Taxonomy of the Neotropical freshwater crab family Trichodactylidae. VI. The genera *Avotrichodactylus* and *Rodriguezia* (Decapoda: Brachyura: Trichodactylidae)

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Abstract

The taxonomy of two trichodactyline genera of the Neotropical freshwater crab family Trichodactylidae are revised. The genus *Avotrichodactylus* Pretzmann, 1968, includes two species, *A. constrictus* (Pearse, 1911) and *A. oaxensis* Rodríguez, 1992; the genus *Rodriguezia* Bott, 1969, also has two species, *R. mensabak* Cottarelli and Argano, 1977, and *R. villalobosi* (Rodríguez and Manrique, 1967). The taxonomic statuses of all the species are discussed and a short diagnosis is provided for each. A complete list of the material examined and a map of geographic distribution of the species are furnished.
Key words: Brachyura, Crustacea, Mexico, Neotropical region, Systematics.

Introduction

The four species of the trichodactylid freshwater crabs that occur in southern Mexico are included in the subfamily Trichodactylinae owing to similarities with the South American representatives of the genus *Trichodactylus* Latreille, 1828, in carapacial and gonopodal morphology (Pretzmann, 1968; Bott, 1969a; Rodríguez, 1992; Magalhães and Türkay, 1996a). The first two species described from this region were in fact assigned to this genus, viz., *Trichodactylus constrictus* Pearse, 1911, and *T. villalobosi* Rodríguez and Manrique, 1967. However, these species have some peculiarities in the morphology of the first and second pair of gonopods, which led Pretzmann (1968) and Bott (1969a) to assign them separate subgeneric ranks under *Trichodactylus*. Pretzmann (1968) erected the subgenus *Avotrichodactylus* for *T. constrictus* based on the curved and tapering apex of the first gonopod, while Bott (1969a) introduced *Trichodactylus* (*Rodriguezia*) for *T. villalobosi,* diagnosed by the second gonopod being shorter than the first one. Bott (1969a) did not recognize *Avotrichodactylus* because he stated that Pretzmann had not in fact examined males of *T. constrictus*. Pretzmann (1978) subsequently raised *Avotrichodactylus* to genus level on the basis of the gonopodal morphology and distribution of the species. In his monographic treatment of the Trichodactylidae, Rodríguez (1992) kept it with this rank and also elevated *Rodriguezia*

to genus. This classification was maintained by Magalhães and Türkay (1996a) in their proposal of a generic system for the family, and more recently followed by other workers (see Ng *et al.*, 2008; De Grave *et al.*, 2009).

In this paper, we continue our ongoing taxonomic revision of the trichodactylid genera (see Magalhães and Türkay, 1996a, b, c; 2008a, b) by presenting brief diagnoses and illustrations of the carapace and the male first pleopods for each species of *Avotrichodactylus* and *Rodriguezia*, as well as remarks about their intraspecific variability. A key to the species of both genera is also provided.

Material and Methods

The measurements are given in millimeters; measurements of the type and the largest specimen examined are usually provided. The terminology used for gonopod description is explained in Magalhães and Türkay (1996a); the number of anterolateral teeth of the carapace includes neither the exorbital angle (when toothed) nor the accessory tooth sometimes present at base of the exorbital angle. Type specimens of species were examined, except where noted otherwise. Synonymies presented include mainly references from 1969 onwards; see Bott (1969a) for synonymies prior to that year. Geographic distribution of the species was mapped on the basis of the records presented in this paper and from the literature.

Abbreviations: Measurements – cb, carapace breadth, measured across the carapace at its widest point; cl, carapace length, measured along the midline, from the frontal to the posterior margin. Repositories of the specimens – CNCR, Colección Nacional de Crustaceos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus; IVIC, Colección de Referencia de Crustáceos Decápodos, Instituto Venezolano de Investigaciones Científicas, Caracas; NHM, The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; NHMW, Naturhistorisches Museum Wien, Wien; RMNH, National Museum of Natural History (*Naturalis*), Leiden; SMF, Senckenberg Museum, Frankfurt am Main; URTV, Universitá degli Studi di Roma "Tor Vergata", Dipartimento di Biologia, Roma; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.; and ZMH, Zoologisches Museum, Universität Hamburg, Hamburg. Other abbreviations – alt., altitude; coll., collector(s); juv., juvenile; and plp 1 and plp 2, first and second male gonopods, respectively.

Systematic

Avotrichodactylus Pretzmann, 1968

Trichodactylus (*Trichodactylus*). – Coifmann, 1939: 111 [part.] [not *Trichodactylus* Latreille, 1828].

Trichodactylus (*Avotrichodactylus*) Pretzmann, 1968: 71.

Trichodactylus (*Rodriguezia*). – Bott, 1969a: 25 [part.] [not *Trichodactylus* (*Rodriguezia*) Bott, 1969].

Avotrichodactylus. – Pretzmann, 1978: 4. – Pretzmann, 1980: 661. – Rodríguez, 1992: 63. – Villalobos-Hiriart *et al.*, 1993: 284. – Álvarez *et al.*, 1996: 129. – Magalhães and Türkay, 1996a: 772. – Suárez, 2005: 155. – De Grave *et al.*, 2009: 42. – Álvarez *et al.*, 2011: 275.

Trichodactylus. – Guinot, 1988: 19 [part.] [not *Trichodactylus* Latreille, 1828].

Type species: Trichodactylus constrictus Pearse, 1911 [by monotypy].

Remarks: Although the plp 2 is similar to that of *Rodriguezia* in being shorter than the plp 1, the tapered distal part of the plp 1 and its strong curvature in ventrolateral direction, as well as the fused III-V abdominal somites (as opposed to the straight plp 1 with broad apex, and all abdominal somites free in *Rodriguezia*),

justify the status of *Avotrichodactylus* as a distinct genus.

Key to the species of *Avotrichodactylus*

1. Male plp 1 with apical portion strongly curved ventrolaterally (Figs. 7, 8); carapace usually with 2-3 anterolateral teeth.....*A. constrictus*
-. Male plp 1 with apical portion nearly straight (Figs. 11, 12); carapace usually with 4-5 anterolateral teeth.....*A. oaxensis*

Avotrichodactylus constrictus (Pearse, 1911)
(Figs. 1 - 9)

Trichodactylus constrictus Pearse, 1911: 4, fig. 4. – Rodríguez and Manrique, 1967: 183. – Smalley, 1970: 104, fig. 9.
Trichodactylus (*Trichodactylus*) *constrictus*. – Coifmann, 1939: 111.
Trichodactylus (*Avotrichodactylus*) *constrictus*. – Pretzmann, 1968: 71.
Trichodactylus (*Rodriguezia*) *bidens* Bott, 1969a: 25, pl. 24, figs. 68-69. – Cottarelli and Argano, 1977: figs. 3-4. – Reddell, 1981: 114.
Trichodactylus (*Rodiguezia*) [sic !] *constrictus*. – Bott, 1969a: 26 [error].
Rodriguezia bidens. – Bott, 1969b: 270.
Avotrichodactylus constrictus. – Pretzmann, 1980: 661, pl. 14, figs. 61-63; pl. 15, fig. 69; pl. 18, fig. 81. – Rodríguez and Hobbs Jr., 1989: 399. – Rodríguez, 1992: 66, figs. 2A, 10I, 12F, 23A-E. – Villalobos-Hiriart *et al.*, 1993: 284. – Magalhães and Türkay, 1996a: 67, 68, 72. – Álvarez and Villalobos, 1997a: 416. – Álvarez and Villalobos, 1997b: 438. – Álvarez *et al.*, 1999: 23, fig. 3. – Álvarez *et al.*, 2005: 191. – Álvarez *et al.*, 2011: 275.
Trichodactylus bidens. – Holthuis, 1986: 614. – Guinot and Geoffroy, 1987: 21. – Guinot, 1988: 19.
Avotrichodactylus bidens. – Rodríguez and Hobbs Jr., 1989: 399. – Rodríguez, 1992: 65, fig. 23F. – Villalobos-Hiriart *et al.*, 1993: 284. – Álvarez *et al.*, 2005: 191. – Klaus and Plath, 2011: 411.

Holotype: Female (USNM 98399), Mexico, Veracruz, lago Catemaco, 27.VII.1910, A.G. Ruthven and H.B. Baker. It was first deposited in the University of Michigan Museum (cat. number 41717), but was subsequently transferred to the USNM.

Paratypes: 7 females (cb 11.8, cl 10.6; to cb 21.0. cl 19.1), (USNM 98400), 1 female (USNM 79361), all with same data as in holotype.

Material: Mexico — No precise locality: 3 males, 1 female (NHMW 1829), V.1883. — State of Veracruz: 2 males, 1 female (USNM 234436), NW+N sides of mesa San Lorenzo, SSW of Tenochtetlán, 03.II.1968, R.R. Miller *et al.*; 2 males, 4 females (USNM 128406), Zanja la Mina, off Mesa San Lorenzo, ca. 6 Km SSW of Tenochtitlán, 10.VII.1968, E.S. Wing *et al.*; 2 males, 1 female (INPA-CR 503), idem; 12 males, 10 females (CNCR 2200), El Zapotal, Catemaco, 18.IX.1954, A. Villalobos; 6 males, 4 females (CNCR 13347), río Maquinas, entre la Estación de Biología Tropical Los Tuxtlas y Montepio, 5.V.1995, F. Álvarez; 3 males, 1 female (CNCR 13385), río La Palma, entre Catemaco y Montepio, 2.VI.1995, J.C. Molinero and R. Robles; 1 female (CNCR 10624), arroyo entre los río La Palma y río Maquinas, Los Tuxtlas, San Andres Tuxtla, 12.XII.1986, coll. unknown; 2 males, 1 female (CNCR 16830), río La Palma, entre Catemaco y Montepio, San Andres Tuxtla, 11.VIII.1985, coll. unknown; 1 female (CNCR 9261), río Palma, San Andres Tuxtla, 27.IX.2008, coll. unknown; 1 male, 1 female (CNCR 15529), río Maquinas, San Andres Tuxtla, 12.viii.1995, coll. unknown; 3 males (CNCR 13277), entre El Potrero y Medellin, Los Tuxtlas, 7.VII.1986, F. Álvarez; 1 male (CNCR 12917), Santiago Tuxtla, Medellín, desviación a Tres Zapotes, 7.VII.1986, F. Álvarez; 6 males, 2 females (CNCR 13348), La Playita, río Tepango, Santiago Tuxtla, 3.V.1995, R. Robles; 3 males, 5 females (CNCR 17045), La Playita, río Santiago, Santiago Tuxtla, 23.I.1997, R. Robles and F. Álvarez; 1 female (USNM 102215), arroyo Tapalapan, Santiago Tuxtla, 17.IV.1957, A. Villalobos *et al.*; 1 male, 1 female, 1 juv. (USNM 189307), arroyo Escuinapan, tributary of lake Catemaco,

15.II.1974, F.H. Miller; 2 males, 1 female (CNCR 12962), Catemaco, primer puente de Las Margaritas a Tebanca, Catemaco, 4.VIII.1994, M.E. Camacho *et al.*; 2 males (NHMW 4072), Lago Catemaco, 14.V.1975, I. P.-Neuwall; 2 males (CNCR 12971), lago de Catemaco, Playa Azul, 18º26'N 95º05'W, 15.IV.1957, H.H. Hobbs Jr. and A. Villalobos; 15 males, 3 females (CNCR 12960), arroyo 1 km S de Coyame, orilla del lago de Catemaco, Catemaco, 1.VIII.1994, M. Hermoso *et al.*; 1 male (CNCR 12955), idem locality, 1.VIII.1994, M. Hermoso *et al.*; 2 males (CNCR 12957), idem locality, 1.VIII.1994, M. Hermoso *et al.*; 3 males, 2 females (CNCR 12999), lago de Catemaco, 13.VI.1965, J. Cabrera; 1 male, 1 female (CNCR 12897), arroyo Posalapan, Los Tuxtlas, 13.VII.1986, F. Álvarez; 1 male (CNCR 13342), río entre Las Margaritas y Tebanca, lago de Catemaco, 6.V.1995, J.L. Villalobos; 1 female (CNCR 12953), río entre Las Margaritas y Tebanca, lago de Catemaco, 4.VIII.1994, F. Álvarez; 1 male (CNCR 12916), río en el poblado de Tebanca, 10.VII.1986, F. Álvarez; 17 males, 2 females (CNCR 12959), lago de Catemaco, en la orilla entre Las Margaritas y Tebanca, 1.VIII.1994, F. Álvarez; 16 males, 7 females (CNCR 2150), Playa Hermosa, lago Catemaco, Catemaco, 21.VIII.1966, L.B. Holthuis, J. Cabrera and F. Manrique; 2 males (INPA 1918), idem; 7 males, 2 females (CNCR 6128), idem locality, 31.VIII.1966, L.B. Holthuis, J. Cabrera and F. Manrique; 1 male, 1 female (MZUSP 9766), idem; 1 male, 1 female (IVIC 717), Playa Hermosa, lago Catemaco, 3.VIII.1966, L.B. Holthuis *et al.*; 1 male, 2 females (CNCR 1241), lago de Catemaco, Catemaco, 2.I.1953, M. Bopp; 5 males, 5 females (CNCR 20346), arroyo 4 km antes de Posa Reina, ejido las Margaritas, Catemaco, 5.IV.2002, J.L. Villalobos and A. Botello; 1 male, 1 female (CNCR 12903), salto de Eyipantia, 29.IX.1984, F. Álvarez; 4 females (CNCR 21314), puente Tezizapa, manantial Platanillo, Tatahuicapan de Juárez, X.1984, J.L. Villalobos; 1 male, 1 female (CNCR 12918), río en el poblado de Hueyapan de Ocampo, 9.VII.1986, F. Álvarez; 3 males, 7 females (CNCR 17084), río Tonalá, estación 8, balneario San Antonio en San José, Las Choapas, 17°51.98'N 94°05.25'W, 11.VI.1997, R. Robles; 2 males (CNCR 17241), idem locality, 24.III.1998, R. Robles. — State of Tabasco: 1 male (INPA 1828), Teapa, stream 500 m before entrance of Coconá caves, 22.III.1981, R.P. López; 5 males, 3 females (NHM 1907.5.15.5-9), Teapa; 1 male, 1 female (SMF 31867), idem; 7 males, 7 females, 4 juv. (CNCR 16620), Los Azufres, Teapa, 10.X.1996, J. L. Villalobos and R. Robles; 1 male, 1 female (INPA 1917), idem; 1 female (CNCR 16621), idem locality, III.1996, M. Mendoza; 1 male (CNCR 5855), río Puyacatengo, Teapa, 15.IV.1986, J.P.G. Reynoso; 5 males, 2 females (CNCR 18688), arroyo cercano a la cueva de las Sardinas, Tapijulapa [17°27'N 92°47'W], 29.III.1998, R. Robles; 1 male (INPA 1916), idem; 1 female (CNCR 21031), cueva de las Sardinitas, cerca de Tapijulapa, 31.V.1988, R. Robles and J.L. Villalobos; 3 males, 1 female (URTV), Tocotalpa, Tapijulapa, cueva El Azzufre, 9.IV.1971, V.S. Sbordoni; 1 male, 1 female (INPA 1931), cueva los Azufres, Parque de la Luz, 17°26,54'N 92°46,47"W, 3.X.2010, S. Klaus and M. Plath; 1 female (ZMH K-34550), Tapijulapa, cueva el Azzufre, 1.II.1982, H. Wilkens; 1 male (15.7:13.9), holotype of *Trichodactylus* (*Rodriguezia*) *bidens* Bott, (ZMH K-28323), arroyo del Solpho, near Tapijulapa, 26.III.1964, Zander; 2 females, paratypes of *T.* (*R.*) *bidens*, (ZMH K-28642), idem; 1 female, paratype of *T.* (*R.*) *bidens*, (SMF 29991, ex-4888), idem; 1 female (RMNH D 29853), idem, 1970, H. Wilkens. — State of Oaxaca: 7 males, 8 females (USNM 189308), arroyo Zacatiapan, approximately 6 mi. S of Paploapan [? = Papaloapan], 28.II.1939, G.F. Atz; 1 female (CNCR 1026), Piedra de Amolar Montebello, San Juan Bautista Tuxtepec, 20.IX.1947, coll. unknown; 2 juv. (CNCR 13101), Nuevo Montebello, San Juan Bautista Tuxtepec, 31.VII.1994, M. Hermoso *et al.* — State of Chiapas: 5 males, 2 females (CNCR 26312.), Río Michol, poblado El Michol, Salto del Agua, 17°34'10"N 92°17'03"W, 18.I.2002,

coll. unknown; 1 male, 1 female (INPA 1920), idem; 2 males (USNM 230085), 1 km N Palenque, 25.VII.1973, J. Redell *et al.*; 2 females (CNCR 19052), about 4 miles W of Mayabel campgroud on road to ruínas de Palenque, 4.I.1977, D. Felder *et al.*; 1 male, 1 female (CNCR 13352), arroyo de las ruínas de Palenque, 1985, J.C. Nates; A. Cantú and J.L. Villalobos; 2 males, 1 female (CNCR 13627), arroyo de las ruínas de Palenque, 4.X.1978, col. unknown; 1 female (CNCR 5801), arroyo de las ruínas de Palenque, Palenque, 11.VI.1986, E. Lira; 4 males, 1 female (CNCR 9797), idem locality, 1.VIII.1988, coll. unknown; 1 female (CNCR 5590), arroyo que pasa por las ruínas de Palenque, Palenque, 4.IX.1986, A. Cantú *et al.*; 5 males, 6 females (CNCR 5593), arroyo en las ruínas de Palenque, Palenque, 4.IX.1986, Cantú *et al.*; 6 males, 2 females (CNCR 19226), arroyo en la entrada de las ruínas de Palenque, Palenque, 31.VII.2001, J.L. and M.C. Villalobos; 1 male, 1 female (INPA 1919), idem; 1 female (USNM 88055), las ruínas de Palenque, C. Goodnight; 4 males, 11 female (NHMW 4071), 1 km NW Palenque, VI.1975, I.P.-Neuwall; 2 males (NHMW 21821), Palenque, IV-V.1975, I.P.-Neuwall; 6 males, 3 females (CNCR 2945), acueducto Baño de la Reina, ruínas de Palenque, Palenque, 8.VIII.1983, Nates, Villalobos and Cantú; 2 males, 1 female (CNCR 5597), km 4 de la desviación hacia Palenque, 4.IV.1986, Cantú *et al.*; 1 female (CNCR 8682), carretera Palenque-Chancalá, km 27, 18.X.1987, J.L. Villalobos and E. Lira; 2 males (CNCR 12587), Estación Chajul, río Lacantún, Marqués de Comillas, 28.VII.1993, M. Palma; 1 male (CNCR 8696), afluente del Lacanjá, río Maya, camino hacia Bonampak, 19.X.1987, E. Lira and J. L. Villalobos; 3 males, 4 females (CNCR 20347), río Usumacinta, 16°49'24.9"N 90°53'18.3"W, 19.I.2002, coll. unknown.

Diagnosis: Carapace subquadrate; anterolateral margins of carapace with two to three teeth behind external orbital tooth. Abdominal somites III-V fused. Male plp 1 with distal portion tapering and strongly bent in ventrolateral direction. Marginal suture running along mesial side of stem, not twisted to other sides. Subterminal spine fields well developed, discontinuous, situated on lateral and mesial sides, with latter broader and larger than former. Distal opening subcircular, small, situated terminally. Plp 2 about half of length of plp 1.

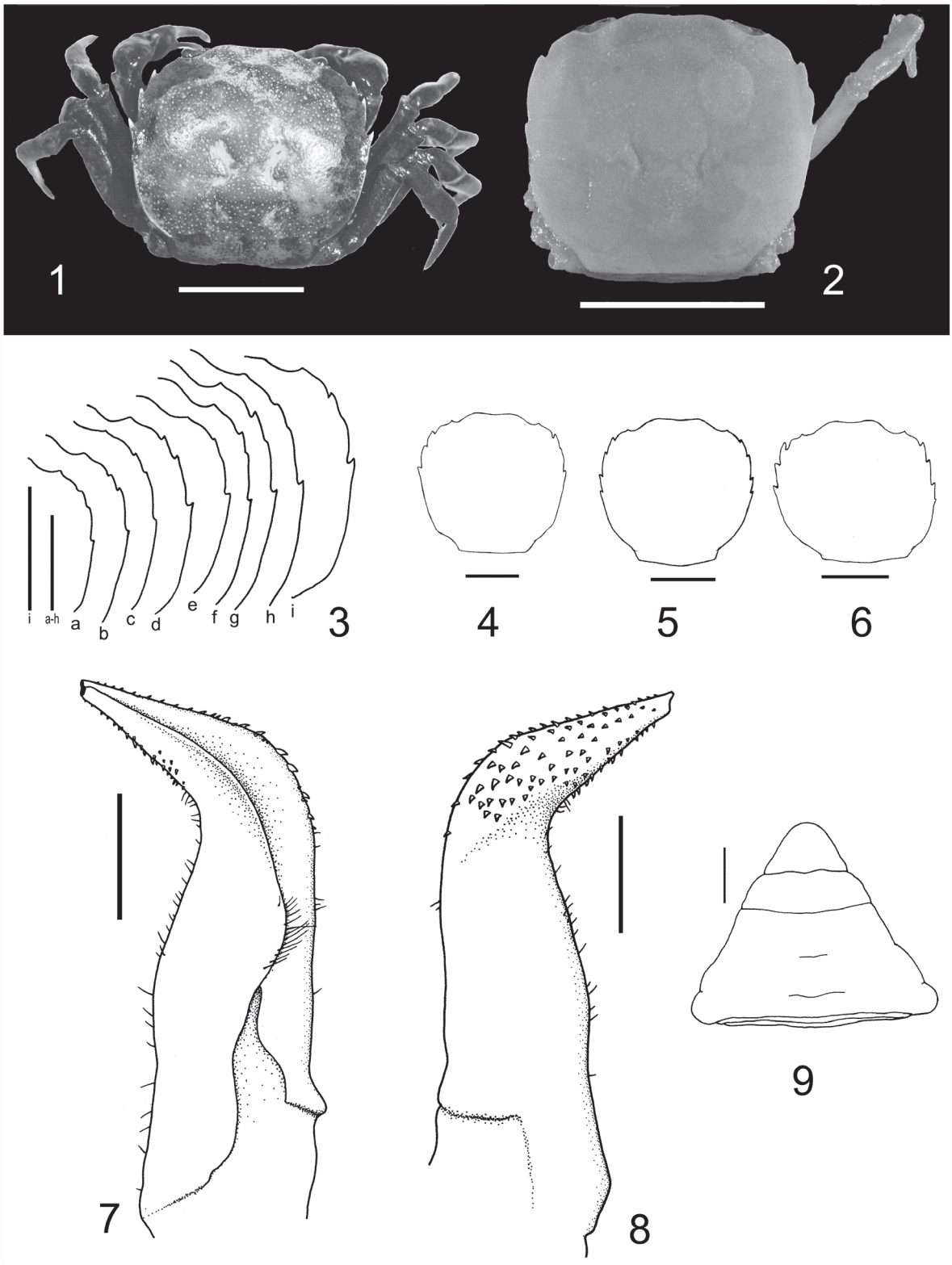
Measurements: cb 19.1, cl 16.8 (holotype); largest specimen examined: cb 24.1, cl 21.7 (male, CNCR 13385).

Type locality: Mexico, state of Veracruz, lake Catemaco.

Distribution: Southern Mexico, in the states of Veracruz, Tabasco, Oaxaca, and Chiapas (Fig. 20). Additional records from these states were also provided by Rodríguez and Manrique (1967) and Rodríguez and Hobbs Jr. (1989).

Remarks: Bott (1969a) included *A. constrictus* in his newly-erected subgenus *Trichodactylus* (*Rodriguezia*) probable based on the geographical distribution of the species, as he did not have access to any male specimens of this species and, therefore, could not examine its gonopodal morphology. In the same paper, he described *T.* (*R.*) *bidens* and distinguished it from *T.* (*R.*) *constrictus* only by the number of teeth on the anterolateral margins of the carapace (2 versus 3, respectively), as both left and right gonopods of the holotype of *T.* (*R.*) *bidens* were already severely damaged, thus precluding an evaluation of gonopod morphology. Cottarelli and Argano (1977) also identified their specimens of *T.* (*R.*) *bidens* on the basis of the number of anterolateral teeth.

We have examined most of the specimens mentioned in the literature that were assigned to both taxa, as well as additional material from southern Mexico, and found a clear variation in the shape and number of the teeth on the anterolateral margins of the carapace. Usually, the second tooth is sharp as in the holotype specimen (Fig. 1), but it can be smaller, rounded, vestigial or even evanescent (Figs. 2,



Figures 1 - 9. *Avotrichodactylus constrictus* (Pearse, 1911): 1, female, holotype, USNM 98399, dorsal view; 2, male, holotype of *Trichodactylus* (*Rodriguezia*) *bidens* Bott, 1969, ZMH K-28323, dorsal view; 3, outline of the right margin of the carapace (a-h, NHM 1907.5.15.5-9, a,b,d-g: males, c,h: females; i, male, holotype of *T.* (*R.*) *bidens* Bott, 1969, ZMH K-28323); 4, outline of the carapace, CNCR 13385, male; 5, outline of the carapace, CNCR 17084, male; 6, outline of the carapace, CNCR 12587, male; 7, right first gonopod, USNM 189307, mesioventral view; 8, right first gonopod, USNM 189307, dorsolateral view; 8, outline of the male abdomen and telson. Scale bars: 10 mm (1, 2, 4-6); 5 mm (3); 2 mm (9), 1 mm (7, 8).

3). Specimens from the state of Veracruz usually have three low and sharp teeth while there is a tendency for reduction of the second tooth in those specimens from the states of Tabasco and Chiapas. This is particularly evident among the specimens from the lots NHM 1907.5.15.5-9 (Fig. 3a-h) and ZMH K-28323 (Fig. 3i). It is also rather common that the shape of the teeth vary between the left and right margins of the same specimen (for instance, a specimen from the lot CNCR 13385 – Fig. 4). A few specimens can even bear four teeth on the lateral margin (for instance, some specimens of the lots CNCR 17084 and CNCR 12587 – Figs. 5, 6), but usually the fourth pair consists of vestigial teeth (for instance, in the specimen of the lot CNCR 12587 – Fig. 6, or in the holotype of *A. constrictus* itself – Fig. 1). Rodríguez and Hobbs Jr. (1989) also recognized the variability in the anterolateral teeth of these taxa.

Moreover, the distal part of the plp 1 can be more or less tapered and the lateral and mesial patches of the subterminal spine field partially continuous in some specimens (Figs. 7, 8). The curvature of the plp 1's distal part is not so pronounced in immature males.

Ojeda (2010), in an unpublished academic thesis on the distribution patterns of the Trichodactylidae from Mexico, presented a detailed morphological study of the carapace and gonopod of *Avotrichodactylus constrictus* and presumptive *A. bidens* from different river basins within their area of distribution. He found great variability in carapace, third maxilliped and gonopod characters among populations of *A. constrictus* from different hydrographic basins, although no particular morphology could be associated with each basin or population (Ojeda, 2010). He also noticed a high degree of similarity between the specimens assigned to both species, but preferred to keep them separated until additional material can be obtained from the area of occurrence of *A. bidens*.

Our study of a good series of specimens (including adult male specimens with intact gonopods) from and near the type locality of *T.* (*R.*) *bidens*, the "Cueva de los Azufres", in Tapijulapa, state of Tabasco, has shown no taxonomically significant difference in the carapace and gonopod morphology to justify assigning specific status to them. Therefore, in spite of the impossibility of evaluating the gonopod morphology of the holotype of *T.* (*R.*) *bidens*, we propose that this species be considered a junior synonym of *A. constrictus* owing to the overlapping of their occurrences and overall similarities in morphology of the specimens, taking into account also that the characters used to separate both taxa are subject to strong variability as described above.

Avotrichodactylus oaxensis Rodríguez, 1992
(Figs. 10 - 14)

Avotrichodactylus oaxensis Rodríguez, 1992: 67, figs. 3C, 4G, 6G, 12G, 15C, 24A-H. – Villalobos-Hiriart *et al.*, 1993: 284. – Magalhães and Türkay, 1996a: 67, 69, 72. – Álvarez and Villalobos, 1997a: 416. – Álvarez and Villalobos, 1997b: 438. – Álvarez *et al.*, 1999: 23, fig. 3. – Suárez, 2005: 155.

Holotype: Male (ZMH 34549a), Mexico, state of Oaxaca, cañada Acatlán, río San Antonio, 20.II.1988, H. Wilkens.

Paratypes: 2 males juv. (cb 11.9, cl 11.2; cb 18.1, cl 16.6) 1 female juv. (cb 12.2, cl 11.0) (ZMH 34549b); 2 males (MNHN B-24317); 1 male (cb 18.0, cl 16.7) (IVIC 718), all with same data as in holotype.

Material: Mexico — No precise locality: 1 male (USNM 268896). — State of Veracruz: 4 males, 8 females (USNM 285034), 50 yds in back of hacienda Potrero [? region of Los Tuxtlas], 23.XII.1940, Marchand; 1 male, 1 female (INPA 1260), idem; 1 male, 1 female (SMF 39110), idem; 3 males, 3 females (USNM 285033), idem; 9 males, 7 females, 2 carapaces (CNCR 26311), laguna de Majahual, carretera El Trópico-Montepio, San Andres Tuxtlas, 18º39'13.6"N 95º08'20.1"W, 21.IV.2005, J.L. Villalobos; 3 males, 2 females (INPA 1921), idem; 2 males (CNCR 12915), carretera entre Tres Zapotes y Tlapacoyan, 18º27'N 95º23'W, 7.VII.1986, F. Álvarez;

1 female (CNCR 1117), arroyo de la Pita, Ciudad Alemán, date and coll. unknown. — State of Oaxaca: 1 female (USNM 230086), cueva de Juan Sanchez, NW Acatlán, 7.I.1973, T. Byrd, A.G. Grubbs and M. Cassey; 4 males, 2 females (CNCR 25505), La Junta, cerca de Acatlán, 5.IV.2002, M.L. Mejía and L.M. Mejía; 1 male (INPA 1922), idem; 2 females (CNCR 1773), río en Rancho San Ricardo, Playa Vicente, date and coll. unknown.

Diagnosis: Carapace subquadrate; anterolateral margins of carapace with four to five teeth behind external orbital tooth. Abdominal somites III-V fused (segmentation between somites II-III and III-IV sometimes marked by pigmentation). Male plp 1 slender, with distal portion tapering and nearly straight or slightly bent in ventrolateral direction. Marginal suture running along mesial side of stem, not twisted to other sides. Subterminal spine fields well developed, situated on lateral and mesial sides, with latter broader and larger than former and both patches partially joined on dorsal side. Distal opening subcircular, very narrow, situated terminally and directed towards mesioventral side. Plp 2 about 0.6 times length of plp 1.

Measurements: cb 22.8, cl 21.2 (holotype); largest specimen examined: cb 27.2, cl 23.6 (male, CNCR 25505).

Type locality: Mexico, state of Oaxaca, cañada Acatlán, río San Antonio.

Distribution: Southern Mexico, in the states of Veracruz and Oaxaca (Fig. 20).

Remarks: Like the previous species, the shape and number of the teeth in the anterolateral margin of the carapace is also variable in *A. oaxensis*. Most of the examined specimens have four to five sharp teeth, but the fourth to fifth teeth can be more or less reduced in some specimens (Fig. 11); occasionally, a sixth tooth may be present (Fig. 10), but this seems to be an abnormal situation.

Avotrichodactylus oaxensis resembles *A. constrictus* in carapace morphology, but they can be distinguished from each other by the number of anterolateral teeth (4-5 in the former; 2-3 in the latter) and by the gonopod morphology (the plp 1 of *A. oaxensis* is nearly straight or weakly bent in a mesioventral direction, while it is strongly bent in a lateroventral direction in *A. constrictus*) (Figs. 12-13, 7-8, respectively). Moreover, the molecular analysis made by Ojeda (2010) using two mitochondrial genes from individuals of one population of each species (*A. oaxensis* from laguna Majahual; *A. constrictus* from río Tuxtla) showed a clear genetic divergence between them: 8% for cytochrome oxidase I (COI) gene and 10% for the 16S rRNA gene.

Rodríguez (1992) stated that the repository of the type material of *A. oaxensis* was the MNHN in Paris. In fact, only two male paratypes remain in the collection of this museum. The holotype, two males and one female paratypes have been returned to the ZMH in Hamburg, and the other male paratype has been deposited in the IVIC's collection.

Rodriguezia Bott, 1969

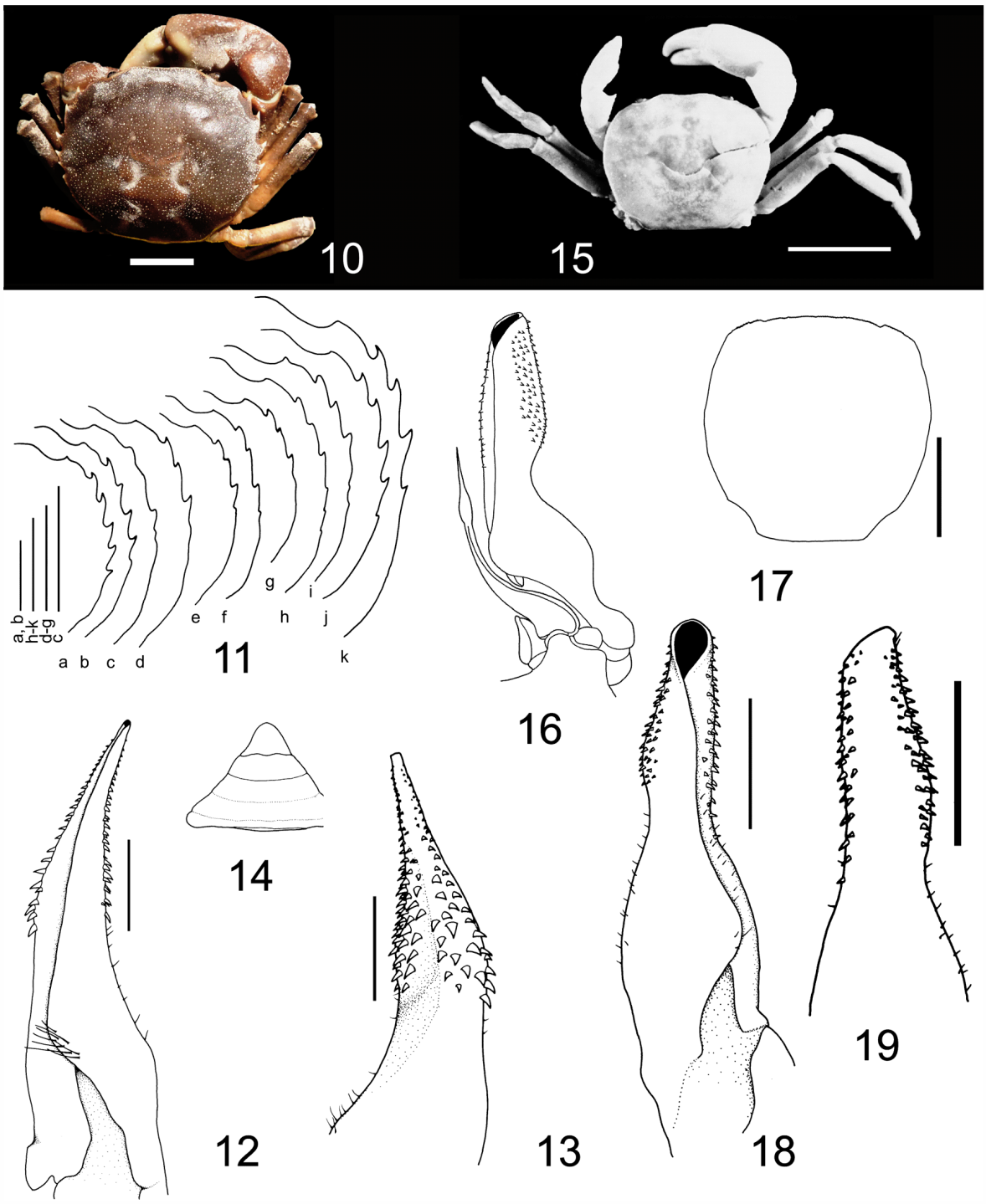
Trichodactylus (*Trichodactylus*). – Pretzmann, 1968: 70 [part.] [not *Trichodactylus* Latreille, 1828].

Trichodactylus (*Rodriguezia*) Bott, 1969a: 25 [part.].

Trichodactylus. – Guinot, 1988: 19 [part.] [not *Trichodactylus* Latreille, 1828].

Rodriguezia. – Rodríguez, 1992: 62. – Villalobos-Hiriart *et al.*, 1993: 284. – Álvarez *et al.*, 1996: 129. – Magalhães and Türkay, 1996a: 72. – De Grave *et al.*, 2009: 42. – Álvarez *et al.*, 2011: 276.

Type-species: Trichodactylus villalobosi Rodríguez and Manrique, 1967 [by original designation].



Figures 10 - 14. *Avotrichodactylus oaxensis* Rodríguez, 1982; 15 – 16. *Rodriguezia villalobosi* (Rodríguez and Manrique, 1967), holotype, CNCR 7832; 17 – 19. *Rodriguezia mensabak* (Cottarelli and Argano, 1977), holotype, URTV: 10, male, CNCR 25505, dorsal view; 11, outline of the right margin of the carapace (a, USNM 230086, male; b, male paratype, MNHN B-24317; c, USNM 285033, male; d, INPA 1260, male; e, INPA 1260, female; f, SMF 39110, male; g, SMF 39110, female; h-i, USNM 285033, females; j, male paratype, ZMH K-24317; k, male holotype, ZMH K-34549a); 12, left first gonopod, holotype, ZMH K-34549a, mesioventral view; 13, left first gonopod, distal half, holotype, ZMH K-34549a, dorsolateral view; 14, outline of the male abdomen and telson; 15, dorsal view; 16, left first and second gonopods, holotype, CNCR 7832 (reproduced from Rodríguez and Manrique, 1966); 17, outline of the carapace; 18, right first gonopod, mesioventral view; 19, right first gonopod, distal half, dorsolateral view. Scale bars: 10 mm (10, 15); 5 mm (11, 17); 2 mm (14), 1 mm (12, 13, 18, 19) (14, no scale was informed in the original figure).

Key to the species of *Rodriguezia*

1. Ocular peduncle well developed; cornea present; plp 2 with subdistal part of mesial border smooth, apex lanceolate; epigean.....*R. villalobosi*
-. Ocular peduncle reduced, weakly movable; cornea absent; plp 2 with mesial border bearing minute spines, apex subtriangular; troglobious.....*R. mensabak*

Rodriguezia villalobosi (Rodríguez and Manrique, 1967)
(Figs. 15 - 16)

Trichodactylus villalobosi Rodríguez and Manrique, 1967: 183, pl. 1, figs. 1-3, text-fig. 1. – Smalley, 1970: 104.
Trichodactylus (*Trichodactylus*) *villalobosi*. – Pretzmann, 1968: 70.
Trichodactylus (*Rodriguezia*) *villalobosi*. – Bott, 1969a: 27, text-fig. 4.
Rodriguezia villalobosi. – Rodríguez, 1992: 63, fig. 23G-H. – Villalobos-Hiriart *et al.*, 1993: 284. – Álvarez and Villalobos, 1995: 94. – Magalhães and Türkay, 1996a: 67, 69, 72. – Álvarez *et al.*, 2011: 276.

Holotype: Male, damaged (CNCR 7832), Mexico, state of Chiapas, rancho La Esperanza, 28.XI.1949, A. Villalobos.

Diagnosis: Carapace subquadrate, regions well defined; frontal margin smooth, slightly bilobed. Anterolateral margins of carapace smooth, unarmed. Dactylus of pereiopods 2 to 5 covered by dense pubescence. Abdominal somites free. Male plp 1 with distal part straight, lateral borders with median constriction. Marginal suture straight, situated on mesial side. Subterminal spine fields well developed, discontinuous, with lateroventral and mesiodorsal patch, respectively. Apex simple and symmetrical, distal border rounded. Distal opening large, obliquely directed towards mesial side. Male plp 2 with lanceolate apex, reaching slightly beyond median constriction of plp 1.

Measurements: cb 16.5, cl 14.5 (holotype, according to Rodríguez and Manrique, 1967).

Type locality: Mexico, state of Chiapas, Rancho La Esperanza. According to Álvarez & Villalobos (1995), this locality is situated at 17°02'N 92°44'W, municipality of El Bosque.

Distribution: Southern Mexico, in the state of Chiapas (Fig. 20). An additional record from this state, San Juan Bosque [El Bosque] was provided by Rodríguez and Manrique (1967).

Remarks: The morphology of the carapace and the first gonopod of this species are very similar to that of *Trichodactylus* species, particularly to those with smooth anterolateral carapace margins (e.g., some forms of *T. fluviatilis* Latreille, 1828). However, the relative length of the male second pleopod and the zoogeographic distribution clearly distinguish this species from *Trichodactylus* species.

The holotype and currently the only specimen available for this taxon is partially damaged with oblique and transversal clefts on the dorsal side of the carapace, and the lateral part of the right side of the 3rd and 4th abdominal somites broken (Fig. 15). Furthermore, the additional male specimens mentioned by Rodríguez and Manrique (1967) as well as both left gonopods 1 and 2, that were detached from the holotype specimen, could not be found during a subsequent reorganization of the CNCR collection (J.L. Villalobos, pers. comm.). Therefore, the figure provided by Rodríguez and Manrique (1967: 184, fig. 1) is reproduced here to illustrate the morphology of the first gonopod of the species (Fig. 16).

Rodriguezia mensabak (Cottarelli and Argano, 1977)
(Figs. 17 - 19)

Trichodactylus (*Rodriguezia*) *mensabak* Cottarelli and Argano, 1977: 207, figs. 1-2. – Reddell, 1981: 17, 111, 114, 319, fig. 16. – Rodríguez, 1985: 76.
Trichodactylus mensabak. – Holthuis, 1980:

319. – Holthuis, 1986: 614. – Guinot and Geoffroy, 1987: 21. – Guinot, 1988: 19.
Rodriguezia mensabak. – Rodríguez, 1992: 62. – Villalobos-Hiriart *et al.*, 1993: 284. – Magalhães and Türkay, 1996a: 67, 69, 72. – Álvarez *et al.*, 2011: 276.

Holotype: Male (URTV), Mexico, state of Chiapas: Tila, cueva de Nicolas Bravo, 1160 m alt., 1.X.1975, V. Sbordoni and R. Argano.

Paratypes: 3 males (URTV). Same data as in holotype.

Diagnosis: Carapace subquadrate, regions ill defined, orbits small and very shallow, nearly indistinct; frontal margin fringed with faint papillae, with slight median concavity. Exorbital angle indistinct. Anterolateral margins of carapace unarmed, with very faint papillae near orbit. Ocular peduncle short and barely movable; cornea absent. Pereiopods 2 to 5 very long and slender, dactylus and propodus with few scattered setae. Abdominal somites free. Male plp 1 with gentle median constriction in ventromesial view; distal part straight. Marginal suture straight, situated on mesial side. Subterminal spine fields well developed, discontinuous, with lateroventral and mesiodorsal patch, respectively. Apex simple and symmetrical, distal border rounded. Distal opening large, obliquely directed towards mesial side. Male plp 2 well developed, distinctly shorter than plp 1, bearing few minute spines on subdistal mesial border.

Measurements: cb 11.2, cl 10.7 (holotype); largest specimen examined: cb 17.6, cl 16,4 (male, paratype, UTRV).

Type locality: Mexico, state of Chiapas, Tila [17º23'15"N 92º27'56"W], cueva de Nicolas Bravo.

Distribution: Known only from the type locality (Fig. 20).

Remarks: This is the only truly troglobious species of Trichodactylidae, and most of its morphological features (ocular peduncle much reduced, very shallow orbit, absence of cornea, and very long and slender legs) are adaptations to a cavernicolous environment. Otherwise the male first pleopod shows a similar morphological structure to that of *R. villalobosi* and some species of the genus *Trichodactylus*. The second male pleopod of *R. mensabak* has a very peculiar morphology. In this species, the plp 2 has a subtriangular apex, which is rounded distally, and bears minute spines on the mesial border (see Cottarelli and Argano, 1977: 208, fig. 1e), while in *R. villalobosi* the apex is lanceolate and sharp distally, and the subdistal part of the mesial border is smooth, without trace of spines (Fig. 16).

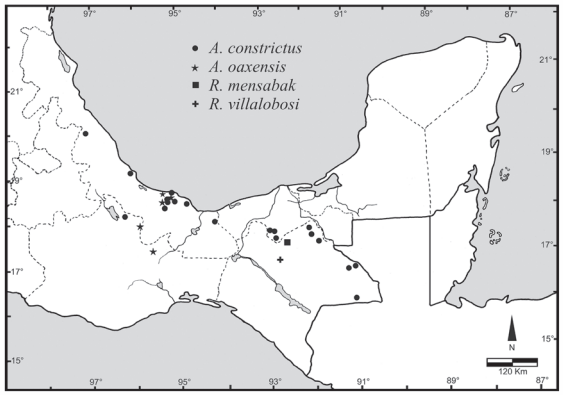


Figure 20. Distribution of *Avotrichodactylus constrictus*, *A. oaxensis*, *Rodriguezia mensabak*, and *R. villalobosi* (some symbols refer to more than one close set of localities).

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