Cah. Biol. Mar. (1993), **34** : 387-399
Roscoff

Redescription and ecology of *Batillipes phreaticus* Renaud-Debyser, 1959 (Arthrotardigrada, Batillipedidae) in the gulf of Valencia (western mediterranean)

S. Villora-Moreno* and S. de Zio Grimaldi**
* Department of Animal Biology. Faculty of Biological Sciences, University of Valencia, Burjassot E-46100, Valencia (Spain)
** Istituto di Zoologia ed Anatomia Comparata dell'Università di Bari. Via Amendola, 165A. 70126 Bari (Italy).

Abstract : Three sandy beach localities along the Mediterranean coast of the Iberian Peninsula were sampled for meiofauna : two in Valencia and one in Tarragona. The samples revealed two species of marine tardigrades, *Batillipes pennaki* and *B. phreaticus,* that are new additions to the Iberian fauna. Here we provide life history and morphometric data for *B. phreaticus,* as well as a redescription of their adult morphology. An analysis of spatial distribution shows that this species is particularly abundant in the retention zone (midlittoral level) and in the shallow infralittoral level.

Résumé : Des prélèvements de méiofaune ont été réalisés à partir de plages de sable situées le long de la côte méditerranéenne de la péninsule ibérique : deux à Valence et une à Tarragone. Les échantillons révèlent deux espèces de tardigrades, *Batillipes pennaki* et *B. phreaticus :* espèces nouvelles pour la faune ibérique. *B. phreaticus* est étudiée ici et une analyse de la distribution spatiale montre que cette espèce est particulièrement abondante dans la zone de rétention (niveau mediolittoral) et au niveau de l'infralittoral.

INTRODUCTION

According to the review of Maucci and Durante (1984), the phylum Tardigrada has been scarcely studied in the Iberian Peninsula. Until recently, only two members of the order Arthrotardigrada (*Bathyechiniscus tetronyx* Steiner, 1926, and *Batillipes dicrocercus* Pollock, 1970) were known to occur in the Iberian coasts.

The present report extends our knowledge of the marine tardigrade fauna of the Iberian coasts through the addition of two new species belonging to the family Batillipedidae : *Batillipes pennaki* and *B. phreaticus*. The latter species has an additional interest, this being its first record in the Mediterranean Sea.

Information on the life history and adult morphology of *B. phreaticus* is scant, and little has been added since the original description of the species in 1959. Based on McKirdy's (1975) review of the genus *Batillipes*, we provide a redescription of *B. phreaticus* together with morphometric data. Finally, in this paper we contribute data on the spatial distribution of natural populations which add to our knowledge of the ecology of the genus *Batillipes*.

MATERIALS AND METHODS

Collections were made in April and June 1990 in two sandy beaches in the Gulf of Valencia (El Saler and Mareny de San Lorenzo) and one in Tarragona (cala Romana). Sampling stations were located in the water table (in the zone of dry sand), in the zone of retention, in the zone of resurgence, and in the zone of saturation at the infralitoral level up to a depth of 1,5 m (Fig. 1).

Quantitative samples were taken at each of seven stations with a coring device (10 cm^2 area and 30 cm long). The cores were immediately sectioned at 5 cm intervals. Samples were treated with 7,5 percent $MgCI_2$ as a narcotic agent and fixed with 5 % buffered formaldehyde. Decantation was used to separate out the meiofauna, repeating the procedure four times. Supernatant water was decanted through a sieve with 42 μm meshes and meiofauna stained with Rose Bengal. The meiofauna was observed and classified under a stereomicroscope at 40x magnification.

Sediment analysis for particle size was carried out using an electromechanical sifter. The different granulometrical classes were coded according to the Wenthworth scale (Buchanan, 1984) to assess characteristic sediment indices. Porosity was estimated using the Amoureux (1966) method.

Observations of tardigrades were made on specimens mounted in glycerin, using a coverslip with supports to prevent body deformations. Morphometric data were obtained using an interference or phase contrast microscope at a magnification of 1000x.

Descriptive statistics for the morphometric data (frequency analysis) and Pearson product-moment correlations were calculated using the SPSS/PC+ software package.

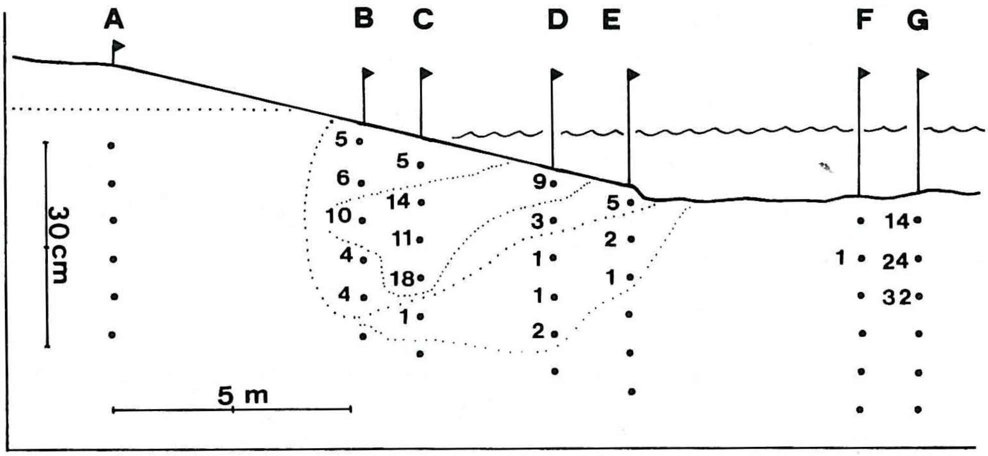

Fig. 1 : Sampling stations and abundance (specimens/50 ml) of *Batillipes phreaticus* at Mareny de San Lorenzo beach, Valencia.

RESULTS

Two species of tardigrades belonging to the family Batillipedidae were identified : *Batillipes pennaki* Marcus, 1946 and *Batillipes phreaticus* Renaud-Debyser, 1959. The first species was only observed in Tarragona and its morphological features agree with Marcus' original description and with the subsequent revision of McKirdy (1975).

Batillipes phreaticus Renaud-Debyser, 1959

Renaud-Debyser, 1959.
Renaud-Debyser and Salvat, 1963.
Riemann, 1966.
Pollock, 1971.
Morgan and King, 1976.

Material examined

A total of 217 specimens were identified. Biometric data were obtained from 36 specimens, including 8 larvae-I, 6 larvae-II, 7 preadults, and 15 adults (6 males, 9 females). Developmental stages were established according to Grimaldi de Zio and D'Addabbo Gallo (1975).

Description (Figs. 2 and 3)

General body shape

The body of adult and preadult specimens is wider posteriorly than anteriorly. In larvae-I and larvae-II, the anterior-posterior variation in body width is less noticeable. In specimens observed without pressure from the coverslip, body lobes are clearly visible.

There is a pair of conspicuous lateral auricles between the posterior end of the head and the first pair of legs. Between the 3rd and 4th pair of legs there is the 3rd laterodorsal projection, which changes its size as the tardigrade grows. The 3rd lateral projection is ventrolaterally directed and round in larvae-I, larger and pointed in larvae-II and well developed in immature (preadults) and mature adults (adults). Body lobes and lateral projections are always dorsal. In uncompressed specimens, a reduced conical ventrolaterally directed projection can be observed between the 2nd and 3rd pair of legs.

Cephalic appendages and head

The rostral edge between external cirri (e.c.) and lateral cirri (l.c.) is flat. There are two small tubercles between the internal and external cirri. In accordance with the description of Pollock (1971), the tubercles are larger in adults than in larvae. Following Pollock's (1989) diagnosis of genus *Batillipes*, the cephalic tubercles or papillae are identified as secondary clavae.

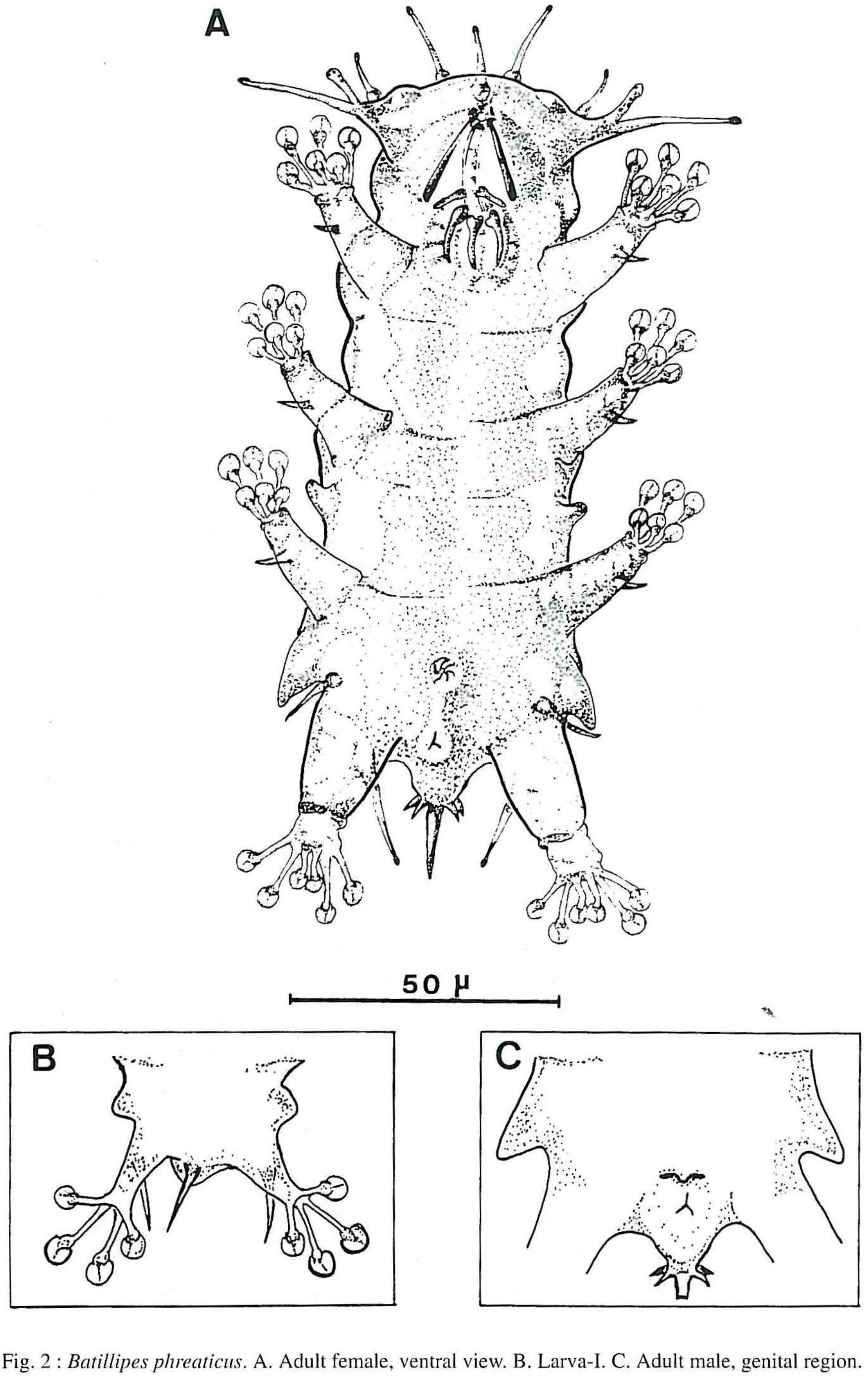

Fig. 2 : *Batillipes phreaticus*. A. Adult female, ventral view. B. Larva-I. C. Adult male, genital region.

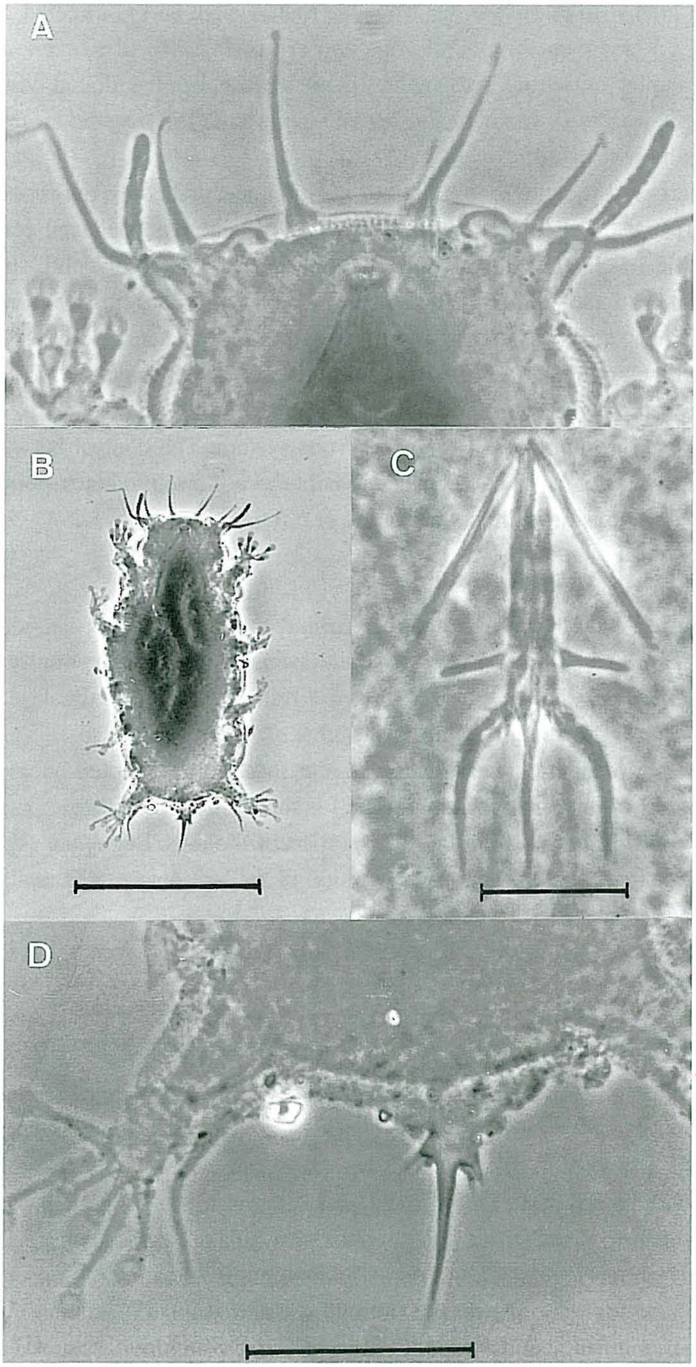

Fig. 3 : *Batillipes phreaticus*. A. Cephalic appendages and head. B. General view. C. Buccal apparatus. D. Caudal apparatus. Bar in A and D 50 μm, in B 100 μm, in C 10 μm.

The median cirrus (m.c.) inserts far from the rostral edge and is directed upwards. The internal cirri (i.c.) insert on the rostral edge and are oriented forwards. The external cirri (e.c.) have a medial curvature that makes them visible from a dorsal view. However, McKirdy (1975) suggested that cephalic appendage orientation may be an unreliable character due to its high variability.

The e.c. insert near the clava, in a ventral position and preceding the mouth. The clava and lateral cirrus A (c.A) insert together on the same enlarged pedestal (cirrophore) on either side of the head. The clava inserts below c.A ; it is roughly club-shaped, with a conspicuous van der Land's body inside its base. According to our observations the clava is less undulating than suggested in the original description of Renaud-Debyser (1959). Using phase contrast, black punctuations are evident on the surface of the clava. The c.A is directed sideways over the clava.

All cephalic cirri are innervated by the nervous system. The contact between the nerve endings and the inner cavity of each cirrus is visible as a refractive black point. This structure is more conspicuous in the m.c. than in i.c. or c.A.

Spines and other appendages

The lateral cirrus E (c.E) inserts dorsally behind the 3rd lateral projection. The c.E is more prominent in larvae-I and II than in adults, because it is proportionally larger in the former specimens. In adults, the c.E is absent or difficult to see, as is the case in other species such as *Batillipes adriaticus* Grimaldi de Zio *et al.*, 1979.

On the proximal portion of each leg, there is a short spine directed backwards. Of the spines on the anterior three pairs of legs, spine I is the shortest ; the three spines have similar morphology and are inserted on the tibial portion of the legs. Leg spine IV is strong and long, it has a wide insertion on the femoral portion of the leg. A van der Land's body is evident near the basal zone of leg spine IV.

In the larvae, as in the adults, all cephalic cirri, c.E and leg spines IV have enlarged spear-shaped tips.

Caudal apparatus

The caudal spine is strong and directed upwards. The morphology of the caudal apparatus changes throughout the tardigrade life history. Larvae-I have the caudal spine directly inserted on the caudal end. In the larvae-II, the caudal spine and two small lateral spines are inserted on a wide conical base. This conical base is larger in adults, with two pairs of small lateral spines attaching to the strong caudal spine. One pair of lateral spines is long and ventrally directed, the other is smaller and dorsally directed. It is difficult to observe the lateral spines because adhering debris is usually present in the caudal body surface.

The morphology of the caudal apparatus as well as the number of lateral spines, show little variation within each developmental stage. In this study we found a single adult specimen lacking the caudal appendage.

TABLE I

Measurements (in μm) of adults and larvae.

	LARVAE		IMMATURE	MATURE	
	1st. STAGE x σ (n) min - max	2nd. STAGE x̄ σ (n) min - max	x̄ σ (n) min - max	MALES x̄ σ (n) min - max	FEMALES x̄ σ (n) min - max
L	78.5 6.0 (8) 72-84	101.8 11.5 (6) 80-112	124.3 8.0 (7) 110-130	139.7 13.1 (6) 120-150	135.4 12.8 (9) 120-150
m.c.	13.3 0.5 (4) 13-14	15.4 1.3 (5) 14-17	- - -	14.8 1.0 (4) 14-16	15.8 3.1 (5) 13-20
i.c.	13.16 2.3 (6) 11-16	16.0 0.7 (5) 15-17	19.5 0.7 (2) 19-20	20.5 1.3 (4) 19-22	19.0 0.8 (7) 18-20
ve.c.	12.4 1.8 (5) 10-15	13.8 1.1 (5) 12-15	13.5 0.7 (2) 13-14	12.8 2.8 (4) 11-16	13.5 1.4 (8) 12-16
cl.	10.0 1.4 (5) 8-12	11.0 1.0 (5) 10-12	11.0 - (1)	12.8 2.1 (4) - 10-15	12.4 1.1 (8) 11-14
c.A	21.5 1.6 (6) 19-23	23.0 1.2 (5) 22-25	23.0 - (1) -	25.8 2.6 (4) 22-28	25.3 2.5 (7) 22-29
c.E	13.0 - (1) -	15.3 1.7 (4) 13-17	- - -	18.0 - (1) -	12.0 - (1) -
p4	9.8 1.3 (4) 8-11	13.4 1.3 (5) 12-15	20.0 1.4 (2) 19-19	19.5 1.3 (4) 18-21	19.6 1.5 (5) 18-22
c.s.	12.7 1.4 (6) 13-14	13.8 2.5 (4) 10-15	18.7 0.6 (3) 18-19	18.0 1.4 (4) 16-19	18.0 1.8 (6) 16-21

Abbreviations
L. total length ; m.c. medial cirrus ; i.c. internal cirri ; e.c. external cirri A ; cl. clavae ; c.A cirris ; c.E cirri E ; p4 leg spine IV ; c.s. caudal spine

Morphometry

The study of morphometric data confirms the ontogenic variation in all cephalic appendages, in the caudal spine and in leg spine IV. Table II shows the correlations between body length and selected appendages. The correlation values are high, with $r > 0.6$ ($P < 0.001$, 1-tailed test).

Toe lengths and toe disc morphology

Feet I through IV possess toes of varying lengths (long, intermediate, short). On feet I, II and III, the two long digits are completely dorsal. The three intermediate length toes are only slightly dorsal and their insertions alternate with those of the two long toes. The intermediate length toe between the two long digits is the more ventral toe. Finally, the short digit is completely ventral.

On feet IV, length and arrangement of toes are symmetrical. The two long digits are dorsal and the two short digits are ventrally inserted between them. Two intermediate length digits insert beside the long digits.

In larvae-I, there are only four digits on each feet. The short toe and the ventral intermediate length toe are missing from feet I, II and III. On feet IV, the two short digits are missing.

Toe discs are large (3-4 μm) and circular. Morphology varies according to toe disc position, therefore our descriptions refer to toe discs observed under coverslip pressure.

Cuticle punctuation pattern

The punctuations of the external cuticle are spaced and prominent on the dorsal surface. The cuticle around the m.c. and c.E is devoid of punctuations. On the ventral surface, punctuations are small and closely spaced. Gonopore field, anal field and surface between legs are devoid of punctuations.

Buccal apparatus

The overall appearance of the buccal apparatus is, according to McKirdy's (1975) classification, delicate and symmetrical. The stilets lack enlarged basal tips, and are located dorsal and lateral to the mouth tube. The stylets' supports are straight with proximal end furca-like. Furcae equal. Mouth tube straight.

Placoids slender with furcate tips. The pharyngeal bulb is spheric (12 μm in larvae and 19-22 μm in adults), located between the first pair of legs.

Male and female gonoporal field

Female gonoporal apparatus consists of a gonopore surrounded by six identical plates (rosette morphology). The distance between female gonopore and anus is 12-13 μm.

Male gonoporal-anal field consists of a slight elevation over the gonopore and the trefoil anal opening.

DISCUSSION

Morphology

Gross morphological features suggest that our specimens of *Batillipes* belong to the group formed by *B. phreaticus, B. carnonensis* Fize, 1957 an *B. littoralis* Renaud-Debyser, 1959.

The close relationship between *Batillipes phreaticus* and *B. carnonensis* was already established by Fize (1963), who after further review of *B. carnonensis* concluded that the sole difference between the two species pertains to the morphology of the clava. In *B. carnonensis* the clava is similar to that in *B. similis*, whereas in *B. phreaticus* the clava is curved outwards and with black punctuations on its surface (Renaud-Debyser, 1959). Pollock (1971) comments that his specimens of *B. phreaticus* have clava that are identical to those in the original description of Renaud-Debyser. However, Pollock misinterprets the reference about *B. pennaki* Marcus, 1946. Renaud-Debyser (1959, p. 139) writes "Les clavas sont aussi caractéristiques de cette espèce que le sont celles de *B. pennaki*", indicating that the clavae are very different, whereas Pollock interprets instead that the clavae are very much alike.

In our specimens, the clava is similar to that originally described by Renaud-Debyser, but we can not consider this feature as conclusive from a taxonomic point of view because we have observed considerable variability within our populations.

According to McGinty and Higgins (1968), the mounting media (glycerin or Hoyer) can destroy characters or introduce externally imposed alterations. Appendage orientation, on the other hand, may be unreliable since the appendages are flexible, particularly the clava, and their morphology is variable.

We have relied heavily on the morphology of the caudal apparatus to distinguish our specimens of *Batillipes phreaticus* from *B. carnonensis*. Fize (1963) describes a pair of small lateral bristles in *B. carnonensis* but our specimens have two pairs of spines. On the other hand, *Batillipes carnonensis* has a strong and very long spine on the fourth pair of legs "exceeding the toe end" (Fize, 1957 ; p. 432), whereas leg spine IV in *Batillipes phreaticus* never exceeds the toe end.

Although cephalic papillae (secondary clavae) are more evident in juvenile than in adult *Batillipes phreaticus*, Fize does not consider this character in the original description or in the subsequent correction of *Batillipes carnonensis* (Fize, 1963).

In Renaud-Debyser's original illustrations, the head is more massive in *Batillipes phreaticus* than in *B. carnonensis*. However, using light microscopy, we have observed that this character varies according to the plane of observation. Body size is larger in *B. carnonensis* than in *B. phreaticus* (180 µm). A remarkable feature of our Mediterranean specimens is their small size, which in the mature adults is only 135-140 µm.

In 1970, D'Hondt described a new subspecies, *Batillipes littoralis submersus*, based on the morphology of the caudal apparatus. D'Hondt's description did not include details which may be of taxonomic importance, such as the presence or not of the gonopore, the insertion of e.c. (on independent cirrophori in *B. littoralis*), and the presence of a spur on the fourth pair of legs (this character was missing in D'Hondt's illustration). The present data lead us to consider the subspecies *Batillipes littoralis submersus* as a larvae-II of *Batillipes phreaticus*, since before the present work these larvae were unknown.

Ontogenetic variation of some taxonomic characters was already reported in *Batillipes mirus* Richters, 1909 and *B. bullacaudatus* (McGinty & Higgins, 1968). In the present work, we consider that the ratio "appendage sizes/body size" is unreliable from a taxonomic point of view because body growth is independent from the growth of the appendages. Upon careful scrutiny of our morphometric data, we note the rapid growth of some appendages (i.c., leg spine IV and caudal spine) compared to others such as m.c., e.c., c.A, and clava which have about the same length in larvae as well as in adults (Tab. I).

A correspondence can be established between McGinty and Higgins' (1968) size classes, and the age classes of Grimaldi de Zio and D'Addabbo Gallo (1975). Size classes I and II are larvae-I, size class III is the larva-II, and size classes IV and V are preadults and adults.

The lateral projections are missing in the adults of *Batillipes mirus* (McGinty & Higgins, 1968). In *Batillipes phreaticus* we have observed variation in the morphology of the lateral projections between the 3rd and the 4th pair of legs. In larvae-I they are round, in larvae-II they are pointed, and they are well developed in preadults or adults.

Our data suggest that the morphology of the caudal appendage and the number of its lateral spines are also ontogenetically variable characters.

In the genus *Batillipes*, length and arrangement of the toes are variable. The angle between the leg and the plane of the toe disc is related to the length and the arrangement of digits. In toe descriptions it is important to take as a reference the long digits, which are always dorsal. The length of the remaining digits varies according to their position relative to that of the long digits. In order to reach the surface of sand grains with the toe discs, short and intermediate length digits must be lateral or ventral to the long digits.

The general arrangement of toes is similar in the first, second and third pair of legs because their position in relationship to the body axis is identical. The fourth pair of legs, which is used only in backwards movements, has a different orientation in order to enable adhesion of the toe discs to the surface of sand grains, this resulting in a different arrangement of the digits.

Ecology

Batillipes phreaticus was observed by Renaud-Debyser (1959) in dunar, well rounded sand with a mean grain size of 250 µm, without fine sediment fraction and a porosity of 35 %. Temperature was between 15 and 27 °C and salinity between 31 and 34 ‰.

Our specimens were observed in subangular sand, with a mean grain size of 235-365 µm. Porosity between 33 and 43 %. Salinity between 34-38 ‰. Next to the sampling zone, there is discharge of continental fresh water from a littoral lagoon (La Albufera de Valencia).

This species is absent from the phreatic zone (water table) at the dry sand zone (A). Density of *Batillipes phreaticus* is high at the retention zone (B-C), decreasing at the resur-

TABLE II A

Pearson product-moment correlations. Minimum pairwise N of cases : 7. One-tailed. Signification : * 0.001.

	L
p4	0.93*
i.c.	0.91*
c.A	0.81*
c.s.	0.82*
cl.	0.68*
m.c.	0.44
c.E	0.29
e.c.	0.11

TABLE II B

Descriptive statistics for the morphometric data used in Pearson correlations.

Variable	Cases	Mean	Std Dev
L	37	115.4324	26.2335
m.c.	18	14.8889	1.9670
i.c.	24	17.2083	3.0925
e.c.	24	13.2083	1.6413
cl.	23	11.5652	1.6188
c.A	24	23.7500	2.5065
c.E	7	14.8571	2.2678
p4	20	16.1000	4.3758
c.s.	23	15.9565	3.0072

gence zone (D) and at the mesolittoral berma (E) where hydrodynamism is more elevated. The species reaches its higher density at the infralittoral zone (F-G) with remarkable density differences between nearest points. This feature denotes the pathchy distribution pattern of the species.

In Arcachon (Renaud-Debyser, 1959), the distribution of *B. phreaticus* is limited to the resurgence zone, the species being absent from the infralittoral zone.

As far as its vertical distribution, the species was only observed up to a depth of 25 cm into the sediment, at the middlittoral level. In the infralittoral zone, it only reaches a depth of 15 cm, probably because of the low oxygen concentration.

In agreement with other reports (McGinty & Higgins, 1968), we have not found any relationship between sediment granulometry and abundance of *Batillipes phreaticus*. Water saturation and oxygen concentration seem to correlate better with the abundance and distribution of the species.

The population composition in age stages varies throughout the year. In spring the highest percentage corresponds to the larvae-II, followed by larvae-I, and, finally, adults. In summer, nearly all the specimens were adults (males and females) or preadults, followed by larvae-II and some larvae-I. These differences between spring and summer, agree with other reports that suggest that the species is particularly abundant in the spring (De Zio & Grimaldi, 1966 ; McGinty & Higgins, 1968).

Geographical distribution

British Isles and the Northwest of Europa : Bassin d'Arcachon and La Manche Channel in France (Renaud-Debyser, 1959, Renaud-Debyser & Salvat, 1963) ; Elbe Estuary in Germany (Riemann, 1966) ; Yorkshire in England (Pollock, 1971). This work is the first record of the species in the Mediterranean Sea (Grimaldi de Zio *et al.*, 1983).

TABLE III

Sediment indices from sampling stations (A to G).

	A	B	C	D	E	F	G
Md	285	350	365	235	280	260	245
QD (Φ)	0.28	0.22	0.24	0.29	0.34	0.35	0.32
IGSD	0.39	0.33	0.38	0.41	0.48	0.47	0.43
SKI	- 0.04	0.12	0.01	0.01	- 0.30	0.03	0.03
KG	0.89	1.03	1.14	0.91	0.94	0.88	0.85
HF	0.60	0.80	0.89	0.61	0.60	0.54	0.52

Abbreviations
Md Mean grain size
QD Quartile deviation
IGSD Inclusive Graphic Standard Deviation
SKI Inclusive Graphic Skewness
KG Graphic Kurtosis
HF Hydrodynamic Factor

ACKNOWLEDGMENTS

We are grateful to Dr. E. Font for critically reading the manuscript. SVM was supported through an F.P.I. fellowship from the Spanish Ministry of Science and Education.

REFERENCES

AMOUREUX, L., 1966. Étude bionomique et écologique de quelques annélides Polychètes des sables intertidaux de côtes Ouest de la France. *Arch. Zool. Exp. Gen.*, 107 : 1-218.

BUCHANAN, J.B., 1984. Sediment analysis. In N. A. Holme & A. D. McIntyre (Eds.). *Methods for the study of marine benthos*. Blackwell Scientific Publications, Oxford. 1 : 41-65.

D'HONDT, J.L., 1970. Inventaire de la faune marine de Roscoff. *Ed. Station Biol. Roscoff*, 30 pp.

DE ZIO S., & P. GRIMALDI, 1966. Ecological aspects of Tardigrada distribution in South Adriatic beaches. *Veröff. Inst. Meeresf. Bremerh.*, 2 : 87-94.

FIZE, A., 1957. Description d'une espèce nouvelle de tardigrade *Batillipes carnonensis* n. sp. *Bull. Soc. Zool. France*, 82 (5-6) : 430-433.

FIZE, A., 1963. Contribution à l'étude de la microfaune des sables littoraux du Golfe d'Aigues Mortes. *Vie et Milieu*, 14 : 669-774.

GRIMALDI DE ZIO, S., & M. D'ADDABBO GALLO, 1975. Sviluppo postembrionale e mute in *Batillipes pennaki* Marcus (Heterotardigrada). *Riv. Biol.*, 68 (3) : 244-275.

GRIMALDI DE ZIO, S., M. MORONE DE LUCIA & M. D'ADDABO GALLO, 1983. Marine tardigrades ecology. *Oebalia*, 9 : 15-31.

GRIMALDI DE ZIO, S., M. MORONE DE LUCIA, M. D'ADDABBO GALLO & P. GRIMALDI, 1979. Observazioni su alcuni tardigradi di una spiaggia pugliese e descripzione di *Batillipes adriaticus* sp. nov. (Heterotardigrada). *Thalassia Salentina*, 9 : 39-50.

MARCUS, E., 1946. *Batillipes pennaki*, a new marine Tardigrade from the north and south American Atlantic coast. *Comm. Zool. Mus. Hist. Nat. Montevideo*, 2 : 1-3.

MAUCCI, W. & M.V. DURANTE, 1984. Il Tardigradi di la peninsola iberica. *Misc. Zool.*, 8 : 67-80.

McGINTY M.M. & R.P. HIGGINS, 1968. Ontogenetic variation of taxonomic characters of two marine tardigrades with the description of *Batillipes bullocaudatus* n. sp. *Trans. Amer. Microc. Soc.*, 87 (2) : 252-262.

McKIRDY, D.J., 1975. *Batillipes* (Heterotardigrada) : comparison of six species from Florida (USA) and a discussion of taxonomic characters within the genus. *Mem. Ist. Ital. Idrobiol.*, 32 : 177-223.

MORGAN & KING, 1976. Synopis of the British Fauna (New Series). British Tardigrada. Linnean Soc., London.

POLLOCK, L.W., 1970. *Batillipes dicrocercus* n. sp., *Stygarctus granulatus* n. sp., and other Tardigrada from Woods Hole, Massachussets USA. *Trans. Amer. Microsc. Soc.*, 89 : 38-52.

POLLOCK, L.W., 1971. On some british marine tardigrada, including two new species of *Batillipes*. *J. mar. biol. Ass. U.K.*, 51 : 93-103.

POLLOCK, L.W., 1989. Marine interstitial Heterotardigrada from the Pacific coast of the United States, including a description of *Batillipes tridentatus* n. sp. *Trans. Amer. Microsc.* Soc., 108 (2) : 169-189.

RENAUD-DEBYSER, J., 1959. Sur quelques tardigrades du bassin d'Arcachon. *Vie et Milieu*,10 : 135-146.

RENAUD-DEBYSER, J. & B. SALVAT, 1963. Éléments de prospérité des biotopes des sédiments meubles interdidaux et écologie de leurs populations en microfaune et macrofaune. *Vie et Milieu*, 14 (3) : 463-550.

RICHTERS, F., 1909. Tardigraden. Studien. B*er. Senck. Natur. Ges. Frankfurt a. M.*, 1909 : 28-45.

RIEMANN, F., 1966. Die interstitielle Faune in Elbe-Aestuar. Verbreitung und Systematik. *Arch. Hydrobiol.*, Suppl. 31 : 1-279.