OBSERVATIONS ON MARINE HETEROTARDIGRADA, INCLUDING A NEW GENUS FROM THE WESTERN ATLANTIC OCEAN.

by

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Résumé

Etude de deux espèces d'Hétérotardigrades marins. Chez les Oreellidae, un nouveau genre est créé et la description *d'Anisonyches diakidius* n.g., n.sp., est donnée. L'auteur étudie également la morphologie et l'écologie d'une espèce cosmopolite : *Echiniscoides sigismundi.*

The Heterotardigrada Marcus, 1927, is the most diverse of the three orders in the phylum Tardigrada. Sixteen marine genera, comprising 41 species, compared to six semi-terrestrial genera, comprising more than 140 species, demonstrate the basically marine nature of this order. Approximately 350 species occur in thirteen closely related genera in the other major order, Eutardigrada Marcus, 1927 (Pilato, 1969, 1971). Marine heterotardigrades are generally regarded as primitive on the basis of morphological diversity at the generic level and their broad array of ornamentation and appendages.

Seven of the sixteen genera of marine heterotardigrades have been described since 1950. Among the most recent of these, *Tanarctus* Renaud-Debyser, 1959, *Parastygarctus* Renaud-Debyser, 1965 and *Florarctus* Delamare and Renaud-Mornant, 1965, were found in coralline sand collected in tropical or sub-tropical areas. With new species of marine tardigrades frequently reported in studies of meiofauna from new geographical localities, we can look forward to gaining much more knowledge of the range of heterotardigrade diversity in the near future.

Observations made in this paper are drawn together from two separate sources. Intertidal coral sand collected at the Bahamas in 1968 included a new genus as well as *Batillipes mirus* Richters, 1909 a, *Pleocola limnoriae* Cantacuzène, 1951 and *Halechiniscus subterraneus* Renaud-Debyser, 1959. Finally, the cosmopolitan species, *Echiniscoides sigismundi* (M. Schultze, 1865), was the subject of mor-

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phological review and ecological study at Woods Hole in 1970. This material follows the phylogenetic sequence proposed by Ramazzotti (1972).

Suborder: ECHINISCOIDEA Marcus, 1927

Family: Oreellidae (I) Ramazzotti, 1962

Genus: *Echiniscoides* (M. Schultze, 1865)

Diagnosis: Unplated Oreellidae with more than four claws on each leg; claws without accessory basal spurs.

Type species: *Echiniscoides sigismundi* (M. Schultze, 1865).

Discussion: *Echiniscoides* is the oldest currently recognized genus of marine Tardigrada. It has remained monotypic since its distinction from the genus *Echiniscus* was recognized by Plate (1889). Its systematic placement within the Heterotardigrada is clear, but it is morphologically unique among described forms. Consequently, its familial placement has been problematical.

Because toes and distinct dorsal plates are lacking, *Echiniscoides* has been placed within the suborder Echiniscoidea near the point of its apparent divergence from the suborder of toe-bearing Arthrotardigrada (Marcus, 1927 ; Thulin, 1928 ; Cuénot, 1932 ; Puglia, 1959 ; Schulz, 1963 ; Ramazzotti, 1962). In this position, it has been most closely allied with the genus *Oreella* Murray, 1910 (Thulin, 1928 ; Schulz, 1963) and with *Oreella* and *Archechiniscus* Schulz, 1953 (Puglia, 1959 ; Ramazzotti, 1962) in the family Oreellidae.

Echiniscoides sigismundi (M. Schultze, 1865)
(Fig. 1 ; Table 1).

Echiniscus sigismundi, M. Schultze, 1865 ; *Emydium sigismundi* Lameere, 1895 ; *Echiniscus sigismundi* Loman, 1921.

Diagnosis: *Echiniscoides* with 5-11 claws, without accessory spurs, directly inserted on each leg; papillae present on legs III and IV.

Distribution: East and south coasts of the North Sea, Norway to Belgium (M. Schultze, 1865; Lameere, 1895; Richters, 1909 a and b ; Carlzon, 1909; Loman, 1921; Marcus, 1927, 1936; Cuénot, 1932; Grell, 1937; Tambs-Lyche, 1939-40); British Isles (Murray, 1911; Green, 1950; Crisp and Hobart, 1954); Roscoff, France (d'Hondt, 1970); Tenerife, Spain (Rodriquez-Roda, 1946; Mediterranean at Naples (Richters, 1908) ; Adriatic at Rovigno (Richters, 1908) ; Bulgarian coast

(1) The family name « Oreellidae » was introduced by Puglia (1959) in a doctoral thesis to the University of Illinois. However, according to the International Code on Zoological Nomenclature (1964, Section III, Articles 8 and 9), a dissertation does not constitute publication. Consequently, the family name Oreellidae has been credited to Ramazzotti (1962), who was first to use it validly.

of the Black Sea (Valkanov, 1949; Caspers, 1951); Romanian coast of the Black Sea (Rudescu, 1964) ; Dead Sea (Teunissen, 1938) ; Belgian Congo, Africa - at 1000 m altitude! (Teunissen, 1938) ; Yellow Sea, China (Mathews, 1937); Galapagos Islands (Schuster and Grigarick, 1966); El Salvador (Schulz, 1953); California (Schuster and Grigarick, 1965, 1970) ; Brazil (du Bois-Reymond Marcus, 1952 ; Bonaire (du Bois-Reymond Marcus, 1960) ; North Carolina and Massachusetts (McGinty and Higgins, 1968); New Hampshire and Maine (Pollock, 1970 a).

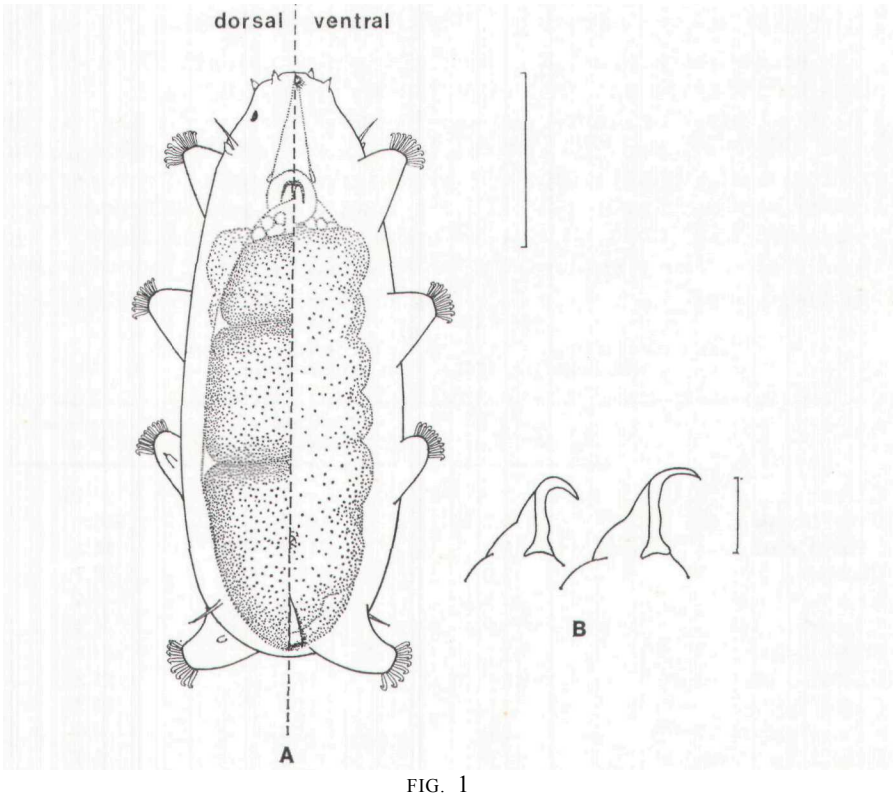

FIG. 1
Echiniscoides sigismundi.

A: adult female, composite of dorsal (left) and ventral (right) aspects, scale - 50 µm; B: claws from fourth pair of legs, innermost (left) and outermost (right). Scale: 10 µm.

Description: Measurements ± standard error are based on 31 individuals from Woods Hole, collected from a single barnacle plate, 2 August 1970. These data are grouped into three arbitrary size categories in table 1.

Body contour smooth, without projections or spurs. Body length, 185.3 ±7.0 µm. Cephalic cirri reduced in size; median cirrus absent; paired internal cephalic cirri from papillate base, 4.0 ± 0.1 µm; paired external cephalic cirri also from enlarged base, slightly longer than internal cirri, 4.4 ± 0.1 µm. Internal cirri dorsal to mouth, external cirri are ventral. Clavae and lateral cephalic cirri in dorso-lateral

location on head. Clavae as flattened papillae often with roughened distal margin, 3.2 ± 0.1 um. Lateral cephalic cirri, 10.0 ± 0.4 u.*m,* taper from broad base, located slightly anteriad to clavae. Eyes present as dark red-brown to black bodies, distally concave with roughened surface; located antero-ventrally to lateral cirri.

Mouth subterminal, surrounded by circular cuticular thickening. Pharyngeal bulb slightly flattened antero-posteriorly, 18.0 ± 0.6 um in length. Placoids short, of typical fused heterotardigrade shape. Stylets stout, 37.7 ± 1.4 u.*m* in length; enter buccal canal near mouth via short sheaths; slightly dorsal placement on pharyngeal bulb. Stylet base nearly rectangular. Stylet supports absent.

Cuticle finely punctate; thickened plates absent. Dorso-lateral somatic cirrus E an irregularly tapered cone, dorsal to legs IV, 10.7 ± 0.5 um. Cephalic tubercles (homolog to «cephalic papillae» in some other echinscoids) lateral to mouth, between internal and external cirri. Slight cuticular ridge dorsal to mouth. Anus postero-ventral between fourth pair of legs; flanked by two flattened triangular, cuticular ridges. On some, distal margins of each ridge raised slightly above body contour. Otherwise body contour smooth without projections.

TABLE 1
Mean measurements (un) of *Echiniscoides sigismundi* (M. Schultze, 1865) from Woods Hole

	Juveniles 101-150 μm	Small adults 151-200 μm	Large adults 201-250 μm
Character	N = 6	N = 15	N = 10
Body length	120.7	185.3	224.0
Lateral cirri	7.3	10.2	11.2
Clavae	2.6	3.2	3.7
External cirri	3.3	4.1	4.5
Internal cirri	3.8	4.4	4.8
Stylet length	27.7	38.9	42.0
Diameter of pharynx	13.3	17.7	21.2
Cirrus E	7.9	11.5	11.3
Papilla on fourth leg	2.5	3.3	3.6
Papilla on third leg	4.0	5.5	5.8

Dimorphism exists in gonopore shape and location. Female gonopore, of six, pointed, cuticular projections joining apically in light, rosette-shaped apposition; located mid-ventrally, approximately one-half distance between legs III and IV. Male gonopore, a raised rounded opening, mid-ventral but slightly closer to anal ridges. Configuration of gonoducts could not be ascertained. Since no animal examined possessed mature gametes, sex distinctions were assumed by comparison with similar dimorphism in other genera (Pollock, 1970b).

Legs stubby, of approximately equal length. Anterior three pairs in ventro-lateral orientation, directed forward; legs IV ventro-lateral but nearly terminal and oriented in opposite direction. Toes absent. Terminal appendages long un-spurred claws; from 5-10 per leg. Size of claws increases slightly from proximal to distal side of each foot (see Fig. 1B). Basal membranes connect all but the curved tip of

each claw to the foot. Single papilla, 3.2 ± 0.1 um long, on outside of legs IV near their junction with body; identical in appearance to clavae. Larger papillae, 5.3 ± 0.2 um, with spinous extension near the base of legs III and body; similar in appearance to internal and external cephalic cirri. Spines and papillae absent from legs I and II.

The size structure of populations was studied by grouping all individuals collected from a single mural plate of the barnacle *Balanus balanoides* (L.) into arbitrary size categories and comparing the percentage of each population occurring in each size class. Results from four such studies reveal that considerable variation in size composition is found even when comparing fauna from the same locality collected on the same day. In all cases, however, larger middle-sized animals dominated the population.

Discussion: Although *E. sigismundi* is widely distributed, frequently collected and extensively described anatomically (Marcus, 1927), aspects of its external morphology have been overlooked. Most noteworthy of these are the arrangement of claws and the occurrence of dimorphism in the shape and location of gonopores. Papillae on legs IV and a second pair of cephalic cirri do not appear in the original description (Schultze, 1865, Taf. XXVI, 1 and 2), while clavae and lateral cirri are shown to be approximately equal in size. These variations are assumed to be observational or artistic errors.

The claws of *E. sigismundi* are its most distinctive feature. Only one other, extremely rare (now possibly extinct) species, *Thermozodium esakii* Rahm, 1937, reportedly possesses more than four claws per leg. *E. sigismundi* always has more than four (with a single exceptional observation, Richters, 1909 b).

Marcus (1927) observed that the number of claws on legs of a single individual may be variable. In examining this feature, I found that in all but three cases among 31 individuals, the number of claws per foot found on legs IV was one less than on each of the anterior three pairs. In the three exceptions, claws on each foot were equal in number. The smallest specimen (107 un body length) had five claws on each leg. Cuénot (1932) observed the same number on embryos 95 ¡un in length still contained within the egg shell. Animals possessing a 6/5 formula (i.e., number of claws per foot on anterior legs/number of claws per foot on legs IV), were 110-112 ¡un in length (N = 3). An exceptional animal of 190 um body length had a 7/6 formulae. The remainder had either 8/7 (N = 15) or 9/8 (N = 9) formulae. There is considerable overlap in size between these groups, especially in the 200-220 um size range, indicating that the correlation between size and claw number is not sharply defined. This peculiar characteristic of one less claw on legs IV than on legs I-III is shared by a new genus to be described below and provides the strongest evidence of the relationship between these genera.

Another ontogenetic change occurs in the appearance of the gonopore and of cuticular ridges flanking the anus. Individuals in the 107-112 um size range showed no signs of either of these structures. Animals measuring 135-180 um in length possessed cuticular ridges but not obvious gonopores. Both ridges and pores were found on larger animals. A similar sequence of development occurred in juve-

nile stages of *Stygarctus bradypus* Schulz, 1951 (Renaud-Mornant et Anselme-Moizan, 1969).

At Woods Hole, *E. sigismundi* is found most commonly on the intertidal barnacle *Balanus balanoides.* This relationship previously has been reported from Holland (Loman, 1921), the British Isles (Crisp and Hobart, 1954) and from California, USA (Schuster and Grigarick, 1965, 1970). In their studies of the *Echiniscoides-Balanus* association, Crisp and Hobard (1954) found tardigrades more abundant on barnacles from exposed shores than on those from sheltered conditions. While *E. sigismundi* occurred year-round, they postulated that greater abundance observed in winter may have been related to decreased availability of microalgae in summer. They concluded that the barnacle species involved is unimportant to the occurrence of tardigrades, provided it occupies the proper type of shore.

TABLE 2

Comparison of *E. sigismundi* distribution on six adjacent mural plates comprising a dead *Balanus balanoides,* including density on each plate (No. *E. sigismundi/mm*^{2} plate surface) and proportional abundance (in percent) in each of four micro-habitats on each plate. N = 125.

	Mural Plates						
	1	2	3	4	5	6	$\bar{x}$
Density	0.48	1.40	0.80	0.46	0.82	0.31	0.71
Cavities	70	64	75	50	94	50	67.2
External surface	30	36	9	41	6	50	28.7
Internal surface	0	0	3	3	0	0	1.0
Sides	0	0	13	6	0	0	3.0

Tardigrades studied here were collected from *B. balanoides* from the upper intertidal region of rectangular rock slabs forming the « Fisheries Jetty » at Woods Hole. No significant difference occurred in abundance of *E. sigismundi* on the mural plates of adjacent living and dead barnacles of the same size and appearance. However, on living barnacles, *E. sigismundi* was unusually abundant (4.57 *E. sigismundi/mm*^{2} plate surface, as compared to more typical densities of 0.5-0.8/mm^2) on the four opercular plates which usually are lost along with soft parts in dead barnacles. Other than through the loss of these particularly favored opercular plates, differences in desirability did not occur between plates of living and dead barnacles. Barnacle plates themselves merely provide substratum regardless of the condition of the barnacle inside. Density of distribution of *E. sigismundi* was random ,index of aggregation (S^2/x) = 0.218) among the six mural plates comprising a single dead barnacle (Table 2).

Microdistribution on each of these six plates was observed and results are shown also in Table 2. Generally more than 2/3 of the *E. sigismundi* had found their way into longitudinal cavities existing between outer and inner lamellae of each plate. In most cases, the external surfaces were next most heavily populated, while internal surfaces harbored the lowest densities of tardigrades.

In comparison with other available sites, it is not surprising that longitudinal cavities are favored microhabitats. These cavities are packed with blue-green algae, maintained by light penetrating the outer lamella or mural plates, and remain full of capillary water in all but the most extreme drying conditions. They are accessible to only the smallest meiofauna and the microfauna. Much lower densities of *E. sigismundi* reported previously in the literature may result from ignoring the fauna of these cavities which harbored as many as 94 per cent of the fauna.

As in Crisp and Hobart (1954), high visual correlation was found between tardigrade frequency and irregular patches of filamentous blue-green algae and both thin sheets and filaments of green algae. Greatest algal and tardigrade densities occurred on the opercular plates, in those longitudinal cavities to which access had been made by fracture or erosion through the external lamella of the mural plate, and among vertical ridges around the base of each mural plate.

E. sigismundi was the dominant epizoan on nearly every plate examined. Occasionally an orange-colored bdelloid rotifer was abundant, as were at least two species of mites.

Genus : Anisonyches n.g.

Diagnosis: Oreellidae with four claws each on the first three pairs of legs and three claws each on the fourth pair of legs; claws with accessory basal spurs.

Etymology: *Aniso* (G.) - unequal + *onyches* (G.) - claws; referring to the unequal number of claws among legs on the same individual.

Anisonyches *diakidius* n. sp.
(Fig. 2; Table 3)

Diagnosis: *Anisonyches* with two basal spurs present on each claw; papillae present on base of fourth pair of legs only.

TABLE 3

Measurements (uun) of *Anisonyches diakidius* n. g., n. sp. Column 1, the type specimen; columns 2-5, others from the type locality; column 6, mean ± standard error of the mean of preceding 5 representatives.

Body length	77	156	147	123	168	154.2	9.3
Body width (middle)	45	45	42	28.5	45	41.1	3.2
Lateral cirri	4	4	4	4	4.5	4.1	0.1
Clavae	4.5	4.5	4	4	4	4.2	0.1
External cirri	3	3	3	3	3	3.0	0.0
Internal cirri	3	3	3	2.5	3	2.9	0.1
Stylet length (bulb to sheath)	15	18	18	13.5	17.5	16.4	0.9
Stylet sheath	18	21	18	15	18	18.0	1.0
Placoid length	6	3	4	4.5	4	4.3	0.5
Pharyngeal bulb	13.5	9	9	9	10.5	10.2	0.9
Cirrus E	9	6.8	6	6	7.5	7.1	0.6
Claw length	4.5	3.6	6.6	6	3.3	4.8	0.7

Holotype: Adult (USNM No. 50901); collected by **L.W.** Pollock, **1968.**

Type locality: East Plana Cay (easternmost of the French Cays) between Crooked and Mayaguna Islands, Bahamas (22° 23' N, 73°30'W). Beach on southern coast, mid-tidal level, 0-3" depth in coralline sand. From samples gathered by Dr. G.C. Clough and made available by Dr. D.J. Zinn.

Distribution: East Plana Cay; and Conway Bay Beach, Isla Santa Cruz, Galapagos Islands, Ecuador (00° 32.7' S; 90° 32.2' W) ; high tidal area, fine to medium sand, 0-20 cm depth. From material provided by M. McGinty Bayly.

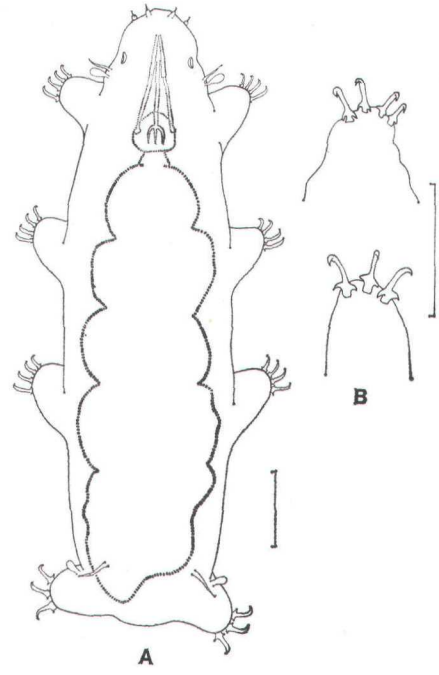

FIG. 2
Anisonyches diakidius n. g., n. sp.

A: adult, composite from dorsal aspect; B: leg and claws from leg I (top); leg and claws from leg IV (bottom).
Scales: 20 μm.

Etymology: Di (G.) - two + *akidius* (G.) - diminutive of spur, referring to the two basal spurs found on all claws.

Description of holotype: Body length, **177 um.** Cephalic cirri reduced in size. Paired internal cephalic cirri, 3 u*m,* somewhat dorsal to external cephalic cirri, **3u;** measurements of both including thickened basal section. Median cirrus absent. Small, ovaloid clavae, **4.5 um:** thin, short lateral cirri, 4 um, located slightly anteriad to clavae. Clavae and lateral cirri dorso-lateral position. Eye spots present as black bodies, antero-lateral to lateral cirri.

Mouth subterminal; pharyngeal bulb small, 13.5 µm diameter, somewhat flattened posteriorly. Thin stylets, 33 µm long with narrow rectangular base; extend from dorso-lateral placement on pharyngeal bulb, enter buccal canal through prominent sheaths extending 18 µm from the mouth laterally along buccal canal. Stylet supports absent. Placoids, 6 µm in length, fused anteriorly as in most other Heterotardigrada.

Body « eutardigrade-like » in shape. Cuticle transparent, without thickened plates, ornamentation or obvious punctations. Cirri E, 9 µm in length, located dorso-anteriad to legs IV. Slight constrictions both anterior to lateral cirri and posterior to clavae. Otherwise, body outline smooth, without cephalic, somatic or caudal projections. Gonopore a rosette of six small cuticular plates, located mid-ventrally anteriad to anus. Mid-gut formed into six diverticulae. Anus as crossed, pursed lines between fourth pair of legs.

Stubby legs of approximately equal length. Toes absent. Terminal appendages stout claws slightly curved apically, each bearing two opposing nearly basal accessory spurs. Basal spurs oriented at right angles to one another so that as one is in focus, the other is directed away or toward the observer giving the claw an assymetrical appearance. Claws progressively longer from innermost to outermost; mean length of claws, 4.5 µm. Basal membranes connect each claw to foot. Four claws on each of legs I-III; only three claws on each of legs IV. Papillae present near the base of legs IV. Papillae and spines absent from anterior three pairs of legs.

Mrs. M. McGinty Bayly generously provided individuals of this species from her collections in the Galapagos Islands. In all aspects, specimens from both locations appear identical. In addition, juveniles in her material differed from adults by possessing only two claws on all legs.

Discussion: *Anisonyches* falls within the limits of the order Heterotardigrada by the presence of cephalic appendages and the morphology of its buccal apparatus. The absence of toes places it within the suborder Echiniscoidea.

The absence of cuticular plates or a gelatinous body coating and possession of claws without toes distinguishes *Anisonyches* from all known tardigrades except *Oreela minor* and *E. sigismundi.* Further similarities among these three forms include the number of cephalic cirri, presence of papillae on legs IV and general morphology of the buccal apparatus. Additional closeness between *A. diakidius* and *E. sigismundi* but to the exclusion of *O. minor,* are found in body shape, morphology of cephalic cirri, presence of eyes, and, most importantly at the generic level, possession of unequal number of claws on different legs of the same specimen. Differences exist between the two genera in the absence of papillae on the pair of legs in *A. diakidius* and in morphology and number of claws. In observations of *A. diakidius* from two localities ($n > 25$), none possessed more than four claws on anterior legs or three claws on legs IV. Never were less than five claws observed on *E. sigismundi* ($n > 100$) at Woods Hole.

The morphology of claws found in *A. diakidius* has no parallel among other Heterotardigrada. Claws with two laterally opposed basal spurs have been recorded previously only from the eutardigrade genus, *Milnesium* Doyère, 1840.

Summary

Systematic and ecological observations are presented on two species of Heterotardigrada.

In the Oreellidae, a new genus and species is described and the morphology and ecology of a cosmopolitan species is presented.

Morphology and ecology of *Echiniscoides sigismundi* living on intertidal barnacles at Woods Hole is discussed. Morphological features include triangular folds of cuticle flanking anus, dimorphism in gonopore shape and location, and presence of one less claw on legs IV than on legs I-III (a major point of similarity to *Anisonyches,* below). Ontogenetic changes include increase in claws per leg and delayed appearance of cuticular anal ridges and gonopores.

Comparable densities of *E. sigismundi* occurred on plates of living and dead barnacles - plates merely providing substratum. Uneven distribution of tardigrades among plates comprising single dead barnacles visually correlated with distribution of green and bleue-green algae. Longitudinal compartments between barnacle plate lamellae and opercular plates were favored microhabitats.

Anisonyches diakidius n.g., n.sp. is described from the Bahamas. The generic diagnosis: unplated Echiniscoidea with four claws each on first three pairs of legs and three claws on each of fourth pair of legs.

Specific diagnosis: *Anisonyches* with two basal spurs on each claw; papillae present on base of fourth pair of legs only.

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Abstract

Two species of the marine heterotardigrade family Oreellidae are treated in this study. A new genus and species is described, *Anisonyches diakidius* n. g., n .sp., and the morphology and ecology of a cosmopolitan species, *Echiniscoides sigismundi,* is examined.

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