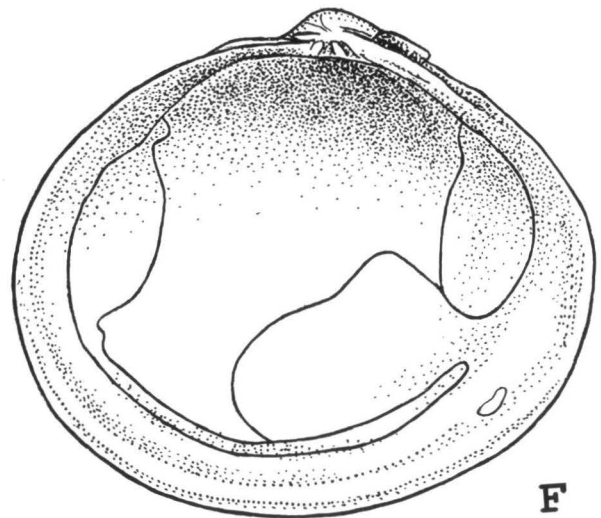
B



C



E



F

Kanno, 1958, p. 192, pl. 4, figs. 13, 14; KAFANOV, 1991, p. 72. *Macoma lukini* KAMENEV, 1989, p. 89 (footnote) [*nomen nudum*]; KAMENEV, 1990, p. 129, text-figs. 2, 3; KAMENEV, 1995, p. 10, text-figs. 7-10.

Type material and localities – *Macoma orbiculata* Scarlato, 1981, holotype – Zoological Institute, Russian Academy of Sciences, St.-Petersburg, no. 9730. Sea of Japan, Tatar Strait, off South Sakhalin, depth 59 m, muddy sand with gravel and stones, coll. O.A. Scarlato, r/v "Toporok", 1949.

Macoma lukini Kamenev, 1990, holotype – Institute Museum, Institute of Marine Biology, Far East Branch of the Russian Academy of Sciences, Vladivostok, no. 1/33220. Kraternaya Bight, Yankicha Island, Ushishir islands, middle Kurile Islands, depth 11 m, muddy sand, coll. G.M. Kamenev, August 26, 1985.

Discussion – The structure of the pallial line and sinus in true *Macoma obliqua* (Sowerby, 1817) and in Recent North Pacific "*Macoma obliqua*", auctt. are very similar. However, the former may be easily distinguished from the latter by its higher, more equilateral shell, sharper apical angle and more protruded beaks. On the other hand, the northeastern Pacific "*Macoma obliqua*", auctt. and *M. orbiculata* Scarlato, 1981, from Tatar Strait, Sea of Japan, are identical (Text-fig. 2). As judged from its original description (Scarlato, 1981, p. 361; unfortunately, this author did not illustrate the inside of the right valve), *M. orbiculata* was said to differ in having a larger pallial sinus and pallial line merging in the left valve. However, in *Macoma* this character is highly variable (Kafanov *et al.*, 1997) and, among other aspects, is age-dependent (Evseev, 1975).

Macoma orbiculata Scarlato, 1981 being preoccupied (Kanno, 1958, p. 192, pl. 4, figs. 13, 14) and should be renamed as *M. golikovi* Scarlato & Kafanov, 1988.

It is clear that *M. lukini* Kamenev, 1990, is a junior synonym of *M. golikovi* Scarlato & Kafanov, 1988. The author himself (Kamenev, 1990, p. 131) noted: "The review of the data on Recent *M. obliqua*, deposited in the collections of the Zoological Institute of the Academy of Sciences of the USSR... revealed, that the only character specific for *M. lukini* sp. n. is the valve somewhat more prolonged and flattened...". The comparison of H/L, B/L and A/L indices that Kamenev (1990, p. 130) presented in a table for *M. lukini* and the North Pacific "*M. obliqua*" (the latter data from Dunnill & Ellis, 1969) is inadequate; the data on *M. lukini* were improperly abbreviated and, as a result, the indices that Kamenev relied upon differ from those calculated in the present study for the specimens of *M. lukini*, excluded by Kamenev (1989; table 2) as "abnormal". Concerning the variability of the pallial sinus and pallial line, it is essentially identical both in the paratypes of *M. luki-*

ni (Kamenev, 1990, text-fig. 3) and in the North Pacific "*M. obliqua*", auctt.

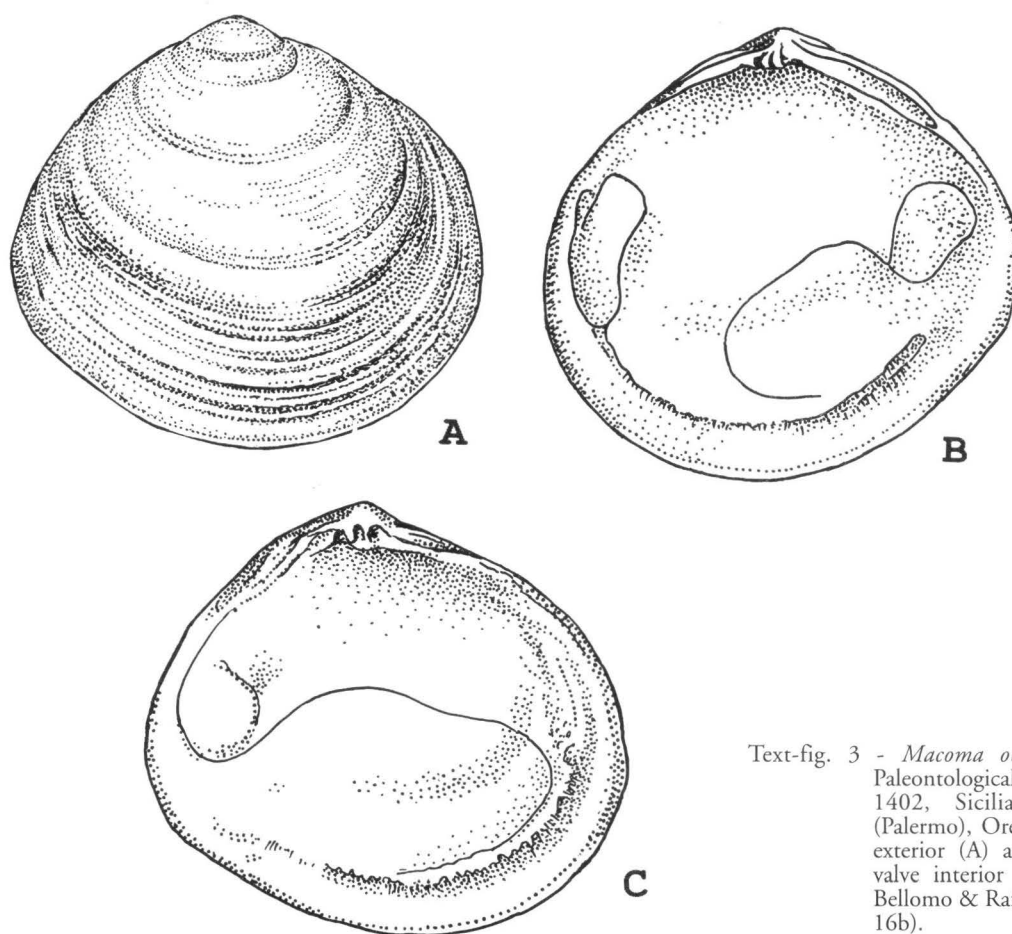
Description – Shell medium-sized (up to 50 mm), triangular-rounded, with a poorly marked right-hand flexure; moderately low (mean H/L = 0.82 ± 0.02), more or less equilateral (mean A/L = 0.57 ± 0.01), moderately bulging (mean B/L = 0.20 ± 0.01), neither beveled nor slanted; somewhat thick, white with an ochre-brown periostracum. Anterodorsal margin, anterior margin, and anteroventral margin forming a semi-oval outline. Posterior margin narrow, drawn posteriorly, beveled. Posterior slope markedly crumpled by a moderately rough radial fold.

Beaks slightly protruded anteriorly, of moderate height, somewhat wide, pointed, elevated. Growth rings (5-6 in an adult shell) alternate with numerous concentric growth wrinkles. Nymph elongate, straight, 0.40 times as long as the valve. Pallial sinus and pallial line in left valve most often fully confluent, with point of merger closer to anterior adductor scar. In right valve, pallial sinus one-third shorter than in the left valve.

Distribution – This species is widely distributed along the Asian and American coasts of the North Pacific, occurring as far as the Arctic Ocean (Point Barrow): Tatar Strait of the Sea of Japan, south to Kievka Bay ($42^{\circ} 50' N$) (Evseev & Kiyashko, 1995); the coast of the Sea of Japan and the Okhotsk Sea off the southern Sakhalin Island, Terpeniya Bay, Kurile (Shimushir, Yankicha), Commander (Bering) and Aleutian Islands, Avacha Inlet (Eastern Kamchatka), to the south off the Pacific coast of North America up to the northern portion of the outer coast of Washington. There are questionable records on the Californian coast (Coan, 1971).

M. golikovi is known from the Middle Miocene Erolonskaya Suite of Western Kamchatka (Gladnikov *et al.*, 1984, p. 219, pl. 53, figs. 9, 14, 16), though sometimes confused with *M. incongrua*. Specimens of "*Macoma inquinata* (Desh.)" from the Oligocene Matchigarskaya and the lower part of Vengeriyskaya Formations of Schmidt Peninsula, northern Sakhalin Island (Khomenko, 1938, p. 50, pl. 13, figs. 1-4) may be identified as *Macoma* cf. *golikovi*. Furthermore, *M. golikovi* has been recorded as "*M. obliqua*" from the Pleistocene (Attarman) deposits of the Karaginsky Island, Eastern Kamchatka (Petrov, 1982), Alaska, southwestern British Columbia, Oregon and southern California (Coan, 1971).

Ecology – *Macoma golikovi* occurs from the lower intertidal zone to a depth of ca. 180 m. In the Avacha Inlet, Eastern Kamchatka, it is abundant in the sandy intertidal and upper subtidal environments with a population density as high as 150 specimens/m² (Oshurkov *et al.*, 1989). At Kraternaya Bight (the flooded crater of Ushishir Volcano), Kurile Islands,



Text-fig. 3 - *Macoma obliqua* (Sowerby, 1817), Paleontological Museum of Palermo no. 1402, Siciliano del Fiume Oreto (Palermo), Oreto (Palermo). Right valve exterior (A) and interior (B), and left valve interior (C), $\times 1.5$; drawn from Bellomo & Raffi (1991, pl. 1, figs. 14a,b, 16b).

M. golikovi lives under strongly peculiar hydrological conditions affected by shallow-water gasohydrothermal vents, dominating on muddy sands at 2-30 m water depth and may occur in abundance up to 2,250 specimens/m², with a biomass up to 600 g/m² (Kamenev, 1989).

MACOMA (MACOMA) OBLIQUA (J.Sowerby, 1817)
Text-figs. 1B-C, 3A-C)

Tellina obliqua J. SOWERBY, 1817, p. 137, pl. 161, fig. 1 [nom. conserv., ICZN Opinion 948, 1971] non W. Wood, 1815, p. 152, pl. 41, figs. 4-5 [nom. reject., ICZN Opinion 948, 1971] (see: Coan & Sealy, 1969); S. V. WOOD, 1848, p. 228, pl. 21, figs. 7a-d; S. V. WOOD, 1874, p. 152, 216; Anonymous, 1963, p. 106, pl. 38, figs. 7-9.

Tellina obliqua f. *perfrigida* DE GREGORIO, 1884, p. 176 [refers to S. V. WOOD, 1848, pl. 21, fig. 7 and SOWERBY, 1817, pl. 161, figs. 3, 4].

Macoma obliqua (J. Sowerby, 1817): HEERING, 1950, p. 168, pl. 15, figs. 3-6 (see for synonymy); SPAINK & NORTON, 1967, p. 39, pl. 1, figs. 1-2, pl. 2, figs. 13a,b; COAN, 1971, p. 26 (part.), pl. 6, fig. 31, non pl. 7, fig. 33 and text-fig. 14; GLADENKOV *et al.*, 1980, p. 48, pl. 9, figs. 11-15a; BELLOMO & RAFFI, 1991, p. 3, tav. 1, figg. 4a,b, 7, 8, 9a,b, 10a,b, 12a,b, 13a,b, 14a,b, 15, 16a,b.

Type material and locality – *Tellina obliqua* J. Sowerby, 1817 - lectotype (selected by Coan, 1971, p. 24) in Natural History Museum, London, Fossil Mollusca Section no. 43058; figured by Coan, 1971, pl. 6, fig. 31. Red Crag, Suffolk, England, coll. G.R. Leathes.

Tellina obliqua f. *perfrigida* De Gregorio, 1884 - syntypes in Natural History Museum, London, Fossil Mollusca Section; "Argille di Ficarazzi, sables del fiume Oreto, Palermo, Post Pliocene".

Discussion – The differences in shell-form between *M. golikovi* and *M. obliqua* are easily seen from Text-figs. 2 and 3. Moreover, the morphometric analysis (Student's t-test)¹, reveals statistically significant differences ($t = 3.687$, $P > 0.999$) in H/L and A/L indices. So, in *M. obliqua* the shell is definitely higher and more equilateral than in *M. golikovi*.

Though *M. obliqua* and *M. golikovi* are considered herein as different species, they are obviously related.

¹ The indice values' distribution could be approximated (Kolmogorov-Smirnov λ -test; $\lambda = 0.223$, $P < 0.001$) well enough by the Gaussian distribution.

Moreover, *M. lyelli* Dall, 1894 (Figs. 4C-D) of the Northwest Atlantic "Late Miocene" (actually Early Pliocene: Hazel, 1983; Tedford & Hunter, 1984; Ward & Blackwelder, 1987) from the "Miocene of Gay Head", Martha's Vineyard, Massachusetts (Dall, 1894: 297; Dall, 1900: 1049, pl. 37, figs. 9-11) and *M. cookei* Gardner, 1944 (Fig. 4A-B) from the Yorktown Formation, Yorktown, York River, Virginia (Gardner, 1944: 100, pl. 17, figs. 8, 11; holotype USNM 325592 also figured: Campbell, 1993, pl. 16, fig. 147) also belong to the same *M. obliqua*-*M. golikovi* species-complex.

Description – Shell medium-sized (up to 50 mm), triangular-rounded, somewhat high (mean H/L = 0.93 ± 0.02), nearly equilateral (mean A/L = 0.48 ± 0.01), moderately bulging or slightly flattened (mean B/L = 0.20 ± 0.02), slanted, and rather thick. Outline oval. Posterior margin broad, usually neither drawn posteriorly nor beveled. A low keel and slight concavity are evident at the posterior margin of the right valve.

The beak is slightly protruded anteriorly, of low height. Growth rings (up to 7 in an adult shell) are pronounced. Hinge plate rather narrow. Pallial sinus not very deep in the right valve, but very deep in the left valve.

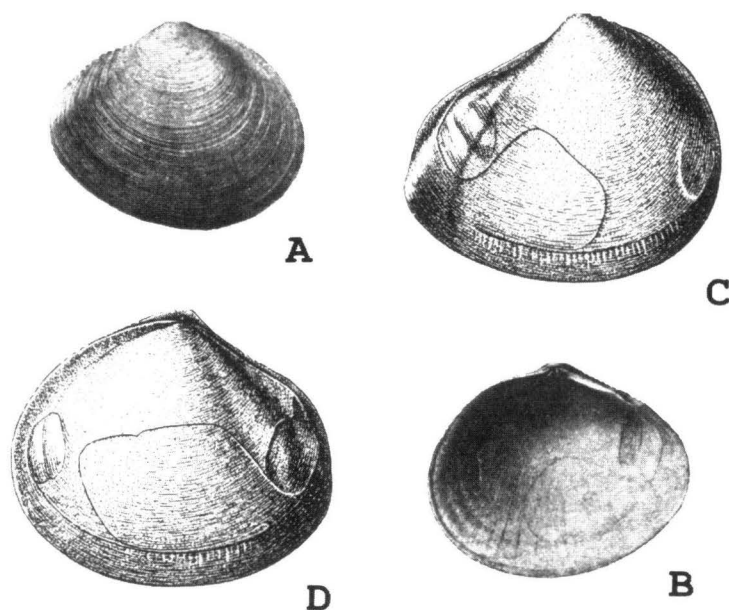
Distribution – *Macoma obliqua* is one of the most common Tellinidae in the Western European and Mediterranean Plio-Pleistocene. It has been recorded from the Coralline Crag, Red Crag, Icenian and Cromer of England, *Serripes* Zone of Tjornes Crag and Breidavik Beds of Iceland, Scaldisien of Doel, Belgium, Breda, Oosterhout and Maassluis Formations of the Netherlands, and in the Late

Emilian and latest Sicilian of the Mediterranean (S.V. Wood, 1848, 1874; Heering, 1950; Anon., 1963; Spaink & Norton, 1967; Coan, 1969; Gladenkov *et al.*, 1980; Gladenkov, 1981; Raffi, 1986; Bellomo & Raffi, 1991; Sami & Taviani, 1997). Its occurrence in the European Pliocene (see Wilkinson, 1980, and Gladenkov, 1981) and Plio-Pleistocene deposits of the Mediterranean (Raffi, 1986; Malatesta & Zarlenga, 1988) suggests that geochronologically *M. obliqua* ranges from the Early Pliocene (Coralline Crag), about 4.0 million years ago (Jenkins *et al.*, 1988) to the latest Early Pleistocene at about 0.8 million years ago. The record of *M. obliqua* in the Mediterranean about 1.2-0.8 million years ago was cited by Raffi (1986) and Malatesta & Zarlenga (1988) as the evidence of the migration of the boreal fauna from the Pacific to the Atlantic Ocean during the Pleistocene. Such a migration, however evidently occurred already in Neogene. Bellomo & Raffi (1991) consider that all the specimens so far quoted for the Lower Pleistocene of the Mediterranean as *Macoma cal-carea* (Gmelin), *M. perfrigida* (De Gregorio) and *M. balthica* (Linnaeus) should be referred to *M. obliqua*.

BIOGEOGRAPHIC COMMENTS

The results obtained are evidencing the problems concerning the timing of the trans-Arctic migrations of marine biota from the North Pacific to the North Atlantic through the Bering Strait during the Neogene.

The first Late Cenozoic migrations are generally believed to have occurred during the Beringian transgression, when the deposits of the Red Crag,



Text-fig. 4 - A,B) *Macoma cookei* Gardner, 1944, Yorktown, York River, Virginia, Yorktown Formation, Lower Pliocene, holotype USNM no. 325592, shell length 34.3mm, right valve exterior (A) and interior (B), reproduced from Gardner, 1944, pl. 17, figs. 8, 11; C,D) *Macoma lyelli* Dall, 1894, "Miocene of Gay Head", Martha's Vineyard, Massachusetts, shell length 43.0mm, internal cast, showing impression of right (C) and left (D) valves. Reproduced from Dall, 1900, pl. 37, figs. 9, 11.

England, and of the Tjornes Beds (*Serripes* Zone), Iceland, took place (Durham & MacNeil, 1967; Einarsson *et al.*, 1967; Gladenkov *et al.*, 1980; Svitoch & Taldenkova, 1994). Accepting a tripartition of the Pliocene (Zanclean, Piacenzian and Gelasian) (Berggren *et al.*, 1995), the Beringian transgression may be dated as early Middle Pliocene (Piacenzian), about 3.5-3.0 million years ago. Numerous authors (Durham & MacNeil, 1967; Kafanov, 1979, 1984 with references therein; Coan, 1969; Vermeij, 1991), however, considered the possibility that such migrations might have taken place as early as the Late Miocene.

Although there is no general consensus on each hypothesis (Herman & Hopkins, 1980; Svitoch & Taldenkova, 1994), the molluscan paleontological data seem to support the latter hypothesis. So, *Macoma obliqua* is present in northeastern Atlantic since the Coralline Crag. The very base of the Coralline Crag has been dated at about 4.0 million years (Jenkins *et al.*, 1988). On the other hand, the representatives of *M. golikovi*-*M. obliqua* species-complex are known in the North Pacific since at least the Middle Miocene even from the Oligocene (*M. golikovi*). Therefore, it is most likely that the first migration through the Bering Strait occurred earlier than the Beringian transgression, in the Late Miocene or in the earliest Pliocene. The last molluscan and diatom evidence in the Bear Lake Formation of the Alaska Peninsula (Marincovich & Gladenkov, 1997) also suggests that the Bering Strait first formed in the latest Miocene or earliest Pliocene, in the time-interval between 5.5-5.6 and 4.7-4.9 million years ago.

So, I agree with Coan (1969, 1971, p. 27) that "Members of this species-complex were apparently among the first group of boreal *Macoma* to reach the Atlantic as a result of the late Miocene submergence of the Bering Strait". During the Late Miocene the predecessors of the modern *M. golikovi* migrated into the North Atlantic via the Canadian Arctic, later originating three separate species - *M. lyelli*, *M. cookei* and *M. obliqua*. The latter widely spread through the Late Neogene basins in Europe and Mediterranean. In the Mediterranean basin *M. obliqua* is rather common from the Early Emilian through the latest Sicilian (Bellomo & Raffi, 1991; Sami & Taviani, 1997), than disappeared in the Middle Pleistocene.

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