

Systematics, distribution and palaeoecology of the genera *Genocidaris* Agassiz, 1869 and *Arbacina* Pomel, 1869 (Trigonocidaridae, Echinoidea)

Sistemática, distribución y paleoecología de los géneros *Genocidaris* Agassiz, 1869 y *Arbacina* Pomel, 1869 (Trigonocidaridae, Echinoidea)

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Abstract: The relationship among members of the echinoid genera *Genocidaris* and *Arbacina* (family Trigonocidaridae) is studied. Distinctive morphological characters of these two genera are discussed, based on recent specimens from the Caribbean and the Mediterranean and on fossils collected from 34 Miocene, Pliocene and Pleistocene European localities. Geographic and biostratigraphic distributions of the two genera and their palaeoecological requirements are reported. Based on this analysis, *Arbacina* is considered a junior synonym of the genus *Genocidaris*.

Resumen: Se estudia la relación entre los géneros de equinoideos *Genocidaris* y *Arbacina*, ambos pertenecientes a la familia Trigonocidaridae. Se discuten los caracteres morfológicos distintivos de estos dos géneros, basados en el estudio de ejemplares de treinta y cuatro localidades europeas, correspondientes al Mioceno, Plioceno y Pleistoceno. Se ha estudiado la distribución geográfica y bioestratigráfica de ambos géneros, así como sus requisitos paleoecológicos. Con base en este análisis, el género *Arbacina* se considera un sinónimo junior de *Genocidaris*.

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INTRODUCTION

Small temnopleuroid echinoids are common in Neogene near-shore deposits of Europe (Mediterranean, Atlantic coast and Paratethys region). Usually restricted to coronal diameters of less than 10 mm, these echinoids are often overlooked in outcrops, especially where preserved as fragments. Contrary to larger “regular” echinoids, however, their corona is quite sturdy and thus frequently preserved in more turbulent, coarse-grained deposits. Unfortunately, their remains are often abraded and susceptible to overgrowth by calcitic cement. Due to this and their complex taxonomy, they are notoriously difficult to identify to species level and have usually been lumped in the species *Arbacina monilis*, *A. catenata*, *A. romana* and *Psammechinus dubius*. Careful revision of these remains often shows that many are juvenile echinaceans that cannot be determined to genus or species level (e.g., Kroh, 2005). A number of records, however, appear correctly

assigned to *Arbacina*. Differentiation from the closely related extant genera *Genocidaris* and *Trigonocidaris* proves difficult due to the poor characterization of the fossil genus *Arbacina* and the variable nature of its putative diagnostic features.

Genocidaris and *Arbacina* were established in 1869 by Agassiz and Pomel, respectively. Mortensen (1943) observed close similarities between these two genera. Kroh (2005) noticed that the indentation at the base of the primary tubercles, which is the main character distinguishing *Genocidaris* from *Arbacina* (Mortensen, 1943; Fell & Pawson, 1966), was present also in *Arbacina catenata* (Desor in Agassiz & Desor, 1846) from the lower Miocene of the Paratethys (Austria and France). Borghi *et al.* (2006) reported the presence of indentations also in Pliocene and Pleistocene samples traditionally assigned to *Arbacina romana* (Merian in Desor, 1858) from Italian localities. In addition,

these authors detected the occurrence of features diagnostic of *Arbacina* in fossil and recent specimens belonging to *Genocidaris maculata* Agassiz, 1869. Vadet and Nicolleau (2017) affirmed that *Arbacina* and *Genocidaris* were indistinguishable on the basis of the results of morphological biometric analyses; however, they maintained them separated by a different ambulacral plate composition and transferred *Arbacina* to the family Parechinidae Mortensen, 1903. *Arbacina* is currently considered as a subjective junior synonym of *Genocidaris* in Smith and Kroh (2011) and Kroh and Mooi (2022). Herein, the investigation has been extended to settle the question of the distinction between these two genera by analysis of the respective type species: *Genocidaris maculata* and *Arbacina monilis* (Desmarest in Defrance, 1825).

MATERIAL AND METHODS

The taxonomy of the genus *Arbacina* is problematic. Several species have been attributed to this genus but most of them are not completely known in their morphology because they were described on the base of single (or a few) specimens, which are often missing or badly preserved. This is the case, for example, with a group of species instituted by Pomel (1887) from the upper Miocene and Pliocene of Algeria, including *A. badinskii*, *A. asperata*, *A. massylea*, *A. sahelensis* and *A. nicaisii*, whose types are wanting (the whereabouts of Pomel collection are unknown; see Stara & Borghi, 2017 for details). Philippe (1998) pointed out this situation, cautioning about the loss of small morphological details, often obscured by abrasion and diagenetic cement growth. He also underlined the presence of a large intraspecific morphological variability, which affects also the test sculpturing. Since the distinction among species is mainly based on the frequency of occurrence of sunken and raised ornamentation in the test surface, studying large samples is needed when working with these small echinoids. Consequently, only species represented by well-preserved type (or topo-typic) material are discussed. In the following we report information about the specimens examined in this study, in particular about the type material available for the two type-species, *Genocidaris maculata*, and *Arbacina monilis*, and of some key species of *Arbacina*.

Genocidaris maculata Agassiz, 1869

Agassiz (1869) provided a short description and no illustration. The type material, dredged in the Caribbean Sea between Cuba and Florida, was housed at the Museum of Comparative Zoology, Harvard. Subsequently, Agassiz (1872) added detailed illustration of three specimens of different size from the same area. The illustration of a syntype (ECH-1411) from Dry Tortugas, Florida, is reported in Smith and Kroh (2011). Mortensen (1903, 1943) considered the specimens from

the Mediterranean Sea as identical to those from the Caribbean. Two complete topo-typic recent specimens (USNM E12092) with well-preserved apical disc from Florida, have been examined in this study.

Arbacina monilis (Desmarest in Defrance, 1816)

Desmarest did not indicate the type locality but regarding the repository of the type material, however, he wrote: “*Echinus monilis* is closely related to the species which is very common in the limestones of Doué in Anjou”, which has been dated to the Serravallian by Nicolleau and Dudicourt (2006). Agassiz and Desor (1846) first figured this species; they considered Doué as the type-locality and extended its distribution to a number of other localities in north-western France. This interpretation was shared by Desor (1856) and Bazin (1884). Ten topotypic specimens (MG 1028 Do.01-10) from the Serravallian of Doué were available for this study. Additionally, 53 specimens from other localities from the upper Miocene of western France (MG 1415 Sv.11-22, MG 1415 SI.01-21, MG 1415 No.01-20) have been used for comparison.

Arbacina blancheti Lambert in Castex, 1930

Two syntypes from the Oligocene of Lesperon (France) are housed at the MNHN (F.J01239, collection Lambert). The illustration of one of them is provided in the MNHN web site (<https://science.mnhn.fr/institution/mnhn/collection/f/item/j01239>, accessed March 2022).

Arbacina catenata Desor in Agassiz & Desor, 1846

Desor provided a short description and no illustration of this species. Locality and repository of the type material are unknown (Lambert, 1910; Philippe, 1998; Kroh, 2005). Desor (1858, p. 122) wrote: “*T. 69. (Original de l'espèce) Tertiaire (Molasse?) du Midi. Très rare. Muséum d'Avignon*”. Philippe (1998) was not able to trace the holotype in French collections. It seems probable that the plaster cast T69 in the collection of Neuchâtel was taken from a corona originating from the Burdigalian of Avignon (south-eastern France), but the cast is not at Lyon and at Neuchâtel (P. Nicolleau, personal communication, 2019). Lambert (1910) proposed a neotype based on a specimen from Plan d'Arren, a locality near Istres, Bouches du Rhône (P. Nicolleau, personal communication, 2019). We based our concept of *A. catenata* on the detailed description and illustration provided by Philippe (1998), who studied specimens from the Miocene of the Rhône Basin, including the Burdigalian of the Bassin d'Avignon (typic horizon for the neotype).

Arbacina romana (Merian in Desor, 1858)

The original diagnosis reported “*Petite espèce renflée, voisine du P. monilis, mais plus tuberculeuse. Tertiaire supérieur (Pliocène) de Palerme. Muséum Bâle. Exemple unique*”. After Lambert (1910),

the whereabouts of the holotype are unknown. The type locality is Palermo (Sicily, southern Italy), but all the specimens known from this area (base of Monte Pellegrino; Ficarazzi) originated from Calabrian deposits (Checchia-Rispoli, 1907), not from Pliocene localities. Lambert (1910) considered the description provided by Checchia-Rispoli (1907) as the reference to this species. The fossil material from the surroundings of Palermo examined by the authors in the Checchia-Rispoli collection, consisting of 220 specimens (MGP/CR 01-220), represents topo-typic material. Checchia-Rispoli (1916, 1923) subsequently extended the distribution of *A. romana* to other Calabrian localities of Sicily, the Pliocene (Piacenzian) of Altavilla (Sicily) and the Gelasian of Anzio, near Rome: 124 specimens were available to study from these localities (Tab. 1).

Arbacina piaë Lovisato in Cotteau, 1895

The type specimens were lost, together with a large part of the Lovisato's collection, when the Museum of Cagliari was destroyed by bombing in 1943 (P. Stara, personal communication, 2019). The illustration reported in the original description (Cotteau, 1895, pl. 3, figs. 1–6) does not show morphological details. The original outcrop is no longer exposed at the type locality, the Burdigalian of Bonorva (Sardinia). However, Lovisato (in Lambert, 1907) attributed to *A. piaë* the

specimens from the Aquitanian–lower Burdigalian of Funtanazza, another Sardinian locality not far from Bonorva. We based our concept of *A. piaë* on 12 specimens (MG 1412 Fu.01-12) from this locality.

Brooding species

A group of sexually dimorphic species of *Arbacina* has been described from upper Miocene and Pliocene localities of the Atlantic coast of France.

Arbacina pareyni Roman, 1983, Pliocene of Saint André de Bohon (Manche). The holotype (MNHN.F. R50799), the sole specimen known of this species, was figured by Roman (1983, pl. 2, figs. 9–12).

Arbacina emmae Néraudeau et al., 2003, Messinian of Bretagne. Also, in this case the holotype (MNHN, collection Barbe), figured in Néraudeau et al. (2003, fig. 2; pl. 1, fig. 5; pl. 2, figs. 4–6), is the sole specimen known.

Arbacina hugueti Dudicourt et al., 2005, Pliocene of Challans (Vendée). The holotype (pl. IV, figs. 1–3) is housed at the Museum of Niort (n. 8279), two paratypes are at the Muséum National d'Histoire Naturelle of Paris. (MNHN-R64551 and MNHN-DHT A24829).

Genocidaris incerta Clark, 1928

Recent, Australia; the holotype (SAM E.623) was figured by Clark (1928, fig. 137).

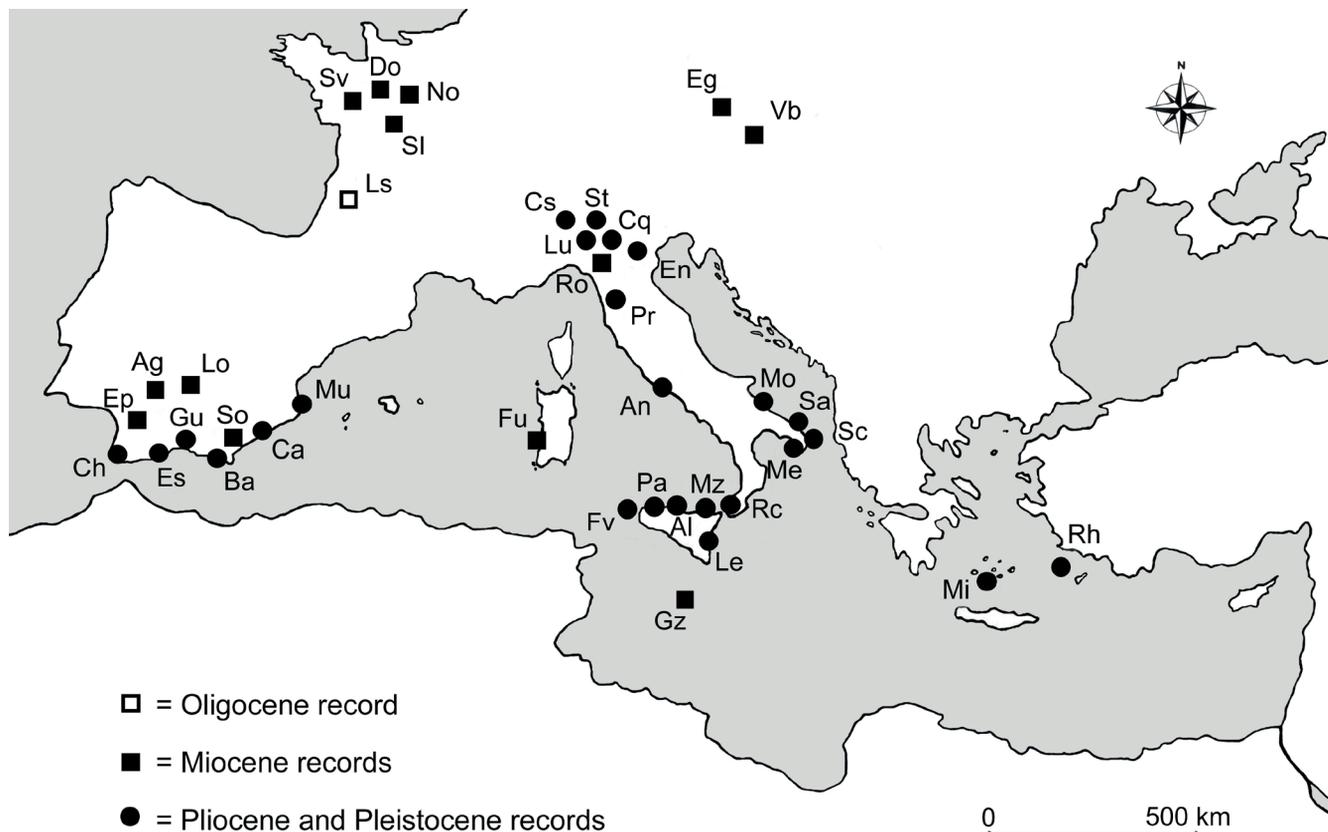


Figure 1. Map with the location of the finding localities cited in the text. Abbreviations are reported in the material and methods section.

Table 1. List of the specimens examined in this study. ** = topo-typic material, * = specimens from the respective type-areas. N, number of specimens.

Species	N.	Catalogue n.	Locality	Age
<i>Genocidaris monilis</i> **	10	MG 1415 Do.01-10	Doué (France)	Serravallian (Nicolleau & Dudicourt, 2006)
<i>Genocidaris monilis</i> *	12	MG 1415 Sv.11-22	Savigné (France)	Langhian (Nicolleau & Dudicourt, 2006)
<i>Genocidaris monilis</i> *	21	MG 1415 Sl.01-21	Saint Laurent de Lin (France)	Langhian (Sztrákos & Sterubaut, 2017)
<i>Genocidaris monilis</i> *	20	MG 1415 No.01-20	Noyant (France)	Serravallian–Tortonian (Nicolleau & Dudicourt, 2006)
<i>Genocidaris catenata</i>	1	MG 1412 Ro.01	Roteglia (Italy)	Langhian (Amorosi, 1997)
<i>Genocidaris catenata</i>	1	MGUS/Bajo Lo.01	Lora del Río (Spain)	Tortonian (Abad, 2005)
<i>Genocidaris catenata</i>	5	AG/Bajo Ac.01-05	Alcalá de Guadaíra (Sevilla, Spain)	Messinian (Bajo <i>et al.</i> , 2008)
<i>Genocidaris catenata</i>	6	MGUS/Bajo So.01-06	Sorbas (Spain)	Messinian (Martin & Braga, 1994)
<i>Genocidaris catenata</i>	6	MGUS/Bajo Ca.01-06	Carboneras (Spain)	Messinian (Aguirre, 1998)
<i>Genocidaris catenata</i>	2	MGUS/Bajo Ep.01-02	Espera (Spain)	Tortonian (Pereira <i>et al.</i> , 2002)
<i>Genocidaris piae</i> *	12	MG 1412 Fu.01-12	Funtanazza (Italy)	Aquitanian–Burdigalian (Spano <i>et al.</i> , 2002)
<i>Genocidaris romana</i> *	2	MGP/CR Al.01-02	Altavilla (Italy)	Pliocene (Cecchia-Rispoli, 1916)
<i>Genocidaris romana</i>	7	MGUS/Bajo Ba.01-06	Balerna (Spain)	Pliocene (Aguirre, 1998)
<i>Genocidaris romana</i>	3	MGUS/Bajo Es.01-03	Estepona (Spain)	Pliocene (Aguirre <i>et al.</i> , 2005)
<i>Genocidaris romana</i>	3	MGUS/Bajo Ch.01-03	Chiclana (Spain)	Pliocene (Aguirre, 1995)
<i>Genocidaris romana</i>	6	MG 1414 Ar.01-06	Aguilas (Spain)	Pliocene (Pajaud, 1977, Montenat <i>et al.</i> , 1978)
<i>Genocidaris romana</i> *	3 4	MG 1412 An.01-03 MSR i.25	Anzio (Italy)	Gelasian (Carboni & Di Bella, 1997)
<i>Genocidaris romana</i>	5	MB/MA 01-05	Parlascio (Italy)	Calabrian (Manzoni, 1879)
<i>Genocidaris romana</i> *	52 64 1	MG 1411 Fv.01-52 MG 1412 Fv.53-116 MG 1579.I	Favignana (Italy)	Calabrian (Borghi & Garilli, 2016)
<i>Genocidaris romana</i> *	2 1	MG 1411 Tr.01-02 MG 1579.F	Terreti (Italy)	Plio-Pleistocene (Bonfiglio, 1974)
<i>Genocidaris romana</i> **	220	MGP/CR 01-220	Palermo (Italy)	Calabrian (Cecchia-Rispoli, 1907)
<i>Genocidaris romana</i> *	1	MSR i.161	Lentini (Italy)	Calabrian (Cecchia-Rispoli, 1938)
<i>Genocidaris maculata</i> **	1	USNM E12092	Florida Keys (USA)	Recent
<i>Genocidaris maculata</i>	3	MG 1414 Cq.01-03	Campore (Italy)	Piacenzian (Ceregato <i>et al.</i> , 2007)
<i>Genocidaris maculata</i>	1	MG 1413 Lu.01	Lugagnano (Italy)	Piacenzian (Monegatti <i>et al.</i> , 2002)
<i>Genocidaris maculata</i>	1	MGUS/Bajo Es.01	Estepona (Spain)	Pliocene (Aguirre <i>et al.</i> , 2005)
<i>Genocidaris maculata</i>	119 36 22 4	MG 1112 St.01-119 MP/S.01-36 MS.01-22 MG 1579.A, C, D, G	Stirone River (Italy)	Calabrian (Crippa <i>et al.</i> , 2019)
<i>Genocidaris maculata</i>	25 45 43 2	MG 1413 Cs.01-25 MG 1414 Cs.26-70 MG 0993 Cs.71-114 MG 1579.J, K	Castell'Arquato (Italy)	Calabrian (Crippa <i>et al.</i> , 2019)
<i>Genocidaris maculata</i>	1	MG 1414 Mi.01	Milos Is. (Greece)	Calabrian (Tsokas, 2000)
<i>Genocidaris maculata</i>	3	MG 1414 En.01-03	San Polo (Italy)	Calabrian (Fornaciari, 1997)
<i>Genocidaris maculata</i>	2	MG 1414 Me.01-02	Punta Melisio (Italy)	Calabrian (Taddei Ruggiero, 1994)
<i>Genocidaris maculata</i>	7	MG 1414 Sc.01-07	S. Cesarea (Italy)	Calabrian (Ragaini, 1994)
<i>Genocidaris maculata</i>	6	MG 1414 Sa.01-06	S. Andrea (Italy)	Calabrian (Ragaini, 1994)
<i>Genocidaris maculata</i>	1	MG 1414 Mo.01	Monopoli (Italy)	Calabrian (Pieri & Moretti, 1999)
<i>Genocidaris maculata</i>	2	MG 1414 Mz.01-02	Milazzo (Italy)	Late Pleistocene (Borghi <i>et al.</i> , 2014)

Species	N.	Catalogue n.	Locality	Age
<i>Genocidaris maculata</i>	1	MG 1579.E1	Capraia Is. (Italy)	Recent
<i>Genocidaris maculata</i>	2	MG 1579.E2, E3	Aci Castello (Italy)	Recent
<i>Genocidaris maculata</i>	1	MG 1579.H	Elba Is. (Italy)	Recent
<i>Genocidaris maculata</i> *	1	MG 1413 RM.01	Capraia Is. (Italy)	Recent
<i>Genocidaris maculata</i> *	1	MG 1413 RM.06	Pantelleria (Italy)	Recent
<i>Genocidaris maculata</i> *	1	MG 1413 RM.04	Otranto (Italy)	Recent

Genocidaris oyeni Osborn, Portell & Mooi, 2020

Upper Pliocene Intracoastal Formation (Florida, USA); the holotype (UF 202640) and 3 paratypes (UF 202635, 202638–39) were figured in Osborn *et al.* (2020; figs. 20–23).

As a whole, 793 fossils from 34 different localities (Fig. 1) and 8 recent specimens (Tab. 1) have been examined by the authors. They include topotypic specimens, as described above.

Most specimens are preserved as whole coronas. In a few specimens, the apical system is preserved, as are –rarely– spines and jaws.

Some of this material was initially attributed in the literature to the genus *Arbacina*. This was the case for specimens from Spain (Roman & Soudet, 1990; Néraudeau *et al.*, 2001; Bajo *et al.*, 2005, 2006, 2008; Bajo & Borghi, 2009), Italy (Checchia-Rispoli, 1907, 1916, 1923, 1938; Borghi *et al.*, 2006), Austria (Kroh & Harzhauser, 1999; Kroh, 2003, 2005), France (Lambert, 1910; Balland, 1948; Roman, 1989; Néraudeau *et al.*, 2003), Greece (Marcopoulou-Diacantoni, 1974) and Malta (Challis, 1980). The remainder of the available specimens was assigned to *Genocidaris* (Borghi, 1995; Kroh, 2003, 2005; Borghi *et al.*, 2006).

The specimens studied from the Miocene and Pliocene of Spain correspond to Bajo's collection and are housed at the Geological Museum of the University of Seville and the Museum of Alcalá de Guadaíra (Seville, Spain). Fossils from Italy, France, Greece (Milos Island), and Malta (Gozo Island) were examined at the Museo Geologico “Cortesi” of Castell'Arquato (Italy), Museo Civico of Salsomaggiore (Italy), Museo “Gemmellaro” of the Geology Institute, University of Palermo (Checchia-Rispoli's collection), Museo “Capellini”, University of Bologna (Manzoni's collection), Museo Palaeontologico, University of Rome, Museo Aquilegia, Masullas (Sardinia, Italy). Photographs of *Arbacina monilis* from the “faluns” de Lublé, near Savigné-sur-Lathan (Indre-et-Loire, France) were provided by the Muséum d'Angers (collection Izvarine). Illustration of specimens from Austria (Eggenburg Region and Vienna Basin) and from Greece (Rhodes Island) have been provided by A. Kroh (Natural History Museum of Vienna).

Scanning electron microscope photography (SEM) was carried out at the Natural History Museum of Vienna (Austria) and the University of Salamanca (Spain).

The systematic palaeontology follows Kroh and Smith (2010) and Kroh and Mooi (2022).

Abbreviations

Institutions. Ang/IZV, Muséum d'Angers, France (collection Izvarine); MB, Museo “Capellini”, Istituto di Geologia, University of Bologna, Italy; MCS, Museo Civico of Salsomaggiore, Italy; MG, Museo Geologico “Cortesi”, Castell'Arquato, Italy; MGP, Museo Geologico “Gemmellaro”, University of Palermo, Italy; MGUS, Geological Museum, University of Seville, Spain; MAG, Museum of Alcalá de Guadaíra, Seville, Spain; MNHN, Muséum National d'Histoire Naturelle of Paris; MP, Istituto di Scienze della Terra, University of Parma, Italy; MSNC, Museo Aquilegia, Masullas (Sardinia, Italy); MSR, Museo Paleontologico, University of Rome, Italy; NHMW, Natural History Museum Vienna, Austria; SAM, South Australian Museum, Adelaide (Australia); UF, Florida Museum of Natural History (U.S.A.).

Localities. Ag, Alcalá de Guadaíra (Seville, Spain); Al, Altavilla (Palermo, Italy); An, Anzio (Rome, Italy); Ba, Balerna (Almería, Spain); Ca, Carboneras (Almería, Spain); Ch, Chiclana (Cádiz, Spain); Cq, Campore (Parma, Italy); Cs, Castell'Arquato (Piacenza, Italy); Do, Doué (France); Eg, Eggenburg region (Austria); En, San Polo d'Enza (Reggio Emilia, Italy); Ep, Espera (Cádiz, Spain); Es, Estepona (Málaga, Spain); Fu, Funtanazza (Sardinia, Italy); Fv, Favignana Island (Trapani, Italy); Gu, Alcalá de Guadaíra (Seville, Spain); Gz, Gozo Island (Malta); Le, Lentini (Sicily, Italy); Lo, Lora del Rio (Seville, Spain); Ls, Lesperon (France), Oligocene; Lu, Lugagnano (Piacenza, Italy); Me, Punta Melisio (Lecce, Italy); Mi, Milos Island (Cyclades, Greece); Mz, Milazzo (Messina, Italy); Mo, Monopoli (Bari, Italy); Mu, Águilas (Murcia, Spain); No, Noyant La Plaine (France); Pa, Palermo (Sicily, Italy); Pr, Parlascio and Usigliano dei Lari (Pisa, Italy); Rc, Terreti and Croce Valanidi, near Reggio Calabria (Italy); Rh, Rhodes Island (Greece); RM, present Mediterranean Sea; Ro, Roteaglia (Reggio Emilia, Italy); Sa, Torre S. Andrea (Lecce, Italy); Sc, Santa Cesarea (Lecce, Italy); Sl, Saint Laurent de Lin (France); So, Sorbas (Almería, Spain); St, Stirone River near San Nicomede (Parma, Italy); Sv, Savigné sur Lathan (France); Vb, Vienna Basin (Austria).

Morphology. D, test diameter measured at the ambitus.

RESULTS

Morphological features

Previous work (Borghi *et al.*, 2006) comparing fossil *Genocidaris* and *Arbacina* from Italian Pliocene and Pleistocene sites and living specimens of *Genocidaris maculata* from the Mediterranean Sea, showed a close similarity in most of their morphological features: test shape, apical system, auricles, primary tubercles, pore arrangement and pattern of the original coloration (Fig. 2A–2H). In the following we present a detailed analysis of the morphological features traditionally utilised in the literature to separate these two genera.

Apical disc. In both the type species of the two studied genera, *Genocidaris maculata* (Fig. 3A) and *Arbacina monilis* (Fig. 3B), the apical disc is regularly dicyclic with widely exert, relatively large ocular plates and a comparatively small periproct. The genital plates bear a few tubercles and raise ornamentation in the form of low ridges. *A. catenata* (Fig. 3C) and *A. romana*

(Fig. 3F), also have apical discs almost identical to that of the type species of *Arbacina*. A single, large suranal plate, as observed in recent specimens of *G. maculata* and in exceptionally well-preserved fossil *G. maculata* from the Italian Pleistocene (Fig. 2G), is so far not documented for *Arbacina*. Based on the great similarity of the apical disc shape, the fact that the suranal plate is rapidly lost after death does not greatly undermine the supposition that some or all species of *Arbacina* had such a plate. Further evidence to support this idea is that isolated platelets highly similar to the suranal plate of *Genocidaris maculata* co-occur with coronal fragments, lantern elements and spines of *A. monilis* in sieved bulk samples from the Serravallian of Noyant la Plaine (France).

Ambulacra. The ambulacra are about 2/3 the width of the interambulacra at the ambitus. Each plate bears a primary tubercle positioned adorally to the plate centre and several smaller, subequal secondary tubercles. The ambulacral plates are composed of three elements, the lowest being the largest. In extant *Genocidaris*

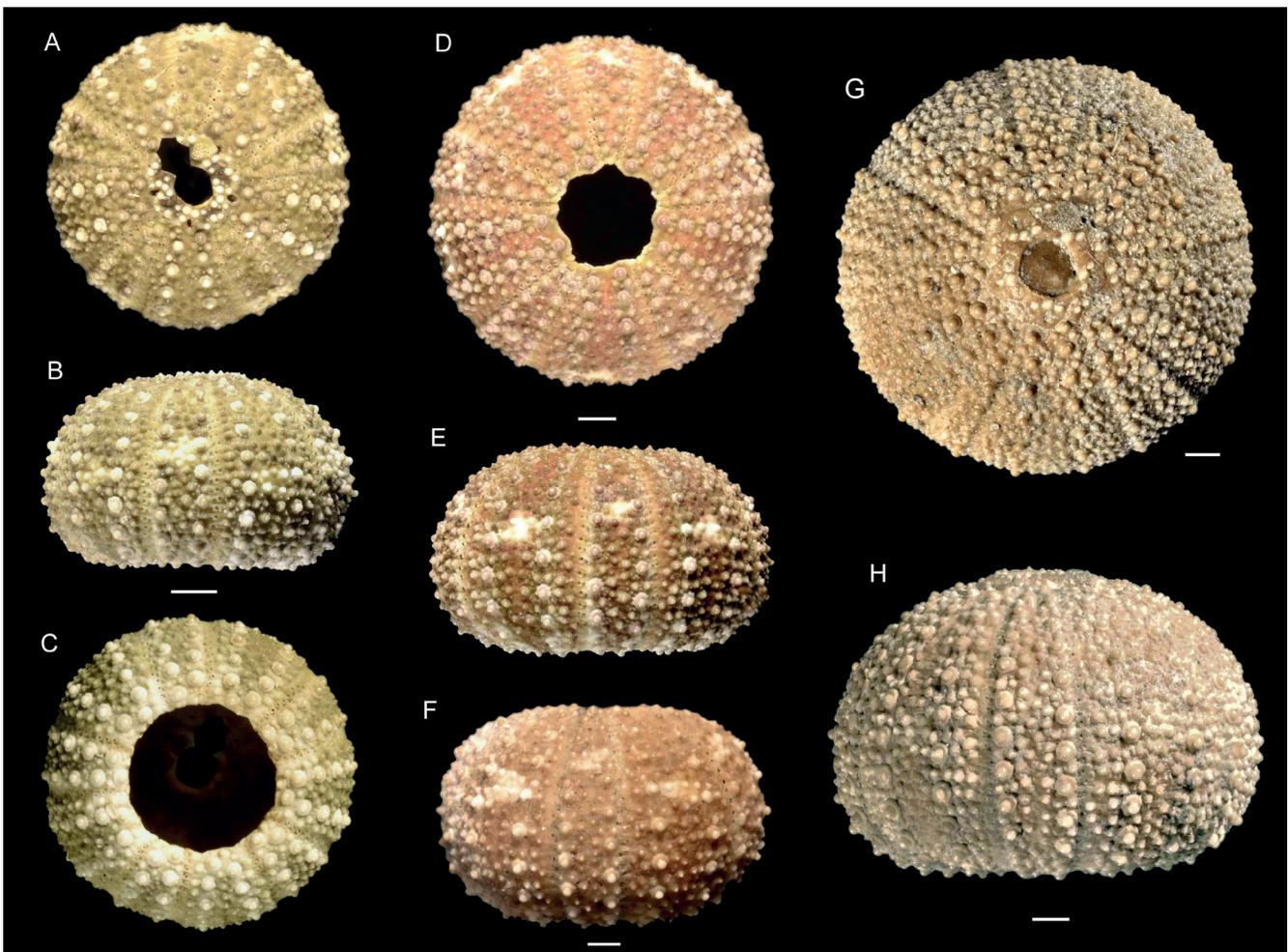


Figure 2. *Genocidaris maculata*. **A–C**, MG 1579.E1, D = 7 mm, Recent, Capraia Island (Italy), greenish colouration; **D–E**, MG 1579.E2, D = 9 mm, Recent, Aci Castello (Italy), brownish colouration; **F**, MG 1579.K, D = 8 mm, Calabrian of the Stirone River, near Parma (Italy), residual colour pattern; **G**, MG 1579.C, D = 11.5 mm, Calabrian of the Stirone River, aboral view of a whole specimen with the suranal plate; **H**, MG.1112.St.37, D = 12 mm, Calabrian, Stirone River, lateral view; scale bars = 1 mm.

maculata all three elements reach the perradial suture (Fig. 4A–4E). This feature has been observed also in the samples from the Pleistocene of Italy (Fig. 4C). In *Arbacina monilis* the lower and the upper elements extend to the perradius, whereas the middle element consists of a small occluded demiplate (Fig. 4B). In this case, the plate compounding corresponds to the echinid-style (Kroh & Smith, 2010, fig. 11M). This kind of plate compounding is present in all the examined Miocene samples in which this morphological detail was visible. Tendency in the lower element to enlarge perradially, thereby restricting the middle element, has been rarely observed also in Calabrian and recent specimens of *Genocidaris maculata* (arrow in Fig. 4A), albeit only in relatively large specimens ($D > 7$ mm). Each ambulacral plate bears a single primary tubercle, close to the poriferous zone, which is superimposed to the two lower elements and sometimes also to a part of the upper element.

Interambulacra. Each interambulacral plate bears a single, subcentral primary tubercle and multiple, smaller secondary tubercles. There is no significant difference in the number or structure of the interambulacral plates in *Genocidaris* and *Arbacina*.

Sunken ornament. The presence of sutural pits and depressions around the primary tubercles and along the horizontal sutures was one of the key characters mentioned by Mortensen (1943) to separate *Genocidaris* and *Arbacina*. However, true, sharply-edged sutural pits resulting in distinct reduction of plate thickness, such as those in *Ternopleurus toreumaticus* (see Kroh & Smith, 2010, fig. 7G), are absent in both genera. In the extant *G. maculata*, these sunken ornaments are hardly visible, due to the small size of most specimens (D rarely exceeding 7–8 mm; Mortensen, 1943) and to the crowded tuberculation and ornamentation. Fossil *Genocidaris* from the Pliocene and Pleistocene of Northern Italy, commonly reaching 12–15 mm (Borghi, 1995), do show these ornamentations: in most cases these “depressions” consist simply of small areas of the test surface free from tuberculation and raised epistromal ridges (“d” in Fig. 5A). These are here named “pseudo-depressions”. Sometimes there are also true small depressions (“p” in Fig. 5A). Contrary to true sutural pits, however, they are shallow in section view and do not result from a significant reduction in plate thickness. All these details are present also in a recent topo-typic specimen of *G. maculata* (Fig. 4F). This is also the case for the other species studied.

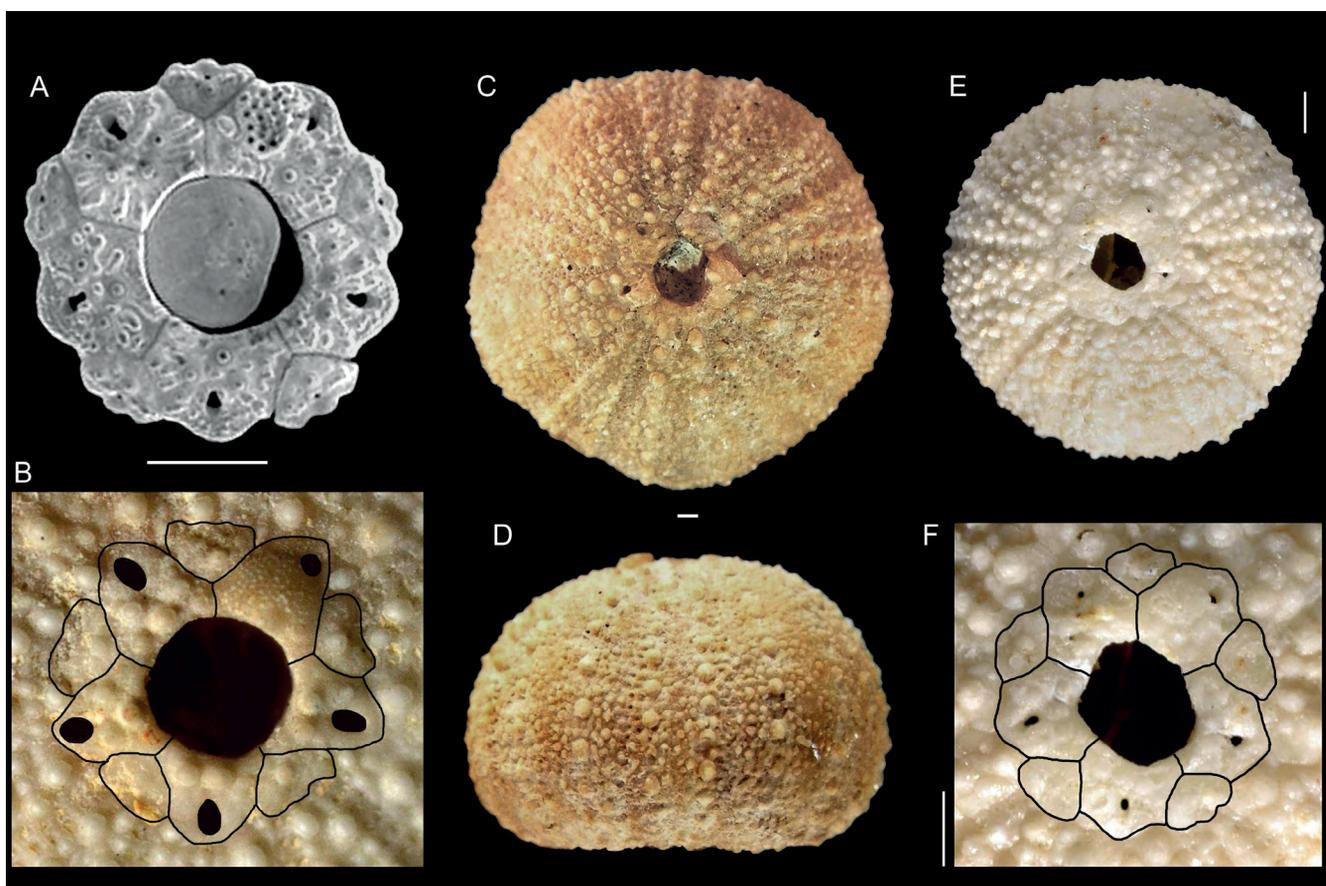


Figure 3. **A**, *Genocidaris maculata*, USNM E12092.1, Recent, Florida, apical disc (SEM photograph); **B**, *Genocidaris monilis*, Ang/IZV.07, Langhian of Savigné-sur-Lathan (France), scheme of the apical system; **C–D**, *Genocidaris catenata*, AG/Bajo. Ac.01, $D = 22$ mm, Messinian of Alcalá de Guadaíra (Spain), aboral (**C**) and oral (**D**) views; **E–F**, *Genocidaris romana*, MG 1579.F, $D = 11$ mm, Calabrian of Terreti (southern Italy), aboral view (**E**) and scheme of the apical system (**F**); scale bars = 1 mm.

In larger specimens (TD > 10 mm) of *A. monilis* (Fig. 5C, 5F), *A. catenata* from the Rhône Basin (Philippe, 1998) and *A. romana* from Sicily (Italy; Fig. 5D) similar, small pseudo-depressions and shallow depressions do occur, mainly along the horizontal sutures and around the primary tubercles.

Raised ornament. Contrary to sunken ornament, which is sparse, raised ornament in the form of epistromal ridges is present to a varying degree in all species of *Genocidaris* and *Arbacina* studied. The basic pattern consists of two to three prominent, subparallel ridges vertically linking the primary tubercles in each interambulacral column; they are commonly named “catenae” in the literature. Although considered characteristic of *Arbacina* (Fig. 5D) these ridges are found in *G. maculata* as well (Tab. 2; Fig. 5B, 5E). *A. monilis* likewise has weakly developed catenae (Fig. 5C, 5F).

Additionally, low ridges connecting the secondary tubercles to the base of the sub-central primary tubercle occur, thereby forming a “radiating pattern” (*sensu* Kroh, 2005). Expression of this ornament seems to depend largely on the density of the secondary tuberculation. In specimens with dense secondary tuberculation made of numerous subequal tubercles this pattern is less evident than in forms in which secondary tuberculation is sparser, such as in specimens of *A. romana* (Fig. 5D) and *A. monilis* (Fig. 5C; Tab. 2). This feature is quite

variable, however, often showing large variation even within single populations.

Indentation. Another feature used for the distinction between *Arbacina* and *Genocidaris* is the presence of “pits” indenting the base of the primary tubercles. Supposedly these indentations are present in *Genocidaris* (Fig. 4E, 4F) but absent in *Arbacina* (Mortensen, 1943). The occurrence of this feature is herein investigated for a sample of 232 specimens of *G. maculata* from the Pleistocene of Emilia (Tab. 2). The results are compared with data taken from 116 specimens of *A. romana* from the Pleistocene of Sicily. Significant differences are observed. In roughly 95% of the analysed *Genocidaris*, primary and marginal tubercles are more (Fig. 5E) or less indented (Fig. 5B). When present, the smooth surface is commonly limited to a portion of the base. In contrast, only two specimens of *A. romana* (out of 84 examined) show clear indentation in some of the tubercles. In *A. monilis* (Tab. 2; Fig. 5C, 5F) indentation is frequent (44% of the specimens studied), as well as in samples attributed to *A. catenata* from the Rhône Basin (France; Philippe, 1998).

Tubercles. The tubercles of both *Arbacina* and *Genocidaris* are imperforate throughout (Figs. 4F, 5A–5D). Contrary to the statement of Mortensen (1943), crenulations can be frequently observed in fossil

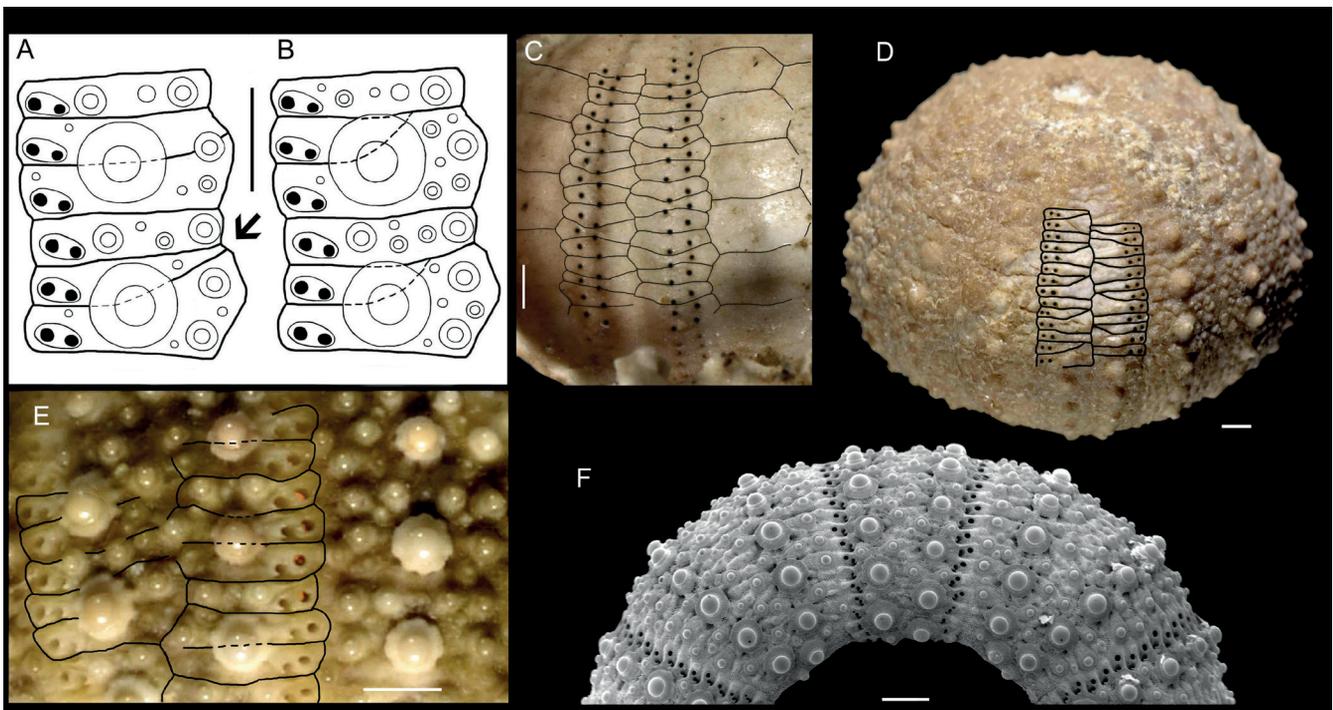


Figure 4. A–E, Scheme of the ambulacral plates compounding. **A**, *Genocidaris maculata*, MG 1579.E3, D = 7 mm, Recent, Aci Castello (Italy); the arrow marks restriction in the lower element; **B**, *Arbacina monilis*, MG 1415 Do.07, D = 15 mm, Miocene, Doué (France); **C**, *Genocidaris maculata*, MG 1579.A, Calabrian of Castell’Arquato (Italy), seen from the interior; **D**, *Echinopsis elegans*, MG 1579.B, D = 11 mm, Eocene of Blaye (France); **E**, *Genocidaris maculata*, MG 1579.E1, D = 7 mm, Recent, Capraia Island (Italy). **F**, *Genocidaris maculata*, Recent, off Florida Keys (USNM E12092), D = 7 mm, oral view; scale bars = 0.5 mm.

(Fig. 6B, 6C) and recent specimens of *Genocidaris maculata* (Fig. 4F). Well preserved specimens of *Arbacina monilis* from Douè and Noyant la Plaine (France) also show crenulation in the primary tubercles (Fig. 6D; Tab. 2), although this feature is easily obscured by abrasion and cement overgrowth. *A. catenata* and *A. romana* usually occur in coarse sands, an environment not favouring the preservation of this feature, and crenulation is apparent only in particularly well-preserved specimens. Fossil *G. maculata* occurring in fine, pelitic sands are largely unaffected by rim cement growth, facilitating the preservation of this feature.

Dorso-ventral stretching of the tubercles has been considered by [Fell and Pawson \(1966\)](#) as one of the characteristic features of the genus *Arbacina*. In the studied material, tubercles that are longer in the dorso-ventral axis than they are wide result from post-mortem growth of small calcite crystals, oriented preferentially in the dorso-ventral axis. The reason for this is the syntaxial nature of the overgrowing diagenetic cement and the genetically fixed orientation of the c-axes of the skeletal calcite, which is tangential to the plate surface

and aligned with the dorso-ventral axis of the corona in temnopleuroids ([Kroh, 2005, fig. 21](#); [Raup, 1962, 1966](#)).

Spines. Primary spines in *Genocidaris* are relatively short (about 1/3 of test diameter), taper slightly to a blunt point distally, longitudinally striated but without small thorns or spines so that the striations appear to be smooth (Fig. 6E–6G). However, minute ornament in form of nodules or thorns can be observed in SEM photography (Fig. 6F). In cross section, spines consist of few (6–7) radial wedges (*costae*) linked by stereom *trabeculae* enclosing a narrow central lumen.

Spine-bearing specimens of *Arbacina* were recovered from two Spanish localities (Estepona and Sorbas). Additionally, isolated spines co-occurring with *Arbacina monilis* at St. Laurent and Noyant La Plaine (France) were obtained from sieved bulk samples. These spines correspond to those in *Genocidaris*, being similarly short, longitudinally striated, and with a blunt point (Fig. 6E–6G). Their maximum length is 2.8 mm and they bear small nodules in the *costae*, similar to those present in fossil and recent spines of *Genocidaris*.

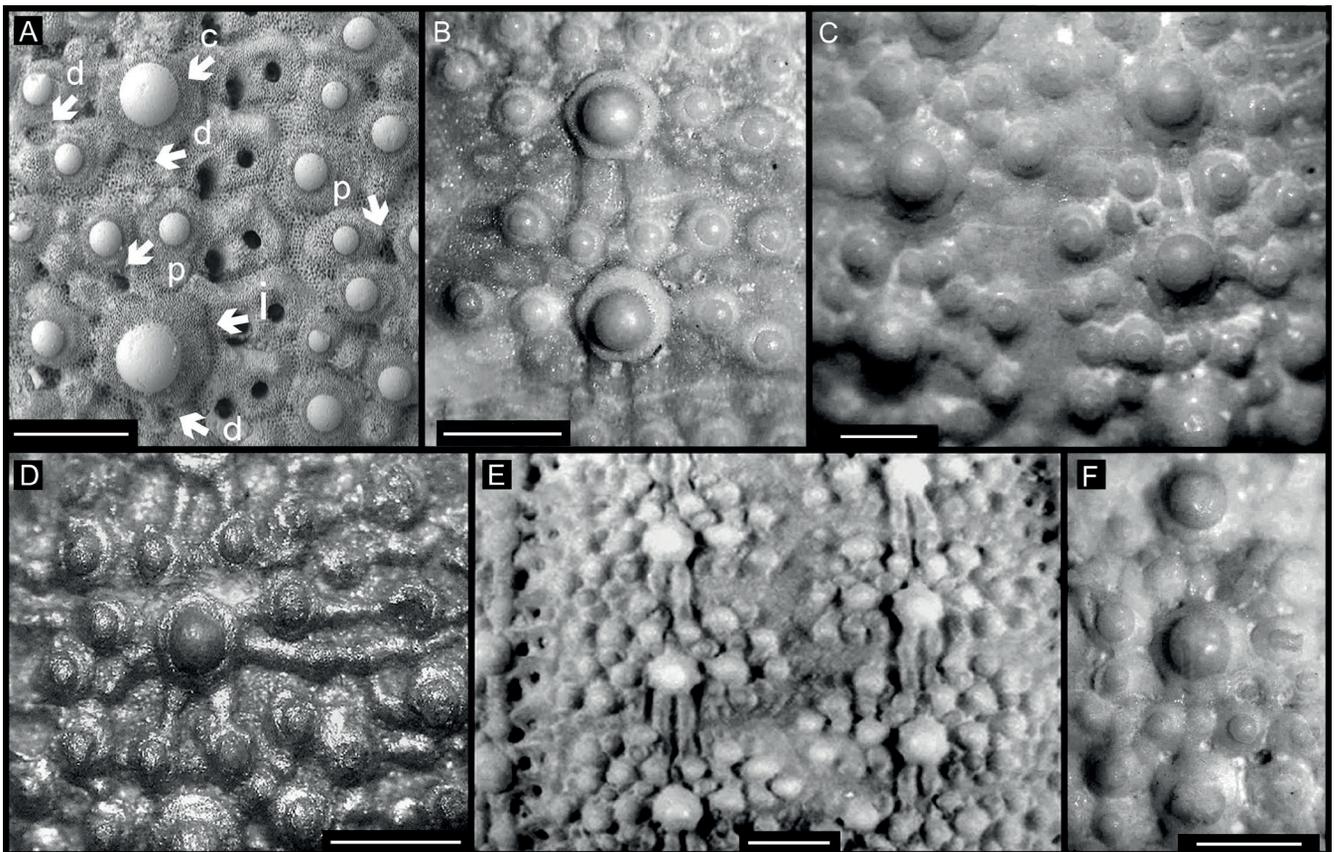


Figure 5. **A**, *Genocidaris maculata* (MG 1026.Cs.13), Calabrian of Castell'Arquato, (Italy), arrows indicate crenulations (**c**), indentation (**i**), pseudo-depressions (**d**) and shallow depressions (**p**); **B**, *Genocidaris maculata* (MG 1413.Cs.18), Calabrian of Castell'Arquato (Italy), tubercles with weak indentation and catenae; **C**, *Genocidaris monilis* (MG 1415.No.20), Serravalian of Noyant La Plaine (France), close up of indentations, small naked areas and pseudo-depressions; **D**, *Genocidaris romana* (MG 1411.Fv.04), Calabrian of Favignana Island (Sicily, Italy), radiating pattern; **E**, *Genocidaris maculata* (MG 1413.Gm.17), Calabrian of Castell'Arquato (Italy), well developed catenae and indentations; **F**, *Genocidaris monilis* (MG 1415.No.20), close up showing indentations and pseudo-depressions, Serravalian of Noyant La Plaine (France); scale bars = 0.5 mm.

Table 2. Frequency of different kinds of ornamentation in *Genocidaris romana*, Pleistocene of Sicily, *G. monilis*, Miocene of western France, and *G. maculata*, Pleistocene of Emilia (Italy). **N**, number of specimens in which these features were preserved.

Test ornamentation	<i>G. romana</i>		<i>G. monilis</i>		<i>G. maculata</i>	
	%	N	%	N	%	N
Indentation at the base of primary tubercles	2	84	44	41	100	211
Most primary tubercles lacking indentation	100	84	78	41	7	211
<i>Catena</i> e linking primary tubercles in longitudinal series	92	87	18	41	62	214
Pseudo-depressions along suture-lines	72	61	56	41	47	157
Pseudo-depressions around primary tubercles	38	58	63	41	100	178
Crenulation in the primary tubercles	5	20	21	19	27	120
Radiating pattern	4	99	10	41	67	210

Lantern. The lantern is known in recent and fossil specimens of *Genocidaris maculata* (Borghi, 1995); it is unknown in *Arbacina monilis*. Although isolated lantern elements commonly co-occur with *Arbacina* tests in the various source localities, they cannot be unambiguously assigned to *Arbacina*, due to the co-occurrence of other small echinaceans.

Girdle. The lantern support structures of *G. maculata* and *A. catenata*, as well as other species assigned to *Arbacina*, are very similar. They consist of arched, distally fused auricles without tags. No consistent differences in shape could be observed between the two putative groups.

Colouration. Well preserved colour patterns in fossil tests of *G. maculata* from the Pleistocene of Italy (Fig. 2F) and the Pliocene of Spain (e.g., MGUS/Bajo/Es. 01), as well as in *Arbacina romana* from the lower Pleistocene of Favignana Island (Borghi et al., 2006, pl. 4, fig. 4), correspond to colouration in extant *G. maculata* (Fig. 2A–2E).

Morphological variability. Considerable morphological variability has been observed in all the samples with respect to the following features:

- size of peristome, apical system and tubercles in proportion to the test diameter.
- test outline circular to subpentagonal (Fig. 3C), coronal profile low (Fig. 7E) to more or less elevated (Fig. 7C).
- number of plates in ambulacral and interambulacral columns.
- frequency of occurrence and degree of sunken and raised ornamentation on the test (Tab. 2).
- density and arrangement of the secondary tubercles: more or less crowded, randomly scattered on the plates or forming more or less regular vertical series, and/or circles around the primary tubercles.

The variations occur within samples attributed to the same species when from different localities, as well

as within samples from single localities. For example: 9% of the sample (44 specimens out of 386 examined by A. Turpin, personal communication, May 2009) of *A. monilis* from the Serravallian–Tortonian of Noyant (France) shows an unusually small peristome and tubercles (Fig. 7B). The presence of intermediate cases indicates that these differences represent only intraspecific variation.

A large variability was highlighted also by Vadet and Nicollaeu (2017), who carried on biometric analysis based on samples of *Arbacina monilis* from the type area and *Genocidaris maculata* from the Caribbean and the Mediterranean Sea. They analysed six morphological parameters: width of the poriferous zones, diameter of the scrobicules at the ambitus in the interambulacra, diameter of the primary ambulacral tubercles and number of plates in the ambulacral and interambulacral columns, they concluded that there were no significant biometric differences between the two genera.

DISCUSSION

Both *Genocidaris* and *Arbacina* differ from *Psammechinus* Agassiz in Agassiz & Desor, 1846 in having larger poriferous zones at the ambitus and triads of pore-pairs almost straight throughout. In *Psammechinus*, they are more arched; in most cases there are also fewer plates in the interambulacral columns in *Psammechinus* (Vadet & Nicolleau, 2017). These features may be useful to distinguish between young individuals of *Psammechinus* and similar-sized adult specimens of *Genocidaris* or *Arbacina*, which are otherwise almost indistinguishable.

Genocidaris and *Arbacina* share all the examined morphological details. In particular, the characters traditionally used to separate these two genera (e.g., Mortensen, 1943; Smith & Kroh, 2011), are present in all recent and fossil samples here examined, although with different frequency of occurrence and degree. Apparently, the sole difference seems to be in the ambulacral plate compounding: in recent and

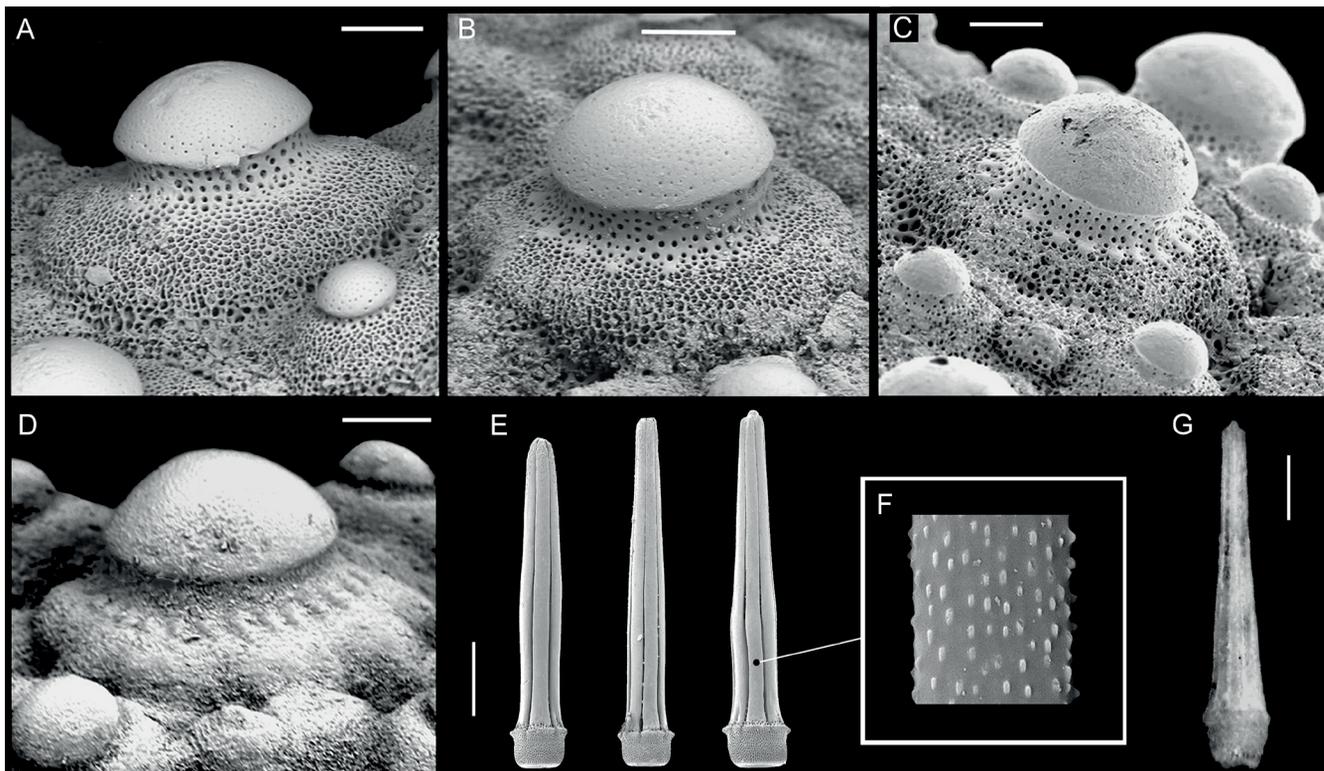


Figure 6. **A**, *Genocidaris maculata* (MG 1413.RM.01), Recent, Capraia Island (Italy), non-crenulate and non-indented primary tubercle; **B**, *Genocidaris maculata* (MG 1413.Cs.13), Calabrian of Castell'Arquato (Italy), weak crenulation; **C**, *Genocidaris maculata* (MG 1112.St.31), Calabrian of Stirone River (Italy), rather strong crenulation; **D**, *Genocidaris monilis* (MG 1415.No.20), Serravallian of Noyant (France), specimen with distinct crenulation; **E–F**, *Genocidaris maculata*, primary spines (MG 1579.G), Calabrian of Castell'Arquato (Italy), with detail of a costa; **G**, *Genocidaris monilis* (MG 1415.No.20s), Serravallian of Noyant La Plaine (France), primary spine; **A–F** are SEM photographs; scale bars = 0.2 mm.

Pleistocene *Genocidaris maculata* the middle element of mature plates always reaches the perradial suture, whereas in the studied Miocene fossils traditionally attributed to *Arbacina*, including *Arbacina monilis*, the middle element consists of a short demiplate not reaching the perradius. [Vadet and Nicollean \(2017\)](#) suggested that this difference could be due to the very small size of recent specimens of *Genocidaris*, rarely exceeding a diameter of 7–8 mm. However, we have observed this feature also in Calabrian specimens with D up to 15–17 mm. After [Kroh and Smith \(2010, p. 197\)](#), there can be in some species a marked change in development from juvenile to adult regarding this feature, with smaller plates initially occupying the full column width and becoming progressively occluded as growth proceeds. This was noticed in *Echinopsis* [Agassiz, 1840](#), another genus belonging to the Temnopleuridea [Kroh & Smith, 2010](#): in Figure 4D we report the illustration of a small (D = 11 mm) specimen of *Echinopsis elegans* [Agassiz & Desor, 1846](#) from the Eocene of Blaye (France), with a weathered portion showing a part of the middle elements extending towards the perradius. We did not observe similar cases in larger specimens (D up to 35 mm) of *Echinopsis* from the same locality, which have the typical echinid compounding scheme as reported

in [Kroh and Smith \(2010, fig. 11M\)](#). Also, the scheme reported in [Mortensen \(1943, fig. 36\)](#) indicates a middle element reaching the perradius.

Differences in the ambulacral plate compounding are commonly used in the systematics of Echinoids. In particular, the presence or absence of demiplates is of great significance in many schemes of higher taxonomy of regular and irregular echinoids. This is the case with the family Temnopleuridae, which is stated to have an echinid-style compounding ([Smith & Kroh, 2011](#)). In the case under study, we think that the tendency of the lower element to enlarge perradially and to occlude the intermediate demiplate may be sometimes delayed (as well as in *Echinopsis*), possibly due to environmental factors. Observations in other temnopleurids in a phylogenetic context would inform if the presence of the demiplate condition is plesiomorphic for the entire temnopleuroid clade.

The above reported observations indicate that *Arbacina* and *Genocidaris* are synonymous.

They were both established as new genera in 1869. *Genocidaris* [Agassiz, 1869](#) (p. 262–263) was published in October 1869. According to the ICZN (4th ed., Article 21.3.1) this corresponds to a publication date of 31.10.1869. *Arbacina* [Pomel, 1869](#) (p. 41) is more problematic since the publication date is not given in the

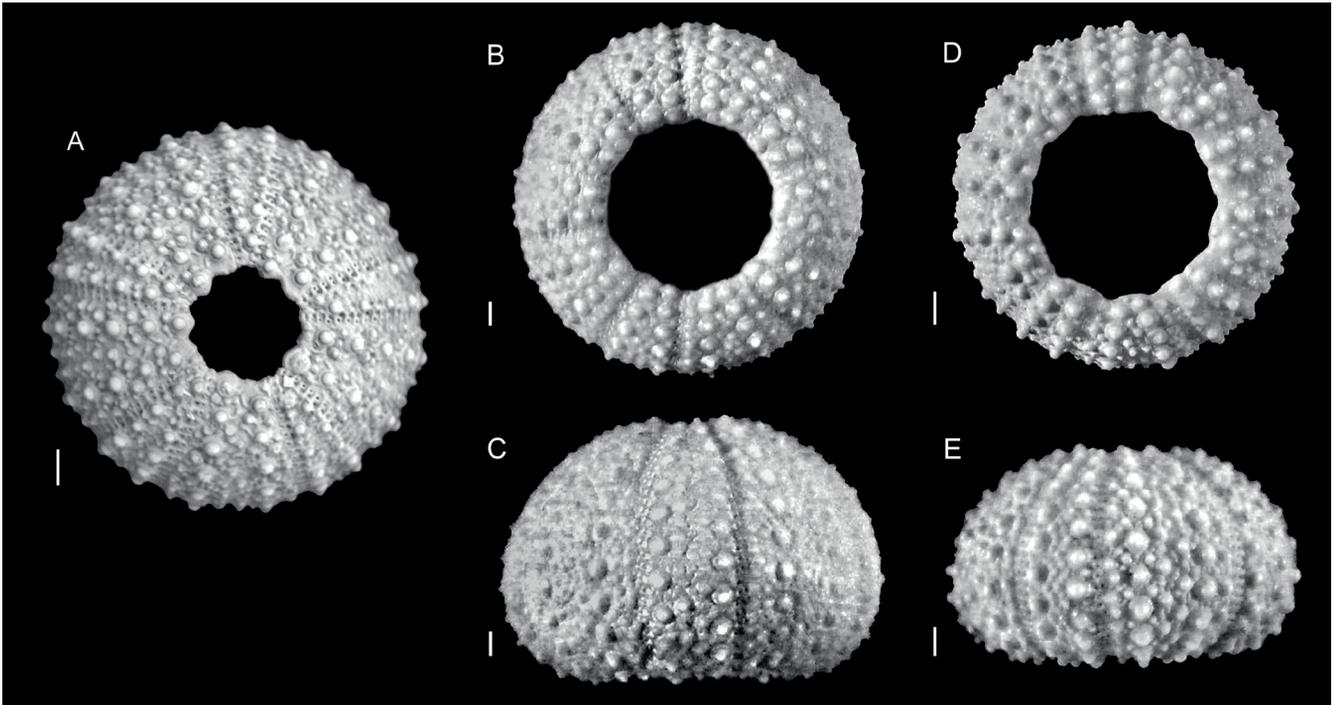


Figure 7. *Genocidaris monilis*. **A–E**, Serravallian, Noyant La Plaine (France); **A**, MG 1415.No.20, D = 11 mm, aboral view; **B–C**, MG 1415.No.06, D = 16 mm, specimen with rather small tubercles, small peristome and elevated profile; **D**, MG 1028.No.20, D = 11 mm, oral view, common size of the peristome; **E**, MG 1415.No.15, D = 11.6 mm, lateral view with typical rather depressed profile; scale bars = 1 mm.

work itself. According to Lambert in Bather (Zoological Record, Vol. 36, for 1899, Pt. XIV Echinodermata) it was published in 1869, without indication of a date on the frontispiece; according to the ICZN (4th ed., Articles 21.7 and 21.3.2) the publication date thus is taken to be 31.12.1869 (A. Kroh, personal communication, 2010). Consequently, *Arbacina* is here considered as a junior synonym of *Genocidaris*, as indicated in [Smith and Kroh \(2011\)](#) and [Kroh and Mooi \(2022\)](#).

Both these genera have traditionally been classified as temnopleuroid echinoids on account of their test sculpturing. Slightly sunken ornament has been recognised both in the fossil and the recent material studied. Because the sculptures are shallow and small, they are consistent with the distinctive characters of the Trigonocidaridae [Mortensen, 1903](#). This family is distinguished from the Temnopleuridae [Agassiz, 1872](#) by the lack of sharply defined sutural pits, the test being ornamented only by radial epistroma and indentations around the primary tubercles ([Smith & Kroh, 2011](#)). *Lamprechinus* [Doderlein, 1905](#) and *Trigonocidaris* [Agassiz, 1869](#), two other extant members of this family, differ from *Genocidaris* by the genital plates, which are smooth and bear only a single tubercle each. In contrast, in *Genocidaris* the genital plates bear several tubercles in adults, both in the recent and the fossil specimens examined in this study.

Accepted species

***Genocidaris maculata* (Fig. 2A–2H).** It is easily distinguished from the other cogenics by the strong development of indentations, pseudo-depressions around the base of the tubercles and radiating pattern (Tab. 2). In particular, indentations are present in all the examined specimens, both fossil and recent ones. Mature ambulacral plates are commonly made by three elements reaching the perradial suture, whereas in all the other species, apart from *G. romana*, the median element (seldom the upper one as well) is represented by a demiplate. Modest differences were noticed between the Pliocene–Pleistocene specimens and the current Mediterranean ones ([Borghi, 1995](#)): the presence of naked areas and crenulations are more frequent in the fossil sample than in the current population. These traits can partially be explained by the larger mean test size in the fossil sample.

***Genocidaris monilis* (Fig. 7A–7E).** This species is also placed in *Genocidaris* due to the frequent indentation around the base of the tubercles and the occurrence, although not frequent, of radiating ridges. *G. monilis* may be distinguished from *G. romana* by the less strong development of *catenae*, the more frequent occurrence of indentations and pseudo-depressions at the base of the primary tubercles (Tab. 2) and the

larger maximum test size: specimens from San Juvat (Bretagne, Western France) reach a diameter up to 25 mm (Bazin, 1884). The original diagnosis of *G. romana* (Merian in Desor, 1858) reported: “species close to *P. monilis*, but more tuberculate”. However, in the examined samples the secondary tubercles are, on the average, more numerous in *G. monilis* than in similar-sized specimens attributed to *G. romana* and *G. maculata*. Differences in the tubercular arrangement were reported in the literature to separate *G. monilis* from the closely related species. Nevertheless, *G. monilis* shows dense secondary tuberculation whose arrangement is generally consistent with that in *G. romana*. Particular features, such as the “scarcity of the secondary tubercles” (Lambert, 1910) and “grains forming a circular corona around the primary tubercles” (Balland, 1948), are likely local variations shown only by part of the population and do not represent reliable distinctive characters. Balland (1948) underlined the close similarity between *Arbacina monilis* and *A. blancheti* (Lambert in Castex, 1930) from the Oligocene of Lesperon (western France) and proposed synonymy of the two species. The illustration of a syntype of *A. blancheti* (MNHN.F.J01239) corroborates this opinion. The fossil material studied by Lambert probably came from the Quarry of Lesperon from limestones belonging to the Formation de Gaas, dated to the Rupelian (Sztrákos & Steurbaut, 2017), thus representing the oldest record for *Genocidaris*.

***Genocidaris catenata* (Fig. 3C–3D).** This species is characterized by remarkable variability. Differences are recognisable even when comparing the neotype of *G. catenata* designated by Lambert (1910) with the other specimens from the Rhône Basin described by Philippe (1998): the neotype shows denser granulation, fewer secondary tubercles and lacks indentation, which are visible in some tests from the Rhône Basin (Philippe, 1998, pl. 8, figs. 1c, 2c). Since differentiation between *G. catenata* and *G. romana* was difficult, the Miocene samples have been traditionally assigned to *G. catenata*, the Pliocene and Pleistocene ones to *G. romana*. However, *G. romana* from the type area is distinctly separated by indentation in the primary tubercles, which is almost absent, and the ambulacral plate compounding, which is of the echinid style in *A. catenata*, whereas in *A. romana* the middle elements reach the perradius.

***Genocidaris romana* (Fig. 3E–3F).** Based on the topo-typic specimens from Sicily also this species is assigned to *Genocidaris*. It is distinguished from *G. monilis* and *G. maculata* by much lower frequency of indentation and pseudo-depressions around the base of the primary tubercles, whereas *catenae* are more frequent (Tab. 2). Additionally, *G. romana* differs from all the Miocene species attributed to *Arbacina* here examined by its ambulacral plate compounding, with all three elements reaching the perradius.

***Genocidaris piaë*.** Based on the original diagnosis and the specimens from Funtanazza available to study, this species has frequent indentations and pseudo-depressions. It is distinguished by its dense secondary tuberculation made of small granules, whereas secondary tubercles are almost absent.

Brooding species. *A. pareyni*, *A. emmae* and *A. hugueti* show highly modified apical discs, including internal structures in some species (e.g., in *A. hugueti*, Dudicourt *et al.*, 2005, pl. 4, fig. 6), and an absence of a radiating sculpture (epistromal ridges). Nevertheless, they are close to the *Genocidaris* species discussed above. Because a genus can be represented by marsupiate species in one region and non-marsupiate species in others (Dudicourt *et al.*, 2005; Hambrey *et al.*, 2013), also these species could belong to *Genocidaris*. However, since they have been based on a few and poorly preserved specimens (mainly the highly modified female phenotypes), it is desirable to verify their generic attribution on the basis of additional topotypic material.

***Genocidaris incerta*.** The Australian extant species differs from *G. maculata* by larger primary tubercles, sculpturing almost wanting and the border of the poriferous areas not sharply cut (Clark, 1928, fig. 137). As highlighted by Clark (p. 457), the poor condition of the original material was the cause for the uncertainty as for the status of that new taxon and the reason for the attribution to the genus *Genocidaris* was only the apparent close resemblance to *G. maculata*. The very much larger tubercles and the test sculpturing reduced to a minimum raise doubt about the generic attribution of this taxon. This species is currently assigned to the genus *Genocidaris* by Kroh and Mooi (2022).

***Genocidaris oyeri*.** The species from the upper Pliocene Intracoastal Formation is distinguished from *G. maculata* by proportionally smaller apical system and smaller peristome. After Osborne *et al.* (2020), another difference consists of three sharply defined vertical depressions below the primary tubercles in the interambulacral areas.

SYSTEMATIC PALAEONTOLOGY

Class Echinoidea Leske, 1778

Subclass Euechinoidea Bronn, 1860

Infraclass Carinacea Kroh & Smith, 2010

Superorder Echinacea Claus, 1876

Order Camarodonta Jackson, 1912

Infraorder Temnopleuroidea Kroh & Smith, 2010

Family Trigonocidaridae Mortensen, 1903

Genus *Genocidaris* Agassiz, 1869

Type-species. *Genocidaris maculata* Agassiz, 1869, p. 262; by original designation.

[= *Arbacina* Pomel, 1869; p. 41; type species *Echinus monilis* Desmarest, in DeFrance, 1825, p. 100; by original designation].

Distribution and temporal range of the type species. Originally described upon recent specimens from between the Florida Keys and Cuba.

Description (modified from Smith & Kroh, 2011). Test small, low domed, with ambitus slightly below mid-height. Apical disc small, firmly bound to corona, dicyclic with oculars well separated from periproct. Genital plates with only a few tubercles, not forming a perianal ring. Periproct small, subcircular covered, with a large glassy suranal plate in the type species. Periproct strongly offset. Ambulacra straight, pore-pairs uniserial throughout, no phyllodes. Small primary tubercle to each compound plate. A few much smaller secondary tubercles between primaries and perradially. Plating trigeminate with echinid-style compounding; however, in some species also the middle element reaches the perradius. Interambulacral plates a little wider than tall. Small sub-central primary tubercle, clearly distinct from secondary tubercles (except for the most adoral plates). Secondary tuberculation well developed, but of varying density in the various species. Primary tubercles imperforate and non-crenulate to weakly crenulate. Base of primary tubercles commonly indented. Test ornament in form of small, weakly sunken pits and low epistromal ridges connecting the tubercles. Often a weak radiating pattern around the primary tubercles may be present. Peristome almost half test diameter; buccal notches extremely feeble. Membrane almost naked except for buccal pores. Perignathic girdle with auricles joined perradially. Lantern camarodont.

Species included. *Genocidaris monilis* (Desmarest in DeFrance, 1816), Oligocene to Pliocene of western France (Lambert, 1910; Lambert in Castex, 1930; Balland, 1948; Roman, 1989; Néraudeau *et al.*, 2003). *Genocidaris catenata* (Desor in Agassiz & Desor, 1846), Miocene (Burdigalian, Langhian, Messinian) of France (Lambert, 1910; Philippe, 1998), Spain (Roman & Soudet, 1990; Néraudeau *et al.*, 2001; Bajo *et al.*, 2008), Italy (Ragaini, 1994). *Genocidaris romana* (Merian in Desor, 1858), Pliocene and Pleistocene of Spain (Roman & Soudet, 1990; Bajo *et al.*, 2005) and Italy (Checchia-Rispoli, 1907, 1916, 1923; Borghi *et al.*, 2006). *Genocidaris maculata* Agassiz, 1869, Pliocene and Pleistocene of the Mediterranean, Recent, Atlantic and Mediterranean (Agassiz, 1869; Mortensen, 1943). *Genocidaris piae* (Lovisato in Cotteau, 1895). Lower Miocene (Aquitanian-Burdigalian) of Sardinia (Lovisato in Cotteau, 1895; Lambert, 1907; Comaschi-Caria, 1963). *Genocidaris incerta* Clark, 1928, Recent, southern Australia. *Genocidaris oyeri* Osborn, Portell & Mooi, 2020, Upper Pliocene of Florida (USA).

Distribution. Oligocene to Recent; Mediterranean, tropical Atlantic, Australia.

PALAEOECOLOGY

Arbacina romana from the Pleistocene of Sicily inhabited shallow water bottoms with bryozoans thickets and algal patches (Borghi *et al.*, 2006). This hypothesis is consistent with the results of recent palaeoecological studies dealing with other *Arbacina*-bearing sites. Néraudeau *et al.* (2001) affirmed that *A. catenata* from the Messinian of Sorbas Basin (Spain) lived on alga-rich bottoms, between 20–40 m water depth. Similarly, the specimens of *Arbacina* from the Tortonian of Espera (Spain) were associated with *Tripneustes*, *Schizaster* and *Clypeaster* on muddy seafloors in the lower infralittoral (Bajo & Borghi, 2009). Those from the Miocene and the Pliocene of south-western Spain were commonly associated to shallow water echinoids: *Schizechinus*, *Plagiobrissus* and *Echinolampas* (Bajo *et al.*, 2005, 2006, 2008). In the Greensand Formation of Gozo Island (Malta; Messinian, upper Miocene) *Arbacina* was interpreted to live in shallow water soft bottoms, with active currents (Pedley *et al.*, 2002). *Arbacina* from the lower Miocene of Gebel Gharra (Egypt) lived in high wave energy environments on shallow water, coarse sandy bottoms with sea grass and macroalgal patches (Kroh & Nebelsick, 2003). According to Nicolleau and Dudicourt (2006) the “Savignèen” facies (Langhian) of the French “faluns” is very rich in bryozoans and was deposited in the infralittoral. There, shallow water echinoids are commonly associated with *A. monilis*.

Genocidaris maculata is widespread in the present Mediterranean and Atlantic, inhabiting sandy bottoms rich in bioclastic detritus and muddy sands with *Peyssonnelia* (Riedl, 1991). Populations are also frequently encountered in seagrass meadows and *Posidonia* fields. *G. maculata* is common at 50 m off Naples (Koehler, 1927), but is usually found in shallower waters elsewhere. The studied Pleistocene specimens from Punta Ristola and Punta Melisio (Italy) are usually associated with an infralittoral fauna, which is typical of a coarse biotrititic substratum (Taddei-Ruggiero, 1994). Kroh (2003) interpreted the palaeoenvironment of *Genocidaris* sp. from the Langhian of Niederleis (Paratethys, Austria) as a “shallow sublittoral seafloor, characterised by sand flats with bryozoan’s thickets and algal patches”.

Based on these observations, the species originally attributed to *Arbacina* share similar ecological preferences with extant and fossil *Genocidaris*.

BIOGEOGRAPHY AND STRATIGRAPHY

Genocidaris is known from the Oligocene (Lambert in Castex, 1930) to Recent. It firstly appeared in the Atlantic, finding most favourable environmental conditions in western France. In the lower Miocene, *Genocidaris* could be found in the Mediterranean and then the Paratethys: *G. piae* was present in Sardinia during the Aquitanian–lower Burdigalian (Cotteau,

1895; Lambert, 1907), *G. catenata* was widespread in the Burdigalian of the Mediterranean (Philippe, 1998) and Central Paratethys (Kroh, 2005). The genus extended as far east as Poland during the Langhian (Kroh & Harzhauser, 1999). During the Pliocene and the Pleistocene *Genocidaris* has been frequently recorded in the Mediterranean: Italy, Spain, Greece and along the North African coasts. In particular, *G. maculata* became common during the Pleistocene (Gelasian-Calabrian) in the Adriatic Basin, *G. romana* in the Ionian and Tyrrhenian Seas. The first record in south-eastern United States is from the upper Pliocene (*G. oyeri*). Today, *G. maculata* lives in the Mediterranean Sea, along the European Atlantic coast and westward as far as the Azores Islands (Portugal) and the Caribbean. Another recent species, *G. incerta*, has been rarely recorded along the southern coasts of Australia.

CONCLUSIONS

The morphological characters traditionally used to separate the genus *Arbacina* Pomel, 1869 from *Genocidaris* Agassiz, 1869 are present, although with different frequency of occurrence, in all fossil and recent samples examined in this study. In addition, the species attributed to these two genera share similar ecological requirements. The sole morphological difference consists of the ambulacral plate compounding: all three elements reach the perradius in Pleistocene (Gelasian and Calabrian) and recent *Genocidaris maculata* Agassiz, 1869 and *G. romana* (Merian in Desor, 1858), whereas the Miocene species show the typical echinid style. This difference is here interpreted as a delayed development in the lower element, without systematic significance.

Based on these observations, *Arbacina* is considered as a junior synonym of *Genocidaris* following previous works.

The species *Arbacina monilis*, *A. catenata*, *A. romana* and *A. piae* are transferred to *Genocidaris*.

Distinction among species of *Genocidaris* is mainly based on the different frequency of occurrence of the test sculpture, made of raised epistromal ridges, indentations, crenulation and pseudo-depressions. *G. maculata* is distinguished from the other congeneric species by the strong development of indentations and pseudo-depressions. In *G. romana* indentation is almost absent and the test sculpturing, made of pseudo-depressions and radiating pattern, is less developed. *G. monilis*, *G. catenata* (Desor in Agassiz & Desor, 1846) and *G. piae* (Lovisato in Cotteau, 1895) are distinguished from *G. maculata* and *G. romana* by the echinid-style compounding of the ambulacral plates, with the lower element more enlarged perradially and occluding the middle platelet. Additionally, in *G. piae* secondary tubercles are almost missing, replaced by a dense and fine granulation.

Based on the recombination of four fossil species so far attributed to *Arbacina*, the genus *Genocidaris*

originated in the Oligocene of western France, then migrated eastwards during the lower Miocene, colonising the Mediterranean (Aquitanian of Sardinia) and the Paratethys (Langhian). In the upper Pliocene it became common in the Mediterranean and colonised the Caribbean Sea (south-eastern United States). Today, the type species, *G. maculata* Agassiz, 1869 is widespread in the Atlantic and in the Mediterranean, whereas *G. incerta* is rare in southern Australia.

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