Increased sampling blurs morphological and molecular species limits: revision of the Hispaniolan endemic spider genus *Tainonia* (Araneae: Pholcidae)

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**Abstract.** The genus *Tainonia* comprises unusually large pholcids endemic to Hispaniola. Previously, only the type species had been formally described, represented in collections by no more than 12 adult specimens. However, the existence of more species has been hypothesised based on a few further individuals. The present paper is based on a sample of 205 mostly newly collected adult specimens from 18 localities in the Dominican Republic and four localities in Haiti. The increased sampling reveals a wide range of variation, including intermediate levels of divergence that often blur rather than clarify species limits. Therefore, although not all taxonomic questions can be settled here, morphological (including morphometric) and molecular (mitochondrial 16S, CO1) data strongly support two new species: one in La Visite National Park, Haiti (*T. visite*, sp. nov.) and another on Samaná Peninsula and parts of the eastern Dominican Republic (*T. samana*, sp. nov.). Species limits among the other populations are more difficult to support or reject. Specimens from Bayahibe (eastern Dominican Republic) and from La Ciénaga (Cordillera Central) are each assigned species status on the basis of consistent morphological differences (*T. bayahibe*, sp. nov., *T. cienaga*, sp. nov.), but no molecular data are available due to lack of specimens. All other specimens are provisionally assigned to a possibly paraphyletic *T. serripes* (Simon). There is considerable morphological variation within this widely distributed group of populations but this variation is rather continuous and molecular distances fill most of the range between morphologically unambiguous conspecifics and unambiguous heterospecifics.

**Additional keywords:** 16S, barcoding, CO1, Dominican Republic, Haiti, morphometrics, taxonomy.

**Introduction**

High levels of diversity and endemism (Myers et al. 2000; Santiago-Valentin and Olmstead 2004; Smith et al. 2005), a complex geological history resulting in complex biogeographic patterns (Iturralde-Vinent and MacPhee 1999; Ricklefs and Bermingham 2008) and drastic deforestation (Paryski et al. 1989; Hedges and Woods 1993; Sergile and Woods 2001) combine to make the West Indies a hotspot not only of biodiversity, but also of research into the origin and loss of this diversity. In comparison to vertebrates, however, invertebrates have played a relatively minor role in these debates, mostly because their basic taxonomy is still rather fragmentary (see references in Hedges 2001, 2006 for some exceptions; also: Liebherr 1998; Bell 2001; Miller and Miller 2001; Wilder and Hollocher 2003).

In spiders, the amber fauna of Hispaniola has attracted considerable attention, while the recent fauna of many taxa remains poorly studied (Penney 2008). About one-third of described Hispaniolan spider species are based on amber material, and only one more family is recorded from extant than from fossil species (46 versus 45; Penney 2008). Little work has been done on extant spiders since the review by Bryant (1948): in more than five decades the species number had increased from 224 to just 296 (Penney and Pérez-Gelabert 2002), and it is now at ~325 (Penney 2008). Pholcidae are one of those families that until recently contained about equal numbers of described fossil and extant species. Excluding the synanthropic species that are most probably recent introductions, Penney (2008) listed no more than eight extant but eleven fossil species.

Two recent collecting trips of about 3 weeks each to the Dominican Republic (2005) and Haiti (2007) have shown that the actual number of extant species is much higher. Collections at 41 localities within this relatively short period of time have resulted in ~38 pholcid species. Most of these (~29) belong to the genus *Modisimus* (Huber et al. in press), four to *Leptopholcus* (partly published by Huber and Wunderlich 2006) and the rest to *Tainonia*. The latter genus is the focus of the present paper.

The genus *Tainonia* was erected recently (Huber 2000) to accommodate a Hispaniolan pholcid spider originally described as *Blechroscelis serripes* Simon, 1893. Further species have been known to exist (Huber 2000), but none has been described. *Tainonia* spiders are easily distinguished from representatives of the two other pholcid genera on Hispaniola.
(Modisimus, Leptopholcus) by their large size, reaching a leg span of up to 15 cm. In a wider taxonomic context, Tainonia specimens are unusual among pholcids in having the femora and tibiae of all legs covered with strong short spines. Spines of similar morphology occur in other genera too, but there they are usually confined to a single ventral row on the male anterior legs, whereas in Tainonia they occur in several rows all around the femora and tibiae in both sexes and on all legs. The only comparable and most probably convergent case is the Brazilian species Mesabolivar spinulosus (Mello-Leitão) (see Huber 2000: fig. 823). Also unusual among pholcids are the barely modified male chelicerae. In most pholcid genera, the armature of the male chelicerae is a valuable species-specific character, presumably shaped by sexual selection (Huber 1999). Tainonia male chelicerae bear no more than an inconspicuous proximal bulge that is not species-specific. All comparable cases refer to single exceptional species in genera with strongly modified male chelicerae (Tupigea nadleri Huber, Coryssocnemis viridescens Kraus, Psilocorus acanthus Chamberlin & Ivie).

In this paper we redescribe Tainonia serripes, providing first ultrastructural and molecular data for the genus, and describe four new species of Tainonia, with special emphasis on the problem of species limits.

Materials and methods

Most of the material studied herein (~200 adult specimens) was collected during two trips to the Dominican Republic (Nov. 2005) and to Haiti (Nov.–Dec. 2007). All new material is currently deposited in the Alexander Koenig Research Museum of Zoology, Bonn (ZFMK), but will later be partly transferred to the Museo de Historia Natural, Santo Domingo. Further material (nine adult specimens) was borrowed from the American Museum of Natural History, New York (AMNH), the Museum of Comparative Zoology, Cambridge (MCZ) and the National Museum of Natural History, Washington, DC (USNM). The type specimen of the type species T. serripes has been investigated previously (Huber 1997) and was restudied (by BAH) in Paris in August 2008.

Morphological methods and terminology are as in Huber (2000). Measurements are in mm (±0.02 mm if two decimals are given) unless otherwise noted; eye measurements are ± 5 μm. Drawings were done with a camera lucida on a Labophot-2 compound microscope (Nikon, Tokyo). Photographs were taken with a Nikon Coolpix 995 digital camera (2048 × 1536 pixels) mounted on a Nikon SMZ-U dissecting microscope. For SEM photos, specimens were cleaned ultrasonically, dried in hexamethyldisilazane (HMDS; Brown 1993) and photographed with a S-2460 scanning electron microscope (Hitachi, Tokyo). Cleared epigyna were stained with chlorazol black.

In an effort to evaluate minor genital shape differences that were difficult to interpret, we performed both a morphometric analysis of linear distances (~1040 measurements in three species from which adequate samples were available) and an analysis of DNA sequences from two mitochondrial genes: 16S rRNA and the DNA barcoding available) and an analysis of DNA sequences from two mitochondrial genes: 16S rRNA and the DNA barcoding standard CO1 (also limited to three species of which suitable material for DNA sequencing was available).

The DNA of 15 pholcid specimens (Table 1) was isolated from ethanol-preserved prosomata and legs or from whole individuals using the Nucleo Spin Tissue extraction kit (Macherey-Nagel, Düren, Germany). PCR conditions and primers (the latter also specified in the GenBank records) were those used by Astrin et al. (2006). Where this routine failed, we used the Qiagen (Hilden, Germany) Multiplex PCR kit. Double-stranded sequencing of PCR products was performed by a sequencing facility (Macrogen, Seoul, South Korea).

As outgroups for the phylogenetic analysis, we used several published sequences of Neotropical pholcids: Ciboneya antrai (Huber & Pérez, 2001, Mesabolivar aurantiacus (Mello-Leitão, 1930) (from Bruvo-Madaric et al. 2005), Coryssocnemis simia Huber, 2000, Priscula venezuelana Simon, 1893, Tupigea sp. (from Astrin et al. 2006) and Modisimus vittatus Bryant, 1948 (from Huber et al. in press).

Table 1. GenBank accession numbers

Specimens sequenced, DNA voucher numbers and GenBank accession numbers; for more detailed information, see ‘Material examined’ sections and/or the respective GenBank records. H: Haiti; DR: Dominican Republic

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<th>Species</th>
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<th>DNA voucher</th>
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<th>Acc. # CO1</th>
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Alignments (available from the authors and as an Accessory Publication on the Invertebrate Systematics site) were obtained manually (CO1) or with MUSCLE ver. 3.6 (Edgar 2004), run with default parameters. Aligned 16S sequences had a length of 473 bp and CO1 sequence length was 439 bp. We used PAUP* ver. 4.0b10 (Swofford 1998) to compute p-distances (i.e. uncorrected distances). Modelfest ver. 3.7 (Posada and Crandall 1998; Posada and Buckley 2004), implementing the Bayesian information criterion (BIC), identified the generalised time reversible (GTR) + gamma distribution (I) (Lanave et al. 1984) model of nucleotide substitution as the best-fit model for 16S. The best-fit model for CO1 was the Hasegawa–Kishino–Yano (HKY) + invariable sites (I) + Γ model (Hasegawa et al. 1985). For phylogenetic analysis, we concatenated the alignments of the two mitochondrial genes in BioEdit ver. 7.0.4.1 (Hall 1999). Within the genus Tainonia, homology of sequence positions seemed unambiguous. Adding the outgroup species, however, resulted in regions of ambiguous alignment, so that 51 characters of the 16S gene had to be excluded from the analysis in order to guarantee positional homology (these were positions 478–490, 504–509, 710–726, 743–757 of the combined alignment, cf. Accessory Publication). Gaps were treated as missing information. Parallel Bayesian Markov chain Monte Carlo (MCMC) analyses were conducted with the MrBayes ver. 3.1.2 software (Ronquist and Huelsenbeck 2003) to infer phylogenetic reconstructions. We applied the models of sequence evolution as diagnosed by the BIC, while letting MrBayes equate the values of the parameters through the use of ‘flat’ prior distributions. Parameters were unlinked among partitions and also between the 3rd versus 1st plus 2nd codon positions in CO1. The analysis was run for 10^7 generations (using the default chain number and temperatures). Every 1000th tree was sampled (20 000 trees retained for the two parallel – converging – runs taken together). Negative log-likelihood score stabilisation (‘burnin’) was determined graphically and checked using the TRACER ver. 1.4.1 software (Rambaut and Drummond 2007). Accordingly, we used 19 900 trees for building a 50%-majority rule consensus dendrogram (with posterior probabilities).

Results

Although genital shape differences among specimens were not strictly quantified, an ordering of specimens according to subjective degrees of similarity revealed interesting results when compared with molecular distances (Fig. 1). As expected, specimens that showed no or minimal genital differences (and would thus by traditional criteria unambiguously be considered conspecific), had the lowest values (p-distances: 0–0.9% for 16S, 0–2.8% for CO1). On the other extreme, comparisons of specimens from La Visite (that any traditional taxonomist would likely consider to be clearly not conspecific with specimens from any other locality and that are thus assigned to the new species T. visite) with other specimens had the highest values (7.1–8.6 for 16S, 12.2–14.2 for CO1).

Pairs of specimens that showed intermediate morphological differences (and that are here tentatively all classified as T. serripes) also showed intermediate molecular distances. The largest values within this group were for comparisons between ‘eastern’ and ‘western’ (cf. Fig. 4) T. serripes specimens (4.6–6.0 for 16S, 8.0–11.5 for CO1); the lowest values were for comparisons among different ‘western’ populations (2.2–3.1 for 16S, 5.3–8.5 for CO1).

Unexpected were the low distances between specimens assigned to the new species T. samana and T. serripes.

Fig. 1. Pairwise genetic p-distances among all sequenced specimens. Horizontal bar colours are explained by the vertical bars. Note that a distinct barcoding gap is absent between those specimens that are morphologically unambiguous conspecifics (‘clearly conspecific’) and those that are morphologically unambiguous heterospecifics (‘visite versus other sp.’, ‘samana versus serripes’). For further discussion see text.
Morphologically, several characters clearly separate *T. samana* from all other species (see species diagnosis below) and by traditional criteria it would as clearly deserve species status as *T. visite*. However, molecular distances between *T. samana* and *T. serripes* were relatively low (5.1–6.4 for 16S, 7.6–11.3 for CO1), largely overlapping with distances among *T. serripes* populations.

Morphometric analyses revealed clear quantitative differences between the species-level taxa described below (Fig. 2), but failed to support the separation between the problematic *T. serripes* populations. Only the relationship between male palpal bulb and tibia lengths tended to differentiate eastern and western populations, though with a wide range of overlap (Fig. 2a). Surprisingly, allometric values of male genital characters on carapace width were even lower for *T. serripes* than for the other two species measured (except for the non-significant values for palpal tibia width; Table 2), indicating relatively uniform genital size. That this was not simply a correlate of more uniform overall size is shown by the allometric values of tibia 1 length, which were highest in *T. serripes* (Table 2).

Separate phylogenetic analyses of the CO1 and 16S sequences resulted in quite different relationships among outgroup taxa...
but in basically the same relationships among taxa within *Tainonia*. The only minor differences concerned the support for the ‘eastern group’ of *T. serripes* (posterior probability: 1.00 for 16S versus 0.67 for CO1) and the relationships among western *T. serripes* populations. We therefore show only the results of the combined analysis (Fig. 3). It suggests that *T. serripes* as construed here may represent a paraphyletic species. However, the low posterior probability of 0.53 for *T. samana* + ‘eastern group’ of *T. serripes* indicates that it is more appropriate to consider this an unresolved trichotomy (*T. serripes* ‘eastern group’ + ‘western group’ + *T. samana*). Both the ‘eastern’ and ‘western’ groups of *T. serripes* appear highly supported. We nevertheless decided not to formally split these groups for several reasons discussed below.

### Discussion

Species boundaries are usually distinct and clear in the ‘non-dimensional’ situation (*sensu* Mayr 1955), i.e. at one place and one time. In spiders (and most other arthropods), species-specific structures such as genitalia and other copulatory contact structures are usually both easily distinguished among species and relatively invariant within species (Eberhard 1985; Eberhard et al. 1998; Huber 2004). This may change dramatically as soon as populations from different localities are included. Whatever the species concept preferred by the taxonomist, it is often a subjective decision as to how to interpret minor genitalic differences among populations. Large samples of many localities may provide statistical data and reveal significant morphological or molecular gaps (e.g. Coyle 1971; Thorpe 1975; Bond and Stockman 2008), and ecological and behavioural observations may support reproductive isolation among morphologically similar populations (e.g. Hebert et al. 2004) or lack of isolation despite considerable morphological differences (e.g. Huber and Pérez 2001). However, both the samples and the data (statistical, ecological, behavioural) are notoriously difficult to obtain and are not available nor feasible for the large majority of invertebrate taxa.

Molecular distances have been discussed as a potential solution to the problem, or at least as independent data to support or reject species limits (Bond 2004; Hebert et al. 2004; Paquin and Hedin 2004; Coleman 2009; further references in Meier et al. 2008). We agree that mitochondrial DNA divergence is neither necessary nor sufficient as a criterion for delineating species (Moritz and Cicero 2004) and that a simplistic approach for identifying species limits will often fail (Meier et al. 2006; Boyer et al. 2007). However, we also see the need to further explore the potential of short DNA sequences both for helping to solve basic taxonomic problems and for quick biodiversity estimates. In pholcid spiders, two previous studies have explored this option, and both concluded that CO1 and 16S may indeed help draw species limits in a large majority of cases (Astrin et al. 2006; Huber et al. in press). However, most species in these previous studies were morphologically distinct enough to provide no major problems for traditional methodology. The current study differs in consisting to a large extent of borderline cases with morphologically ambiguous species status.

Our results show that the molecular data do not give a clear answer and are about equally ambiguous to morphology. The dataset of pairwise distances fails to show a distinct ‘barcoding gap’ between intra- and interspecific comparisons (cf. Fig. 1) and more evidence than the two mitochondrial genes sequenced here will be necessary in order to fruitfully apply any form of ‘DNA taxonomy’. Relatively high *p*-distances between eastern and western populations of *T. serripes* would rather seem to support species-level distinction. For the 16S gene, this would imply a fairly wide gap between inter- and intraspecific distances (3.1–4.6) not very different from that found for Hispaniolan *Modisimus* spiders by Huber et al. (in press) (3.5–5.5 after exclusion of one ambiguous case).

### Table 2. Allometric values of male characters

<table>
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<tr>
<th>Species</th>
<th>Tibia 1</th>
<th>Bulb length</th>
<th>Palpal tibia length</th>
<th>Palpal tibia width</th>
<th>Palpal femur length</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tainonia serripes</em></td>
<td>1.36 *** (30)</td>
<td>0.45 *** (34)</td>
<td>0.30 * (34)</td>
<td>0.15 n.s. (34)</td>
<td>0.35 ** (34)</td>
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<tr>
<td><em>Tainonia samana</em></td>
<td>1.04 *** (27)</td>
<td>0.67 *** (29)</td>
<td>0.45 *** (29)</td>
<td>0.07 n.s. (29)</td>
<td>0.56 *** (29)</td>
</tr>
<tr>
<td><em>Tainonia cienaga</em></td>
<td>1.06 *** (9)</td>
<td>0.66 *** (10)</td>
<td>0.43 ** (10)</td>
<td>0.16 n.s. (10)</td>
<td>0.48 ** (10)</td>
</tr>
</tbody>
</table>

Slopes of regressions on carapace width as an indicator of body size, using ordinary least-squares regression of log-transformed data. Slopes significantly different from 0 are indicated by * (P < 0.05), ** (P < 0.01), and *** (P < 0.001); n.s.: not significant; sample sizes in parentheses.

*Fig. 3.* Bayesian 50% majority rule consensus tree for molecular sequence data (mitochondrial 16S and CO1). Posterior probability values are indicated at the respective nodes. The scale shows the expected nucleotide substitutions per site.
We nevertheless opted against formally splitting *T. serripes* for three reasons. (1) With the material available, it seems not possible to draw unambiguous morphological species boundaries. Morphological differences among populations that initially appeared significant were blurred by additional specimens collected from intermediate localities. (2) The CO1 gene does not replicate the 16S result above. Although there is a tendency of eastern versus western comparisons to give relatively high values, there is no gap in comparisons among western populations (Fig. 1). Rather than that, about half of the comparisons among ambiguous *T. serripes* populations fall within the gap previously identified for *Modisimus* spiders (4.6–9.6; Huber *et al.* in press). (3) Although it is very probable that the type specimen of *T. serripes* in fact belongs into the group for which we use this name, it is currently not possible to decide whether it belongs to the ‘eastern’ or ‘western’ group (see below). Splitting the two would thus require an additional arbitrary decision. In conclusion, it seems preferable at the present state of knowledge to have a possibly arbitrary decision. In conclusion, it seems preferable at the present state of knowledge to have a possibly arbitrary decision.

**Taxonomy**

**Genus Tainonia** Huber


Type species: *Bleuroscelis serripes* Simon, 1893.

**Diagnosis**

Large pholcids (body length 5–8 mm, leg span up to 15 cm) with femora and tibiae of both sexes covered with short spines arranged in several rows (Figs 50, 74), male chelicerae with inconspicuous proximal bulge (Figs 40, 58), male palpal femur with distinctive ventral apophysis (Figs 28, 66), procursus massive and relatively simple except distally, bulb simple with curved apophysis originating from ‘embolar division’ (conical projection of bulb carrying the sperm duct opening; Figs 27, 36, 38). Legs long (leg 1 \( \approx 10 \times \) body length), leg formula 1243, femora and tibiae usually with lighter tips and more-or-less distinct subdistal darker rings, legs with several rows of spines on femora and tibiae (Figs 50, 74; sometimes also proximo-dorsally on metatarsi), without curved hairs, vertical hairs in higher-than-usual density on femora, tibiae and metatarsi (in rows), retrolateral trichobothrium of tibia 1 at 4–6\%, retrolateral trichobothrium present on all tibiae; tarsi pseudosegmented \( \approx 40–45 \) on tarsi 1), tarsi 4 with complex comb-hairs distally (Figs 48, 49). Abdomen usually cylindrical, tapering posteriorly, in life ochre to brown, in alcohol bluish, often with white spots dorsally and laterally, ventrally with median line behind gonopore, genital plate light brown, without epiandrous spigots (Figs 43, 57, 69); six spinnerets (Fig. 44), anterior lateral spinnerets (ALS) with two spigots (one widened, one cylindrical to conical) and hole of unknown function at basis of terminal segment (Figs 41, 54, 80, 81), posterior median spinnerets (PMS) with two small pointed spigots (Figs 41, 61, 80), posterior lateral spinnerets (PLS) without spigots.

Sexual dimorphism slight, females with slightly shorter legs, sometimes rather oval abdomen, unmodified chelicerae, hairs ventrally on abdomen characteristically directed to sides (Fig. 53). Epigynum brown, sclerotised plate of varying shape, internal genitalia with round to elongated pore plates (Figs 55, 56, 76).

**Natural history**

Like most pholcids, *Tainonia* spiders prefer shady, humid, protected habitats like caves, overhangs and hollows in ravines (Fig. 7), spaces under logs or large palm leaf shafts (Fig. 8), or among large rocks in forests. Although most adults were found in such microhabitats, juveniles also occur in more exposed situations and higher in the vegetation. The only exception is *T. samana* where adults also build their webs higher in the vegetation, up to 2 m above the ground (Fig. 6). Webs are typically slightly domed sheets, often with a diameter of 70 cm or more.

**Distribution**

*Tainonia* spiders occur only on Hispaniola (Fig. 4). Large collections from Cuba and Puerto Rico as well as from mainland Central and South America have never been found to contain *Tainonia*. The genus is not known from Dominican amber.

**Composition and relationships**

We propose five nominal species, but the number should not be regarded as closed (see above). *Tainonia* is clearly part of the ‘New World clade’, a group of genera mostly or entirely restricted to the Americas (Huber 2000). Characters supporting this are the absence of epiandrous spigots and ALS piriform gland spigots, the exposed tarsal organ, the large distance between posterior median eyes (PME) and anterior lateral eyes (ALE) and the retrolateral coxa apophysis (cf. Huber 2000: p. 36). The phylogenetic analysis (Fig. 3) does not support a closer relationship between these taxa having a ventral apophysis on
the male palpal femur (Tainonia, Modisimus, Tupigea; cf. Fig. 66). Beyond that, Tainonia is not known to share any convincing apomorphy with another New World genus, so its exact position remains unknown.

**Tainonia serripes** (Simon)
(Figs 4a, 5, 7–14, 27–55)

_Blechroscelis serripes_ Simon, 1893: 479–481, 483; Bryant, 1948: 366–367, fig. 46; Huber, 1997: 578, fig. 2a–d.
_Tainonia serripes_: Huber, 2000: 146, figs 560–569.

**Material examined**

_Holotype_. ♀, unspecified locality on Hispaniola (’St. Dom.’, see Remarks below), date and collector not given, MNHN (6832), examined (see Huber 1997).

_Non-type material. Dominican Republic: San Cristóbal Prov._: degraded forest at river near Medina (18°30.8′N, 70°07.4′W), 100 m a.s.l., 7.xi.2005 (coll. BAH) 1♀, 1♂ (+ 3 juv. in pure ethanol, ZFMK Ar 1445, 46).
_Monserr Suelo Prov._: degraded forest at brook through plantation near Jima (19°01.4′N, 70°28.8′W), ~700 m a.s.l., near ground, 8.xi.2005 (coll. BAH) 5♂, 7♀ (+ 1 juv. in pure ethanol, ZFMK Ar 1447, 45). _Duarte Prov._: Reserva Scientifica Loma Quita Espuela, ~500 m a.s.l. (19°21.5′N, 70°09′W), 10.xi.2005 (coll. BAH) 3♂, 6♀ (+ 1 ♂ in pure ethanol, ZFMK Ar 1449, 50). _Maria Trinidad Sánchez Prov._: near La Entrada, forest above rocks at Santuario de La Virgen (19°34.9′N, 69°54.0′W), 15 m a.s.l., 12.xi.2005 (coll. BAH) 1♂, 3♀ (+ 1 ♂ in pure ethanol; ZFMK Ar 1451, 52).
_Puerto Plata Prov._: N of La Cumbre (19°34.3′N, 70°38.0′W), degraded forest near plantations, 600 m a.s.l., at rocks along dried brook, 13.xi.2005 (coll. BAH) 2♂, 5♀ (ZFMK Ar 1453); S of Puerto Plata, forest along path towards Isabel Torres National Park (19°46.4′N, 70°42.3′W), 350 m a.s.l., in vegetation and under overhangs, 14.xi.2005 (coll. BAH) 6♂, 5♀ (+ 1 juv. in pure ethanol, ZFMK Ar 1454, 55); Puerto Plata, iv.–v.1941 (coll. D. Hurst). _Barahona Prov._: 5 km NE Paraiso (18°01.9′N, 71°08.4′W), forest along brook, 60–150 m a.s.l., at rocks, under logs and overhangs, 18.xi.2005 (coll. BAH) 2♂, 8♀ (+ 3 juv. in pure ethanol, ZFMK Ar 1456, 57); 7 km NW Paraiso (18°02.4′N, 71°11.6′W), degraded forest along river, in vegetation and under logs, 180 m a.s.l., 7.xii.2007 (coll. BAH) 1♂, 5♀ (+ 4 juv. in pure ethanol, ZFMK Ar 1458, 59). _Peravia Prov._: near Nizao (18°36.0′N, 70°29.2′W), degraded forest along river, 670 m a.s.l., 19.xi.2005 (coll. BAH) 6♂, 3♀ (ZFMK Ar 1460). _Monte Plata Prov._: near Yamasa (18°45.9′N, 70°01.2′W), degraded forest along river, 70 m a.s.l., low vegetation and under logs, 20.xi.2005 (coll. BAH) 2♂, 4♀ (+ 2 juv. in pure ethanol, ZFMK Ar 1461, 62). _Hato Mayor Prov._: N of Manchado (18°50.2′N, 69°18.5′W), degraded forest near river, 150 m a.s.l., low vegetation and small cavities, 21.xi.2005 (coll. BAH) 1♂, 4♀ (+ 1 juv. in pure ethanol, ZFMK Ar 1463, 64). _La Romana Prov._: forest at Rio Chavón (18°26.5′N, 68°53.3′W), 20 m a.s.l., 23.xi.2005 (coll. BAH) 3♂ (ZFMK Ar 1465). _Haiti: Dept. Ouest._: Kenscoff, 6.i.x.1935 (collector not given). 1♂, 1♀ (AMNH); near Kenscoff (18°27.5′N, 72°17.4′W), degraded forest along brook, 1200 m a.s.l., 10.xii.2007 (coll. BAH) 2♀ (+ 4 juv. in pure ethanol, ZFMK Ar 1466, 67). _Dept. Sud._: Macaya Biosphere Reserve at 18°20.4′N, 74°00.9′W (’loc. 2′), degraded forest along ravine, 1290 m a.s.l., 29.xi.2007 (coll. BAH) 1♂, 2♀ (+ 3 juv. in pure ethanol; ZFMK Ar 1468, 69); same locality but 18°20.2′N, 74°01.3′W, degraded forest along ravine, 1220 m a.s.l., 1.xii.2007 (coll. BAH) 1♂, (ZFMK Ar 1470); same locality but 18°20.5′N, 74°01.0′W (’loc. 3′), 1350 m a.s.l., 30.xi.2007 (coll. BAH), 1 juv in pure ethanol (ZFMK Ar 1471). _Dept. Nord._: forest near

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**Fig. 4.** Known distributions of _Tainonia_ species. (a) _Tainonia serripes_. (b) The four new species described herein.
Labadie at 19°47.1′N, 72°14.5′W, 10–30 m a.s.l., domed sheets among rocks, 4.xii.2007 (coll. BAH), 2 juv. in pure ethanol (ZFMK Ar 1472). Unidentified locality: ‘Savanette, Valley of the Ex-2-Cheval′, cavernicolous, 23.iv.1958 (coll. S. Lazell), 1<,2> (AMNH).

Remarks

In previous publications (Huber 1997, 2000), the type locality was erroneously given as ‘Dominican Republic: Santo Domingo’. However, ‘St. Dom.’ denotes Saint Domingue (Simon 1893: 479) rather than Santo Domingo. Saint-Domingue was the name of the French colony that is now Haiti, but the name continued to be used until the 20th century. Saint-Domingue has sometimes also been used to refer to all of Hispaniola, but it is more likely that the Frenchman Eugène Simon referred to the French western part that is now the Republic of Haiti. The assignment of this name to the specimens above rather than to those of another species is not unambiguous. Only *T. samana* can be clearly excluded based on its female genitalia. The other three species are restricted to areas that are relatively difficult to access. In contrast, *T. serripes* as construed here occurs close to all major cities and ports (Port-au-Prince, Cap Haïtien, Puerto Plata, Santiago, San Francisco, Santo Domingo). We consider it most likely that the type specimen originates from a place near one of these cities.

Diagnosis

The type species as delimited here is distinguished primarily by negative characters: it does not have the flattened procursus tip and long epigynum with frontal hump like *T. samana* (cf. Figs 65, 66, 79); it does not have a monochromous carapace and relatively small male palps and small female pore plates like *T. bayahibe* (cf. Figs 2b, 24, 87); and it does not have the strongly curved procursus with distinctive distal sclerite like *T. cienaga* (cf. Figs 63, 64). The only positive distinguishing feature we found concerns the relationship between genital bulb length and palpal tibia length: *T. serripes* has a relatively shorter bulb than all other species, with only minimal overlap (Fig. 2a). Apart from that, there is considerable variation, both in the shape of the procursus and in the shape of the epigynum (Figs 29–35).

Description

**Male (near Jima)**

Total length 6.7, carapace width 2.4. Leg 1: 75.8 (20.4 + 0.9 + 18.0 + 30.9 + 5.6), tibia 2: 12.4, tibia 3: 9.7, tibia 4: 11.6. Tibia 1 L/d: 78. Habitus as in Fig. 5; carapace pale whitish with large brown marks laterally that reach median line frontally and posteriorly; ocular area brown with narrow light median stripe; clypeus brown; sternum medially orange-brown, laterally yellow, margins dark brown; legs brown, tips of femora and tibiae lighter, subdistal darker rings; abdomen bluish grey with darker bluish marks, ventrally bluish stripe behind gonopore; genital plate light brown. Distance PME–PME 275 μm; diameter PME 175 μm; distance PME–ALE 185 μm; distance AME–AME 25 μm; diameter AME 60 μm. Sternum wider than long (1.6/1.2). Chelicerae as in Fig. 40. Palps as in Figs 27, 28; coxa with retrolateral ridge and weakly sclerotised (light) depression, trochanter simple, femur proximal apophysis without distal projection, distal apophysis with subdivided tip, tibia without dorso-distal hump, procursus slightly curved, with distal structures as in Figs 36, 39. Retrolateral trichobothrium of tibia 1 at 5%; tarsus 1 with ~45 pseudosegments, very distinct.
Variation

Tibia 1 ($N=30$): 12.9–19.2 (mean: 16.1); carapace width ($N=34$): 1.4–2.8 (mean: 2.2); bulb length ($N=34$): 0.72–1.22 (mean: 1.01); palpal femur length ($N=34$): 0.84–1.54 (mean: 1.17); palpal tibia length ($N=34$): 0.72–1.26 (mean: 1.01); palpal tibia width ($N=34$): 0.40–0.76 (mean: 0.57). In some specimens the sternum is homogenous orange with brown margins, in others there are light marks at the bases of the coxae; some specimens with only lateral marks on carapace (especially smaller specimens); in specimens from Santuario de la Virgen the lateral marks are rather yellow with smaller dark spots; some specimens with monochromous bluish-grey abdomen. These colour variations are found also within populations. Genital morphology is in contrast very constant within populations, but shows considerable variation among populations. Figs 28–32 show the procursi of specimens from five localities (see also Huber 2000: fig. 563 for a sixth locality); in contrast, the bulbal apophyses show only minimal variation.

Female

In general similar to male, including colour variation. Tibia 1 ($N=61$): 11.2–19.2 (mean 15.3); carapace width ($N=63$): 1.33–2.83 (mean: 2.20); epigynum length ($N=65$): 0.60–1.40 (mean: 1.06); epigynum width frontally ($N=65$): 0.30–1.02
(mean: 0.65); epigynum width posteriorly (N = 66): 0.60–1.50 (mean: 1.10). Epigynum quite flat, slightly elevated frontally in specimens from Loma Quita Espuela and Santuario de la Virgen, much wider posteriorly in females from SW-Dominican Republic and Haiti (Figs 34, 35); internally with round to oval pore plates (Figs 33–35, 55). Egg-sacs round with a diameter of ~3.5–5.0 mm.

**Distribution**

Widely distributed on Hispaniola (Fig. 4a).

**Tainonia cienaga**, sp. nov.

(Figs 4b, 18–20, 56–64, 84)

**Material examined**

Holotype. ♂ near La Ciénaga, (~19°03’N, 70°53’W), La Vega Prov., Dominican Republic; path along river at ~1100 m a.s.l., at rocks, 9.xi.2005 (coll. BAH), in ZFMK (Ar 1473).

Non-type material. Dominican Republic: La Vega Prov.: near La Ciénaga, same data as holotype, 7♂, 2♀ (ZFMK Ar 1474); near La Ciénaga, path to Los Tablones (19°03.5’N, 70°53.0’W), ~1200 m a.s.l., 8.xi.2005 (coll. BAH) 1♂, 3♀ (ZFMK Ar 1475); Ciénaga, Parque Nacional A. Bermudez, tropical evergreen forest, 1100 m a.s.l., 19.vii.–2.viii. 1995 (coll. S. & J. Peck) 1♂, (AMNH); La Ciénaga, along Arroyo Frío (19°04’N, 70°51’W), at night, 8.i.1986 (coll. S. Larcher, C. Domínguez, F. Mora) 1♂, (USNM).

**Diagnosis**

Distinguished from congeners by the shape of the procursus with distinctive distal sclerite (Figs 63, 64) and by the dorsal hump distally on the male palpal tibia (Figs 63, 64); apparently also by the longer sclerites posteriorly attached to the pore plates (Fig. 84). *T. cienaga* differs from *T. serripes* also by the longer bulb in relation to the palpal tibia (Fig. 2a).

**Description**

**Male (holotype)**

Total length 7.7, carapace width 2.6. Leg 1: 74.9 (19.7 + 1.1 + 18.1 + 29.7 + 6.3), tibia 2: 12.7, tibia 3: 10.1, tibia 4: 12.1. Tibia 1 L/d: 76. Habitus as in Fig. 18; carapace pale ochre with large brown marks that reach median line frontally and posteriorly; ocular area dark brown with narrow light median stripe; clypeus dark brown; sternum ochre with brown median mark and dark brown margins; legs brown, femora almost black, tips of femora and tibiae ochre-yellow; abdomen almost monochromous grey, genital plate light brown. Distance PME–PME 275 µm; diameter PME 195 µm; distance PME–ALE 185 µm; distance AME–AME 45 µm; diameter AME 80 µm. Sternum wider than long (2.0/1.5). Palps as in Figs 63, 64; coxa with retrolateral ridge and weakly sclerotised (light) depression, trochanter simple, femur proximal apophysis without distal projection, distal apophysis with subdivided tip, tibia with distinctive dorso-distal hump, procursus strongly curved, with distal structures as in Fig. 60. Retrolateral trichobothria of tibia 1 at 4%; tarsus 1 with ~45 pseudosegments, very distinct.

**Variation**

Tibia 1 (N = 10): 13.7–18.4 (mean: 15.9); carapace width (N = 10): 1.7–2.6 (mean: 2.1); bulb length (N = 11): 0.94–1.26

Figs 27, 28. *Tainonia serripes* from Jima, left male palp in prolateral and retrolateral views. b, genital bulb; ba, bulbal apophysis; fe, femur; pr, procursus; ti, tibia. Scale line: 0.5 mm.
(mean: 1.08); palpal femur length \((N=11)\): 0.94–1.38 (mean: 1.14); palpal tibia length \((N=11)\): 0.74–1.04 (mean: 0.88); palpal tibia width \((N=11)\): 0.42–0.58 (mean: 0.48).

Most specimens lighter than type specimen, especially legs; pattern on abdomen often quite distinct: dark bluish marks on bluish-grey background, ventrally short median bluish line behind gonopore; some specimens also with rows of white spots on abdomen; femora and tibiae often with dark subdistal ring before light tip. Both carapace pattern and shape of genitalia very constant.

**Female**

In general similar to male, including colour variation. Tibia 1 \((N=5)\): 12.8–18.7 (mean 14.8); carapace width \((N=4)\): 1.7–3.0 (mean: 2.1); epigynum length \((N=5)\): 0.86–1.46 (mean: 1.04); epigynum width frontally \((N=5)\): 0.50–1.00 (mean: 0.69); epigynum width posteriorly \((N=5)\): 0.82–1.54 (mean: 1.02). Epigynum a bulging plate without median hump, with whitish area uniformly wide across entire width (Fig. 20); internally with round pore plates with long sclerotised structures posteriorly (Figs 56, 84).

**Distribution**

Known from La Ciénaga area only (Fig. 4b).

**Etymology**

The species name is a noun in apposition, derived from the type locality.

*Tainonia samana*, sp. nov.

(Figs 4b, 6, 21–23, 65–81, 85)

**Material examined**

*Holotype*. ♂, S of Las Galeras \(19^\circ12.8'\mathrm{N}, 69^\circ13.1'\mathrm{W}\), Samaná Prov., Dominican Republic; forest above rocks, domed webs in vegetation, 20 m a.s.l., 12.xi.2005 (coll. BAH), in ZFMK (Ar 1476).

*Non-type material*. **Dominican Republic: Samaná Prov.**; degraded forest near Sánchez (road to Las Terrenas) \(19^\circ14.5'\mathrm{N}, 69^\circ35.9'\mathrm{W}\), in low vegetation and sheltered areas, 290 m a.s.l., 11.xi.2005 (coll. BAH), 8♀, 14♂ (+ 2♂, 2♀ in pure ethanol, ZFMK Ar 1477, 78); degraded forests near Salto de Limón \(19^\circ16.6'\mathrm{N}, 69^\circ26.5'\mathrm{W}\), ~120 m a.s.l., in low vegetation, at rocks, in cave, 11.xi.2005 (coll. BAH), 9♀, 16♂ (+ 1♂, 3♀ in pure ethanol, ZFMK Ar 1479, 80); S of Las Galeras \(19^\circ12.8'\mathrm{N}, 69^\circ13.1'\mathrm{W}\), forest above rocks, domed webs in vegetation, 20 m a.s.l., 12.xi.2005 (coll.
BAH), 10.5, 8(3 juv. in pure ethanol, ZFMK Ar 1481, 82). La Romana Prov.: near Batey El Gato (18°27.7'N, 69°04.7'W), near entrance to cave, 80 m a.s.l., at rocks, 24.xi.2005 (coll. BAH), 1♂, 3♀ (ZFMK Ar 1483). El Seibo Prov.: near Miches (18°56.8'N, 69°05.2'W), forest with plantations, ~300 m a.s.l., low vegetation, 22.xi.2005 (coll. BAH), 1♂, 1♀ (ZFMK Ar 1484).

Diagnosis
Easily distinguished from congeners by the flattened sclerite distally on the procursus (Figs 65, 66, 70), the long male palpal tibia (in relation to its diameter; Fig. 2c), the shapes of the proximal and distal male palpal femur apophyses (Fig. 66), the long epigynum with almost parallel lateral margins and distinct frontal hump (Figs 2d, 23, 79) and the long pore plates (Figs 76, 85).

Description

Male (holotype)

Total length 7.5, carapace width 2.2. Leg 1: 69.8 (18.1+0.9+16.4+29.9+4.5), tibia 2: 10.5, tibia 3: 8.4, tibia 4: 9.7. Tibia 1 L/d: 74. Habitus as in Fig. 21; carapace pale ochre-yellow with brown marks laterally; ocular area laterally brown; clypeus slightly darker than carapace; sternum light brown to orange, with dark brown margins and lighter bands laterally; legs light brown, tips of femora and tibiae whitish; abdomen bluish-grey with darker bluish marks, long bluish stripe ventrally behind gonopore, genital plate light brown. Distance PME–PME 240 μm; diameter PME 150 μm; distance PME–ALE 150 μm; distance AME–AME 45 μm; diameter AME 60 μm. Sternum wider than long (1.5/1.2). Chelicerae as in Fig. 67. Palps as in Figs 65, 66; coxa with retrorotateral ridge and weakly slerotised (light) depression, trochanter simple, femur proximal apophysis with distinctive distal projection, distal apophysis with undivided simple tip, tibia without dorso-distal hump, relatively longer than in other species (Fig. 2c), procursus weakly curved, with distinctively flattened distal structure. Rotorotateral trichobothrium of tibia 1 at 5%; tarsus 1 with ~40 pseudosegments, very distinct.

Variation

Tibia 1 (N=27): 11.5–17.1 (mean: 14.0); carapace width (N=29): 1.3–2.2 (mean: 1.7); bulb length (N=29): 0.82–1.14
Some specimens with additional brown margin posteriorly on carapace; sternum either monochromous orange or with lighter lateral bands; some specimens with distinct rows of white spots on abdomen.

Female

In general similar to male, including colour variation. One specimen only with lateral marks reaching midline frontally (large specimen from S Las Galeras). Tibia 1 (N = 37): 8.5–16.9 (mean 13.5); carapace width (N = 40): 1.0–2.5 (mean: 1.7); epigynum length (N = 42): 0.50–1.20 (mean: 0.90); epigynum width frontally (N = 42): 0.40–0.94 (mean: 0.64); epigynum width posteriorly (N = 42): 0.40–1.10 (mean: 0.78). Epigynum a long bulging plate with distinctive frontal median hump (Fig. 79); internally with very elongated pore plates (Figs 76, 85).

Natural history

In contrast to all other species of *Tainonia*, *T. samana* was mainly found in the forest vegetation up to 2 m above the ground rather than in protected habitats like crevices and hollows in ravines or under logs on the ground.

Distribution

Known from several localities on Samaná Peninsula and two localities in eastern Dominican Republic (Fig. 4b).

Etymology

The species name is a noun in apposition, derived from the type locality.

*Tainonia visite*, sp. nov.

(Figs 4b, 15–17, 82, 83, 86)

Material examined

**Holotype.** ♀, La Visite National Park, Case Dent (18°20.2’N, 72°16.4’W), Dept. Sud-Est, Haiti; 1880 m a.s.l., ravine in pine forest, 27.xi.2007 (coll. BAH), in ZFMK (Ar 1485).

**Non-type material.** Same data as holotype: 1♀, 2♂ (+ 2♂ 1 juv. in pure ethanol; ZFMK Ar 1486, 87).
Fig. 52–62. *Tainonia serripes* (52–55) and *T. cienaga* (56–62). 52, Epigynum. 53, Area behind epigynum. 54, Female anterior lateral spinneret. 55, 56, Cleared internal genitalia with pore plates. 57, Male gonopore. 58, Portrait of male, showing barely modified chelicerae. 59, Male palpal tarsal organ. 60, Left procursus and bulb tip, prolateral view. 61, Male functional spinnerets. 62, Male palpal trichobothrium base. b, genital bulb; pr, procursus. Scale lines: 10 μm (59, 62), 40 μm (54, 61), 60 μm (57), 200 μm (56), 300 μm (53, 55, 60), 500 μm (52), 600 μm (58).
Diagnosis

Distinguished from congeners by the slender procursus (Fig. 83), the long bulbal apophysis (Fig. 82), the relatively long bulb (in relation to palpal tibia length; Fig. 2a) and the small palp in relation to body size (Fig. 2b; similar in T. bayahibe).

Figs 63, 64. *Tainonia cienaga*, left male palp in prolateral and retrolateral views. Scale line: 0.5 mm.

Figs 65, 66. *Tainonia samana*, left male palp in prolateral and retrolateral views. Scale line: 0.5 mm.
Description

Male (holotype)

Total length 7.5, carapace width 2.8. Leg 1: 74.9 (19.7 + 1.2 + 18.4 + 29.5 + 6.1), tibia 2: 13.1, tibia 3: 10.7, tibia 4: 12.5. Tibia 1 L/d: 52. Habitus as in Fig. 15; carapace yellowish with dark brown marks, ocular area dark except median light stripe, on both sides of ocular area whitish, clypeus light brown, sternum light brown with dark brown margins, labium dark brown, legs brown, patella area and tibia subdistally darker, abdomen bluish grey, dorsally darker than ventrally, genital plate brown. Distance PME–PME 370 μm; diameter PME 205 μm; distance PME–ALE 175 μm; distance AME–AME 45 μm; diameter AME 90 μm. Sternum wider than long (2.0/1.4). Palps as in Figs 82, 83; coxa with retrolateral ridge and weakly sclerotised (light) depression, very large in relation to other palpal segments, trochanter simple, femur proximal apophysis without distal projection, distal apophysis with subdivided tip, tibia without dorso-distal hump, procursus very slender, weakly curved, with simple distal structures, bulbal apophysis very long. Retrolateral trichobothrium of tibia 1 at 6%; tarsus 1 with ~45 pseudosegments, very distinct except proximally.

Variation

The second male is paler (younger?), carapace pattern similar, abdomen with distinct pattern of white spots arranged...
in lines (dorsal and lateral) or patches. Tibia 1: 18.0, carapace width: 2.6.

**Female**

In general similar to male, abdomen in both females without distinct white spots. Tibia 1: 16.4, 16.5; carapace width: 2.6, 2.8. Epigynum only slightly wider posteriorly (Fig. 17); internally with oval pore plates (Fig. 86).

**Distribution**

Known from type locality only (Fig. 4b).

**Etymology**

The species name is a noun in apposition, derived from the type locality.
Figs 82, 83. *Tainonia visite*, left male palp in prolateral and retrolateral views. Scale line: 0.5 mm.

Figs 84–88. 84–87, Cleared epigyna (all at same scale) in dorsal views, *Tainonia cienaga* (84), *T. samana* (85), *T. visite* (86), and *T. bayahibe* (87). 88, *T. bayahibe*, left procursus, retrolateral view. Scale lines: 0.5 mm.
**Tainonia bayahibe**, sp. nov.  
(Figs 4b, 24–26, 87, 88)

**Material examined**

Holotype. ♀, near Bayahibe (18°23.0’N, 68°49.9’W), La Altugracia Prov., Dominican Republic; arid forest along road, 30 m a.s.l., in small cavity, 23.xi.2005 (coll. BAH), in ZFMK (Ar 1488).

Non-type material. Same data as holotype: ♂, 1 juvenile (Ar 1489).

**Diagnosis**

Distinguished from congeners by the monochromous whitish carapace (Figs 24, 25), by the relatively small male palps (Fig. 2b; similar only in *T. visite*) and by the relatively small female pore plates (Fig. 87).

**Description**

**Male (holotype)**

Total length ~7.5 (abdomen damaged), carapace width 2.8. Leg 1: 77.0 (20.1 + 1.1 + 18.4 + 32.5 + 4.9), tibia 2: 11.7, tibia 3: 9.5, tibia 4 missing. Tibia 1 L/d: 77. Habitus as in Fig. 24; carapace distinctively whitish, ocular area brown with dark lateral marks, clypeus also light brown, chelicerae dark brown; sternum orange-brown with dark brown margins and slightly lighter (yellowish) marks at bases of coxae; legs brown, tips of femora and tibiae whitish, dark brown before whitish tip; abdomen almost monochromous whitish, genital plate light brown. Distance PME–PME 320 μm; diameter PME 175 μm; distance PME–ALE 175 μm; distance AME–AME 35 μm; diameter AME 70 μm. Sternum wider than long (1.6/1.2). Palps in general similar to *T. serripes* (cf. Figs 27, 28) but femur distal apophysis with undivided tip, procursus as in Fig. 88. Retrolateral trichobothrium of tibia 1 at 5%, tarsus 1 with ~40 pseudosegments, very distinct.

**Female**

In general similar to male, including whitish carapace, but abdomen bluish to greenish-grey, with rows of large white spots (Fig. 25) and sternum monochromous orange-brown with dark margin. Tibia 1: 17.3; carapace width: 2.5. Epigynum distinctly wider posteriorly (Fig. 26); internally with very small oval pore plates (Fig. 87).

**Distribution**

Known from type locality only (Fig. 4b).

**Etymology**

The species name is a noun in apposition, derived from the type locality.

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