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**DISTRIBUTION OF CREVICE SPECIES
ALONG THE IBERIAN PENINSULA
AND NORTHWEST AFRICA**

by Craig B. KENSLER,
*Marine Science Laboratories,
Menai Bridge, Anglesey,
Great Britain **

ABSTRACT

The distribution of fifty-nine selected intertidal crevice species in southwest Europe and northwest Africa has been investigated. From the detailed study of twenty-eight species, six distinct patterns of geographical distribution have been recognised.

INTRODUCTION

Papers describing the intertidal rock crevice habitat, and the crevice fauna, have been few in number. GLYNNE-WILLIAMS & HOBART (1952), investigated the habitat and fauna at Anglesey, in North Wales, whilst MORTON (1954), examined similar crevice habitats and faunas at Plymouth, in southwest England. More recently, KENSLER investigated and described the crevice habitat in western Norway (1964*b*), and in the Mediterranean (1965), and listed the crevice fauna for each region. The colonization of artificial crevices by marine invertebrates has been studied by KENSLER & CRISP (1965).

Several other workers have observed the habitat or noted members of its fauna (MONIEZ, 1889; STELFOX, 1916; BARNES, 1924; BAUDOIN, 1939, 1946; MORTON, 1960; SCARRATT, 1961; KENSLER, 1964*a*, 1965). Limited information is available in the literature concerning the distribution of crevice species.

* Present address : Fisheries Research Division, 327 Willis Street, Wellington, New Zealand.

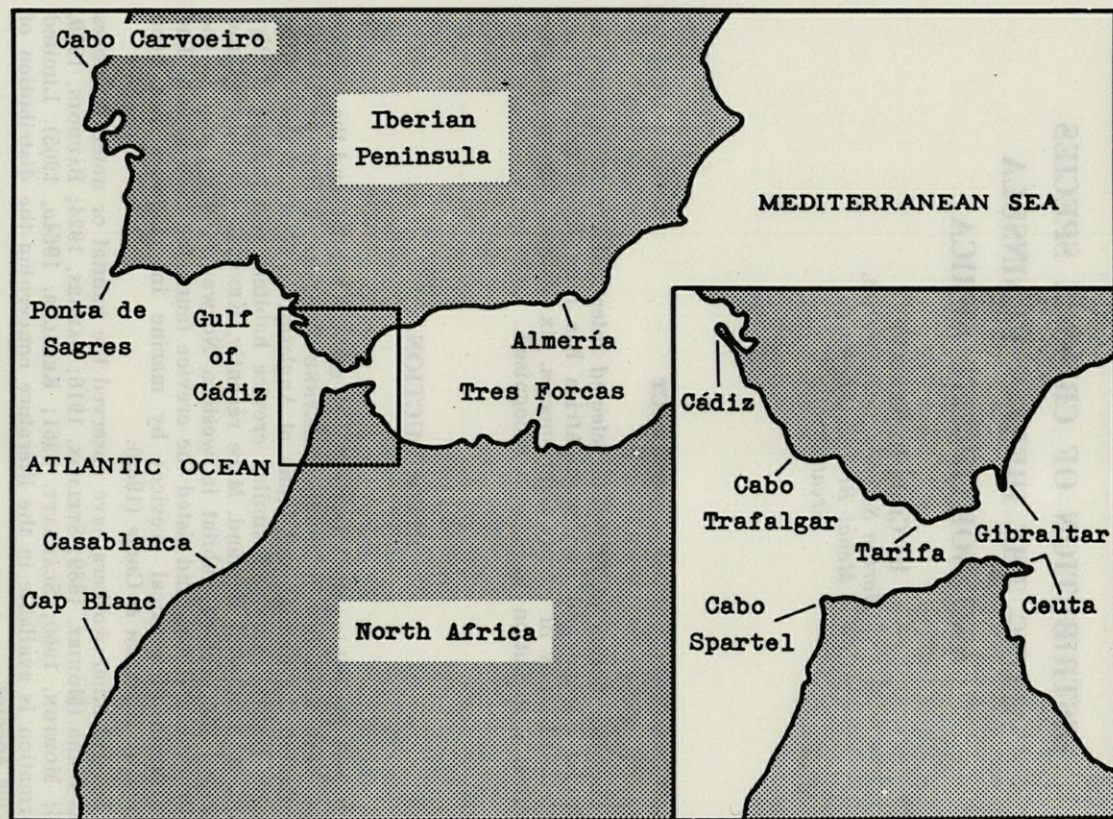


FIG. 1. — Map of the area investigated along the Iberian Peninsula and northwest Africa, showing places mentioned in the text.

KENSLER (1964b) gives the distribution of selected crevice species in western Norway, and also compares the more northern fauna of west Norwegian crevices with that of North Wales and southwest England. In his paper on the Mediterranean crevice habitat KENSLER (1965), delineates the southern and northern limits of distribution for a number of species occurring at Banyuls (in the Mediterranean), North Wales, and western Norway.

During the latter months of 1963, I investigated the distribution of fifty-nine selected crevice species in southwest Europe and North Africa, examining suitable sites in France, Spain, Gibraltar, Portugal and Morocco. Unfortunately I was not able to visit Algeria as originally planned (due to the border fighting at the time between the Moroccan and Algerian armies) and therefore my North African investigations were limited to the coast of Morocco only.

The *Plymouth Marine Fauna* (1957) has been followed, wherever possible, in regard to scientific nomenclature and authorities.

AREA AND STATIONS INVESTIGATED

Figure 1 shows the general area of the study, ranging from Cabo Caroveiro, Portugal and Cap Blanc, Morocco in the west, to Almeria, Spain and to Tres Forcas, Morocco, in the east. In Figure 2 are shown the localities of the twenty-five stations investigated, with the place names given in Table 1. These stations

TABLE 1
List of the stations investigated along the Iberian Peninsula and northwest Africa.

IBERIAN PENINSULA	
1. Cabo Carvoeiro, Portugal.	9. Cabo Trafalgar, Spain.
2. Ericeira, Portugal.	10. Tarifa, Spain.
3. Cascais, Portugal.	11. Gibraltar, east coast.
4. Cabo de Espichel, Portugal.	12. Punta Chullera, Spain.
5. Cabo de Sines, Portugal.	13. Fuengirola, Spain.
6. Sagres, Portugal.	14. Almuñecar, Spain.
7. Albufeira, Portugal.	15. Almeria, Spain.
8. Cádiz, Spain.	
NORTH AFRICA	
16. Cap Blanc, Morocco.	21. Benzou, Morocco.
17. Temara, Morocco.	22. Moroccan-Spanish Frontier.
18. Larache, Morocco.	23. Cap Mazari, Morocco.
19. Cabo Spartel, Morocco.	24. Al Hoceima, Morocco.
20. Cabo Malabata, Morocco.	25. Tres Forcas, Morocco.

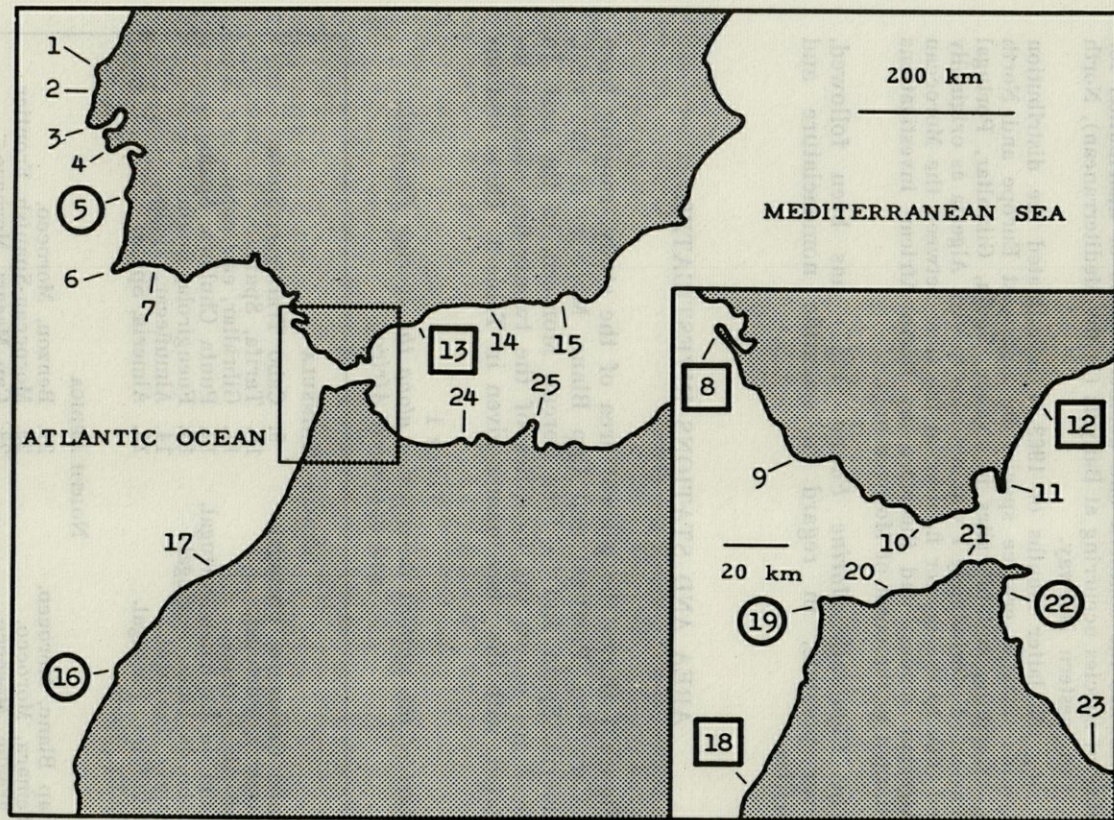


FIG. 2. — Location of the stations investigated, with the place names given in Table 1. Localities particularly suitable for the development of a crevice fauna are indicated by circles (O), and particularly unsuitable localities are indicated by squares (□).

represent rocky localities, on both European and African sides of the Strait of Gibraltar, suitable for the development of a crevice fauna. Particularly suitable localities with well formed crevices favourable for the development of the fauna (see Fig. 2), are indicated by circles (e.g. ⑤, ⑬, ⑰, ⑳), whereas particularly unsuitable localities with few or with unsuitable fissures are indicated by squares (e.g. ⑧, ⑫, ⑭, ⑱). The remaining stations where crevices of an average character and frequency were present were not considered to be particularly suitable, or unsuitable, and therefore appear without symbols.

THE FAUNA

As noted by several previous workers (GLYNNE-WILLIAMS & HOBART, 1952; MORTON, 1954; KENSLER, 1964*b*, 1965) the crevice community is composed of two faunal elements, those intertidal animals of terrestrial origin, and those which are truly marine. The number of marine forms are generally greater than the number of terrestrial forms (KENSLER, 1964*c*). Also, the fauna is extremely varied and composed of a number of ecological groups. KENSLER (1964*c*) recognised five ecological groups, with decreasing affinity for the habitat, 1) permanent crevice species, 2) temporary crevice species, 3) juvenile crevice species, 4) hypobiotic species, and 5) accidental crevice species.

Fifty-nine species were investigated during the study, and the detailed distribution of these species for each of the twenty-five stations visited is given in Table 2. The distribution symbols used in the illustrations of this paper have the following meanings, open circle ○ = no specimens found, full circle ● = specimens found.

THE DISTRIBUTIONS

As can be seen from Table 2, some species were widely distributed and were present at all, or the majority, of the stations investigated. Examples of such species are, the nemertean, *Emplectonema gracile* and *Eunemertes peronea*; juvenile forms of the decapods, *Eriphia spinifrons* and *Pachygrapsus marmoratus*; the gastropod, *Littorina neritoides*; the lamellibranchs, *Lasaea rubra* and *Hiatella arctica*; the mite, *Halotydeus hydrodromus*; and the chilopod, *Hydroschendyla submarina*. Other species were more

Station	1. Cabo Carvoeiro	2. Ericeira	3. Cascais	4. Cabo de Espichel	5. Cabo de Sines	6. Sagres	7. Albufeira	8. Cádiz	9. Cabo Trafalgar	10. Tarifa	11. Gibraltar	12. Punta Chullera	13. Fuenfrola	14. Almuñecar	15. Almería	16. Cap Blanc	17. Temara	18. Larache	19. Cabo Spartei	20. Cabo Malabata	21. Benzou	22. Fronther	23. Cap Mazari	24. Al Hoceima	25. Tres Forcas	
Marine Forms :																										
Coelenterata	●	●	○	●	●	●	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○
Anthozoa																										
<u>Actinia equina</u> L.	●	●	○	●	●	●	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○
<u>Anemonia sulcata</u> (Pennant)	●	●	○	●	●	●	●	○	○	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	○	○
Platyhelminthes																										
Turbellaria																										
<u>Leptoplana alcinoi</u> Schmidt	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Nemertini																										
Anopla																										
<u>Lineus longissimus</u> (Gunnerus)	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
Enopla																										
<u>Emplectonema gracile</u> (Johnston)	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<u>Eunemertes peronea</u>	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<u>Amphiporus lactifloreus</u> (Johnston)	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<u>Tetrastemma melanocephalum</u> (Johnston)	●	●	●	●	●	●	●	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○

TABLE 2

The Detailed Distributions of the fifty-nine Species investigated.

The table summarises observations made on the distributions of fifty-nine species at each of the twenty-five stations visited during the study. The distribution symbols used in the table have the following meanings, open circle (○) = no specimens found, full circle (●) = specimens found.

- 25. •
- 24. •
- 23. •
- 22. •
- 21. •
- 20. •
- 19. •
- 18. •
- 17. •
- 16. •
- 15. •
- 14. •
- 13. •
- 12. •
- 11. •
- 10. •
- 9. •
- 8. •
- 7. •
- 6. •
- 5. •
- 4. •
- 3. •
- 2. •
- 1. •

Pachygrapsus marmoratus Fabricius

Mollusca

Polyplacophora

Lepidochitona cinereus (L.)

Gastropoda

Diodora apertura (Montagu)

Patella tarentina von Salis

Patella safiana Lamarck

Acmaea unicolor Forbes

Monodonta turbinatâ Born

Gibbula umbilicalis (da Costa)

Littorina neritoides (L.)

Littorina littorea (L.)

Littorina saxatilis (Olivi)

Littorina punctata Gmelin

Cerithiopsis tubercularis Montagu

Triphora perversa (L.)

Fossarus ambiguus Linné

Cingula (Cingula) cingillus (Montagu)

Nucella lapillus (L.)

Pulmonata

Ovatella myosotis (Draparnaud)

Otina ovata (Brown)

Siphonaria algerisae Quoy et Gaimard

Onchidella celtica Forbes and Hanley

restricted in their distribution, as also can be seen from Table 2. Some forms were present mainly in the Mediterranean, whilst other species were found only along the western European shores, or along the western European and African shores, or on both, but were not found within the Mediterranean.

The detailed distributions of seventeen selected species, showing definite patterns, are given in Figures 3-14. A check of the literature revealed scattered, and sometimes doubtful, reference to the general distribution of these seventeen species. Therefore, Tables 3-6 have been compiled from the works of many investigators, supplemented by personal unpublished observations, in order to give the general zoögeography of each species. The seventeen selected species revealed four distinct distribution patterns, which will be elaborated below, and are illustrated in Figures 3-14. A fifth group of ten species was found at the majority of the stations visited during the study. The centre of distribution of these ten species lies within the area studied and they reach their northern limits somewhere along the Atlantic coasts of Europe, not occurring as far as Britain. Table 7, compiled from the literature, gives information on the northern limits of distribution for each of these ten species. A sixth pattern of distribution was shown by a single species, the Mediterranean barnacle, *Chthamalus depressus*.

The following types of distributions were recognised :

I. *Lusitanian-Mediterranean*.

Species present along European Atlantic and Mediterranean coasts, but not found along coasts of Morocco (Figs. 3-4).

II. *Boreal*.

Species present along European Atlantic coasts, but not found along Moroccan Atlantic coast nor in the Mediterranean (Figs. 5-8).

III. *Lusitanian*.

Species present along Atlantic coasts of Europe and Morocco, but not found along Mediterranean coasts (Figs. 9-10).

IV. *Tropical Atlantic*.

Species present in the Mediterranean and along the Atlantic coast of Morocco, but not found along European Atlantic coasts north of Cádiz, Spain (Figs. 11-14).

V. *Atlanto-Mediterranean*.

Species present in the Mediterranean and along Atlantic coasts of Morocco and Europe as far north as mid-Portugal, northern Spain, or western France, but not found in Britain.

VI. Mediterranean.

Species present in the Mediterranean and the Strait of Gibraltar, but not found along Atlantic coasts of Europe and North Africa.

I. LUSITANIAN-MEDITERRANEAN

Figures 3 and 4 show the distribution of the isopods, *Campepeoa hirsuta* and *Dynamene bidentata*, with their zoögeography given in Table 3.

Campepeoa hirsuta occurs along Atlantic coasts of Britain and Europe and enters the Mediterranean, where its distribution is limited. Apparently, it is restricted to a small stretch of shore on the European side of the Strait of Gibraltar. The species was not found in any rock crevices examined at Banyuls (KENSLE, 1965), nor was it observed at any of the several sites examined along the south coast of Spain (unpublished observations), nor has it been recorded from the Mediterranean by previous workers. *Dynamene bidentata*, also found along British and European Atlantic coasts, is in contrast widespread in the Mediterranean, and has been reported from as far east as the Black Sea (see Table 3).

MONOD (1932) reported *C. hirsuta* and *D. bidentata* from Mauretania in West Africa, and therefore both species would seem to be present along the Atlantic coast of Morocco south to Mauretania. However, neither species was noted at the several stations I visited along the Moroccan Atlantic coast, but perhaps further investigations of the restricted habitats occupied by these two isopods will reveal specimens. *Dynamene bidentata* is usually found in crevices and similar hypobiotic habitats in the lower intertidal zone. *Campepeoa hirsuta* is normally restricted to the high tide zone. Where either species is scarce, careful and patient searching is necessary to reveal specimens in crevices, tufts of lichen, or in empty barnacle shells.

II. BOREAL

Figures 5-8 show the distributions of *Otina ovata*, *Nucella lapillus*, *Jaera albifrons*, *Littorina saxatilis*, *Lineus longissimus*, *Cirratulus cirratus*, *Littorina littorea*, and *Aëpopsis robinii*, with the zoögeography of each species given in Table 4. Apparently these eight species are absent or rare from the Mediterranean and from the coasts of Morocco.

The cryptozoic pulmonate, *Otina* extended southward along Portugal to Tarifa, Spain, at the western entrance to the Strait of Gibraltar (see Fig. 5), but was not found at any stations on the Moroccan coast nor from localities within the Mediterranean, although many suitable

crevices were examined. A search through the literature revealed that *Otina* had previously been reported only as far south as Lagos, in southern Portugal (NOBRE, 1932). Therefore, the discovery of *Otina* at Tarifa extends its southern limit of distribution to south Spain, and also records *Otina* for the first time from Spanish coasts.

The remaining seven species apparently reach their southern limits of distribution in Portugal. Figure 6 shows the distribution of the gastropod, *N. lapillus*, and the isopod, *J. albifrons*. These species extended south along the coast to Cabo de Sines (station 5), and were not found at any stations to the south, although *N. lapillus* has been reported from the Atlantic coast of Morocco and the Mediterranean coast of France (PASTEUR-HUMBERT, 1962a), and *J. albifrons* has been listed as « rare in the Mediterranean » (PERRIER, 1954). These species were not recorded from the crevice habitat at Banyuls (KENSLE, 1965), nor noted at several suitable sites along the Mediterranean coast of Spain (unpublished observations), but perhaps are present and are found as isolated populations only.

The gastropod, *L. saxatilis* (see Fig. 7), extended along the west coast of Portugal to station 6, where the species apparently attains its southern limit of distribution. *Littorina saxatilis* was not noted at any stations to the east nor further to the south on the coasts of Morocco, although a careful search was made of rock crevices and other suitable intertidal habitats.

The nemertean, *L. longissimus*; the annelid, *C. cirratus*; the gastropod, *L. littorea*; and the coleoptern, *A. robinii*, were present at all seven stations investigated in Portugal but did not extend eastward into the Gulf of Cádiz, nor south to the northwest coast of Africa (see Fig. 8).

III. LUSITANIAN

The distribution of the tanaid, *Tanais chevreuxi*, is seen in Fig. 9. This species is usually restricted to crevices on exposed shores, and was found along Atlantic coasts of Portugal, Spain and Morocco, all of which experience heavy surf, but was not recorded from any localities within the Mediterranean, all of which however were relatively sheltered. KENSLE (1965) concluded that *T. chevreuxi* was not present at Banyuls because the crevices lacked suitable coarse deposits of broken shell and gravel, used in the construction of the « galleries » inhabited by the species, and organic detritus on which the species feeds.

A number of marine laboratories, universities, and research institutions along Mediterranean coasts have reported to me that *T. che-*

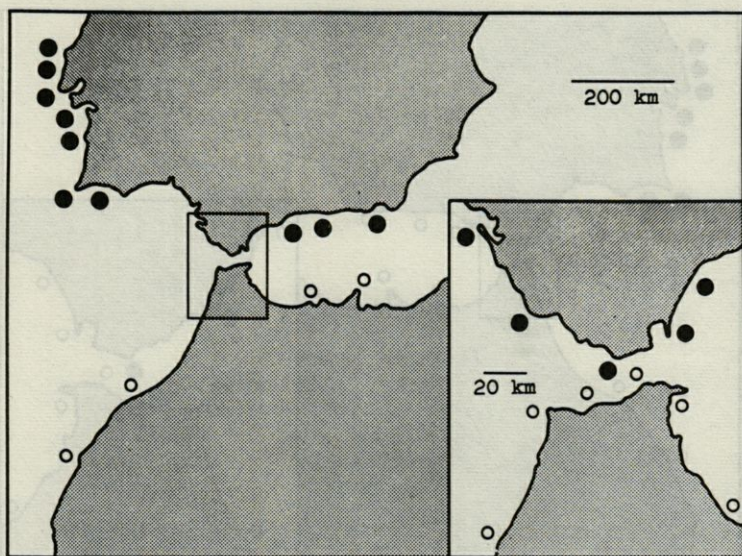


FIG. 3. — Distribution of *Campecopea hirsuta*.

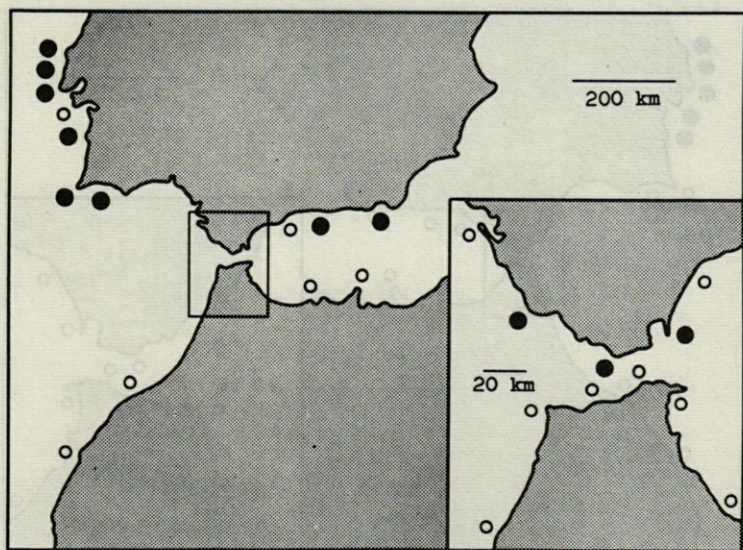


FIG. 4. — Distribution of *Dynamene bidentata*.

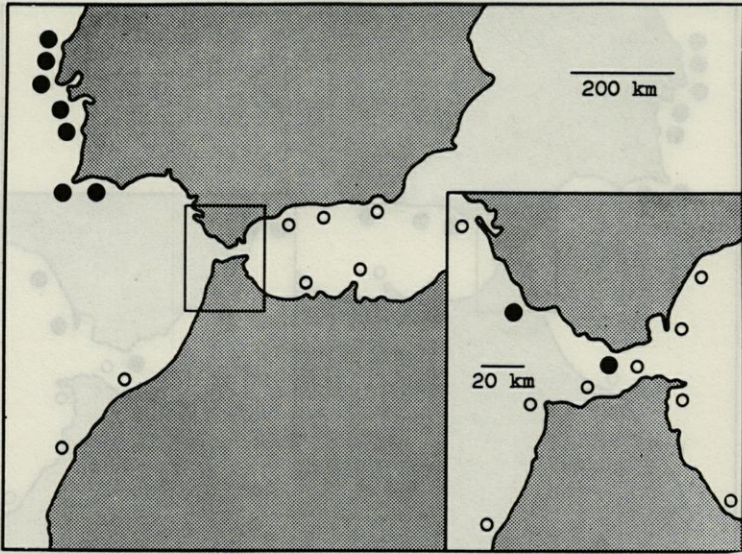


FIG. 5. — Distribution of *Otina ovata*.

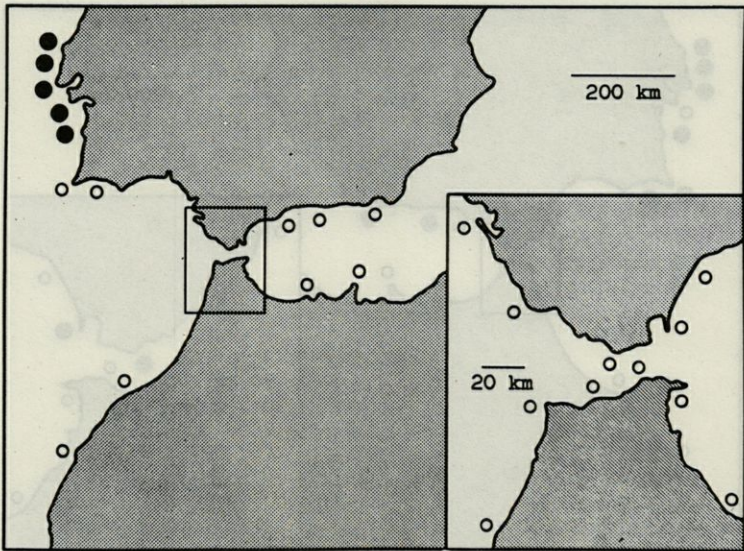


FIG. 6. — Distribution of *Nucella lapillus* and *Jaera albifrons*.

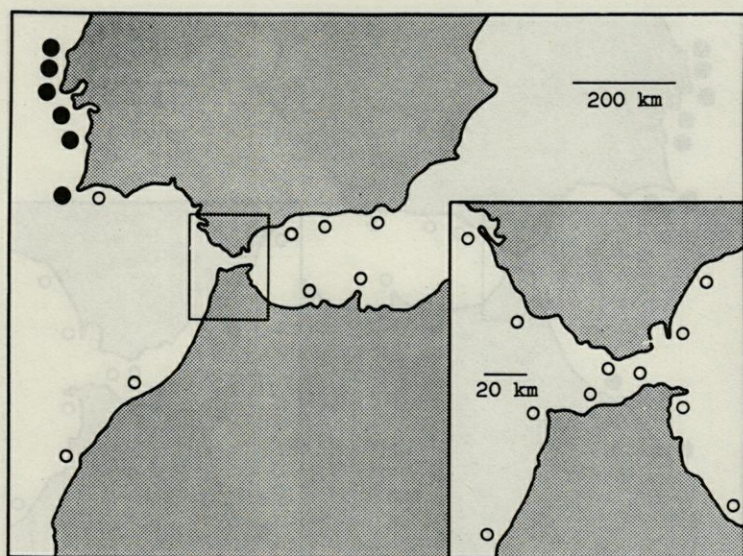


FIG. 7. — Distribution of *Littorina saxatilis*.

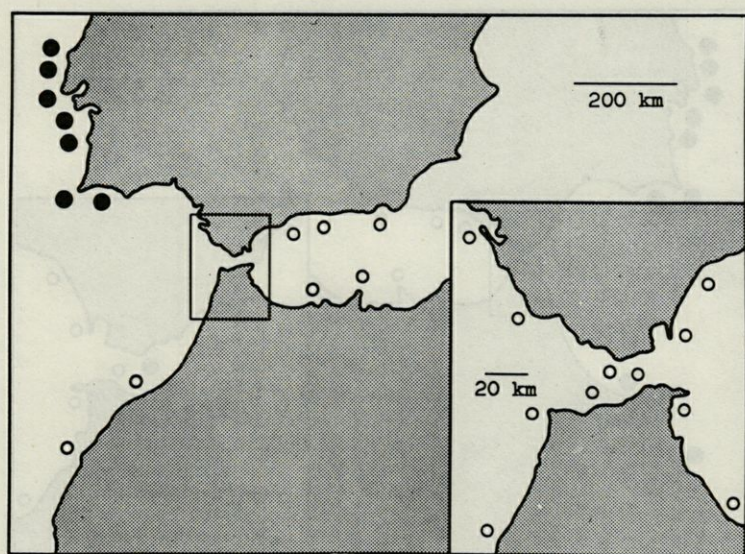


FIG. 8. — Distribution of *Lineus longissimus*, *Cirratulus cirratus*, *Littorina littorea* and *Aëpopsis robinii*.

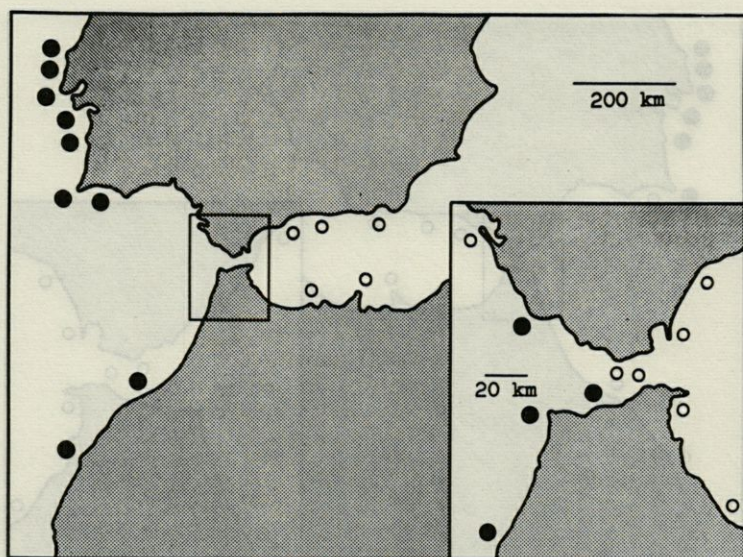


FIG. 9. — Distribution of *Tanais chevreuxi*.

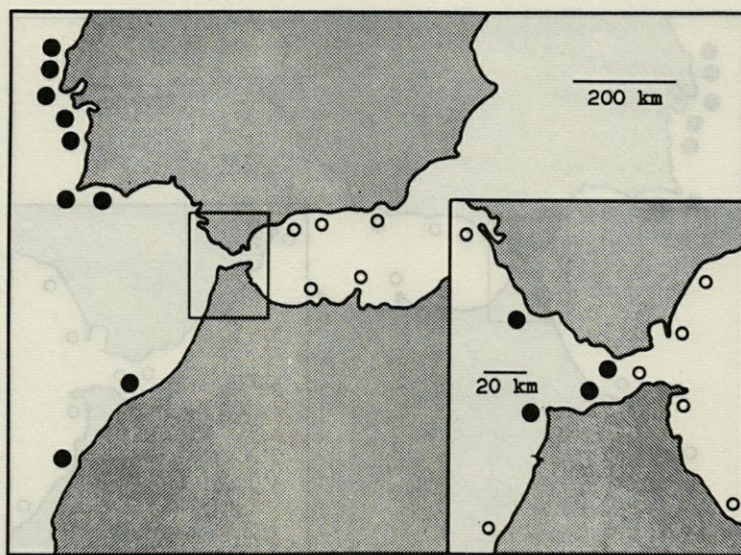


FIG. 10. — Distribution of *Cingula cingillus* and *Ovatella myosotis*.

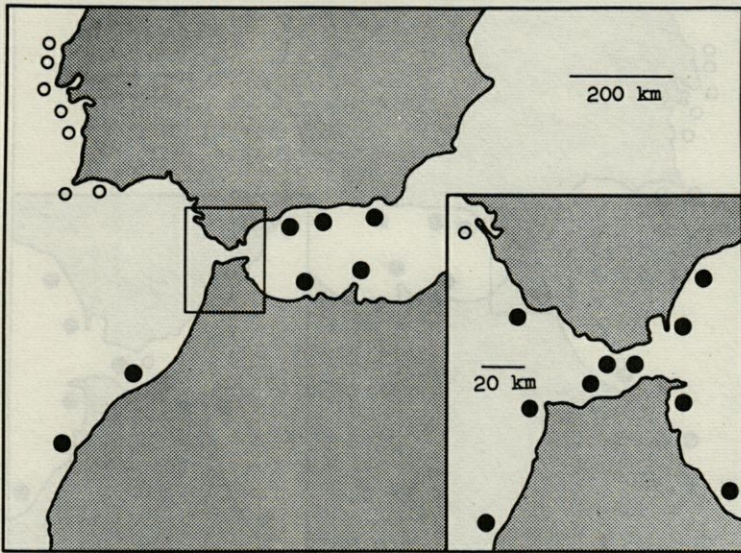


FIG. 11. — Distribution of *Littorina punctata*.

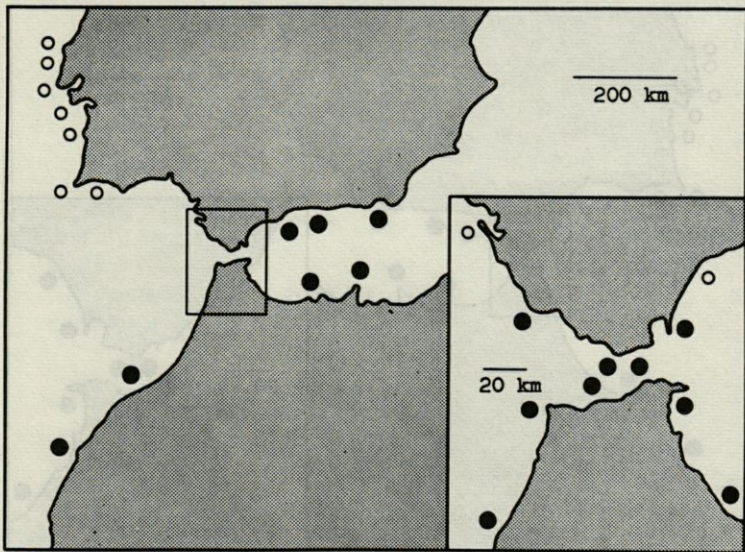


FIG. 12. — Distribution of *Patella safiana*.

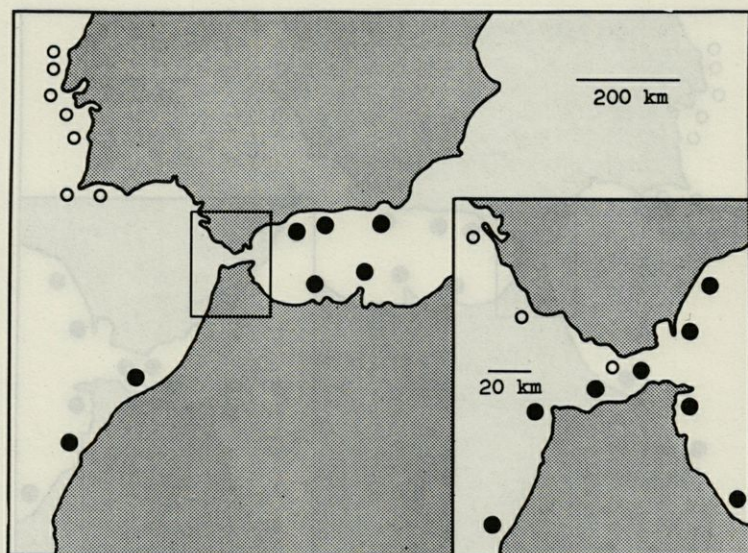


FIG. 13. — Distribution of *Fossarus ambiguus*.

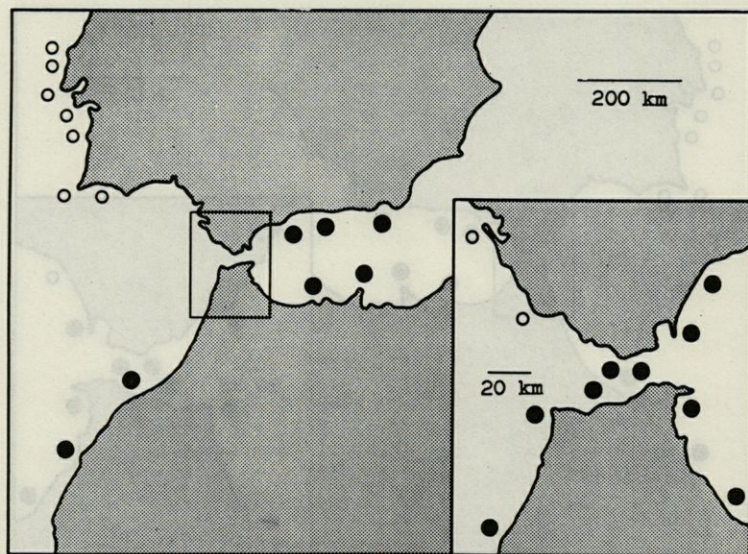


FIG. 14. — Distribution of *Leptoplana alcinoi*.

vreuxi has not been found in their region. However, as noted in Table 5, T. MONOD (1923) has reported the species from Naples and the Adriatic, but unfortunately did not mention the habitat occupied by this species of *Tanais*. Perhaps further investigations on suitable rock crevice habitats will disclose the presence of *T. chevreuxi* at a number of localities from within the Mediterranean. But, our present knowledge of this species indicates that its distribution in the Mediterranean is limited.

Figure 10 shows the distribution of two gastropods, the rissoid, *Cingula cingillus*, and the pulmonate, *Ovatella myosotis*, with their zoögeography given in Table 5. These species were present along Atlantic coasts of Europe and Africa but apparently do not penetrate the Strait of Gibraltar and Mediterranean basin. Both *Cingula* and *Ovatella* are usually restricted to crevices containing considerable deposits of organic material. Therefore, the apparent absence of *C. cingillus* and *O. myosotis*, like that of *T. chevreuxi*, from Mediterranean crevices might be ascribed to the scarcity of organic suspended matter in the clear oligotrophic waters of the Mediterranean, as suggested by KENSLER (1965).

IV. TROPICAL ATLANTIC

Figures 11-14 show the distributions of *Littorina punctata*, *Patella safiana*, *Fossarus ambiguus*, and *Leptoplana alcinoi*. Information on their northern limits of distribution is given in Table 6.

The gastropods, *L. punctata* and *P. safiana* (Figs. 11-12) are tropical species which extend up the Atlantic coast from West Africa, and enter the Mediterranean, but have a limited northern distribution along the Atlantic coast of Europe. Apparently, both species reach their northern limit at Cabo Trafalgar, Spain, and were not recorded from any localities further north. It is interesting to note that neither *L. punctata* or *P. safiana* was recorded at Banyuls (KENSLER, 1965). Therefore, it is probable that the Mediterranean distribution of these species is mainly confined to the coasts of North Africa. PASTEUR-HUMBERT (1962a) lists *L. punctata* only from Spain on the European coast of the Mediterranean, but from Morocco, Algeria, Tunisia and Egypt, on the African coast, continuing eastward to Syria. The Mediterranean distribution of *P. safiana* is much less widespread than that of *L. punctata*, the species being recorded only from Morocco and Algeria (PASTEUR-HUMBERT, 1962a).

The cryptozoic gastropod, *F. ambiguus*, is a tropical Atlantic species which extends northwards along the Atlantic coast from Angola (PASTEUR-HUMBERT, 1962a) and enters the Mediterranean. The species is

widely distributed throughout the Mediterranean (see Table 6), and penetrates into the Adriatic and Aegean Seas, but was not found to extend west of the Strait of Gibraltar along the Atlantic coasts of Spain or Portugal, as may be seen from Fig. 13.

The turbellarian, *L. alcinoi*, was found to be present along the Atlantic coast of Morocco, and was recorded at all stations within the Mediterranean (Fig. 14). On the European coast, the species extended westward only as far as Tarifa (station 10), and was not found at any stations northwest of the Strait of Gibraltar.

V. ATLANTO-MEDITERRANEAN

The following ten species were commonly noted at the majority of the stations investigated during the study, and reach their northern limits of distribution along Atlantic coasts of Europe: *Eunemertes peronea*, *Eriphia spinifrons*, *Pachygrapsus marmoratus*, *Acmaea unicolor*, *Siphonaria algesirae*, *Arca pulchella*, *Cardita calyculata*, *Chama gryphoides*, *Mytilus minimus*, and *Ligia italica*. Information on the northern limit of distribution for each species is given in Table 7.

Juvenile specimens of the decapods, *E. spinifrons* and *P. marmoratus*, and of the lamellibranch, *M. minimus*, were a common feature of the numerous crevices examined during the course of this study. The three species are widespread throughout the Mediterranean basin, and their distribution extends northward along the Atlantic coast of Europe. CRISP & FISCHER-PIETTE (1959) investigated the distribution of these three intertidal species, as well as a number of others, along the Atlantic coast of western France. Their study showed that *E. spinifrons* and *P. marmoratus* reached their northern frontier near Concarneau, in southwest Brittany, whilst *M. minimus* was not found north of Arcachon, in the Bay of Biscay.

The exact northern limits of distribution for the remaining seven species are unknown, as the crevice habitat along Atlantic coasts of Spain and France has yet to be examined and fauna lists compiled. The gastropod, *A. unicolor*, was present in western Portugal (see Table 2), and has been listed for the Atlantic coast of France (PASTEUR-HUMBERT, 1962a), but has not been reported from Roscoff in northwest France (CORNET & MARCHE-MARCHAD, 1951), nor from Plymouth in southwest England (Plymouth Marine Fauna, 1957). Therefore, the northern frontier for *A. unicolor* lies at some point on the Atlantic coast of France, south of Roscoff.

The northern frontier for each of the remaining six species is even less certain than is that of *A. unicolor*. The colourful nemertean, *E. peronea*; the pulmonate, *S. algesirae*; and the lamellibranchs, *A. pulchella*, *C. calyculata* and *C. gryphoides*, were present

TABLE 3

Detailed Distribution of Lusitanian-Mediterranean Group.

Two species present along European Atlantic and Mediterranean coasts, but not found along coasts of Morocco.

Species	Information on the southern and Mediterranean limits of distribution	Reference
<i>Campecopea hirsuta</i>	Listed for Plymouth in southwest England; present on Atlantic coast of France; not found in Mediterranean at Banyuls; but also reported from Atlantic coast of Morocco, south to Mauritania, West Africa.	Plymouth Marine Fauna, 1957; Monod, 1923; Kensler, 1965; Monod, 1932.
<i>Dynamene bidentata</i>	Listed for Plymouth in southwest England; present on Atlantic coast of France; found in Mediterranean at Banyuls; listed from Mediterranean and Black Sea; listed for Naples; reported from Adriatic; but also reported from Atlantic coast of Morocco, south to Mauritania, West Africa.	Plymouth Marine Fauna, 1957; Monod, 1923; Kensler, 1965; Omer-Cooper & Rawson, 1934; Torelli, 1930; Riedl, 1963; Monod, 1932.

TABLE 4

Detailed Distribution of Boreal Group.

Species present along European Atlantic coasts, but not found along Moroccan Atlantic coast or in the Mediterranean.

Species	Information on the southern limits of distribution	Reference
<i>Lineus longissimus</i>	Listed for Plymouth in southwest England; reported from Roscoff in northwest France; not listed for the Mediterranean; not found in Mediterranean at Banyuls.	Plymouth Marine Fauna, 1957; Gontcharoff, 1955; Delphy, 1935; Kensler, 1965.
<i>Cirratulus cirratus</i>	Listed for Plymouth in southwest England; reported from Roscoff in northwest France; not listed for northwest Africa; not listed for the Mediterranean.	Plymouth Marine Fauna, 1957; Cornet & Rullier, 1951; Fauvel, 1936; Fauvel, 1923; Laubier & Paris, 1962.
<i>Littorina saxatilis</i>	Common along English Channel, southwest Brittany, and Atlantic coast of France; listed for northern Portugal; not found in Mediterranean at Banyuls; not reported from Morocco.	Crisp & Fischer-Piette, 1959; Nobre, 1932; Kensler, 1965; Pasteur-Humbert, 1962a.

<i>Littorina littorea</i>	Found along English Channel, southwest Brittany, and Atlantic coast of France; listed for southern Portugal; not found in Mediterranean at Banyuls.	Crisp & Fischer-Piette, 1959; Nobre, 1932; Kensler, 1965.
<i>Nucella lapillus</i>	Found along English Channel, southwest Brittany, and Atlantic coast of France; listed for Portugal; not found in Mediterranean at Banyuls; but also reported from Mediterranean coast of France.	Crisp & Fischer-Piette, 1959; Nobre, 1932; Kensler, 1965; Pasteur-Humbert, 1962a.
<i>Otina ovata</i>	Listed for Plymouth in southwest England; reported from Roscoff in northwest France; listed for southwest Portugal; not found in Mediterranean at Banyuls.	Plymouth Marine Fauna, 1957; Cornet & Marche-Marchad, 1951; Nobre, 1932; Kensler, 1965.
<i>Jaera albifrons</i>	Listed for Plymouth in southwest England; not found in Mediterranean at Banyuls; Neapel (?); rare in Mediterranean.	Plymouth Marine Fauna, 1957; Kensler, 1964c; Nierstrasz & Schuurmans Stekhoven, 1930; Perrier, 1954.
<i>Aëpopsis robinii</i>	Listed for Plymouth in southwest England; reported from Roscoff in northwest France; not found in Mediterranean at Banyuls.	Plymouth Marine Fauna, 1957; Le Masne, 1938; Baudoin, 1946; Kensler, 1965.

TABLE 5
Detailed Distribution of Lusitanian Group.
 Three species present along Atlantic coasts of Europe and Morocco,
 but not found along Mediterranean coasts.

Species	Information on the southern limits of distribution	Reference
<i>Tanais chevreuxi</i>	Listed for Plymouth in southwest England; present Atlantic coast of France; reported from Casablanca, Italy and the Adriatic; not found in Mediterranean at Banyuls.	Plymouth Marine Fauna, 1957; Dollfus, 1897; Monod, 1923, 1925; Kensler, 1965.
<i>Cingula cingillus</i>	Listed for Plymouth in southwest England; reported from Roscoff in northwest France; listed for southwest Portugal; listed for Mediterranean; not found in Mediterranean at Banyuls.	Plymouth Marine Fauna, 1957; Cornet & Marche-Marchad, 1951; Nobre, 1932; Pasteur-Humbert, 1962a; Kensler, 1965.
<i>Ovatella myosotis</i>	Listed for Plymouth in southwest England; reported from Roscoff in northwest France; reported from Mediterranean and Madeira; not found in Mediterranean at Banyuls.	Plymouth Marine Fauna, 1957; Cornet & Marche-Marchad, 1951; Jeffreys, 1869; Kensler, 1965.

TABLE 6

Detailed Distribution of Tropical Atlantic Group.

Four species present in the Mediterranean and along Atlantic coast of Morocco, but not found along European Atlantic coasts north of Cádiz, Spain.

Species	Information on northern limits of distribution	Reference
<i>Littorina punctata</i>	Not found in Mediterranean at Banyuls; listed for Mediterranean coast of Spain and Atlantic coast of Morocco; not listed for Portugal; not found at San Sebastián in northeast Spain; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Kensler, 1965; Pasteur-Humbert, 1962a; Nobre, 1932; Kensler, unpublished observat.; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Patella safiana</i>	Not found in Mediterranean at Banyuls; listed for Mediterranean region and for Atlantic coast of Morocco; not listed for Portugal; not found at San Sebastián in northeast Spain; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Kensler, 1965; Pasteur-Humbert, 1962a ; Nobre, 1932; Kensler, unpublished observat.; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Fossarus ambiguus</i>	Found in Mediterranean at Banyuls; common throughout Mediterranean region; not listed for Portugal; not found at San Sebastián in northeast Spain; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Kensler, 1965; Pasteur-Humbert, 1962a; Nobre, 1932; Kensler, unpublished observat.; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Leptoplana alcinoi</i>	Found in Mediterranean at Banyuls; not listed for Plymouth in southwest England; not listed for the Isle of Man.	Kensler, 1965; Plymouth Marine Fauna, 1957; Marine Fauna of the Isle of Man, 1963.

TABLE 7

Detailed Distribution of Atlanto-Mediterranean Group.

Ten species present in the Mediterranean and along Atlantic coasts of Morocco and Europe as far north as mid-Portugal, northern Spain, or western France, but not found in Britain.

Species	Information on northern limits of distribution	Reference
<i>Eunemertes peronea</i>	Listed for Mediterranean; reported from Mediterranean only (Marseille, Neapel, Sicilen); found in Mediterranean at Banyuls; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Joubin, 1894; Bürger, 1895; Kensler, 1965; Gontcharoff, 1955; Plymouth Marine Fauna, 1957.
<i>Eriphia spinifrons</i>	Common in Mediterranean; extends northward along Atlantic coast of France to southwest Brittany; not listed for Plymouth in southwest England.	Zariquiez Alvarez, 1946; Crisp & Fischer-Piette, 1959; Plymouth Marine Fauna, 1957.
<i>Pachygrapsus marmoratus</i>	Common in Mediterranean; extends northward along Atlantic coast of France to southwest Brittany; not listed for Plymouth in southwest England.	Zariquiez Alvarez, 1946; Crisp & Fischer-Piette, 1959; Plymouth Marine Fauna, 1957.
<i>Acmaea unicolor</i>	Found in Mediterranean at Banyuls; listed for Atlantic coasts of Morocco and France; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Kensler, 1965; Pasteur-Humbert, 1962a; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.

<i>Siphonaria algesirae</i>	Present in Mediterranean; listed for Portugal; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Pasteur-Humbert, 1962a; Nobre, 1932; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Arca pulchella</i>	Common in Mediterranean; not listed for Portugal; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Pasteur-Humbert, 1962b; Nobre, 1932; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Cardita calyculata</i>	Found in Mediterranean at Banyuls; listed for south and west Portugal; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Kensler, 1965; Nobre, 1932; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Chama gryphoides</i>	Common in Mediterranean; listed for western Portugal; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Pasteur-Humbert, 1962b; Nobre, 1932; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Mytilus minimus</i>	Present in Mediterranean and along Atlantic coasts of Portugal and France; extends northward along Atlantic coast of France to Arcachon; not reported from Roscoff in northwest France; not listed for Plymouth in southwest England.	Pasteur-Humbert, 1962b; Crisp & Fischer-Piette, 1959; Cornet & Marche-Marchad, 1951; Plymouth Marine Fauna, 1957.
<i>Ligia italica</i>	Commonly found in Mediterranean at Banyuls; not listed for Plymouth in southwest England; not listed for the Isle of Man.	Kensler, 1965; Plymouth Marine Fauna, 1957; Marine Fauna of the Isle of Man, 1963.

in southern or western Portugal (see Table 2), but were not reported from Roscoff in northwest France (GONTCHAROFF, 1955; CORNET & MARCHE-MARCHAD, 1951), nor from Plymouth in southwest England (Plymouth Marine Fauna, 1957). The terrestrial isopod, *L. italica*, was common at Banyuls (KENSLE, 1965), and along southwest Portugal (Table 2), but has not been found at Roscoff (personal communication, Monsieur L. CABIOCH), nor listed from Plymouth (Plymouth Marine Fauna, 1957). Thus, the northern distribution limits for the latter six species lie along European Atlantic coasts between northern Portugal and northwestern France.

VI. MEDITERRANEAN

The sixth and final distribution pattern recognised was that of the Mediterranean barnacle, *Chthamalus depressus*. The distribution and ecological variation of *Chthamalus* species in the Mediterranean area has been studied by SOUTHWARD (1964) and by KENSLE, BHATNAGAR & CRISP (1965). Their findings show that *C. depressus* is all but confined to the Mediterranean basin and the Strait of Gibraltar, as is also shown in Table 2.

RELATION BETWEEN DISTRIBUTIONS AND ABIOTIC FACTORS

The Strait of Gibraltar connects two characteristically different water masses, the Atlantic Ocean, to the west, and the Mediterranean Sea to the east. The shores bathed by these two water masses are subjected to diverse, and sometimes extreme, physical conditions. Three environmental factors change as one passes from the Atlantic, through the Strait of Gibraltar, into the Mediterranean. Firstly, the tidal amplitude is 3 to 5 times greater along Atlantic shores than in the Mediterranean basin (Admiralty Tide Tables, Vol. I & II, 1963). The degree of wave exposure also changes considerably. Atlantic coasts of Portugal, Spain and Morocco are subjected to constant and heavy wave action, whereas Mediterranean shores are relatively sheltered and receive only limited wave exposure caused by winds. Lastly, the water masses of the Atlantic are different from those of the neighbouring Mediterranean in regard to salinity, temperature, and suspended organic matter. Generally, Atlantic water is of relatively low salinity and not subject to great extremes of temperature, whilst Mediterranean

water is of higher salinity and experiences much greater temperature extremes. Also, the suspended organic matter in Atlantic waters is considerably richer than in clear oligotrophic waters of the Mediterranean.

For Boreal, Tropical Atlantic, and Atlanto-Mediterranean species, discussed in this paper, temperature is apparently the most important factor limiting their distribution. The general southern and northern distributions of these species are given in Table 8. It is seen that all species in the Boreal group reach Britain, whilst the majority extend to Norway. The metropolis of these cold water species lies well to the north, and they are near to their southern limits of distribution in warm waters of southwest Europe. The southern limit for *Nucella lapillus*, *Jaera albifrons*, *Littorina saxatilis*, *Lineus longissimus*, *Cirratulus cirratus*, *Littorina littorea* and *Aëpopsis robinii* is reached in southwest Portugal, whilst only the pulmonate *Otina ovata* extends south to the entrance of the Strait of Gibraltar.

Colder inshore water temperatures apparently limit the northward spread of the Tropical Atlantic species, *Littorina punctata*, *Patella safiana*, *Fossarus ambiguus* and *Leptoplana alcinoi*. The metropolis of these species is well to the south, on West African shores (see Table 8). All of these species extend northward to the Strait of Gibraltar, and are present in the western Mediterranean. They reach their northern frontier along the southwest coast of Spain, seemingly due to the lower temperatures of the inshore waters.

The Atlanto-Mediterranean species, *Eunemertes peronea*, *Eriphia spinifrons*, *Pachygrapsus marmoratus*, *Acmaea unicolor*, *Siphonaria algesirae*, *Arca pulchella*, *Cardita calyculata*, *Chama gryphoides*, *Mytilis minimus* and *Ligia italica*, are abundant and near the centre of their geographical range in the area of study. The majority of these species reach their northern limits of distribution in the Bay of Biscay, whilst *Siphonaria algesirae* extends only to western Portugal. The exact frontiers of these ten species are not fully known. Apparently the northern spread of these warm water species is limited by the lower temperatures encountered in the more northern latitudes.

Species of the Mediterranean and Lusitanian groups are limited in their distribution in relation to conditions inside and outside the Mediterranean basin. Apparently, *Chthamalus depressus* favours the sheltered localities and high summer temperatures which characterise the Mediterranean, as it does not extend west of the Strait of Gibraltar. It has also been suggested by KENSLER, BHATNAGAR & CRISP (1965) that *C. depressus* may be metabolically adjusted to the poorer nutrient conditions of the Mediterranean,

TABLE 8
The General Southern and Northern Distributions
of the Six Groups Recognised.

Groups and Species	Southern limit	Northern limit
<i>Otina ovata</i>	Southern Spain	S.W. Scotland
<i>Nucella lapillus</i>	Southern Portugal	North Norway
<i>Jaera albifrons</i>	Southern Portugal	Norway
<i>Littorina saxatilis</i>	Southern Portugal	Arctic
<i>Lineus longissimus</i>	Southern Portugal	Norway
<i>Cirratulus cirratus</i>	Southern Portugal	Norway
<i>Littorina littorea</i>	Southern Portugal	Norway
<i>Aëpopsis robinii</i>	Southern Portugal	Western Scotland
Tropical Atlantic		
<i>Littorina punctata</i>	Sénégal	N.W. Mediterranean
<i>Patella safiana</i>	Angola	N.W. Mediterranean
<i>Fossarus ambiguus</i>	Angola	N.W. Mediterranean
<i>Leptoplana alcinoi</i>	West Africa	N.W. Mediterranean
Atlanto-Mediterranean		
<i>Eunemertes peronea</i>	West Africa	Bay of Biscay
<i>Eriphia spinifrons</i>	West Africa	Bay of Biscay
<i>Pachygrapsus marmoratus</i>	West Africa	Bay of Biscay
<i>Acmaea unicolor</i>	West Africa	Bay of Biscay
<i>Siphonaria algesirae</i>	West Africa	Western Portugal
<i>Arca pulchella</i>	West Africa	Bay of Biscay
<i>Cardita calyculata</i>	West Africa	Bay of Biscay
<i>Chama gryphoides</i>	West Africa	Bay of Biscay
<i>Mytilis minimus</i>	West Africa	Bay of Biscay
<i>Ligia italica</i>	West Africa	Bay of Biscay
Mediterranean		
<i>Chthamalus depressus</i>	Southern Mediterranean	Northern Mediterranean
Lusitanian		
<i>Tanais chevreuxi</i>	Southern Morocco	North Wales
<i>Cingula cingillus</i>	Morocco ?	Norway
<i>Ovatella myosotis</i>	Morocco ?	Scotland
Lusitanian-Mediterranean		
<i>Campeopea hirsuta</i>	Mauritania ?	Scotland
<i>Dynamene bidentata</i>	Mauritania ?	Scotland

and that outside this area its low metabolic rate may be disadvantageous leading to its replacement by *C. stellatus*.

Several factors can be suggested which explain the apparent absence of the Lusitanian species, *Tanais chevreuxi*, *Cingula cingillus* and *Ovatella myosotis* from Mediterranean crevices. The three species are true crevice forms, and require exposed shores with crevices containing rich deposits of sediment and organic matter. These ecological requirements are found within crevices along Atlantic coasts of Britain, Europe and North Africa, where the species are present, but not along shores that I examined within the western Mediterranean.

The distributions shown by *Campecopea hirsuta* and *Dynamene bidentata* are difficult to correlate with the abiotic factors. In view of the discrepancies between my observations and records in the literature, more detailed investigations of a greater number of suitable sites along North African coasts are necessary before any firm conclusions can be reached.

The existence of « critical limits » in intertidal distributions was demonstrated by CRISP & KNIGHT-JONES (1955), and discussed by CRISP & SOUTHWARD (1958). Two critical limits, separated by an unsuitable sandy coast, were recognised in the area of study; a) southwest Portugal, and b) the Strait of Gibraltar.

Southwest Portugal was noted to be a barrier to the majority of the Boreal species extending southwards. The coast along the Gulf of Cádiz, to the east of Portugal, is an unfavourable area of sand, and this may explain why many intertidal species are unable to reach further south. It is indicative of the unsuitability of this stretch of coast that the great majority of Boreal forms stop short of the northern arm of the Gulf of Cádiz, and all the Tropical Atlantic forms stop at or before its southern arm.

The Strait of Gibraltar forms a barrier to the spread of a number of species. The pulmonate, *Otina ovata*, reached its southern limit at the western entrance of the Strait, whilst the Tropical Atlantic species, *Littorina punctata*, *Patella safiana*, *Fossarus ambiguus* and *Leptoplana alcinoi*, reached their northern limits of distribution at the Strait of Gibraltar. This same area also formed a barrier to the westward spread of the warm water barnacle, *Chthamalus depressus*, and to the eastward spread of the Lusitanian species, *Tanais chevreuxi*, *Cingula cingillus*, and *Ovatella myosotis*. As already mentioned, there is an abrupt change in physical conditions (exposure, temperature and tidal range) in the region of the Strait of Gibraltar, and this change may well explain why a number of species meet their distributional limits in this particular area.

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RÉSUMÉ

La distribution de cinquante-neuf espèces particulières des crevasses rocheuses intertidales a été étudiée dans le Sud-Ouest de l'Europe et le Nord-Ouest de l'Afrique. Vingt-cinq stations ont été examinées le long des côtes atlantiques et méditerranéennes du Portugal, de l'Espagne, de Gibraltar et du Maroc pendant les derniers mois de l'année 1963.

Un grand nombre d'espèces sont largement distribuées, et ont été rencontrées dans la majorité ou dans toutes les stations prospectées: les Némertes *Emplectonema gracile* et *Eunemertes peronea*; les formes juvéniles des Décapodes *Eriphia spinifrons* et *Pachygrapsus marmoratus*; le Gastropode *Littorina neritoides*; les Bivalves *Lasaea rubra* et *Hiatella arctica*; l'Acarien *Halotydeus hydrodromus*; et le Chilopode *Hydroschendyla submarina*.

Vingt-huit espèces ont été étudiées plus en détail, et six types bien distincts de distribution géographique ont pu être mis en évidence. Ces types de distribution caractérisés par leurs contingents faunistiques, sont les suivants:

- I. Lusitano-méditerranéen
Campecopea hirsuta, *Dynamene bidentata*.
- II. Boréal
Otina ovata, *Nucella lapillus*, *Jaera albifrons*, *Littorina saxatilis*, *Lineus longissimus*, *Cirratulus cirratus*, *Littorina littorea*, *Aëpopsis robinii*.
- III. Lusitanien
Tanais chevreuxi, *Cingula cingillus*, *Ovatella myosotis*.
- IV. Tropical-atlantique
Littorina punctata, *Patella safiana*, *Fossarus ambiguus*, *Leptoplana alcinoi*.

V. Atlantico-méditerranéen

Eunemertes peronea, *Eriphia spinifrons*, *Pachygrapsus marmoratus*, *Acmaea unicolor*, *Siphonaria algesirae*, *Arca pulchella*, *Cardita calyculata*, *Chama gryphoides*, *Mytilus minimus*, *Ligia italica*.

VI. Méditerranéen

Chthamalus depressus.

Les rapports entre les diverses distributions et les facteurs abiotiques ont montré que la température est probablement le facteur le plus important limitant la distribution des formes boréales, tropicales atlantiques et atlantico-méditerranéennes. Les espèces des groupes lusitanien et méditerranéen ont leur répartition limitée par rapport aux conditions régnant à l'intérieur et à l'extérieur du bassin méditerranéen.

Deux limites critiques, séparées par une côte sableuse impropre à l'installation des espèces des crevasses, ont été observées dans la région étudiée :

- a) Le Sud-Ouest du Portugal, et
- b) Le Déroit de Gibraltar.

SUMMARY

The distribution of fifty-nine selected intertidal crevice species in southwest Europe and northwest Africa has been investigated. Twenty-five stations were examined along Atlantic and Mediterranean coasts of Portugal, Spain, Gibraltar and Morocco, during the latter months of 1963.

A number of species were widely distributed, and were present at all or the majority of the stations visited, namely : the nermer-teans, *Emplectonema gracile* and *Eunemertes peronea*; juvenile forms of the decapods, *Eriphia spinifrons* and *Pachygrapsus marmoratus*; the gastropod, *Littorina neritoides*; the lamellibranchs, *Lasaea rubra* and *Hiatella arctica*; the mite, *Halotydeus hydrodromus*; and the chilopod, *Hydroschendyla submarina*.

Twenty-eight species were examined in detail, and six distinct patterns of distribution were recognised. The patterns, and their respective species, are as follows :

I. Lusitanian-Mediterranean

Campeopea hirsuta, *Dynamene bidentata*.

- II. Boreal
Otina ovata, *Nucella lapillus*, *Jaera albifrons*, *Littorina saxatilis*, *Lineus longissimus*, *Cirratulus cirratus*, *Littorina littorea*, *Aëpopsis robinii*.
- III. Lusitanian
Tanais chevreuxi, *Cingula cingillus*, *Ovatella myosotis*.
- IV. Tropical Atlantic
Littorina punctata, *Patella safiana*, *Fossarus ambiguus*, *Leptoplana alcinoi*.
- V. Atlanto-Mediterranean
Eunemertes peronea, *Eriphia spinifrons*, *Pachygrapsus marmoratus*, *Acmaea unicolor*, *Siphonaria algesirae*, *Arca pulchella*, *Cardita calyculata*, *Chama gryphoides*, *Mytilus minimus*, *Ligia italica*.
- VI. Mediterranean
Chthamalus depressus.

A correlation of the distributions and the abiotic factors showed that temperature is probably the most important factor limiting the distribution of Boreal, Tropical Atlantic, and Atlanto-Mediterranean forms. Species of the Mediterranean and Lusitanian groups are limited in their distribution in relation to conditions inside and outside the Mediterranean basin.

Two critical limits, separated by an unsuitable sandy coast, were recognised in the area of study,

- a) southwest Portugal, and
- b) the Strait of Gibraltar.

ZUSAMMENFASSUNG

Die Verbreitung von 59 Arten aus dem intertidalen Felsspaltensystem wurde in Südwest Europa und Nordwest Afrika untersucht. 25 Stationen wurden während der letzten Monate des Jahres 1963 an den atlantischen und mediterranen Küsten Portugals, Spaniens, Gibaltars und Marokkos besucht.

Eine grosse Anzahl der untersuchten Arten zeigt eine weite Verbreitung und wurde in den meisten oder sogar in allen Stationen gefunden: die Nemertinen *Emplectonema gracile* und *Eunemertes peronea*; die Jugendformen der Dekapoden: *Eriphia spinifrons* und *Pachygrapsus marmoratus*; der Gastropode *Littorina neritoides*; die Muscheln *Lasaea rubra* und *Hiatella arctica*; der Akarier

Halotydeus hydrodromus und der Chilopode *Hydroschendyla submarina*.

28 Arten wurden gründlicher beobachtet und 6 durch ihre faunistische Zusammenstellung gut zu unterscheidende Verbreitungstypen konnten bestimmt werden :

- I. Lusitanisch-mediterran
Campeopea hirsuta, *Dynamene bidentata*.
- II. Borealisch
Otina ovata, *Nucella lapillus*, *Jaera albifrons*, *Littorina saxatilis*, *Lineus longissimus*, *Cirratulus cirratus*, *Littorina littorea*, *Aëpopsis robinii*.
- III. Lusitanisch
Tanais chevreuxi, *Cingula cingillus*, *Ovatella myosotis*.
- IV. Tropisch-atlantisch
Littorina punctata, *Patella safiana*, *Fossarus ambiguus*, *Leptoplana alcinoi*.
- V. Atlantisch-mediterran
Eunemertes peronea, *Eriphia spinifrons*, *Pachygrapsus marmoratus*, *Acmaea unicolor*, *Siphonaria algesirae*, *Arca pulchella*, *Cardita calyculata*, *Chama gryphoides*, *Mytilus minimus*, *Ligia italica*.
- VI. Mediterran
Chthamalus depressus.

Die zwischen den verschiedenen Verbreitungstypen und den abiotischen Faktoren herrschenden Verhältnisse zeigen dass die Temperatur wahrscheinlich der wichtigste Begrenzungsfaktor der borealen, tropischatlantischen und atlantisch-mediterranen Formen ist. Die Verbreitung der lusitanischen und mediterranen Formen entspricht den Verhältnissen innerhalb und ausserhalb des Mittelmeerbeckens.

In der untersuchten Gegend wurden zwei kritische durch felspaltlose Sandküsten getrennte Grenzen entdeckt :

- a) Südwest Portugal,
- b) Gibraltar Meerenge.

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