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Phylogenetic and biogeographic analysis of the genus *Caribeacarus* (Acari : Opilioacarida), with description of a new South American species

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Abstract. The mite order Opilioacarida is widely distributed in the tropical and sub-tropical zones of the world, where it is rare and poorly known. On the American continent only two genera, 14 species and one subspecies are known. This work aimed to describe a new species of *Caribeacarus* from the state of Pará, in the eastern part of the Brazilian Amazon. A phylogenetic analysis of the species in this genus is also presented, and interpreted along with the historical biogeography of this genus in Central and South America. A key to the species of *Caribeacarus* is provided.

Additional keywords: Amazon, Biogeography, Brazil, Opilioacaridae, Parasitiformes.

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Introduction

The mite order Opilioacarida retains many ancestral features, suggesting it may be one of the most primitive groups among the living Parasitiformes (Grandjean 1936; Walter and Harvey 2009). One of the most important primitive aspects of Opilioacarida is the presence of a complete acarine ontogenetic sequence: they are the only parasitiform mites known to have a prelarva. This morphological feature and others makes these mites one of the most important groups in the study of relationships among the two major lineages of mites, Acariformes and Parasitiformes. Unfortunately Opilioacarida species are still poorly known, with a limited number of collections throughout the world (Walter and Harvey 2009).

The order Opilioacarida is distributed throughout the tropics and subtropics but contains a relatively small number of species compared with other mite orders. Only 11 genera, 33 species and one subspecies have been described. The majority of genera and species are found in the Old World, with only two genera, 14 species and one subspecies described from the USA, Mexico, Cuba, Nicaragua, Panama, Venezuela, Brazil, Uruguay and Argentina (Vázquez and Klompen 2009).

Among the two genera found on the American continent, *Neocarus* Chamberlin & Mulaik, 1942 includes the majority of species. This genus also has the widest geographic distribution; specimens have been collected from Uruguay to the southern United States. In contrast, the genus *Caribeacarus* Vázquez & Klompen, 2009 includes only three described species that are restricted to the Caribbean region and Central America.

Biospeleological inventories have become more common in Brazil, especially in recent years. This is certainly due to some changes in the Brazilian laws regarding cave heritage. During work on such inventories a new species of *Caribeacarus* was found in iron ore caves. Therefore, as well as carrying out a phylogenetic and biogeographic analysis for the species of this genus, this work also has the objective of describing a new South American species.

Materials and methods

Study area

Collections of mites were carried out principally in caves and epigean areas of iron karst located in the municipal districts of Carajás, Curionópolis, Parauapebas and Canaã dos Carajás, all located in south-eastern Pará state. The ferriferous formation of Carajás, where such caves are located, is within the domain of the Amazon forest, in the north of Brazil. Some of the caves are found

within a National Forest (Flona de Carajás). This area, although comprising a protected area, shows multiple anthropogenic uses, such as iron ore exploration.

The ferriferous formation of Carajás is composed of plateaus whose topography is maintained by a ferruginous topmost breccia, named 'canga', under which the lateritic ore occurs, with a thickness that can surpass, locally, 200 m (Lindenmayer *et al*. 2001). The entrances of the caves are in this lateritic crust, and the development of conduits and galleries mainly occur below this thick layer of iron.

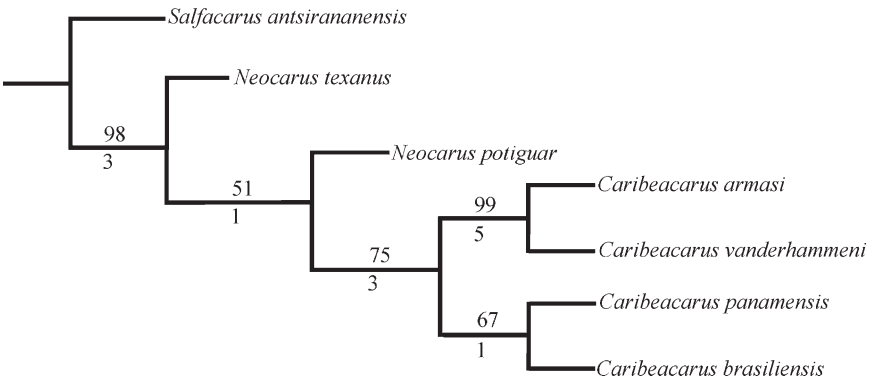


Fig. 1. Bootstrap (above to nodes) and Bremer (below to nodes) values reported in support of the most parsimonious cladogram recovered according to the simple parsimony method.

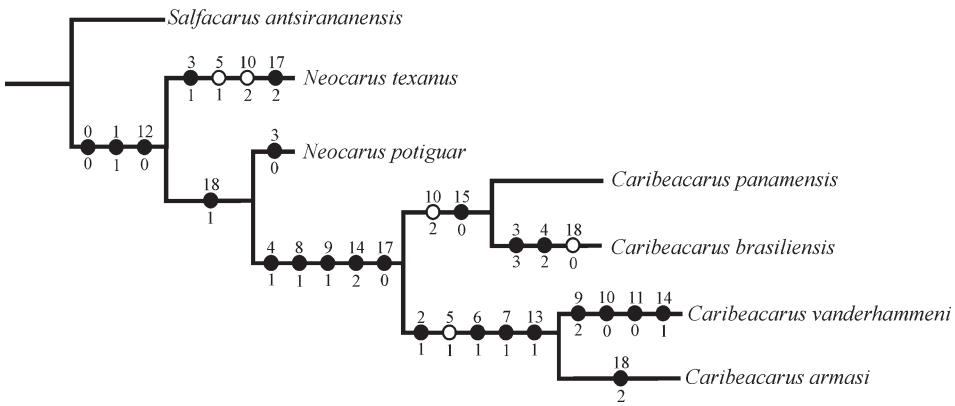


Fig. 2. Single most parsimonious cladogram recovered by simple parsimony method (L = 31; Ci =87; Ri = 85). Black circles indicate synapomorphies; white circles indicate homoplasy. Numbers above and below circles represent, respectively, character number (as in Appendix 1) and character states.

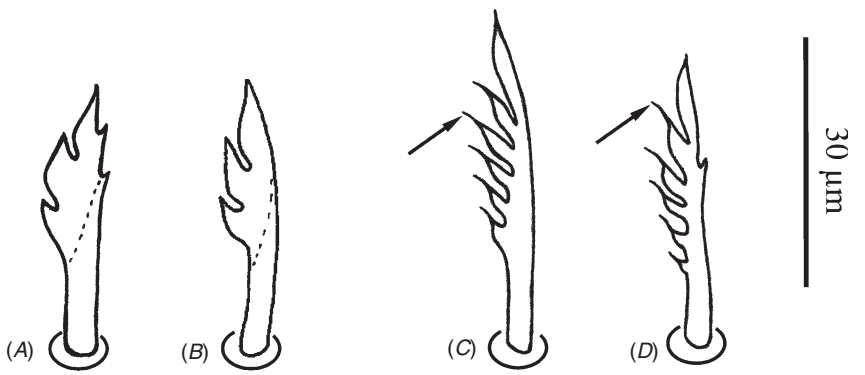
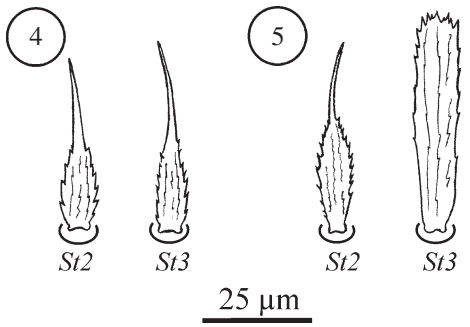


Fig. 3. Shape of *d*-type setae present on palp tarsus of *Caribeacarus* Vázquez & Klompen, 2009 and *Neocarus* species. (*A*) *Neocarus texanus* Chamberlin & Mulaik, 1942; (*B*) *N. potiguar* Bernardi et al 2012; (*C*) *C. armasi* Vázquez & Klompen, 2009; (*D*) *C. brasiliensis*, sp. nov.



Figs 4, 5. *4*, *Caribeacarus brasiliensis*, sp. nov typical sternal setae found in the sternal area of the 'Continental' species-group. *5*, *Caribeacarus armasi* Vázquez & Klompen, 2009, typical sternal setae found in the sternal area of the 'Caribbean' species-group.

Another area where Opilioacarida specimens were collected is in the municipality of Altamira, in southern Pará state. This location is also within the Amazon forest and specimens of Opilioacarida were also found inside caves, but caves in this area are situated in different geological formations, where the predominant rock is sandstone.

Methods of description

All of the specimens were collected with the aid of a brush and stored in vials with 70% ethanol. The majority of the material was studied as slide-mounted specimens. For this purpose, specimens were dissected (due to size), cleared in Nesbitt's solution and mounted on slides using Hoyer's medium for microscopy studies (Walter and Krantz 2009).

Identification and the drawings of the specimens was done with the aid of a Leica MDLS phase contrast microscope (Leica Microsystens, Wetzlar, Germany) connected to a drawing tube. Measurements were taken using an ocular micrometer, and are presented in micrometers (µm). The nomenclature of setae and other morphological characters follow that of Van der Hammen (1969, 1976) and Vázquez and Klompen (2002, 2009). The terminology used for the sternal setae (*St1*, *St2*, *St3* and *St5*) is an attempt to unify the nomenclature used in Parasitiformes mites (H. Klompen and M.M. Vázquez, unpubl. data).

Ultrastructural analyses were also conducted through use of scanning electron microscopy. A female was placed on an aluminium support stub covered with a film of aluminium foil with carbon tape, sputter-covered with gold (Baltec SCD 050), and observed in a LEO EVO 40 XVP scanning electron microscope (Carls Zeiss AG, Oberkochen, Germany).

Collection sites of the specimens examined were georeferenced using coordinates in degrees, minutes and seconds with the local geodesic system South American Datum (SAD 69).

The material of the new species studied are deposited at the Universidade de São Paulo, Escola Superior de Agricultura 'Luiz de Queiroz', Department of Entomology and Acarology, Mite Reference Collection (MZLQ), Piracicaba, São Paulo, Brazil; at the Universidade Federal de Lavras, Department of Biology, Section of Zoology, Collection of Subterrean Invertebrates (ISLA), Lavras, Minas Gerais, Brazil; and at the Ohio State University Acarology Collection (OSAL), Columbus, Ohio, USA.

Phylogenetic analysis

The phylogenetic analysis was based on the morphological characters of adult individuals. A total of 19 characters was used to hypothesise the relationships among the taxa analysed. Among these characters, six were multi-state. The matrix of characters, with their respective states (Appendix 1), was analysed by the simple parsimony method with NONA ver.

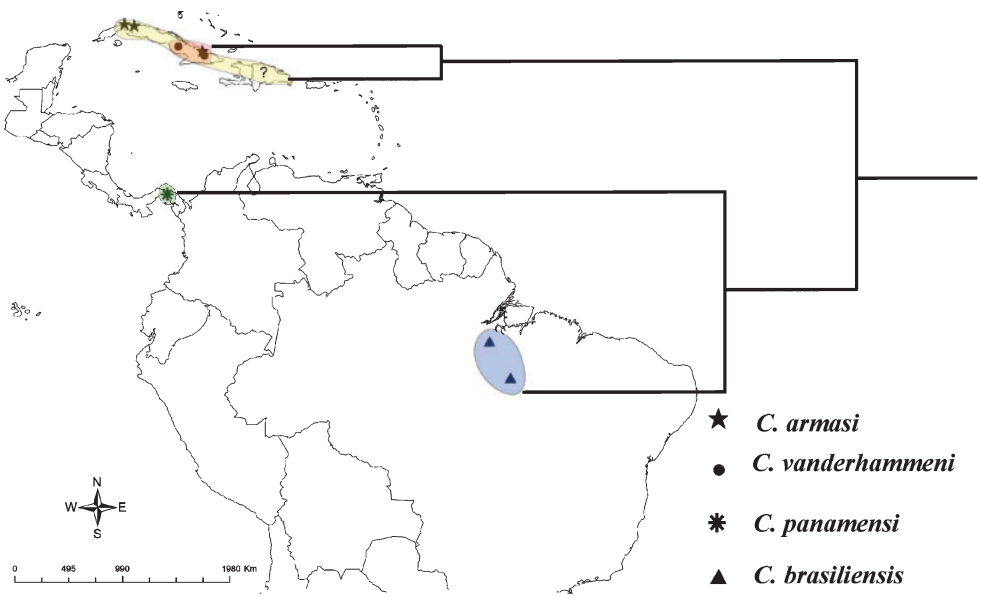


Fig. 6. Area cladograms based on data from phylogeny and geographic distribution of *Caribeacarus* Vázquez & Klompen, 2009 species.

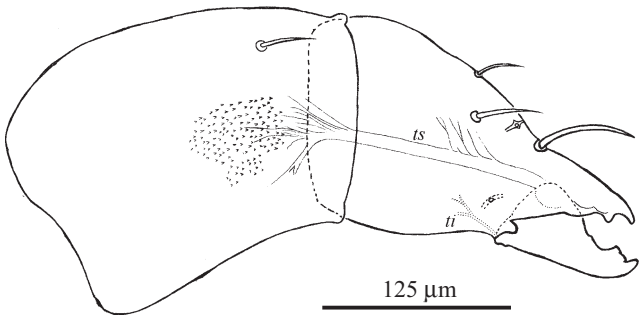


Fig. 7. *Caribeacarus brasiliensis*, sp. nov., male adult, paratype. Lateral view of chelicera: ts, superior tendon; ti, inferior tendon.

2.0 (Goloboff 1993). The search strategy used was TBR (tree bisection–reconnection), with replication equal to 100 (mult*100), followed by SPR (subtree pruning and regrafting) with the same number of replications. The maximum number of trees retained in the program memory was 1000 (hold = 1000). No characters were weighted or ordered *a priori*. Bremer support analysis (the decay index), with up to 10 extra steps, and bootstrap with 1000 repetitions were used to determine node support. The cladograms resulting from these procedures were analysed with WinClada ver. 1.00.08 (Nixon 2002). A list of characters used for this analysis, with their respective states, is provided in Appendix I.

Salfacarus antsirananensis Vázquez & Klompen, 2010, an African species, was used as distant outgroup for the

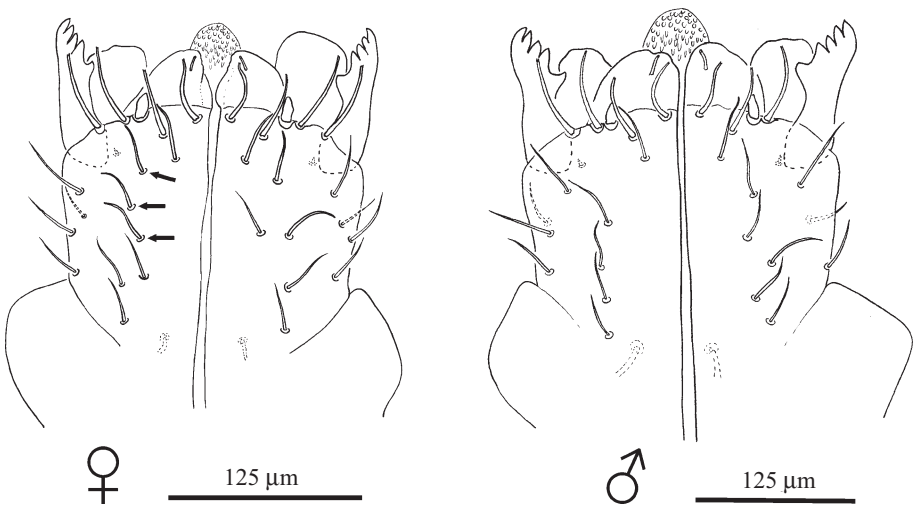
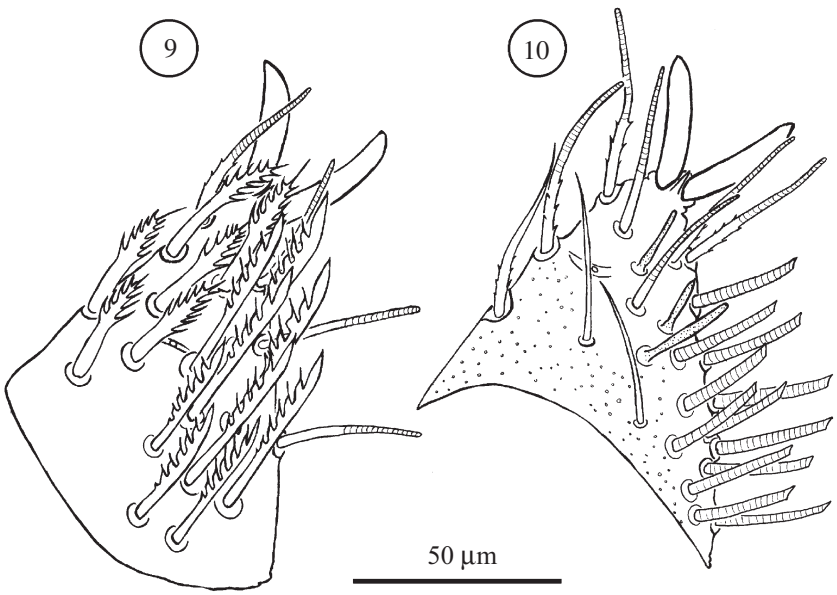
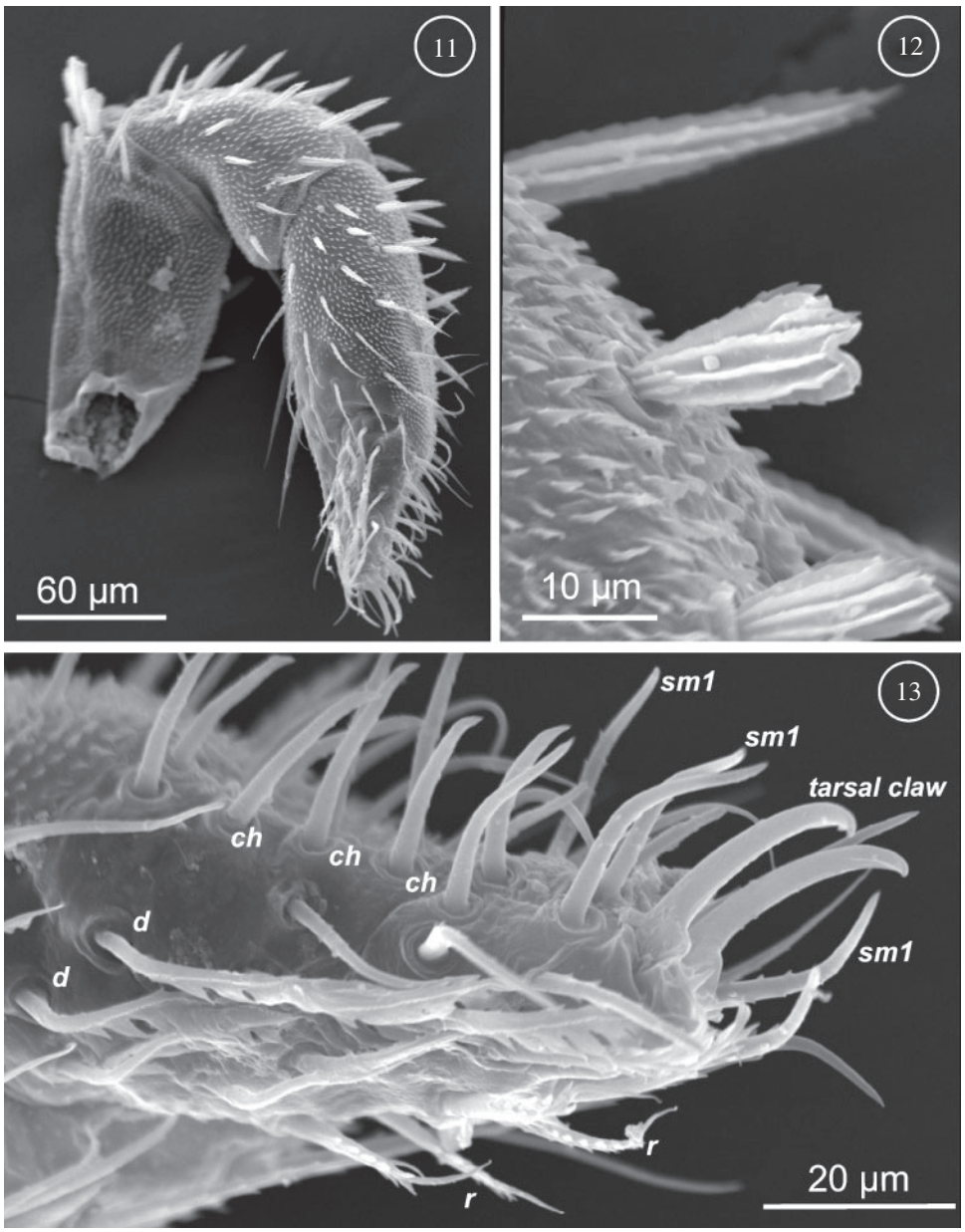


Fig. 8. *Caribeacarus brasiliensis*, sp. nov., female adult, holotype and male adult paratype. Rounded-tip ventral setae restricted to females indicated by arrows.



Figs 9, 10. *Caribeacarus brasiliensis*, sp. nov., female adult, holotype. *9*, Palp tarsus dorsal view; *10*, palp tarsus ventral view.



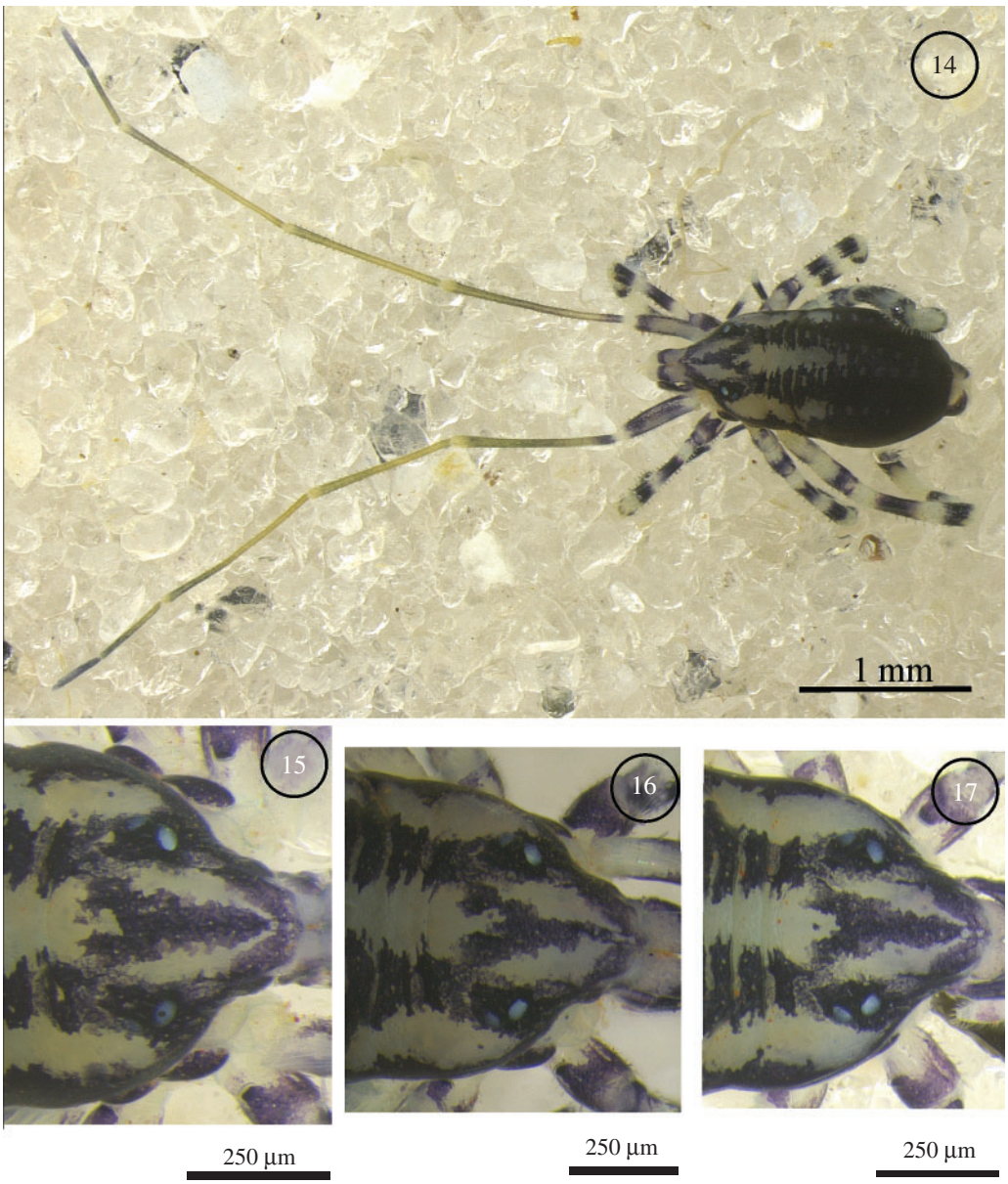
Figs 11–13. *Caribeacarus brasiliensis*, sp. nov., tritonynph. *11*, Geral view of the palp; *12*, detail of the ribbed setae on femur; and *13*, detail of the setae on the tarsal palp.

phylogenetic analysis. Two *Neocarus* species, *N. potiguar* Bernardi *et al*., 2012 from north-eastern Brazil, and *N. texanus* Chamberlin & Mulaik, 1942, the type species of the genus, were used as close outgroups. All species listed in the present work had a holotype or paratype specimens examined. Examined material included newly identified additional material of *C. panamensis* Vázquez & Klompen, 2009 (with data similar to those of the type specimens). This added material is deposited at OSAL. The only exception was *Caribeacarus vanderhammeni* Juvara-Balş & Baltac, 1975. The type of this species was not available for examination, and coding was based on the original description.

Biogeographic analysis

Distribution maps were generated based on the known occurrence records for *Caribeacarus* species. To represent the dispersion patterns of each species on the map, a method adapted from that proposed by Croizat to obtain individual tracks was used (Croizat 1958). These tracks were outlined by the disjoint localities and were created through a range (area) which connects all separate locations where all representatives of the species are present. Points are usually connected by the shortest route.

A cladogram of areas based on the results from the phylogenetic analysis developed in this study was used to



Figs 14–17. *Caribeacarus brasiliensis*, sp. nov., adult. Dorsal view. *14*, *15*, *16* female; *17*, male.

recover the relationships among the areas where species occurred. The area cladogram was obtained by replacing the species of terminal groups with the respective occurrences of their individuals.

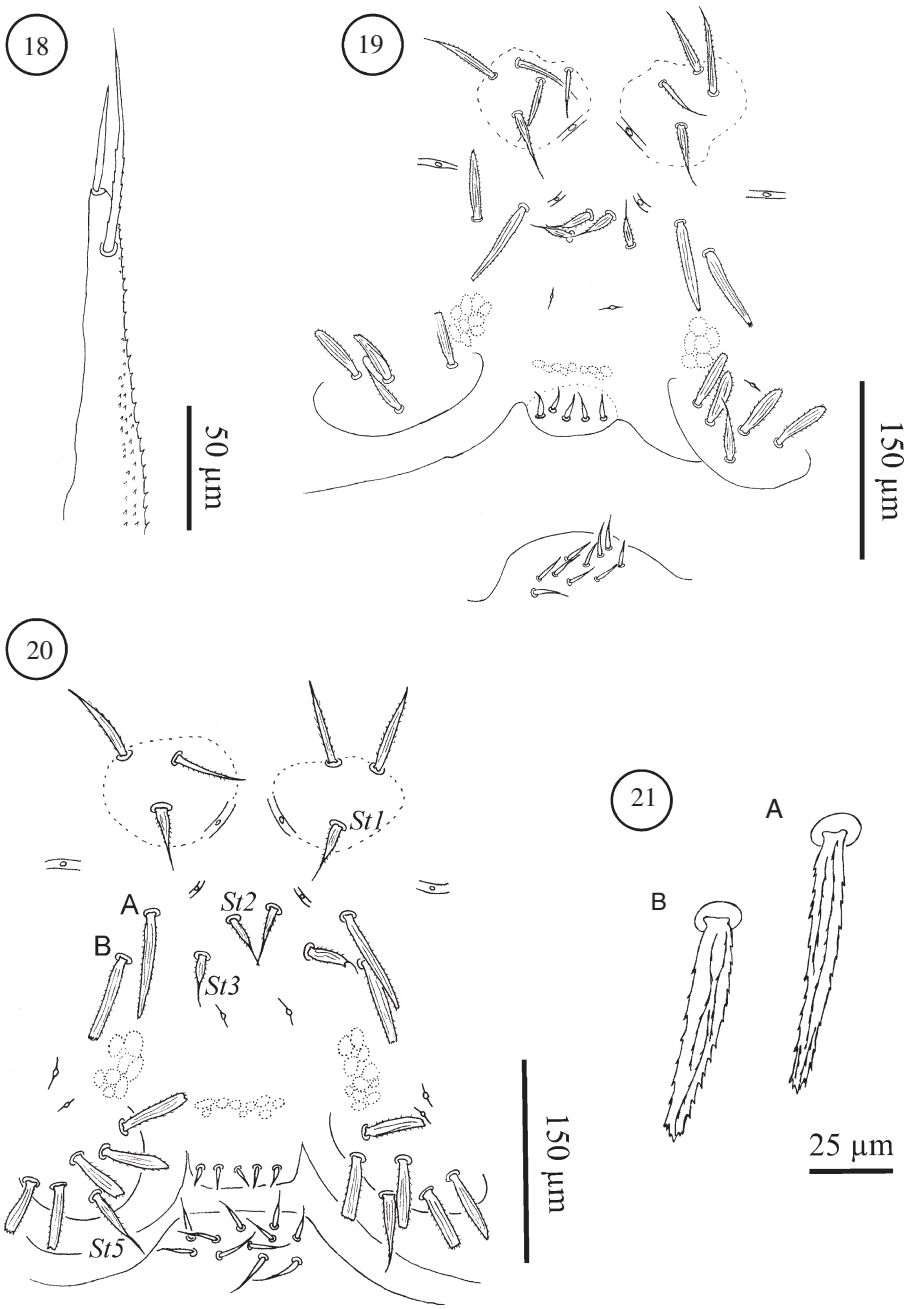
Results and discussion

Phylogenetic results

After an exhaustive search, the simple parsimony analysis recovered a single most parsimonious cladogram with a length of (L) = 31, consistency index (Ci) = 87 and retention index (Ri) = 85 (Fig. 1). Support measures indicate good support for all clades of the ingroup (Fig. 2). The calculation of Bremer support was based on a search of all trees up to 41 steps long.

Notably, monophyly or paraphyly of the genus *Neocarus* could not be established with any confidence based on this analysis, because taxon sampling for that genus is clearly inadequate for that purpose. Preferentially, all species, including multiple undescribed species from Brazil, need to be added to the matrix for that purpose.

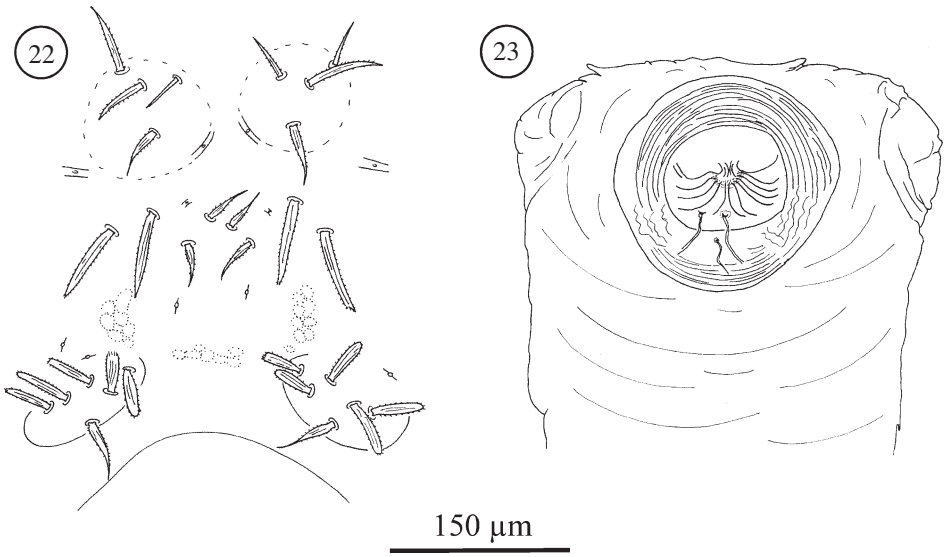
The monophyly of *Caribeacarus* was suggested by Vázquez and Klompen (2009) and seems well supported. Support is based largely on four characters: (1) presence of large number of foliate (*d*-type) setae on the palp tarsus (character 9); (2) shape of those *d*-type setae (slender, with six or more lobules that are attenuate) (character 8) (Fig. 3*C*, *D*); (3) lack of setae



Figs 18–21. *Caribeacarus brasiliensis*, sp. nov., female adult, holotype: *18*, detail of the sternapophysis. Male adult: *19*, *20*, sternitogenital area; *21*, details of the setae in sternal seta.

in the pre-genital region of the female (character 17); and (4) presence of at least five pairs of ventral/ventrolateral setae on acrotarsi II–IV (character 14).

The above results require an update of the generic diagnosis of *Caribeacarus*. The large number of *d*-type setae, the primary diagnostic character for the genus (Vázquez and Klompen 2009), consistently distinguishes *Neocarus* from *Caribeacarus*. However, it is worth noting that larger numbers of *d*-type setae are also found in several Old World taxa (Grandjean 1936; Naudo 1963; Vázquez and Klompen 2010). The shape of the *d-type* setae may be added as a diagnostic character for *Caribeacarus*. Relative to the condition in *Neocarus* species, the *d*-type setae in all *Caribeacarus* species are (1) more slender, (2) have six or more lobules (versus three or four), and (3) have lobules with attenuate ends (smooth in *Neocarus*) (Fig. 3). The combination of large numbers of *d*-type setae and the characteristic shape may be unique within Opilioacaridae. The position of the crown-like sensillum of tarsus I on the tip of the tarsus, rather than in the dorsal sensory field, was listed in the original generic diagnosis



Figs 22, 23. *Caribeacarus brasiliensis*, sp. nov., female adult, holotype: *22*, sternitogenital area; *23*, ovipositor.

(Vázquez and Klompen 2009), but is not characteristic of the genus. It is absent in *C. brasiliensis*, sp. nov. and *C. panamensis* and this modification appears restricted to *C. armasi* Vázquez & Klompen, 2009 and *C. vanderhammeni* (the 'Caribbean' species-group). Of the remaining characters, the setation of the pregenital area in females is variable among Opilioacaridae in general, while the setation of acrotarsi II–IV has not been studied in the majority of opilioacarid genera.

Caribeacarus includes two distinct clades, one containing continental species ('Continental' species-group) and another one containing species present on islands ('Caribbean' species-group). The 'Caribbean' species-group is particularly well supported, sharing: (1) the modification of sternal setae *St3* to stout and ribbed (Figs 4, 5), (2) the high number of setae on the basal segment and fixed digit of the male chelicerae, (3) the distal position of the crown-like sensillum on tarsus I, and (4) the median position of solenidion ω_d on basitarsi II–IV. Support for the 'Continental' species-group is more tentative, species in this group sharing: (1) the presence of fine setae with attenuate tips in the pregenital region of the males and (2) relatively small numbers of *ch*-type sensilla on the palp tarsus. Both of these characters appear in various other Opilioacaridae.

Biogeographic considerations

The genus *Caribeacarus* is the smaller of the two opilioacarid genera recorded in the Neotropical region. By comparing occurrence records of *Caribeacarus* species with our hypothesis of phylogenetic relationships within the genus, and associating this data with knowledge on the geological evolution of the Americas, it is possible to propose some hypotheses with respect to the diversification of this group.

Although the etymology of the genus *Caribeacarus* refers to collection sites where the first described specimens were recorded, it is unlikely that it originated in the Caribbean Island complex. One of the greatest geological events in Central America was the displacement of the Proto-Caribbean plate, which is currently represented by the Caribbean islands, from their west to east position, where they formed the first land bridge between South and North America. During this displacement, which started ~80 Mya, subsidence events occurred on these landmasses. Therefore, the maintenance of terrestrial biota in this period was unlikely (Pindell 1994; Iturralde-Vinent and MacPhee 1999; Iturralde-Vinent 2004/

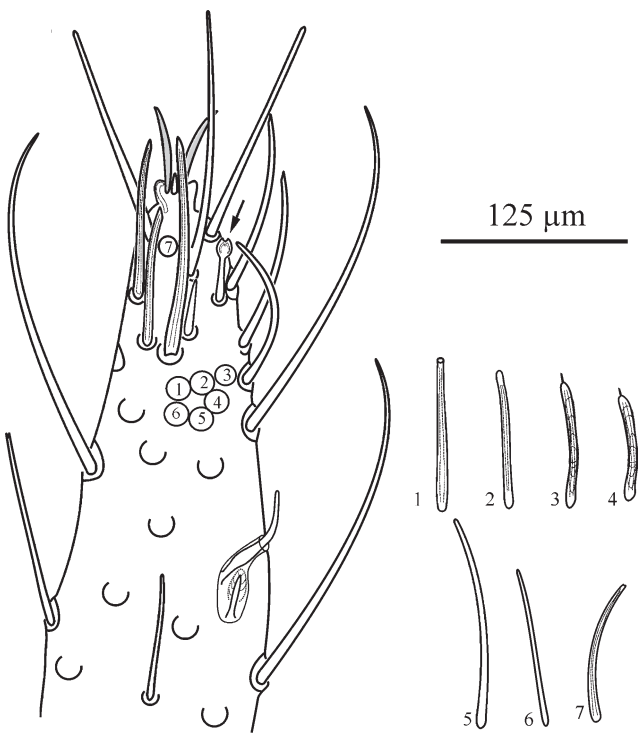
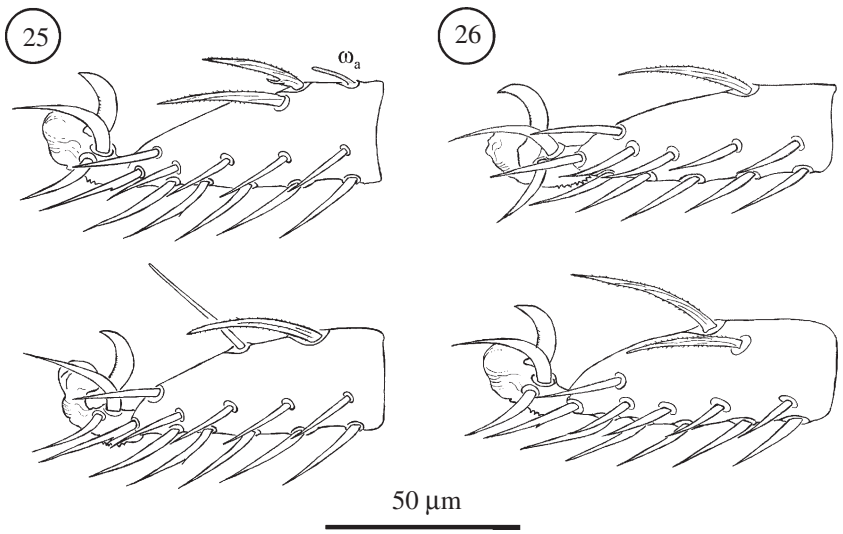


Fig. 24. *Caribeacarus brasiliensis*, sp. nov., female adult, holotype. Partial dorsal view of telotarsus I. The open semicircles represent insertions of setae. Arrow indicates the sensillum with 'crown-like' tip.

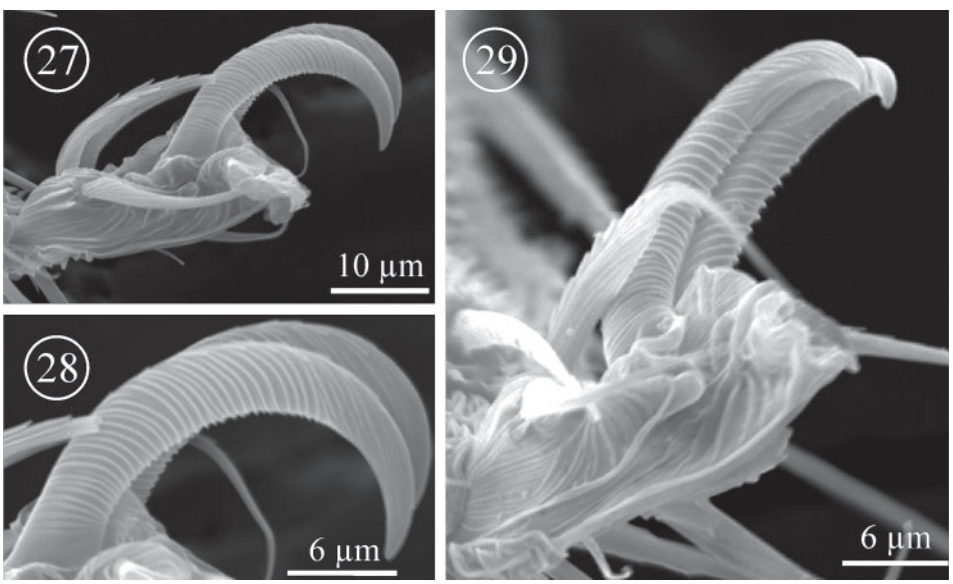
2005). The most probable period for the colonisation of these islands by terrestrial organisms would have occurred only during the Eocene and Oligocene periods (between 35 and 32 Mya), during an uplift event. This event allowed for contact between the South American continent and the future Antilles, up to the area currently occupied by Cuba. This land bridge allowed colonisation of the islands by continental terrestrial fauna, including previously isolated parts (Iturralde-Vinent and MacPhee 1999). The Opilioacarida were not the only taxon benefitting from the emergence of this land bridge, as a large number of mammals, reptiles, invertebrates and other groups is hypothesised to have crossed this land bridge.

Another possible hypothesis for colonisation is through over-water dispersal of propagates. However, studies have demonstrated that surface-current dispersal of propagates is inadequate as an explanation of the observed distribution patterns of terrestrial fauna in the Greater Antilles (Iturralde-Vinent and MacPhee 1999). In the past, the destination of propagates originating from the north of South America was Central America or other parts of the land recently created in this region (Iturralde-Vinent and MacPhee 1999).

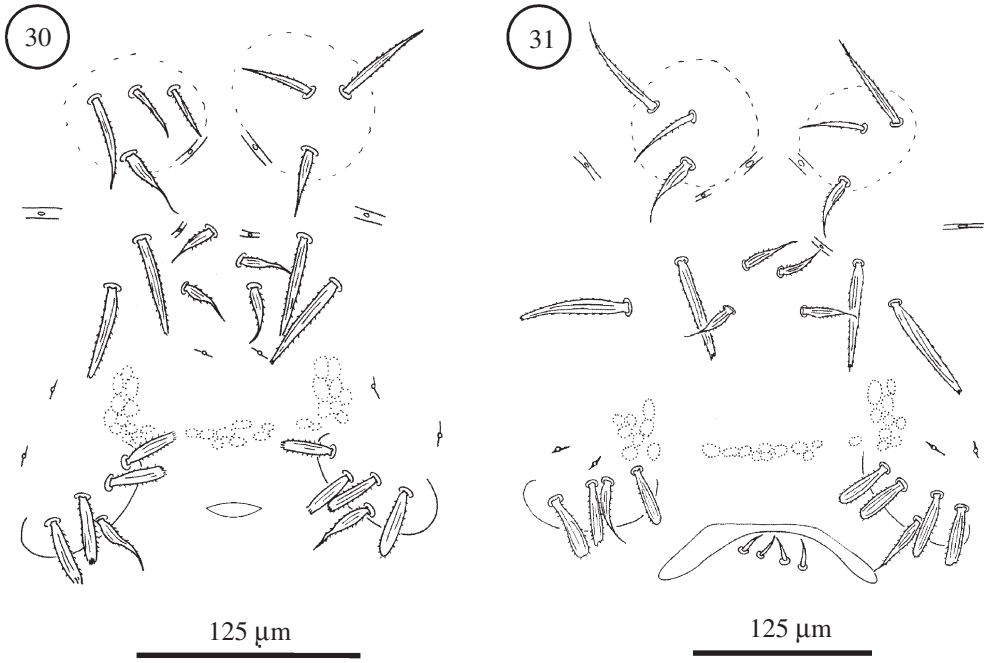
New subsidence events have been verified after the Eocene-Oligocene (between 33–35 Mya), resulting in a large period of isolation. These events may have been responsible for the



Figs 25, 26. *Caribeacarus brasiliensis*, sp. nov., female adult, holotype: *25*, anterolateral and posterolateral view of the acrotarsus of leg II; *26*, anterolateral and posterolateral view of the acrotarsus of leg III.



Figs 27–29. *Caribeacarus brasiliensis*, sp. nov., tritonynph: *27*, *28*, tarsal claw of the tarsus of leg II; *29*, tarsal claw of the tarsus of leg IV.



Figs 30, 31. *Caribeacarus brasiliensis*, sp. nov., tritonymph, paratypes, sternitogenital area: *30*, female tritonymph; *31*, male tritonymph.

emergence of the ancestral species from the clade formed by *Caribeacarus armasi* and *C. vanderhammeni*, the 'Caribbean' species-group. The ancestor of the clade formed by the species *C. brasiliensis* and *C. panamensis* remained in the continental part of South America (Fig. 6). The events which would have caused speciation within the 'Caribbean' species-group are difficult to determine, as this region presents complex and controversial aspects of geology, with various cyclic events of uplift and subsidence.

Finally, the establishment of *Caribeacarus* species in Panama might be the most recent event occurring in this group. The colonisation of this region was only possible after the emergence of the Panama Isthmus, which, according to Hoorn *et al*. (2010), was completed between the end of the Pliocene and beginning of the Pleistocene (~2.5 Mya).

Taxonomy

Family **OPILIOACARIDAE** With, 1904

Genus ***Caribeacarus*** Vázquez & Klompen, 2009

Caribeacarus Vázquez & Klompen, 2009: 34.

Type species: *Caribeacarus armasi* Vázquez & Klompen, 2009, by original designation.

Caribeacarus brasiliensis, sp. nov.

(Figs 1–24)

Material examined

Holotype. Brazil: Pará State: ♀, Gruta S11D-11 (06°24′38.3″S 50°19′38.7″W), municipality of Parauapebas, 19.iii.2010, R. Andrade (MZLQ).

Paratypes. Brazil: Pará State: 1 ♂, Gruta N4WS-46 (06°04′27.9″S 50°11′39.1″W) Carajás, 19.v.2011, R. Andrade (MZLQ); 2 ♀, Gruta Cav34-S11 (06°24′0.8.8″S 50°22′56″W), municipality of Parauapebas, 25.xi.2010, R. Andrade (MZLQ); 1 ♂, Gruta N5SM2–72 (06°07′31.2″S 50°07′54.1″W), municipality of Parauapebas, 11.iii.2011, R.A. Zampaulo (MZLQ); 1 ♂, Gruta N5SM2–66 (06°07′41.4″S 50°08′04.6″W), municipality of Parauapebas, 30.ix.2010, R.A. Zampaulo (MZLQ); 1 ♂, 2 ♀, Gruta N5SM2–03 (06°08′26.2″S 50°08′04.2″W), municipality of Parauapebas, 22.xi.2010, R.A. Zampaulo (MZLQ); 1 ♀, Gruta N5S-31 (06°08′26.2″S 50°08′04.2″W), municipality of Parauapebas, 15.vii.2010, R.A. Zampaulo (OSAL); 1 ♂, Gruta S11–22 (06°25′02.7″S 50°18′06.5″W), municipality of Carajás, 2.ix.2011, R. Andrade (OSAL); 1 ♂, Gruta N5SM2–43 (06°07′18.6″S 50°07′41.4″W), municipality of Parauapebas, 6.iv.2010, R.A. Zampaulo (OSAL); 1 ♂, Gruta N5SM2–30 (06°08′15.8″S 50°07′57.6″W), municipality of Parauapebas, 8.iv.2011, R. Andrade (OSAL); 1 ♂, Gruta N5SM2–03 (06°08′26.2″S 50°08′04.2″W), municipality of Parauapebas, 22.xi.2010, R.A. Zampaulo (OSAL); 1 ♀, Gruta N4WS-46 (06°04′27.9″S 50°11′39.1″W) Carajás, 19.v.2011, R. Andrade (OSAL); 1 ♀, Gruta N5S-39 (06°06′19.9″S 50°08′00.4″W), municipality of Carajás, 4.iv.2010, R. Andrade (ISLA); 1 ♀, Gruta S11D-11 (06°23′50.8'S 50°21′30.4'W), municipality of Parauapebas, 25.ix.2010, R. Andrade (ISLA); 2 ♂, Gruta N5SM2–43 (06°07′18.6″S 50°07′41.4″W), municipality of Parauapebas, 6.iv.2010, R. A. Zampaulo (ISLA); 2 ♀, Gruta N5SM2–03 (06°08′26.2″S 50°08′04.2″W), municipality of Parauapebas, 22.xi.2010, R.A. Zampaulo (ISLA); 1 ♂, Gruta N5SM2–98 (06°08′17″S 50°08′00″W), municipality of Parauapebas, 30.x.2010, R. Andrade (ISLA); 1 ♂, Gruta N5SM2–21 (06°07′53.2″S 50°08′04.1″W), municipality of Parauapebas, 27.x.2010, R.A. Zampaulo (OSAL); 1 ♂, Gruta N5SM1–29 (06°06′28.1″S 50°08′07.2″W), municipality of Parauapebas, 19.ii.2010, R.A. Zampaulo (ISLA); 2 ♂, Cave Abrigo do Abutre (06°24′0.8.8″S 50°22′56″W), municipality of Altamira, 11.x.2010, M.E. Bichuette (ISLA); 2 ♂, 1 ♀, Gruta S11D-92 (06°23′42.3″S 50°19′19.1″W), municipality of Parauapebas, 18.i.2010, R. Andrade (ISLA).

Diagnosis

Male with three setae on fixed digit of chelicerae, like *C. panamensis* (4–6 setae in *C. armasi* and five in *C. vanderhammeni*). Palp tarsus with 8–9 foliate setae as in *C. panamensis* and *C. armasi* (12 in *C. vanderhammeni*). Only 11–12 *ch*-type setae on palp tarsus (unique for this species): 15 in *C. panamensis*, 25 in *C. armasi* and 32 in *C. vanderhammeni*). Setae *St2–St3*, in the sternal area barbed and tapering, as in *C. panamensis* (in *C. armasi* and *C. vanderhammeni St2* are barbed, ribbed and tapering, but *St3* are barbed, ribbed and stout, appearing rectangular in shape). In addition to setae *St2–St3*, sternal area with only four barbed and long setae, as in *C. armasi* (3–4 pairs in *C. panamensis* and 6–5 pairs in *C. vanderhammeni*). Female pregenital area lacking any setae (with fine setae in *C. panamensis*, ribbed in *C. armasi* and *C. vanderhammeni*).

Description of adults

Chelicera (Fig. 7): basal segment with one dorsal seta, fixed digit with three. All setae smooth. Dorsal and antiaxial lyrifissures present. Fixed digit with one pronounced tooth. Movable digit with one anterior and pronounced tooth, and one very small denticle situated posteriorly. Basal portion of movable digit smooth. Superior (*ts*) and inferior (*ti*) tendons most distinct in the median part of chelicerae. Superior tendon strong and extends to anterior part of segment I, inferior tendon appears short and slender. Basal segment 147–175 µm, fixed digit 210–250 µm, movable digit 73–90 µm.

Subcapitulum (Fig. 8): all four pairs of paralabial setae present: *pl1* small, conical; With's organ (*pl2*) membranous, smooth and discoid; rutellum (*pl3*) with five teeth and inserted dorso-laterally; *pl4* small, conical and inserted dorsally. In addition, four circumbuccal setae (*cb*), and 8–13 median and subcapitular smooth setae. Lateral lips with two distinct canals, *ogl1* thick and shorter than *ogl2*. Distinct sexual dimorphism expressed in adults. In females three or four pairs of the ventral setae have a rounded tip (rather than fine and tapering). In males only one pair, placed near *cb3*, is rounded (Fig. 8; rounded tip of ventral setae indicated by arrows).

Palp tarsus (Figs 9, 10): setation includes two pointed and smooth setae, three *s*-type, 8–9 *d*-type, 5–6 *v1*-type, 1–3 *v2*-type, 11–12 *ch*-type and 11 *sm*-type setae. Pretarsus with well-developed claws. No distinct sexual differentiation observed. Tibia/tarsus 205–240 µm, genu 132–155 µm, femur 185–205 µm, trochanter 85–107 µm.

Idiosoma (Figs 14–17): longer (1.3–1.8 mm) than wide (0.68–0.83 mm), oval. Body lightly coloured with dark blue patches. Some leg segments, mainly femur and trochanter, are violet coloured. Body sometimes with a brownish background resulting from ingested food.

Dorsum: anterior dorsal shield with two pairs of eyes and 82–98 stout, ribbed setae. Dorsal idiosoma between the shield and the preanal segment without setae, but with numerous lyrifissures arranged in transverse rows. Preanal segment with one dorsal and two ventral stout, ribbed setae; anal plates each with 10–14 stout, ribbed setae.

Sternapophyses (Fig. 18): with two setae, including one small seta at the tip and one long and barbed seta positioned more basally.

Sternitogenital region (Figs 19–21): with one pair of capsules, each carrying one tapered and barbed seta (*St1*) and 3–6 barbed setae. Remaining sternal area with: (1) two pairs of small setae, both barbed and tapering (*St2* and *St3*); (2) two pairs of long, stout, ribbed barbed setae placed laterally of *St2* and *St3*; and (3) three pairs of lyrifissures, two pairs large and the third smaller.

Pregenital and genital area: male (Figs 19, 20) with one pair of capsules, each carrying one tapered and barbed seta (*St5*) and 3–6 stout, ribbed setae. Pregenital area between capsules with 4–7 (rarely two) small and smooth setae. Genital area with 7–13 small and smooth setae. Female (Fig. 22) with one pair of capsules, each with one tapering and barbed seta, and 3–6 stout, ribbed setae. Pregenital area between capsules without setae. Genital area without setae.

Ovipositor (Fig. 23): simple, cylindrical, tube like, without setae, but with a single pair of gland-like structures situated medially.

Legs (Figs 24–29): leg I longer than others. Tarsi I without acrotarsus, but with a distinct basitarsus. Acrotarsus present in legs II–IV. Dorsal portion of acrotarsus of legs II with a ribbed and bifurcate seta, one small solenidion, one long and smooth sensillum (probably a solenidion) and two barbed, long and large setae. Dorsal portion of acrotarsi III and IV with three barbed, long setae, and one pair of smooth and fine setae. Median and ventral portion of acrotarsi II–IV with five pairs of smooth or weakly barbed setae, arranged in five whorls. Pretarsi with one pair of claws, one pair of long and curved setae, and a pair of small and straight setae. Pretarsal claws with fine striations, a feature recognised only under scanning electron microscopy. Dimensions (µm): leg I: telotarsus 370–485, basitarsus 525–590, tibia I 460–475, tibia II 730–855, genu 970–1100, basifemur 565–630, telofemur 675–745, trochanter 500–585. Leg II: acrotarsus 95–105, basitarsus 300–350, telotarsus 395–455, tíbia 340–400, genu 300–365, femur 600–680, trochanter 190–250. Leg III: acrotarsus 95–107, basitarsus 300–360, telotarsus 350–425, tíbia 310–380, genu 295–380, basifemur 400–475, telofemur 160–200, trochanter 165–190. Leg IV: acrotarsus 100–125, basitarsus 350–445, telotarsus 470–545, tíbia 500–555, genu 470–585, femur 670–790, basitrochanter 260–340, telotrochanter 245–310.

Development notes

The only nymphal instar collected was the tritonymph, probably due to the larger size of this type of immature. All collections were made by visual search and this can be the reason for the small number of immatures found.

The tritonymphs are very similar to the adults, but there are some differences especially in setal numbers for some structures. The palp tarsus of tritonymphs carries only seven or eight *d-type* setae (rarely six) and nine or ten *r-type* setae (rarely eight), while the sternal verrucae carry only three or four setae (some specimens carry only two, *St1* and one setae tapering and barbed).

Similar to the adult species, sexual dimorphism is present in the tritonymphs stages. The subcapitulum of female tritonymphs carries at least two rounded-tip setae, while setae in the pregenital and genital area are always absent (Figs 8, 30). Male tritonymphs lack rounded-tip setae on the subcaptulum, lack setae in the

pregenital area, and have a few (2–5) small tapering setae in the genital area (Fig. 31).

Distribution and ecology

Specimens were collected in two distinct areas of Pará state, Brazil. In the south, three specimens were found in litter of a sandstone cave during a brief collecting session. Most specimens were recovered in the east-central region of the state, as part of an extensive biospeleological inventory of a large number of iron caves. The majority of these specimens were found in litter and under rocks near the cave entrances, sometimes as single individuals but frequently in small groups, with four or more specimens. These groups included mixtures of juveniles, females and males.

The main focus of this inventory was biospeleological studies and, for this reason, only occasional collections were conducted in the surrounding epigeal habitat, resulting in a small number of specimens (four). There is therefore still little information about the occurrence of these mites in epigeal habitats. Even so, it seems clear that *C. brasiliensis* is a troglophile, a species that can complete its entire life cycle in an epigeal and cave habitat.

Etymology

The specific epithet is an adjective referring to the occurrence of this species in Brazil.

Key to adult species of *Caribeacarus* (adapted from Vázquez and Klompen 2009)

1. Setae *St2* and *St3* tapering in shape; basal segment of chelicera in male with one seta; 'crown-like' sensillum on tarsus I small and not on tip ..... Continental species-group 2
   Setae *St2* tapering in shape and *St3* stout, never fine; basal segment of chelicera in male with two or more setae; 'crown-like' sensillum on tarsus I conspicuous, inserted on tip ..... Caribbean species-group. . .3
2. Fine setae present in genital area of female; 3–4 pairs of setae in sternal area, in addition to setae *St2* and *St3*; palp with 15 *ch*-type setae ..... *C. panamensis*
   Genital area in female without setae; two pairs of setae in sternal area, in addition to setae *St2* and *St3*; palp with 11–12 *ch*-type setae ..... *C. brasiliensis*
3. Palp tarsus with eight foliate (*d*-type) setae; two pairs of setae in sternal area, in addition to setae *St2* and *St3* ..... *C. armasi*
   Palp tarsus in adults with 10–12 foliate (*d*-type) setae; four or more pairs of setae on sternal area, in addition to setae *St2* and *St3* ..... *C. vanderhammeni*

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Appendix 1. List of characters and character states in phylogenetic analysis

Opisthosoma

0. Setae on opisthosomal segments in adults
   0. Setae absent
   1. Setae present
1. Number of the papilliform setae on penultimate segment of idiosoma
   0. More than three
   1. Only three

Legs

2. Position of 'crown-like' sensillum on tarsus I
   0. In dorsal sensory field, not on tip of tarsus
   1. On tip of tarsus
3. Number of the setae on lateral portion of the acrotarsi II–IV
   0. Two pairs
   1. Three pairs
   2. Four pairs
   3. Five pairs
4. Number of the setae on the ventral portion of the acrotarsi II–IV
   0. Three pairs
   1. Four pairs
   2. Five pairs
5. Position of the solenidion ω_d on the basitarsi III and IV
   0. Distal, often partially sunk into basitarsus
   1. Median, not sunk in basitarsus

Gnathosoma

6. Number of the setae on the fixed digit of the male chelicerae
   0. Three
   1. Four or more
7. Number of the setae on basal segment of male chelicerae
   0. One
   1. Two or more
8. Type of the *d*-type setae on palp
   0. Stout, with less than five lobules
   1. Slender, with more than six lobules and lobules with filiform tips
9. Number of the *d*-type setae on palp
   0. Five or six

(*continued next column*)

Appendix 1. (*continued*)

   1. Eight or nine
   2. More than 10
10. Number of the *ch*-type setae on palp tarsus
   0. 32
   1. 25 or 26
   2. 15 or less
11. Number of the pairs of median and subcapitular setae
   0. More than 15
   1. 13 or less

Genital and sternal area

12. Papilliform setae in sternal area of adults
   0. Absent
   1. Present
13. Shape of *St2* and *St3* setae
   0. Tapering and ribbed
   1. Setae *St2* tapering and ribbed, setae *St3* stout and ribbed
14. Number of pairs of setae in sternal area in addition to setae *St2* and *St3*
   0. Four or more
   1. Three
   2. Two
15. Shape of setae in pre-genital area of the male
   0. Fine, tip attenuate
   1. Stout and ribbed
16. Shape of setae in genital area of the male
   0. Fine, tip attenuate
   1. Fine and ribbed
   2. Stout and ribbed
17. Shape of setae in pre-genital area of the female
   0. Absent
   1. Attenuate and ribbed
   2. Stout and ribbed
18. Shape of setae in genital area of the female
   0. Absent
   1. Fine, tip attenuate
   2. Stout and ribbed

Appendix 2. Matrix used in phylogenetic analysis

Taxa	Characters																		
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
S. antsirananensis	1	0	0	2	0	0	0	0	0	0	1	1	1	0	0	1	1	1	0
N. potiguar	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	2	1	1
N. texanus	0	1	0	1	0	1	0	0	0	0	2	1	0	0	0	1	0	2	0
C. vanderhammeni	0	1	1	2	1	1	1	1	1	2	0	0	0	1	1	1	2	0	1
C. armasi	0	1	1	2	1	1	1	1	1	1	1	1	0	1	2	1	2	0	2
C. panamensis	0	1	–	2	1	0	0	0	1	1	2	1	0	0	2	0	0	0	1
C. brasiliensis	0	1	0	3	2	0	0	0	1	1	2	1	0	0	2	0	0	0	0