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General Palaeontology, Systematics and Evolution (Invertebrate Palaeontology)

A new whale barnacle from the early Pleistocene of Italy suggests an ancient right whale breeding ground in the Mediterranean



Une nouvelle balane de baleine du Pléistocène inférieur de l'Italie suggère l'existence d'une ancienne zone de reproduction des baleines noires dans la Méditerranée

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ABSTRACT

The fragmentary fossil history of whale barnacles (Cirripedia: Coronulidae) is mainly constituted by remains of *Coronula* spp. in Plio-Pleistocene deposits found along extant humpback whale migration routes, and especially in occurrence of breeding areas. Here we report the presence of a single compartment of *Cetopirus* along with remains of *Coronula bifida* in Lower Pleistocene open shelf deposits of Salento (South Italy). This is the first occurrence of the genus *Cetopirus* prior to the Late Glacial period (ca. 15–10 ky before Present), and the specimen here studied is designated as the holotype of the new fossil species *Cetopirus fragilis*. Since *Cetopirus* is currently found exclusively inhabiting the skin of the right whales (*Eubalaena* spp.), the fossil material here studied suggests the persistence of Balaenidae in the Mediterranean Basin during the Early Pleistocene and supports the existence of a baleen whale migratory route active between the central Mediterranean and the North Atlantic during the Plio-Pleistocene.

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R É S U M É

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L'histoire fossile des balanes qui affectent les baleines (Cirripedia: Coronulidae) est fragmentaire et principalement constituée par des restes de *Coronula* spp. dans des sédiments du Plio-Pléistocène. Ces restes sont typiquement placés le long des parcours migratoires des baleines à bosse, et spécialement près des leurs zones de reproduction. Nous rapportons sur un compartiment isolé de *Cetopirus*, découvert avec quelques restes de *Coronula bifida* dans des sédiments de plate-forme ouverte du Pléistocène inférieur de Salento (Italie méridionale). Il s'agit de la première occurrence du genre *Cetopirus* avant la période Tardiglaciaire (environ 15 à 10 000 ans avant le présent), et le spécimen décrit ici est désigné comme holotype de la nouvelle espèce fossile *Cetopirus fragilis*. Étant donné que *Cetopirus* est actuellement connu comme un symbiote spécifique du genre *Eubalaena* (comprenant les baleines noires), les fossiles étudiés ici suggèrent la persistance des balénidés dans la Méditerranée pendant le Pléistocène inférieur et plaident en faveur de l'existence d'une route migratoire active entre la Méditerranée centrale et l'Atlantique septentrional pendant le Plio-Pléistocène.

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1. Introduction

Whale barnacles are epizoid crustacean cirripedes that live exclusively on the cetacean skin (Fertl, 2002). Among the extant whale barnacles, the currently monospecific genus *Cetopirus* (Fig. 1) is known as a genus-specific symbiont on the three species of right whales (family Balaenidae): *Eubalaena australis*, *E. glacialis* and *E. japonica*. Therefore, this whale barnacle is found in both the Southern and the Northern Hemisphere (Holthuis et al., 1998; Scarff, 1986). Except for a few subfossil records from Recent (Holocene) deposits of Argentina (Pastorino and Griffin, 1996) and the Netherlands (Holthuis et al., 1998) and from the Late Glacial of South Spain (Álvarez-Fernández et al., 2014), *Cetopirus* was until now completely unknown as a fossil. In this work we record the presence of *Cetopirus* in Lower Pleistocene marine deposits of the central Mediterranean Basin. The specimen, consisting of a single complete left latus (or carinolatus), was collected together with remains of *Coronula bifida*. In this paper we describe the

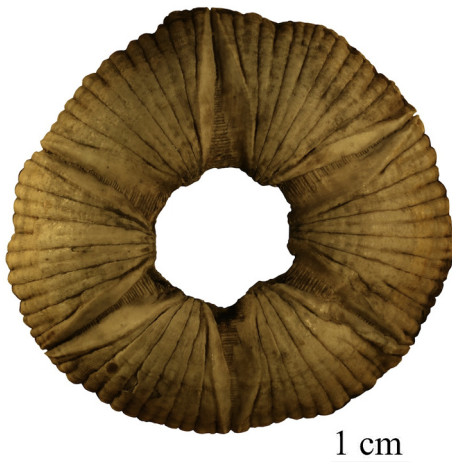


Fig. 1. Recent *Cetopirus complanatus* shell (KBIN 95996), in apical view.
 Fig. 1. Coquille récente de *Cetopirus complanatus* (KBIN 95996), en vue apicale.

Cetopirus specimen, designating it as the holotype of the new species *C. fragilis*; then we discuss its palaeobiological significance with regard to the coeval Mediterranean baleen whale fauna.

2. Materials and methods

2.1. Institutional abbreviations

KBIN, Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussel, Belgium); MSNUP, Museo di Storia Naturale dell'Università di Pisa (Pisa, Italy); MZUF, Museo di Storia Naturale, Sezione di Zoologia "La Specola", Università degli Studi di Firenze (Firenze, Italy); SAM-PK, Natural History Iziko South African Museum (Cape Town, South Africa).

2.2. Calcareous nannofossil biostratigraphy

One sample of the marly sediment embedding the *Cetopirus* specimen described in this work (MSNUP I16903) was collected for biostratigraphic study. Calcareous nannofossil analysis was carried out using a polarized light microscope on a smear-slide prepared from the sample, following standard techniques (Bown and Young, 1998). The nannofossil content was evaluated applying a semi-quantitative method to record the abundance of each species per Field of View (FOV) counting specimens on 100 FOV. The abundance terminology was as follow:

- abundant ≥ 10 specimens/FOV;
- common ≥ 1 specimens/FOV;
- few ≤ 1 specimens/FOV;
- rare = only 1 specimen observed.

All the recognized taxa are referenced in Bown (1998). We followed Gibbard and Head (2009) and Gibbard et al. (2010) in considering the Gelasian stage/age as belonging to the Pleistocene series/epoch, thus complying with the 2009 decision of the Executive Committee of the International Union of Geological Sciences.

2.3. Systematics

The anatomical terminology here used derives mainly from various papers by Buckeridge (1983), Darwin (1854), Pastorino and Griffin (1996), Pilsbry (1916), and Zullo (1979). Throughout all the paper, the newly coined expression “terminal transverse loops of the ribs” is used as a synonymous of “transverse loops of the folded wall” as used by Darwin (1854).

The following specimens were directly examined for comparisons: *Cetopirus complanatus* (MZUF 83; MZUF 85; MZUF 86; MZUF 88; KBIN 95994; KBIN 95995; KBIN 95996; KBIN 95997; KBIN 95998; plus various uncatalogued specimen kept in the personal collection of Mark Bosselaers); *Coronula bifida* (MSNUP I16907; MSNUP I16908; MSNUP I16909; MSNUP I16910; MSNUP I16911; MSNUP I16912; MSNUP I16913); *Coronula diadema* (MSNUP I13971; MSNUP I13980; MSNUP I13982; MSNUP I13988; MSNUP I14392; MSNUP I14393; MSNUP I15762; MSNUP I15767; MZUF 76; MZUF 77; MZUF 89; SAM-PK, various uncatalogued specimens); *Coronula reginae* (MZUF 84); *Cryptolepas rhachianecti* (one uncatalogued specimen kept in the personal collection of Mark Bosselaers); *Platylepas bisexlobata* (KBIN 102006; KBIN 102009); *Platylepas hexastylus* (MZUF 6; MZUF 7); *Tubicinella major* (MZUF 71; MZUF 72).

3. Geological framework

The *Cetopirus* specimen here studied (MSNUP I16903) was collected by A.V. from a rocky cliff (known as “Il Fascio”) outcropping in the area of Porto Craulo, inside the port of Otranto (Salento, southern Italy) (Fig. 2a). The rocks exposed at Il Fascio belong to the Uggiano La Chiesa Formation (UCF), a Plio-Pleistocene unit deposited within the Adriatic foredeep (Bossio et al., 2002).

From a lithostratigraphic viewpoint, in southeastern Salento the UCF mainly consists of fossiliferous, well stratified biodetritical limestones and yellowish calcareous sands and marls deposited in an open shelf environment (Bossio et al., 1993). The benthic assemblages indicate

typical depths of the inner neritic zone, although slightly greater depths have been recorded occasionally (Bossio et al., 2005). In the Otranto area, the UCF shows a maximum thickness of ca. 35 m and ranges from the Uppermost Piacenzian stage (D'Alessandro et al., 2004) to the basal part of the Calabrian stage (Bossio et al., 1987).

At the port of Otranto, the UCF is well exposed. In particular, the outcrop of Il Fascio (Fig. 2b) is characterized by levels of marlstones which alternate with intensively bioturbated, decimetric calcarenitic layers. Main fossils are decapod crustaceans (including *Lobocarcinus sismondai*) and ichthyoliths (Menesini, 1967; Varola, 1965, 1981); they are common and particularly concentrated in the marly levels. Brachiopods, echinoids, bivalves, gastropods, corals, and turtle remains have been also recognized. Whale barnacle shells and isolated plates belonging to the fossil species *Coronula bifida* are known from three marly beds sited near the top of the succession (Fig. 2c); the specimen here studied was found in the middle marly bed.

For more details on the geological setting see the supplementary online material file *Cetopirus_ESM.pdf*.

4. Calcareous nannofossil biostratigraphy

The assemblage observed in the sample contains: common to abundant specimens of small (between >2 and <7 μm) unidentified *Reticulofenestra*; few specimens of *Calcidiscus leptoporus*, *Calcidiscus macintyreii*, *Coccolithus pelagicus*, *Cricolithus jonesi*, small (<3 μm) unidentified *Gephyrocapsa* with closed central area, *Helicosphaera carteri*, *Pontosphaera japonica*, *Pontosphaera* sp., *Pseudoemiliania lacunosa*, *Pseudoemiliania ovata*, *Syracosphaera histrica*; rare specimens of *Braarudosphaera bigelowii* and *Helicosphaera sellii*.

Based on the occurrence of *Calcidiscus macintyreii* and the absence of *Discoaster brouweri*, the analyzed assemblage was attributed to the *Calcidiscus macintyreii* subzone of Gartner (1977); furthermore, the absence of large *Gephyrocapsa oceanica*, allows the identification of Mediterranean Neogene Nannoplankton zone 19a of Rio et al. (1990). The sample is dated to the late



Fig. 2. a: location of the town of Otranto (Salento, South Italy); b: the exposure of the Uggiano La Chiesa Formation at Il Fascio (photo by S.M.); c: A *Coronula bifida* specimen cropping out from a marly bed at Il Fascio (photo by S.M.).

Fig. 2. a : localisation de la ville d'Otrante (Salento, Italie méridionale) ; b : affleurement de la formation de Uggiano La Chiesa à Il Fascio (photographie par S.M.) ; c : spécimen de *Coronula bifida* affleurant d'un banc marneux à Il Fascio (photographie par S.M.).

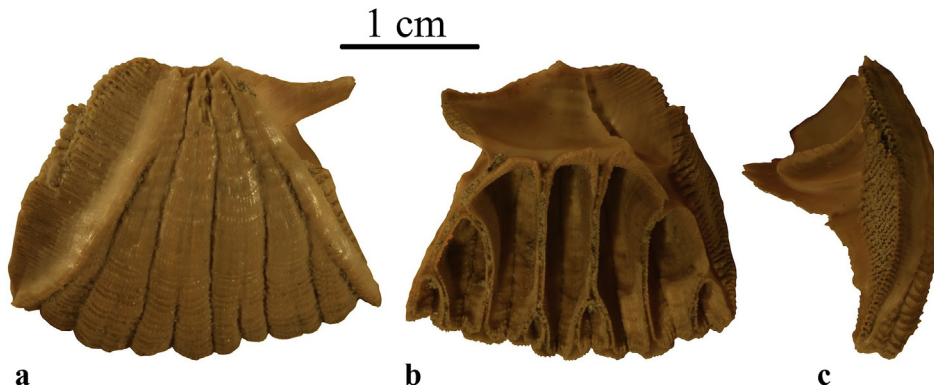


Fig. 3. MSNUP I16903, *Cetopirus fragilis*, sp. nov. (holotype), single left compartment (latus or carinolatus) collected in the town of Otranto (Apulia region, South Italy) in Lower Pleistocene deposits: a, apical view; b, basal view; c, radial view.

Fig. 3. MSNUP I16903, *Cetopirus fragilis*, sp. nov. (holotype), compartiment gauche isolé (latus ou carinolatus) recueilli dans la ville d'Otrante (région des Pouilles, Italie du Sud) dans des dépôts du Pléistocène inférieur : a, vue apicale ; b, vue basale ; c, vue radiale.

Gelasian-early Calabrian (early Santernian substage of the 'Italian Marine Stages' regional scheme, following [Gibbard and Cohen \(2008\)](#)), with absolute ages ranging from 1.95 Ma to 1.73 Ma as reported by [Raffi et al. \(2006\)](#), respectively for the highest occurrence of *D. brouweri* and the lowest occurrence of large *G. oceanica* in the Mediterranean area.

5. Systematic palaeontology

Class Maxillopoda [Dahl, 1956](#)

Subclass Cirripedia [Burmeister, 1834](#)

Order Sessilia [Lamarck, 1818](#)

Suborder Balanomorpha [Pilsbry, 1916](#)

Family Coronulidae [Leach, 1817](#)

Genus *Cetopirus* [Ranzani, 1817](#)

Type species: *Lepas complanata* [Mörch, 1853](#), Late Pleistocene to Recent.

Distribution: Early Pleistocene to Recent. Known as fossil from Lower Pleistocene deposits of Italy, Upper Pleistocene deposits of Spain, and Holocene deposits of Argentina and the Netherlands. Currently known as an exclusive symbiont of *Eubalaena* spp., living in temperate seas.

Emended diagnosis: Body within a dome-shaped shell, consisting of 6 sub-equal compartments; circumference circular in apical view; rounded-hexagonal orifice of the body chamber, not larger than the basal opening; opercular valves present, much smaller than the orifice; sheath short and smooth, whose basal edge does not project freely; ala square and thin; compound radius moderately thick to very thick, whose closely spaced, completely branched sutural septa are inclined with respect to the true radius and originate from a main septum running along the outer edge of the radius; external radius rather narrow and transversely striated; paries thin, ornamented with broad longitudinal ribs having simple, T-shaped terminations; terminal transverse loops of the ribs flattened towards the outside and affected by longitudinally elongated tubes or tubules; core of the ribs solidly calcified, no tubes or tubules present in the core of the ribs outside the lateral lobes of the terminal transverse loops of the ribs; ribs

flattened, ornamented by transverse lamellae (externally) and weak longitudinal striae (both externally and internally); apex of the shell presenting four ribs forming three cavities; secondary branching very symmetrical and frequent, occurring near the apex of the shell and causing the basal edge of each plate to present a treelike pattern.

Cetopirus fragilis, sp. nov. ([Figs. 3, 4b](#))

Holotype and only referred specimen: MSNUP I16903, a complete left compartment (latus or carinolatus).

Type horizon and locality: Lower Pleistocene marlstones at Il Fascio (Latitude: 40°09'09" N; Longitude: 19°09'29" E), Porto Craulo (Otranto, Apulia region, Italy), characterized by the presence of fossil remains of *Coronula bifida*. The type horizon, which is part of the Plio-Pleistocene Uggiano La Chiesa Formation, is attributed to the Mediterranean Neogene Nannoplankton zone 19a *sensu* [Rio et al. \(1990\)](#), that is, to the 1.95 Ma - 1.73 Ma time span (according to [Raffi et al., 2006](#)).

Derivation of the name: From the Latin "fragilis" (fragile), considering its rather thin radius with respect to the very thick radius of the extant species *Cetopirus complanatus*.

Diagnosis: Radius moderately thick, able to fill only the external half of the cavity between two neighbouring plates; terminal transverse loops of the ribs whose lateral lobes present subcylindrical tubules affecting the solid surface originated by the calcification of the space sited between the opposite inner faces of the inner lamina.

Description, remarks and comparisons: This medium-sized specimen ([Fig. 3](#)) is very well preserved, and various details of the shell ornamentation are exquisitely observable. A weak degree of erosional smoothing is limited to the upper, more convex part of the compartment; fine features of the ribs are instead perfectly preserved in the lower part of the compartment. In fact, the upper part of the specimen corresponds to the portion of the shell which in life emerged from its host's skin, thus explaining the moderate smoothing there observed ([Bianucci et al., 2006a](#); [Dominici et al., 2011](#)).

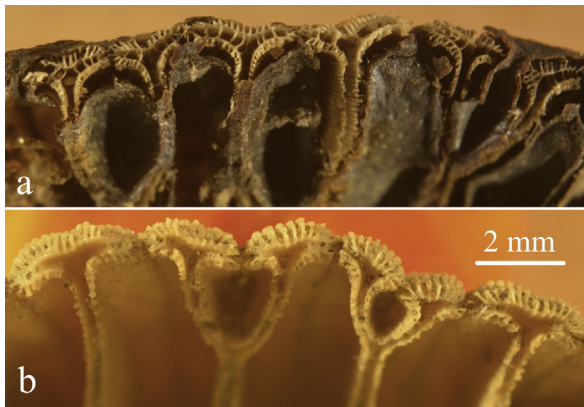


Fig. 4. Comparison between the inner structure of the terminal transverse loops of the ribs in recent and fossil species of the genus *Cetopirus*: a: KBIN 95996, *C. complanatus*; septa-filled terminal transverse loops of the ribs. According to Darwin (1854), “In *C. balaenaris* [= *Cetopirus complanatus*]. . . the opposite sides [of each loop] are seen to be connected by shelly longitudinal plates”; b: MSNUP I16903, *Cetopirus fragilis*, sp. nov.; septa-free terminal transverse loops of the ribs whose lateral lobes present subcylindrical tubules affecting the solid surface originated by the calcification of the space sited between the opposite inner faces of the inner lamina (note the tear-shaped, smooth and tubule-free area in the centre of the loop).

Fig. 4. Comparaison entre la structure interne de boucles transversales terminales de côtes dans des espèces récentes et fossiles du genre *Cetopirus* : a : KBIN 95996, *C. complanatus*; boucles transversales terminales de côtes remplies d'alvéoles. Selon Darwin (1854), « En *C. balaenaris* [= *Cetopirus complanatus*]. . . les côtés opposés [de chaque boucle] sont reliés par des plaques longitudinales coquillières » ; b : MSNUP I16903, *Cetopirus fragilis*, sp. nov.; boucles transversales terminales de côtes sans cloisons dont les lobes latéraux présentent des tubules subcylindriques affectant la surface solide générée par la calcification de l'espace situé entre les faces internes opposées de la lame intérieure (notez la zone lisse et sans tubule, en forme de larme, dans le centre de chaque boucle).

The well developed treelike pattern of the basal edge of MSNUP I16903 means that it belonged to a still-growing mature individual rather than to a juvenile (Seilacher, 2005), as also the overall size of the plate indicates.

Although the type material consists just of a single compartment, various features which on the whole characterize the well recognizable genus established by Ranzani (1817), distinguishing it from the other whale barnacles, have been detected by us; some of these features are, to our knowledge, exclusive of *Cetopirus*. The observed characters include:

- the flat and broad ribs, which bifurcate abundantly and symmetrically (Darwin, 1854), thus generating the tree-like pattern of the basal edge of the shell (Seilacher, 2005);
- the thin and square ala (Darwin, 1854);
- the basal edge of the sheath which does not project freely (Darwin, 1854);
- the estimated depressed shape of the shell (Pastorino and Griffin, 1996);
- the external radius being rather narrow (Pastorino and Griffin, 1996) and strongly striated transversely (our observation);
- the estimated diameter of the body chamber orifice being smaller than the basal opening (Pastorino and Griffin, 1996);

- the terminal transverse loops of the ribs which flatten towards the outside (Darwin, 1854).

According to Scarff (1986), the coronulid species most similar to *Cetopirus complanatus* is *Coronula reginae*. MSNUP I16903 differs from *C. reginae*, the former suggesting a significantly convex shell, the latter being typically conical and straight-shaped outside (Darwin, 1854); moreover, the compound radius of MSNUP I16903 is remarkably thicker and narrower than in *C. reginae*. Anyway, the compound radius of MSNUP I16903 is significantly thinner than observed in any *C. complanatus* specimen (in which the radius virtually fills the cavity between neighbouring compartments, Pastorino and Griffin (1996); see Fig. S3 of the supplementary online material file *Cetopirus.ESM.pdf*) and, in its middle portion, it does not reach the basis of the sheath by about half the thickness of the compartment. Darwin (1854) observed that in the genus *Cetopirus* the terminal transverse loops of the ribs are remarkably flatter towards the outside compared to other whale barnacles. In *C. complanatus* these loops are affected by thin, well-spaced and rather symmetrical planar septa which connect the opposite inner faces of the inner lamina, thus defining tubes whose transverse section is subrectangular and rather wide (Fig. 4a; Darwin, 1854). These septa affect even the very central portion of the loop. On the contrary, MSNUP I16903 displays a few very fine tubules affecting only the lateral lobes of the loops, far from the medial plane of symmetry of the rib (which instead presents a tear-shaped, smooth and septa-free area). These distal tubules (Fig. 4b) are roughly cylindrical and thick-walled (namely, they can be described as asymmetrical and irregular cylindrical openings within a solid surface originated by the calcification of the space sited between the opposite inner faces of the inner lamina).

The fossil coronulid species *Cetolepas hertleini* (from the Lower Pleistocene of the San Diego Formation, California, USA) shows striking similarities with *Cetopirus complanatus*. MSNUP I16903 mainly differs from *Cetolepas hertleini* by showing:

- a significantly convex sutural edge of the radius (instead of a simple, linear one);
- a smooth sheath (instead of a decidedly grooved one).

The coronulid genus *Cryptolepas* includes two species: the extant *C. rhachianecti* and the fossil *C. murata*; the latter presents strong affinities with both *Cetopirus complanatus* and MSNUP I16903 (Zullo, 1961). However, MSNUP I16903 presents a moderately thick compound radius, while *Cryptolepas* spp. presents a thick, *C. complanatus*-like radius (Davis, 1972; Pilsbry, 1916). Moreover, three features associate MSNUP I16903 to *C. complanatus* while distinguishing them from both *C. murata* and *C. rhachianecti*. First, the texture of the sutural edge of the radius, which presents closely spaced, completely branched sutural septa that project inward and downward and originate from a main septum running along the outside edge of the radius; in turn, in *Cryptolepas* spp. the pattern is crenulate and originates from a central septum running along the inner edge

of the radius (Davis, 1972; Zullo, 1969). Second, the core of each of the ribs ("buttresses proper" *sensu* Davis (1972)) is solidly calcified (with the important exception of the terminal transverse loops of the ribs, which show the above reported tube-like features), while Davis (1972) and Zullo (1961) report on longitudinal septa, forming longitudinal tubes within the largely uncalcified buttresses proper of *Cryptolepas* spp. Third, the sheath is remarkably smooth, while it is affected by deeply incised transverse grooves in *Cryptolepas* spp. (Zullo, 1961, 1969). Finally, both *C. complanatus* and MSNUP I16903 strongly differ from *C. rhachianecti* by presenting T-shaped terminations of the ribs which build up a complete outer wall (see Pilsbry, 1916).

As reported above, MSNUP I16903 belongs to the genus *Cetopirus* owing to a number of features which distinguish the genus established by Ranzani (1817) from the other coronulids; anyway, the above mentioned differences between MSNUP I16903 and the recent species *C. complanatus* (i.e., the presence in MSNUP I16903 of a thin radius and a peculiar inner structure of the terminal transverse loops of the ribs) allow and recommend us to establish a new species – *Cetopirus fragilis* – within the genus *Cetopirus*. Since the coronulid Bauplan - paraphrasing Darwin (1854): six compartments of equal size, having the same outline, arranged in a crown-shaped, more or less depressed, shell - is well known and suffers no remarkable variations among the various species of Coronulidae, a complete single plate is enough to provide a reliable reconstruction of its complete skeleton and consequently to describe a new taxon.

6. Palaeobiogeographical implications

The fossil record of the whale barnacles is quite fragmentary and localized in few areas of the world. In the Mediterranean Basin, fossil whale barnacles are known from various Pliocene to Pleistocene Italian and Cypriot shallow marine deposits (De Alessandri, 1895, 1906; De Gregorio, 1895; Dominici et al., 2011; Menesini, 1968; Seguenza, 1873). This record also includes some *C. bifida* specimens from the Uggiano La Chiesa Formation (Bossio et al., 1993). However, only whale barnacles belonging to the genus *Coronula* (namely: *C. bifida*, *C. diadema*, and the dubious *C. (Flabelcorona) ficarazzensis*) have been recorded from the Mediterranean Basin to this day, with the exception of some fragments of *Tubicinella major* and *Cetopirus complanatus* found in the Late Glacial settlement of Nerja Cave (South Spain) which have been regarded as an indirect evidence of human feeding on a displaced southern right whale (Álvarez-Fernández et al., 2014). The only other fossil records of *Cetopirus complanatus* published to this date are from Holocene deposits of Argentina (ca. 7500–2000 years ago; Pastorino & Griffin, 1996) and the Netherlands (10th century A.D.; Holthuis et al., 1998). Therefore, the Early Pleistocene plate here described (MSNUP I16903) allows us to extend back the global fossil record of *Cetopirus* for more than 1.7 My; moreover, it represents the first record of *Cetopirus* for the Mediterranean fauna before the Late Glacial period.

Considering that:

- today *Coronula* spp. live preferentially on the skin of the humpback whale *Megaptera novaeangliae*;
- the fossil shells of *Coronula* spp. have primarily been recorded from breeding areas or migratory routes of living humpback whale.

Bianucci et al. (2006b) proposed that, unlike the present, humpback or related whales may have used the Mediterranean as a breeding ground during the Pliocene and Pleistocene.

Now, MSNUP I16903 suggests that the diversity of the migratory mysticetes in the Mediterranean during the Pleistocene was greater than previous suggested by the fossil record of *Coronula* spp. In fact, we propose that MSNUP I16903 was hosted by a balaenid whale, since *Cetopirus complanatus* is currently known as an exclusive symbiont of both the North Atlantic and the southern right whales and considering that the general high host specificity of the whale barnacles is believed to date to the Pliocene (e.g., Bianucci et al., 2006a; Dominici et al., 2011). We suggest that a right whale migratory route was active between the Mediterranean (the putative breeding ground) and the Northeast Atlantic (the putative feeding ground) during the Plio-Pleistocene. In this regard, the presence in Italian Pliocene deposits of:

- at least three genera of balaenids (including *Eubalaena*, see Bisconti, 2002, 2009);
- a neonate balaenid (Bisconti, 2003), coupled with the Plio-Pleistocene record of *Eubalaena* spp. along the coast of the Northeast Atlantic (Aaris-Sørensen et al., 2010; Churchill et al., 2012; Newton, 1882), are noteworthy.

The Plio-Pleistocene balaenid migratory path here proposed (Fig. 5) could represent the fossil analogues of the historical (and possibly no longer extant) *Eubalaena glacialis* migration route spanning between the Biscay Bay and the Northeast Atlantic (Brown, 1986). In this framework, the modern occurrence of the North Atlantic right whale in the Biscay Bay wintering area (Aguilar, 1986) could be a recent product of the northward repositioning of the Gulf Stream which is believed to have occurred during the Last Glacial Termination and, possibly, during all other Late Quaternary deglaciation phases (Keffer et al., 1988).

MSNUP I16903 also indicates the persistence of Balaenidae in the Mediterranean Basin during the Early Pleistocene, at least until the Gelasian-Calabrian transition which corresponds to the Mediterranean Neogene Nannoplankton zone 19a *sensu* Rio et al. (1990) spanning in time from 1.95 Ma to 1.73 Ma (according to Raffi et al., 2006). Until today, fossil balaenids from the Mediterranean were reported from Upper Miocene to Pliocene deposits (Bianucci and Landini, 2007; Bianucci et al., 2009). The coexistence of both *Coronula* and *Cetopirus* (documented by fossil shells of *Coronula bifida* from the horizon in which the holotype of *Cetopirus fragilis* was found) suggests that Balaenidae and Balaenopteridae shared the same breeding ground: the shallow sea covering the easternmost part

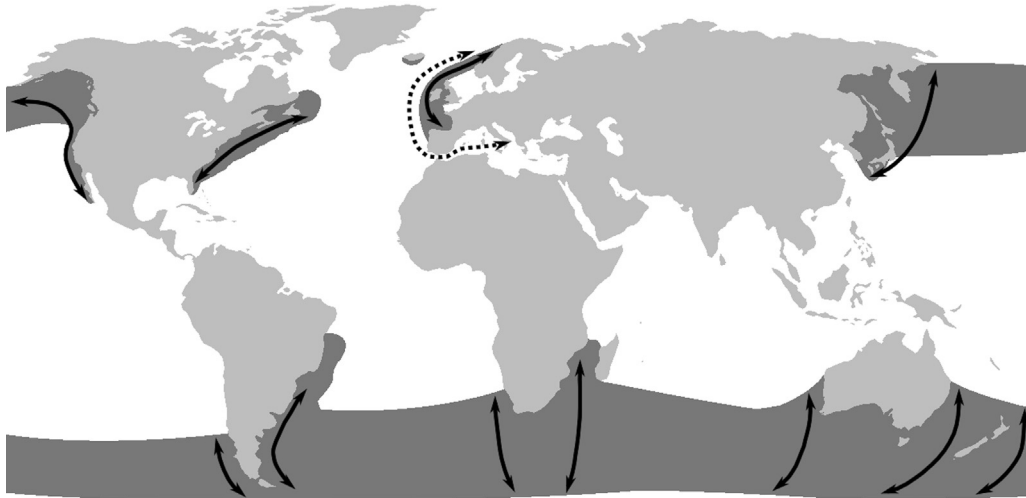


Fig. 5. The worldwide distribution of the genus *Eubalaena*, the balaenid whale which currently hosts *Cetopirus complanatus*, is indicated by light grey areas. Solid black arrows indicate extant or historical migration paths between the high-latitude feeding grounds and the low-latitude breeding grounds. The dotted black arrow indicates the putative fossil migration route of *Eubalaena* sp. or related balaenid whales between the North Atlantic (the feeding area?) and the Mediterranean Sea (the breeding area?).

Fig. 5. Distribution mondiale du genre *Eubalaena*, le baléniidé qui inclut actuellement *Cetopirus complanatus*, indiquée par des zones gris clair. Les flèches pleines noires indiquent les chemins de migration existants ou historiques entre les zones d'alimentation (situées aux hautes latitudes) et les zones de reproduction (situées aux basses latitudes) des baleines noires. La flèche noire pointillée indique une hypothétique route migratoire fossile de *Eubalaena* sp. (ou baleines apparentées), comprise entre la Méditerranée centrale (la zone de reproduction ?) et l'Atlantique septentrional (la zone d'alimentation ?). Cartographic base after wikimedia.org. Distributional data source: National Oceanic and Atmospheric Administration, National Marine Fisheries Services.

of Salento during the Early Pleistocene. This observation finds an analogous in the distribution of the extant *Eubalaena japonica*, which is believed to breed and calve south of Baja California (Gendron et al., 1999; Gilmore, 1956), just as the preferential host of *Coronula* spp., the rorqual *Megaptera novaeangliae*, does (Gendron and Urban, 1993; Scammon, 1874). A similar sympatric distribution during the cold breeding season (a most unusual case among extant mysticetes) has been hypothesized for the Hawaiian waters (Herman et al., 1980). In this respect, it's noteworthy that *E. japonica* and *M. novaeangliae* have occasionally been observed while interacting in their winter low-latitude grounds (Salden and Mickelsen, 1999; Scarff, 1986).

The fossil coronulids from Otranto suggest the preservation of a rather high baleen whale biodiversity in the Mediterranean during the Early Pleistocene, despite the scarcity of fossil mysticetes (Bianucci et al., 2009). Recent findings from South Italy, comprising two mysticetes from the Lower Pleistocene beds of Cutrofiano (Margiotta and Varola, 2007) and a large balaenopterid (approaching the size of *Balaenoptera musculus*) from the Calabrian deposits of Matera (Bianucci et al., 2012), partially fill the gap in the Pleistocene fossil record of the Mediterranean baleen whales, thus supporting the continuation of a diverse mysticete fauna.

Finally, it should be noted that, in contrast to some tens of specimens of *Coronula* spp., only one isolated specimen belonging to the genus *Cetopirus* has been collected from the Lower Pleistocene deposits of the Mediterranean Basin. This observation does not necessarily indicate that the abundance of Balaenopteridae was much greater than that of Balaenidae: in fact, field research suggests that, while virtually every extant humpback whale hosts at least some

Coronula diadema individuals (e.g., Nishiwaki, 1959), reaching eventually more than 450 kg of coronulid hosts (Fertl, 2002), on extant right whales the frequency and abundance of *Cetopirus complanatus* seem to be much lower, and roughly comparable to those of the more host-generalist symbiont *Coronula diadema* (Scarff, 1986).

7. Conclusions and perspectives

This work provides the first unambiguous report of *Cetopirus* prior to the Late Glacial Period, thus greatly extending back the stratigraphic distribution of this genus and significantly contributing to expand our scarce knowledge about the fossil history of the whale barnacles. On the basis of some anatomical differences (regarding the thickness of the radius and the inner structure of the terminal transverse loops of the ribs) with the Recent species *Cetopirus complanatus*, MSNUP I16903 was here described as the holotype of the new fossil species *Cetopirus fragilis*.

Since *Cetopirus* is currently regarded as exclusively inhabiting the skin of the balaenids, the *Cetopirus fragilis* specimen MSNUP I16903 strongly suggests the persistence of at least one population of Balaenidae in the Mediterranean Basin during the early Pleistocene, as well as the *Coronula bifida* remains suggest with regard to Balaenopteridae. Therefore, since *Cetopirus* is currently known as a symbiont of the North Atlantic right whale, MSNUP I16903 supports the existence of a baleen whale migratory route active between the Mediterranean and the North Atlantic during the Plio-Pleistocene.

According to Dominici et al. (2011), the fossil coronulid *Coronula bifida* is the direct ancestor of the most common extant species *Coronula diadema*; a similar model

could possibly be suggested for *Cetopirus fragilis* - *Cetopirus complanatus*. No phylogenetic analyses comprising both extant and fossil coronulid taxa have been published to this date, and the evolutionary relationships between the extant whale barnacles and their Plio-Pleistocene relatives is unknown and largely speculative. Future work should undertake comprehensive phylogenetic analyses of Coronulidae that would further enhance our understanding of the evolutionary links between baleen whales and their barnacles during the Late Neogene and the Quaternary.

Authors' contribution

A.V. collected the specimen MSNUP I16903. A.C., M.B., and G.B. undertook the systematic study and elaborated the palaeobiogeographical hypotheses. S.M. provided the geological setting and R.C. the biostratigraphical framework. A.C. wrote the paper and prepared the illustrations. All authors discussed the results and commented on the manuscript at all stages.

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