

Ecology and distribution of the Diurodrilidae (Polychaeta), with redescription of *Diurodrilus benazzii*

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Abstract: The ecology and distribution of *Diurodrilus* species have been studied after a bibliographic review. The species of this genus are often restricted to the upper moist sand substratum (medium water level, *D. subterraneus*, *D. ankei*, and *D. benazzii*), or to the lower midlittoral and upper sublittoral (*D. minimus*, and *D. dohrni*). In natural environments a single species occurs at each horizontal level. The distribution pattern between upper and lower levels may be controlled by physical factors. Interspecific competition between congeneric species of *Diurodrilus* may be considered as a possible cause controlling populations within each horizontal sandy beach level. It is possible to identify morphological differences between species inhabiting each horizontal level of a sandy beach. In the lower level, always scoured by the waves, *Diurodrilus minimus* and *D. dohrni* have well developed toes, reacting with adhesion to increased water currents, while in the more stable upper level, *D. benazzii* and *D. subterraneus* display reduced adhesive toes, both in size and number. *Diurodrilus benazzii* was collected from the midlittoral phreatic system in a sandy beach at the Gulf of Valencia (W. Mediterranean). Since no information is available on taxonomical characters of *D. benazzii*, e.g., the sensorial pattern, ciliophores, or ventral ciliation, this paper provides a redescription of the species, comparing the taxonomically relevant characters of all known *Diurodrilus* species.

Résumé : L'écologie et la distribution des espèces de *Diurodrilus* ont été étudiées après une revue des données bibliographiques. Les espèces de ce genre sont souvent limitées au substrat sableux humides des niveaux supérieurs (méditerranéen moyen, *D. subterraneus*, *D. ankei*, and *D. benazzii*), ou au niveau du méditerranéen inférieur et du sublittoral supérieur (*D. minimus* et *D. dohrni*). Dans la nature, une seule espèce habite chaque niveau horizontal et le schéma de distribution entre les niveaux supérieurs et inférieurs est contrôlé par des facteurs physiques. Une compétition interspécifique au sein du genre *Diurodrilus* peut-être considérée comme une cause possible contrôlant les populations dans chaque niveau horizontal d'une plage sableuse. Il est possible d'identifier des différences morphologiques entre les espèces habitant chaque niveau horizontal. Au niveau inférieur, toujours agité par les vagues, *Diurodrilus minimus* et *D. dohrni* ont des orteils bien développés permettant l'adhésion dans le milieu agité, tandis que dans les niveaux supérieurs plus stables, *D. benazzii* et *D. subterraneus*, ont des orteils réduits à la fois en taille et en nombre. *Diurodrilus benazzii* a été récolté dans le système phréatique méditerranéen d'une plage sableuse du golfe de Valence (Méditerranée Occidentale). Étant donné qu'il n'y avait pas jusqu'ici de données sur les caractères taxonomiques importants tels que la disposition des organes sensoriels, des ciliophores, de la ciliation ventrale, une redescription de cette espèce est donnée, permettant une comparaison des caractères taxonomiques essentiels de toutes les espèces actuellement connues du genre *Diurodrilus*.

Keywords: interstitial Polychaeta, Diurodrilidae, distribution, ecology, redescription, Mediterranean.

Introduction

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The genus *Diurodrilus* Remane was separated from the family Dinophilidae by Kristensen and Niilonen (1982).

According to ultrastructural details such as cuticle, pharynx and sperm, these authors created the new family Diurodrilidae. Although, body plan, and specially cuticle structure (synapomorphy), place the Diurodrilidae among the polychaetes (Kristensen and Niilonen, 1982), relationships with a particular polychaete family are difficult to establish. This is not the case for other Dinophilidae (mainly *Dinophilus* and *Trilobodrilus*) which recently have added new evidences as a monophyletic subgroup within the Dorvilleidae (Eibye-Jacobsen and Kristensen, 1994).

Taxonomical differences between the six species of *Diurodrilus* were mainly based on caudal structure. Until the description of *Diurodrilus ankei* Ax, 1967, taxonomical characters as sense organs and ciliophores, were not considered. In the redescription of *D. subterraneus* Remane, 1934, Mock (1981) shows many new data which were missing in the Remane's original description. The last discovered species, *D. westheidei* Kristensen and Niilonen, 1982 is given with an extensive description, that should serve as a model to describe new species and to complete old descriptions for *D. minimus* Remane, 1925, *D. benazzii* Gerlach, 1952 and *D. dohrni* Gerlach, 1953.

In a previous paper faunistic composition of interstitial polychaetes and other meiofauna were used to discriminate between sandy beaches with and without macrophytic cover (Villora-Moreno *et al.*, 1991). During new surveys of sandy beaches meiofauna in the Gulf of Valencia (Spain), *Diurodrilus benazzii* was identified inhabiting the phreatic system. The first part of this paper deals with the redescription of *D. benazzii*. The analysis of the results obtained indicates that the pattern of sense organs and the ciliated areas, for the genus *Diurodrilus*, may be more conservative than originally expected.

The last described species of the genus *Diurodrilus* was found in the Arctic circle. As many other interstitial taxa this genus shows a world wide geographical distribution. Moreover, each *Diurodrilus* species has its definite spatial pattern, which is similar from beach to beach. The second part of this paper will present a bibliographic review of the *Diurodrilus* ecology, considering some physical and biological factors controlling the horizontal distribution of *Diurodrilus* species.

Materials and methods

Samples were collected (29 May 1991) from the water table at the high water mark of the beach (El Saler, Valencia), using the Karaman-Chappuis sampling technique: the fauna is concentrated by filtration (42 µm mesh net) from the water that seeps into the bottom of a pit dug in the sand. The sediment consisted of moderately well sorted medium siliceous sand.

Most of the animals were observed alive in squash preparations using phase-contrast and interference (Nomarski technique) microscopy. A sample of 1 l was kept at room temperature. Relaxation with isotonic MgCl₂ was used before and during microscopical observations, then animals were fixed with neutralized 5% formaldehyde, mounted in glycerin and slides were sealed. Specimens were illustrated with the aid of a camera lucida (Olympus interference microscope).

Results and discussion

Diurodrilus benazzii Gerlach, 1952

(Figures 1, 2G-I, Table I)

Diurodrilus benazzii Gerlach, 1952, p. 186, fig. 1-3; Gerlach, 1955, p. 61; Delamare-Deboutteville, 1953, p. 747; Rao and Ganapati, 1968b, p. 28; Ax, 1969, p. 76; Rao, 1969, p. 97; Westheide, 1972a, p. 460, fig. 2b.

Diurodrilus Benazzii: Delamare-Deboutteville, 1960, p. 476; Fize, 1957, p. 379.

Diurodrilus benazzi: Jouin, 1971, p.54; Kristensen & Niilonen, 1982.

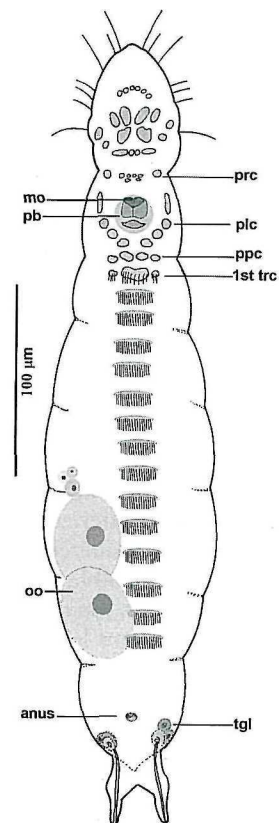


Figure 1. Semidiagrammatic representation of *Diurodrilus benazzii* (ventral view).

Figure 1. Représentation semi-schématique de *Diurodrilus benazzii* (vue ventrale).

Table 1. Comparative table of main morphological and ecological characters of *Diurodrilus* species. Abbreviations for Distribution: AN, North Atlantic. ANE, Northeast Atlantic. ANW, Northwest Atlantic. INE, East Indopacific. ISW, Southwest Indopacific. MED, Mediterranean.

Tableau 1. Comparaison des principaux caractères morphologiques et écologiques des espèces de *Diurodrilus*. Abréviations pour la distribution : AN : Atlantique Nord. ANE, Atlantique Nord-Est. ANW, Atlantique Nord-Ouest. INE, Indopacifique Est. ISW, Indopacifique Sud-Ouest. MED, Méditerranée.

	<i>minimus</i>	<i>subterraneus</i>	<i>benazzii</i>	<i>dohrni</i>	<i>ankeli</i>	<i>westheidei</i>
Length ((m)	250-450	350-440	250-425	320	400-500	325-423
Prostomium						
constriction ciliated	?	-	-	?	-	+
cuticular plates	-	+	-	-	+	-
stiff sensory cilia	+	+, long	+	+	+	+
sensorial pattern known	-	+(?)	+	-	+(?)	+
prostomial ciliated areas known	-	+(?)	+	+(?)	+	+
Trunk						
segments well marked	-	-	+	+	+	-
stiff sensory cilia	+, long	+, long	-	-	+	+
ciliophores / segment	?	5	3	?	3	3
triangular ciliary fields	?	-	-	?	-(?)	+
Pygidium						
anal cone	small	-	-	-	-	+large
number of toes	4	4	2	4	4	4
toes equal sized	+	-	+	-	-	-
length of toes (μm)	10-12	7, 19	20	5, 15	6, 21	12, 33
stiff sensory cilia	+, long	+, long	-	-(?)	+	+
Maturity						
females	IV(Sylt)	summer	summer	spring	summer	winter
vitellogenic oocytes (n°)	2	2	2	1	1-2(?)	2
males		summer	summer	spring	summer	unknown
Habitat						
sediment	fine-coarse /shell	medium /quartz		medium-coarse /shell	coarse /rocky	coarse
Tidal beaches	LW	LW, MW		LW	MW(?)	-
Tideless beaches		damp sand	MW	MW, LW	-	-
Sublittoral	+	-	-	- 15 m	-	- 2 - 3m
Distribution	ANE, MED	AN, MED	ISW, MED	ANE, MED	INE	ANW

Type Locality: San Rossore, Pisa (Tyrrhenian Sea)

Material examined: 20 animals (males and females) from a sample with more than 100 specimens, collected in El Saler beach (Valencia, Spain). Specimens are deposited in the Marine Invertebrates collection of the Laboratorio de Biología Marina, Facultad de Biología de Valencia, Spain.

External morphology

Adult length of *Diurodrilus benazzii* range from 250-300 μm (Gerlach, 1952) to 400-425 μm (Fig. 1). Segmentation pattern is similar to other species of the genus *Diurodrilus*. Body comprising a prostomium fused with

buccal region (peristomium), five trunk segments (well marked), and a pygidium. Prostomium and peristomium appear separated by an evident constriction, not ciliated. Mouth opening is oval, located ventrally on the peristomium. Pharyngeal apparatus consists of a muscular pharynx bulb. Intestine ciliated all through the alimentary tract. Trunk width increases from the first to the fourth segment, decreasing towards the caudal region. The fusiform appearance is more noticeable in mature females carrying large eggs in the fourth and fifth segments (Fig. 1). Pygidium with one pair of toe-like lateral appendages (20 μm long, proximally 14 μm broad, distally 6.2 μm)

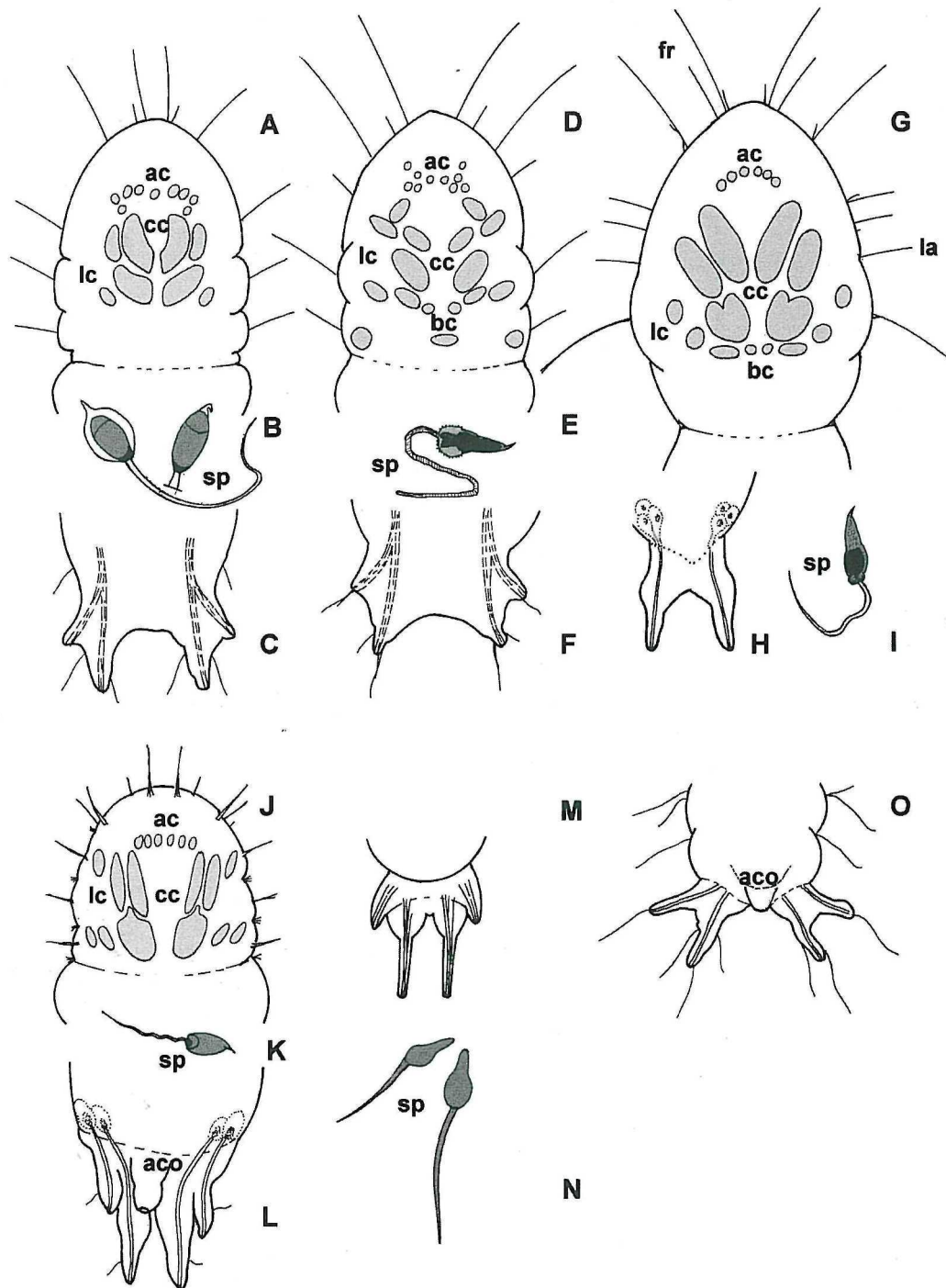


Figure 2. Semidiagrammatic representation of prostomial sensoria and ciliophores (ventral view), spermatozoa, and pygidium (ventral view) of *Diurodrilus* species. A-C *Diurodrilus ankei* (modified from Ax, 1967); D-E *D. subterraneus* (modified from Mock, 1981); F *D. subterraneus* (modified from Kristensen & Eibye-Jacobsen, 1995); G-I *D. benazzii*; J-L *D. westheidei* (from Kristensen & Niilonen, 1982); M-N *D. dohrni* (from Gerlach, 1953); O *D. minimus* (drawn from a micrography of G. Teuchert, in Ax, 1967: 15, fig.6A).

Figure 2. Représentation semi-schématique des formations sensorielles du prostomium et des ciliophores (vue ventrale), des spermatozoïdes et du pygidium (vue ventrale) des espèces de *Diurodrilus*. (A-C) *Diurodrilus ankei* (modifié d'après Ax, 1967) ; (D-F) *D. subterraneus* (modifié d'après Mock, 1981) ; (G-I) *D. benazzii* ; (J-L) *D. westheidei* (d'après Kristensen & Niilonen, 1982) ; (M-N) *D. dohrni* (d'après Gerlach, 1953) ; (O) *D. minimus* (dessiné d'après une micrographie de G. Teuchert, in Ax, 1967 : 15, fig.6A).

provided with adhesive glands (Fig. 2H). Anal pore situated ventrally and distally on the fifth trunk segment, without anal cone.

Sensorial pattern, ciliophores and ventral ciliation

Diurodrilus benazzii lacks cuticular reinforcements or plates, as described in *D. ankei* and *D. subterraneus* (Ax, 1967; Mock, 1981). Following the terminology of Kristensen and Niilonen (1982), tactile bristles or sensoria (stiff sensory or adjoined cilia) may be present on the prostomium, trunk segments or the pygidium of *Diurodrilus* species. Tactile bristles (stiff sensory cilia) have been recorded on the prostomium of all species of the genus *Diurodrilus*, and laterally on the trunk segments of the species *D. ankei*, *D. minimus*, *D. westheidei*, and *D. subterraneus*. Stiff sensory cilia are lacking on the trunk segments and pygidium of *Diurodrilus dohrni* and *D. benazzii*. Sensorial pattern is known after the original description of *D. ankei* and *D. westheidei*, and also for *D. subterraneus* after its redescription by Mock (1981).

Sensorial pattern of *Diurodrilus benazzii* differs from the original description by Gerlach (1952). There are 3 pairs of long frontalia with short bristles at the basis and 4 pairs of lateral alia (Fig. 2G).

Ventral prostomial ciliation is represented by specialized ciliated areas, ciliophores (Kristensen and Niilonen, 1982). Pattern of ciliated areas was first known for *D. ankei* (Fig. 2A) and then for *D. westheidei* (Fig. 2J). In the redescription of *D. subterraneus*, Mock (1981) described several ciliated areas, which are very difficult to delimit (Fig. 2D).

Original description of *D. benazzii* shows correctly the number, size and situation of anterior ciliophores, nevertheless the other ciliated areas are shown as two lateral rings. The specimens from the Gulf of Valencia have a ciliary pattern corresponding partially to the ciliary pattern of *D. ankei* and *D. westheidei*. Size and situation of anterior ciliophores seem to be very similar, changing only the number of areas, 6 in *D. westheidei* and *D. benazzii*, and 9 or more in *D. ankei* and *D. subterraneus*. Central ciliophores are very close in size and number (6) in *D. ankei*, *D. westheidei* and *D. benazzii*.

Prostomial ciliophore-complex of *Diurodrilus benazzii* consists of 5 groups, with a total of 20 ciliophores, placed in the first and second partition of the prostomium (Fig. 2G). The anterior group of ciliophores (ac) is formed by 6 small rectangular ciliophores, arranged in an arc (14 μ m length). The central group (cc) is formed by 6 large ciliophores, 4 anterior and club-like ones (22 x 7 μ m, and 11 x 7 μ m), and 2 heart-shaped (9 x 11 μ m). Below the central group there are 4 small basal ciliophores (bc) in a transverse row, 2 rounded (2 μ m) and 2 club-like (7 x 2 μ m). The lateral groups (lc) consist of 2 ciliophores at each side, lateral to the heart-shaped ciliophores.

Prostomium and peristomium are separated by transverse rows of 8-10 small prepharyngeal ciliophores (prc, Fig. 1), just before the mouth opening. Beside the mouth there are several peristomial lateral ciliophores (plc, Fig. 1). There are no triangular ciliary fields as in *D. westheidei*. Between the mouth opening and the first trunk ciliophore there are four postpharyngeal ciliophores arranged in a transverse row (ppc). The ciliated area of the first trunk segment is modified in a similar way, but consists of only 3 ciliophores, with the central one enlarged (1st trc, Fig. 1). In the original description, Gerlach (1952) showed 2 transverse ciliophores all situated on the trunk. However, the specimens collected in the Gulf of Valencia show a total of 15 ciliophores on the trunk. Each trunk segment carries 3 ciliophores in transverse rows. The known patterns of ciliophores for both, prostomium and trunk segments, are very close in the four investigated species. It seems that the ciliophore pattern may be more conservative than expected, over all in the trunk segments. Only a detailed study of prostomial ciliophores should be used as taxonomic characters.

The morphology of the pygidium has been used as the more valuable character to identify the species of *Diurodrilus*, however, the shape of the pygidium may be intermediate between the species, as found by Wolff *et al.* (1980), who stated that differences between *D. subterraneus* and *D. minimus* were not always clear.

Reproductive system

Mature males and females of *D. benazzii* are nearly equal in size, sex ratio was 1 : 1 in the Gulf of Valencia. Females have paired ovaries, and usually carry two large oocytes in the 4th and 5th trunk segments. Trunk segments of males were filled up with sperm. In agreement with Kristensen and Eibye-Jacobsen (1995) for *D. subterraneus*, the reproductive system of mature males consists exclusively of mature spermatozoa lying free in the coelom. Morphology of the spermatozoa of *D. benazzii* has been investigated by light microscopy and shows a pattern similar to that found in other species of the genus *Diurodrilus* (Fig. 2B, E, I, K, N). The spermatozoon is tripartite, with a round or elongated head containing a giant acrosome, then a nucleus in the middle-piece, followed by a collar and a medium sized flagellum (Fig. 2I). Morphology of mature spermatozoa are very close to those described by Kristensen and Eibye-Jacobsen (1995) for *D. subterraneus*. According to TEM-investigations by Kristensen and Niilonen (1982), this spermatozoon "is unique, different to spermatozoa previously described in other archiannelids" (Franzén, 1977; Franzén and Sensenbaugh, 1984; Kristensen and Eibye-Jacobsen, 1995).

Emended diagnosis of Diurodrilus benazzii

Medium-sized (250-425 μ m) distinctly segmented species. Prostomium with 3 pairs of frontal sensoria

(frontalia) and 4 pairs of lateral sensoria (lateralialia). Trunk without lateral sensoria. Ventral side of prostomium covered by 20 ciliophores. Four postpharyngeal ciliophores arranged in a transverse row, as the first trunk ciliophore. On the trunk 15 midventral ciliophores present, 3 transverse rows on each segment. One pair of caudal toes, length 20 μm . Anal cone absent.

Ecology and geographical distribution of Diurodrilidae

The species of the genus *Diurodrilus* inhabit the interstitial system of medium to coarse sand biotopes, from the upper shore to the shallow sublittoral (Fig. 3a). Across sandy midlittoral habitats, species of *Diurodrilus* are often restricted to certain zones, showing two main distributional patterns: 1) species restricted to upper moist sand substratum and medium water level (*D. subterraneus*, *D. ankei* and *D. benazzii*), 2) species of lower midlittoral and upper sublittoral (*D. minimus* and *D. dohrni*).

Diurodrilus subterraneus, *D. ankei* and *D. benazzii* have been recorded exclusively from the moist sand substratum (high to medium water level). In this habitat the species were identified together with typical stygobionts such as the polychaete *Stygocapitella subterranea* Knöllner, 1934, or the mystacocarid *Derocheilocaris remanei* Delamare-Deboutteville and Chappuis, 1951.

Belonging to the first group, *Diurodrilus subterraneus* was originally described by Remane (1934) from the "Küstengrundwasser" of the Kiel Bay, and was later identified by Schmidt (1969, 1972a) from the same bay and the island of Sylt (Fig. 3e). In the Mediterranean, *D. subterraneus* has been recorded by Delamare-Deboutteville (1960) from the phreatic system together with *Derocheilocaris remanei*, and by Fize (1963) inhabiting a phreatic system of sand together with species of Gnathostomulida. In the Rhine estuary *D. subterraneus* reaches high densities (500 indivs./0.1 m²) in the midlittoral zone, and also inhabits medium sand flats kept free from silt by tidal scour (Wolff *et al.*, 1980) (Fig. 3f). The high dominance of this species was previously stated by Schmidt (1969) for the damp sand zone in the island of Sylt, where *D. subterraneus* may reach 30% of the total meiofauna.

Diurodrilus benazzii also inhabits exclusively the midlittoral moist sand substratum, where it may be identified together with *Derocheilocaris remanei* (Delamare-Deboutteville, 1953; Fize, 1963). These two species have been recorded from the same habitat in the Gulf of Valencia, where both species may reach more than 80% of the total meiofauna. Other records, outside the Mediterranean Sea, are referred to Waltair and Orissa coast, in the bay of Bengal, Indian Ocean, where *D. benazzii* inhabits medium to coarse midlittoral sand (Rao and Ganapati, 1968a, b; Rao, 1969) (Fig. 3b).

Diurodrilus minimus shows a larger horizontal distributional pattern, inhabiting areas from the

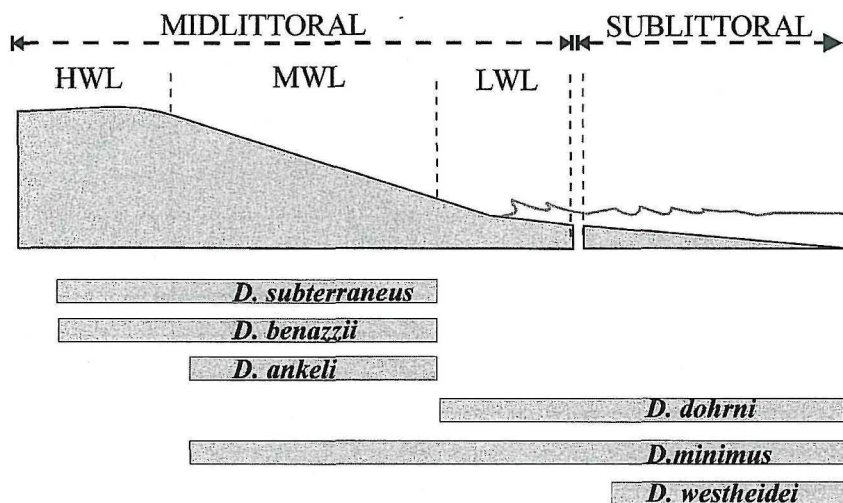
"Küstengrundwasser" (Remane, 1925), to always moist sand in the lower midlittoral level (Renaud-Debyser and Salvat, 1963; Rao and Ganapati, 1968a; Schmidt, 1969, 1972b; Wolff *et al.*, 1980; von Nordheim, 1984). Exceptionally, *D. minimus* has been recorded from *Amphioxus* sands (Fize, 1963).

According to or despite their patchy or gregarious distribution, as mentioned for *D. benazzii* by Rao and Ganapati (1968b), *Diurodrilus* species display an evident zonation pattern, already reported by Westheide (1972a) in the Gulf of Tunis. Along a beach profile, Westheide (*op. cit.*) identified a differentiated distributional pattern for some interstitial polychaetes, including two species of the genus *Diurodrilus*, *D. benazzii* in the phreatic system (upper midlittoral), and one unidentified species (c.f. *D. dohrni*) in the lower midlittoral, in contact with the sublittoral (Fig. 3c). The same distribution pattern was recorded by Wolff *et al.* (1980) in the North Sea, where *D. dohrni* occurred lower in the intertidal zone than *D. subterraneus* (Fig. 3f). The latter species inhabited the damp sand zone, as *D. benazzii* does in the Mediterranean Sea.

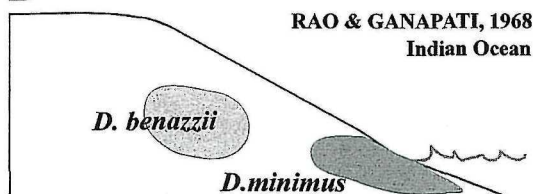
After a bibliographic review on Diurodrilidae, it was possible to select several references with simultaneous occurrence of different species of *Diurodrilus* from the same sandy beach. Despite the noticeable scarcity of data about *Diurodrilus*, figures 3b-f allow us to assume that only two species of *Diurodrilus* may be identified in the midlittoral zone of sandy beaches, one species at each horizontal level. In the upper levels (HW-MW) *D. benazzii* or *D. subterraneus*, and for the lower levels (LW) *D. minimus* or *D. dohrni* (Fig. 3g). There is no record of two or more *Diurodrilus* species inhabiting the same horizontal level of sandy beaches at the same time.

The presence of different congeneric species of interstitial polychaetes at each beach level were interpreted by Westheide (1972a, b) as the result of a historic intrageneric isolation, through the competitive exclusion principle (*Hesionides gohari* vs. *H. arenaria*, and *Diurodrilus benazzii* vs. *Diurodrilus spec.*, c.f. *D. dohrni*). Exclusion by actual competition cannot explain the actual distribution of *Diurodrilus* species. Environmental factors are strongly different between the upper and lower levels of surf-beaten sandy beaches. In this way, the distribution pattern of *Diurodrilus* species across a sandy beach firstly depends on the physiological tolerance of the individual species to the environmental factors of each sandy level. According to the bibliographic review, each horizontal level may be inhabited by several species of *Diurodrilus*. Nevertheless, in natural environments a sole species occurs at each level. Interspecific competition between congeneric species of *Diurodrilus* may be regarded as a possible cause controlling populations within a sandy beach level, while the distribution pattern between upper and lower levels are

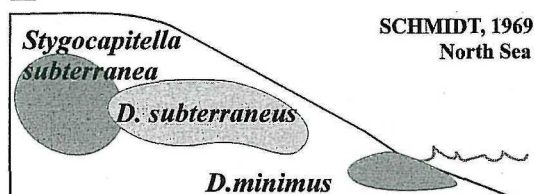
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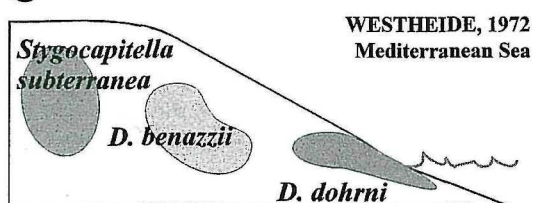
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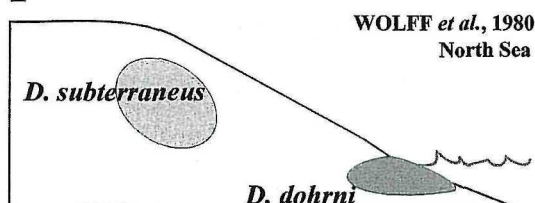
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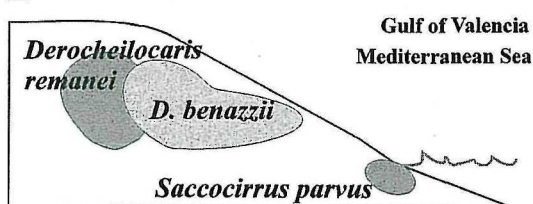
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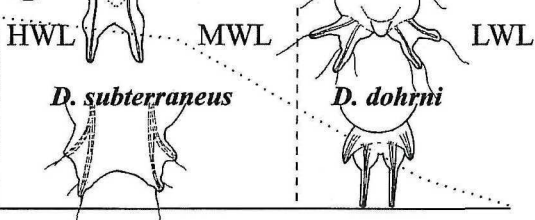


Figure 3. Distribution of *Diurodrilus* species in sandy beaches. A Diagramatic representation of the distribution of each of the 6 species. B-F Simultaneous occurrence of different species of *Diurodrilus* in the same sandy beach (modified from different authors, see text). G Morphological differences (pygidium) between species inhabiting upper and lower levels of sandy beaches.

Figure 3. Distribution des espèces de *Diurodrilus* dans les plages sableuses. A Représentation schématique de la distribution horizontale de chacune des six espèces. B-F localisation précise de chaque espèce dans des plages où 2 espèces sont présentes à la fois ; les localisations de *Stygocapitella subterranea*, *Deirocheilocaris remanei* et *Saccocirrus parvus* sont également indiquées (modifié d'après différents auteurs, voir texte). G Différences morphologiques dans les structures adhésives du pygidium des espèces habitant les niveaux supérieurs et inférieurs des plages sableuses.

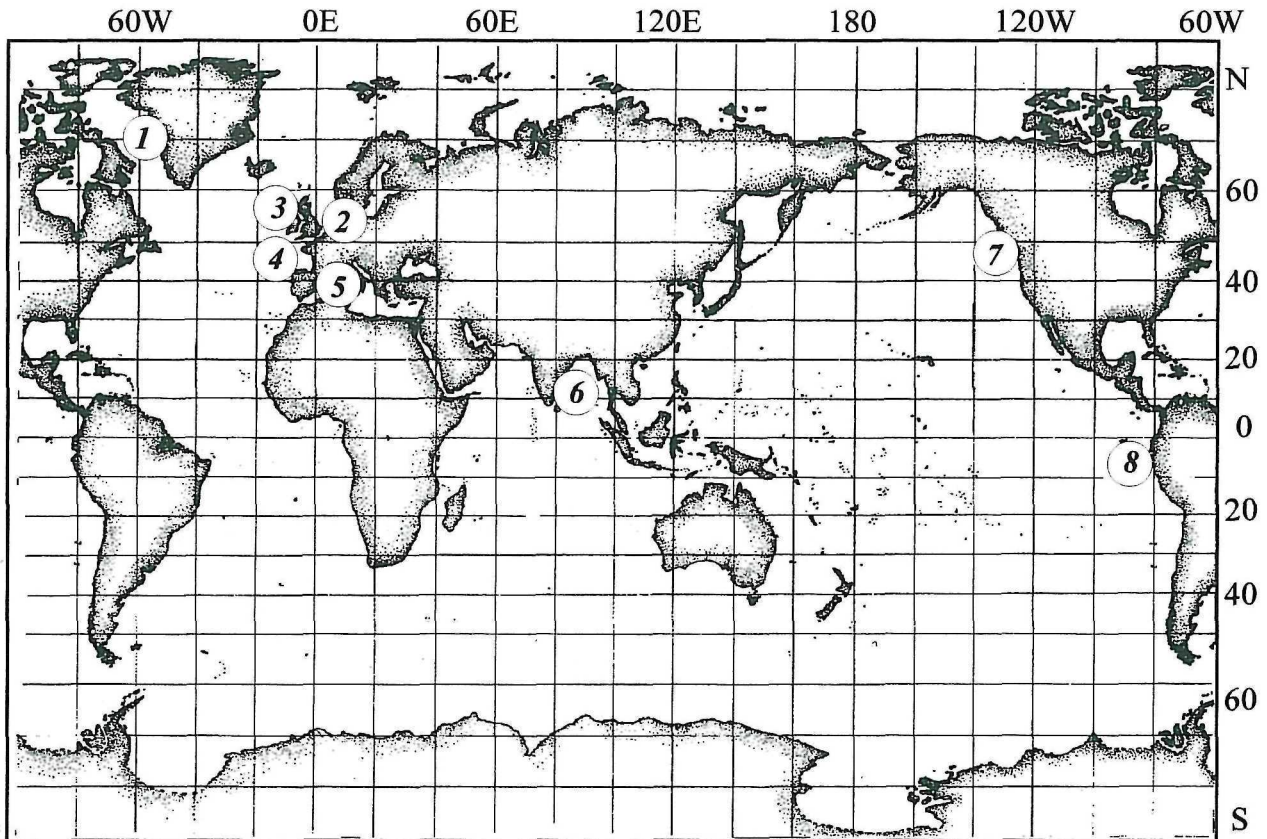


Figure 4. Geographical distribution of *Diurodrilus* species. (1) W. Greenland: *D. westheidei*, and *D. subterraneus*. (2) North Sea: *D. minimus*, *D. dohrni*, and *D. subterraneus*. (3) British Islands: *D. minimus*. (4) Bay of Biscay: *D. minimus*. (5) Mediterranean Sea: *D. benazzii*, *D. minimus*, *D. dohrni*, and *D. subterraneus*. (6) Gulf of Bengal: *D. benazzii*, and *D. minimus*. (7) False Bay, Washington: *D. ankei*. (8) Galapagos Islands: *D. ankei* (?).

Figure 4. Distribution géographique des espèces de *Diurodrilus*. (1) Ouest Groenland : *D. westheidei*, and *D. subterraneus*. (2) Mer du Nord : *D. minimus*, *D. dohrni*, and *D. subterraneus*. (3) Iles Britanniques : *D. minimus*. (4) Golfe de Gascogne : *D. minimus*. (5) Méditerranée : *D. benazzii*, *D. minimus*, *D. dohrni*, and *D. subterraneus*. (6) Golfe du Bengale: *D. benazzii*, and *D. minimus*. (7) False Bay, Washington : *D. ankei*. (8) Iles Galapagos : *D. ankei* (?).

controlled by external factors (sensu Sanders, 1968). This hypothesis may also explain the distribution pattern for sandy beaches with a sole species of *Diurodrilus*. In these beaches, the species only colonizes its characteristic level, according to its physiological tolerances, remaining empty the other level.

There is no experimental data about physiological tolerances of *Diurodrilus* species to support their distribution patterns. However, it is possible to identify morphological differences between species inhabiting each horizontal level of a sandy beach. Lower levels (contact between midlittoral and sublittoral), are largely determined by the impact of waves, while upper levels (phreatic or moist sand) may be considered as a more stable habitat. Inhabiting the lower level of sandy beaches *Diurodrilus minimus* and *D. dohrni* have well developed toes, reacting

with adhesion to increased water currents, while in the upper level *D. benazzii* and *D. subterraneus* display reduced adhesive toes, both in size and number (Fig. 3g). Kristensen and Niilonen (1982) found two species of *Diurodrilus* in West Greenland, *D. subterraneus*, with reduced adhesive toes in the midlittoral moist sand, and *D. westheidei*, with well-developed adhesive toes, in the sublittoral (-2-5 m) under strong tidal currents (more than 100 cm/s).

The reproductive period of *Diurodrilus* species seems to be related to summer months, however, a detailed study of literature shows that mature animals have been recorded during all seasons. In Greenland the reproductive period of *D. subterraneus* is summer (Kristensen and Niilonen, 1982). Animals with eggs are especially common in August (Westheide, 1990), and juvenile peaks in the North Sea occur during summer and autumn months (Schmidt, 1969).

In the Island of Sylt, females of *D. minimus* occur in April (Westheide, 1990), but mature animals are common in Roscoff during summer (Jouin, 1968 in Cabioch *et al.*, 1968). Mature animals of *D. dohrni* have been reported from the North Sea during winter (Wolff *et al.*, 1980). Probably the same species is found sexually mature during March in the Mediterranean Sea (Westheide, 1972a). Mature specimens of *D. benazzii* have been collected in the Mediterranean sea during late spring and summer (Westheide, 1972a, this work). Mature animals of *D. ankeli* were originally described during summer from False Bay, NE Pacific (Ax, 1967). Finally, mature females of *D. westheidei* were originally described from Greenland, during winter period (Kristensen and Niilonen, 1982).

The records of the geographical distribution of Diurodrilidae should be considered with caution, mainly because references from the literature are very scarce. The Mediterranean Sea shows the richest distribution of

Diurodrilus species: *D. minimus*, *D. subterraneus*, *D. benazzii* and *D. dohrni* (Fig. 4). The type species *D. minimus* is widely distributed from the Northeastern Atlantic to the Mediterranean and Southwestern Indopacific (Westheide, 1990). *Diurodrilus dohrni* and *D. subterraneus* have a North Atlantic and Mediterranean distribution (Gerlach, 1953; Westheide, 1990), while *D. benazzii* is known from the Mediterranean (Gerlach, 1952; Fize, 1963; Delamare-Deboutteville, 1953; Westheide, 1972a), and also from the Southwestern Indopacific (Rao, 1969; Rao and Ganapati, 1968a, b; Rao, 1972). *Diurodrilus westheidei* has never been identified after its original description from Greenland (Kristensen and Niilonen, 1982) and *D. ankeli*, only known with certitude from the NE Pacific (Ax, 1967), may also occur in the Galapagos Islands (Schmidt and Westheide, 1977). An additional record is referred to an undescribed new species, *Diurodrilus* sp.1, found at 20-60 m depths off Beaufort N.C., U.S.A (Rieger and Rieger, 1976).

Abbreviations in the figures

ac	anterior ciliophores
aco	anal cone
bc	basal ciliophores
cc	central ciliophores
fr	frontalia
la	lateralial
lc	lateral ciliophores
plc	peristomial lateral ciliophores
mo	mouth
oo	oocyte
pb	pharyngeal bulb
ppc	postpharyngeal ciliophores
prc	prepharyngeal ciliophores
sp	spermatozoon
tgl	toe gland
trc	ciliary area of the trunk

Abréviations dans les figures

ac	ciliophores antérieurs
aco	cône anal
bc	ciliophores basaux
cc	ciliophores centraux
fr	frontalia
la	lateralial
lc	ciliophores latéraux
plc	ciliophores latéraux du péristomium
mo	bouche
oo	ovocyte
pb	bulbe pharyngien
ppc	ciliophores post-pharyngiens
prc	ciliophores pré-pharyngiens
sp	spermatozoïde
tgl	glandes adhésives pygidiales
trc	aire ciliée du tronc

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