# Three new cavernicolous species of dragon millipedes, genus Desmoxytes Chamberlin, 1923, from southern China, with notes on a formal congener from the Philippines (Diplopoda, Polydesmida, Paradoxosomatidae) 

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#### Abstract

The large Southeast Asian genus Desmoxytes is slightly rediagnosed. A number of troglomorphic, most likely troglobitic, species occur in southern China. A key is provided to all 10 Desmoxytes spp. currently known from China, including three new presumed troglobites: D. eupterygota sp. n. from Hunan Province, as well as D. spinissima sp. n. and D. lui sp. n. from Guangxi Province. "Desmoxytes" philippina Nguyen Duc \& Sierwald, 2010, from the Philippines, is formally removed from Desmoxytes, but not assigned to another genus. It probably belongs in a new genus in the subfamily Australiosomatinae, tribe Antichiropodini, close to the Bornean Euphyodesmus Attems, 1931 and Borneochiropus Golovatch, 1996.


## Keywords

Millipede, cave, Desmoxytes, new species, key, China

## Introduction

Originally, the name "dragon millipedes" was proposed as a vernacular name to distinguish Hylomus draco Cook \& Loomis, 1924, a Chinese species showing unusually spiny paraterga, Apparently, Cook and Loomis (1924) were so impressed by this feature that they placed the species not only in a new genus, but also created a new family. However, Jeekel $(1968,1980)$ demonstrated that actually several Southeast Asian species share this peculiar character, referring to Hylomus as a synonym of the slightly older Desmoxytes Chamberlin, 1923, assigning the latter genus to the tribe Orthomorphini, and sinking Hylomidae under Paradoxosomatidae. Golovatch and Enghoff (1994), followed by Nguyen Duc et al. (2005), adopted the notion "dragon millipedes" as a fairly compact and homogeneous group of species composing the genus Desmoxytes, tribe Orthomorphini, subfamily Paradoxosomatinae, in which the paraterga are wingor antler-shaped, or even spiniform. Since the genus was based only on a couple of equivocal apomorphies, the generic diagnosis of Desmoxytes as presented by Golovatch and Enghoff (1994) remained rather shaky whilst their cladistic analysis showed no meaningful resolution.

After Mesibov (2006) had described Desmoxytoides, a monobasic genus from eastern Australia which also demonstrates antler-like paraterga, the "dragon millipedes" again became a vernacular name meaningless from a taxonomic or evolutionary viewpoint (Enghoff et al. 2007, Nguyen Duc and Sierwald 2010). Even though Mesibov (2006) had failed to assign Desmoxytoides to a tribe or subfamily, due to the presence of a thick solenomere lacking a nearby solenophore the type species $D$. hasenpuschorum Mesibov, 2006 shows, it clearly represented a different subfamily, Australiosomatinae, albeit rather untypical of it because male legs 1 were devoid of adenostyles. This alone suggested multiple origins of conspicuously hypertrophied paraterga within Paradoxosomatidae. Parallelisms have been reconfirmed and further extended by Golovatch and Stoev (2010) who described a similarly spinigerous species of Tectoporus Carl, 1914 (Tectoporini, Paradoxosomatinae) from Papua New Guinea. Based on gonopod features alone, these authors also suggested placing provisionally both Desmoxytoides and Desmoxytes philippina Nguyen Duc and Sierwald, 2010, the latter species from the Philippines, into the Australasian tribe Antichiropodini (Australiosomatinae). This agrees far better with biogeographical evidence as well, because Borneo supports still another few species in Euphyodesmus Attems, 1931 and Borneochiropus Golovatch, 1996, both latter genera again in Antichiropodini, which show spine-shaped paraterga (Golovatch 1996). Furthermore, Golovatch and Stoev (2010) have proposed to restrict the usage of the term "dragon millipedes" solely to the genus Desmoxytes, a group
still fairly well diagnosed earlier by Golovatch and Enghoff (1994) despite certain shortcomings (Mesibov 2006; Enghoff et al. 2007). An updated, only slightly modified diagnosis will be provided below.

In other words, antler-like or spiniform paraterga must have evolved independently at least in three different lineages of Paradoxosomatidae representing three tribes and two subfamilies: Desmoxytes (Orthomorphini, Paradoxosomatinae), or "dragon millipedes" in the proper sense; Tectoporus (Tectoporini, Paradoxosomatinae); as well as Desmoxytoides, Euphyodesmus, Borneochiropus and "D." philippina (see below) (Antichiropodini, Australiosomatinae).

The genus Desmoxytes s. str. is currently represented by 26 species ranging from southern China in the North to about the middle of Malay Peninsula within both Thailand and Malaysia in the South. Most of the species diversity is found in Vietnam (9 species), followed by Thailand (8), southern China (7) and Myanmar (2), while neither Cambodia nor Laos has hitherto been known to support any Desmoxytes, even the sole pantropical congener, D. planata (Pocock, 1895). Most of the species are quite local in distribution: the few which have been reported from southern China tend to be restricted to a single locality each. This alone suggests that many more new species of Desmoxytes will be revealed in the future.

Several Desmoxytes species show remarkably bright, apparently aposematic live colorations ranging from intense carmine to pink or purple-pink (see review in Enghoff et al. 2007). One such species, D. purpurosea Enghoff, Sutcharit and Panha, 2007, comes from a small karstic area in northern Thailand, originally probably a cave, but later having its roof collapse, resulting in the present cavernous mountain with high humidity throughout (Enghoff et al. 2007). However, all three heretofore known troglomorphic, most likely even troglobitic congeners, D. longispina (Loksa, 1960), D. scutigeroides Golovatch, Geoffroy and Mauriès, 2010 and D. scolopendroides Golovatch, Geoffroy and Mauriès, 2010, are pallid to pale brownish in coloration, being confined to karst caves in Guangxi Province (Golovatch et al. 2010). Both latter species come from Mulun Karst which probably contains the richest cave fauna not only in China, but even globally (Deharveng et al. 2008). Epigean congeners from China have only been recorded in Jiangxi ( $D$. draco (Cook and Loomis, 1924)), Guangxi ( $D$. cornutus (Zhang and Li, 1982) and D. minutubercula (Zhang, 1986)) and Yunnan provinces ( $D$. planata). At least the latter species shows an intense red, aposematic live coloration which fades out completely during preservation in alcohol, whereas the coloration in the remaining trio is light, yellowish to light brown in alcohol (Zhang and Li 1982, Zhang 1986, Golovatch and Enghoff 1994). Another interesting observation is that the few species of Desmoxytes which have spiniform paraterga are all confined to Guangxi Province, several being presumed troglobites.

Generally speaking, the family Paradoxosomatidae, one of the largest in Diplopoda as a whole, contains surprisingly few cavernicoles. It is only the large genus Desmoxytes that appears to harbour several troglomorphic species, with caves in southern China hosting virtually all of them.

The present note is devoted to descriptions of three new cave-dwelling Desmoxytes from southern China, i.e. two more from Guangxi Province, as well as the first species from Hunan Province. A key is also given to all ten species of Desmoxytes known to occur in China. In addition, a recent error concerning the identity of a formal congener from the Philippines is being corrected here.

The holotypes will be deposited in the collection of the Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IZAS), with paratypes to be housed in the collections of the South China Agricultural University, Guangzhou, China (SCAU), Guangxi Normal University, Guilin, China (GNUG), Zoological Museum, University of Moscow, Russia (ZMUM), and Muséum national d'Histoire naturelle, Paris, France (MNHN).

A dynamic web page for each taxon name mentioned in the paper is generated on the fly by the Pensoft Taxon Profile tool (see Penev et al. 2010). All species descriptions are automatically exported at the time of publication to a wiki platform (www. species-id.net) through the Pensoft Wiki Convertor (see Penev et al. 2011, Stoev and Enghoff 2011).

## Taxonomic part

## Desmoxytes Chamberlin, 1923

http://species-id.net/wiki/Desmoxytes
Diagnosis. A genus of medium-sized to larger (up to 43 mm long) Orthomorphini with 20 segments and conspicuously enlarged and elevated paraterga (antler-like, wing-shaped or spiniform). Metaterga often granulate, tuberculate and/or spiculate. Certain male femora (5, 6, 7 and/or 9) often inflated ventrally. A setose central lobe or a paramedian pair of setose tubercles between male coxae 4 present.

Gonopods with rather short, subcylindrical, distoventrally setose coxae. Telopodites mostly suberect, only seldom subfalcate. Prefemoral (= densely setose) portion from $1 / 3$ to $1 / 2$ as long to nearly as long as femorite, the latter not twisted, at most only slightly enlarged distad and devoid both of a mesal groove/hollow and any processes. Seminal groove running entirely mesally to pass onto a usually shortened solenomere, the latter mostly sheathed by a usually condensed, rather simple solenophore, much shorter than femorite, composed of a smaller lamina medialis and a larger lamina lateralis. Solenophore demarcated from femorite by a clear-cut sulcus or cingulum at base, poorly or strongly set off from base of solenomere.

Type species. Desmoxytes coniger Chamberlin, 1923
Species composition. Currently 29 described species.
Remarks. The above diagnosis largely repeats that given by Golovatch and Enghoff (1994). Here it only emphasizes variation in relative lengths of the femoral and solenophore parts of the gonopod telopodite.

## Species descriptions

## Desmoxytes eupterygota sp. n.

urn:lsid:zoobank.org:act:F7B1C583-5E3C-4980-8EB1-7BB9D3BFB5F3
http://species-id.net/wiki/Desmoxytes_eupterygota
Figs 1, 2

Holotype. đ (IZAS), China, Hunan Prov., Chenzhou City, Linwu County, Tianhe, Cave 1, 500 m a.s.l., 19.VI.2009, leg. Tian Mingyi \& Xue Zhihong (CHIhn09LWX02).

Paratypes. 1 § (SCAU), 1 \& (ZMUM), same locality, together with holotype. $1 \jmath^{\lambda}(\mathrm{MNHN}$ JA 130), 1 § juv., 1 q juv., 1 fragment (SCAU), 1 q juv. (GNUG), same county, Changshali, Cave 1, 500 m a.s.l., 19.VI.2009, leg. Tian Mingyi \& Xue Zhihong (CHIhn09-LWX03).

Name. To emphasize the paraterga being true wings.
Diagnosis. Differs in the paraterga being mostly wing-shaped, rather long and strongly curved, combined with a short gonopod femorite and a condensed solenophore, as well as $\widehat{\jmath}$ legs totally devoid of femoral humps. See also Key below.

Description. Length ca 25-29 ( $\delta^{\pi}$ ) or $32 \mathrm{~mm}(q)$, juveniles ( $q$ with 18 segments) up to 26 mm ; width of proterga and metaterga+paraterga 1.8 and 2.0-2.3 ( $\AA^{\top}$ ), or 2.3 and $2.8 \mathrm{~mm}(q)$, respectively. Holotype 27 mm long, 1.8 and 2.3 mm wide on midbody pro- and metazona, respectively. Juveniles ( $q$ with 18 segments) up to 1.9 and 2.8 mm wide on midbody pro- and metazona, respectively.

Body moniliform (Fig. 1D). Coloration of alcohol material ( $\delta^{\lambda}, q$ and advanced juvenile instars) rather uniformly light grey-brownish to yellowish, anterior body part often a little darker brownish (Fig. 1A-C). In width, head $\ll$ collum $=$ segment $2=3$ $<4=16$; thereafter body gradually tapering towards telson. Front part of head densely setose, vertex bare, epicranial suture distinct. Antennae very long and slender, reaching back to segment 5 or $6\left(\widehat{o}^{\top}\right)($ Fig. 1A-C), or 4 ( ( ) dorsally, antennomeres 5 and 6 each with an apicodorsal compact group of bacilliform sensilla.

Tegument rather smooth and shining, both pro- and metazona very delicately microalveolate, metaterga finely shagreened and rugulose transversely, surface below paraterga finely shagreened. Collum with $3+3$ small, but rather evident teeth in a row at front margin, behind it with $2+2$ and $2+2$ extremely small denticles, knobs or insertion points (setae invariably obliterated) in two transverse, often barely visible rows. Metatergum 2 with a pattern of similar, barely visible $2+2$ and $2+2$ knobs or insertion points in two transverse rows. Starting from metatergum 3, setation pattern entirely or nearly untraceable. Collum and all following metaterga with large, mostly subfalcate, wing-shaped, high paraterga (Fig. 1A-D) directed dorsolaterally and ending up clearly above dorsum on collum, as well as segments $2-7$ and 17 $\& 18$, remaining paraterga subhorizontal and about level with dorsum in $\widehat{\delta}$, but slightly lower and shorter in $q$ and juveniles. Paraterga with two indentations at


Figure I. Desmoxytes eupterygota sp. n., Ə̄ paratype from near Tianhe. A-C anterior part of body, dorsal, ventral and lateral views, respectively $\mathbf{D}$ midbody segments, dorsal view $\mathbf{E}$ telson, ventral view $\mathbf{F}$ midbody leg, front view. Photographed not to scale.
front margin, starting from collum these becoming less distinct and nearly fully disappearing in segments 15 to 18 . Paraterga 17-19 directed caudad, subspiniform (Fig. 1E). Stricture between pro- and metazona narrow only in a few anteriormost segments, thereafter much wider and only vaguely delimited, always smooth at bottom (Fig. 1D). Pore formula normal; ozopores inconspicuous, located about midway on ventral side of poriferous paraterga. Transverse sulcus evident on metaterga 3-18 (Fig. 1D). Pleurosternal carinae poorly developed in segments 2 and 3, absent from others (Fig. 1C). Epiproct (Fig. 1E) rather simple, dorsal subapical and, especially, lateral pre-apical papillae very distinct, tuberculiform. Hypoproct (Fig. 1E) subtrapeziform, caudal margin very slightly concave, setigerous cones at caudal edge very small, widely separated. Axial line missing.


Figure 2. Desmoxytes eupterygota sp. n., ${ }^{2}$ paratype from near Tianhe. A sternal cones between coxae 4, ventral view $\mathbf{B}$ and $\mathbf{C}$ right gonopod, mesal and lateral views, respectively. Scale bar: $1.0(\mathbf{A})$ and 0.5 mm (B, C). Designations: fe femorite sph solenophore sl solenomere $\mathbf{l l}$ lamina lateralis $\mathbf{l m}$ lamina medialis $\boldsymbol{s}$ spinule on lm

Sterna quite densely setose, cross-impressions faint. A paramedian pair of entirely separated, short, rounded, setose tubercles between $\widehat{0}$ coxae 4 (Fig. 2A). Legs (Fig. 1A, B, F) very long and slender, devoid of modifications, ca 3.2-3.5 ( $\widehat{O}^{\top}$ ) or 2.5 ( $q$ ) times longer than midbody height.

Gonopods (Fig. 2B, C) short. Coxite rather short, subcylindrical, poorly setose distodorsally, about half as long as telopodite. Prefemoral (= densely setose) portion less than half as long as acropodite. Femorite (fe) quite stout, slightly enlarged distad, with seminal groove running entirely on mesal face, apically with a distinct sulcus demarcating a short, strongly condensed solenophore (sph). The latter distinguished by a parabasally spinigerous (s) and terminally poorly trifid lamina medialis (lm) and a simpler and somewhat larger lamina lateralis (ll). Solenomere (sl) similarly short, flagelliform, well separated at base from solenophore.

## Desmoxytes spinissima sp. n.

urn:Isid:zoobank.org:act:805A9FDB-02DC-4449-93AE-5C514FD59D0E
http://species-id.net/wiki/Desmoxytes_spinissima
Figs 3, 4

Holotype. đ龴 (IZAS), China, Guangxi Prov., Fuchuan County, Guanyuan, Cave Guanyuan Dong, 25.I.2012, leg. Li Youbang, Li Youting and Tang Kewen (CHIgx12LYB04).

Paratype. $1 \not+$ (GNUG), same locality, together with holotype.
Name. To emphasize the extremely long and spiniform paraterga.
Diagnosis. Differs in the paraterga being long and spiniform throughout, combined with a strongly condensed solenophore and both of femora 6 and 7 being humped. See also Key below.

Description. Length ca $27\left(\widehat{\sigma}^{\top}\right)$ or $36 \mathrm{~mm}(q)$; width of pro- and metaterga together with paraterga 1.6 and $4.0\left(\sigma^{\top}\right)$ or 2.0 and $4.0 \mathrm{~mm}(q)$, respectively.

Body strongly moniliform (Fig. 3A, B). Coloration of alcohol material rather uniformly light pink-brownish to nearly pallid, anterior body part a little darker, pinkish (Fig. 3). Antennomere 7 dark brown. In width, head $\ll$ collum $=$ segment $2=3<$ $4<5=16$; thereafter body gradually tapering towards telson. Head densely setose throughout, epicranial suture distinct. Antennae very long and slender, reaching back to segment $8\left(\widehat{\sigma}^{\top}\right)$ or $6(q)$ dorsally, antennomeres 5 and 6 each with an apicodorsal compact group of bacilliform sensilla.

Tegument rather smooth and poorly shining, prozona very delicately microalveolate, metaterga finely shagreened to microgranulate/microspiculate, surface below paraterga finely shagreened. Collum with $3+3$ evident setigerous spines in a row at front margin (growing increasingly long laterad), behind it with $1+1$ and $2+2$ similar spinules in two transverse rows. Following metaterga with a pattern of similar $1+1$ and $2+2$ spinules in two transverse rows. Collum and all following metaterga with extremely long, straight, spiniform paraterga (Fig. 3A, B) directed more dorsally than laterally and ending up clearly above dorsum on collum and in segments $2-18$; only paraterga 19 subhorizontal, about level with dorsum, directed clearly caudad and reaching behind until about midlength along telson. Paraterga ca $1.2-1.3$ ( $\widehat{J}^{\top}$ ) or 0.9 times ( $q$ ) as long as midbody height. Paraterga 1-18 with 2-3 evident indentations/spinules frontally (these growing increasingly inconspicuous towards telson) and a short, but evident tooth posteriorly at base. Stricture between pro- and metazona rather narrow and shallow, always smooth at bottom (Fig. 3B). Pore formula normal; ozopores inconspicuous, located just behind last indentation on ventral side of poriferous paraterga. Transverse sulcus missing. Pleurosternal carinae evident only in segments 2 and 3. Epiproct (Fig. 3C, D) rather simple, subapical and, especially, pre-apical papillae very distinct, finger-shaped. Hypoproct (Fig. 3D) subtrapeziform, caudal margin emarginate, setigerous cones at caudal edge small, but evident, widely separated. Axial line missing.

Sterna quite densely setose, cross-impressions faint. A paramedian pair of entirely separated, short, rounded, setose tubercles between ô coxae 4 (Fig. 4A). Legs (Fig.


Figure 3. Desmoxytes spinissima sp. n., $\delta$ holotype. A anterior part of body, lateral view $\mathbf{B}$ midbody segments, lateral view $\mathbf{C}$ posterior part of body, dorsal view $\mathbf{D}$ telson, ventral view $\mathbf{E}$ femora 6 and 7, lateral view. Photographed not to scale.
$3 \mathrm{~A}-\mathrm{C})$ extremely long and slender, $>4.0\left(\mathrm{O}^{\top}\right)$ or $3.2(\uparrow)$ times longer than midbody height. $0^{\lambda}$ femora 6 and 7 strongly inflated ventrally in distal quarter (Fig. 3E)

Gonopods (Fig. 4B, C) simple. Coxite rather short, subcylindrical, poorly setose distodorsally, about $1 / 3$ as long as telopodite. Prefemoral portion (= densely setose)


Figure 4. Desmoxytes spinissima sp. n., $\widehat{\jmath}^{7}$ holotype. A sternal cones between coxae 4, ventral view B-C left gonopod, mesal and lateral views, respectively. Scale bar: 1.0 (A) and $0.5 \mathrm{~mm}(\mathbf{B}, \mathbf{C})$. Designations: fe femorite $\mathbf{s p h}$ solenophore $\mathbf{s l}$ solenomere $\mathbf{l l}$ lamina lateralis $\mathbf{l m}$ lamina medialis
about half as long as acropodite. Femorite (fe) slender, elongate, only slightly enlarged distad, with seminal groove running entirely on mesal face, also with a distinct sulcus demarcating a short, strongly condensed solenophore (sph). The latter distinguished by a smaller, somewhat folded lamina medialis ( $\mathbf{( m m}$ ) and a simpler and larger lamina lateralis (11). Solenomere (sl) similarly short, flagelliform, rather faintly separated at base from solenophore.

## Desmoxytes lui sp. n.

urn:lsid:zoobank.org:act:A0C24C82-1F34-437A-BCFA-C28A1E3BA72F
http://species-id.net/wiki/Desmoxytes_lui
Figs 5, 6

Holotype. đ (IZAS), China, Guangxi Prov., Yongfu County, Shangxiao, Cave Dachong Dong, 17.I.2012, leg. Li Youbang and Lu Shiyi (CHIgx12-LYB03).

Paratypes. 1 \& (GNUG), 1 q juv. (MNHN JA 131), same locality, together with holotype.

Name. To honour Mr Lu Shiyi, one of the collectors.
Diagnosis. Differs in the paraterga being spiniform only until segment 5, combined with the gonopods being strongly condensed, $\begin{gathered} \\ \text { femora } 6 \text { humped. See also Key }\end{gathered}$ below.

Description. Length ca $36\left(\delta^{\lambda}\right), 43 \mathrm{~mm}(q)$ or $40 \mathrm{~mm}(1 q$ juvenile with 19 segments); width of pro- and metaterga together with paraterga 2.0 and $2.2\left(\AA^{\pi}\right), 3.2$ and $3.4 \mathrm{~mm}(q)$ or 3.0 and $3.1 \mathrm{~mm}(1 q$ juvenile with 19 segments), respectively.

Body strongly moniliform (Fig. 5A-C). Coloration of alcohol material rather uniformly light pink-brownish to nearly pallid, anterior body part a little darker, pinkish (Fig. 5). Antennomere 7 dark brown (even in the juvenile). In width, segment $3=4<$ head $<$ collum $=$ segment $2<6=16$; thereafter body gradually tapering towards telson. Head very densely setose throughout, epicranial suture distinct. Antennae extremely long and slender, reaching back to segment 9 ( $\delta^{\top}$ ) or 7 ( $q$ ) dorsally, antennomeres 5 and 6 each with an apicodorsal compact group of bacilliform sensilla.

Tegument rather smooth and poorly shining, prozona very delicately microalveolate, metaterga finely shagreened to microgranulate/microspiculate, surface below paraterga finely shagreened to microgranulate. Collum with $6+6(7)$ evident setigerous spinules in a row at front margin, behind it with about $4+4$ smaller spinules in an irregular transverse row.

Following metaterga with a pattern of similar, smaller, $3+3$ and $3+3$ spinules in two transverse rows, last row gradually growing up to $6+6$ until segment 19 . Collum and following metaterga 2-4 with straight, spiniform paraterga, about as long as body height in $\widehat{\delta}$, a little shorter in $q$ and juvenile (Fig. 5A-C), directed much more dorsally than laterally and ending up clearly above dorsum; paraterga 5 only slightly shorter than preceding ones; paraterga 6-18 contrasting short, coni- to dentiform; paraterga 19 subhorizontal, about level with dorsum, directed clearly caudad and reaching behind until about midlength $\left(\sigma^{\top}\right)$ or front third $(q)$ along telson. Paraterga $1-5$ with two rather evident, setigerous indentations/spinules/knobs frontally and a short tooth posteriorly at base (Fig. 5A). Stricture between pro- and metazona very broad and shallow, always smooth at bottom (Fig. 5B, C). Pore formula normal; ozopores inconspicuous, located just at base on lateral side of poriferous paraterga. Transverse sulcus usually very vague, traceable in segments 4-18. Pleurosternal carinae evident only in segments 2 and 3 (Fig. 5A). Epiproct (Fig. 5C, D) rather simple, lateral pre-apical papillae very distinct, finger-shaped. Hypoproct (Fig. 5D) subtrapeziform,


Figure 5. Desmoxytes lui sp. n., ô holotype. A anterior part of body, lateral view B body segments 5 to 8, lateral view $\mathbf{C}$ posterior part of body, dorsal view $\mathbf{D}$ telson, ventral view. Photographed not to scale.
caudal margin emarginate, setigerous cones at caudal edge very large, widely separated. Axial line missing.

Sterna quite densely setose, cross-impressions faint. A paramedian pair of entirely separated, short, rounded, setose tubercles between or coxae 4 (Fig. 6A). Legs (Fig. $5 \mathrm{~A}, \mathrm{~B})$ extremely long and slender, ca $6.0\left(\delta^{\wedge}\right)$ or 4.5 ( $\%$ ) times longer than midbody height. ${ }^{\lambda}$ femora 6 strongly inflated ventrally in distal quarter (Fig. 5B).

Gonopods (Fig. 6B-D) simple. Coxite rather short, subcylindrical, poorly setose distodorsally, about $1 / 3$ times as long as telopodite. Prefemoral portion (= densely setose) about half as long as acropodite. Femorite (fe) rather slender, elongate, only slightly enlarged distad, with seminal groove running entirely on mesal face, also with a distinct sulcus demarcating a short, strongly condensed solenophore (sph). The latter distinguished by a somewhat folded lamina medialis ( $\mathbf{l m}$ ) and a simpler lamina lateralis (II). Solenomere (sl) similarly short, flagelliform, evidently separated at base from solenophore.


Figure 6. Desmoxytes lui sp. n., ${ }^{\lambda}$ holotype. A sternal cones between coxae 4, ventral view B-D right gonopod telopodite, mesal, dorsal and sublateral views, respectively. Scale bar: $1.0(\mathbf{A})$ and $0.5 \mathrm{~mm}(\mathbf{B}-\mathbf{D})$. Designations: fe femorite sph solenophore sl solenomere $\mathbf{1 1}$ lamina lateralis $\mathbf{l m}$ lamina medialis

## A key to Desmoxytes species currently known to occur in China

1 At least paraterga on collum and following four segments spiniform, mostly very long and directed evidently more dorsally than laterally (Figs 3, 5). Guangxi Province2

- Paraterga wing- (Fig. 1) or antler-shaped ..................................................... 7

2 Paraterga long and spiniform only on collum and following four segments, evidently shorter on segment 5, small and coni- to tuberculiform thereafter (Fig. 5)
)..
Paraterga subequally long and spiniform at least in segments 2-18 (Fig. 3) ... 3
Both $\widehat{0}$ femora 6 and 7 very evidently humped ventrally in distal quarter (Fig. 3E)
D. spinissima sp. n.


## "Desmoxytes"philippina and its true affinities

As we have noted above, spiniform paraterga must have appeared independently in several paradoxosomatid lineages, including the subfamily Australiosomatinae. This latter group is still rather vaguely defined as opposed to the other two subfamilies, Alogolykinae and Paradoxosomatinae, showing no clear-cut apomorphies. Like Alogolykinae, and contrary to Paradoxosomatinae, most of the Australiosomatinae are supplied with adenostyles (= ventral projections) on femora 1, coupled with the gonopod showing a shorter or longer prefemoral portion, and a usually (but not always) shortened femorite crowned with one to several processes at or near the base of a strong solenomere. Contrary to the conditions observed in the other two subfamilies, this strong, thick, often apical solenomere in Australiosomatinae requires no or almost no support from the neighbouring structures, thus never being set off at or near the distal end of the femorite by a lateral sulcus or cingulum to develop a special sheath in the form of a solenophore. A complex, often membranous, apical solenophore that is clearly set off at least by one sulcus or cingulum at or near the distal end of the femorite must have appeared later in order to protect and sheath a mostly thin, weak, flagelliform solenomere.

In short, we see the main evolutionary trend in the family Paradoxosomatidae as the progressive development of a complex solenophore in conjunction with the soleno-
mere's growing flexibility and fragility. The Australiosomatinae would therefore be the basalmost group, with the Alogolykinae (and probably also a few Paradoxosomatinae like the tribe Paradoxosomatini and a few genera of the tribe Chamberlinini which also have solid solenomeres - see Golovatch 2011, Nguyen Duc and Korsós 2011) likely forming the next step by still retaining a strong and thick solenomere, the apical part of which, however, is already protected and sheathed by a solenophore. Finally, in the bulk of the Paradoxosomatinae (and of the Paradoxosomatidae as a whole), a distinctly delimited, complex, mostly membranous solenophore has developed to sheath and protect the weak, flagelliform solenomere.

Jeekel (1968) divided the Australian Australiosomatinae into two tribes, Australiosomatini and Antichiropodini, seeing the main differences between them in gonopod structure alone. Thus, the gonopod in Australiosomatini was stated to show a short to longer prefemoral portion and a stout femorite with several strong branches, including a modestly developed solenomere. In contrast, Antichiropodini were said to be characterized through a short prefemoral portion, an elongated femorite and a similarly long, strong, apically or subapically located solenomere. Golovatch (1996), when treating several Australiosomatinae from Borneo, regarded Euphyodesmus Attems, 1931 and a newly described genus, Borneochiropus Golovatch, 1996, as particularly close to each other, having also transferred both to the tribe Antichiropodini. Not only do at least some of their constituent species show spiniform paraterga so vividly reminding of those observed in certain Desmoxytes, but both lack adenostyles while their gonopod traits are especially similar: the prefemoral portion is medium-sized to hypertrophied, accordingly the femorite is elongate to strongly reduced, and the solenomere is apical to subapical. Both Euphyodesmus and Borneochiropus could have as well been assigned to Australiosomatini, but their placement into the Antichiropodini was favoured because their gonopods looked far simpler than those of most of the Australiosomatini in having only uni- or biramous telopodites, and the solenomere invariably apical or subapical.

In other words, the choice was indeed quite arbitrary. There are a few transitional conditions in gonopod conformation to be observed within Euphyodesmus alone which make it difficult to unequivocally assign this genus to either of the tribes.

This background information is necessary to properly assess the identity of Desmoxytes philippina, described recently from the Philippines (Nguyen Duc and Sierwald 2010). That it is nothing else but an Australiosomatinae has already been noted elsewhere, albeit indirectly because the species had not been described yet (Golovatch and Stoev 2010). Moreover, the gonopod structure (a uniramous telopodite with the prefemoral, femoral and solenomere parts being subequal in length, the femorite also twisted so that the seminal groove runs mostly along its lateral face, the absence both of a solenophore and of its basal delimitation sulcus), the lack of adenostyles, as well as the spiniform paraterga strongly suggest affinities to the Bornean Euphyodesmus and Borneochiropus. The proximity of the Philippines to Borneo supports this view. In no way does D. philippina resemble a species of Orthomorphini, a tribe in which the seminal groove always runs along the mesal side of the gonofemorite before passing
onto a flagelliform solenomere sheathed by an evident apical solenophore, both latter structures being set off at their bases at least by one distinct sulcus or cingulum.

So we are forced to remove " $D$ ". philippina from Desmoxytes and assign it provisionally to a still unclassified genus of Antichiropodini or Australiosomatini, placing it there together with the similar Euphyodesmus and Borneochiropus. For the time being, we refer to this species as "Desmoxytes" in quotation marks to emphasize its highly doubtful generic allocation. The latter is the more so strange as Nguyen Duc and Sierwald (2010) explicitly noted the above basic differences. Placing philippinus provisionally in Euphyodesmus would have been more logical at the subfamily level.

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## References

Cook OF, Loomis HF (1924) A new family of spined millipeds from central China. Journal of the Washington Academy of Sciences 14: 103-108.
Deharveng L, Bréhier F, Bedos A, Mingyi T, Youbang L, Feng Z, Wengeng Q, Xuefeng T (2008) Mulun and surrounding karsts (Guangxi) host the richest cave fauna of China. Subterranean Biology 6: 75-79.
Enghoff H, Sutcharit C, Panha S (2007) The shocking pink dragon millipede, Desmoxytes purpurosea, a colourful new species from Thailand (Diplopoda: Polydesmida: Paradoxosomatidae). Zootaxa 1563: 31-36.
Golovatch SI (1996) The millipede family Paradoxosomatidae on Borneo, with contributions to the faunas of some other islands of the Sunda area (Diplopoda, Polydesmida). Revue suisse de Zoologie 103(1): 151-193.
Golovatch SI (2011) New or poorly-known Oriental Paradoxosomatidae (Diplopoda: Polydesmida), XI. Arthropoda Selecta 20(4): 259-266.
Golovatch SI, Enghoff H (1994) Review of the dragon millipedes, genus Desmoxytes Chamberlin, 1923 (Diplopoda, Polydesmida, Paradoxosomatidae). Steenstrupia 20: 45-71.
Golovatch SI, Stoev P (2010) New or poorly-known millipedes (Diplopoda) from Papua New Guinea, 3. Arthropoda Selecta 19(3): 145-152.
Golovatch SI, Geoffroy JJ, Mauriès JP (2010) Two new species of the millipede genus Desmoxytes Chamberlin, 1923 (Diplopoda: Polydesmida: Paradoxosomatidae) from caves in southern China. Arthropoda Selecta 19(2): 57-61.

Jeekel CAW (1968) On the classification and geographical distribution of the family Paradoxosomatidae (Diplopoda, Polydesmida). Academische Proefschrift, Rotterdam, 162 pp.
Jeekel CAW (1980) The generic allocation of some little-known Paradoxosomatidae from South-East Asia (Diplopoda, Polydesmida). Revue suisse de Zoologie 87: 651-679.
Mesibov R (2006) Dirt-encrusted and dragon millipedes (Diplopoda: Polydesmida: Paradoxosomatidae) from Queensland, Australia. Zootaxa 1354: 31-44.
Nguyen Duc A, Korsós Z (2011) A revision of the millipede genus Riukiupeltis Verhoeff, 1939 (Diplopoda, Polydesmida, Paradoxosomatidae), with comments on the status of related species. ZooKeys 156: 25-40.
Nguyen Duc A, Sierwald P (2010) A new dragon millipede (Polydesmida: Paradoxosomatidae: Orthomorphini) from the Philippines. The Raffles Bulletin of Zoology 58(2): 173-177.
Nguyen Duc A, Golovatch SI, Anichkin AE (2005) The dragon millipedes in Vietnam (Polydesmida: Paradoxosomatidae, genus Desmoxytes Chamberlin, 1923). Arthropoda Selecta 14(3): 251-257.
Penev L, Agosti D, Georgiev T, Catapano T, Miller J, Blagoderov V, Roberts D, Smith VS, Brake I, Ryrcroft S, Scott B, Johnson NF, Morris RA, Sautter G, Chavan V, Robertson T, Remsen D, Stoev P, Parr C, Knapp S, Kress WJ, Thompson FC, Erwin T (2010) Semantic tagging of and semantic enhancements to systematics papers: ZooKeys working examples. ZooKeys 50: 1-16. doi: 10.3897/zookeys.50.538
Penev L, Hagedorn G, Mietchen D, Georgiev T, Stoev P, Sautter G, Agosti D, Plank A, Balke M, Hendrich L, Erwin T (2011) Interlinking journal and wiki publications through joint citation: Working examples from ZooKeys and Plazi on Species-ID. ZooKeys 90: 1-12. doi: 10.3897/zookeys. 90.1369
Stoev P, Enghoff H (2011) A review of the millipede genus Sinocallipus Zhang, 1993 (Diplopoda, Callipodida, Sinocallipodidae), with notes on gonopods monotony vs. peripheral diversity in millipedes. ZooKeys 90: 13-34. doi: 10.3897/zookeys.90.1291
Zhang CZ (1986) On the genus Pratinus and its two new species from China (Diplopoda: Paradoxosomatidae). Acta Zootaxonomica Sinica 11(3): 253-257.
Zhang CZ, Li ZY (1982). Centrodesmus cornutus sp.nov., ein neue Diplopodenart aus dem Süd-China (Paradoxosomatidae: Polydesmida). Acta Zootaxonomica Sinica 7(1): 37-39.

# New species and records of Hydroptilidae (Trichoptera) from Venezuela 

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#### Abstract

Eight new species of Hydroptilidae (Trichoptera) from Venezuela are described: Acostatrichia digitata sp. n., Hydroptila cressae sp. n., Metrichia botrychion sp. n., Ochrotrichia spira sp. n., Oxyethira bettyae sp. n., Oxyethira quiramae sp. n., Oxyethira redunca sp. n., and Rhyacopsyche shorti sp. n. New country records for Venezuela of 2 additional species, Neotrichia feolai Santos \& Nessimian, 2009 and Oxyethira picita Harris \& Davenport, 1999, are also provided. Illustrations of male genitalia are provided with each description.


## Keywords

Trichoptera, caddisflies, Hydroptilidae, Anchitrichia, Hydroptila, Metrichia, Neotrichia, Ochrotrichia, Oxyethira, Rhyacopsyche, new species, Neotropical

## Introduction

Caddisflies, or Trichoptera, are a diverse order of insects with $\sim 15,000$ described species and 100s of new species awaiting description (Holzenthal et al. 2011). Trichoptera faunal diversity is particularly impressive in the Neotropical biogeographical region,
where recent inventories have revealed up to $75 \%$ of collected species to be undescribed (Holzenthal et al. 2007) Hydroptilidae is the largest family in the order, including 75 genera, $\sim 2,000$ described species found all over the world, and a high number of undescribed species. As their common name, microcaddisflies, suggests, hydroptilids are minute with few larger than 5 mm . The aquatic larvae construct portable or fixed silken purse-like cases in the final instar (Wiggins 2004). The larvae of many species feed on algae, while some feed on moss microphylls (Wiggins 2004; Carins and Wells 2008). Some have been known to be predatory, while others are parasitoids (Wells 1985, 2005).

In this paper, we describe 8 new hydroptilid species in 6 genera from Venezuela. We also provide new country records for Venezuela for 2 species, Neotrichia feolai Santos \& Nessimian, 2009 and Oxyethira picita Harris \& Davenport, 1999. The material was collected as part of a project under the direction of Dr. Andrew Short, University of Kansas, USA, to inventory the aquatic Coleoptera and other aquatic insect orders of Venezuela. In June, 2010, a team of 4 American and 4 Venezuelan entomologists collected aquatic insects in the southern half of Venezuela, including the llanos of Guárico state, the southern tributaries of the upper to middle Orinoco River basin, and the Gran Sabana of Bolívar state, and, in northern Venezuela, the Turimiquire Mountains of Monagas state. About 90 species of Trichoptera were collected, including about 25 new species of which the new Hydroptilidae are described here.

## Materials and methods

Morphological terminology used for male genitalia of specimens in the genus $O x y$ ethira follows that of Kelley (1984), for the genus Metrichia that of Flint (1972), and for the genus Rhyacopsyche that of Wasmund and Holzenthal (2007). All others follow the terminology of Marshall (1979). For simplicity, paired structures are discussed in the singular. Procedures for specimen preparation followed those explained in detail by Blahnik et al. (2007). For specimen examination and illustration, cleared genitalia were placed in a watch glass with glycerin and small glass beads. The glass beads held the genitalia in place and allowed structures to be viewed in precise lateral, dorsal, and ventral positions. Genitalia were examined with an Olympus BX41 compound microscope at 250-500 $\times$ magnification. Structures were traced in pencil with the use of a camera lucida (drawing tube) mounted on the microscope. Pencil sketches were then scanned (Fujitsu ScanSnap S1500M scanner), edited in Adobe Photoshop (v. 9.0.2, Adobe Systems Inc.), and used as a template in Adobe Illustrator (v. 13.0.2, Adobe Systems Inc.) to be digitally inked. Electronic "drawing" was completed with the aid of a graphics tablet (Bamboo Fun, Wacom Company, Limited). Species descriptions were constructed using the program DELTA (Dallwitz et al. 1999) and specimen management followed the procedures outlined by Holzenthal and Andersen (2004). Each pinned specimen examined during the study was affixed with a barcode label (4 mil polyester, $8 \times 14 \mathrm{~mm}$, code 49) bearing a unique alphanumeric sequence begin-
ning with the prefix UMSP. Specimens in alcohol were given a single barcode label to represent all those in a single vial. The prefix is not meant to imply ownership by the University of Minnesota Insect Collection (UMSP), but only to indicate that the specimen was databased at that collection. Types of species described and other material examined are deposited in the University of Minnesota Insect Collection, St. Paul, Minnesota (UMSP), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH), and the Museo del Instituto de Zoología Agrícola, Maracay, Venezuela (MIZA).

## Taxonomy

## Acostatrichia digitata Thomson \& Holzenthal, sp. n.

 urn:lsid:zoobank.org:act:85981ECC-3397-4968-ACBC-B6EE2098DA5B http://species-id.net/wiki/Acostatrichia_digitata Fig. 1Diagnosis. This species is most similar to Acostatrichia fimbriata Flint, 1974 but can be distinguished by a mesoventral process on abdominal segment VII with an apex that is truncate and rugose, not pointed. The posterolateral process of abdominal segment VIII bears digitate projections apically, unlike the spines on $A$. fimbriata. Additionally, the subgenital appendage of $A$. digitatus is pointed apically instead of rounded.

Description. Male. Length of forewing $2.7 \mathrm{~mm}(\mathrm{n}=1)$. Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Dorsum of head dark brown with pale yellow setae; thorax dark brown with pale yellow setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine yellow setae and small scattered patches of dark brown setae. Genitalia. Abdominal sternum VII with long mesoventral process, apex truncate, rugose. Segment VIII anterolateral margin straight, posterolateral margin greatly elongate into narrow structure bearing digitate apical projections; ventrally posterior margin concave, mildly crenulated. Segment IX anterolateral margin acute, posterolateral margin broadly convex; with mesolateral quadrate structure bearing prominent setae (see Fig. 1A); dorsally with posterior margin straight. Subgenital appendage paired, broadly rounded with apicoventral point, dorsally with rounded emargination on inner edge. Inferior appendage setose, narrow, rod-like, fused latero-ventrally with subgenital appendage, in ventral view with semiquadrate apical emargination (see Fig. 1D). Tergum X membranous, triangular in dorsal view. Phallus tubular basally with median complex bearing basal loop and pair of circular "windows", apex with pair of elliptic plates, strongly sclerotized mesolaterally.

Material examined. Holotype male: VENEZUELA: Bolívar: E Tumeremo, W Bochinche, Río Botonamo, $07^{\circ} 25.462^{\prime} \mathrm{N}, 61^{\circ} 14.318^{\prime} \mathrm{W}, 150 \mathrm{~m}, 13 . v i i .2010$, UV light, Holzenthal, Thomson, Cressa (UMSP000095201) (UMSP).

Etymology. The Latin word digitatus meaning "having fingers", referring to the digitate projections on the posterolateral process of the VIIIth segment.


Figure I. Acostatrichia digitata sp. n. Male genitalia: A segments IX-X, lateral (base of phallus crosshatched) B segments VII-VIII and segment IX anterolateral margin, lateral C segments IX-X, dorsal D segments VII-IX, ventral $\mathbf{E}$ phallus, lateral $\mathbf{F}$ phallus, dorsal.

## Hydroptila cressae Thomson \& Holzenthal, sp. n.

urn:lsid:zoobank.org:act:22765A69-4EE1-4DA6-BB78-E100D0C6EF33
http://species-id.net/wiki/Hydroptila_cressae
Fig. 2

Diagnosis. This species is most similar to Hydroptila denza Ross, 1948, but differs in the shape of the projection on the posterolateral margin of abdominal segment IX. This projection is more pointed and is curved downward, or decurved, in H. cressae, while it is straight and more blunt in $H$. denza. The triangular subgenital process seen in H. denza is not apparent in H. cressae. Additionally, tergum X of H. cressae contains an internal apodeme that is not apparent in $H$. denza.

Description. Male. Length of forewing $2.0 \mathrm{~mm}(\mathrm{n}=1)$. Head unmodified, without ocelli; antennae unmodified. Tibial spur count $0,2,4$. Dorsum of head brown with pale yellow setae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine light brown setae with small dark brown patch of setae at apex. Genitalia. Abdominal sternum VII with simple, slender, pointed mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin convex, posterolateral margin with pointed projection, curving slightly ventrad; dorsally with posterior margin convex. Inferior appendage setose, with narrow base, apex truncate with pair of dark points on internal face. Tergum X membranous, extending past inferior appendage, containing internal sclerotized apodeme (see Fig. 2A). Phallus narrow, elongate; apex membranous, ovate, with elongate, slender spines extending past membranous region.

Material examined. Holotype male: VENEZUELA: Bolívar: Gran Sabana, E. Pauji, "Río Curvita", $04^{\circ} 31.237^{\prime} \mathrm{N}, 61^{\circ} 31.591^{\prime} \mathrm{W}, 869 \mathrm{~m}, 15-16 . v i i .2010$, UV light, Holzenthal, Thomson, Cressa (UMSP000095196) (UMSP).

Etymology. Named in honor of Dr. Claudia Cressa, an aquatic ecologist at the Universidad Central de Venezuela and friend and colleague of the authors.

## Metrichia bostrychion Thomson \& Holzenthal, sp. n.

urn:Isid:zoobank.org:act:13F7C864-63DB-4360-92FA-D3CB3331DBA3
http://species-id.net/wiki/Metrichia_bostrychion
Fig. 3
Diagnosis. This species is most similar to Metrichia anisoscola (Flint, 1991), but differs in the shape of the inferior appendage, which is less elongate in M. bostrychion and more suborbicular. The dorsolateral hook in M. bostrychion is also stouter than that of M. anisoscola. Metrichia bostrychion can also be distinguished by the 3rd spine on the phallus which spirals dorsally.

Description. Male. Length of forewing $1.8 \mathrm{~mm}(\mathrm{n}=1)$. Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Dorsum of head dark brown with white setae; thorax dark brown with white and dark brown setae dorsally, brown


Figure 2. Hydroptila cressae sp. n. Male genitalia: A segments VII-X, lateral (base of phallus crosshatched) B segments VIII-X, dorsal $\mathbf{C}$ segments VII-IX, ventral $\mathbf{D}$ phallus, lateral $\mathbf{E}$ phallus, dorsal.
ventrally; leg segments with brown setae. Forewings covered with fine dark brown setae with small patch of light brown setae at apex. Abdomen with internal sacs between segments IV-V. Dorsolateral setal brushes on segments IV and V. Genitalia. Abdominal sternum VII with short, pointed mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin very elongate, narrowing, withdrawn into segments VIIVIII, posterolateral margin convex; dorsally with posterior margin membranous, flat. Preanal appendage (cercus) short, rounded. Dorsolateral hook stout, strongly decurved (see Fig. 3A). Inferior appendage suborbicular with shallow posterolateral emargination, extends as high as segment IX. Tergum X membranous, apex subdeltoid in dorsal view. Phallus widest at base, narrowing to median constriction, membranous apex with 3 spines, 1 st and 3rd slender, elongate, 2nd spiraling dorsad.

Material examined. Holotype male: VENEZUELA: Monagas: Guachero Cave National Park at La Paila waterfall, $10^{\circ} 10.322^{\prime} \mathrm{N}, 63^{\circ} 33.315^{\prime} \mathrm{W}, 1110 \mathrm{~m}, 20-21$. vii.2010, sweep net, Holzenthal, Thomson (UMSP000095197) (UMSP).

Paratype. same data as holotype, 1 female (UMSP).
Etymology. The diminutive of the Greek word bostrychos meaning "curl", referring to the small spiral in the second apical spine on the phallus.

## Neotrichia feolai Santos \& Nessimian, 2009, redescription and new country record

 http://species-id.net/wiki/Neotrichia_feolaiFig. 4
Neotrichia feolai Santos \& Nessimian, 2009: 766 [Type locality: Brazil, Amazonas, Rio
Preto da Eva (tributary to Rio Preto da Eva); INPA; male].

Diagnosis. Neotrichia feolai was previously only known from the male holotype collected from Brazil, Amazonas. Eight males were collected for the first time from Venezuela, representing a new record in this study for the country. Original illustrations did not include the distinctive subgenital appendage, but specimens from Venezuela match all other characteristics of the Brazilian species perfectly. Some of our specimens are dry, while the holotype was collected in alcohol, allowing us to to describe coloration. We have also described and illustrated the subgenital plate not seen in the original illustration.

According to the original authors, this species is most similar to Neotrichia biuncifera Flint, 1974. The shapes and lengths of the bracteole and inferior appendage are similar, but $N$. feolai can be distinguished by having only a single spine at the apex of the phallus.

Redescription. Male. Length of forewing 1.6-1.9 mm (n=8). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 0,2 , 3 . Dorsum of head brown with light brown setae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine light brown setae with small patches of dark brown setae. Genitalia. Abdominal sternum VII with-


Figure 3. Metrichia bostrychion sp. n. Male genitalia: A segments VII-X, lateral (base of phallus crosshatched) B segments IX-X, dorsal $\mathbf{C}$ segments VII-IX, ventral D phallus, lateral E phallus, dorsal.
out mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin strongly narrowing, withdrawn into segment VIII, posterolateral margin fused dorsally with tergum X (see Fig. 4B). Subgenital plate fused, diamond-shaped with pair of apico-ventral setae, posterior margin bearing paired row of sclerotized spines within membranous layer (see Figs. 4A, 4C). Bracteole spatulate, extended evenly with inferior appendage. Inferior appendage setose, laterally narrow and rod-like, fused lateroventrally with subgenital appendages, ventrally with semiquadrate apical emargination. Tergum X membranous, bearing minute dorsal setae, with deep emargination both laterally and dorsally, dorsal lobe with sclerotized apex. Phallus with wide tubular base narrowing to median constriction, membranous apex with spiral process and slender apical spines.

Material examined. VENEZUELA: Guárico: Santa Rita, Morichal de los Becerros, $08^{\circ} 09.044^{\prime} \mathrm{N}, 62^{\circ} 35.149^{\prime} \mathrm{W}, 66 \mathrm{~m}, 6 . v i i .2010$, UV light, Holzenthal, Thomson, 8 males ( 5 in alcohol) (UMSP, NMNH, MIZA).

## Ochrotrichia spira Thomson \& Holzenthal, sp. n.

 urn:lsid:zoobank.org:act:83832CD2-268B-4AA3-A5EC-F6FAB463D9F6 http://species-id.net/wiki/Ochrotrichia_spira Fig. 5Diagnosis. This species is most similar to Ochrotrichia raposa Bueno-Soria \& SantiagoFragoso, 1992. Both have a simple, threadlike phallus and the large inferior appendage bears patches of black pegs on its internal face. The inferior appendage of $O$. spiralis, however, is parallel-sided with a truncate apex. Also, the sclerotized processes extending from tergum X of $O$. spiralis are easily distinguishable from those of $O$. raposa, in particular the large, spiral process.

Description. Male. Length of forewing $2.6-2.7 \mathrm{~mm}(\mathrm{n}=3)$. Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count $0,3,4$. Dorsum of head dark brown with pale yellow setae; thorax light brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae and patches of dark brown. Forewings covered with fine brown setae with small patches of dark brown setae near apex. Genitalia. Abdominal sternum VII with short, rounded mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin concave, posterolateral margin fused dorsally with tergum X. Inferior appendage setose, 3 times longer than wide, parallel-sided, apex truncate, inner surface bearing many short, stout spines distributed as in Figs. 5A, 5C. Tergum X sclerotized, highly developed with 3 processes: 1 st simple, slender pointed; 2nd with heavily sclerotized edge, large subapical point, small apical point; 3rd strongly spiraled, extended past other processes. Phallus tubular, elongate, threadlike.

Material examined. Holotype male: VENEZUELA: Monagas: Guachero Cave National Park, $10^{\circ} 10.322^{\prime} \mathrm{N}, 63^{\circ} 33.315^{\prime} \mathrm{W}, 1110 \mathrm{~m}, 20-21 . v i i .2010$, UV light, Holzenthal, Thomson, Cressa (UMSP000095193) (UMSP).


Figure 4. Neotrichia feolai Santos \& Nessimian, 2009. Male genitalia: A segments VIII-X, lateral (base of phallus crosshatched) B segments IX-X, dorsal $\mathbf{C}$ segment IX, ventral $\mathbf{D}$ phallus, lateral $\mathbf{E}$ phallus, dorsal.

Paratypes. same data as holotype, 2 males (UMSP, NMNH).
Etymology. The Latin word spiralis meaing "spiral", referring to the strongly spiraled process extending from tergum X .

## Oxyethira (Tanytrichia) bettyae Thomson \& Holzenthal, sp. n. urn:lsid:zoobank.org:act:9B85F4D2-070A-4192-BD8D-E4DF432D19AA http://species-id.net/wiki/Oxyethira_bettyae <br> Fig. 6

Diagnosis. This species is placed in the subgenus Tanytrichia according to the characters given by Kelley (1985): segment VIII venter excised to anterior margin, segment IX elongate and extending into segment VI, the absence of segment IX dorsum, and a phallus bearing two long lateral processes originating at the midlength. This species is most similar to Oxyethira longissima Flint, 1974. The phallus is very similar, bearing long paired processes sharply bent back anteriorly. However, the subgenital process of O. longissima is more strongly arched and much more slender in lateral view than that of $O$. bettyae. Also, when viewed ventrally, the bilobed process of $O$. bettyae is wider basally than $O$. longissima.

Description. Male. Length of forewing 2.0-2.2 mm (n=6). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count $0,3,4$. Dorsum of head dark brown with pale yellow setae; thorax brown with light brown setae dorsally; leg segments with light brown setae. Forewings covered with fine light brown setae and small scattered patches of dark brown setae and golden brown setae. Genitalia. Abdominal sternum VII with simple, pointed mesoventral process with small patch of stout pegs basally. Segment VIII anterolateral margin straight, posterolateral margin pointed; dorsally posterior margin with rounded emargination; ventrally posterior margin with deeply divided. Segment IX anterolateral margin very narrow and very elongate, withdrawn into segments VI-VIII, posterolateral margin straight, not extended posteriorly past segment VIII. Subgenital process fused, apex with small rounded emargination (see Fig. 6C). Bilobed process slender, extending posteriad. Inferior appendage fused with deep apical emargination, sparsely setose, heavily sclerotized, apex acute, upturned in lateral view. Tergum X membranous, quadrate dorsally, oblong ventrally. Phallus with tubular basal half, apical half membranous; 2 long, lateral processes beginning at midlength, very sharply curved backward, or recurved.

Material examined. Holotype male: VENEZUELA: Guárico: UCV San Nicolasito Field Station, $08^{\circ} 8.296^{\prime} \mathrm{N}, 66^{\circ} 24.459^{\prime} \mathrm{W}, 62 \mathrm{~m}, 5 . v i i .2010$, UV light, Holzenthal, Thomson (UMSP000095178) (UMSP).

Paratypes. same data as holotype, 1 male (UMSP); Venezuela: Bolívar: Los Pijiguaos at rock outcrop, $6^{\circ} 35.617^{\prime} \mathrm{N}, 66^{\circ} 49.238^{\prime} \mathrm{W}, 80 \mathrm{~m}, 7-8$.vii.2010, UV light trap, Holzenthal, Thomson, 5 males (in alcohol) (UMSP, NMNH, MIZA).

Etymology. Named in honor of the first author's grandmother, Betty Welter, who passed away while this work was in progress.


Figure 5. Ochrotrichia spira sp. n. Male genitalia: A segments VII-X, lateral (base of phallus crosshatched) B segments VIII-X, dorsal C segments VII-IX, ventral D phallus, lateral E phallus, dorsal.

## Oxyethira picita Harris \& Davenport, 1999, new country record

 http://species-id.net/wiki/Oxyethira_picitaOxyethira picita Harris \& Davenport, 1999: 35 [Type locality: Peru, Loreto, edge of Rio Sucusari backwater, adjoining Explorama lodge; NMNH; male]. -Santos et al., 2009: 36, 43 [distribution].

Diagnosis. Oxyethira picita was previously known only from the male holotype collected from Peru, Loreto. A single male was collected at a later date from Brazil, Amazonas (Santos et al. 2009). Five males were now collected for the first time from Venezuela, representing a new record for the country. All five males were collected in alcohol.

Oxyethira picita was placed in the subgenus Tanytrichia by Harris \& Davenport (1999), although it was suggested that it also displayed some similarity to the subgenus Loxotrichia. The original description and illustration of O. picita are detailed and well done; further description or illustration was not thought necessary.

Material examined.VENEZUELA: Bolívar: Campamento Río Aro, $07^{\circ} 37.443^{\prime} \mathrm{N}$, $64^{\circ} 08.324^{\prime} \mathrm{W}, 90 \mathrm{~m}, 10-11 . v i i .2010$, UV light, Holzenthal, Thomson, 4 males (in alcohol) (UMSP, MIZA). VENEZUELA: Bolívar: 30 km S Upata, roadside marsh, $07^{\circ} 22.239^{\prime} \mathrm{N}, 61^{\circ} 44.233^{\prime} \mathrm{W}, 163 \mathrm{~m}, 12 . v i i i .2010$, Short, Tellez, Camacho, 1 male (in alcohol) (NMNH).

## Oxyethira (Dactylotrichia) quiramae Thomson \& Holzenthal, sp. n. urn:lsid:zoobank.org:act:6C447B87-EA39-4D06-A28A-0702345D2930 <br> http://species-id.net/wiki/Oxyethira_quiramae

Fig. 7

Diagnosis. This species is placed in the subgenus Dactylotrichia according to the characters given by Kelley (1985): segment VIII venter excised nearly to the anterior margin and segment IX venter extending anteriorly through segments VIII-VI. This species is most similar to Oxyethira hozosa Harris \& Davenport, 1999. Both species have short, blunt, ventrally triangular inferior appendages and a phallus with a distal curved process and an ejaculatory duct enclosed within the membranous apex. O. quiramae can be distinguished by a subgenital plate that is not as strongly decurved and lacks an acute apex in lateral view. Also, in O. quiramae, segment IX extends anteriorly past the posterior margin of abdominal segment VI.

Description. Male. Length of forewing 1.8-1.9 mm ( $\mathrm{n}=3$ ). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count $0,3,4$. Dorsum of head brown with light brown setae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with light brown setae. Forewings covered with fine brown setae with small scattered patches of light brown setae and small patches of dark brown setae near margins and apex. Genitalia. Abdominal sternum VII with simple, digitate


Figure 6. Oxyethira bettyae sp. n. Male genitalia: A segments VI-X, lateral (base of phallus crosshatched) B segments VI-X, dorsal $\mathbf{C}$ segments VI-IX, ventral $\mathbf{D}$ phallus, lateral $\mathbf{E}$ phallus, dorsal.
mesoventral process with large patch of stout pegs basally. Segment VIII anterolateral margin straight, posterolateral margin convex with small mesal emargination; dorsally posterior margin with rounded emargination; ventrally deeply excised. Segment IX anterolateral margin narrow and elongate, withdrawn into segments VI-VIII, posterolateral margin straight, not extended posteriorly past segment VIII. Subgenital process fused distomesally, apex with shallow emargination, curving ventrad (see Fig. 7C). Bilobed process slender, curved, not extending posteriorly past segment VIII. Inferior appendage reduced, triangular, heavily sclerotized (see Fig. 7C). Tergum X not apparent. Phallus with tubular basal half, apical half membranous; apex elongate, slender, pointed, curving dorsad and sharply recurved.

Material examined. Holotype male: VENEZUELA: Guárico: UCV San Nicolasito Field Station, $08^{\circ} 8.296^{\prime} \mathrm{N}, 66^{\circ} 24.459^{\prime} \mathrm{W}, 62 \mathrm{~m}, 5 . v i i .2010$, UV light, Holzenthal, Thomson (UMSP000095179) (UMSP).

Paratypes. same data as holotype, 2 males (NMNH, MIZA).
Etymology. Named in honor of Gina Quiram, a friend and colleague of the first author, for all her help in the field.

## Oxyethira redunca Thomson \& Holzenthal, sp. n. urn:lsid:zoobank.org:act:C8A428D1-6558-479C-8AF8-8857D6E2A5FB <br> http://species-id.net/wiki/Oxyethira_redunca

Fig. 8

Diagnosis. We have been unable to assign this species to a subgenus. The deep ventral excision of abdominal segment VIII and the extension of segment IX anteriorly into segment VII make it somewhat similar to Loxotrichia. However, the absence of a subgenital process precludes it from being placed with certainty in any of the current subgenera and distinguishes it from all other species.

Description. Male. Length of forewing $2.4 \mathrm{~mm}(\mathrm{n}=1)$. Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count $0,3,4$. Dorsum of head brown with pale yellow setae; thorax brown with pale yellow setae dorsally, pale yellow ventrally; leg segments with brown setae. Forewings covered with fine brown setae and elongate patches of light brown setae and small patches of dark brown setae near margins and apex. Genitalia. Abdominal sternum VII with spatulate mesoventral process. Segment VIII anterolateral margin straight, posterolateral margin acutely convex; dorsally posterior margin with deep acute emargination; ventrally posterior margin with deep rounded emargination. Segment IX anterolateral margin very elongate, narrowing, withdrawn into segments VII-VIII, posterolateral margin acute, not extending past segment VIII; dorsally bearing paired, elongate, slender processes, basal half extending posteriorly, apical half strongly bent anteriad. Subgenital process not apparent. Bilobed process not apparent. Inferior appendage setose, laterally narrow and rod-like, fused latero-ventrally with subgenital appendages, ventrally with semiquadrate apical emargination. Tergum X


Figure 7. Oxyethira quiramae sp. n. Male genitalia: A segments VI-IX, lateral (base of phallus crosshatched) B segments VII-IX, dorsal $\mathbf{C}$ segments VII-IX, ventral $\mathbf{D}$ phallus, lateral $\mathbf{E}$ phallus, dorsal.

membranous, large, bearing elliptic patch of minute setae dorsally (see Fig. 8B). Phallus with tubular basal half, apical half membranous, convex ventrally, apex curving dorsad.

Material examined. Holotype male: VENEZUELA: Bolívar: Gran Sabana, E. Pauji, "Río Curvita", $4^{\circ} 31.237^{\prime} \mathrm{N}, 61^{\circ} 31.591$ 'W, $869 \mathrm{~m}, 15-16 . v i i .2010$, UV light, Holzenthal, Thomson, Cressa (UMSP000095176) (UMSP).

Etymology. The Latin word reduncus meaning "bent backward", referring to the sharply bent dorsal processes of segment IX.

## Rhyacopsyche shorti Thomson \& Holzenthal, sp. n.

urn:lsid:zoobank.org:act:56EB1974-52AA-4EE1-9F95-357CD2AC3A4A
http://species-id.net/wiki/Rhyacopsyche_shorti
Fig. 9

Diagnosis. This species is most similar to Rhyacopsyche otarosa Wasmund \& Holzenthal, 2007. Both species display an inferior appendage with a bifid apex bearing a large rounded dorsal lobe. However, the ventral lobe is broadly pointed in $R$. shorti and truncate in $R$. otarosa. Additionally, when seen dorsally, the dorsolateral lobes of segment IX are rounded in $R$. shorti, not acicular as in $R$. otarosa.

Description. Male. Length of forewing 2.6-2.7 mm ( $\mathrm{n}=2$ ). Head unmodified, with 3 ocelli; antennae unmodified. Tibial spur count 1, 3, 4. Dorsum of head brown with dark brown setae and light brown patch between antennae; thorax brown with light brown setae dorsally, light brown ventrally; leg segments with dark brown setae. Forewings covered with golden brown setae with small patches of dark brown setae at margins and apex. Genitalia. Abdominal sternum VII without mesoventral process. Segment VIII unmodified. Segment IX anterolateral margin very elongate, narrowing, withdrawn into segments VII-VIII, posterolateral margin with rounded setae-bearing dorsolateral lobe and truncate mesolateral lobe. Inferior appendage with rounded mesodorsal projection bearing setae, setae directed anteriad; apex heavily sclerotized, curving dorsad, acute. Tergum X membranous, round in dorsal view, contracted inside dorsolateral lobes of segment IX. Phallus basally tubular, elongate, narrow, apex membranous and with thickened spines.

Material examined. Holotype male: VENEZUELA: Bolívar: Gran Sabana, E. Pauji, "Río Curvita", $04^{\circ} 31.237^{\prime} \mathrm{N}, 61^{\circ} 31.591^{\prime} \mathrm{W}, 869 \mathrm{~m}, 15-16 . v i i .2010$, UV light, Holzenthal, Thomson, Cressa (UMSP000095199) (UMSP).

Paratype. same data as holotype, 1 male (UMSP).
Etymology. Named in honor of Dr. Andrew Short, an entomologist at the University of Kansas and friend and colleague of the authors.


Figure 9. Rhyacopsyche shorti sp. n. Male genitalia: A segments IX-X, lateral (base of phallus crosshatched) B segments IX-X, dorsal $\mathbf{C}$ inferior appendages, ventral $\mathbf{D}$ phallus, lateral $\mathbf{E}$ phallus, dorsal.

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## References

Blahnik RJ, Holzenthal RW, Prather A (2007) The lactic acid method for clearing Trichoptera genitalia. In: Bueno-Soria J, Barba-Alvarez R, Armitage B (Eds) Proceedings of the XIIth International Symposium on Trichoptera. The Caddis Press, Columbus, Ohio, 9-14.
Bueno-Soria J, Santiago-Fragoso S (1992) Studies in aquatic insects, XI: seven new species of the genus Ochrotrichia (Ochrotrichia) from South America (Trichoptera: Hydroptilidae). Proceedings of the Entomological Society of Washington 94: 439-446.
Dallwitz MJ, Paine TA, Zurcher EJ (1999) User's guide to the DELTA Editor. http://deltaintkey.com/ [accessed 6 February 2012]
Carins A, Wells A (2008) Contrasting modes of handling moss for feeding and case-building by the caddisfly Scelotrichia willcarinsi (Insecta: Trichoptera). Journal of Natural History 42: 2609-2615. doi: 10.1080/00222930802354308
Flint OS Jr (1972) Studies of Neotropical caddisflies, XIV: on a collection from northern Argentina. Proceedings of the Biological Society of Washington 85: 223-248.
Flint OS Jr (1974) Studies of Neotropical caddisflies, XV: the Trichoptera of Surinam. Studies on the Fauna of Suriname and other Guianas 14: 1-151.
Flint OS Jr (1991) Studies of Neotropical caddisfliesm XLV: the taxonomy, phenology, and faunistics of the Trichoptera of Antioquia, Colombia. Smithsonian Contributions to Zoology 520: 1-113. doi: 10.5479/si.00810282.520
Harris SC, Davenport LJ (1999) New species of Hydroptilidae (Trichoptera) from the Amazon region of northeastern Peru. Proceedings of the Entomological Society of Washington 101: 26-38.
Holzenthal RW, Andersen T (2004) The caddisfly genus Triaenodes in the Neotropics (Trichoptera: Leptoceridae). Zootaxa 511: 1-80.
Holzenthal RW, Blahnik RJ, Prather AL, Kjer KM (2007) Order Trichoptera Kirby, 1813 (Insecta), Caddisflies. Zootaxa 1668: 639-698.

Holzenthal RW, Morse JC, Kjer KM (2011) Order Trichoptera Kirby, 1813. In: Zhang ZQ (Ed) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 209-211.
Kelley RW (1984) Phylogeny, morphology and classification of the micro-caddisfly genus Oxyethira Eaton (Trichoptera: Hydroptilidae). Transactions of the American Entomological Society 110: 435-463.
Marshall JE (1979) A review of the genera of the Hydroptilidae (Trichoptera). Bulletin of the British Museum (Natural History) Entomology Series 39: 135-239.
Ross HH (1948) Notes and descriptions of Nearctic Hydroptilidae (Trichoptera). Journal of the Washington Academy of Sciences 38: 201-206.
Santos APM, Henriques-Oliveira AL, Nessimian JL (2009) New species and records of Oxyethira Eaton (Trichoptera: Hydroptilidae) from Amazonas State, Brazil. Zootaxa 2169: 35-44.
Santos APM, Nessimian JL (2009) New species and records of Neotrichia (Trichoptera: Hydroptilidae) from Central Amazonia, Brazil. Zoologia 26: 758-768.
Wasmund AM, Holzenthal RW (2007) A revision of the Neotropical caddisfly genus Rhyacopsyche, with the description of 13 new species (Trichoptera: Hydroptilidae). Zootaxa 1634: 1-59.
Wells A (1985) Larvae and pupae of Australian Hydroptilidae (Trichoptera), with observations on general bilogy and relationships. Australian Journal of Zoology, Supplementary Series 113: 1-69. doi: 10.1071/AJZS113
Wells A (2005) Parasitism by hydroptilid caddisflies (Trichoptera) and seven new species of Hydroptilidae from northern Queensland. Australian Journal of Entomology 44: 385-391. doi: 10.1111/j.1440-6055.2005.00492.x
Wiggins GB (2004) Caddisflies: The Underwater Architects. University of Toronto Press, Toronto, 292 pp .

# A new Chlerogelloides from northeastern Brazil and French Guiana, with a key to the species (Hymenoptera, Halictidae) 

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#### Abstract

A third species of the rare augochlorine bee genus Chlerogelloides Engel et al. (Halictinae, Augochlorini) is described and figured. Chlerogelloides nexosa sp. $\mathbf{n}$. is most similar to the type species, C. femoralis Engel et al., in that both have modified midlegs in the males. The former, however, can be distinguished on the basis of its terminalia, which in some respects more closely resembles those of $C$. simplex Engel and Brooks. Brief comments on the secondary features of males and relationships of the genus are provided. A key to the species of the genus is provided and floral records of Cordia nodosa Lam. (Boraginaceae) and Gonzalagunia dicocca Cham. \& Schltdl. (Rubiaceae) are noted.


## Keywords

Apoidea, Anthophila, Halictidae, Halictinae, Augochlorini, Chlerogelloides, taxonomy, Brazil

## Introduction

Numerous lineages of bees within the New World tribe Augochlorini (Halictinae) are known to have characteristically elongate heads, typically involving an elongation of the malar space and clypeus, and often the supraclypeal area, and presumably adaptations for obtaining nectar from flowers with deep corollas, although few floral records are available (e.g., Engel 2000, 2007, 2009, 2010a, 2010b; Engel and Brooks 2002; Engel and Gonzalez 2009). Among such bees, one of the more peculiar are the species of the genus Chlerogelloides Engel et al. (Engel et al. 1997; Engel and Brooks 1999), so named for its superficial resemblance to the more diverse and widespread genus Chlerogella Michener (Engel 2009, 2010a), and putatively related to Chlerogella and Ischnomelissa Engel (Engel 2000). Unlike nearly all of the aforementioned cases of augochlorines with noticeably elongate head, in Chlerogelloides the malar space is unmodified and short, but the clypeus remains distinctively elongate. A complete account of the genus has been provided by Engel and Brooks (1999) and Engel (2000). To hitherto known species of Chlerogelloides have been reported from Brazil (Amazonas), Colombia (Putumayo), Ecuador (Morona Santiago, Napo, Sucumbíos), French Guiana (Roura), and Peru (Loreto) for Chlerogelloides femoralis Engel et al. and Brazil (Amapá) and French Guiana for C. simplex Engel and Brooks (Engel et al. 1997; Engel and Brooks 1999; Moure 2007). As the specific epithet suggests, the type species, C. femoralis, is also noteworthy among the Augochlorini for its peculiarly modified midlegs in males, the function of which remains unknown but are presumably used in mating. Tragically, no biological information of any kind has been reported for any species of the genus.

Herein we report the discovery of a third species in the genus, specimens of which were captured while visiting flowers of Cordia nodosa Lam. (Boraginaceae: sometimes placed in its own order, Boraginales) and Gonzalagunia dicocca Cham. \& Schltdl. (Gentianales: Rubiaceae), and representing the first occurrence of the genus in Pará State, Brazil.

## Material and methods

Morphological terminology follows that of Engel (2001, 2009) and Michener (2007), while the format for the description follows those of Engel et al. (1997) and Engel and Brooks (1999). The higher classification of Augochlorini is that of Engel (2000). Abbreviations used for common morphological terms are: S, metasomal sternum; T, metasomal tergum; F, flagellomere; DS, diameter of the antennal scape; and OD, ocellar diameter (based on the median ocellus). Measurements and proportions are adapted from Moure and Sakagami (1962): body length, head length and width, upper and lower interocular distances, and ocellocipital distance. Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscope lens.

## Systematics

Tribe Augochlorini Beebe, 1925
Subtribe Augochlorina Beebe, 1925
Genus Chlerogelloides Engel, Brooks, \& Yanega, 1997

## Chlerogelloides nexosa Oliveira, Engel, \& Mahlmann, sp. n.

 urn:lsid:zoobank.org:act:C5A48B27-0DC1-4AC6-9C17-9AD8E9D3C617 http://species-id.net/wiki/Chlerogelloides_nexosaFigs 1-3, 5, 7-10

Holotype. đ̃, Brazil, Pará (Melgaço, Reserva Caxiuanã, Estação Ecológica Ferreira Penna, $01^{\circ} 43$ 'S, $51^{\circ} 29^{\prime}$ W, 18-21.ix. 2011 [18-21 September 2011], Rech, Coelho, Correa \& Carmo Leg. // coletada na flor: Cordia nodosa Lam. (Boraginales - Cordiaceae) - durante o curso de Polinização 2011 // Holotype male Chlerogelloides nexosa Oliveira, Engel \& Mahlmann. The specimen is deposited in the Entomological Collection of the Museu Paraense Emílio Goeldi (MPEG), in Belém, Pará, Brazil.


Figure I. Male of Chlerogelloides nexosa sp. n. collecting resources at flowers of Cordia nodosa Lam. (Boraginaceae) at the Estação Ecológica Ferreira Penna (Caxiuanã Reserve, Melgaço, Pará, Brazil). Photograph by Rech et al. (in press).


Figures 2-3. Photomicrographs of male paratype of Chlerogelloides nexosa sp. n. $\mathbf{2}$ Lateral habitus $\mathbf{3}$ Facial view.

Paratypes. $1 \delta$, with same label data as holotype and deposited in the Entomological Collection of the Zoological Museum of the Federal University of Bahia (MZUFBA), in Salvador, Bahia, Brazil. $5 \widehat{J}^{\text {ふ }}$, Guyane Française [French Guiana], Saül, Carbet ONF de Galbao, 27.viii. 2003 [27 August 2003], on Gonzalagunia dicocca, leg. J. Munzinger; deposited in the Department of Entomology, Royal Belgian Institute of Natural Sciences, Brussels, Belgium and one in the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA. 1才, Guyane Fr. [French Guiana], Patawa, viii. 1999 [August 1999], PM; deposited in the Department of Entomology, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

Diagnosis. Integument predominantly honey yellow with metallic olive green highlights only on the head, mesoscutum, mesoscutellum, and metanotum (Figs 2, 3); postgena uniformly covered by plumose setae except; mesotrochanter without prominent ventral tubercle and not strongly bent (Fig. 5); mesofemur greatly expanded and flattened along inner surface, with a prominent tubercle on ventral surface in apical third (Fig. 5); mesotibia with inner surface twisted and flanked by non-contiguous, ill-defined carinas converging medioapically (Fig. 5); mesobasitarsus about twice as long as wide and weakly concave on inner surface; male terminalia as in figures 7-10.


Figures 4-6. Male midlegs of species of Chlerogelloides. 4 Chlerogelloides femoralis Engel et al. 5 C. nexosa sp. n. 6 C. simplex Engel and Brooks.

Description. ${ }^{\text {² }}$ : Structure: Total body length 6.60 mm ; forewing length 4.50 mm . Head elongate, length 1.80 mm , width 1.47 mm (Figs 2, 3); clypeus longer than maximum width, length 0.60 mm , width 0.47 mm , almost entirety of clypeus ( $85 \%$ ) set below lower tangent of compound eyes; frontal line weakly carinate between antennae, becoming a faintly impressed line from there to median ocellus; antennal scape relatively short (excluding basal bulb), length 0.50 mm ; pedicel about as long as F1; F1 wider than long, slightly longer than F2; F2-F5 slightly wider than long; F6-11 progressively becoming longer than previous flagellomeres; distance from median ocellus to lateral ocellus 0.05 mm ; between lateral ocelli 0.20 mm ; ocellocular distance 0.22 mm ( $1.46 \times$ ocellar diameter); compound eye about 3.25 x wider than


Figures 7-10. Male terminalia of Chlerogelloides nexosa sp. n. 7 Hidden and fused sterna VII+VIII 8 Genital capsule, lateral view 9 Genital capsule, dorsal view 10 Genital capsule, ventral view.
gena in profile (width of compound eye 0.65 mm , width of gena 0.20 mm ), beginning a little below middle of compound eyes. Intertegular distance 0.95 mm ; mesoscutellum less than twice as long as metanotum (mesoscutellum length 0.35 mm , metanotum length 0.20 mm ); dorsal surface of propodeum faintly concave, elongate (as for the genus: vide Engel et al. 1997; Engel and Brooks 1999; Engel 2000). Mesofemur greatly enlarged, approximately twice as long as wide (measurement made on internal surface: length 1.2 mm , width 0.55 mm ), with flattened inner surface (Fig. 5), ventrally ridged along external border from apex basad to ventral tubercle in apical third; mesotibia slightly twisted on internal surface (in posterior view), with two non-contiguous carinae along borders and converging medioapically, one from


Figures II-I2. Male of Chlerogelloides simplex Engel and Brooks. II Lateral habitus $\mathbf{I} \mathbf{2}$ Facial view.
base of mesotibia and with a small elevation near apex, other more apical on external border, both carinae terminating at a weakly depressed medioapical area from which spur articulates; mesobasitarsus twice as long as wide, flattened on dorsal surface and with carinae bordering weakly depressed inner surface. Forewing pterostigma very long, almost as long as first submarginal cell; hind wing with basal hamuli arranged $2-1$, distal hamuli arranged 2-1-2. Male terminalia as in figures $7-10$.

Sculpturing: Integument smooth and polished, faintly imbricate in some places, with sparse small to minute punctures, except face above level of antennal toruli with punctures more closely spaced as well as on mesoscutum, mesoscutellum, and metanotum; punctures separated by $2-5 \times$ a puncture diameter on mesepisternum; dorsal surface of propodeum smooth, polished, and glabrous.

Coloration: Integument predominantly honey yellow with brownish areas laterally pronotum near pronotal lobe, dorsal surface of propodeum, apex of metafemur, external surface of metatibia, apical third of T1, apical two-thirds of T2-T3, and T4-T7 with yellowish areas slightly darker than elsewhere (darker areas wider and longer in paratype). Head metallic olive green except honey yellow on clypeus (sometimes with some brown areas extending from base in paratypes from French Guiana), labrum, mandible, malar area, and antennal scape; pedicel flagellum dark brown. Mesoscu-


Figures 13-14. Male of Chlerogelloides femoralis Engel et al. 13 Lateral habitus 14 Facial view.
tum, mesoscutellum, and metanotum metallic olive green, less shiny than on head; axilla dark brown with metallic reflections; tegula translucent brown; axillary sclerites brown, base of C+Sc honey yellow otherwise wing venation brown to dark brown; pleura honey yellow except mostly brown on hypoepimeral area, with weak metallic green highlights (almost imperceptible in most places); wing membranes hyaline, slightly and faintly infumate apically, with some iridescence depending on lighting.

Pubescence: Pubescence largely consisting of golden simple setae. Head with scattered, largely simple setae, those on supraclypeal area, vertex, gena, and postgena longer; setae dorso-apically on scape longer, between one-third and one-half DS, remainder much shorter; a few short, branched setae in lower paraocular area and surrounding upper border of supraclypeal area; gena with uniformly distributed branched setae, setae with branches arising from one side of rachis in apical two-thirds; setae along borders with compound eyes very short. Mesosomal setae generally simple except more plumose around pronotal lobe and surrounding propodeal spiracle; disc of mesoscutum with relatively short and sparse setae, shorter than those of mesepisternum, although denser than on the latter; disc of mesoscutellum with setae little longer than those of mesoscutum, distinctly longer along posterior margin; metanotum with yellowish, short, plumose setae intermixed with


Figures 15-22. Male terminalia of species of Chlerogelloides (15-18 Chlerogelloides simplex Engel and Brooks; 19-22 C. femoralis Engel et al.). $1 \mathbf{5}$ Hidden and fused metasomal sterna VII+VIII (in situ with capsule in figure 18) 16 Genital capsule, dorsal view 17 Genital capsule, lateral view 18 Genital capsule, ventral view (with hidden sterna VII + VIII in situ). 19 Hidden and fused sterna VII+VIII 20 Genital capsule, lateral view 21 Genital capsule, lateral view 22 Genital capsule, ventral view.
longer, branched, golden setae, laterally longer, about 1.5DS; lateral and posterior surfaces of propodeum with long (about 2DS), largely-simple, scattered setae, although less numerous than on mesoscutum. Leg pubescence typical for male Augochlorini except distal half of anterior surface of procoxa with dense, long, branched setae, such setae about
1.2DS; anterior area formed by carinae along ventral surface of mesobasitarsus glabrous and separate from posterior area covered by minute setae. Wing membranes uniformly pilose. Metasoma generally with sparsely-scattered, simple, long setae, on T1-T3 simple setae mostly distributed across discs, with apical margins glabrous, such setae varying from $1-1.5$ DS in length, setae becoming progressively longer on more apical segments, on T4-T7 with short, dense, plumose setae intermixed with long setae.
$q$ : Unknown.
Etymology. The specific epithet is taken from the Latin word nexosus, meaning "complicated", and is a reference to the complex morphology of this and other species in the genus.

Comments. A single female, collected in French Guiana with one of the males, is indistinguishable from that of C. simplex (specimen from Patawa, deposited in Brussels). It is possible that it is a female of C. nexosa, but given that definitive C. simplex is known from the same area we cannot be certain that it is a definitive female of the new species. Only further collecting in the region will be able to determine the correct association of females for this complex genus of bees.

## Key to species of Chlerogelloides

The present key is modified from that provided by Engel and Brooks (1999). Females are presently unknown for $C$. nexosa sp. n.

1 Males........................................................................................................... 2

- Females 4
2 Mesofemur greatly swollen and with one or two inner apical teeth (Figs. 4, 5); metallic reflections of head and mesosoma tending toward green (Figs 2, $3,13,14$ ); male terminalia as in figures $7-10$ or 19-223
- Mesofemur simple, unmodified (Fig. 6); metallic reflections of head and mesosoma tending toward blue (Figs 11, 12); gena lacking distinctive tuft of setae; face above level of antennae with minute punctures closely packed; apical quarter to one-third of clypeus yellow; axilla dark brown; male terminalia as in figures 15-18
C. simplex Engel \& Brooks

3 Mesotrochanter with strong inner projection (Fig. 4); gena with distinctive tuft of long, plumose setae; face above level of antennae with minute punctures widely scattered over glabrous integument; apical two-thirds of clypeus yellow (Fig. 14); axilla yellow
C. femoralis Engel et al.

- Mesotrochanter without strong inner projection (Fig. 5); gena without tuft of long, plumose setae; face above level of antennae with minute punctures closely packed; clypeus entirely but sometimes with extensive areas of brown extending from base (Fig. 3); axilla brownish.......................C. nexosa sp. n. Clypeus and basal area of propodeum yellow ......... C. femoralis Engel et al. Clypeus and basal area of propodeum brown
C. simplex Engel \& Brooks


## Discussion

The three known species of Chlerogelloides are all quite similar, immediately noticeable for their modified, elongate clypeus which is basally intruded upon by a deeply acute and projecting epistomal sulcus, such that the narrowed epistomal lobe nearly reaches the clypeal apex. In addition, the species share a short malar space, a pronotum in which the dorsal surface is expanded, and a serrate inner metatibial spur in males and females (Engel et al. 1997; Engel and Brooks 1999; Engel 2000). The bodies are largely yellow but with significantly regions of dark to brilliant metallic coloration, usually green but also blue and coppery (Figs. 2, 3, 11-14). When the genus was first described, the sole species known (C. femoralis) had males with considerably modified midlegs, particularly the mesotrochanter, mesofemur, mesotibia, and mesobasitarsus (Fig. 4). Some of these modifications are now known to be shared with C. nexosa sp. n., such as the greatly enlarged (although somewhat compressed along the anterior-posterior axis) mesofemora with ventral tubercles or teeth and about twice as long as wide, the inner ridges and apically depressed surfaces of the mesotibiae, and the concave inner surfaces of the mesobasitarsi (Fig. 5). The mesotrochanter of C. femoralis is strongly bent and has a strong inner tubercle (Fig. 4), while the same podite in C. nexosa sp. n. lacks such a prominent modification, at most showing a weak swelling (Fig. 5). The mesobasitarsus of C. femoralis is about as long as wide and somewhat triangular, while it is longer than wide and more rectangular in C. nexosa sp. n. In contrast, the midlegs of $C$. simplex are like those of other Augochlorini (Fig. 6), particularly the normal mesofemora which are about four times as long as wide. In C. nexosa sp. n. and C. femoralis the metallic reflections of the head and mesosoma tend to be green while in C. simplex such areas are more bluish, although green highlights are indeed present in the few known specimens. Males of $C$. nexosa sp. n. have the gena uniformly covered by plumose setae in which the branches arise from the rachis on one side in the apical two-thirds, while males of C. femoralis have such setae clustered into a distinctive tuft midway along the gena. Other differences between C. femoralis and C. nexosa sp. n. include the smaller ocellocular distance and narrower gena (by comparison to the width of the compound eye) in the latter species. Lastly, the terminalia of $C$. nexosa sp. n. tend to more closely resemble those of C. simplex rather than C. femoralis. Detailed descriptions of C. femoralis and C. simplex were given relatively recently by Engel et al. (1997) and Engel and Brooks (1999), and that material is not repeated herein.

At present the genus is known only by a meager diversity and relative paucity of material, despite the seemingly wide range of the lineage across South America. Accordingly, it is premature to attempt too contemplative of an investigation into the evolution of this genus, particularly given that the resulting three-taxon statement would have little explanatory power in the absence of more complete life-history or biological data for the constituent species. Nonetheless, if we presume that the modified midlegs of C. femoralis and C. nexosa sp. n. represent a derived feature indicating a close relationship between these two species, then C. simplex would appear to fall basal within the genus. This assumption seems safe for the moment given that such modifications of the midleg podites are not known in related or other genera of Augochlorini (Engel 2000). It would be significant to
discover the uses of these elaborate adaptations as used by the male during courtship and mating, and melittologists should be aware of these bees as they undertake observational studies in those regions where individuals are known to occur. Perhaps more interesting and feasible at this stage would be continued work on the relationship of the genus as a whole in relation to other lineages of Augochlorini. Engel and Brooks (1999) and Engel (2000) highlighted a putative relationship between Chlerogelloides and Chlerogella + Ischnomelissa. This hypothesis has not been supported by preliminary molecular work and Chlerogelloides does seem to occupy a rather isolated place among augochlorine genera, at least phenotypically. Intensive sampling is needed in order to increase the material available for the genus (for both molecular and morphological studies), more thoroughly document the distribution of its species, and to bring to light its presumably unique biology.

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## References

Beebe W (1925) Studies of a tropical jungle; one quarter of a square mile of jungle at Kartabo, British Guiana. Zoologica 6: 5-193.
Engel MS (2000) Classification of the bee tribe Augochlorini (Hymenoptera: Halictidae). Bulletin of the American Museum of Natural History 250: 1-89. doi: 10.1206/0003-0090(2000)250<0001:COTBTA>2.0.CO;2

Engel MS (2001) A monograph of the Baltic amber bees and evolution of the Apoidea (Hymenoptera). Bulletin of the American Museum of Natural History 259: 1-192. doi: 10.1206/0003-0090(2001)259<0001:AMOTBA>2.0.CO;2
Engel MS (2007) Two new augochlorine bees from Ecuador (Hymenoptera: Halictidae). Acta Entomologica Slovenica 15(1): 21-29. doi: 10.3897/zookeys.23.248
Engel MS (2009) Revision of the bee genus Chlerogella (Hymenoptera, Halictidae), Part I: Central American species. ZooKeys 23: 47-75.
Engel MS (2010a) Revision of the bee genus Chlerogella (Hymenoptera, Halictidae), Part II: South American species and generic diagnosis. ZooKeys 47: 1-100. doi: 10.3897/zookeys. 47.416
Engel MS (2010b) The bee genus Chlerogas in Bolivia (Hymenoptera, Halictidae). ZooKeys 46: 61-70. doi: 10.3897/zookeys.46.460
Engel MS, Brooks RW (1999) A new Chlerogelloides from French Guiana, with comments on the genus (Hymenoptera: Halictidae). Journal of the Kansas Entomological Society 72(2): 160-166.
Engel MS, Brooks RW (2002) A new bee of the genus Ischnomelissa, with a key to the known species (Hymenoptera: Halictidae). Entomological News 113(1): 1-5.
Engel MS, Gonzalez VH (2009) A new species of Chlerogas from the Andes of central Colombia (Hymenoptera: Halictidae). Caldasia 31(2): 441-447.
Engel MS, Brooks RW, Yanega D (1997) New genera and subgenera of augochlorine bees (Hymenoptera: Halictidae). Scientific Papers, Natural History Museum, University of Kansas 5: 1-21.
Moure JS (2007) Augochlorini Beebe, 1925. In: Moure JS, Urban D, Melo GAR (Eds) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region, 759-823. Sociedade Brasileira de Entomologia, Curitiba, xiv+1058pp. [Available and updated online at http:// www.moure.cria.org.br/catalogue (last accessed 17 April 2012)].
Moure JS, Sakagami SF (1962) As mamangabas sociais do Brasil (Bombus Latreille) (Hymenoptera, Apoidea). Studia Entomologica 5(1-4): 65-194.
Michener CD (2007) The Bees of the World [2 ${ }^{\text {nd }}$ Edition]. Johns Hopkins University Press, Baltimore, xvi+[i]+953 pp., +20 pls.
Rech AR, Coelho CP, Correa F da S, Carmo VS do, Cavalcante MC, Kanashiro M (In press) Aspectos da biologia reprodutiva pré-dispersiva de Cordia nodosa Lam. (Cordiaceae: Boraginales) na estação Ferreira Pena, Melgaço - Pará - Brasil. Curso de Polinização.

# A new species of Bolitoglossa (Amphibia, Caudata) from the Sierra de Juárez, Oaxaca, Mexico 

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#### Abstract

We describe a new species of Bolitoglossa (Nanotriton) from the Sierra de Juárez and Sierra Mixe of Oaxaca, Mexico. Bolitoglossa chinanteca sp. n. is distinguished from the three other species in the subgenus Nanotriton by its more robust body, by having substantial numbers of maxillary teeth and differences in relative head width, foot width, and limb length. The new species occurs in sympatry with Bolitoglossa (Nanotriton) rufescens at the type locality. The description of another species of salamander from the Sierra de Juárez is noteworthy, given the already high plethodontid salamander species richness of the region.


## Keywords

Caudata, Mexico, morphology, Plethodontidae, Oaxaca, taxonomy

## Introduction

The genus Bolitoglossa, with 117 described species (AmphibiaWeb 2011), is by far the largest genus within the order Caudata. It has the widest range of any tropical salamander genus, from the lowlands of southern Tamaulipas, Mexico to Brazil and Bolivia in

[^0]South America. The monophyly of Bolitoglossa is well supported on molecular (ParraOlea et al. 2004) as well as morphological grounds. The lack of a sublingual fold, short ceratohyals, partially or fully webbed feet, and fused distal tarsal 4 and 5 characterize all the species of the genus (Wake 1966; Wake and Elias 1983).

Parra-Olea et al. (2004) used mtDNA sequence data analyzed phylogenetically to subdivide Bolitoglossa into seven subgenera: Bolitoglossa, Eladinea, Magnadigita, Mayamandra, Nanotriton, Oaxakia, and Pachymandra. The subgenus Nanotriton comprises species previously included in the B. rufescens group: Bolitoglossa occidentalis Taylor 1941, B. rufescens Cope 1869, and the recently described B. nympha Campbell et al. 2010. The species of Nanotriton are small, short-tailed salamanders with small pad-like hands and weakly developed feet, all associated with paedomorphosis (Alberch 1983). These species occur in habitats ranging from sea-level lowland forests, to humid cloud forests up to 2000 m in elevation.

In this paper we describe a new species of the subgenus Nanotriton from the Sierra de Juárez and Sierra Mixe, Oaxaca, based on morphological differences from described species and DNA sequence differences from sympatric B. rufescens and the other two species in the subgenus. The new species is assigned to Bolitoglossa (Nanotriton) (ParraOlea et al. 2004) based on its relatively small body size, fully webbed, pad-like feet with little digital individuation, short tail, overall morphological similarity to other species in the subgenus, and phylogenetic placement with mitochondrial DNA sequence data.

## Materials and methods

External morphology was examined in 17 populations of all known species of Bolitoglossa (Nanotriton) (Table 1). These specimens represent most of the geographic range of the subgenus from the Atlantic coast of Mexico (Veracruz) to western Honduras. We took 14 measurements that reflect size and proportional shape of the salamanders: distance from snout to posterior end of vent (SVL), tail length (TL), snout to gular fold length (SG), head width at angle of jaw (HW), axilla-groin length (AG), forelimb length (FLL), hind limb length (HLL), shoulder width (SW), right foot width (RFW), head depth (HD), interorbital width (IO), internarial width (IN), tip of snout to anterior corner of eye (rostrum length, RL), diameter of eye opening (ED). Measurements were taken to the nearest 0.1 mm using vernier calipers. We also counted the number of costal grooves separating adpressed limbs (limb interval, LI). We counted total numbers of ankylosed vomerine (VT), premaxillary (PMT) and maxillary teeth (MT) under a dissecting microscope.

Species identifications of each population were based on geography and the allozyme results of Larson (1983). Bolitoglossa nympha, recently described from the Sierra de Caral on the Guatemala-Honduras border, is currently known only from the type locality (Campbell et al. 2010). The diagnosis for Bolitoglossa nympha relies largely on molecular characteristics, which are not currently available for most populations of the Bolitoglossa rufescens complex. In Larson's 1983 allozyme study, populations from Finca El Volcán, Guatemala, the San Pedro Sula area, Honduras and Santa Rosa del


Figure I. Map of the localities of Bolitoglossa (Nanotriton) used in the morphological study. Locality numbers correspond to those in Table 1. Green points represent B. chinanteca populations, pink points B. nympha populations, blue points B. occidentalis populations, and red points $B$. rufescens populations.

Copán, Honduras, which are the geographically closest populations included in our study to the type locality of $B$. nympha, cluster together in a distance-based phylogeny. For this reason, we tentatively treat these three populations as belonging to B. nympha. Definitive species identification of populations from eastern Guatemala and Honduras will require detailed molecular study of the complex.

Statistical analyses were run with the program JMP 8 (SAS Institute, Cary, NC, USA). Wilcoxon tests were used to test for differences between group means for selected variables. In order to test for sexual dimorphism within species, variables were tested for normality within each species using the Shapiro-Wilk test. For variables whose distribution did not differ significantly from the normal distribution, a t-test was used to compare the mean for males and females. A Wilcoxon test was used to compare means for males and females of each species for variables whose distributions differed significantly from normal. Significant differences in means between males and females of the same species were found for nearly all variables (see results), indicating that sexual dimorphism exists within these species, so all further analyses were performed separately for males and females.

Table I. Populations and numbers of individuals used in morphological analyses. Numbers of females and males at locality 2 are for B. chinanteca and B. rufescens, respectively.

| Species | Locality | No. females | No. males |
| :--- | :--- | :--- | :--- |
| Bolitoglossa chinanteca | 1) Vista Hermosa area, Oaxaca, Mexico | 5 | 3 |
| Bolitoglossa chinanteca, <br> Bolitoglossa rufescens | 2) 10.3 km S of Valle Nacional, Oaxaca, <br> Mexico | 2,1 | 3,0 |
| Bolitoglossa chinanteca | 3) Sierra Mixe, Oaxaca, Mexico | 1 | 0 |
| Bolitoglossa nympha | 4) Finca El Volcán, Alta Verapaz, <br> Guatemala | 5 | 16 |
| Bolitoglossa nympha | 5) Santa Rosa de Copán, Copán, Honduras | 3 | 7 |
| Bolitoglossa nympha | 6) San Pedro Sula area, Cortés, Honduras | 6 | 5 |
| Bolitoglossa occidentalis | 7) Cerro Baúl, Oaxaca, Mexico | 5 | 6 |
| Bolitoglossa occidentalis | 8) Copainala area, Tuxtla Gutiérrez, <br> Chiapas, Mexico | 10 | 9 |
| Bolitoglossa occidentalis | 9) Berriozabal, Chiapas, Mexico | 5 | 6 |
| Bolitoglossa occidentalis | 10) Tapachula area, Chiapas, Mexico | 7 | 20 |
| Bolitoglossa occidentalis | 11) Finca Santa Julia, San Marcos, <br> Guatemala | 20 | 20 |
| Bolitoglossa rufescens | 12) Cuautlapan, Veracruz, Mexico | 20 | 20 |
| Bolitoglossa rufescens | 13) Catemaco, Veracruz, Mexico | 8 | 19 |
| Bolitoglossa rufescens | 14) Sierra Mazateca, Oaxaca | 1 | 0 |
| Bolitoglossa rufescens | 15) Ocozocoautla area, Chiapas, Mexico | 2 | 3 |
| Bolitoglossa rufescens | 16) Ocosingo, Chiapas, Mexico | 1 | 3 |
| Bolitoglossa rufescens | 17) Palenque, Chiapas, Mexico | 4 | 6 |

Multivariate statistical analyses used all variables except LI, MT, and VT, which were not measured in the same units ( mm ) as the other variables. In order to remove the effect of body size, each variable was regressed against SVL, and the residuals from a linear fit with SVL were used in further analyses. Separate linear fits were used for males and females. Normality of the residuals for each variable was tested using the Shapiro-Wilk test. Given that Discriminant Function Analysis (DFA) can still be used when the assumption of multivariate normality is violated, particularly when the percent of correct classification is high (Klecka 1980), we performed a DFA using residuals from SVL of all variables except TL, which was missing for several individuals of the new species that had missing or regenerated tails.

Because one group (the new species) has a smaller sample size than the total number of variables measured (8 females, 6 males), a Principal Components Analysis (PCA) was used to reduce the dimensionality of the data. The PCA was performed using residuals of the following variables, which passed the normality test: males: SG, FLL, HLL, IO, HW, SW, RFW, ED; females: FLL, HLL, RL, IO, RFW, ED. A second DFA was then performed on the first three principal components.

Although a full molecular analysis of the subgenus Nanotriton is beyond the scope of the present work, several mitochondrial sequences were generated in order to compare
the new species to other members of its subgenus. We sequenced a specimen (paratype) of the undescribed species (IBH 22535), as well as a specimen of B. rufescens (IBH 22536) from the same locality and an individual of B. occidentalis (MVZ 194259) for the 16 S rRNA ( $16 \mathrm{~S}, 518 \mathrm{bp}$ ) and cytochrome b (cyt b, 809 bp ) mitochondrial genes using primers MVZ117 and MVZ98 (Palumbi 1996) for 16S and primers MVZ15 and MVZ16 (Moritz et al. 1992) for cytb. Reactions were run at $94^{\circ} \mathrm{C}$ for $2 \mathrm{~min}, 38$ cycles of $94^{\circ} \mathrm{C}$ for $30 \mathrm{~s}, 48^{\circ} \mathrm{C}$ for $30 \mathrm{~s}(16 \mathrm{~S})$ or $1 \mathrm{~min}(\mathrm{cytb}), 72^{\circ} \mathrm{C}$ for 1 min , with a final cycle at $72{ }^{\circ} \mathrm{C}$ for 8 min . We aligned these sequences with available sequences for B. rufescens (MVZ 194254) and B. nympha (MVZ 194333) from GenBank using the program MUSCLE 3.6 (Edgar 2004) and concatenated alignments for 16 S and cytb. We trimmed cytb sequences to a length of 645 bp to match those from GenBank. Individuals of Bolitoglossa mexicana (MVZ176838) and B. hartwegi (MVZ 263458) were used as outgroups for phylogenetic analysis. We used the program RAxML (Stamatakis 2006) to estimate a phylogeny with maximum likelihood under the GTR+G substitution model in order to determine the relationship of the new Sierra de Juárez species to other members of the subgenus Nanotriton. The data were partioned by gene (16S and cytb), and the cytochrome $b$ gene was partitioned by codon position. One thousand bootstrap replicates were performed to assess nodal support. Pairwise distances between species were calculated using PAUP* v4.0 (Swofford 2003). Additionally, we compared the genetic distance between an individual of the new species from the Sierra Mixe (MZFC 16085), for which only a 16 S sequence was available in GenBank, to our sample from the Sierra de Juárez.

## Results

Means, standard deviations, and ranges of all measurements and tooth counts are given in Table 2. Our new species showed significant sexual dimorphism for only two variables (HLL, RL), although this result may be partially due to small sample size. Males and females of the other species had significantly different means for the following variables: Bolitoglossa nympha - SVL, SG, FLL, HLL, RL, AG, IO, IN, HW, SW, RFW, HD, and VT; B. occidentalis - SVL, AG, IO, SW, MT; B. rufescens - AG, IO, IN, HW, SW, HD.

The Discriminant Function Analysis (DFA) for females using three principal components constructed from residuals from SVL of variables that passed normality tests correctly classified all but one individual of the new species (Table 3). Five of 14 individuals of $B$. nympha were misclassified as $B$. occidentalis, 23 of 46 individuals of $B$. occidentalis were misclassified (12 as B. nympha and 11 as B. rufescens), and 19 of 36 individuals of B. rufescens were misclassified ( 1 as $B$. chinanteca, 8 as B. nympha, 10 as $B$. occidentalis). For males, four of five individuals of the new species were classified correctly while many individuals of the other species were misclassified (Table 3). The number of individuals classified per group differs from the total number of individuals per group because some individuals lack data for measurements such as TL, and
Table 2. Mean $\pm$ SD and range for morphological measurements. Number of individuals is indicated when less than the total number for a species.

|  | Bolitoglossa chinanteca |  | Bolitoglossa nympha |  | Bolitoglossa occidentalis |  | Bolitoglossa rufescens |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Measurement | Females $N=8$ | Males $N=6$ | Females $N=14$ | Males $N=28$ | Females $N=47$ | Males $N=61$ | Females $N=36$ | Males $N=52$ |
| SVL | $\begin{aligned} & 32.3 \pm 5.41 \\ & (28.4-43.4) \end{aligned}$ | $\begin{aligned} & 37.6 \pm 3.19 \\ & (33.4-41.2) \end{aligned}$ | $\begin{aligned} & 37.8 \pm 3.25 \\ & (33.0-43.2) \end{aligned}$ | $\begin{aligned} & 32.8 \pm 4.40 \\ & (23.0-37.9) \end{aligned}$ | $\begin{aligned} & 35.9 \pm 4.86 \\ & (26.2-45.6) \\ & \hline \end{aligned}$ | $\begin{aligned} & 33.7 \pm 2.93 \\ & (25.9-38.9) \end{aligned}$ | $\begin{aligned} & 32.1 \pm 2.51 \\ & (25.9-37.5) \end{aligned}$ | $\begin{aligned} & 31.1 \pm 2.34 \\ & (25.6-37.2) \end{aligned}$ |
| TL | $\begin{gathered} 28.1 \pm 5.46 \\ (18.3-34.0) \\ N=6 \end{gathered}$ | $\begin{aligned} & 29.1 \pm 4.25 \\ & (24.0-35.5) \end{aligned}$ | $\begin{gathered} 27.5 \pm 2.74 \\ (23.9-32.3) \\ N=11 \end{gathered}$ | $\begin{gathered} 25.4 \pm 4.67 \\ (15.0-33.2) \\ N=25 \end{gathered}$ | $\begin{gathered} 25.2 \pm 5.04 \\ (14.7-32.6) \\ N=45 \end{gathered}$ | $\begin{gathered} 24.8 \pm 3.00 \\ (19.0-31.9) \\ N=59 \end{gathered}$ | $\begin{gathered} 22.3 \pm 2.39 \\ (18.5-27.2) \\ N=35 \end{gathered}$ | $\begin{gathered} 22.5 \pm 3.14 \\ (17.7-34.0) \\ N=49 \end{gathered}$ |
| SG | $\begin{aligned} & 9.3 \pm 1.12 \\ & (7.7-10.5) \end{aligned}$ | $\begin{aligned} & 9.8 \pm 0.81 \\ & (8.8-11.1) \end{aligned}$ | $\begin{aligned} & 9.2 \pm 0.71 \\ & (8.0-10.3) \end{aligned}$ | $\begin{gathered} 8.2 \pm 0.87 \\ (6.4-9.5) \end{gathered}$ | $\begin{aligned} & 8.9 \pm 1.09 \\ & (6.6-11.5) \end{aligned}$ | $\begin{aligned} & 8.58 \pm 0.67 \\ & (7.1-10.2) \\ & \hline \end{aligned}$ | $\begin{gathered} 8.1 \pm 0.58 \\ (6.5-9.3) \end{gathered}$ | $\begin{gathered} 8.1 \pm 0.55 \\ (6.6-9.1) \\ \hline \end{gathered}$ |
| HW | $\begin{gathered} 6.1 \pm 0.79 \\ (5.1-7.1) \\ \hline \end{gathered}$ | $\begin{gathered} 6.3 \pm 0.52 \\ (5.7-6.9) \\ \hline \end{gathered}$ | $\begin{gathered} 5.6 \pm 0.40 \\ (4.7-6.0) \\ \hline \end{gathered}$ | $\begin{gathered} 5.0 \pm 0.58 \\ (3.8-6.2) \\ \hline \end{gathered}$ | $\begin{gathered} 5.8 \pm 0.80 \\ (4.2-7.2) \\ \hline \end{gathered}$ | $\begin{gathered} 5.4 \pm 0.47 \\ (4.2-6.5) \\ \hline \end{gathered}$ | $\begin{gathered} 5.1 \pm 0.34 \\ (4.2-5.9) \end{gathered}$ | $\begin{gathered} 5.0 \pm 0.33 \\ (4.3-5.6) \\ \hline \end{gathered}$ |
| HD | $\begin{gathered} 2.9 \pm 0.42 \\ (2.5-3.8) \\ \hline \end{gathered}$ | $\begin{gathered} 2.9 \pm 0.53 \\ (2.4-3.9) \\ \hline \end{gathered}$ | $\begin{gathered} 2.6 \pm 0.19 \\ (2.3-3.0) \\ \hline \end{gathered}$ | $\begin{gathered} 2.4 \pm 0.22 \\ (1.9-2.7) \\ \hline \end{gathered}$ | $\begin{gathered} 2.6 \pm 0.30 \\ (1.9-3.4) \end{gathered}$ | $\begin{gathered} 2.6 \pm 0.22 \\ (2.1-3.4) \\ \hline \end{gathered}$ | $\begin{gathered} 2.5 \pm 0.26 \\ (2.1-3) \\ \hline \end{gathered}$ | $\begin{gathered} 2.4 \pm 0.24 \\ (2.0-3.3) \\ \hline \end{gathered}$ |
| IO | $\begin{gathered} 3.4 \pm 0.44 \\ (2.7-4.1) \end{gathered}$ | $\begin{gathered} 3.5 \pm 0.22 \\ (3.4-3.9) \\ N=5 \end{gathered}$ | $\begin{gathered} 3.2 \pm 0.23 \\ (2.9-3.7) \end{gathered}$ | $\begin{gathered} 2.9 \pm 0.39 \\ (2.0-3.5) \end{gathered}$ | $\begin{gathered} 3.1 \pm 0.36 \\ (2.2-4.1) \end{gathered}$ | $\begin{gathered} 3.0 \pm 0.30 \\ (2.3-4.0) \end{gathered}$ | $\begin{gathered} 3.0 \pm 0.28 \\ (2.3-3.5) \end{gathered}$ | $\begin{gathered} 2.9 \pm 0.23 \\ (2.5-3.4) \end{gathered}$ |
| IN | $\begin{gathered} 2.0 \pm 0.33 \\ (1.5-2.5) \end{gathered}$ | $\begin{gathered} 2.3 \pm 0.13 \\ (2.1-2.5) \\ N=5 \end{gathered}$ | $\begin{gathered} 1.6 \pm 0.19 \\ (1.4-2.0) \end{gathered}$ | $\begin{gathered} 1.6 \pm 0.30 \\ (1.0-2.0) \end{gathered}$ | $\begin{gathered} 1.59 \pm 0.33 \\ (1.0-2.3) \end{gathered}$ | $\begin{gathered} 1.6 \pm 0.26 \\ (1.1-2.2) \end{gathered}$ | $\begin{gathered} 1.47 \pm 0.13 \\ (1.2-1.8) \end{gathered}$ | $\begin{gathered} 1.4 \pm 0.23 \\ (1.0-2.0) \end{gathered}$ |
| ED | $\begin{gathered} 2.1 \pm 0.28 \\ (1.7-2.4) \end{gathered}$ | $\begin{gathered} 1.9 \pm 0.17 \\ (2.2-1.8) \\ N=5 \end{gathered}$ | $\begin{gathered} 1.8 \pm 0.15 \\ (1.5-2.0) \end{gathered}$ | $\begin{gathered} 1.7 \pm 0.27 \\ (1.2-2.3) \end{gathered}$ | $\begin{gathered} 1.7 \pm 0.26 \\ (1.2-2.2) \end{gathered}$ | $\begin{aligned} & 1.7 \pm 0.24 \\ & (1.3-2.2) \end{aligned}$ | $\begin{gathered} 1.7 \pm 0.21 \\ (1.4-2.1) \end{gathered}$ | $\begin{gathered} 1.7 \pm 0.22 \\ (1.4-2.1) \end{gathered}$ |
| RL | $\begin{gathered} 2.6 \pm 0.32 \\ (2.2-3.1) \end{gathered}$ | $\begin{gathered} 2.9 \pm 0.21 \\ (2.6-3.2) \\ N=5 \end{gathered}$ | $\begin{gathered} 2.4 \pm 0.23 \\ (2.0-2.7) \end{gathered}$ | $\begin{gathered} 2.2 \pm 0.32 \\ (1.5-2.7) \end{gathered}$ | $\begin{gathered} 2.2 \pm 0.32 \\ (1.4-3.0) \end{gathered}$ | $\begin{gathered} 2.2 \pm 0.19 \\ (1.9-2.8) \end{gathered}$ | $\begin{gathered} 2.1 \pm 0.17 \\ (1.5-2.3) \end{gathered}$ | $\begin{gathered} 2.1 \pm 0.22 \\ (1.8-3.0) \end{gathered}$ |
| SW | $\begin{gathered} 4.8 \pm 0.75 \\ (3.4-5.5) \end{gathered}$ | $\begin{gathered} 4.4 \pm 0.28 \\ (4.2-4.9) \\ \hline \end{gathered}$ | $\begin{gathered} 4.4 \pm 0.40 \\ (3.9-5.1) \end{gathered}$ | $\begin{gathered} 3.9 \pm 0.47 \\ (3.0-4.8) \\ \hline \end{gathered}$ | $\begin{gathered} 4.2 \pm 0.54 \\ (3.0-5.5) \end{gathered}$ | $\begin{gathered} 3.9 \pm 0.41 \\ (2.6-4.6) \end{gathered}$ | $\begin{gathered} 3.8 \pm 0.42 \\ (3.0-4.6) \\ \hline \end{gathered}$ | $\begin{gathered} 3.5 \pm 0.30 \\ (2.9-4.2) \\ \hline \end{gathered}$ |
| AG | $\begin{aligned} & 18.2 \pm 3.29 \\ & (13.8-23.6 \end{aligned}$ | $\begin{gathered} 19.3 \pm 2.03 \\ (16.7-22.0) \\ \hline \end{gathered}$ | $\begin{aligned} & 20.3 \pm 3.44 \\ & (16.7-29.2) \\ & \hline \end{aligned}$ | $\begin{gathered} 16.9 \pm 2.63 \\ (11.6-20.7) \\ \hline \end{gathered}$ | $\begin{aligned} & 18.7 \pm 3.01 \\ & (12.6-24.5) \end{aligned}$ | $\begin{aligned} & 16.9 \pm 1.76 \\ & (13.2-19.7) \end{aligned}$ | $\begin{aligned} & 16.2 \pm 1.61 \\ & (12.4-19.6) \\ & \hline \end{aligned}$ | $\begin{aligned} & 15.4 \pm 2.28 \\ & (11.6-28.1) \end{aligned}$ |


|  | Bolitoglossa chinanteca |  | Bolitoglossa nympha |  | Bolitoglossa occidentalis |  | Bolitoglossa rufescens |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| FLL | $\begin{gathered} 8.4 \pm 1.04 \\ (6.9-9.8) \end{gathered}$ | $\begin{gathered} 8.7 \pm 0.67 \\ (8.0-9.9) \end{gathered}$ | $\begin{gathered} 6.9 \pm 0.68 \\ (5.7-7.9) \end{gathered}$ | $\begin{gathered} 6.3 \pm 1.02 \\ (3.8-7.5) \end{gathered}$ | $\begin{gathered} 7.1 \pm 1.22 \\ (4.7-9.6) \\ \hline \end{gathered}$ | $\begin{gathered} 7.0 \pm 0.95 \\ (5.3-9.7) \\ \hline \end{gathered}$ | $\begin{gathered} 6.4 \pm 0.63 \\ (5.2-7.9) \end{gathered}$ | $\begin{gathered} 6.5 \pm 0.59 \\ (5.2-8.0) \end{gathered}$ |
| HLL | $\begin{gathered} 8.0 \pm 0.90 \\ (6.9-9.3) \end{gathered}$ | $\begin{aligned} & 9.3 \pm 0.94 \\ & (8.6-10.8) \end{aligned}$ | $\begin{gathered} 7.2 \pm 0.74 \\ (5.7-8.2) \\ \hline \end{gathered}$ | $\begin{gathered} 6.5 \pm 1.00 \\ (3.8-7.7) \\ \hline \end{gathered}$ | $\begin{aligned} & 7.2 \pm 1.39 \\ & (4.7-10.2) \end{aligned}$ | $\begin{gathered} 7.0 \pm 1.07 \\ (4.3-9.5) \end{gathered}$ | $\begin{gathered} 6.5 \pm 0.61 \\ (5.4-7.9) \end{gathered}$ | $\begin{gathered} 6.4 \pm 0.58 \\ (5.1-7.6) \end{gathered}$ |
| RFW | $\begin{gathered} 3.6 \pm 0.73 \\ (2.6-4.7) \\ \hline \end{gathered}$ | $\begin{gathered} 3.9 \pm 0.45 \\ (3.2-4.4) \\ \hline \end{gathered}$ | $\begin{gathered} 3.4 \pm 0.42 \\ (2.8-4.3) \\ \hline \end{gathered}$ | $\begin{gathered} 3.0 \pm 0.46 \\ (1.7-3.6) \end{gathered}$ | $\begin{gathered} 3.3 \pm 0.61 \\ (2.2-4.4) \\ \hline \end{gathered}$ | $\begin{gathered} 3.2 \pm 0.41 \\ (2.1-4.0) \\ \hline \end{gathered}$ | $\begin{gathered} 2.8 \pm 0.33 \\ (1.8-3.4) \end{gathered}$ | $\begin{gathered} 2.8 \pm 0.36 \\ (2.1-3.6) \end{gathered}$ |
| LI | $\begin{gathered} 1.9 \pm 0.35 \\ (1-2) \\ \hline \end{gathered}$ | $\begin{gathered} 1.4 \pm 0.80 \\ (0-2) \\ \hline \end{gathered}$ | $\begin{gathered} 2.7 \pm 0.52 \\ (2-4) \\ \hline \end{gathered}$ | $\begin{gathered} 2.2 \pm 0.67 \\ (1-4) \\ \hline \end{gathered}$ | $\begin{gathered} 3.3 \pm 0.58 \\ (2-4) \\ \hline \end{gathered}$ | $\begin{gathered} 2.8 \pm 0.66 \\ (2-5) \end{gathered}$ | $\begin{gathered} 2.6 \pm 0.70 \\ (0.5-4) \\ \hline \end{gathered}$ | $\begin{gathered} 2.0 \pm 0.58 \\ (1-3) \\ \hline \end{gathered}$ |
| VT | $\begin{gathered} 24.6 \pm 8.10 \\ (11-39) \\ \hline \end{gathered}$ | $\begin{gathered} 22.5 \pm 2.26 \\ (19-25) \\ \hline \end{gathered}$ | $\begin{gathered} 19.6 \pm 3.77 \\ (14-28) \end{gathered}$ | $\begin{gathered} 16.3 \pm 4.50 \\ (10-25) \end{gathered}$ | $\begin{gathered} 20.5 \pm 5.25 \\ (12-34) \\ \hline \end{gathered}$ | $\begin{gathered} 17.8 \pm 5.88 \\ (6-32) \\ \hline \end{gathered}$ | $\begin{gathered} 15.3 \pm 4.76 \\ (5-26) \end{gathered}$ | $\begin{gathered} 15.9 \pm 14.2 \\ (6-33) \end{gathered}$ |
| PMT | $\begin{gathered} 3.3 \pm 1.37 \\ (2-6) \\ N=6 \\ \hline \end{gathered}$ | $\begin{gathered} 2.5 \pm 1.29 \\ (1-4) \\ N=4 \\ \hline \end{gathered}$ | $\begin{gathered} 0.7 \pm 0.83 \\ (0-2) \end{gathered}$ | $\begin{gathered} 2.4 \pm 0.92 \\ (1-4) \end{gathered}$ | $\begin{gathered} 1.4 \pm 1.76 \\ (0-9) \end{gathered}$ | $\begin{gathered} 1.4 \pm 1.13 \\ (0-4) \end{gathered}$ | $\begin{gathered} 1.8 \pm 1.00 \\ (0-4) \end{gathered}$ | $\begin{gathered} 1.8 \pm 0.80 \\ (1-4) \end{gathered}$ |
| MT | $\begin{gathered} 23.1 \pm 10.8 \\ (9-40) \end{gathered}$ | $\begin{gathered} 29.8 \pm 10.68 \\ (21-49) \end{gathered}$ | $\begin{gathered} 0 \\ (0) \end{gathered}$ | $\begin{gathered} 0 \\ (0) \end{gathered}$ | $\begin{gathered} 17.0 \pm 10.40 \\ (1-42) \end{gathered}$ | $\begin{gathered} 11.4 \pm 9.06 \\ (0-42) \\ N=60 \end{gathered}$ | $\begin{gathered} 1.4 \pm 2.91 \\ (0-10) \\ N=35 \end{gathered}$ | $\begin{gathered} 3.6 \pm 5.72 \\ (0-20) \\ N=51 \end{gathered}$ |

Table 3. Discriminant Function Analysis (DFA) results from principal components constructed from residuals of variables that passed normality tests. Rows represent actual species assignments and columns represent predicted group membership from DFA.

| Females | B. chinanteca | B. nympha | B. occidentalis | B. rufescens |
| :--- | :---: | :---: | :---: | :---: |
| B. chinanteca | 7 | 0 | 1 | 0 |
| B. nympha | 0 | 9 | 5 | 0 |
| B. occidentalis | 1 | 12 | 23 | 11 |
| B. rufescens | 1 | 8 | 10 | 17 |
| Males | B. chinanteca | B. nympha | B. occidentalis | B. rufescens |
| B. chinanteca | 5 | 0 | 0 | 0 |
| B. nympha | 1 | 22 | 3 | 2 |
| B. occidentalis | 0 | 10 | 38 | 11 |
| B. rufescens | 3 | 1 | 13 | 35 |

the DFA classifies only individuals with data for all included variables. Using residuals from SVL of all variables except TL, misclassification rates were lower (Table 4). For females, all individuals of the new species were classified correctly, and only one individual of $B$. nympha was misclassified. For males, all individuals of the new species were classified correctly, while misclassification was higher for the other species (Table 4).

The maximum likelihood mitochondrial gene tree places $B$. chinanteca as the sister taxon of Bolitoglossa occidentalis with strong support (BS=99) (Fig. 2). The GTR distance between individuals of the new species (IBH 22535) and B. rufescens from the Sierra de Juárez is 0.08 for 16 S and 0.21 for cyt $b$. The two samples of $B$. chinanteca from the type locality and the Sierra Mixe have a GTR distance of only 0.004 for 16 S .

Based on the correct classification of nearly all individuals of the new species from the Sierra de Juárez and Sierra Mixe, as well as several differences in external morphology and tooth counts from other species of Bolitoglossa (Nanotriton) and differences in mtDNA sequence data, these individuals represent an undescribed species. Type specimens are deposited in the Colección Nacional de Anfibios y Reptiles, Instituto de Biología, Universidad Nacional Autónoma de México (IBH).

## Bolitoglossa (Nanotriton) chinanteca sp. n.

urn:lsid:zoobank.org:act:ADAB4FB3-5B4A-4487-B254-EF9E481013B3
http://species-id.net/wiki/Bolitoglossa_chinanteca
Figure 3A-3I
Bolitoglossa occidentalis (in part). Duellman, 1960.
Bolitoglossa rufescens (in part). Larson, 1983.
Bolitoglossa rufescens. Campbell et al., 2010. Fig. 28A

Vernacular names. Chinanteca Salamander, Salamandra chinanteca

Table 4. Discriminant Function Analysis (DFA) results from residuals from SVL for all variables except TL. Rows represent actual species assignments and columns represent predicted group membership from DFA

| Females | B. chinanteca | B. nympha | B. occidentalis | B. rufescens |
| :--- | :---: | :---: | :---: | :---: |
| B. chinanteca | 8 | 0 | 0 | 0 |
| B. nympha | 0 | 13 | 0 | 1 |
| B. occidentalis | 0 | 4 | 33 | 10 |
| B. rufescens | 0 | 1 | 13 | 22 |
| Males | B. chinanteca | B. nympha | B. occidentalis | B. rufescens |
| B. chinanteca | 5 | 0 | 0 | 0 |
| B. nympha | 1 | 22 | 3 | 2 |
| B. occidentalis | 0 | 10 | 38 | 13 |
| B. rufescens | 3 | 1 | 13 | 35 |

Holotype. Colección Nacional de Anfibios y Reptiles IBH 24708, field number SMR1401, an adult female from 10.3 km south (by rd) of center of Valle Nacional on Hwy. 175, Sierra de Juárez, Oaxaca, Mexico, 676 m elevation, $17.72390^{\circ} \mathrm{N}, 96.32100^{\circ}$ W (WGS84 datum), collected by Sean M. Rovito and Dana Lee on 26 October, 2010.

Paratypes. Thirteen specimens, all from Oaxaca, Mexico. 7 females: Sierra de Juárez: IBH 24709, same locality data as holotype; KU 136428, 4.6 km N Vista Hermosa; KU 86616-86617, Villa Hermosa [=Vista Hermosa]; MZFC 5323, Vista Hermosa; MVZ 131152, along Mexico Hwy. 175, vicinity of Vista Hermosa, Distrito Ixtlán; Sierra Mixe: MZFC 16085, Carretera Coconales-Zacatepec; 6 males: Sierra de Juárez: IBH 22535, IBH 24711, IBH 24712, same locality data as holotype. KU 86618, Villa Hermosa [=Vista Hermosa]; UCM 52439, UMMZ 119647, Vista Hermosa.

## Referred specimens. None.

Diagnosis. Distinguished from species of all other genera of Neotropical salamanders by the lack of a sublingual fold. Distinguished from species of Bolitoglossa (Magnadigita) and Bolitoglossa (Oaxakia) (Parra-Olea et al. 2004) by the presence of fully webbed, pad-like feet and smaller size. Distinguished from species of Bolitoglossa (Pachymandra) and Bolitoglossa (Bolitoglossa) by smaller size, smaller hands and feet, and shorter tail, from species of Bolitoglossa (Mayamandra) by less broad feet, and from Bolitoglossa (Eladinea) by having a complex tail base in which the transverse processes of the first caudal vertebrae extend forward and cross those of the more anterior vertebra (Parra-Olea et al. 2004). Distinguished from all species of Bolitoglossa (Nanotriton) by more robust body. Distinguished from $B$. nympha by the presence of maxillary teeth, a relatively wider head (HW/SVL females: B. chinanteca: $0.17 \pm 0.018$ vs. B. nympha $0.15 \pm 0.0063$, Wilcoxon test, $\mathrm{Z}=-3.44, \mathrm{p}=0.0006$; males: B. chinanteca: $0.17 \pm 0.010$ vs. $B$. nympha $0.15 \pm 0.008$, Wilcoxon test, $Z=-2.78, p=0.0055$ ), relatively longer forelimbs (FLL/ SVL females: B. chinanteca: $0.24 \pm 0.014$ vs $B$. nympha: $0.18 \pm 0.010$, Wilcoxon test, Z $=-3.79, \mathrm{p}=0.0002$; males: B. chinanteca: $0.24 \pm 0.0067$ vs. B. nympha: $0.19 \pm 0.014$, Wilcoxon test, $\mathrm{Z}=-3.77, \mathrm{p}=0.0002$ ), and relatively wider feet (RFW/SVL females: $B$. chinanteca: $0.10 \pm 0.0081$ vs $B$. nympha $0.089 \pm 0.0077$, Wilcoxon test., $Z=-2.70$, p


Figure 2. Maximum likelihood gene tree of $16 \mathrm{~S}+$ cytb genes. Numbers above branches represent support values from 1000 bootstrap replicates.
$=0.0070$; males: B. chinanteca: $0.10 \pm 0.0009$ vs B. nympha: $0.09 \pm 0.073$, Wilcoxon test, $\mathrm{Z}=-2.87, \mathrm{p}=0.0041$ ). Distinguished from $B$. occidentalis by having more maxillary teeth in males (B. chinanteca: $29.8 \pm 10.7$ vs. B. occidentalis: $11.4 \pm 9.1$; Wilcoxon test, $\mathrm{Z}=-3.43, \mathrm{p}=0.0006$ ), a wider head in females (HW/SVL B. chinanteca: $0.17 \pm$ 0.018 vs. B. occidentalis $0.16 \pm 0.0054$, Wilcoxon test, $Z=-2.85, \mathrm{p}=0.0043$ ), relatively longer forelimbs (FLL/SVL females: B. chinanteca: $0.24 \pm 0.014$ vs B. occidentalis: $0.20 \pm$ 0.017, Wilcoxon test, $\mathrm{Z}=-4.40, \mathrm{p}<0.0001$; males: $B$. chinanteca: $0.24 \pm 0.0067$ vs. $B$. occidentalis: $0.21 \pm 0.017$, Wilcoxon test, $Z=-3.55, \mathrm{p}=0.0004$ ), and relatively wider feet in females (RFW/SVL B. chinanteca: $0.10 \pm 0.0081$ vs B. occidentalis: $0.092 \pm 0.0074$, Wilcoxon test., $\mathrm{Z}=-2.14, \mathrm{p}=0.0326$ ). Distinguished from $B$. rufescens by having more maxillary teeth (females: B. chinanteca: $23.1 \pm 10.8$ vs. B. rufescens: $1.4 \pm 2.9$, Wilcoxon test, $\mathrm{Z}=4.19$, $\mathrm{p}<0.0001$; males: B. chinanteca: $29.8 \pm 10.7$ vs. $B$. rufescens: $3.6 \pm 5.7$, Wilcoxon test, $\mathrm{Z}=6.50, \mathrm{p}<0.0001$ ), relatively longer forelimbs (females: B. chinanteca: $0.24 \pm 0.014$ vs $B$. rufescens: $0.20 \pm 0.015$, Wilcoxon test, $Z=-4.31, \mathrm{p}<0.0001$; males:


Figure 3. Photographs of the live and preserved holotype. A Holotype of Bolitoglossa chinanteca B Holotype of $B$. chinanteca with a sympatric individual of B. rufescens $\mathbf{C}$ Dorsum and $\mathbf{D}$ venter of preserved holotype E Ventral view of holotype before preservation, showing color in life $\mathbf{F}$ Right hand, $\mathbf{G}$ right foot $\mathbf{H}$ gular region and I side view of head of preserved holotype. J Photograph of the type locality of $B$. chinanteca, including banana plants where the type series was collected. All photographs by S. M. Rovito.
B. chinanteca: $0.24 \pm 0.0067$ vs. B. rufescens: $0.21 \pm 0.015$, Wilcoxon test, $Z=-3.55, \mathrm{p}$ $=0.0004$ ), relatively wider feet (RFW/SVL females: B. chinanteca: $0.10 \pm 0.0081$ vs $B$. rufescens: $0.088 \pm 0.0079$, Wilcoxon test., $\mathrm{Z}=-3.24, \mathrm{p}=0.0012$; males: B. chinanteca: $0.10 \pm 0.0009$ vs $B$. rufescens: $0.09 \pm 0.0074$, Wilcoxon test, $Z=-3.03, \mathrm{p}=0.0025$ ), and a relatively wider head in females (HW/SVL B. chinanteca: $0.17 \pm 0.018$ vs. B. rufescens $0.16 \pm 0.0075$, Wilcoxon test, $\mathrm{Z}=-2.81, \mathrm{p}=0.0049$ ).

Description of the holotype. A large adult female (SVL 37.2). Head broad (HW/ SVL 0.15); snout truncate; eyes weakly protuberant, not visible when viewed from below. Maxillary teeth numerous ( 40 maxillary teeth), 6 premaxillary teeth anterior to line of maxillary teeth, do not pierce lip. Vomerine teeth numerous (29), extending in an irregular row to below the center of the internal nares, forming a more numerous patch near internal nares. Labial protruberances moderately developed. Tail fairly rectangular at base, becoming more rounded only at tip and tapering more sharply on posterior one-third; very weakly constricted at base; relatively short (SVL/TAL 0.78). Limbs relatively short (FLL/SLV 0.24, HLL/SVL 0.22); adpressed limbs separated by approximately 2 costal folds. Hands and feet strongly webbed, with only digit 3 emerging from web. Digits poorly defined except near distal tips; third digit on hands and feet pointed, others rounded; subterminal pad not evident; digits in order of increasing length I-II-IV-III on hands and I-V-II $\approx$ IV-III on feet.

Measurements (in mm), limb interval and tooth counts of the holotype. SVL 37.2; HW 5.6; SG 9.8; HD 2.8; eyelid length 2.5 ; eyelid width 1.6; eye-nostril distance 2.0; ED 1.8; IO 3.8; IN 2.2; RL 3.0; snout to forelimb 10.6; snout to anterior angle of vent 34.2; AG 19.3; TL 29.2; tail width at base 3.0; tail depth at base 2.8; FLL 8.8; HLL 8.3; width of right hand 2.8; RFW 3.8; length of third toe 0.6 ; length of fifth toe 0.2 ; maximum nostril diameter 0.4 ; SW 5.1. Limb interval 2. Maxillary teeth 40 ; premaxillary teeth 6 ; vomerine teeth 29 .

Coloration (in life) of the holotype (Fig. 3A, 3B, 3E). Dorsum nearly uniform orange-brown with scattered darker brown specks. Dorsal surface of head slightly darker brown between interorbital region and dorsal midline behind eyes, forming a triangle of darker coloration. Rostrum pale brown. Iris coppery. Labial surfaces and sides of head to insertion of forelimb pale brown with tiny cream spots. Dorsal surface of tail similar to dorsum. Dorsal surface of legs, lateral surfaces of body and tail brown with tiny pale flecks scattered throughout. Gular surface pale with cream and brown mottling. Ventral surface pale brown with fine cream mottling. Underside of tail and limbs pale brown with tiny cream and darker brown specks throughout. Underside of feet pale brown.

Coloration (in alcohol) of the holotype. Dorsum and dorsal surface of tail dark golden brown with scattered dark brown specks. Head and upper surface of limbs brown. Upper surface of feet golden brown. Sides of body and tail, and head greybrown with scattered pale flecks. Gular region, underside of forelimbs, and anterior portion of venter (to approximately 2 costal grooves past insertion of forelimbs) cream colored with light brown mottling. Brown mottling more extensive on posterior portion of venter, underside of tail, and underside of hind limbs. Underside of hands pale, underside of feet slightly darker brown.

Color variation. Several of the paratypes exhibit lighter grey dorsal coloration with more dark brown or black specks in alcohol. MZFC 21178 has a lighter reddish brown dorsum, becoming lighter yellow-brown towards the sides of the body, with numerous dark brown flecks throughout. MZFC 21178 has a more yellowish venter, with extensive brown mottling, while IBH 22523 has a darker brown venter with some pale yellow mottling, and a yellowish gular region with brown mottling.

Osteology. A radiograph of a single adult paratype (UMMZ 119647) shows that the species has osteology typical of Nanotriton. The hands and feet bear foreshortened digits that taper strongly to their tips. The terminal phalanges are irregular in shape and even number, with a maximal formula of 1-2-3-2 and 1-2-3-2-2. The skull is well formed and has a small dorsal fontanelle between the frontal and parietal bones. The nasal bones are well formed and relatively protuberant from the rest of the skull. Prefrontal bones appear to be present. The preorbital processes of the vomer are long and relatively straight. The vertebral column includes an atlas, 14 trunk, one sacral, two caudosacral and 27 caudal vertebrae. The first caudal vertebra has very elongate transverse processes that arise near the anterior end of the vertebra and extend sharply anterolaterally, strongly overlapping the processes of the last caudosacral vertebra. The long process of the first caudal is bifurcated near its base on one side but less evidently so on the other.

Distribution. This species is known from the Sierra de Juárez, between the small settlement of Vista Hermosa (at approximately 1500 m elevation) and the type locality to the north, along Hwy. 175, as well as from the Sierra Mixe, near the town of Santiago Zacatepec. The two known localities are approximately 70 km (by air) apart. The species presumably occurs on the Atlantic slopes of the Sierra de Juárez and the Sierra Mixe between known populations, and perhaps more widely in the Sierra Mixe.

Natural History. All specimens of Bolitoglossa chinanteca for which information is available were collected in the axils of banana plants during the day, and on vegetation at night. The species is presumably arboreal, like other members of the subgenus Nanotriton.

Etymology. This species is named after the Chinanteco people from the municipalities of Santiago Comaltepec and San Pedro Yolox (Sierra de Juárez) in the Chinantla region of Oaxaca, where most specimens were collected. The language spoken in Santiago Comaltepec is also called Chinanteco.

## Discussion

The Bolitoglossa rufescens group (subgenus Nanotriton, following Parra-Olea et al., 2004) long included only two species (B. rufescens and B. occidentalis) (the taxon Bolitoglossa bilineata was synonymized with B. occidentalis by Wake and Brame, (1969)). Populations assigned to $B$. rufescens and $B$. occidentalis showed high levels of genetic divergence from one another (Larson 1983). The diminutive body size of these animals, coupled with variation in traits considered to be diagnostic for species (such as the
presence or absence of maxillary teeth (Larson 1983)), hindered the taxonomic recognition of additional species within the complex. While B. occidentalis, B. rufescens, and B. nympha strongly resemble each other in overall external morphology (as evidenced by high misclassification rates of these species in the DFA), B. chinanteca is easily distinguished from these three species by its more robust body, as well as by the combination of characters given above. The occurrence of B. chinanteca and B. rufescens at the type locality of $B$. chinanteca is the second demonstrated instance of sympatry between two members of the subgenus Nanotriton, which further strengthens the case for the recognition of $B$. chinanteca as a distinct species. Poglayen and Smith (1958) reported B. occidentalis and B. rufescens from 10 km N San Fernando, Chiapas in the Atlantic drainage, and Larson (1983) showed very close geographic proximity between B. rufescens and B. occidentalis in the vicinity of Berriozabal, Chiapas.

No information is currently available on the population size or status of B. chinante$c a$, although individuals were found at the type locality on two recent visits. Although the distribution of Bolitoglossa chinanteca is not known precisely, a polygon drawn between the three known localities has an area of approximately $255 \mathrm{~km}^{2}$. This extent of occurrence, coupled with a decline in extent of occurrence due to habitat destruction, would classify B. chinanteca as Endangered under IUCN Red List Criterion B1ab(i) (B1. Extent of occurrence $<5000 \mathrm{~km}^{2}$, a. known from $<5$ localities, $\mathrm{b}(\mathrm{i})$. continuing decline in extent of occurrence). The fact that $B$. chinanteca has been taken in banana trees in disturbed habitat, however, suggests that it may tolerate disturbance reasonably well. At this time, it does not appear that B. chinanteca qualifies for any of the threatened IUCN categories (CR, EN, VU). This assessment could change if evidence arises that it cannot live away from forest (the banana trees at the type locality are on the forest edge) or that habitat destruction in the region is adversely affecting the species. Because of this, we believe that B. chinanteca should be classified as Near Threatened (NT).

The Sierra de Juárez is among the areas of highest species richness for Neotropical salamanders, and morphologically distinct species continue to be described from the region (Hanken and Wake 2001; Parra-Olea et al. 2005) despite decades of taxonomic study of its salamanders (Wake et al. 1992). Not including the nearby Sierra Aloapaneca, the Sierra de Juárez was previously known to contain 18 salamander species of five genera (Bolitoglossa, Chiropterotriton, Cryptotriton, Pseudoeurycea, and Thorius) (Hanken and Wake 2001; Parra-Olea et al. 2005; Wake et al. 1992); the description of $B$. chinanteca brings the total number to 19 . Such a high diversity of salamanders is notable even for Mexico, and highlights the need for continued taxonomic study of the salamanders of the region and of southern Mexico in general.

## Acknowledgments

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CONACyT postdoctoral fellowship and partially funded by the National Science Foundation (grant DEB 1026393). We wish to thank the Comisariados de Bienes Comunales of Santiago Comaltepec and San Pedro Yolox for permission to work in the area, and to the people of both Santiago Comaltepec and San Pedro Yolox for their hospitality and friendship during our visits to their communities. Collecting permits for this study were provided by the Secretaria del Medio Ambiente y Recursos Naturales (SEMARNAT) to G. Parra-Olea.

## References

Alberch P (1983) Morphological variation in the neotropical salamander genus Bolitoglossa. Evolution 37: 906-919. doi: 10.2307/2408406
AmphibiaWeb (2011) Information on Amphibian Biology and Conservation. Available at www.AmphibiaWeb.org [accessed 22.VI.2011]
Campbell JA, Smith EN, Streicher J, Acevedo ME, Brodie ED Jr (2010) New salamanders (Caudata: Plethodontidae) from Guatemala with miscellaneous notes on known species. Miscellaneous Publications of the Museum of Zoology, University of Michigan 200: 1-60.
Duellman WE (1960) A distributional study of the amphibians of the Isthmus of Tehuantepec, México. University of Kansas Publications, Museum of Natural History 13: 19-72.
Edgar RC (2004) MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 5: 1-19. doi: 10.1186/1471-2105-5-113
Hanken J, Wake DB (2001) A seventh species of minute salamander (Thorius: Plethodontidae) from the Sierra de Juárez, Oaxaca, México. Herpetologica 57: 515-523.
Klecka WR (1980) Discriminant Analysis Sage Publications, Beverly Hills, CA, 70 pp.
Larson A (1983) A molecular phylogenetic perspective on the origins of a lowland tropical salamander fauna 1. Phylogenetic inferences from protein comparisons. Herpetologica 39: 85-99.
Moritz C, Schneider CJ, Wake DB (1992) Evolutionary relationships within the Ensatina eschscholtzii complex confirm the ring species interpretation. Systematic Biology 41: 273-291.
Palumbi SR (1996) Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK (Eds) Molecular Systematics. Sinauer Associates, Sunderland, MA, 204-247.
Parra-Olea G, García-París M, Hanken J, Wake DB (2005) Two new species of Pseudoeurycea (Caudata : Plethodontidae) from the mountains of northern Oaxaca, Mexico. Copeia 2005: 461-469. doi: 10.1643/CH-04-112R
Parra-Olea G, García-París M, Wake DB (2004) Molecular diversification of salamanders of the tropical American genus Bolitoglossa (Caudata: Plethodontidae) and its evolutionary and biogeographical implications. Biological Journal of the Linnean Society 81: 325-346. doi: 10.1111/j.1095-8312.2003.00303.x
Poglayen I, Smith HM (1958) Noteworthy herptiles from Mexico. Herpetologica 14: 11-15.
Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688-2690. doi: 10.1093/bioinformatics/btl446

Swofford DL (2003) PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, MA.
Wake DB (1966) Comparative osteology and evolution of the lungiess salamanders, family Plethodontidae. Memoir of the Southern California Academy of Sciences 4: 1-111.
Wake DB, Brame AH (1969) Systematics and evolution of neotropical salamanders of the Bolitoglossa helmrichi group. Contributions in Science (Los Angeles) 175: 1-40.
Wake DB, Elias P (1983) New genera and a new species of Central American salamanders, with a review of the tropical genera (Amphibia, Caudata, Plethodontidae). Contributions in Science (Los Angeles) 175: 1-19.
Wake DB, Papenfuss TJ, Lynch JF (1992) Distribution of salamanders along elevational transects in Mexico and Guatemala. Tulane Studies in Zoology and Botany Supplementary Publication 1: 303-319.

## Appendix I

Additional specimens examined
Bolitoglossa occidentalis: Guatemala: San Marcos: MVZ 100849, 108794, 108804, 108808, 108814, 108818, 115755, 138521, 138536, 138542, 138552, 138553, 138556, 138557, 138566, 138572, 138573, 138577, 138581, 138583, 138584, 138588, 138592, Finca Santa Julia, ca. 1.25 km E, 0.75 km S (by air) San Rafael Pie de La Cuesta; MVZ 130110, 130118, 132039, 132075, 132102, 132106, 102109, 132110, 132114, 132117, 132118, 132121, 132123, 165298, 165305, Finca Santa Julia, ca. 1.5 km SE (by air) San Rafael Pie de La Cuesta; MVZ 160865, Finca Santa Julia, ca. 2 km S San Rafael Pie de La Cuesta. Mexico: Chiapas: MVZ 132442, 132443, 132447-132449, 132451, 132455, 132456, 132458, 132459, 132464132465 , 146461, Cafetal along road from Tapachula de Córdova y Ordóñez to Nueva Alemania, 13.6 km N (by road) junction Mexico Hwy. 200; MVZ 132468, 132470, 132473, 132475-132477, 132483, 132485, 132486, 132490, 132490, Finca Cruz Blanca, along road from Tapachula de Córdova y Ordóñez to Nueva Alemania, 8.0 km N (by road) junction Mexico Hwy. 200; MVZ 161019, 13 km N Tapachula de Córdova y Ordóñez on road to Nuevo Alemania; MVZ 176843, 176905, 23.3 km NNW (by road) Tapachula de Córdova y Ordóñez at Rancho El Naranjo; MVZ 160964, 160965, 7.5 mi N Berriozabal; MVZ 194204, 194205, 194207-194211, 194214, $-194216,194218,194219$, banana grove on side of road from Tuxtla Gutiérrez to Chicoasen, 11.2 km N (by road) San Fernando; MVZ 194222-194224, 194230, 194233, 15.3 km ENE (by road) Copainala, along road to Coapilla; MVZ 194225, 194235-194239, 194243-194245, Cafetal 11.4 km NW (by road) Berriozabal; MVZ 163817, 176857, SE face Cerro Baúl; MVZ 163818, 163819, 16.8 km NW (by road) Rizo de Oro, slopes of Cerro Baúl; MVZ 196013-163015, ridge SE Cerro Baúl, 21 km W Rizo de Oro (in Chiapas); MVZ 194255-194258, 194269, Cerro Baúl, 23 km N (by road) Rizo de Oro.

Bolitoglossa nympha: Guatemala: Alta Verapaz: MVZ 161047-161056, 161091161101; Finca El Volcán, 25 km NW (by road) Senahu. Honduras: Cortés: 115293115303, Sierra del Espíritu Santo, 10 km W (by air) San Pedro Sula. Copán: MVZ 167983-167988, 16851, 168511, 171068, 171069, 171071, 2 km N Santa Rosa de Copán.

Bolitoglossa rufescens: Mexico: Chiapas: MVZ 176882-176885, 30.7 km NNW (by road) Ocosingo; MVZ 176890-176899, 23 km SSW (by road) Palenque, Ruiz Cortines; MVZ 176900-176904 26 km N Ocozocoautla de Espinosa; MVZ 194254, Cafetal 12.4 km (by road) N Berriozabal on road to Cairo. Oaxaca: IBH 24710, 10.3 km S (by rd) of center of Valle Nacional on Hwy. 175; MZFC 15756, Tuxtepec; Veracruz: MVZ 85501-85503, 85505, 85510-85514, 85522-85524, 85526, 85528, 85529, 85531, 85532, 85534, 85537, 85538, 85541, 85546, 85547, 85549, 85552, 85553, in banana and coffee fields W of Cuautlapan on side of hill; MVZ 85543, 85560, 85564, 85565, 85568, 86670, 86675, 85576, 85579, 85581-85583, near Cuautlapan; MVZ 85573, 85574, 163801-163803, 163805-163814; Lake Catemaco, 2.5 km SE Coyame; MVZ 171840, 171841, Ojoxapam, 2.5 km SE Coyame, edge of L. Catemaco; MVZ 163827-163832, 171842, 9.3 km N Catemaco; MVZ 171836, Dos Amates, 12 km N Catemaco; MVZ 185992, Rancho El Encanto, 13 km N Catemaco; MVZ 172684, 172685, Forest above Playa Escondida, 30 km NNE Catemaco; MVZ 222515, Playa Escondida, 18.5 mi N (by road) Catemaco.

# Antarctic Starfish (Echinodermata,Asteroidea) from the ANDEEP3 expedition 

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#### Abstract

This dataset includes information on sea stars collected during the ANDEEP3 expedition, which took place in 2005. The expedition focused on deep-sea stations in the Powell Basin and Weddell Sea.

Sea stars were collected using an Agassiz trawl ( 3 m , mesh-size $500 \mu \mathrm{~m}$ ), deployed in 16 stations during the ANTXXII/3 (ANDEEP3, PS72) expedition of the RV Polarstern. Sampling depth ranged from 1047 to 4931 m . Trawling distance ranged from 731 to 3841 m . The sampling area ranges from $-41^{\circ} \mathrm{S}$ to $-71^{\circ} \mathrm{S}$ (latitude) and from 0 to $-65^{\circ} \mathrm{W}$ (longitude). A complete list of stations is available from the PANGAEA data system (http://www.pangaea.de/PHP/CruiseReports.php?b=Polarstern), including a cruise report (http://epic-reports.awi.de/3694/1/PE_72.pdf).

The dataset includes 50 records, with individual counts ranging from 1-10, reaching a total of 132 specimens.

The andeep3-Asteroidea is a unique dataset as it covers an under-explored region of the Southern Ocean, and that very little information was available regarding Antarctic deep-sea starfish. Before this study, most of the information available focused on starfish from shallower depths than 1000 m . This dataset allowed to make unique observations, such as the fact that some species were only present at very high depths (Hymenaster crucifer, Hymenaster pellucidus, Hymenaster praecoquis, Psilaster charcoti, Freyella attenuata, Freyastera tuberculata, Styrachaster chuni and Vemaster sudatlanticus were all found below -3770 m ), while others displayed remarkable eurybathy, with very high depths amplitudes (Bathybiaster loripes ( 4842 m ), Lysasterias adeliae ( 4832 m ), Lophaster stellans ( 4752 m ), Cheiraster planeta (4708m), Eremicaster crassus ( 4626 m ), Lophaster gaini ( 4560 m ) and Ctenodiscus australis ( 4489 m )).

Even if the number of records is relatively small, the data bring many new insights on the taxonomic, bathymetric and geographic distributions of Southern starfish, covering a very large sampling zone. The dataset also brings to light six species, newly reported in the Southern Ocean.

The quality of the data was controlled very thoroughly, by means of on-board Polarstern GPS systems, checking of identification by a renowned specialist (Prof. Michel Jangoux, Université Libre de Brux-


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elles), and matching to the Register of Antarctic Marine Species (RAMS) and World Register of Marine Species (WoRMS). The data is therefore fit for completing checklists, for inclusion in biodiversity patterns analysis, or niche modeling. It also nicely fills an information gap regarding deep-sea starfish from the Southern Ocean, for which data is very scarce at this time. The authors may be contacted if any additional information is needed before carrying out detailed biodiversity or biogeographic studies.

## Keywords

Asteroidea, Biodiversity, Deep-Sea, Census of Antarctic Marine Life, Census of Marine Life, ANDEEP cruises, Polarstern, Sea-stars, Starfish

## Project details

## Project title: Bianzo - Biodiversity of Antarctic Zoobenthos

Personnel: Bruno Danis
Funding: Belgian Science Policy Office (BELSPO, cash), Alfred Wegener Institute (AWI, in kind), Marine Biology Lab (ULB, in kind)

Study area descriptions/descriptor: The study area of this dataset was set in the Southern Ocean and focused on deep sea stations distributed on the continental slopes of the eastern Weddell Sea (off Kapp Norvegia) and western Weddell Sea and the South Orkney Islands, and deep Cape, Agulhas, Weddell and Powell Basins Southern Ocean. The Southern Ocean deep-sea is a very under sampled area, according to a recent gap analysis carried out by Griffiths et al. (2010).

Design description: BIANZO (Biodiversity of Antarctic Zoobenthos) investigated biodiversity patterns of the Antarctic zoobenthos and their causal processes for three representative groups of different size categories: nematodes (meiobenthos), amphipods (macrobenthos) and echinoids (megabenthos). Trophodynamic aspects of these benthic groups and their ability to cope with temperature and temperature-related changes (food composition and availability, pH of the seawater...) will be studied mainly in an experimental approach. Information collected in previous studies and in the first two work packages will be used to initiate the development of a model about the possible changes in the benthic communities due to global environmental change. BIANZO generated the initial core data system upon which SCAR's Marine Biodiversity Information Network (SCAR-MarBIN) was built. As SCAR-MarBIN is the Antarctic Node of the international OBIS network, the BIANZO data system was designed to comply with the OBIS standards. BIANZO served as a model to give a single access to three heterogeneous databases, each focusing on the specific groups of interest (Amphipoda, Nematoda, Echinoidea).

Regarding the dataset, the existing Data Toolkit from SCAR-MarBIN was used (http://www.scarmarbin.be/documents/SM-FATv1.zip), following the OBIS schema (http://iobis.org/data/schema-and-metadata). The dataset was uploaded in the ANTOBIS database (the geospatial component of SCAR-MarBIN), and the taxonomy was matched against the Register of Antarctic Marine Species, using the Taxon Match tool (http://www.scarmarbin.be/rams.php?p=match)

## Taxonomic coverage

General taxonomic coverage description: This dataset focuses on Starfish (Echinodermata: Asteroidea). It includes data on 6 orders (Forcipulatida, Notomyotida, Paxillosida, Spinulosida, Valvatida, Velatida) and 11 families (Asteriidae, Astropectinidae, Benthopectinidae, Echinasteridae, Freyellidae, Goniasteridae, Labidiasteridae, Notasteriinae, Porcellanasteridae, Pterasteridae, Solasteridae). The most represented families are the Astropectinidae (Paxillosida), followed by Porcellanasteridae (Paxillosida) and Pterasteridae (Velatida).

## Taxonomic ranks

Order: Forcipulatida, Notomyotida, Paxillosida, Spinulosida, Valvatida, Velatida
Family: Asteriidae, Astropectinidae, Benthopectinidae, Echinasteridae, Freyellidae, Goniasteridae, Labidiasteridae, Notasteriinae, Porcellanasteridae, Pterasteridae, Solasteridae
Genus: Freyella, Bathibiaster, Cheiraster, Diplasterias, Dytaster, Eremicaster, Freyastera, Freyella, Hymenaster, Hyphalaster, Lophaster, Lysasterias, Marsipaster, Notasterias, Notioceramus, Parachaster, Psalidaster, Psilaster, Rhopiella, Ripaster, Styracaster
Species: Dytaster felix, Freyella attenuata, Psalidaster mordax, Lophaster gaini, Bathybiaster loripes, Psilaster charcoti, Pteraster hirsutus, Freyastera tuberculata, Hymenaster pellucidus, Hymenaster praecoquis, Benthopecten pedicifer, Hyphalaster inermis, Eremicaster pacificus, Lophaster stellans, Eremicaster crassus, Rhopiella hirsuta, Notioceramus anomalus, Hymenaster crucifer, Styracaster chuni, Cheiraster planeta, Pteraster spinosissimus, Hyphalaster scotiae, Notasterias pedicellaris, Diplasterias brucei, Lysasterias adeliae

## Spatial coverage

General spatial coverage: ANDEEP 3 cruise track, from Cape Town (SA) to Punta Arenas (CH). Four study regions were selected, but the main focus was on the Powell Basin and the Weddell Basin of the Weddell Sea, and their slopes. Two comparative samples were taken further north in the adjacent Agulhas and southern Cape Basins, which are separated from each other by the Agulhas Ridge. Four study regions were selected, but the main focus was on the Powell Basin and the Weddell Basin of the Weddell Sea, and their slopes. The major South Atlantic deep-sea basins started forming during Jurassic and Cretaceous times in connection with the Gondwana break-up and seafloor spreading (Brandt et al. 2004, 2007; Lawver and Gahagan 2003). The Weddell Basin is separated from the northerly basins by the South- west India Ridge (LaBrecque 1986). The Powell Basin on the western side of the Weddell Sea was formed in the Tertiary by geological processes opening the Drake Passage and tectonic move-
ments in the Scotia Sea (Lawver and Gahagan 2003; Mitchell et al. 2000). The oceanography of the deep South Atlantic seafloor is defined by its prominent water mass, the Antarctic Bottom Water (Tomczak and Godfrey 2001). The Antarctic Bottom Water expands north- wards into the Atlantic basins east and west of the Mid-Atlantic Ridge, like the Agulhas Basin, but can only enter the basins north of the Walvis Ridge (e.g., Cape Basin) via the northerly Romanche Fracture Zone. The Weddell Sea Bottom Water (WSBW), defined by a temperature of 0.71 C and a salinity of 34.64 ppt (Orsi et al. 1993), is the main water mass above the Weddell Sea benthos (Fahrbach et al. 2001). The WSBW flows from the western Weddell Sea into the Scotia Sea and South Sandwich Forearc, and its circulation is driven by the Weddell Sea gyre. The sediments in the bathyal and abyssal Weddell and Powell Basins are dominated by silt and clay.

Coordinates: $71^{\circ} 18^{\prime} 36^{\prime \prime} \mathrm{S}$ and $61^{\circ} 30^{\prime} 0$ "S Latitude; $64^{\circ} 38^{\prime} 24^{\prime \prime} \mathrm{W}$ and $0^{\circ} 0^{\prime} 0^{\prime \prime} \mathrm{E}$ Longitude

Temporal coverage: January 26, 2005 - March 30, 2005
Natural collections description
Parent collection identifier: Marine Biology Lab, Free University of Brussels. Antarctic Echinoderms Collection

Collection name: ANDEEP3 Seastars
Collection identifier: Michel Jangoux
Formation period: January to March 2005
Specimen preservation method: Alcohol

## Methods

Method step description: see quality control above.
Study extent description: Four study regions were selected, but the main focus was on the Powell Basin and the Weddell Basin of the Weddell Sea, and their slopes. Two comparative samples were taken further north in the adjacent Agulhas and southern Cape Basins, which are separated from each other by the Agulhas Ridge.

Sampling description: A 3-m wide Agassiz trawl (AGT) was deployed at two locations in the South Atlantic and 14 locations in the Southern Ocean during the PFS Polarstern expedition ANT XXII/3 WECCON 2005- ANDEEP III in January-April 2005. The sample depths ranged from 1047 to 4931 m , sampling continental slopes of the eastern Weddell Sea (off Kapp Norvegia) and western Weddell Sea and the South Orkney Islands, and deep Cape, Agulhas, Weddell and Powell Basins. At the stations 074-7, 07811 and 081-9, the cod end mesh size was 10 mm , while at all other stations, an inlet of 500 mm mesh size was inserted. The 500 mm mesh size was used because of smaller adult size of deep- sea macrobenthos compared to shelf macrobenthos. The deployment protocol was standardised to 10 min trawling at 1 knot with $1.5 \times$ cable length to water depth to facilitate comparability between the different sites. At station 059-10, the AGT was trawled for 20 min . The haul distances were calculated from the time the Agassiz trawl travelled on the ground. The tension meter of the winch clearly indicated when the AGT left the
seabed. Haul length varied from 731 to 3841 m . Sample volumes were estimated and the general sediment composition was noted. Mega- and larger macrofauna were separated by eye on deck. The taxa of each trawl sample were identified to morphospecies level.

Quality control description: The initial geo-referencing was done by means of the RV Polarstern onboard GPS systems. Geospatial data was directly imported from those systems to avoid potential errors in transcribing. Samples identification was supervised and checked by Michel Jangoux, Marine Biology Lab, Université Libre de Bruxelles. The taxonomic names were matched against two authoritative, expert-driven species registers: the Register of Antarctic Marine Species (RAMS) and the World Register of Marine Species (WoRMS). The automatic matching tools available on both these web sites were utilized.

## Data resources

The data underpinning the analyses reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, http://ipt.biodiversity.aq/resource. do? $\mathrm{r}=$ andeep 3 _asteroidea.

## Datasets

## Dataset description

There is no dataset published through Darwin Core Archive format for this resource. Currently described datasets are listed in the section External datasets.

Language: English
Licenses of use: This work is licensed under a Creative Commons CCZero 1.0 License http://creativecommons.org/publicdomain/zero/1.0/legalcode

## External datasets

## Dataset description

Object name: SCAR-MarBIN DiGIR Server
Format name: OBIS schema
Format version: v1.1
Distribution: http://w2.scarmarbin.be/digir2/digir.php
Dataset description
Object name: GBIF data portal
Format name: DarwinCore
Distribution: http://data.gbif.org/datasets/resource/7928/
Metadata language: English
Date of metadata creation: 2011-12-03
Hierarchy level: Dataset

## References

Brandt A, De Broyer C, De Mesel I, Ellingsen KE, Gooday AJ, Hilbig B, Linse K, Thomson MRA, Tyler PA (2007) The Biodiversity of the Deep Southern Ocean Benthos. Philosophical Transactions of the Royal Society B: Biological Sciences 362 (1477) (January): 39-66. doi: 10.1098/rstb.2006.1952
Brandt A, De Broyer C, Gooday AJ, Hilbig B, Thomson MRA (2004) Introduction to ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) - a tribute to Howard L. Sanders. Deep-Sea Research II 51: 1457-1465. doi: 10.1016/j.dsr2.2004.08.006
Fahrbach E, Harms A, Rohardt G (2001). Flow of bottom water in the northwestern Weddell Sea. Journal of Geophysical Research Ocean 106: 2761-2778. doi: 10.1029/2000JC900142
Griffiths HJ, Danis B, Clarke A (2010) Quantifying Antarctic marine biodiversity: The SCARMarBIN data portal. Deep Sea Research Part II: Topical Studies in Oceanography (October): $1-12$.
LaBrecque JL (1986). South Atlantic Ocean and Adjacent Continental Margins, Atlas 13. Ocean Margin Drilling Program Atlas Series 13.
Lawver LA, Gahagan LM (2003). Evolution of Cenozoic seaways in the circum-Antarctic region. Palaeogeography Palaeoclimatology Palaeoecology 198: 11-37. doi: 10.1016/S0031-0182(03)00392-4
Mitchell NC, Livermore RA, Fabretti P, Carrara G (2000). The Bouvet triple junction, 20 to 10 Ma , and extensive transtensional deformation adjacent to the Bouvet and Conrad transforms. Journal of Geophysical Research-Solid Earth 105: 8279-8296. doi: 10.1029/1999JB900399

Orsi AH, Nowlin WD, Whitworth T (1993) On the circulation and stratification of the Weddell Gyre. Deep-Sea Research 40: 169-203. doi: 10.1016/0967-0637(93)90060-G
Tomczak M, Godfrey JS (2003) Regional Oceanography: an Introduction 2nd edn, Daya Publishing House, xi+390p


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