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# Fossil whale barnacles from the lower Pleistocene of Sicily shed light on the coeval Mediterranean cetacean fauna

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**Abstract:** We report on three shells of whale barnacle (Cirripedia: Coronulidae) collected from Pleistocene shallow-marine deposits exposed at Cinisi (northwestern Sicily, southern Italy). These specimens are identified as belonging to the extinct species *Coronula bifida* BRONN, 1831. Calcareous nannoplankton analysis of the sediment hosting the coronulid remains places the time of deposition between 1.93 and 1.71 Ma (*i.e.*, at the Gelasian-Calabrian transition), an interval during which another deposit rich in whale barnacles exposed in southeastern Apulia (southern Italy) formed. Since *Coronula* LAMARCK, 1802, is currently found inhabiting the skin of humpback whales [Cetacea: Balaenopteridae: *Megaptera novaeangliae* (BOROWSKI, 1781)], and considering that the detachment of extant coronulids from their hosts' skin has been mainly observed in occurrence of cetacean breeding/calving areas, the material here studied supports the existence of a baleen whale migration route between the central Mediterranean Sea (the putative reproductive ground) and the North Atlantic (the putative feeding ground) around 1.8 Ma, when several portions of present-day southern Italy were still submerged. The early Pleistocene utilization of the epeiric seas of southern Italy as breeding/calving areas by migrating mysticetes appears to be linked to the severe climatic degradation that has been recognized at the Gelasian-Calabrian transition and that is marked in the fossil record of the Mediterranean Basin by the appearance of "northern guests" such as *Arctica islandica* (LINNAEUS, 1767) (Bivalvia: Veneroida). The subsequent abandonment of the Mediterranean Sea by most species of mysticetes is likely to have resulted from the progressive emergence of shallow-water coastal environments that occurred in Calabrian and Middle Pleistocene times.

**Key-words:**

- Cirripedia;
- Coronulidae;
- Mysticeti;
- Balaenopteridae;
- habitat loss;
- Mediterranean Basin;

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- cetacean migrations;
- phoresis;
- palaeobiogeography

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**Résumé : *Des balanes de baleine fossiles du Pléistocène inférieur de Sicile renseignent sur la faune de cétacés contemporaine en mer Méditerranée.-*** Nous signalons trois coquilles de balanes de baleine (Cirripedia: Coronulidae) provenant des dépôts marins peu profonds du Pléistocène de Cinisi (nord-ouest de la Sicile, Italie méridionale). Ces spécimens sont identifiés comme appartenant à l'espèce disparue *Coronula bifida* Bronn, 1831. L'analyse du nannoplancton calcaire du sédiment renfermant les restes de coronulidés date la période de dépôt entre 1,93 et 1,71 Ma (c'est-à-dire au passage Gélasien-Calabrien), période à laquelle est également connu un autre dépôt riche en balanes de baleine, situé au sud-est de l'Apulie (Italie méridionale). Bien que *Coronula* Lamarck, 1802, soit actuellement trouvée en position fixée sur la peau de baleines à bosse [Cetacea : Balaenopteridae : *Megaptera novaeangliae* (Borowski, 1781)], et sachant que le décollement des coronulidés actuels de la peau de leur hôte a principalement été observé sur les sites de reproduction et de vêlage des cétacés, le matériel présenté plaide en faveur de l'existence d'une route migratoire active pour les baleines à fanons entre la mer Méditerranée centrale (le site de reproduction présumé) et l'Atlantique nord (l'aire d'alimentation présumée) autour de 1,8 Ma, alors que plusieurs parties de l'Italie méridionale actuelle étaient encore sous les eaux. La fréquentation au Pléistocène inférieur des mers épicontinentales d'Italie méridionale comme aires de reproduction et de vêlage par les mysticètes migrateurs semble être liée à la dégradation climatique dramatique qui a eu lieu au passage Gélasien-Calabrien et qui se marque dans le registre fossile du bassin méditerranéen par l'apparition d' "espèces nordiques" telles qu'*Arctica islandica* (Linnaeus, 1767) (Bivalvia : Veneroida). Le délaissement consécutif de la mer Méditerranée par la plupart des espèces de mysticètes est probablement la conséquence de l'émersion progressive des environnements côtiers peu profonds qui s'est produite au Calabrien et au Pléistocène moyen.

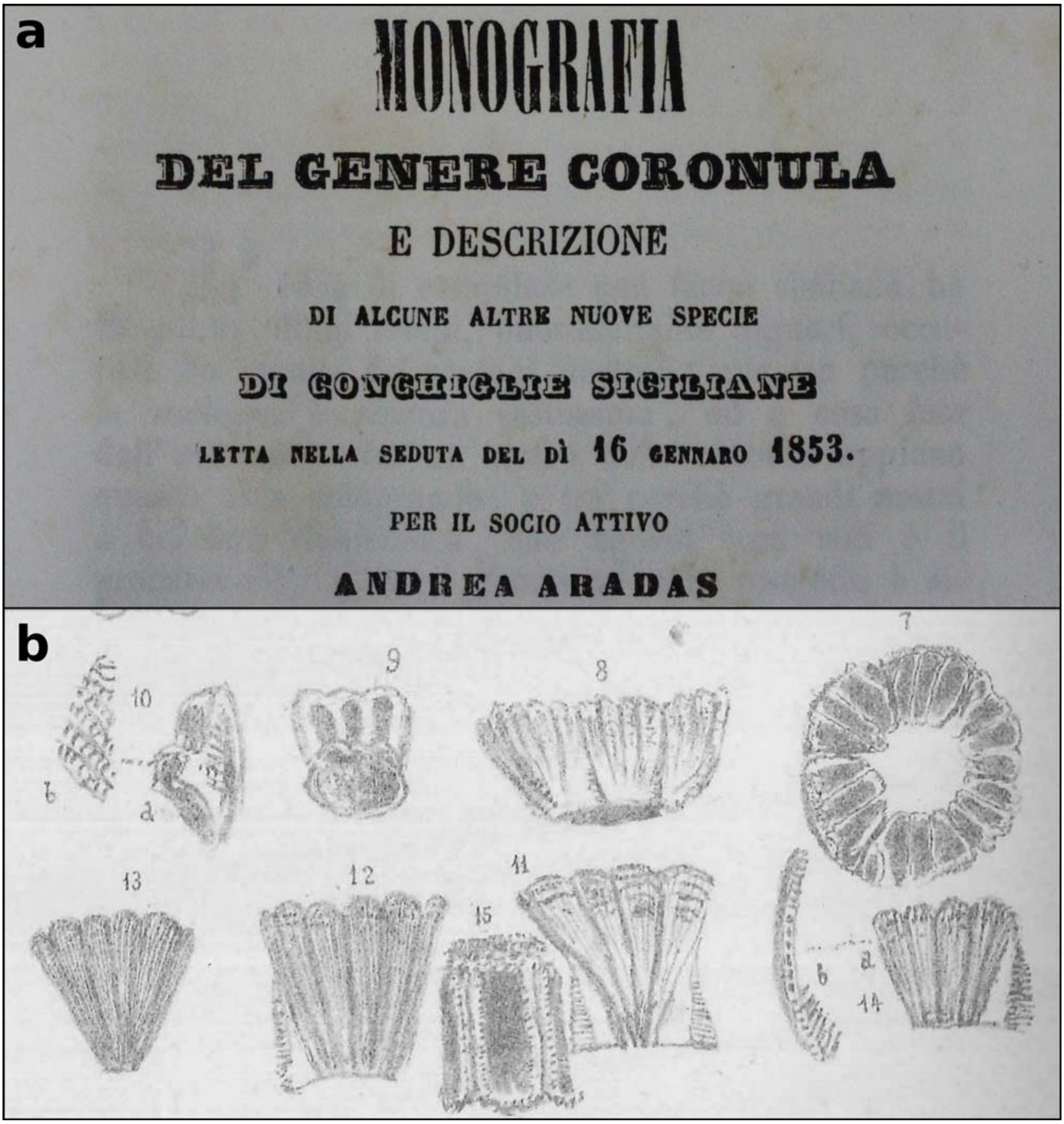
**Mots-clefs :**

- Cirripedia ;
- Coronulidae ;
- Mysticeti ;
- Balaenopteridae ;
- perte d'habitat ;
- bassin méditerranéen ;
- migration des cétacés ;
- phorésie ;
- paléobiogéographie

## 1. Whale barnacles: What they are and how they can serve the vertebrate palaeontologist?

Whale barnacles (Crustacea: Cirripedia: Coronulidae) are epizoic organisms that live exclusively on the skin of cetaceans (*e.g.*, Fertl, 2002). While also present on a few species of toothed whales (Cetacea: Odontoceti), these crown-shaped, symbiotic cirripedes are typically found in association with baleen-bearing whales (Cetacea: Mysticeti). The whale barnacles that currently inhabit the skin of mysticetes show a high degree of host specificity; for example, *Coronula diadema* (Linnaeus, 1767), which likely represents the most widespread coronulid species, attaches preferentially to the humpback whale *Megaptera novaeangliae* (Borowski, 1781), a member of the family Balaenopteridae, although it has occasionally been reported from other cetacean taxa (including two other balaenopterid species). Other species of whale barnacles exhibit an even greater host specificity; for example, *Cetopirus complanatus* (Mörch, 1853) is considered exclusive to the skin of the right whales (genus *Eubalaena* Gray, 1864, currently comprising three species belonging to the family Balaenidae), and *Cryptolepas rhachianecti* Dall, 1872, is regarded as characteristic of the gray whales (*Eschricthius robustus* (Lilljeborg, 1861), the sole living member of the family Eschrichtiidae).

The fossil record of the family Coronulidae is rather scanty. Whale barnacles appear to have originated from an ancient dispersal of members of the family Chelonibiidae (a cirripedian lineage of epizoic phoronts of turtles, sirenians, crabs, and other marine vertebrates and invertebrates) on mysticete cetaceans (Collareta *et al.*, 2016a). Although all the fossil occurrences of whale barnacles published so far are reasonably referable to the Pliocene or Quaternary (Collareta *et al.*, 2016a, and previous references therein), some unpublished coronulid specimens from Taiwan may be older (*i.e.*, late Miocene; John Buckeridge, personal communication, 2018). Based on the remarkable host preferences of extant whale barnacle species, and considering that the detachment of coronulid shells from their host's skin has been observed along migration routes and especially in cetacean breeding/calving grounds (Bianucci *et al.*, 2006b, and references therein), the fossil remains of whale barnacles have recently



MONOGRAFIA
DEL GENERE CORONULA
E DESCRIZIONE
DI ALCUNE ALTRE NUOVE SPECIE
DI CONCHIGLIE SICILIANE
LETTA NELLA SEDUTA DEL DÌ 16 GENNARO 1853.
PER IL SOCIO ATTIVO
ANDREA ARADAS

**Figure 1:** Early works on the fossil record of whale barnacles from Sicily. **a.** Frontispiece of the pioneering work by ARADAS (1854). **b.** Original illustration of the holotype of *Coronula (Flabelcorona) ficarazzensis* DE GREGORIO, 1895. A description of the features depicted in Fig. 1b is provided in the main text of the paper by DE GREGORIO (1895).

been interpreted as markers of ancient mysticete distributional and migration patterns (BIANUCCI *et al.*, 2006a, 2006b; ÁLVAREZ-FERNÁNDEZ *et al.*, 2014; BOSSELAERS & COLLARETA, 2016; COLLARETA, 2016; COLLARETA *et al.*, 2016b, 2017, in press; BOSSELAERS *et al.*, 2017). From this perspective, whale barnacle remains cease to be exclusively regarded as body fossils, assuming instead an additional role – *i.e.*, providing indirect evidence for the passage of their cetacean hosts – that makes them conceptually similar to trace fossils.

The present paper aims at (1) reporting on new fossil remains of coronulid barnacles from lower Pleistocene deposits exposed at Cinisi (northwestern Sicily, southern Italy, central Mediterranean) and (2) outlining their palaeobiogeographical and palaeoecological implications for the coeval cetacean fauna. In doing so, a brief account of the history of scientific research on fossil whale barnacles in Sicily is provided here for the first time.

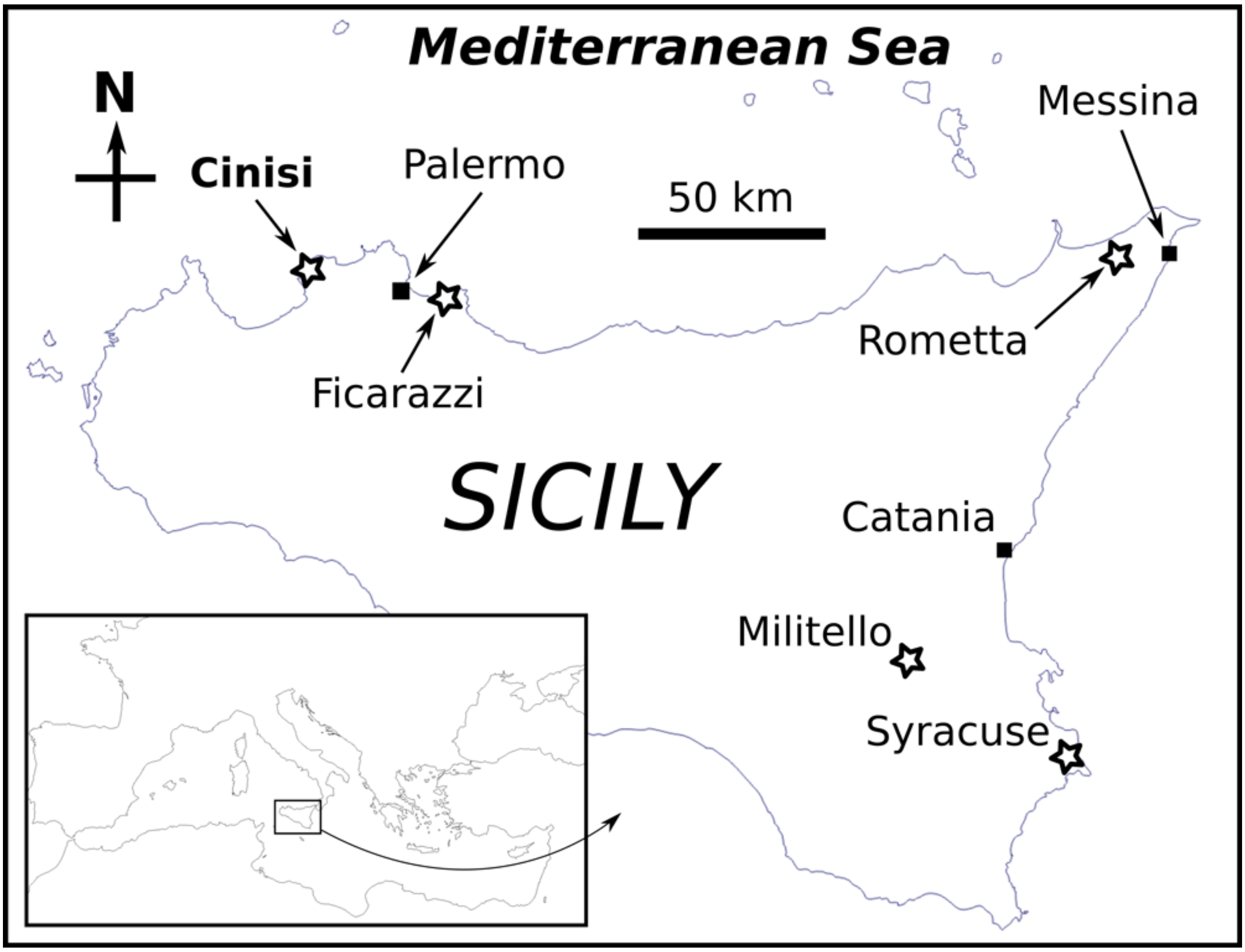


**Figure 2:** Location of the finds of fossil whale barnacles (stars) from Sicily (see text for details and sources of data). The toponym of the study site is highlighted in bold.

## 2. Fossil whale barnacles from Sicily: A brief historical review

The still fragmentary Mediterranean fossil record of Coronulidae consists of findings from a few upper Pliocene to Recent sites of Italy (*e.g.*, De Alessandri, 1895, 1906; Menesini, 1968; Bossio *et al.*, 1993; Dominici *et al.*, 2011; Collareta, 2016; Collareta *et al.*, 2016b, in press), Cyprus (Simonelli, 1893; De Alessandri, 1906), and Spain (Álvarez-Fernández *et al.*, 2014; Bosselaers *et al.*, 2017). Based on this record, mainly consisting of upper Pliocene to mid-lower Pleistocene occurrences of the extinct species *Coronula bifida* Bronn, 1831, and few upper lower Pleistocene (Calabrian) occurrences of the extant species *Coronula diadema*, Bianucci *et al.* (2006a, 2006b) proposed that, unlike today, balaenopteroid whales may have used the Mediterranean as a breeding ground during the latest Neogene and part of the Quaternary.

In Sicily (southern Italy, central Mediterranean), fossil whale barnacles have a long but largely neglected history of discovery and study. To our knowledge, Aradas (1854) was the first scientist to report on fossil whale barnacles from Sicily (Fig. 1.a). Aradas (1854) described a complete shell (which he attributed to *Coronula diadema*) from 'Tertiary' beds exposed at Militello (Catania Province, Fig. 2), and mentioned also a similar specimen previously found in calcareous deposits near Syracuse (Fig. 2).

Seguenza (1873) reattributed the coronulid specimen from Militello described by Aradas (1854) to *Coronula bifida* (a species that is also known from a few other Italian localities) and tentatively proposed a Zanclean (*i.e.*, early Pliocene) age for that record. Seguenza (1873) also cited the presence of shells of *C. bifida* at Syracuse (Fig. 2) and reported on three wall plates belonging to the same species found at Rometta (Messina Province, Fig. 2) in 'upper Zanclean marls', without providing any further indication. Marls and marly clays are common lithologies in the Piacenzian (*i.e.*, upper Pliocene) to middle Pleistocene shallow-marine 'Rometta Succession' exposed in northeastern Sicily and investigated by Seguenza in the 1870s (Di Stefano *et al.*, 2007). Therefore, the fossil remains of *C. bifida* from Rometta described by Seguenza (1873) are most likely not older than the late Pliocene.

In 1895, De Gregorio created the new species (and subgenus) *Coronula (Flabelcorona) ficarazzensis* De Gregorio, 1895, based on a complete coronulid shell from the "Post-Pliocène" of Ficarazzi (Palermo Province, Fig. 2). On the basis of the very approximate and generic description and figures (Fig. 1.b) provided by De Gregorio (1895), this taxon was tentatively synonymized with *Coronula balaenaris* Darwin, 1854 (= *Cetopirus complanatus*) by De Alessandri (1906), whereas Pilsbry (1916) considered the "perfectly useless subgenus *Flabelcorona*" as possibly indistinguishable from *Coronula reginae* Darwin, 1854 (a probable junior synonym of *C. diadema*: see Dominici *et al.*, 2011, and Bosselaers & Collareta, 2016, for further comment). The current location of the holotype of *Coronula (Flabelcorona) ficarazzensis* is not known (Carolina D'Arpa, 2015, personal communication); as such, its systematic assignment remains an open question. Nevertheless, some characters illustrated by De Gregorio (1895) – *e.g.*, the dome-like shape of the shell, the narrow and transversely striated true radius, the moderately thick compound radius, and the presence of rather frequently bifurcating external ribs flaring downwards in a fan-like triangular fashion (Fig. 1.b) – could suggest a relationship between *Coronula (Flabelcorona) ficarazzensis* and *Cetopirus fragilis* Collareta *et al.*, 2016b, whose holotype and only known specimen comes from lower Pleistocene deposits exposed at Otranto (southeastern Apulia, southern Italy: see Discussion below for further details).

Finally, Cipolla (1978) reported on shell elements of *Coronula bifida* from lower Pleistocene sediments exposed along a coastal cliff west of the city of Cinisi (Palermo Province, Fig. 2), without providing any illustration or description of these remains. Unfortunately, the work of Cipolla (1978) was published in a local magazine of natural sciences (*Il Naturalista Siciliano*), which is not widely distributed outside Sicily; as a result, the presence of fossil whale barnacles in the lower Pleistocene of Cinisi was almost completely overlooked by the scientific community. Here we report on the discovery of three new fossil specimens of *Coronula bifida* from the coastal cliff studied by Cipolla (1978) and discuss their palaeobiological meaning.

## 3. Geological and biostratigraphic framework

The sedimentary succession studied by Cipolla (1978) is about 12 m thick and crops out just west of Cinisi, along a coastal cliff running between two localities known as "La Ciucca" and "Torre Molinazzo" (indicative geographic coordinates: N 38°09'50", E 13°05'07"). This succession belongs to the "Calcareniti e sabbie di Castellammare lithofacies", a lower Pleistocene sedimentary unit lying unconformably on pre-Quaternary rocks (Catalano *et al.*, 2004). This unit consists mostly of calcarenites, yellowish carbonate-rich sands, and minor conglomeratic and clayey beds, deposited in an inner-shelf environment (Catalano *et al.*, 2004). The portion of this unit exposed at the study site (Fig. 3.a) hosts a macrofossil assemblage that includes bivalves, gastropods, echinoids, cirripedes, bryozoans, brachiopods, ostracods, and fragmentary remains of crabs and fish (Ruggieri, 1976; Cipolla, 1978). Indeterminate cetacean remains including worn fragmentary postcrania are also present (personal observation by A.C., G.I., and G.B.; Fig. 3.b). A 12-m-thick stratigraphic section (Fig. 4) was measured by Cipolla (1978). The whale barnacle specimens described herein were reported by M.M. and collected by G.I. during fieldwork on behalf of Museo di Storia Naturale di Comiso (Comiso, Ragusa Province, Sicily), and come from the base of an interval of yellowish, bioturbated, fossil-rich, locally indurated sand located in the upper portion of the Cinisi section (Fig. 4). This interval has also produced shelly remains referred by Cipolla (1978) to the veneroid bivalve *Arctica islandica* (Linnaeus, 1767).

Samples of the sandy sediment body hosting the coronulid specimens were collected for biostratigraphic purposes. Calcareous nannofossil analyses were carried out by one of us (R.C.) using a polarized light microscope on a smear-slide prepared from the sample, following standard techniques (Bown & Young, 1998). The calcareous nannofossil assemblages of the samples studied do not differ significantly from each other. The co-occurrence of abundant *Calcidiscus macintyrei* (Bukry & Bramlette, 1969) Loeblich & Tappan, 1978, and rare, small (<3.5 µm), unidentified *Gephyrocapsa* Kamptner, 1943, coupled with the absence of *Discoaster brouweri* Tan, 1927, *emend.* Bramlette & Riedel, 1954, allowed us to attribute the assemblage detected in the analyzed samples to the lower Pleistocene Mediterranean Neogene Nannoplankton (= MNN) zone 19a of Rio *et al.* (1990), corresponding to the Calcareous Nannofossil Plio-Pleistocene (= CNPL) zone 7 of the more recent Neogene and Quaternary biozonation of Backman *et al.* (2012). The bioevents that bound this zone have recently been calibrated by Backman *et al.* (2012) to 1.93 Ma and 1.71 Ma; consequently, the analyzed samples should be regarded as latest Gelasian to earliest Calabrian (*i.e.*, early Santernian, following the 'Italian Marine Stages' regional scheme of Gibbard & Cohen, 2008). Our biostratigraphic results partially contradict those of Ruggieri (1976, 1987) and Cipolla (1978), who referred to the deposits exposed at Cinisi as middle Calabrian (*i.e.*, Emilian substage of the 'Italian Marine Stages' regional scheme) while evoking the persistence or reappearance of some 'Pliocene' (*i.e.*, pre-Emilian) taxa.

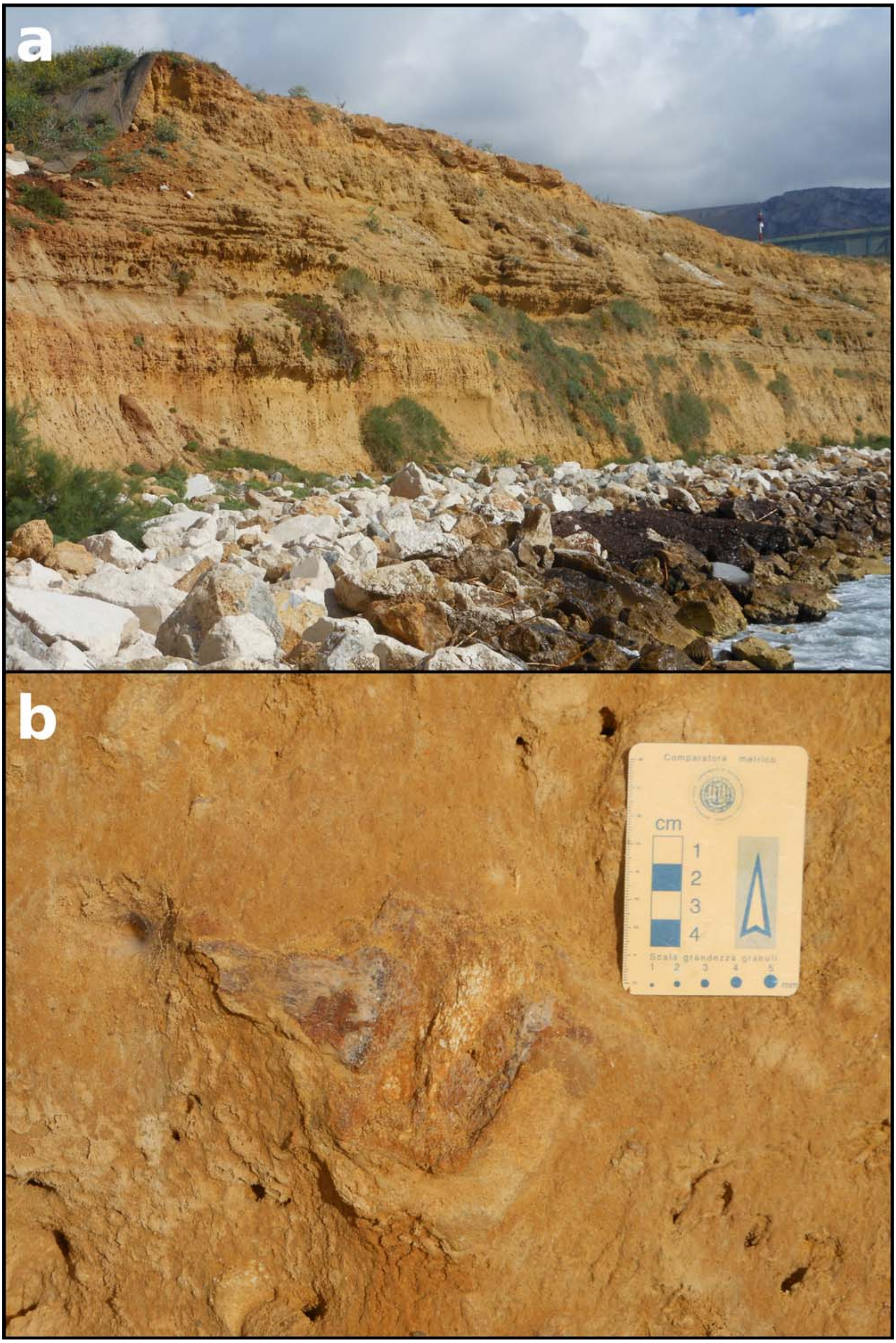


**Figure 3: a.** Exposure of the "Calcareniti e sabbie di Castellammare lithofacies" west of the city of Cinisi. **b.** An indeterminate cetacean vertebra cropping out from a sandy horizon at the study site.

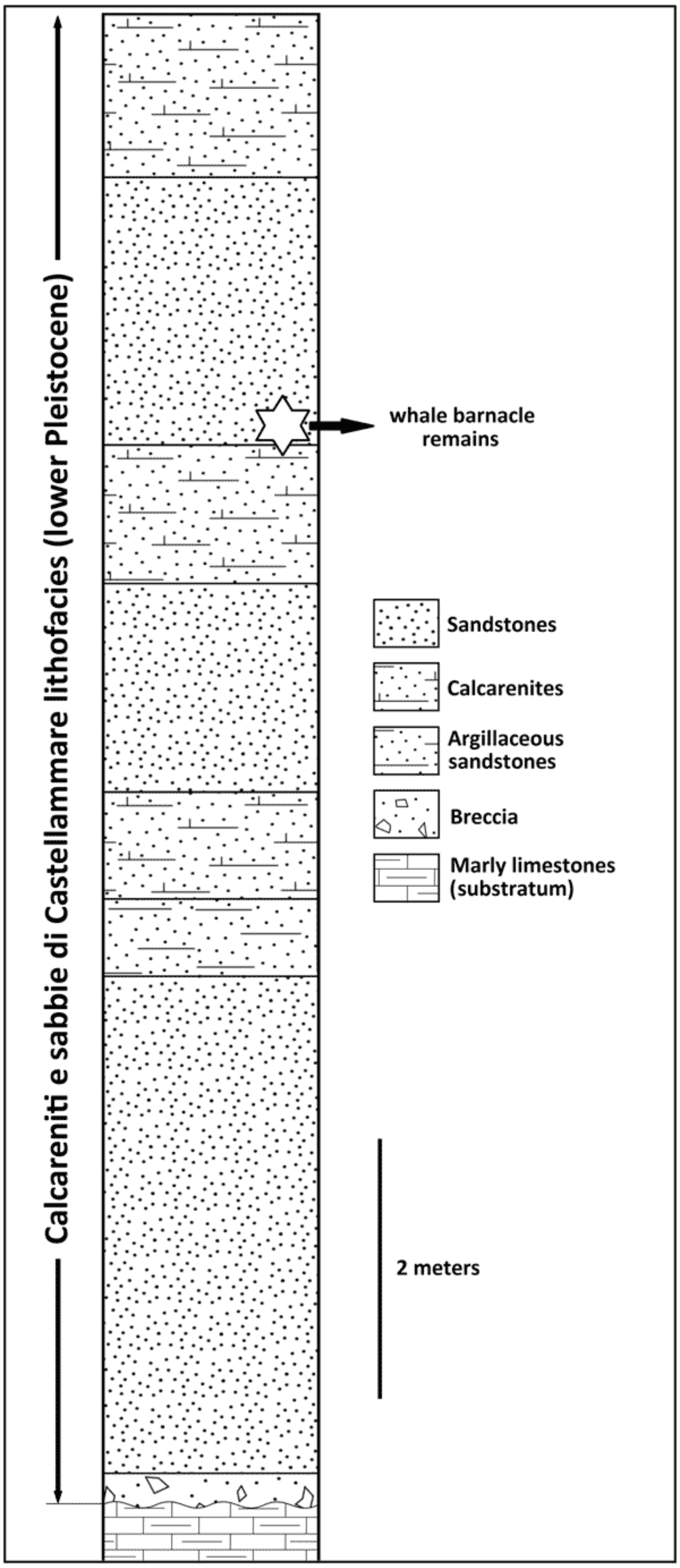


**Figure 4:** Schematic stratigraphic section of the sedimentary succession exposed at the study site (indicative geographic coordinates: N 38°09'50", E 13°05'07"). Redrawn and modified after Cipolla (1978).

## 4. Systematic palaeontology

### Class MAXILLOPODA Dahl, 1956

### Subclass CIRRIPEDIA Burmeister, 1834

### Order SESSILIA Lamarck, 1818

### Suborder BALANOMORPHA Pilsbry, 1916

### Family CORONULIDAE Leach, 1817

### Genus *Coronula* Lamarck, 1802

**Diagnosis** (after Buckeridge, 1983). Body within shell wall composed of six equal-sized compartments; opercular valves present; parietes with similar structure throughout, without internal midribs; parietal ribs radiate accordion-like to end as T-shaped flanges forming exterior of wall; radii less than half thickness of parietes, orifice of body chamber larger than basal opening; sheath smooth, extending entire length of inner wall; radiating ribs on either side of sutures unbranched or asymmetrically branched; opposed sides of terminal flanges crenulate.

**Type species.** *Lepas diadema* Linnaeus, 1767. Early Pleistocene to Recent, cosmopolitan.

**Distribution.** Upper Pliocene (Piacenzian) to Recent (Collareta *et al.*, 2016a), cosmopolitan (Buckeridge, 1983). Currently known as an exclusive symbiont of cetaceans, displaying a high host specificity for the balaenopterid baleen whale species *Megaptera novaeangliae* (Borowski, 1781).

### *Coronula bifida* Bronn, 1831

(Fig. 5)

1831 *Coronula bifida* Bronn, p. 126.
1854 *Coronula barbara* Darwin, p. 421, Pl. 15, fig. 6.
1951 *Coronula dormitor* Pilsbry & Olsson, p. 202.
1968 *Coronula bifida bifida* Menesini, p. 387, Pls. 1-3, figs. 1a-2b; Pl. 4, figs. 1, 3, 5.
1968 *Coronula bifida barbara* Menesini, p. 395, Pl. 3, figs. 3a-5c; Pl. 4, figs. 2, 4, 6.

**Diagnosis.** Shell globose, with longitudinal convex parietal ribs that often bifurcate, and with strong transverse ridges; radii moderately thick, displaying a roughly constant width (or slightly widening downwards) in the upper two thirds of the shell, and then becoming progressively narrower downwards in their lowermost third; body chamber relatively shallow, sub-cylindrical; sheath less than half of the total height of the shell.

**Distribution.** Upper Pliocene (Piacenzian) to mid-lower Pleistocene. Known as fossil from marine deposits of Belgium (as "*C. barbata*", *error pro C. barbara*: Marquet *et al.*, 2009), California (U.S.A.) (as *C. barbara*: Zullo, 1969), Ecuador (as *C. dormitor*: Pilsbry & Olsson, 1951), England (as *C. barbara*: Darwin, 1854), and Italy (both as *C. barbara* and *C. bifida*: Bianucci *et al.*, 2006b, and previous references therein; Collareta, 2016; Collareta *et al.*, 2016b, in press).

**Material and repository.** Three rather large specimens kept at Museo Civico di Storia Naturale di Comiso (= MSNC), Comiso, Ragusa Province, Sicily, under accession numbers MSNC 4454 (Fig. 5.a-c), MSNC 4555 (Fig. 5.d-f), and MSNC 4556 (Fig. 5.g-h). MSNC 4554 and MSNC 4555 are two complete and articulated shells, whereas MSNC 4556 is an incomplete shell consisting of two articulated compartments (rostrum and right latus).

**Occurrence.** Lower Pleistocene shallow-marine deposits outcropping at Cinisi (Palermo Province, northwestern Sicily, southern Italy; indicative geographic coordinates: N 38°09'50", E 13°05' 07") and belonging to the "Calcareniti e sabbie di Castellammare lithofacies" as defined by Catalano *et al.* (2004). The sediment embedding the whale barnacles is attributed to the calcareous nannoplankton zone MNN 19a of Rio *et al.* (1990), that is, to the interval 1.93 - 1.71 Ma (according to Backman *et al.*, 2012).

**Remarks.** The following set of characters helps in distinguishing the extinct species *Coronula bifida* from other coronulid taxa (including the extant species *Coronula diadema*): (1) prominent transverse growth ridges on the external surface of the parietal ribs (*e.g.*, Fig. 5.f); (2) frequently bifurcated parietal ribs (*e.g.*, Fig. 5.b-c); (3) external radii displaying a roughly constant width (or slightly expanding in width downwards) in the upper two thirds of the shell, and then becoming progressively narrower downwards in their lowermost third (*e.g.*, Fig. 5.c, e-f); (4) basal margin of the sheath which does not project freely (*e.g.*, Fig. 5.h); and (5) relatively shallow body chamber, shorter than half of the total height of the shell (*e.g.*, Fig. 5.h) (see also Menesini, 1968). All these characters can be observed in the fossil coronulid specimens from Cinisi, thus allowing an unambiguous species-level determination. Smoothed surfaces (*e.g.*, Fig. 5.a) and fractures (*e.g.*, Fig. 5.d, g) are mostly observed in the upper half of the three specimens, suggesting that this part of the shells was exposed above the skin of the cetacean, as also indicated by the shallow body chamber of MSNC 4554. By contrast, in *C. diadema* most of the shell is exposed outside the skin of the host, so that specimens belonging to this extant species frequently display evidences of abrasion and wearing in the upper two thirds (or more) of the shell (Bianucci *et al.*, 2006a; Dominici *et al.*, 2011). Marks due to encrustation by non-epizoic barnacles (cf. *Anellusichnus* isp. Santos *et al.*, 2005) and other invertebrates (*e.g.*, bryozoans) are observable on all specimens (*e.g.*, Fig. 5.c), similar to features reported by Bianucci *et al.* (2006a) for fossil shells of *C. diadema* from the lower Pleistocene (probably Calabrian; Collareta, 2016) of Ecuador.

Based on the occurrence of a single, well-preserved, large (*i.e.*, displaying a diameter of 60 - 70 mm) shell of *Coronula diadema* from the upper lower Pleistocene of Riparbella (Tuscany, central Italy), Dominici *et al.* (2011) proposed that *C. diadema* is a direct descendant of *C. bifida* and that the evolution of the former included a pronounced increase in size of the adult shell. Interestingly, one of the specimens of *C. bifida* described herein (MSNC 4554) exhibits a maximum diameter of 73 mm, that is, seemingly slightly larger than that of the specimen of *C. diadema* described by Dominici *et al.* (2011). Moreover, with regard to 56 well-preserved shells of *Coronula diadema* from the lower Pleistocene Canoa and Tablazo Formations of Ecuador, Bianucci *et al.* (2006b) noted that their average size is distinctly greater than that observed for extant individuals of *Coronula diadema* from the skin of humpback whales taken off Madagascar (Angot *et al.*, 1951). Bianucci *et al.* (2006b) argued that the fragile construction apparent in juveniles of *Coronula* could render them less likely to fossilize, at least as complete and articulated shells, thus significantly biasing the size parameters of fossil whale barnacle assemblages. Therefore, we contend that the evolutionary trend towards an increase in size proposed by Dominici *et al.* (2011) for *Coronula* still needs to be confirmed.

## 5. Palaeobiogeographical and palaeoecological implications

During the Pliocene, mysticetes were abundant and diverse along the coasts of Italy, being represented by several skeletons referred to species of at least three families (Balaenidae, Balaenopteridae, and Eschrichtiidae) (*e.g.*, Bisconti, 2002, 2003, 2007, 2008, 2009; Bianucci *et al.*, 2009). In turn, the balaenopterid fin whale *Balaenoptera physalus* (Linnaeus, 1758) is the sole baleen whale species known to inhabit the modern waters of the Mediterranean Sea regularly (*e.g.*, Cagnolaro *et al.*, 1993) and is recognized as forming a genetically distinct sub-population displaying largely resident (*i.e.*, non-migratory) habits (Panigada & Notarbartolo di Sciara, 2012, and references therein). The transition from the Pliocene to the extant baleen whale fauna of the Mediterranean Sea is still obscure, as the Pleistocene record of mysticetes (and of cetaceans generally) is very poor in this basin (*e.g.*, Collareta *et al.*, 2016b, and references therein), although a few recent discoveries from Italy

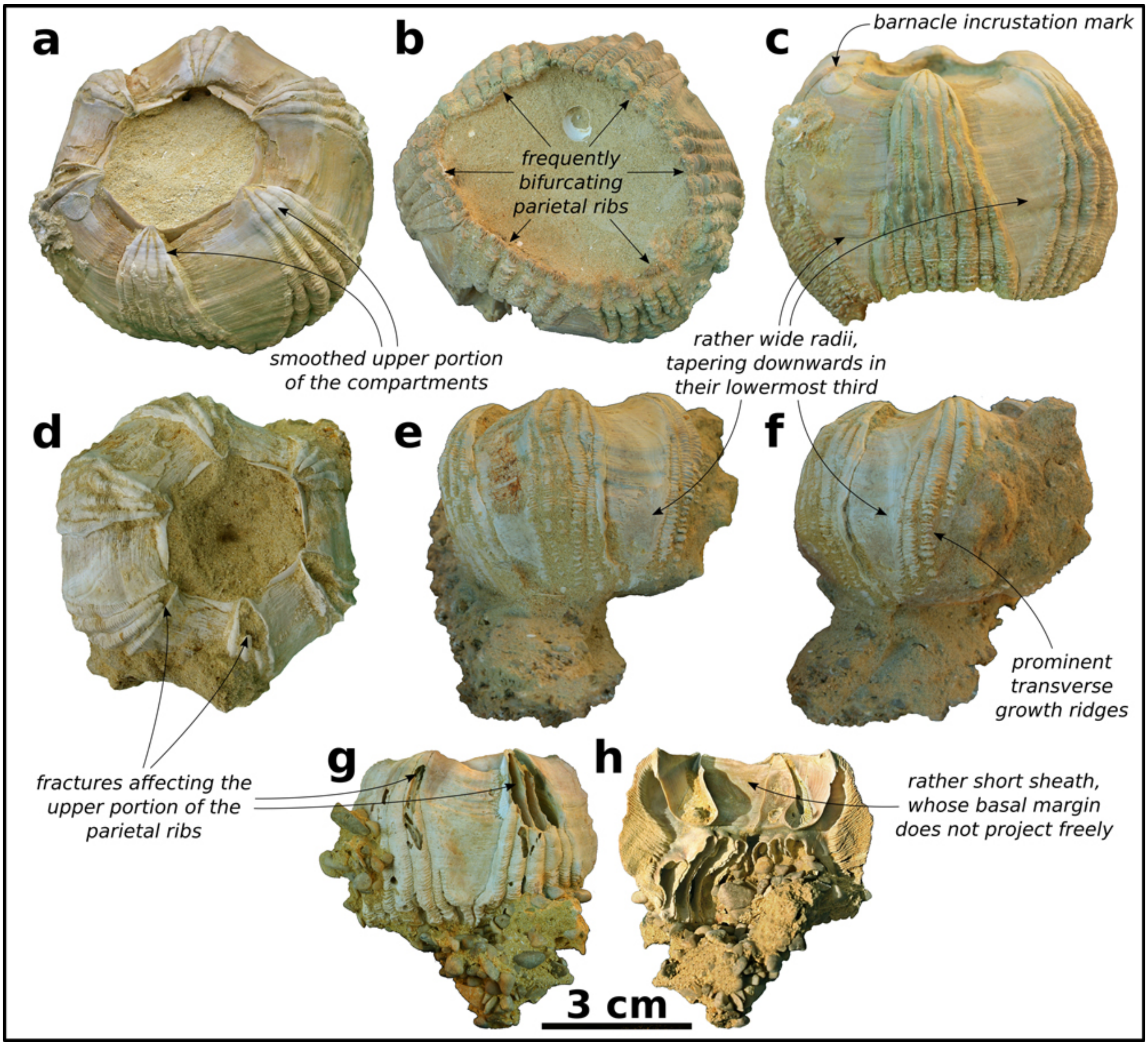


**Figure 5:** MSNC 4554, MSNC 4555, and MSNC 4556, three fossil shells of *Coronula bifida* BRONN, 1831, from lower Pleistocene deposits exposed near Cinisi (Palermo Province, western Sicily, southern Italy). **a-c.** Specimen MSNC 4554. **d-f.** Specimen MSNC 4555. **g-h.** Specimen MSNC 4556. Panels a and d: subapical view; panel b: basal view; panels c, e, f, and g: lateral view; panel h: central view.

(*e.g.*, MARGIOTTA & VAROLA, 2007; BIANUCCI *et al.*, 2012; TSAI *et al.*, 2017) are helping to close this gap. Nevertheless, Pleistocene remains of whale barnacles still play a pivotal role in illustrating the dynamics of the cetacean fauna of the Mediterranean Sea during the Quaternary as reliable indicators of ancient baleen whale populations.

As reported above, the sediment hosting the coronulid specimens from Cinisi was referred to zone MNN 19a of RIO *et al.* (1990) by means of calcareous nannoplankton biostratigraphy. Interestingly, the same lower Pleistocene biozone was identified in fossiliferous deposits of southeastern Sicily featuring remains of a pygmy right whale (cf. *Caperea* sp. GRAY, 1864) (TSAI *et al.*, 2017), as well as in inner-neritic deposits of southeastern Apulia (southern Italy) containing fossil whale barnacles (attributed to *Coronula bifida* and *Cetopirus fragilis*) (COLLARETA, 2016; COLLARETA *et al.*, 2016b, in press). The latter occurrence was recently interpreted as indirect evidence of an ancient breeding/calving ground shared by humpback whales (or other balaenopterids closely related to *Megaptera* GRAY, 1846) and right whales (or other balaenids closely related to *Eubalaena*) (COLLARETA *et al.*, 2016b). Our new finds from Cinisi confirm that, during the early Pleistocene, whales colonized by *Coronula bifida* (most likely belonging to the family Balaenopteridae, in light of the host preferences of the Recent species *Coronula diadema*) frequented the shallow coastal waters of the central Mediterranean Sea (presumably for breeding and calving purposes, considering that the detachment of whale barnacles from living whales has been primarily observed in zones of reproduction). Furthermore, since the fossil whale barnacles from Otranto and Cinisi come from sedimentary units that were deposited during the same, relatively short period of time (*i.e.*, between 1.93 and 1.71 Ma), they seemingly depict the same phase of dispersal of migrating North Atlantic cetaceans within the Mediterranean Basin, and in particular in the epeiric seas located off the coasts of modern southern Italy. From this perspective, baleen whales inhabiting the high-latitude areas of the northeastern Atlantic could have chosen to use the central region of the Mediterranean Basin as a winter breeding/calving ground during the Gelasian-Calabrian transition, possibly as a response to Northern Hemisphere climate change (see also Clementz *et al.* (2014), Boessenecker & Fordyce (2015), Marx & Fordyce (2015), and Tsai (2017) for an updated discussion about the emergence of migratory habits in mysticetes). Indeed, recent research indicates that the waters of the central Mediterranean Sea saw a strong increase in thermal seasonality, coupled with a strong decrease of average winter temperature, around 1.80 Ma (Crippa *et al.*, 2016). This severe climatic degradation is famously marked by the appearance of cold-water North Atlantic invertebrate taxa ("northern guests") such as the ocean quahog bivalve *Arctica islandica* (a species that has been reported as occurring alongside *Coronula bifida* in the deposits exposed at the study site) in the Mediterranean fossil record around 2.0-1.8 Ma (*e.g.*, Gibbard & Head, 2010; Crippa & Raineri, 2015, and references therein). Such a drastic basin-wide cooling episode reflected global climate degradation that implies, in the Atlantic Ocean, both a significant shift of the polar/subpolar water fronts towards the Equator and a remarkable lowering of sea surface temperatures at low latitudes, thus ultimately allowing a cool-temperate Southern Hemisphere form such as *Caperea* to cross the normally impassable tropics and enter the Mediterranean Basin (Tsai *et al.*, 2017).

Since several currently emerged portions of southern Italy were still submerged at the time of the Gelasian-Calabrian transition (Santangelo *et al.*, 2012), lagoons punctuated by islands and other sheltered shallow neritic habitats potentially suitable as breeding/calving grounds for mysticete cetaceans should have been probably well-represented in the central part of the Mediterranean Basin, at the foot of the rising southern Apennine chain (a palaeoenvironmental scenario somewhat reminiscent of today's inshore reproduction sites of *Eschrichtius robustus* and *Megaptera novaeangliae* along the coasts of Baja California; *e.g.*, Scammon, 1968; Gendron & Urban, 1993; Hindell, 2009). Due to a long-lasting pattern of widespread emergence of coastal epeiric sea regions, most of these key environments suffered a progressive reduction during the late early (Calabrian) and Middle Pleistocene (Santangelo *et al.*, 2012), thus possibly leading to the abandonment of the central Mediterranean nursery areas by most large species of migrating mysticetes in favor of breeding and calving grounds located outside the Mediterranean Basin (*e.g.*, in the Gulf of Biscay or off the coasts of northwest Africa). The persistence of large mysticetes in the central Mediterranean at the end of the early Pleistocene is nevertheless witnessed by a partial balaenopterid skeleton, provisionally attributed to the genus *Balaenoptera* Lacépède, 1804, from Calabrian deposits exposed at San Giuliano (Matera Province, Basilicata, Italy) (Bianucci *et al.*, 2012). As reported above, the youngest fossil occurrence of *Coronula* from the Mediterranean Basin is represented so far by a single shell collected from inner-shelf deposits exposed near Riparbella (Tuscany, central Italy) in mudstones tentatively referred by Dominici *et al.* (2011) to the mid-upper Calabrian zone MNN 19e of Rio *et al.* (1990), corresponding to zone CNPL 9 of Backman *et al.* (2012), regarded as ranging from 1.25 to 1.06 Ma.

In conclusion, investigations focusing on the fossil record of whale barnacles (*Coronula* and allied forms) highlight a rather complex and previously unexpected Quaternary history for the Mediterranean mysticetes. New additions to the still fragmentary Italian Pleistocene record of fossil mysticetes will hopefully further elucidate the biogeographical patterns and dynamics of the Mediterranean baleen whale fauna during the Quaternary.

**Note added in proofs:** During the proofreading of the present paper, another contribution (Collareta *et al.*, in press) dealing with the Mediterranean record of *Coronula* was accepted for publication in an international journal. In this forthcoming paper, the hypothesis of a baleen whale migratory route active in early Pleistocene times between the central Mediterranean Sea and the northeastern Atlantic is further investigated in the light of oxygen-isotope analyses of a fossil whale barnacle shell from Apulia.

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