



A new species of *Coronarctus* (Tardigrada, Heterotardigrada) in the deep sea from the Gulf of Mexico revealed by geometric morphometrics and an updated genus key

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Abstract

Coronarctus Renaud-Mornant, 1974, is currently composed of eleven species, which are found in deep sea and shallow environments. We described a new species of *Coronarctus*, as well as doing a morphometric analysis and providing an identification key, from specimens collected in deep-sea sediments (1,182–2,822 m) in the southern Gulf of Mexico. *Coronarctus xiximii* sp. nov. is characterized by spherical primary clavae and flattened secondary clavae, each with two dorsal and two ventral lobes; sensory organs on each pair of legs and additional flexible spine-like processes on legs IV, and heteromorphic, simple claws, with the internal claw of leg IV being twice the size of the external claws. This discovery increases the number of *Coronarctus* species worldwide to twelve.

Keywords Coronarctidae – deep sea · Marine tardigrade · Morphometric analysis · México

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Introduction

Marine tardigrades are micrometazoans that can be found on different substrates, detritus, or other organisms. However, they are mainly found in the interstitial environment (Nelson et al. 2018). They are present in all oceans, from the intertidal zone to abyssal depths ([to > 5,000 m] Fontoura et al. 2017), in marine caves, abyssal mud, deep-sea ooze and associated with manganese nodules (Hansen and Kristensen 2020; Nelson et al. 2018). Almost all marine tardigrades belong to the class Heterotardigrada Marcus, 1927 from the order Arthrotardigrada Marcus, 1927. This order is possibly a non-phylogenetic taxon (Grollmann et al. 2023), but it is still used in the literature and on websites such as <https://www.marinespecies.org>, <https://www.marinespecies.org>, <http://www.tardigrada.net>, and <https://www.gbif.org>. This taxon includes about 229 described species (Degma and Guidetti 2025). However, some estimates indicate that this group could be made up of close to 1,000 species (Bartels et al. 2016).

Coronarctus Renaud-Mornant, 1974, is a marine genus whose species have been described from deep-sea sediments. Currently, eleven species are assigned to the genus, most of which have also been found elsewhere with a geographical distribution that covers the Indian, Atlantic, and Pacific oceans (Degma and Guidetti 2025).

A total of 16 marine tardigrade taxa have been recorded from the Gulf of Mexico (Pérez-Pech et al. 2020; Romano, 2009; Romano et al. 2011; Santos et al. 2018), mainly from the more explored northern region, where *Coronarctus* is represented by *C. disparilis* Reunad-Mornant, 1987, *C. laubieri* Reunad-Mornant, 1987, *C. stylisetus* Reunad-Mornant, 1987, and *C. mexicus* Romano III, Gallo, D'Addabbo, Accogli, Baguley & Montagna, 2011 (Romano et al. 2011; Pérez-Pech et al. 2020). In the Mexican Economic Exclusive Zone (EEZ), five juvenile *Coronarctus* specimens were recently recorded by Pérez-Pech et al. (2020), namely from *C. mexicus* and another undescribed species. The latter possessed larvae much larger than those of other species of *Coronarctus*, which have uniquely-shaped secondary clavae. The organisms could not be described as a novel species due to the absence of corresponding adults.

Coronarctus specimens were collected from the meiofauna of the southern Gulf of Mexico as part of the oceanographic campaigns XIXIMI-3 and XIXIMI-7 conducted by the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE) and the Consorcio de Investigación del Golfo de México (CIGoM). In this study, we perform an interspecific geometric morphometric analysis of the secondary clavae and claws among congeners of the 11 recognized *Coronarctus* to assess morphological distinctiveness, from which we describe a new species. Based on these results, we also provide an updated identification key for the genus, thereby expanding upon the framework of (Gomes-Junior et al. 2020).

Materials and methods

Sampling

Coronarctus specimens were obtained during the oceanographic campaigns XIXIMI-3 and XIXIMI-7. Sediment samples were collected in the Mexican Exclusive Economic Zone (EEZ) of the Gulf of Mexico aboard the oceanographic vessel R/V Justo Sierra (UNAM) as part of the Gulf of Mexico Research Consortium (CIGoM) project. Five *Coronarctus* specimens were found on three samples from different geositions and depths (Fig. 1, Table 1).

Specimens were extracted from the sediment matrix according to Cisterna-Céliz et al. (2019) by decantation and

flotation with colloidal silica (Ludox™ with 1.15 g cm^{-3} of specific gravity), and were then sieved through a $1,000 \text{ }\mu\text{m}$ mesh, collected on a $45 \text{ }\mu\text{m}$ mesh (the process was repeated three times to maximize the number of specimens extracted), and fixed in 4% formalin. Specimens were mounted on microslides under a coverslip and treated with a graded series of glycerin (10, 25, 75, and 100%) before sealing the coverslip with nail polish (Anguas-Escalante et al. 2020; Pérez-Pech et al. 2020).

Morphological and morphometric analyses

Tardigrades were observed on a Zeiss™ Scope.A1 microscope at 20, 40, and 100x magnification using differential interference contrast (DIC). Measurements and photographs were obtained using a Labomed® camera and PixelPro 3.0 software. The key to the genera by Hansen and Kristensen (2020) and Fontoura et al. (2017) was used for genus identification and the original species descriptions to ascertain specific identity (Gomes-Junior et al. 2020; Hansen 2007; Renaud-Mornant 1974; Renaud-Mornant 1987; Romano et al. 2011; Saulenko et al. 2022). Our specimens exhibited a distinctive combination of morphological characters that differentiated them from all known congeners, including the position of the median cirrus, the specific arrangement and number of accessory spines on the claws of legs I–IV, as well as unique morphologies of cephalic cirri, secondary clavae, and sensory organs. To quantitatively support these qualitative observations, we conducted a detailed morphometric analysis focusing on key structures known to be taxonomically informative. Specifically, measurements and shape analyses were performed on the secondary clavae and the claws of legs I and IV (both internal and external claws), structures previously demonstrated as reliable diagnostic characters for species delimitation within the group (Gomes-Junior et al. 2020) (Fig. 2, Table 2). This integrative approach combining qualitative and quantitative data strengthens the resolution of species boundaries and provides a robust framework for morphological differentiation (Table 3).

Morphometric data were obtained from five morphological structures; the secondary clavae, internal claw four, external claw one, and external claw four, which are considered reliable for species identification (Fig. 2, Table 2)(Gomes-Junior et al. 2020) and were taken from illustrations in the

Table 1 Sampling sites where *Coronarctus* specimens were collected during oceanographic campaigns XIXIMI-3 and XIXIMI-7

Cruise	Station	Depth (m)	Latitude (decimal degrees)	Longitude (decimal degrees)	Number of specimens	Sampling date
XIXIMI-3	E27	1,182	24.004233	−86.80632	2	2013–02–28
XIXIMI-7	B11	2,400	24.014517	−96.00765	1	2019–05–10
XIXIMI-7	F38	2,822	21.008183	−94.00295	2	2019–06–08

Mexican Economic Exclusive Zone of the Gulf of Mexico

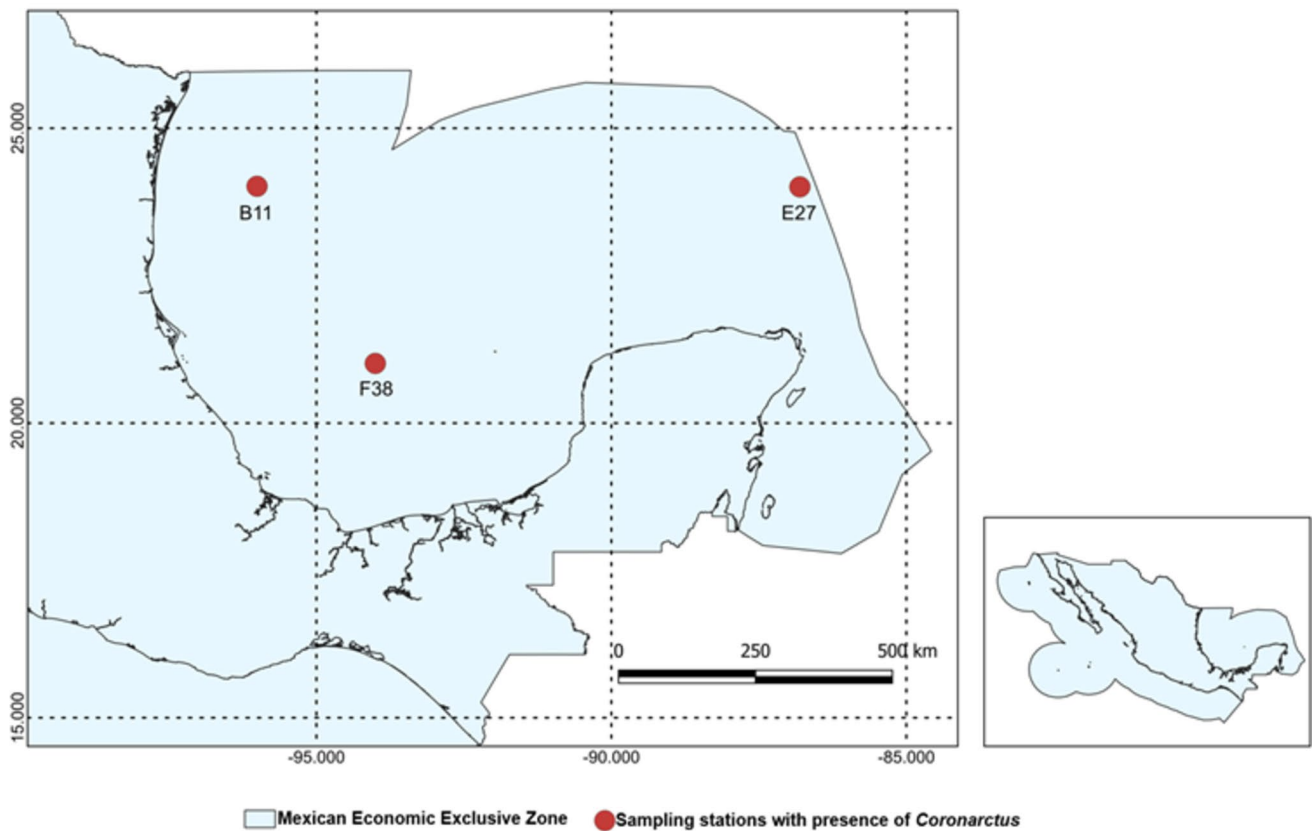


Fig. 1 Location of sampling stations with the presence of *Coronarctus*

original descriptions of the eleven described species of *Coronarctus*. In certain cases, these had to be made from available images of the species (Gomes-Junior et al. 2020; Hansen 2007; Renaud-Mornant 1974; Renaud-Mornant 1987; Romano et al. 2011; Saulenko et al. 2022). We performed six geometric analyses from the morphological structures and the different positions of each: (1) secondary clavae in the ventral region, (2) secondary clavae in the dorsal region, (3) the internal claw of leg I, (4) the external claw of leg I, (5) the internal claw of leg IV and (6) the external claw of leg IV.

A TPS file of each analysis was compiled with the tpsUtil software before importing images into the tpsdig2 software where the corresponding landmarks and semi-landmarks were placed. The shape of structures was defined by landmarks type I (LI) and (LII) (Zelditch et al. 2004). Semi-landmarks were defined using digital curves of equidistant points on photographs of aedeagus spines in lateral view with TPS tpsDig 1.40 software (Rohlf 2004).

The shape of secondary clavae in ventral view was defined by eight LM1 (1–6, 11, 12) and four LM2 (7–10) (Fig. 2A); L1 and L2 correspond to the medial bases of left and right internal cirri, respectively; L3 and L4 mark the

lateral bases of left and right medial cirri; L5 and L6 indicate the anterolateral margins of the left and right clavae; L7 and L8 are positioned at the inner curvature near the primary spines; L9 and L10 represent the posteromedial bases of the left and right clavae, and L11 and L12 mark their posterolateral tips. The shape of secondary clavae in dorsal view was defined by five LMI (1–3, 8, 9) and four LMII (4–7) (Fig. 2B); L1 is located at the central dorsal midline, at the base of the medium cirrus; L2 and L3 indicate the anterolateral margins of the left and right clavae; L4 and L5 are placed at the inner curvature adjacent to anterior lobes of clavae; L6 and L7 represent the posteromedial bases; and L8 and L9 mark the posterolateral tips of the left and right clavae, respectively. The shape of internal and external claws was represented by three LM1 each (Fig. 2C). For both internal and external claws, L1 corresponds to the proximal articulation point with the leg, L2 to the first major inflection point along the proximal shaft, and L3 to the tip of the main branch of the claw.

Once the landmarks were digitized, the files were imported into RStudio 4.3.3 software, where Procrustes analysis was performed to determine which combination of

Table 2 Description and location of landmarks for the cephalic region (ventral and dorsal) as well as the internal and external claws of legs I and IV

Landmark	Type	Unit	Description
1	1	Head (ventral)	Insertion of the left internal cirrus
2	1	Head (ventral)	Insertion of the right internal cirrus
3	1	Head (ventral)	Insertion of the left external cirrus
4	1	Head (ventral)	Insertion of the right external cirrus
5	2	Head (ventral)	Upper vertical crest of the left lobe of the secondary clava
6	2	Head (ventral)	Upper vertical crest of the right lobe of the secondary clava
7	2	Head (ventral)	Crest of the left anterior lobe of the secondary clava
8	2	Head (ventral)	Crest of the right anterior lobe of the secondary clava
9	2	Head (ventral)	Crest of the left posterior lobe of the secondary clava
10	2	Head (ventral)	Crest of the right posterior lobe of the secondary clava
11	2	Head (ventral)	Lower vertical crest of the left lobe of the secondary clava
12	2	Head (ventral)	Lower vertical crest of the right lobe of the secondary clava
Curve	3	Head (ventral)	Curve between lm5 and lm7
Curve	3	Head (ventral)	Curve between lm6 and lm8
Curve	3	Head (ventral)	Curve between lm7 and lm9
Curve	3	Head (ventral)	Curve between lm8 and lm10
Curve	3	Head (ventral)	Curve between lm9 and lm11
Curve	3	Head (ventral)	Curve between lm10 and lm12
1	1	Head (dorsal)	Insertion of the median cirrus
2	1	Head (dorsal)	Upper vertical crest of the left lobe of the secondary clava
3	1	Head (dorsal)	Upper vertical crest of the right lobe of the secondary clava
4	1	Head (dorsal)	Crest of the left anterior lobe of the secondary clava
5	2	Head (dorsal)	Crest of the right anterior lobe of the secondary clava
6	2	Head (dorsal)	Crest of the left posterior lobe of the secondary clava
7	2	Head (dorsal)	Crest of the right posterior lobe of the secondary clava
8	2	Head (dorsal)	Lower vertical crest of the left lobe of the secondary clava
9	2	Head (dorsal)	Lower vertical crest of the right lobe of the secondary clava
Curve	3	Head (dorsal)	Curve between lm2 and lm4
Curve	3	Head (dorsal)	Curve between lm3 and lm5
Curve	3	Head (dorsal)	Curve between lm4 and lm6
Curve	3	Head (dorsal)	Curve between lm5 and lm7
Curve	3	Head (dorsal)	Curve between lm6 and lm8
Curve	3	Head (dorsal)	Curve between lm7 and lm9
1	1	Head (dorsal)	Insertion of the median cirrus
2	1	Head (dorsal)	Upper vertical crest of the left lobe of the secondary clava
3	1	Head (dorsal)	Upper vertical crest of the right lobe of the secondary clava
4	1	Head (dorsal)	Crest of the left anterior lobe of the secondary clava
5	2	Head (dorsal)	Crest of the right anterior lobe of the secondary clava
6	2	Head (dorsal)	Crest of the left posterior lobe of the secondary clava
7	2	Head (dorsal)	Crest of the right posterior lobe of the secondary clava
8	2	Head (dorsal)	Lower vertical crest of the left lobe of the secondary clava
9	2	Head (dorsal)	Lower vertical crest of the right lobe of the secondary clava
Curve	3	Head (dorsal)	Curve between lm2 and lm4
Curve	3	Head (dorsal)	Curve between lm3 and lm5
Curve	3	Head (dorsal)	Curve between lm4 and lm6
Curve	3	Head (dorsal)	Curve between lm5 and lm7
Curve	3	Head (dorsal)	Curve between lm6 and lm8
Curve	3	Head (dorsal)	Curve between lm7 and lm9
1	2	Internal and external claws	Anterior part of the base of the claw
2	2	Internal and external claws	Posterior part of the base of the claw
3	2	Internal and external claws	Claw tip
Curve	3	Internal and external claws	Curve between lm2 and lm3
Curve	3	Internal and external claws	Curve between lm3 and lm1

Table 3 *Coronarctus xiximii* sp. nov. measurements (μm) of the type series. n = number of specimens measured

Character	Holotype		Paratypes			
	Female	n	Adults (females)		Larvae	
			Range	n	Range	n
Body length	331.6	2	253–325.7	2	195.5–220.7	2
Body width	74.9	2	66.8–87.2	2	39.2–86.5	2
Median cirrus	5.4	1	4.2	1	2.6	1
Internal cirrus	4.6	2	4.9–5.5	2	4.1–4.5	2
External cirrus	4.7	2	5.3–8.4	1	4.2	1
Lateral cirrus	4	-	-	2	4.6–5	2
Primary clava	6	2	5–5.8	-	-	-
Cirrus B	7.3	-	-	-	-	-
Cirrus C	17.8	1	11.2	-	-	-
Cirrus E	21.7	2	18.6–19.6	2	4.6–5	2
Coxal process of leg IV	16.4	-	-	-	-	-
Sensory organ of IV	2.5	-	-	-	-	-
Internal claw of leg I	22.7	2	22.3–2	2	17.2–19.4	2
External claw of leg I	17.3	2	14.1–15.6	2	16.9–18.5	2
Internal claw of leg IV	39.4	2	32.6–35.7	2	21.3–22.7	2
External claw of leg IV	17.2	2	16.8–17.4	2	20.7–21.7	2

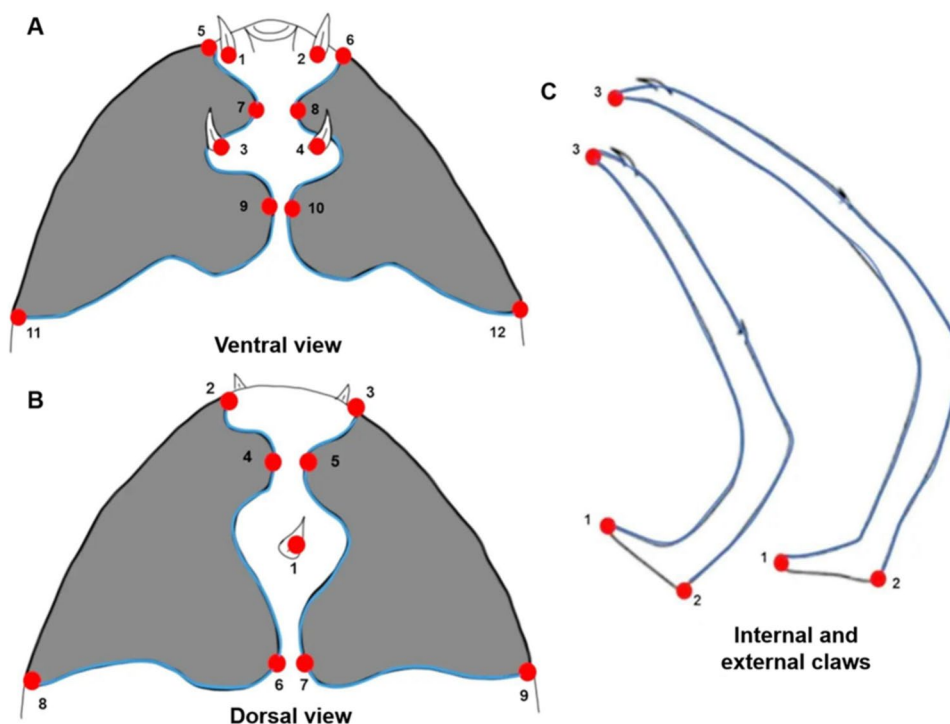
scale change and rigid movements allows for the optimal superposition of different configurations of landmarks that represent structures (Torcida and Perez 2012), with the “gpa-gen()” function of “geomorph” package. Once the analysis

had been performed, the files were saved again in TPS format. The data were plotted using the “plotAllSpecimens()” function in RStudio 4.3.3 (Supplementary information).

A Principal Component Analysis (PCA), a multivariate statistical procedure that normally seeks linear combinations of the original variables that best represent the variability present in the data, was performed. Thus, a few linear combinations, which will be the principal components, would be sufficient to understand the information contained in the data. The objective is to reveal patterns in the correlated variables to classify the samples into possible groups (Laskar et al. 2013). This was performed with the “gm.prcomp()” function of the “geomorph” package and then the Principal Component 1 (PC1) and the Principal Component 2 (PC2) were graphed in Rstudio 4.3.3.

The highest proportion of shape variation in the data sets was quantified by means of principal component analyses (PCA) from adjusted coordinates (Zelditch et al. 2004). Shape variation was analyzed with the first two PCs and shape changes were visualized with the Thin-Plate Spline technique by means of deformation grids. A. The objective was to explore whether the variation of shape structures allows the segregation of species within multidimensional spaces (Laskar et al. 2013). The PCAs were performed with the “gm.prcomp()” function of the “geomorph” package and then the Principal Component 1 (PC1) and the Principal Component 2 (PC2) were graphed in Rstudio 4.3.3.

Finally, to provide a geographic context for the new species, we include a distribution map of all known species

Fig. 2 Location of the landmarks and semilandmarks on the ventral cephalic region; (A) dorsal; (B) internal and external claws (C). Red dots: landmarks, blue curves: semilandmarks

within the genus. The map was drawn up using all available geographic records of *Coronarctus* from original descriptions and records in additional publications (Gomes-Junior et al. 2020; Hansen 2007; Hansen et al. 2001; Pérez-Pech et al. 2020; Renaud-Mornant 1974; Renaud-Mornant 1975; Renaud-Mornant 1980; Renaud-Mornant 1987; Romano et al. 2011; Saulenko et al. 2022). These records were compiled into decimal coordinates to be processed in QGIS software and displayed on a world map (QGIS.org 2025).

Results

Morphometric analysis

According to the six Principal Component Analysis (PCAs), all *Coronarctus* members were segregated in the multidimensional morphospace, which supported shape differences among species (Figs. 3, 4, 5). The analyses corresponding to the shape of internal claws IV and ventral cephalic region support *Coronarctus* sp. nov. as well-differentiated taxon. In the case of the external claws of leg I, Principal Component (PC) 1 and PC 2 represent

52.56% and 33.65% of the total variance respectively. In addition, a clustering of three species is observed: *C. fastigatus* Reunad-Mornant, 1987, *C. stylisetus* and *C. verrucatus* Hansen, 2007 (Fig. 3A, B). In the rest of species, except *C. sonne* Saulenko, Maiorova, Martínez Arbizu & Mordukhovich, 2022, and *Coronarctus* sp. nov., they are observed to be very closely related. The shape of the claws between *Coronarctus* sp. nov. and *C. sonne* is very similar; only in *Coronarctus* sp. nov. is it more curved (Figs. 3A, B). In the internal claws of leg I, PC 1 and PC 2 represent 59.18% and 23.47% of the total variance; once again, clustering is observed in the same three species of the *C. stylisetus* group, while in the rest of species there is no clustering and they are more dispersed except for *Coronarctus* sp. nov., *C. sonne* and *C. disparilis*, which are grouped together. There is a similar pattern in the shape as in the external claw of leg I; *Coronarctus* sp. nov. is differentiated from *C. sonne* and *C. disparilis* mainly by the curvature of the claws (Fig. 3C, D).

For external claws of leg IV PC 1 has a value of 48.67%, while PC 2 represents 33.65% of the total variance. Again, clustering is observed among species in the *C. stylisetus* group. The rest of the species are gathered

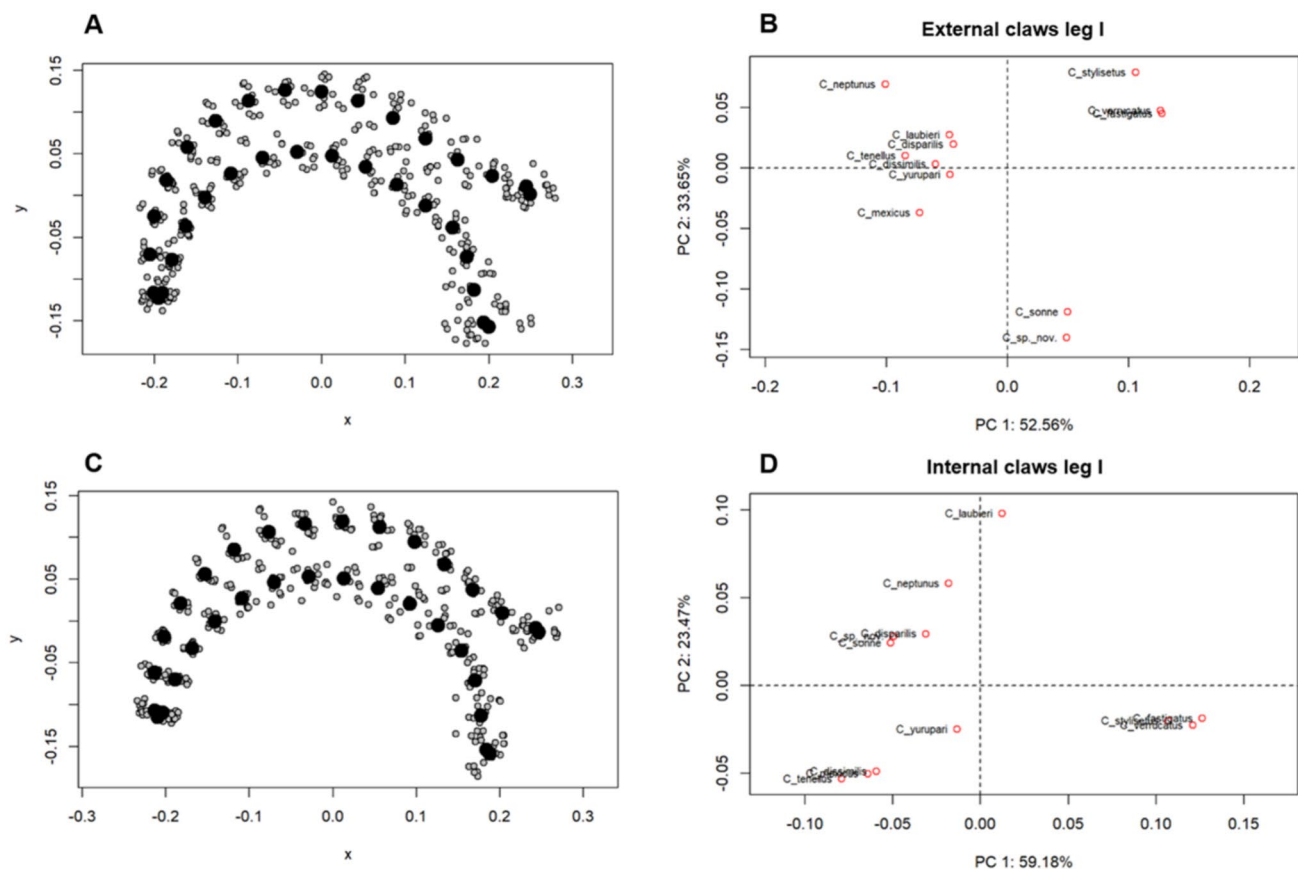


Fig. 3 Procrustes analysis and Principal Component Analysis of the external claws of leg I (A & B) and internal claws of leg I (C & D)

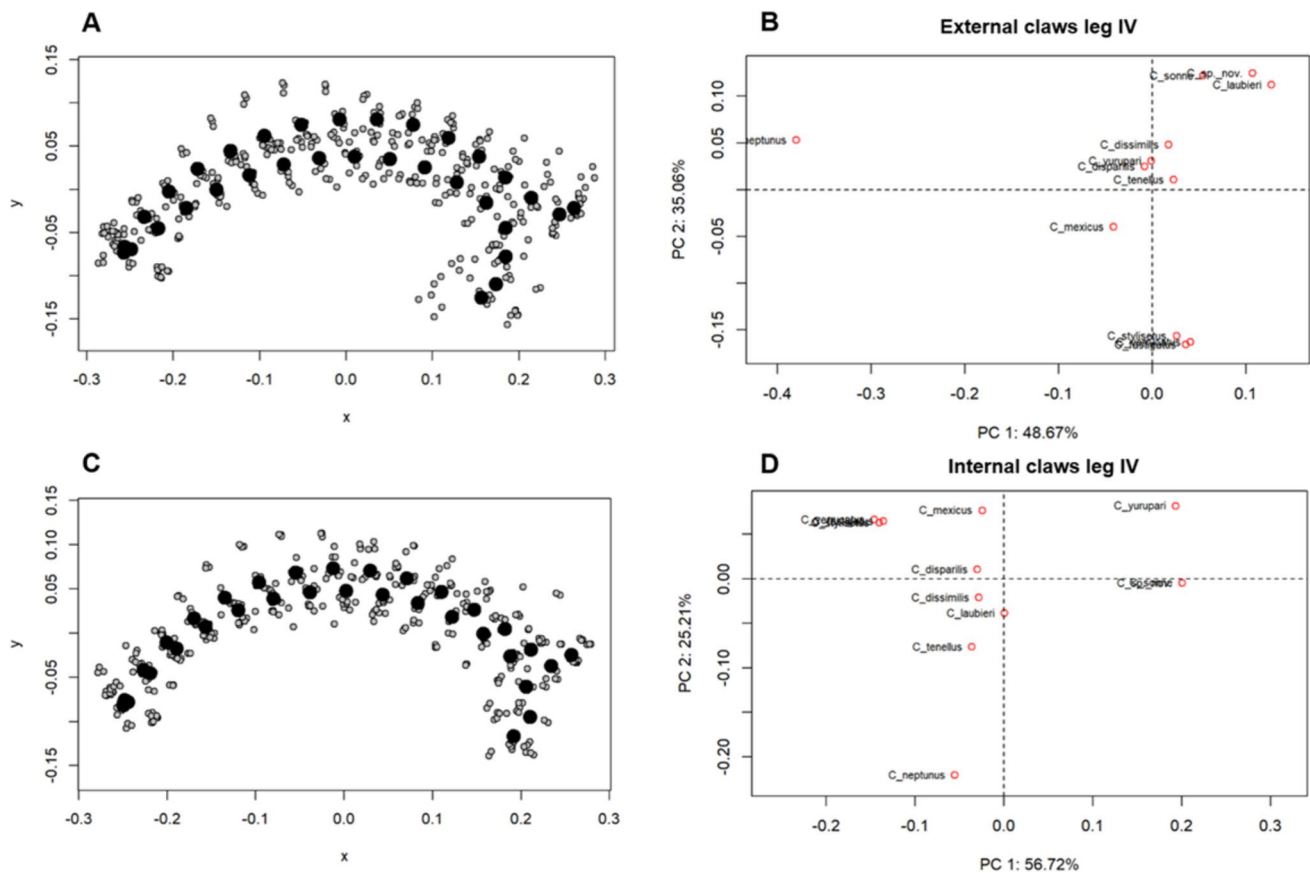


Fig. 4 Procrustes analysis and Principal Component Analysis of the external claws of leg IV (**A** & **B**) and internal claws of leg IV (**C** & **D**)

tightly together in two groups: *Coronarctus* sp. nov., *C. laubieri*, and *C. sonne* are in one group, while all other species except for *C. neptunus* Gomes-Júnior, E. Santos, da Rocha, P.J.P. Santos & Fontoura, 2020, which is far from all the species, form another group. *Coronarctus* sp. nov. differs from *C. sonne* and *C. laubieri* in that the shape of the external claws IV is more curved (Fig. 4A, B). With regard to the internal claws of leg IV, PC 1 and PC 2 show 56.72% and 25.21% variance respectively, and clustering is observed in the species in the *C. stylisetus* group. No grouping is evident in the rest of the species except for *Coronarctus* sp. nov. and *C. sonne*, while *C. neptunus* again is the farthest away. There are no evident differences between the shapes of *Coronarctus* sp. nov. and *C. sonne* (Fig. 4C, D).

In the ventral cephalic region, PC 1 and PC 2 show 51.1% and 28% total variance respectively. Most of the species are closely grouped: *Coronarctus* sp. nov. is in close proximity to *C. laubieri*, while *C. fastigatus* is the furthest away. With regard to variations in shape, *Coronarctus* sp. nov. and *C. laubieri* are easily recognized by a deep indentation between their anterior and posterior lobes; the posterior lobes are very similar in shape and are

thinner than the anterior lobes where there is more difference. The crests are more evident (Fig. 5A, B) in *Coronarctus* sp. nov. Finally, in the dorsal cephalic region, PC 1 and PC 2 show 63.16% and 17.49% respectively. *Coronarctus* sp. nov. is grouped with most of the species except for *C. stylisetus*, *C. yurupari* Gomes-Júnior, E. Santos, da Rocha, P.J.P. Santos & Fontoura, 2020, and *C. neptunus* which is found further away from all of them. The shape of the dorsal lobes is very similar in all species, which is why they are grouped together. *C. neptunus* has the most distinct shape because it does not have evident lobes (Fig. 5C, D).

Taxonomic Accounts

Phylum Tardigrada Doyère, 1840

Class Heterotardigrada Marcus, 1927

Order Arthrotardigrada Marcus, 1927

Family Coronarctidae Renaud-Mornant, 1974

Genus *Coronarctus* Renaud-Mornant, 1974

Coronarctus xiximii sp. nov.

Figs. 6, 7, 8, 9, 10.

<https://zoobank.org/A41E9D07-273F-48F9-85C1-5AA3E6E518C0>

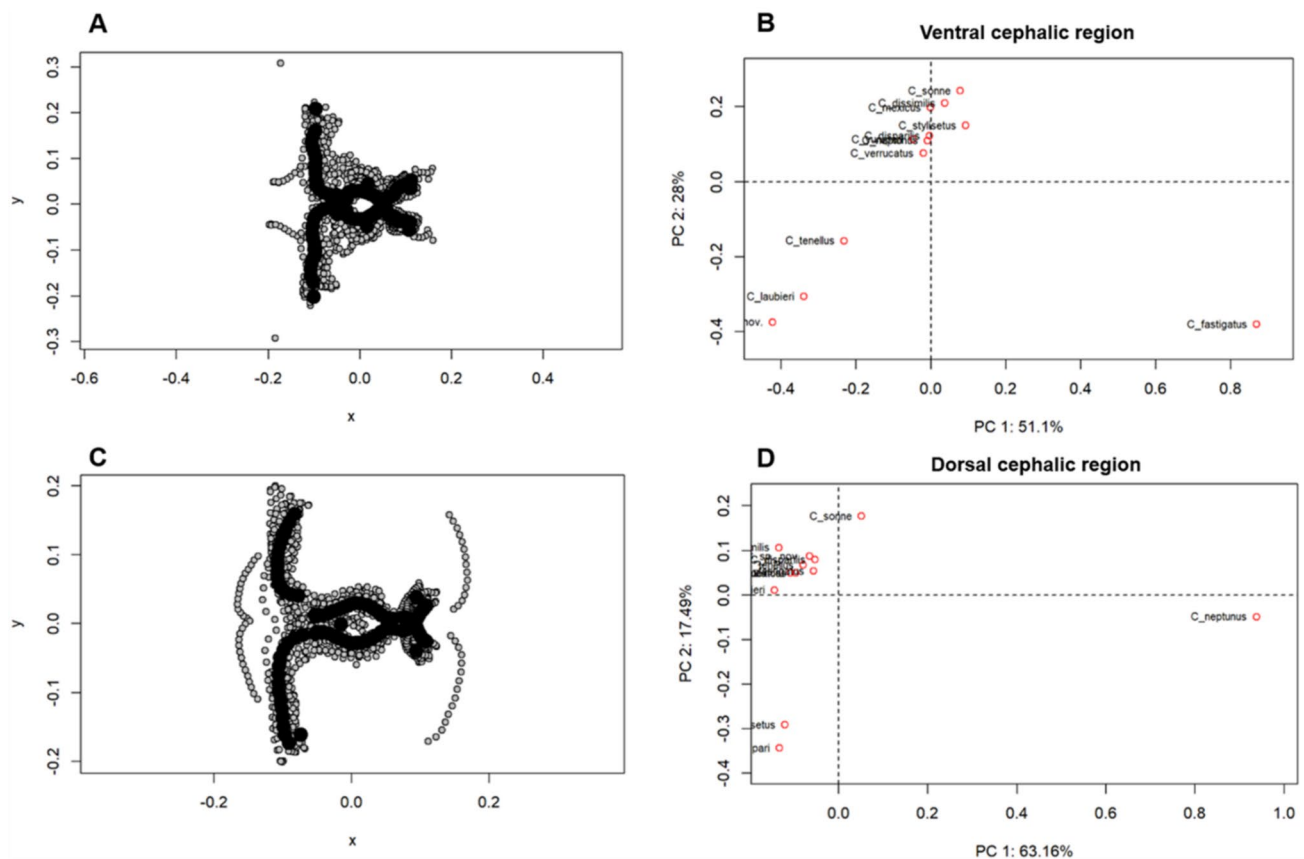


Fig. 5 Procrustes analysis and Principal Component Analysis of ventral (A & B) and dorsal cephalic region (C & D)

Type locality

Mexican Exclusive Economic Zone (EEZ) of the Gulf of Mexico at 2,822 m depth at station F38 (21.008183, −94.00295).

Type material and type repository

Female holotype (CNAC-Ttar000495) at a depth of 2,822 m at the sampling station F38 (21.008183, −94.00295) and four paratypes; two adults of unknown sex CNAC-Ttar000496 at a depth of 2,400 m at the sampling station B11 (24.014517, −96.00765), CNAC-Ttar000497 at a depth of 2,822 m at the sampling station F38 (21.008183, −94.00295). Two larvae with two claws CNAC-Ttar000498 and CNAC-Ttar000499, both at a depth of 1,182 m at the sampling station E27 (24.004233, −86.80632). All specimens have been deposited in the Colección de Tardígrados in the Colección Nacional de Ácaros (CNAC) del Instituto de Biología, UNAM.

Etymology

The specific epithet refers to “Xiximi”, which is the name given to oceanographic campaigns in the Gulf of Mexico Research Consortium (CIGoM). Xiximi means “to spill” in the ancient Nahuatl language.

Diagnosis

Tardigrades with reduced leaf-like cephalic appendages. Median cirrus inserted between the anterior dorsal lobes and posterior lobes of the secondary clavae (Fig. 7C). Spherical primary clavae (Fig. 8A). Flattened secondary clavae have two dorsal lobes and two ventral lobes each. The posterior dorsal lobes are very wide and closely joined. The anterior ventral lobes are separated from the posterior lobes by a deep indentation (Fig. 7B, C). Cuticle smooth. Sensory organs on each pair of legs and additional flexible spine-like processes on legs IV present (Fig. 8C). Heteromorphic claws: the claws of legs IV are much longer than the claws of the first three pairs of legs. On legs I–III the external claws are slightly shorter than the internal claws, while on legs IV the internal claws are twice the size of the external claws. All claws are simple (Fig. 8C, D).

Description of the holotype

Adult female 331.6 µm long and 74.9 µm wide (Figs. 6A, 7A). The cylindrical, elongated body is covered by a smooth, transparent cuticle. The head, narrower than the body, comprises two parts and features short leaf-like cephalic cirri: the first conical part features paired internal (4.6 µm long) and external cirri (4.7 µm long), and the unpaired median

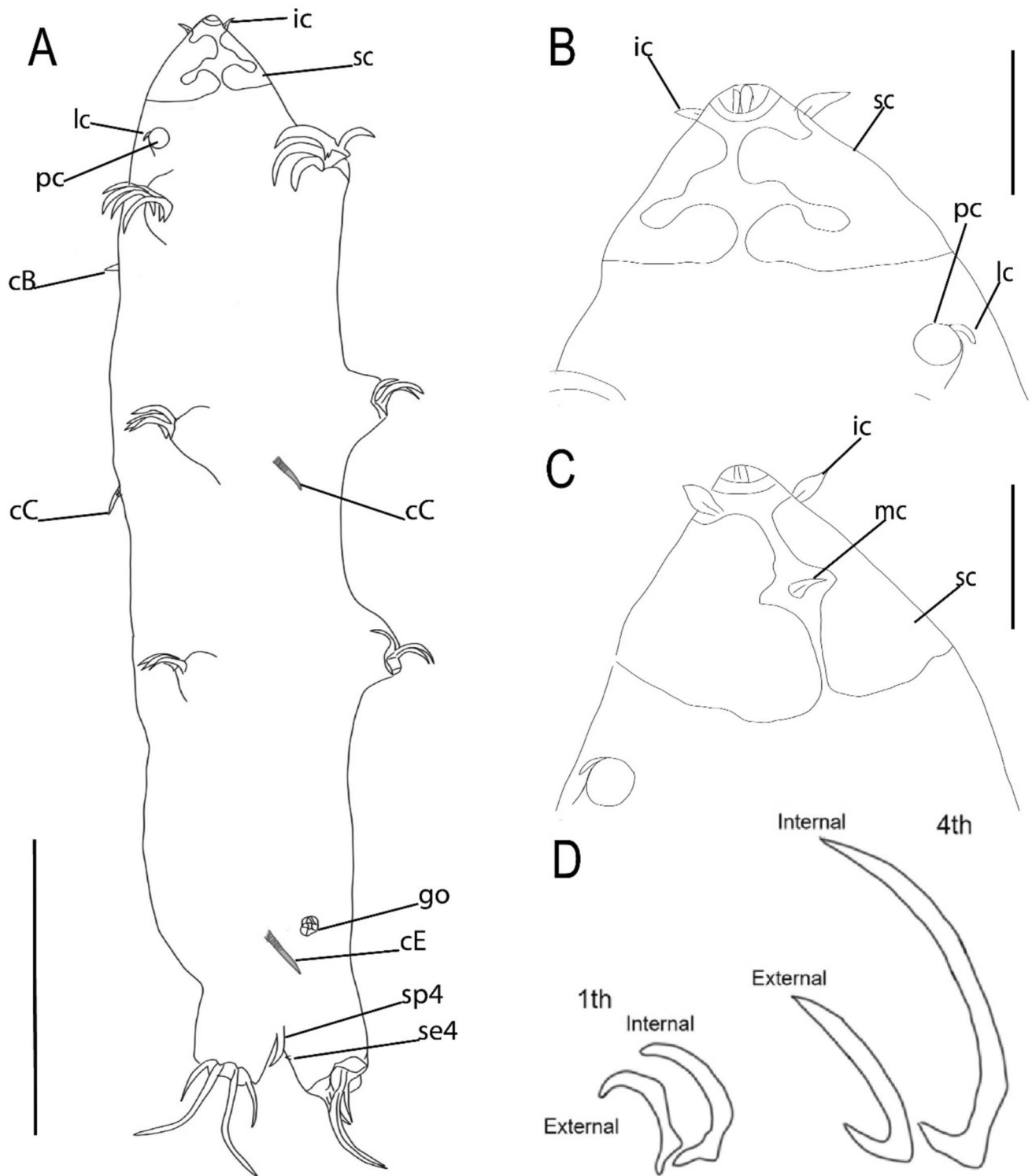


Fig. 6 *Coronarctus xiximii* sp. nov. Adult. **A** Ventral habitus; **B** Ventral view of the head; **C** Dorsal view of the head; **D** Claws of the first and fourth pair of legs. Abbreviations. *cB* cirrus B, *cC* cirrus

C, *cE* cirrus E, *ic* internal cirrus, *lc* lateral cirrus, *mc* median cirrus, *pc* primary clava, *sc* secondary clava, *se4* sensory organ on leg IV, *sp4* coxal process on leg IV. Scale: 100 μ m (**A**), 20 μ m (**B** and **C**)

Fig. 7 *Coronarctus xiximii* sp. nov. Adult. **A** Ventral habitus; **B** Ventral lobes of the secondary clavae and internal cirrus; **C** Dorsal lobes of the secondary clavae and median cirrus. Abbreviations. *ic* internal cirrus, *mc* median cirrus, *mo* mouth, *sc* secondary clava. Scale: 50 μ m (**A**), 20 μ m (**B** and **C**)

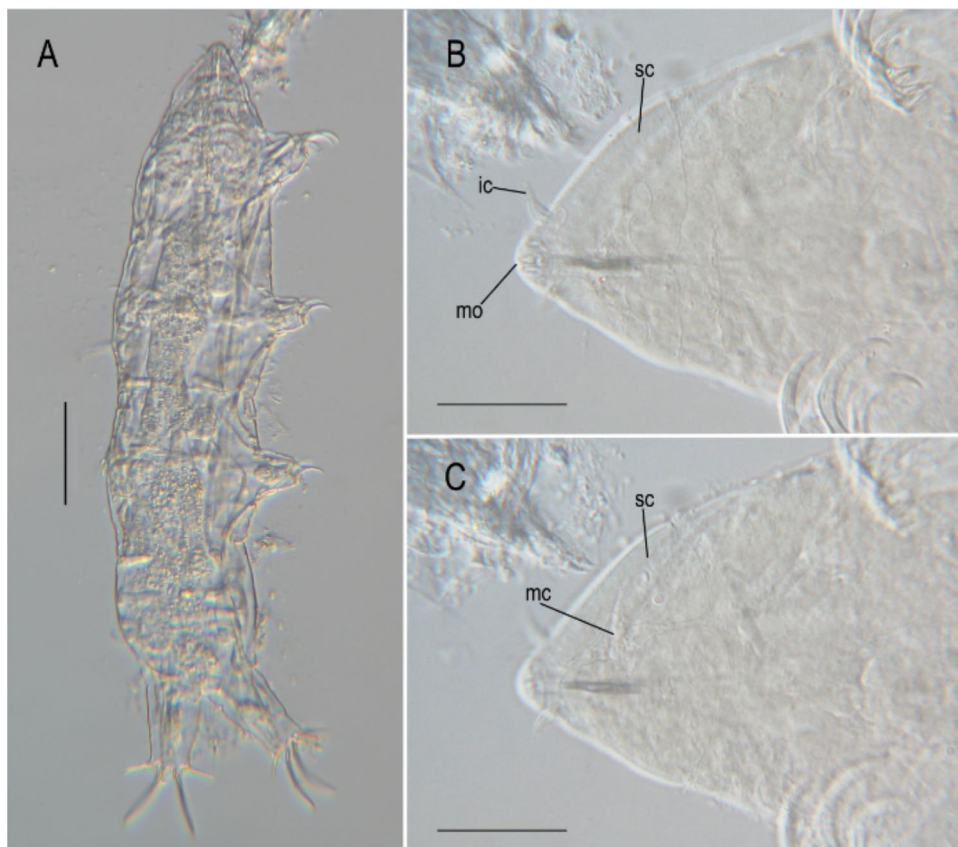


Fig. 8 *Coronarctus xiximii* sp. nov. Adult. **A** Primary clava and lateral cirrus; **B** Cirrus C; **C** Legs IV showing the sensory organ and coxal process; **D** Claws of leg IV. Abbreviations. *cC*: cirrus C, *lc*: lateral cirrus, *pc*: primary clava, *se4*: sensory organ on leg IV, *sp4*: coxal process on leg IV. Scale: 20 μ m (**A-D**)

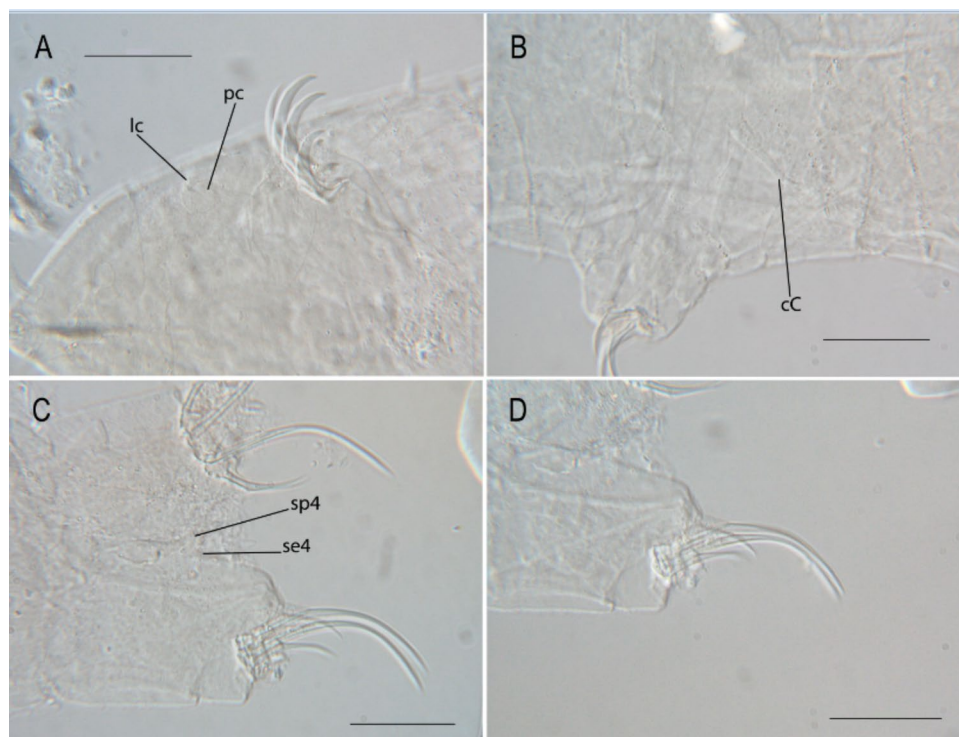
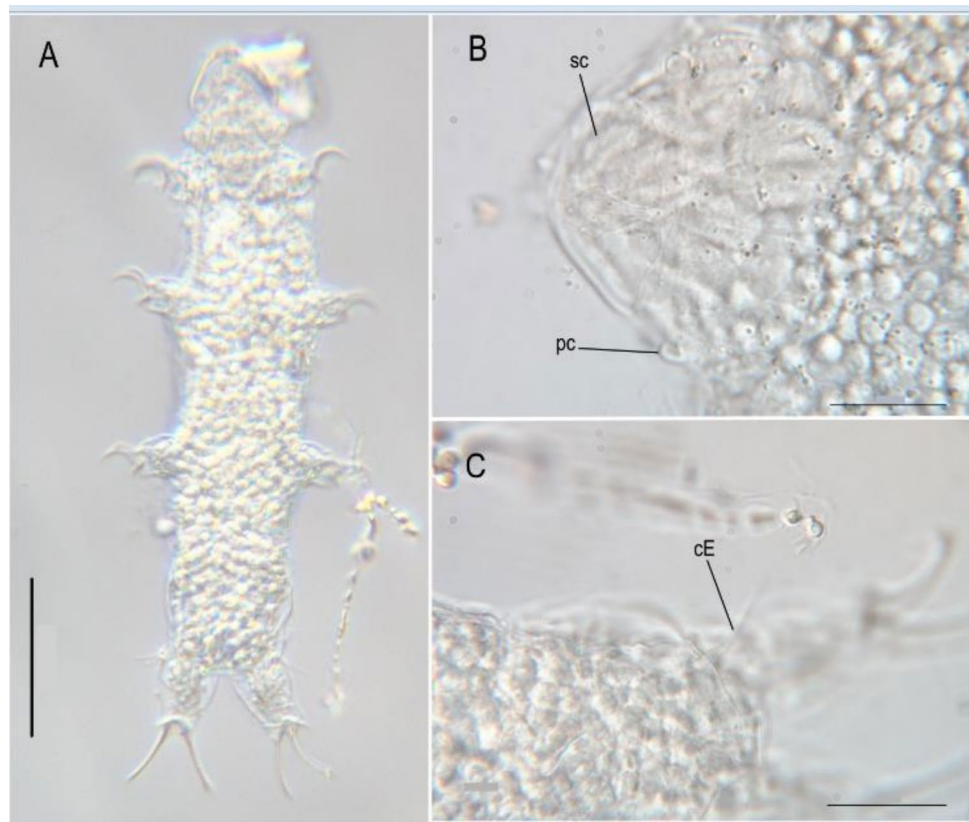


Fig. 9 *Coronarctus xiximii* sp. nov. Larva. **A** Ventral habitus; **B** Ventral view of the head; **C** Dorsal view of the head. *Abbreviations.* *cE* cirrus E, *ic* internal cirrus, *lc* lateral cirrus, *mo* mouth, *pc* primary clava, *sc* secondary clava. Scale: 50 μ m (**A**), 20 μ m (**B** and **C**)



cirrus (5.4 μ m long) (Figs. 6B–C, 7B–C); the posterior second part features the spherical primary clavae and the leaf-like lateral cirri A (Figs. 6B, 8A). Primary clavae (6 μ m in diameter) are separated from the short lateral cirri A (4 μ m long).

The flattened secondary clavae have two dorsal and two ventral lobes each. The dorsal and ventral posterior lobes are closely joined. The two dorsal posterior lobes are very wide and closely joined (Figs. 6C, 7C). The anterior ventral lobes are separated from the posterior lobes by a deep indentation (Figs. 6B, 7B). The median cirrus is inserted between the anterior and posterior dorsal lobes at about equal distance from the mouth and posterior edges of secondary clavae (Figs. 6C, 7C).

Trunk cirri B (7.3 μ m long), C (17.8 μ m long), and E (21.7 μ m long) are present as typical of the genus. Each trunk cirrus consists of a very short cirrophore, accordion-like scapus and tubular flagellum (Figs. 6A, 8B).

The mouth opening is terminal and surrounded by cuticular folds. Details of the buccal apparatus were not observed (Fig. 7B).

The legs are short and robust. The fourth pair of legs is longer than the first three pairs. Short spine-like sensory organs are present on all pairs of legs. A flexible spine-like process (16.4 μ m long) is inserted dorsally in the coxa of leg IV above the sensory organ (Fig. 8C).

The claws, featuring basal spurs and connected by a membrane, display heteromorphy: the claws on legs IV (external claws 16.1 and 17.2 μ m long/internal claws 39.5 and 37.7 μ m long) are much longer than the claws on the first three leg pairs (legs I: external claws 17.2 and 17.3 μ m long/internal claws 22.7 and 22.5 μ m long). On all legs, the external claws are shorter than the internal claws. On legs IV, the internal claws are almost twice as long as the external claws (Figs. 6D, 8A, 8D). The claws on legs I are more robust than those on legs II and III. Only the main tip of all claws is visible. All claws are simple: just a main spine.

The gonopore is rosette-like and the anus could not be observed due to the unfavorable position of the specimen (Fig. 6A).

Larva

The body is 195.5–220.7 μ m long and 39.2–86.5 μ m wide (Figs. 9A, 10A). The cylindrical, elongated body is covered by a smooth, transparent cuticle. The head features paired internal (4.1–4.5 μ m long) and external cirri (4.2 μ m long), the unpaired median cirrus (2.6 μ m long), the spherical primary clavae (4.6–5 μ m long) and leaf-like lateral cirri A (3–3.4 μ m long) (Figs. 9B, 10B,C).

The flattened secondary clavae have two dorsal and two ventral lobes each. The dorsal and ventral posterior lobes are closely joined. The two dorsal posterior lobes

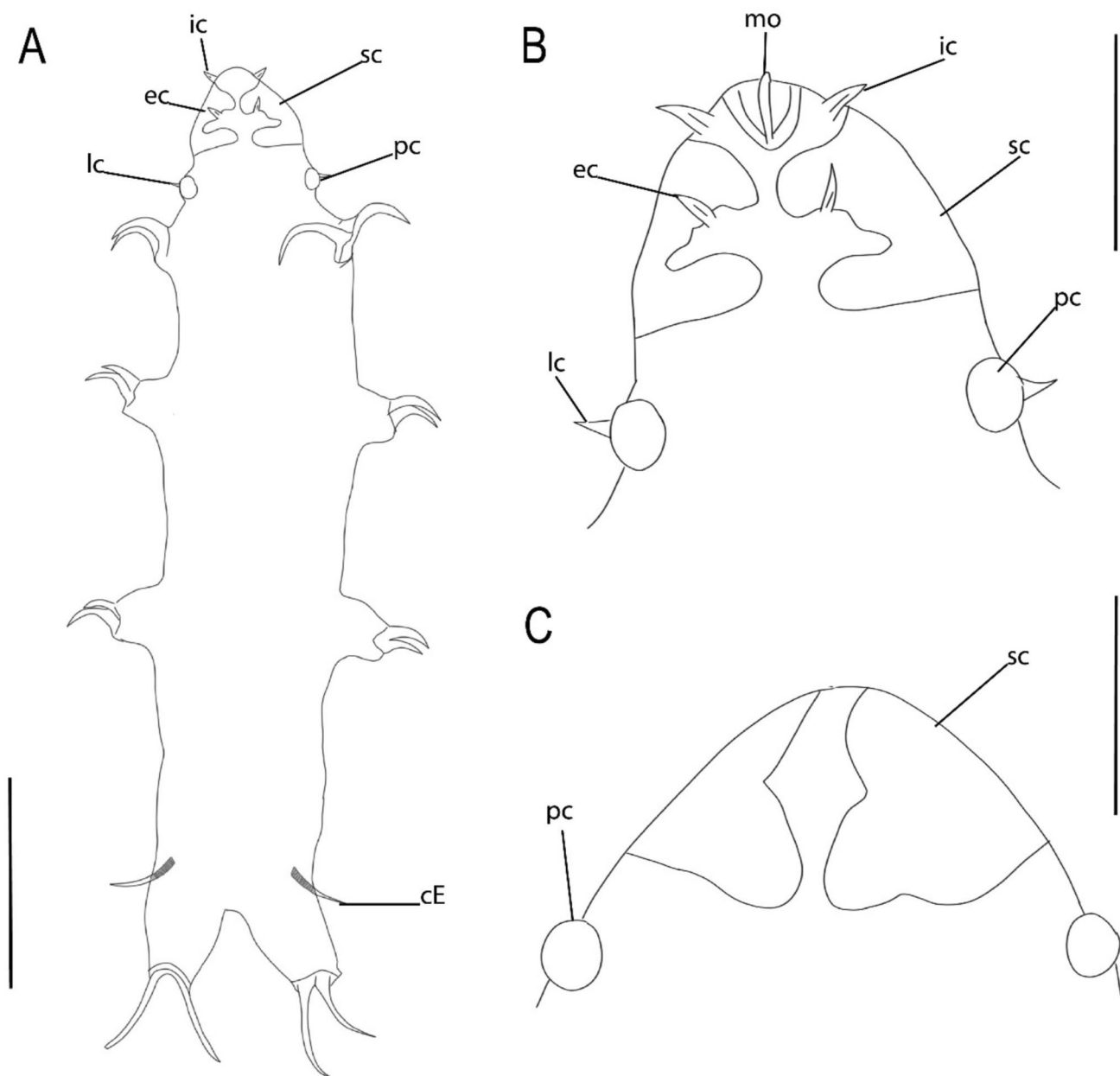


Fig. 10 Larva *Coronarctus xiximii* sp. nov. **A** Ventral habitus; **B** Dorsal view of the head; **C** Cirrus E. *Abbreviations.* *cE* cirrus E, *pc* primary clava, *sc* secondary clava. Scale: 50 μm (**A**), 20 μm (**B** and **C**)

are very wide and closely joined (Figs. 9B, 10C). The anterior ventral lobes are separated from the posterior lobes by a deep indentation (Fig. 10B). The median cirrus is inserted between the anterior and posterior dorsal lobes at about equal distance from the mouth and posterior edges of the secondary clavae.

Only the trunk cirri E (17.1 μm long) is present as is typical for the genus. It consists of a very short cirrophore, an accordion-shaped scape, and a tubular flagellum (Figs. 9C, 10A).

The mouth opening is terminal and surrounded by cuticular folds (Fig. 9B). The oval pharyngeal bulb (16–18.5 μm long and 12.9–13.9 μm wide) is devoid from placoids.

The legs are short and robust. The fourth pair of legs is longer than the first three pairs (Fig. 10A). Sensory organs and coxal processes were not observed.

Only two claws were observed on each leg, featuring basal spurs and connected by a membrane and display heteromorphy: the claws on legs IV (20.7–22.7 μm long) are longer than claws on the first three leg pairs (on legs I:

17.2–18.7 μm long). All claws are simple: just a main spine (Figs. 9A, 10A).

Remarks

The currently known *Coronarctus* species are classified into two main groups based on the size of cephalic appendages and the size ratio of claws to legs I–III and IV lengths. Both groups are named according to the first species described in each. *Coronarctus tenellus* group displays claw heteromorphy (the claws on legs IV are much longer than the claws on legs I–III) and short cephalic appendages ($> 10 \mu\text{m}$ long). This group contains: *C. disparilis* Renaud-Mornant 1987, *C. dissimilis* Gomes-Júnior, E. Santos, da Rocha, P.J.P. Santos & Fontoura, 2020, *C. laubieri* Renaud-Mornant 1987, *C. mexicus* Romano III, Gallo, D'Addabbo, Accogli, Baguley & Montagna, 2011, *C. neptunus* Gomes-Júnior, E. Santos, da Rocha, P.J.P. Santos & Fontoura, 2020, *C. sonne* Saulenko, Maiorova, Martínez Arbizu & Mordukhovich, 2022, *C. tenellus* Renaud-Mornant 1974, and *C. yurupari* Gomes-Júnior, E. Santos, da Rocha, P.J.P. Santos & Fontoura, 2020.

The second group of *Coronarctus stylisetus* display claw homomorphy (the claws of all legs are similar in length) and long cephalic appendages ($< 10 \mu\text{m}$ long). This group contains *C. stylisetus* Renaud-Mornant, 1987, *C. fastigatus* Renaud-Mornant, 1987, and *C. verrucatus* Hansen, 2007 (Gomes-Junior et al. 2020; Saulenko et al. 2022).

The number of specimens of *Coronarctus xiximii* sp. nov. separated from our samples was much lower compared to other meiofauna groups. Male specimens were not found. Of the five specimens of *C. xiximii* sp. nov., only one was identified as female. No characteristics for sexual identification such as the anus, gonopore and seminal receptacles were observed in the rest of the specimens. *Coronarctus xiximii* sp. nov. has short, leaf-like cephalic appendages and

claws with evident heteromorphy, so it belongs to the *C. tenellus* group.

Coronarctus xiximii sp. nov. can be distinguished as follows:

From *C. laubieri* and *C. dissimilis* by the median cirrus located behind the posterior dorsal lobes and near the posterior edges of the secondary clavae and different numbers of accessory spines on the claws. *C. dissimilis* has an apical accessory spine on each claw and *C. laubieri* has two accessory spines on the internal claws of legs IV.

From *C. disparilis* by the presence of an accessory spine on the internal claws of legs I–III; the claws of legs IV, which feature an accessory spine; and the internal claws, which have an additional spine.

From *C. mexicus* by short cephalic cirri with a long accordion-like scapus instead of leaf-like cephalic cirri and the presence of apical accessory spines on all claws of legs I–III and claws of legs IV, which have two accessory spines.

From *C. neptunus* by a leg I–III sensory organ consisting of a needle-like structure protruding from the wrinkled broad cylindrical basal portion. Also, lateral cirri A consist of unannulated scapus followed by a smooth flagellum ending in a spherical tip.

From *C. sonne* by the flattened secondary clavae with two dorsal and two ventral lobes that are not closely joined and the presence of an accessory spine on all claws of legs IV.

From *C. tenellus* by the lack of coxal spine-like processes on legs IV.

From *C. yurupari* by the pedunculated primary clavae, the presence of an accessory spine on all claws in addition to a mediodorsal accessory spine on the claws of leg IV.

A dichotomous key for the identification of *Coronarctus* species (Modified from Gomes-Junior et al. (2020)).

- 1a. Long cephalic cirri ($> 10 \mu\text{m}$ long). Claws displaying homomorphy: claws on legs I–III and claws IV similar in length (*C. stylisetus* group).....2
- 1b. Short cephalic cirri ($< 10 \mu\text{m}$ long). Claws displaying heteromorphy: claws on legs IV much longer than claws on legs I–III (*C. tenellus* group).....4
- 2a. Cuticle smooth. Pedunculated, with or without a pedestalate socket, primary clava. Secondary clava with ventral lobes not posteriorly indented.....3
- 2b. Cuticle studded with numerous small wart-like excrescences. Primary clava not pedunculated. Secondary clavae with closely jointed posterior ventral lobes that have a posterior narrowing indentation (Fig. 11).....*C. verrucatus*
- 3a. Secondary clavae with posterior ventral lobes jointed. Females with seminal ducts directed posteriorly to the gonopore.....*C. stylisetus*

- 3b. Secondary clavae with posterior ventral lobes widely separated (Fig. 11). Females with seminal ducts ascending anteriorly.....*C. fastigatus*
- 4a. Median cephalic cirrus inserted posteriorly at the level of posterior edges or inserted at about equal distance from the posterior and anterior edges of secondary clavae. Narrow and elongated posterior ventral lobes separated from the anterior lobes by a deep indentation.....5
- 4b. Median cephalic cirrus inserted at about equal distance from the posterior and anterior edges of secondary clavae. Broad and short posterior ventral lobes of secondary clavae.....7
- 5a. Median cephalic cirrus inserted posteriorly at the level of posterior edges of secondary clavae.....6
- 5b. Median cephalic cirrus inserted at about equal distance from the posterior and anterior edges of secondary clavae. Claws of hind legs displaying marked heteromorphy, i.e., internal claws are much bigger than external claws. Posterior dorsal lobes of secondary clavae converging to the midsagittal line (Fig. 11). All claws are simple..... *Coronartus xiximii* sp. nov.
- 6a. Claws of hind legs displaying marked heteromorphy, i.e., internal claws are much longer than external (external/external ≤ 0.50). Posterior dorsal lobes of the secondary clavae converging from the midsagittal line (Fig. 11). Claws of legs IV with accessory spines on internal claws and simple external claws.....*C. laubieri*
- 6b. Claws of hind legs with poorly marked heteromorphy, i.e., internal claws slightly longer than external claws (external/external ≥ 0.70). Posterior dorsal lobes of the secondary clavae diverging from the midsagittal line (Fig. 11). All claws of the legs IV with dorsal accessory spines.....*C. dissimilis*
- 7a. Cephalic appendages with annulated scapi and short terminal tube. Wrinkled leg sensory organs.....8
- 7b. Leaf-like or stylet-like cephalic appendages, without annulated scapi. Leg sensory organs smooth.....9
- 8a. Secondary clavae with two very close dorsal lobes and two ventral lobes (Fig. 11). Claws of legs IV with two accessory spines, the rest of the claws with a single accessory spine. Similar sized sensory organs and coxal processes on legs IV.....*C. mexicus*
- 8b. Secondary clavae not displaying dorsal lobes with the mid-dorsal edges diverging posteriorly from the midsagittal line and having two ventral lobes (Fig. 11). On legs IV apical accessory spines present on internal claws while external claws with a well-developed spine located mediodorsally. Sensory organs on legs IV smaller than coxal processes..... *C. neptunus*
- 9a. Posterior ventral lobes of secondary clavae, although converging to the midsagittal line not closely jointed.....10
- 9b. Posterior ventral lobes of secondary clavae closely jointed, coxal processes on legs IV present. All claws on legs IV with apical accessory spines, and at least on internal claws an additional spine is present.....11
- 10a. Coxal processes on legs IV smaller than sensory organs. Claws of legs IV with an accessory spine, the rest of the claws are simple.....*C. sonne*
- 10b. Coxal processes on legs IV absent. Internal claws from legs IV with an accessory spine and external claws simple..... *C. tenellus*
- 11a. Posterior ventral lobes of secondary clavae very wide and with a straight edge in the midsagittal line (Fig. 11). On hind legs, all claws with an apical accessory spine; a conspicuous supplementary spine is present on internal claws IV only (located on the ventral side of claws). Internal claws of the first three pairs of legs with an accessory spine, external claws simple (a minute bulge can be present).....*C. disparilis*
- 11b. Posterior ventral lobes of secondary clavae with a curved edge in the midsagittal line (Fig. 11). On hind legs, a minute supplementary spine is present on all claws (located on the dorsal side of claws). All claws on the first three pairs of legs with an accessory spine..... *C. yurupari*

Geographical distribution

Coronartus xiximii sp. nov. and *C. mexicus* and *C. stylisetus* are species from the Gulf of Mexico and, taken in conjunction with *C. laubieri* and *C. verrucatus* (near the Norwegian Sea), the only ones from the North Atlantic

(Fig. 12). The other seven species of genus have restrictive geographic distribution (*C. dissimilis*, *C. neptunus*, and *C. yurupari*) from the southern Atlantic; *C. disparilis* and *C. fastigatus* from the Indian Ocean; and *C. sonne* from the northern Pacific, except *C. tenellus* that inhabit southern

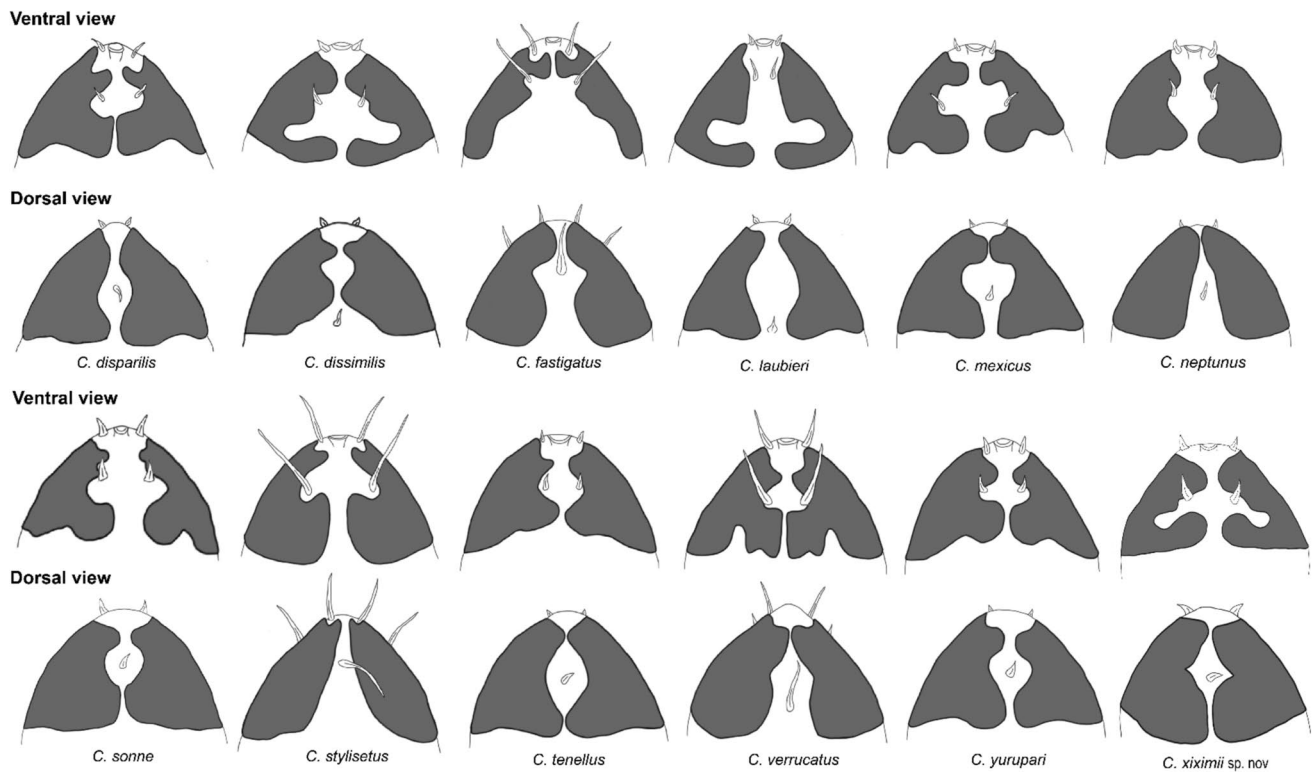


Fig. 11 Secondary clavae of *Coronarctus* species (*C. mexicus* modified from Pérez-Pech et al. 2020, *C. sonne* modified from Saulenko et al. 2022, *C. sp. nov.* is a original drawing and the rest of species are modified from Gomes-Junior et al. (2020))

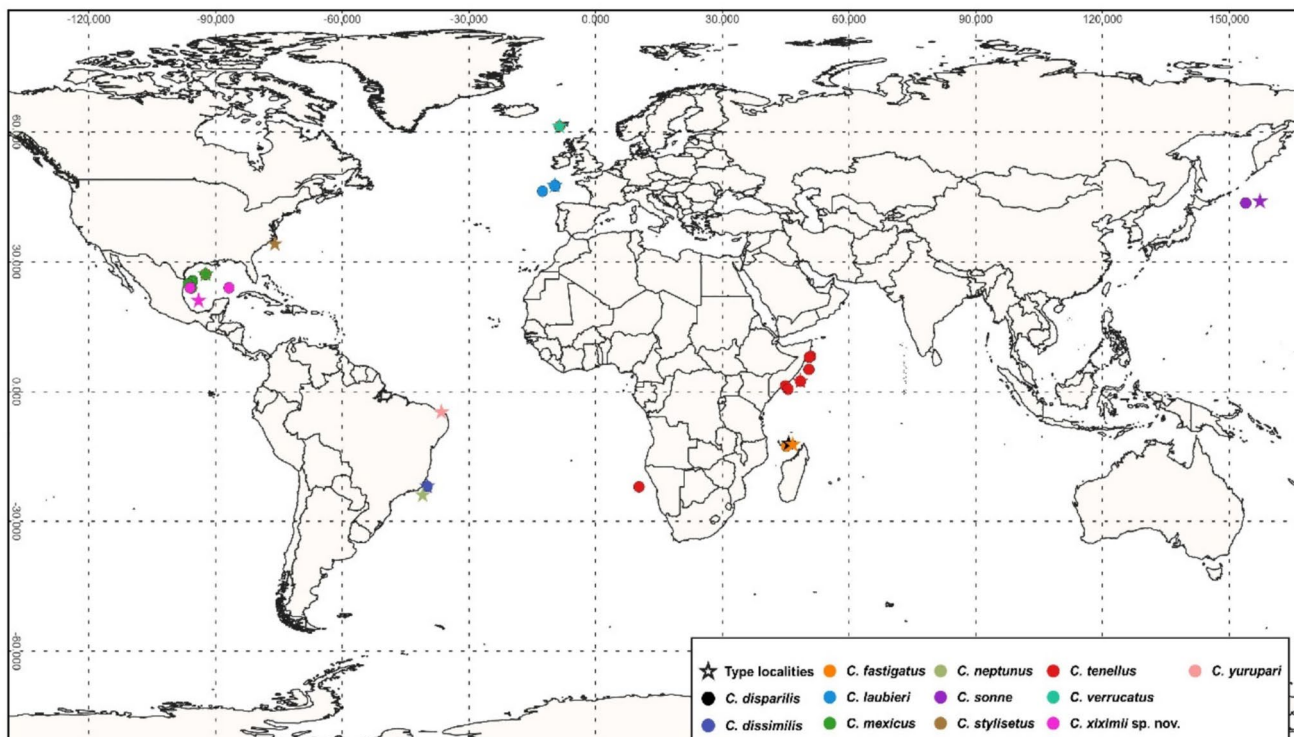


Fig. 12 Geographic distribution of *Coronarctus* species (type localities indicated with [☆])

Atlantic and the Indian Ocean (Fig. 12). Particularly, only six species: *C. disparilis*, *C. laubieri*, *C. mexicus*, *C. stylisetus* and *C. tenellus* have additional records other than those in the original description (Fig. 12).

Discussion

The geometric morphometric approach in this study represents the second approach of its kind to tardigrades (Fontoura and Morais 2011) and the first in marine tardigrades. The morphometric characters have a potential to infer low-level phylogenetic relationships when describing and comparing complex forms, ideally individual homologous elements, complex forms that cannot be easily and objectively described with traditional discrete states (Palci and Lee 2019). In this case, these elements are the secondary clavae and claws. Despite having potential, there are a series of problems that complicate their use: the small number of available specimens and difficulties encountered by not having adequate specimen orientation. Moreover, cryptic speciation may occur as it does in other marine genera. Therefore, care must be taken when using these elements in the analyses (Gomes-Junior et al. 2020).

A new species belonging to the *C. tenellus* group (Gomes-Junior et al. 2020) was described from specimens collected in the Mexican Exclusive Economic Zone of the Gulf of Mexico: *Coronarctus xiximii* sp. nov. which features short, leaf-shaped cephalic appendages and claws with evident heteromorphy. To date, there are only records of marine tardigrades in the marine regions of the northern Gulf of Mexico and the Caribbean Sea (García-Román et al. 2022). Occurrences of *C. xiximii* sp. nov. in the southern Gulf of Mexico are the first records for this region; consequently, three of the eight marine regions now have records of marine tardigrades.

This new species has secondary clavae with the posterior ventral lobes separated from the anterior ventral lobes by a deep indentation, as in the case of *C. laubieri* and *C. dissimilis*. However, *C. xiximii* sp. nov. is clearly distinguished from both of these by the insertion of median cirrus. Other differences are present in the secondary clavae and claws although the shape of the ventral lobes of *C. sp. nov.* are very similar to those of *C. dissimilis*. Nevertheless, upon detailed observation, an important difference is noted in terms of the thickness of the deep indentation. With regard to the claws, no accessory spines are observed in any of the claws in the new species unlike *C. dissimilis*, which has an apical accessory spine on each claw, and *C. laubieri*, which has two accessory spines on internal claws of leg IV, so the shape of the secondary clavae and the characterization of the claws remain reliable taxonomic characters at the time of identification (Gomes-Junior et al. 2020).

C. xiximii sp. nov. has similar characteristics to the undescribed *Coronarctus* sp. specimen recorded by Pérez-Pech et al. (2020), such as the shape of the secondary clavae and

the insertion of the median cirrus. However, body sizes are significantly different: the four-clawed larva of undescribed *Coronarctus* sp. is 398 µm long, while the holotype of *C. xiximii* sp. nov. is 331.6 µm.

In addition to the heteromorphic condition in their claws, an important characteristic shared by *C. xiximii* sp. nov. and *C. laubieri* is that the external claws of legs IV are much smaller than the internal claws. This characteristic has only been observed in these two species and is independent of heteromorphy (Gomes-Junior et al. 2020), which implies that it may be important regarding their phylogenetic relationship.

Unfortunately, we do not have a male specimen to complete the taxonomic description. However, in *Coronarctus*, the presence of external sexual dimorphism has not been observed except for the shape of the gonopore, which in males is a slit in a cuticular fold, whereas in females it is rossete-like (Gomes-Junior et al. 2020).

The family Coronarctidae included only two genera: the monospecific genus *Trogloarctus* and the genus *Coronarctus*. With the description of *C. xiximii* sp. nov., the number of species assigned to this genus, which has a wide geographic distribution (Fig. 12), increases to twelve. With regard to geographic distribution, in some species such as *C. dissimilis*, *C. fastigatus*, *C. neptunus*, *C. sonne*, *C. verrucatus* and *C. yurupari*, only the records of the original description are available. On the other hand, species such as *C. disparilis*, *C. laubieri*, *C. mexicus*, *C. stylisetus* and *C. tenellus* have additional records other than those in the original description. In these species we found two distribution patterns: a distribution restricted to a certain region, such as *C. mexicus* restricted to the Gulf of Mexico and *C. tenellus*, which is restricted to the Indian Ocean and the southern Atlantic Ocean (Fig. 12). These distribution patterns in *Coronarctus* correspond with the variable patterns already observed from a regional to a more cosmopolitan distribution (Gašiorek 2023). However, there are cases in which species have a false transatlantic distribution due to errors in records at the time of identification (Santos et al. 2018). An exhaustive review of the recorded specimens would make it possible to verify that these species have a very wide distribution.

Further exploration of deep-sea biodiversity will allow for a better understanding of less abundant taxa within the meiofauna, such as tardigrades. Marine tardigrades are among the least studied invertebrate taxa, so aspects of their ecology, biogeography, and phylogeny can only be addressed through a basic taxonomic work of this still largely unexplored part of marine biodiversity, both in the Gulf of Mexico and in the rest of the world's oceans.

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