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Original article

Balanomorphs from late Upper Pleistocene and Holocene caves in northern Spain, with a new genus and species, and their palaeoclimatological implications

Les balanomorphes des grottes du Pleistocène supérieur terminal et de l'Holocène du nord de l'Espagne, dont un genre et une espèce nouveaux, et leurs implications paléoclimatologiques

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ABSTRACT

Sampling in archaeological caves in northern Spain, within levels dated between ca. 23,000 and 3500 cal BP, revealed the presence of six species of sessile cirripedes. A new genus and a new species are described in the Lower Magdalenian (ca. 18,000 cal BP). *Titobustillobalanus tubutubulus* gen. nov., sp. nov. is characterised by parietes permeated by a single row of secondary small tubes between primary and secondary inner lamina and a sheath with tubes and cells. For each of the other five species, the current geographic distribution and ecologic data are given. A change of fauna is noticed from the Upper Magdalenian (ca. 14,500 cal BP) indicating global warming.

Mots clés :
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Taxonomie
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Nouvelle espèce
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Pleistocène supérieur
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Asturies et Pays basque)

RÉSUMÉ

Les collectes faites dans les grottes archéologiques du nord de l'Espagne, dans des niveaux datés entre ca. 23 000 et 3 500 cal BP, ont mis en évidence la présence de 6 espèces de cirripèdes sessiles. Un nouveau genre et une nouvelle espèce, du Magdalénien inférieur (ca. 18 000 cal BP), sont décrits. *Titobustillobalanus tubutubulus* gen. nov., nov. sp. est caractérisé, par des parois perforées par une rangée unique de petits tubes secondaires située entre les lames internes primaire et secondaire, et une gaine présentant des tubes et des cellules. Pour chacune des autres espèces, la répartion géographique et les données écologiques concernant leur représentants actuels sont précisées. Un changement de faune est constaté à partir du Magdalénien supérieur (ca. 14 500 cal BP) indiquant un réchauffement climatique.

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1. Introduction

Marine molluscs gathered by humans have been recorded at prehistoric sites in Cantabrian Spain from the Middle Pleistocene (late Mousterian). The evidence, from the Upper Pleistocene onwards (ca. 42,000 cal BP), clearly indicates that species were being gathered as food (above all limpets and periwinkles) (Álvarez-Fernández, 2011). The large volume of information available about the marine molluscs contrasts with the smaller number of studies that have been made about other sea animals, among them, crustaceans (e.g. Moreno, 1994; Gutiérrez, 2009; Álvarez-Fernández, 2010a, 2011, in press; Fano et al., 2013).

Crab remains (chelipeds and fragments of carapace) are documented from the Solutrean period (ca. 23,000 cal BC) onwards, but above all at sites dated in the Holocene. Several species have been classified, all of them present on the coast today. Their rare presence at sites in Cantabrian Spain seems to suggest their capture was opportunist, which is to say that they were caught while the human groups gathered molluscs in the intertidal zone (Álvarez-Fernández, 2011).

The goose barnacle *P. pollicipes* was also collected and consumed as food in this region. Its plates have been documented in sites dated from the Upper Holocene (from the Mesolithic) onwards (Álvarez-Fernández et al., 2013).

Sessile barnacles are cited in some Upper Pleistocene and Holocene archaeological sites (Aranzadi and Barandiarán, 1935; Gutiérrez, 2009; Álvarez-Fernández, 2011), but with few exceptions (determination of Y. Gruet in Álvarez-Fernández et al., 2013; Álvarez-Fernández et al., 2014), no classifications to specific level are established.

In this study, the balanomorphs from 15 archaeological sites located in Cantabrian Spain are analyzed (Figs. 1 and 2). They come from 21 archaeological levels dated from the late Pleistocene to the Holocene (from the Solutrean to the Bronze Age, ca. 23,000–3500 cal BP). Most of those extracted, using fine-mesh screens to sieve sediment, are found in association with shells (mainly limpet specimens). Plates of acorn barnacles are also found isolated in the sediment. Possibly they became detached from the external surface of the molluscs taken to the site as food.

2. Systematic palaeontology

Superorder THORACICA Darwin, 1854
Order SESSILIA Lamarck et al., 1818
Suborder BALANOMORPHA Pilsbry, 1916
Superfamily CHTHAMALOIDEA Darwin, 1854
Family CHTHAMALIDAE Darwin, 1854
Subfamily CHTHAMALINAE Darwin, 1854
Genus ***Chthamalus*** Ranzani, 1817

In the absence of opercular plates, "according to Southward (1976), *Chthamalus stellatus* (Poli, 1791) differs from *C. montagui* Southward, 1976 in having an oval, rather than a kite-shaped apertural opening, and is showing very deep, slit-like pits interiorly at the plate sutures, which are much more obvious than the corresponding ones in *C. montagui*" (in Jagt and Carriol, 2008).

Chthamalus montagui Southward, 1976

Occurrence and material: Bronze Age [Asturias: Arangas (level F), 1 specimen (shell without opercular plates)]. Mesolithic [Basque Country: Marizulo (level III), 6 specimens (shells and fragments of shells of which one with 1 scutum and 1 tergum); Jaizkibel 3 (level D), 75 specimens (shells and fragments of shells of which one with 1 scutum and 1 tergum) and Cantabria: La Cuesta de la Encina B (level A), 1 specimen (shell without opercular plates)].

Current geographic distribution: *C. montagui* occurs from the North of Scotland to Senegal and also in the Mediterranean Sea (Southward, 2008).

Ecology: *C. montagui* is present in the intertidal zone where it dominates in the upper half. Representatives of the species are attached to *Patella vulgata* in Marizulo, to *P. intermedia* in Jaizkibel 3, and to *Mytilus galloprovincialis* in La Cuesta de la Encina B.

Chthamalus stellatus (Poli, 1791)

Occurrence and material: Chalcolithic/Bronze age [Basque Country: Goikolau (level III + IV), 27 specimens (shells and fragments of shells of which one with one scutum and another with one tergum); Urtiaga (level B), 6 specimens (shells and fragments of shells of which one with opercular plates)]. Neolithic/Chalcolithic? [Basque Country: Jaizkibel 3 (level C), 48 specimens (isolated plates)]. Mesolithic/Neolithic? [Basque Country: Jaizkibel 3 (level C/D), 277 specimens (shells and fragments of shells without opercular plates)]. Neolithic [Cantabria: Los Gitanos (level A3), 10 specimens (shells of which one with opercular plates)]. Mesolithic [Basque Country: Marizulo (level III), 1 specimen (shell without opercular plates); Jaizkibel 3 (level F and D), 5 specimens (shells and fragments of shells without opercular plates)].

Current geographic distribution: *C. stellatus* is present from the Shetland Islands, in the north of Scotland, to the northwest coast of Africa and Canary Islands, and in the Mediterranean and Black Seas (Southward, 2008).

Ecology: *C. stellatus* inhabits in the mid and low intertidal zone. Representatives of the species are attached to *P. ulyssiponensis* in Goikolau, in Marizulo and in Los Gitanos, and to *P. intermedia* in Goikolau and in Urtiaga.

***Chthamalus* sp.** (Fig. 3: 7-8)

Remark: *Chthamalus* sp. denotes specimens of which it was not possible to determine whether they belong to *C. montagui* or to *C. stellatus*.

Occurrence and material: Neolithic/Chalcolithic? [Basque Country: Jaizkibel 3 (level B), 28 specimens (isolated wall plates). Mesolithic [Basque Country: Marizulo (level II), 3 specimens (fragments of shells); Jaizkibel 3 (level D), 52 specimens (shells and fragments of shells without opercular plates). Cantabria: La Garma B (level A), 4 specimens (shells without opercular plates); La Cueva del Mar (shell midden), 4 specimens (shells and fragments of shells without opercular plates). Asturias: La Poza l'Egua (shell midden), 1 specimen (shell); El Pindal (level 2), 8 specimens (shells and fragments of shells without opercular plates)]. Upper Magdalenian [Cantabria: La Garma A (level N), 1 specimen (shell without opercular plates)].

Ecology: Some *Chthamalus* sp. are fixed to *Patella* sp. in La Garma B, to *P. intermedia* in El Pindal and to *P. ulyssiponensis* in Marizulo.

Superfamily BALANOIDEA Leach, 1817
Family ARCHAEOBALANIDAE Newman and Ross, 1976
Subfamily SEMIBALANINAE Newman and Ross, 1976
Genus ***Semibalanus*** Pilsbry, 1916

Semibalanus balanoides balanoides (Linnaeus, 1767) (Fig. 3: 1-3, 6)

Occurrence and material: Azilian? [Asturias: El Cierro (level C), 6 specimens (5 wall plates and 1 scutum)]. Middle Magdalenian [Cantabria: La Garma A (level L), 2 specimens (2 wall plates)]. Lower Magdalenian [Cantabria: Altamira (level 2), numerous specimens (shells and fragments of shells of which several with opercular plates). Asturias: El Cierro (level F), 1 specimen (one broken wall plate)].

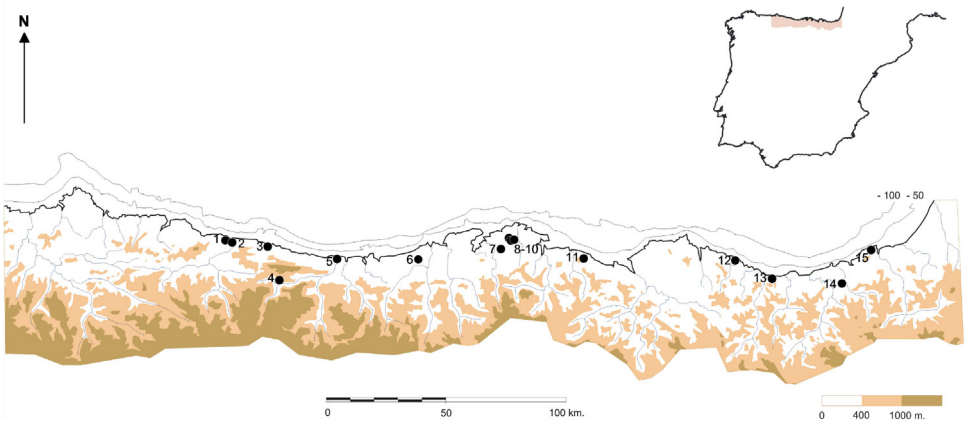

Fig. 1. Prehistoric sites in Cantabrian Spain with remains of Balanomorphs. Asturias: 1, El Cierro; 2, Tito Bustillo; 3, La Poza L'Egua; 4, Arangas; 5. El Pindal. Cantabria: 6, Altamira; 7, La Cuesta de la Encina B; 8, La Cueva del Mar; 9, La Garma A; 10, La Garma B; 11, Los Gitanos. Basque Country: 12, Goikolau; 13, Urtiaga; 14, Marizulo; 15, Jaizkibel 3.

Sites préhistoriques de l'Espagne cantabrique d'où proviennent les Balanomorphes étudiés. Asturies: 1, El Cierro; 2, Tito Bustillo; 3, La Poza L'Egua; 4, Arangas; 5. El Pindal. Cantabrie: 6, Altamira; 7, La Cuesta de la Encina B; 8, La Cueva del Mar; 9, La Garma A; 10, La Garma B; 11, Los Gitanos. Pays basque: 12, Goikolau; 13, Urtiaga; 14, Marizulo; 15, Jaizkibel 3.

Current geographic distribution: *S. balanoides* lives in the boreo-arctic regions of the Atlantic and Pacific Oceans (Kerckhof, 2002). In Europe the species occurs from Svalbard to Gironde (France) but also in the relatively cold rias of the North of Spain (Galicia) (Southward, 2008).

Ecology: The species is mostly found in the intertidal zone with a maximum of abundance at the mid tide level. Representatives of the species are attached to *P. vulgata* in Altamira.

Family BALANIDAE Leach, 1817
Subfamily BALANINAE Leach, 1817
Genus ***Balanus*** Mendes da Costa, 1778
Balanus crenatus crenatus Bruguière, 1789 (Fig. 3: 4-5)

Occurrence and material: Azilian? [Asturias: El Cierro (level C), 4 specimens (4 wall plates)]. Middle Magdalenian [Cantabria: La Garma A (level L), 3 specimens (3 wall plates)].

Current geographic distribution: *B. crenatus crenatus* is an arctic-boreal-temperate species (Southward, 2008) of the North Pacific and the North Atlantic. In Europe the species occurs from the Arctic to the west coast of France as far south as Bordeaux. Currently, the presence of *B. crenatus crenatus* in the Mediterranean Sea is not proved true. It is indicated by Kolosvary (1951) who quotes Darwin (1854), Drensky (1951), Demir (1952-1954), Geldiay and Kocatas (1972) and Granier (1973), but nevertheless Newman and Ross (1976) do not include the Mediterranean Sea in the distribution of *B. crenatus crenatus*. They are followed by Koukouras and Matsa (1998) in their check list of the Mediterranean species.

	Sites	Levels	Archeological Periods	Chronology (ca.)	NR Balanomorphs								NR Molluscs	Marine Fauna Bibliography
					TT	BC	SB	PP	CM	CS	C	Ind.		
HOLOCENE	Arangas	F	Bronze Age	3500 cal BP					1				Indet.	Arias et al. (2013); Álvarez-Fernández (in prep.)
	Urtiaga	B	Chacolithic/Bronze Age	4500-3500 cal BP				1		6			779	Álvarez-Fernández (in press)
	Goikolau	III+IV								27			363	Ontañón (2003); Álvarez-Fernández (in prep.)
	Los Gitanos	A3	Neolithic	6000 cal BP						10			4664	Álvarez-Fernández et al. (2014)
	Jaizkibel 3	C+B	Neolithic/Chalcolithic?	>6000 cal BP				2		48	28		12355	Álvarez-Fernández et al. (in press b)
	Jaizkibel 3	D/C	Mesolithic/Neolithic?	>9500 cal BP				3		277			9013	
	Jaizkibel 3	F+D	Mesolithic	9500-7500 cal BP					75	5	52		21701	
	Marizulo	II+III							6	1	3		704	Álvarez-Fernández & Altuna (2013)
	La Cuesta de la Encina B	A							1				430	Álvarez-Fernández (in press)
	La Garma B	A						1			4		10133	
	La Poza l´Egua	SM									1		3515	
	La Cueva del Mar	SM									4		499	
	El Pindal	2									8		468	Álvarez-Fernández et al. (in press a)
PLEISTOCENE	El Cierro	C	Azilian?	13.000 cal BP		4	6						201	Álvarez-Fernández et al. (in prep.)
	La Garma A	N	Upper Magdalenian	14.500 cal BP							1		4132	Álvarez-Fernández (2012)
	La Garma A	L	Middle Magdalenian	16.500 cal BP		3	2						116	Arias et al. (2005)
	El Cierro	F	Lower Magdalenian	18.000-19.000 cal BP			1						721	Álvarez-Fernández et al. (in prep.)
	Tito Bustillo	1			1							3	40125	Álvarez-Fernández (2013)
	Altamira	2					numerous						5368	Álvarez-Fernández (2009)
	Altamira	III	Solutrean	23.000 cal BP								a few	518	Álvarez-Fernández (2010b)

Fig. 2. Prehistoric sites in Cantabrian Spain with number (NR) of Balanomorph remains, indicating the levels, the archaeological periods and the chronology of the different levels where they have been found. SM: Shell midden. The information about the marine molluscs (determination by E. A.-F.) in the different levels with which the Balanomorpha (determination by R.-P. C.) are associated, and their bibliographical references, are also indicated. BC = *Balanus crenatus crenatus*; C = *Chthamalus* sp.; CM = *Chthamalus montagui*; CS = *Chthamalus stellatus*; Ind = indeterminable; PP = *Perforatus perforatus perforatus*; SB = *Semibalanus balanoides*; TT = *Titobustillobalanus tubutubulus* gen. nov., sp. nov.; Ind = indeterminable. The radiocarbon determinations have been calibrated with the program OxCal version 4.1.7 (Bronk Ramsey, 2001, 2009) against the IntCal09 calibration curve (Reimer et al., 2013). (Álvarez-Fernández, 2009, 2010b, 2012, 2013; Álvarez-Fernández et al., in press a; Alvarez-Fernández et al., in press b; Álvarez-Fernández and Altuna, 2013; Arias et al., 2013, 2005; Ontañón, 2003).

Le nombre (NR) de restes de Balanomorphes des sites préhistoriques de l'Espagne cantabrique, ainsi que les niveaux, les périodes archéologiques et la chronologie des différents niveaux où ils ont été trouvés. SM: Shell midden (amas coquilliers). Les informations sur les Mollusques marins (détermination E. A.-F.) des différents niveaux, auxquels les Balanomorphes (détermination R.-P. C.) sont associés, et les références bibliographiques les concernant, sont aussi indiquées. BC = Balanus crenatus crenatus *; C* = Chthamalus *sp. ; CM* = Chthamalus montagui *; CS* = Chthamalus stellatus *; Ind = indeterminable ; PP* = Perforatus perforatus perforatus *; SB* = Semibalanus balanoides *; TT* = Titobustillobalanus tubutubulus *gen. nov., sp. nov. ; Ind = indéterminable. La datation par le radiocarbone a été calibrée à l'aide du programme OxCal version 4.1.7 (Bronk Ramsey, 2001, 2009) avec la courbe de calibrage IntCa109 (Reimer et al., 2013). (Álvarez-Fernández, 2009, 2010b, 2012, 2013; Álvarez-Fernández et al., in press a; Alvarez-Fernández et al., in press b; Álvarez-Fernández et Altuna, 2013; Arias et al., 2013, 2005; Ontañón, 2003).*

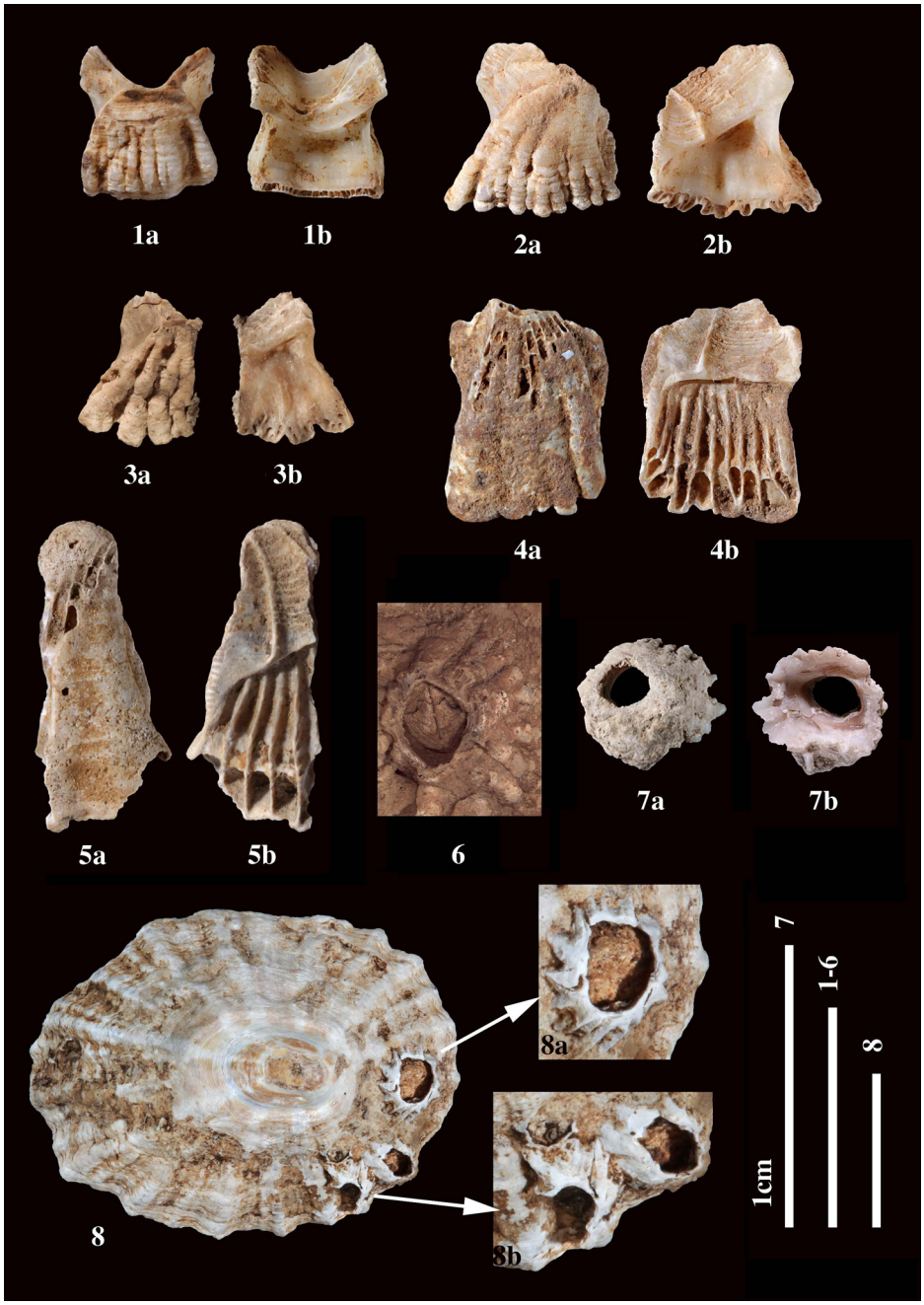

Fig. 3. 1-3 and 6, *Semibalanus balanoides balanoides*: 1a-b, external and internal sides of carina [La Garma A, L; Middle Magdalenian]; 2a-b, external and internal sides of lateral [La Garma A, L; Middle Magdalenian]; 3a-b, external and internal sides of broken plate [El Cierro, F; Lower Magdalenian]; 6, shell with opercular plates [Altamira, 2; Lower Magdalenian]. 4-5, *Balanus crenatus crenatus*: 4a-b, external and internal sides of lateral [La Garma A, L; Middle Magdalenian]; 5a-b, external and internal sides of rostrum [La Garma A, L; Middle Magdalenian]. 7-8, *Chthamalus* sp.: 7a-b, external and internal sides of shell [La Garma A, N; Lower Magdalenian]; 8, shells on *Patella* sp. (8a-b same shells enlarged) [La Cueva del Mar, SM; Mesolithic].
1-3 and 6, Semibalanus balanoides balanoides *: 1a-b, faces externe et interne d'une carène [La Garma A, L ; Magdalénien moyen] ; 2a-b, faces externe et interne d'une latérale [La Garma A, L ; Magdalénien moyen] ; 3a-b, faces externe et interne d'une plaque cassée [El Cierro, F ; Magdalénien inférieur]; 6, test avec valves operculaires [Altamira, 2 ; Magdalénien inférieur]. 4-5,* Balanus crenatus crenatus *: 4a-b, faces externe et interne d'une latérale [La Garma A, L ; Magdalénien moyen] ; 5a-b, faces externe et interne d'un rostrum [La Garma A, L ; Magdalénien moyen]. 7-8,* Chthamalus *sp. : 7a-b, faces externe et interne d'un test [La Garma A, N ; Magdalénien inférieur] ; 8, tests sur* Patella *sp. (8a-b même tests agrandis) [La Cueva del Mar, SM ; Mésolithique].*

Southward (2008) reports that occurrences in warmer climates are probably mistaken identification. More recently Topaloglu and Gönülal (2012) incorporate *B. crenatus crenatus* in their list of 35 thoracic cirripede species from the Mediterranean Sea, but their list is a compilation of former data.

Ecology: The species is mainly from the sublittoral zone, but can rise to the lower intertidal zone. No known support for the specimen found in the caves of northern Spain.

Subfamily CONCAVINAE Zullo, 1992
Genus ***Perforatus*** Pitombo, 2004
Perforatus perforatus perforatus (Bruguière, 1789)

Occurrence and material: Chalcolithic/Bronze Age [Basque Country: Urtiaga (level B), 1 specimen (1 shell)]. Neolithic/Chacolithic? [Basque Country: Jaizkibel 3 (level C), 2 specimens (2 wall plates)]. Mesolithic/Neolithic? [Basque Country: Jaizkibel 3 (level C/D), 3 specimens (shells and fragments of shells without

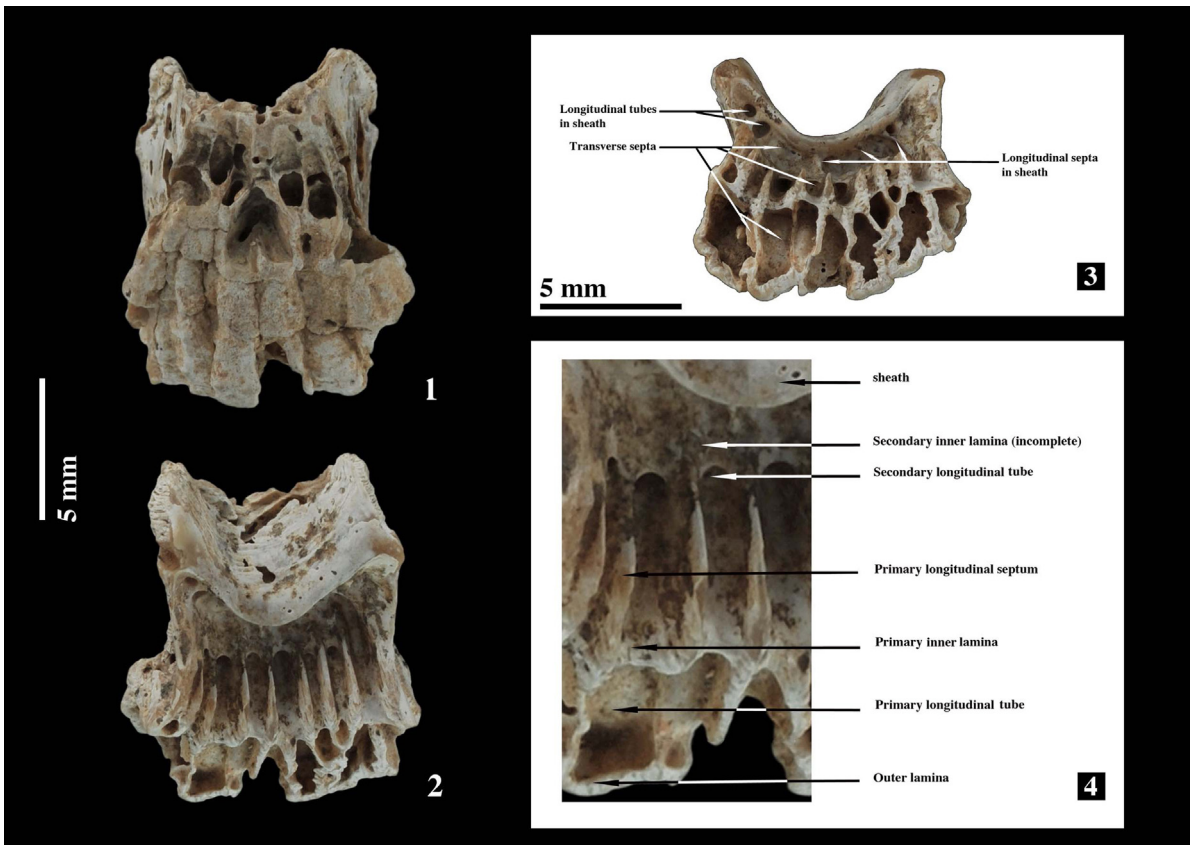

Fig. 4. *Titobustillobalanus tubutubulus* gen. nov., sp. nov., holotype n° TB77.1a.Balano.001: 1-2, external and internal sides; 3, basal view; 4, enlarged part of the external side. Titobustillobalanus tubutubulus *gen. nov., sp. nov., holotype n° TB77.1a.Balano.001 : 1-2, faces externe et interne ; 3, vue basale ; 4, portion agrandie de la face externe.*

opercular plates)]. Mesolithic [La Garma B (level A), 1 specimen (carina)].

Current geographic distribution: *B. perforatus perforatus* is present in the Mediterranean and Black Seas, on French and English coasts of the English Channel, and on Atlantic Coasts from Wales (Cardigan Bay) to Angola (Lobito Bay) (Carriol, 1982).

Ecology: The species is present in the lower half of the intertidal zone and penetrates into the sublittoral zone.

Subfamily INCERTAE SEDIS

Discussion: Following Pitombo (2004) the Balanidae encompass 4 subfamilies. In the absence of observable radii, *Titobustillobalanus* gen. nov. can be classified with certainty in none of them. Among these subfamilies, only two have representatives with more than one row of longitudinal parietal tubes: the Amphibalaninae and the Megabalaninae. *Titobustillobalanus* gen. nov. has a single row of small secondary tubes between primary and secondary inner lamina. The secondary tubes of Amphibalaninae are different. They are formed by the ramification of the septa close to the outer lamina and by anastomosis or linkage of the primary and secondary septa by an inner or secondary lamina (Pitombo, 1999). The secondary tubes are known among the Megabalaninae in *Megabalanus vinaceus* and in the genus *Fosterella* of which they are characteristic. The secondary tubes of *Fosterella* differ from those of the *Titobustillobalanus* gen. nov. because they are on one or more rows in outer lamina, and those of *M. vinaceus* can be distinguished because they are numerous in the inner lamina giving it a cancellated aspect.

Remark: The existence of several representatives of the Balanidae having more than one row of longitudinal parietal tubes allows to reject the hypothesis of a teratological phenomenon for the specimen of Titobustillo.

Genus ***Titobustillobalanus*** Carriol gen. nov. (Fig. 4: 1-4)

Diagnosis: Balanidae with parietes permeated by a single row of secondary small tubes, crossed by transverse septa, between primary and secondary inner lamina. Sheath with tubes and cells.

Type species: Titobustillobalanus tubutubulus sp. nov.

Etymology: In reference to Tito Bustillo Cave, Asturias, Spain.

Affinities: Belonging of *Titobustillobalanus* gen. nov. to a subfamily of Balanidae cannot be established. Only the later discovery of plates with radii will allow a conclusion. Porous radii would indicate a belonging to Megabalaninae and this *Titobustillobalanus* gen. nov. would be classified near the southern genera *Fosterella*, *Notomegabalanus* and *Austromegabalanus*. Thus, it would be the first case of a genus known only in the north hemisphere, taxonomically close to endemic genera of the south hemisphere. The current endemism of these taxa could be the result of extinction of the allied forms of the north hemisphere, as already known with *Notomegabalanus*, of which the representatives in the north hemisphere (four species from North America and one from Europe, *N. buckeridgei* Carriol, 2002) are known only as fossils.

Titobustillobalanus tubutubulus Carriol sp. nov. (Fig. 4: 1-4)

Diagnosis: As for genus.

Etymology: Morphological, alluding to the presence of two sorts of tubes in the paries (in latin *tubus* = tube and *tubulus* = small tube).

Occurrence: Tito Bustillo (Upper Complex, sublevel 1a), Asturias, Spain; Upper Pleistocene, Lower Magdalenian.

Type material: The sole specimen (holotype), a carina, number TB77.1a.Balano.001, is deposited in the Museo Arqueológico de Asturias (Oviedo)

Description: Plate folded under an angle of about 30 degrees at sheath level. Paries outer surface heavily ribbed, yellowish white in colour, mid-height at least 10.2 mm. Internally (Fig. 4: 1-4), primary longitudinal septa have basal teeth with denticles suggesting the existence of a calcareous basis. These septa, which are between primary inner lamina and outer lamina, bound longitudinal primary tubes, with wide quadrangular section and transversal septa. Between the primary inner lamina, and a secondary inner lamina (incomplete), secondary longitudinal septa alternate with secondary longitudinal tubes transversely septed. These tubes, arranged on a unique row, have a small rounded section. The margin of the outer lamina raised. Sheath (Fig. 4: 2) with growth ridges, lacking longitudinal ribs, occupying about 1/2 of interior of plate, with longitudinal tubes in each lateral part, and in the central part the space between the inner lamina and the projection of the edge of the sheath is divided into cellular space by longitudinal and transverse septa. Radii with transverse teeth on sutural edge which seem to be smooth (characteristic deduced from traces left by sutural edge of radii of carinolateral on paries). Alae with secondary alar increment, sutural edge toothed.

Remark: We consider the tubes between the primary inner lamina and a secondary inner lamina to be secondary longitudinal tubes because they are the smallest and partially bounded by an incomplete lamina.

Ecology: It is a cold water species like *S. balanoides balanoides*, the species found in nearby caves, and in levels of the same period.

3. Palaeoclimatic data

In archaeological levels in Cantabrian Spain, dated in the Last Glacial Maximum (from Solutrean to Middle Magdalenian; ca. 23,000-16,500 cal BP) (Fig. 2), three species of sessile cirripedes are present: *S. balanoides balanoides, B. crenatus crenatus* and *T. tubutubulus* sp. nov. In the levels from Upper Magdalenian (Greenland Interestadial 1) to Bronze Age; ca. 15,000-3500 cal BP) (Fig. 2) three other species are present: *C. montagui*, *C. stellatus* and *P. perforatus perforatus*. In view of the current species distribution, *S. balanoides balanoides* and *B. crenatus crenatus* are considered to be species tolerating water colder than the two *Chthamalus* and *P. perforatus perforatus. B. crenatus crenatus* mostly inhabits the infralittoral zone, and after Kerckhof (2002), this species replaces *S. balanoides balanoides*, which lives in the intertidal zone of the boreo-arctic regions of the Atlantic Ocean, in the lower intertidal zone. From the Upper Magdalenian, *C. montagui* (middle and upper intertidal species) and *C. stellatus* (lower half intertidal species) replace *S. balanoides balanoides*, and *P. perforatus perforatus* which inhabits both lower intertidal and infralittoral zones, replaces *B. crenatus crenatus.* So it is likely that the change of cirripede fauna is the result of global warming. This global warming appears in the Upper Magdalenian and the new fauna remained until the Bronze Age (ca. 3500 cal BP) excepted during the last cold period before the Holocene (Younger Dryas, Azilian period) (see Johnsen et al., 2001).

The same conclusion is inferred from the study of the gastropod fauna gathered as food in Cantabrian Spain by human groups. Regarding *Patella*, the most abundant genus during the late Pleistocene in this region, until the Upper Magdalenian *P. vulgata*, considered a cold-climate species, predominated at archaeological sites in Cantabrian Spain. From the Upper Magdalenian the temperate species (*P. intermedia* and *P. ulyssiponensis*) increase in importance, but the percentage of *P. vulgata* is always greater (Álvarez-Fernández, 2011; in press). In this case, it is not a simple substitution of one species by others, but rather a case of greater or lesser presence of each species due to climate change (Moreno, 1994; Craighead, 1999; Bailey and Craighead, 2004; Álvarez-Fernández et al., 2011).

Disclosure of interest

The authors declare that they have no conflicts of interest concerning this article.

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