

Exceptional diversity of *Stefania* (Anura, Cryptobatrachidae) II: Six species from Mount Wokomung, Guyana

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Abstract

Exceptional diversity of *Stefania* (Anura, Cryptobatrachidae) II: Six species from Mount Wokomung, Guyana. Six species of *Stefania* were collected on Mount Wokomung, a tepui in the Pakaraima Mountains of Guyana. This unusually high diversity of *Stefania* is similar to that found on a neighbouring tepui, Mt. Ayanganna. The two tepuis support slightly different habitats. Conspecific *Stefania* from the two mountains differ somewhat in body size, toe disc size and colouration. Specimens from Mt. Wokomung are used to expand descriptions and distributions of some species.

Keywords: Anura, Cryptobatrachidae, *Stefania*, diversity, tepuis, Guyana.

Introduction

Since the genus *Stefania* was erected by Rivero ("1966" [1968]), 18 species have been described (Rivero "1966" [1968], 1970, Duellman and Hoogmoed 1984, Myers and Donnelly 1997, Señaris *et al.* "1996" [1997], MacCulloch and Lathrop 2002, Barrio-Amorós and Fuentes 2003). Recently *Stefania* has been removed from the Hylidae and placed into a new family, the Cryptobatrachidae (Frost *et al.* 2006). As in other Cryptobatrachids, the eggs of *Stefania* are carried on the female's back, and hatch into froglets, without a tadpole stage (Duellman and Hoogmoed 1984, Jungfer and Boehme 1991).

Stefania is a Guiana Shield endemic, occurring from the Essequibo River in Guyana to western Amazonas State, Venezuela, and in northern Brazil (MacCulloch and Lathrop 2002, Barrio-Amorós and Fuentes 2003, Caramaschi and Niemeyer 2005). Many species occur at high elevations on tepuis in the Guiana Shield region. Most accounts of *Stefania* report only one or two species per mountain, with the exception of Mount Ayanganna, Guyana, where five species were collected sympatrically on the slopes at 1490–1550 m, plus two other species at the base, at 870 m (MacCulloch and Lathrop 2002).

Mount Wokomung (05°04'53" N, 59°50'28" W), south of Mt. Ayanganna, is one of the easternmost tepuis in the Guiana Shield (Figure 1). It is separated from Ayanganna by 37 km of uplands, which support lower montane forest

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habitat (Huber *et al.* 1995). Herein we report on *Stefania* from Mount Wokomung. Comparison of the faunas of these neighbouring mountains provides insight into the zoogeography of the Guiana region.

In October–November 2004, collections were made at four locations on Mount Wokomung: the base of the mountain in lower montane forest, 698 m; two locations on the north face in montane or upper montane forest, 1234 and 1411 m; and on the summit in tepui bog habitat, 1698 m. Additional collections were made en route to the mountain in lower montane forest, 600–700 m.

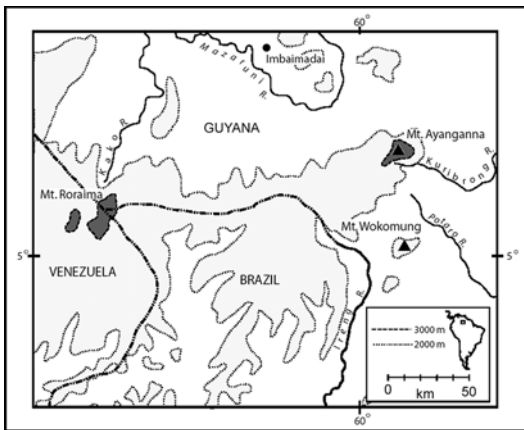


Figure 1 - Map of western Guyana showing the locations of Mount Wokomung and Mount Ayanganna.

The higher-elevation habitat on Wokomung is different from that on Ayanganna. The northeastern slope of Ayanganna, where the specimens reported in MacCulloch and Lathrop (2002) were collected, consists of a series of relatively flat plateaus separated by steep slopes. Above 1200 m the plateaus support low-canopy high-tepui forest with dense ground cover, whereas the slopes are covered by medium-canopy montane forest. Most collections from Ayanganna were made on the plateaus. In contrast, Wokomung has only a few small plateaus, and its slopes at comparable elevations are covered in medium-canopy montane forest, with a more open understory than is found on Ayanganna (Figure 2A; contrast with Figure 1 in MacCulloch and Lathrop 2002). The summit of Wokomung is a shallow bowl, with tepui bog habitat at its centre and montane forest at the edge of the summit (Figure 2B).

Material and Methods

Specimens were collected by hand, usually at night. Most *Stefania* were on vegetation, with few on the ground. Specimens were euthanized using clove oil diluted in 95% ethanol, then fixed in formalin; tissue (liver) was removed and preserved in 95% ethanol. Collected specimens were compared with museum specimens (Appendix I) or published descriptions. New collections of *Stefania* were used to redefine



Figure 2 - Habitat of *Stefania* on Mount Wokomung. (A) Montane forest on the north slope, 1411 m; (B) Evergreen tepui bog habitat at the summit, 1698 m.

distributions and elaborate upon existing species descriptions. All measurements were made with digital calipers and rounded to 0.1 mm. Interdigital webbing is described using the formula of Lescure (1975) and Myers and Duellman (1982), as refined by Savage and Heyer (1997). All specimens described herein are in the collections of the Centre for the Study of Biological Diversity at the University of Guyana (CSBD) or the Royal Ontario Museum (ROM).

Results

Six species of *Stefania* (*S. ackawaio*, *S. ayangannae*, *S. coxi*, *S. evansi*, *S. roraimae* and *S. woodleyi*) were collected from various habitats on Mount Wokomung. Each species is treated separately, below.

Stefania ackawaio MacCulloch and Lathrop
Stefania ackawaio MacCulloch and Lathrop
[Holotype ROM 39473,
from Mt. Ayanganna, Guyana] 2002: 334.

At Ayanganna only one adult male of 46 mm SVL, two subadult females and one juvenile were collected at 1490–1550 m. At Wokomung this species was abundant at both 1234 m and 1411 m and the number of specimens collected was greater: 14 females ranging from 39–66 mm SVL, nine males, 34–48 mm SVL and six independent juveniles, 20–22 mm SVL. Additional individuals were seen but not captured.

In general, specimens from Wokomung resemble the type series from Mount Ayanganna, although some individuals at Wokomung have a grey background colour, rather than the brown background which is present in animals from Ayanganna. Some individuals from Wokomung have patches of reddish colour on dorsum and limbs, which are also found in sympatric *S. ayangannae* and *S. evansi* (Figure 3A). The number of vomerine teeth is 6–9.

Inclusion of the specimens from Wokomung expands the webbing formula of *S. ackawaio* to

I (2-2½) – (2-2½) **II** (1¾-2) – (2½-3) **III** (2¼-2½) – (3-3¼) **IV** (3-3¼) – (2-2¼) **V**.

Stefania ackawaio from Wokomung exhibited variation in size of finger discs, although this variation is less marked than in some other species of *Stefania* (see below). In larger specimens, finger and toe discs are proportionally larger than in smaller individuals. The largest finger disc, on the largest specimen, covers 75% of the tympanum, while in individuals with smaller discs about 66% of the tympanum is covered.

No females were carrying eggs or juveniles, and none had enlarged ova. However, two females retained remnants of the dorsal mucoid layer, indicating that they had recently carried juveniles.

Stefania ackawaio was much more abundant at Wokomung than at Ayanganna, where few were collected at 1490–1550 m. The reason for this is unknown, although it may be that *S. ackawaio* prefers the more open higher-canopy habitat found on Wokomung rather than the dense low-canopy habitat on Ayanganna.

Stefania ayangannae MacCulloch and Lathrop
Stefania ayangannae MacCulloch and Lathrop
[Holotype ROM 39501,
from Mt. Ayanganna, Guyana] 2002: 329.

Stefania ayangannae was the most abundant anuran species encountered at 1411 m, and was fairly numerous at 1234 m. At both locations *S. ayangannae* were found primarily on leaves or branches. On the summit of Wokomung (1698 m), in tepui bog habitat, five adult females were found concealed in the centre of large terrestrial bromeliads. At the rim of the summit, in low-canopy forest habitat, a subadult of 29 mm SVL was collected. In all 15 females of 32–50 mm SVL, six males, 32–40 mm SVL and five juveniles or subadults, 16–30 mm SVL were collected. Additional individuals were seen but not captured.

Stefania ayangannae from Wokomung are similar to those from Ayanganna except that the

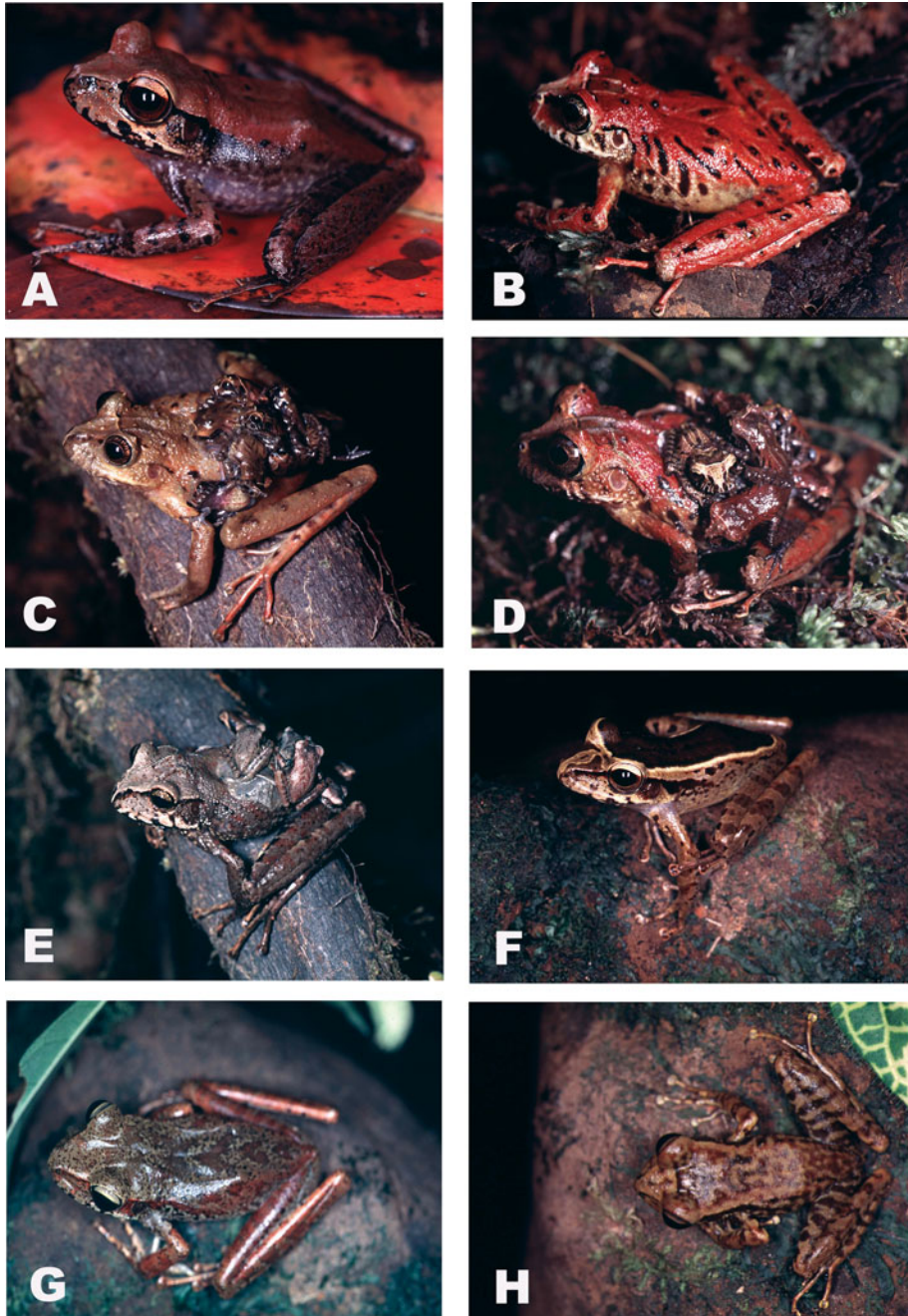


Figure 3 - *Stefania* from Mount Wokomung. (A) *Stefania ackawaio*, ROM 42807, female, 57 mm SVL; (B) *Stefania ayangannae* ROM 42907, female, 42 mm SVL; (C) *Stefania ayangannae* ROM 42952, 50 mm SVL; (D) *Stefania ayangannae*, ROM 42918, 50 mm SVL; (E) *Stefania coxi*, ROM 42856, female, 62 mm SVL; (F) *Stefania evansi*, striped morph, ROM 42891, female, 50 mm SVL; (G) *Stefania evansi*, brown morph with chevron pattern, ROM 42879, female, 72 mm SVL; (H) *Stefania woodleyi*, ROM 42832, male, 41 mm SVL.

second finger is slightly shorter in specimens from Wokomung, reaching the ultimate joint on the first finger (reaches base of disc in frogs from Ayanganna). Maximum size at Wokomung (51 mm for females, 40 mm for males) exceeded that recorded from Ayanganna (48 and 37 mm). Many specimens from Wokomung, of all sizes, had reddish dorsal background colour rather than the yellow background which predominated at Ayanganna (Figure 3B – contrast with Figure 3 in MacCulloch and Lathrop 2002); reddish colour occurred in *S. ackawao* and *S. evansi* from Wokomung as well.

In general, larger individuals of *S. ayangannae* of both sexes have a more tubercular dorsum and darker colouration than do smaller individuals (Figure 3C). In some larger individuals the upper rim of the palpebrum carries a dark brown band, rather than the yellow band present in most specimens from Wokomung and all individuals from Ayanganna. Vomerine teeth 5.

The webbing formula for *S. ayangannae*, based on specimens from Wokomung and Ayanganna, is **I** (2½-3) – (2½-3) **II** (2-2⁺) – (3-3¼) **III** (2¼-2½) – (3½-3¾) **IV** (3½-3¾) – (2-2¼) **V**. Although there is a slight tendency for larger individuals to have more extensive webbing, this correlation is not as marked as it is in *S. evansi*. *Stefania ayangannae* has the least toe webbing of any *Stefania* (MacCulloch and Lathrop 2002).

Stefania ayangannae also exhibits variation in size of finger discs (Figure 4). In most individuals from Wokomung the largest finger disc is 75% of the tympanum diameter, as reported in MacCulloch and Lathrop (2002), while in others it is equal to or greater than the tympanum diameter. About one-third of *S. ayangannae* from Wokomung have large discs; increase in disc size is not related to sex, but it is more common in larger individuals. Re-examination of the specimens from Ayanganna found that the phenomenon of large discs is less common there, with larger discs present in only two large females and one subadult.

The five females collected on the summit of Wokomung are all large, 47–50 mm SVL. All

were carrying juveniles, either five (N=2) or eight (N=3) juveniles (Figure 3D). Two other females, 48 and 50 mm SVL, collected in forest habitat at 1411 m, were carrying four and six juveniles respectively. The largest number of offspring reported in *S. ayangannae* at Ayanganna was four (MacCulloch and Lathrop 2002).

Intra- and interpopulation variation in disc size, finger length, skin texture and colouration occurs in *Stefania ayangannae* from Wokomung and Ayanganna. This variation may be indicative of the presence of cryptic species. However, until a more detailed study can be undertaken, we provisionally assign the specimens from both locations to the same species.

Stefania coxi MacCulloch and Lathrop

Stefania coxi MacCulloch and Lathrop

[Holotype ROM 39477,

from Mt. Ayanganna, Guyana] 2002: 336.

One female of 62 mm SVL, carrying 4 juveniles, was collected on the summit of Mt. Wokomung in tepui bog habitat, on a dense mat of bromeliads (Figure 3E).

The adult resembles the specimens from Ayanganna with the following differences: head less broad, although still wider than long (width 1.1 X length); supratympanic crests slightly less prominent; largest finger disc slightly smaller than tympanum diameter; supernumerary palmar and plantar tubercles less prominent; colour grey, rather than brown. Vomerine teeth 5. These differences are within the range of interpopulation variation.

The foot webbing formula for all individuals from both locations is **I** (2⁺-2¼) – 2¼ **II** (2-2⁺) – (3-3⁺) **III** (2-2⁺) – (3½-3¾) **IV** 3½ – (2-2⁺) **V**.

The four juveniles measured 18–19 mm SVL, and none retained any visible vestige of yolk, so it is assumed that they are near to attaining independence. The mucoid layer on the female's back retained the impression of 7–8 eggs, indicating that other juveniles had recently left the female's care. This species is the only

representative of the broad-headed *S. goini* group that is known from Guyana. Members of this group seem to prefer tepui summit habitat (Señaris *et al.* “1996” [1997]). *Stefania coxi* was found only on the summit of Wokomung, despite intensive collecting on the slopes. On Ayan-ganna it was found in low-canopy forest (MacCulloch and Lathrop 2002). This indicates that *S. coxi* prefers low-canopy or summit habitat rather than medium- or high-canopy forest.

Stefania evansi Rivero

Hyla evansi Boulenger [Holotype BMNH 1947.106 from Groete Creek, Guyana] 1904: 106.

Stefania evansi Rivero “1966” [1968]: 143.

This species was abundant in suitable habitat at lower elevations, at two locations near the base of Mount Wokomung between 680–698 m. None were encountered at the next highest site (1234 m). All specimens were found on vegetation near streams in the forest. Two colour morphs, uniform brown and dorsolaterally striped (morphs A and B of Duellman and Hoogmoed 1984) were collected, the former at both low-elevation locations, the latter at one location only, 698 m elevation. Of the 32 specimens collected, 26 were uniform and six were striped (Figure 3F).

Females measured 45–78 mm SVL (N=9), males 46–52 mm (N=6), subadults 29–40 mm (N=13). The largest striped individuals, two females, measured 50 mm SVL. One adult female of 72 mm SVL (Figure 3G) retained an indistinct dorsal chevron pattern, which is typically present in juveniles (Duellman and Hoogmoed 1984, MacCulloch and Lathrop 2002). Four independent juveniles measuring 19.5–22 mm SVL were collected; three have the dorsal chevron pattern while one was unmarked. Vomerine teeth 7–10.

The foot webbing formula of individuals from several locations in the Pakaraima region is **I** 1 – (1⁺-1¼) **II** 1 – (1⁺-1½) **III** (1-1⁺) – (2-

2¼) **IV** (2-2¼) – (1-1⁺) **V**. Foot webbing is slightly more extensive on larger specimens than on smaller individuals. *Stefania evansi* has the most extensive webbing of the genus.

Most adults, regardless of colour pattern, had red canthal and supratympanic lines. Some individuals of uniform brown colour pattern had reddish patches or spots on dorsum, flanks and limbs (Figure 3G). The red colour fades in preservative. Venter white, with or without brown mottling. Dark brown or black cross-bands on thighs present or absent, but all individuals have black spots on the distal portion of the anterior surface of the thigh.

Specimens of *S. evansi* with dorsolateral stripes (Pattern B of Duellman and Hoogmoed 1984) bear a superficial resemblance to *S. roraimae*. In addition to the obvious differences in toe webbing and elevational preference, they can be readily distinguished by canthal profile, skin texture and colouration of thigh, flank and venter (MacCulloch and Lathrop 2002).

Some individuals have unusually large finger discs. It has been stated that the finger and toe discs in *S. evansi* are approximately equal in size (Señaris *et al.* “1996” [1997], Duellman and Hoogmoed 1984). This is true for most individuals, but in some specimens, the finger discs are unusually large (Figure 5). Most specimens with proportionally larger discs are larger individuals, although not all large *S. evansi* had larger discs, and larger discs were present in some smaller animals of both sexes as well. This situation seems the same as in *S. ayangannae*.

No enlarged ova or other internal evidence of impending reproductive activity were seen. Dry season was ending, and the November–December rainy season imminent. However, the collection of several small juveniles, apparently newly independent, indicated that the reproductive season was nearing completion. At Ayan-ganna one female *S. evansi* with juveniles was collected at the same time of year.

Many characteristics traditionally used to identify this species are variable. The name *Stefania evansi* has been applied to all *Stefania*



Figure 4 - Variation in size of finger discs in similar-sized *Stefania ayangannae* from Mount Wokomung. Left, ROM 42913 (49 mm SVL); right, ROM 42946 (50 mm SVL). Scale bar = 2 mm.



Figure 5 - Variation in size of finger discs in similar-sized *Stefania evansi* from Mount Wokomung. Left, ROM 42891 (49 mm SVL); right, ROM 42875 (49 mm SVL). Scale bar = 2 mm.

with extensive toe webbing from below 900 m. A detailed study of these specimens is needed to determine the possible presence of cryptic species.

Stefania roraimae Duellman and Hoogmoed
Stefania roraimae Duellman and Hoogmoed
 [Holotype UGDB 10, from Mt. Roraima,
 Guyana] 1984: 24–25.
Stefania sp “A” Hoogmoed 1979: 272.

This species has been reported from both Mount Roraima and Mt. Ayanganna, but only females and subadults were collected at these two locations (Duellman and Hoogmoed 1984, MacCulloch and Lathrop 2002). At Wokomung both sexes were collected, at 1234 and 1411 m. Females ranged from 36–68 mm SVL (N=8), males 36–46 mm SVL (N=6). No females had enlarged ova, or exhibited any sign of recent reproductive activity. Five juveniles, SVL 19–22 mm, identified as *S. roraimae* because of their pattern of dorsolateral light stripes and reduced toe webbing, were collected at 1234 and 1411 m.

Stefania roraimae from Wokomung conform to the descriptions from other locations. In the specimen collected at Roraima, the largest finger

disc covered 33% of the tympanum diameter, while in the adults from Ayanganna the disc covered 75% of the tympanum diameter (Duellman and Hoogmoed 1984, MacCulloch and Lathrop 2002). In the more extensive sample from Wokomung this ratio varies from about 50% to about 75%, with no difference between sexes. Although smaller individuals (<40 mm SVL) tend to have relatively smaller discs than larger animals, variation in disc size is not completely correlated with SVL. Variation in disc size in *S. roraimae* between Ayanganna and Wokomung is not as marked as it is in *S. ayangannae*.

Foot webbing formula for individuals from Ayanganna, Wokomung and Roraima is **I** (2–2) – (2–2½) **II** (1¾–2) – (2½–3) **III** (2–2½) – (3–3¾) **IV** (3–3½) – (2–2½) **V**. Vomerine teeth 8–10.

In general the specimens from Wokomung have darker mottling ventrally than do specimens from Ayanganna. Some specimens from Wokomung have small dark spots in the cream-coloured dorsolateral and interorbital lines; these spots are not present in specimens from Ayanganna. In the specimens from Wokomung the dark colours are predominantly grey, whereas the specimens from Ayanganna are

brown. Juvenile *S. roraimae* are uniformly yellow-green at night, with only the outline of the stripes visible. By day they resemble adults, with dark ground colour and light stripes.

Stefania woodleyi Rivero

Stefania woodleyi Rivero [Holotype BMNH 1967.654 from Mount Kanaima, Guyana] 1968: 147.

Two adult males of 40 and 41 mm SVL and two juveniles of 19 mm SVL were collected at the base of Wokomung, at 698 m (Figure 3H). The latter were identified as *S. woodleyi* because their reduced toe webbing and dorsal colouration conform to the unique mottled pattern of this species. The only other species of *Stefania* collected at this location was *S. evansi*, which has more extensive toe webbing.

Following examination of *S. woodleyi* from several locations, the toe webbing formula can be expanded to **I** (2⁺-2¹/₄) – 2¹/₂ **II** (2-2) – (3-3⁺) **III** (2¹/₄-2¹/₂) – (3¹/₂-3³/₄) **IV** 3¹/₂ – (2⁺-2¹/₂) **V**. Vomerine teeth 5. The largest finger disc covers about 66% of the tympanum diameter.

Mount Wokomung is within the range of *S. woodleyi*, which has been collected from several locations in the southern Pakaraima region (MacCulloch and Lathrop 2002).

Discussion

Morphology

Toe disc size variation was found in four species of the *S. evansi* group at Mt. Wokomung – *S. ackawaio*, *S. ayanganna*, *S. evansi* and *S. roraimae*. Examination of specimens from Mt. Ayanganna shows that disc size variation occurs in some *S. ayanganna* from that location. Variation was not apparent in *S. ackawaio*, *S. evansi* or *S. roraimae* from Mt. Ayanganna, but sampling of these species at Ayanganna was low in comparison with Mt. Wokomung. In the single specimen of *S. roraimae* from Mt. Roraima, the finger discs are notably smaller than in

the specimens from Wokomung or Ayanganna (Duellman and Hoogmoed 1984, MacCulloch and Lathrop 2002). Although larger discs occur more frequently in larger animals, the relationship between body size and disc size is not clear. This phenomenon merits further study.

Many *Stefania* from Mt. Wokomung exhibited a reddish colouration not seen in specimens from other locations (Figure 3A, B, D, G). This colour was also seen in some other amphibian taxa (unpublished data). There were many plants with red leaves on Wokomung, and red colour may confer a selective advantage in amphibian camouflage.

MacCulloch and Lathrop (2002) pointed out that juvenile *Stefania* can be difficult to identify because many of the characters used for identification, such as skin texture, webbing and frontoparietal ridges, are not well-developed in juveniles. Juvenile colour pattern is also an unreliable identification tool; conspecific juveniles and even juveniles from the same brood may have different colour patterns (Figure 3D).

Reproduction

It is difficult to reach any conclusions about reproduction in *Stefania* at Mt. Wokomung. All females encountered on the summit of Wokomung, five *S. ayanganna* and one *S. coxi*, were carrying juveniles. Of the 10 female *S. ayanganna* collected on the slopes, two from 1411 m were carrying juveniles. Females of *S. ayanganna* that carried juveniles measured 47–50 mm SVL; numbers of juveniles carried were 4, 5, 6, or 8, with no correlation between size of female and number of offspring. Juveniles measured 14–16 mm SVL.

Two of 14 female *S. ackawaio* collected retained some remnant of the dorsal mucoid layer. No female *S. evansi* or *S. roraimae* had any indication of reproductive activity, although newly independent juveniles of both species were collected. Similarly, two juvenile *S. woodleyi* were collected, although no adult females of this species were encountered.

It appears that *Stefania* species, even those that occur syntopically, do not reproduce at exactly the same time. The humid environment on tepuis and the absence of an aquatic larval stage may render these frogs relatively independent of seasonal reproductive patterns.

Reproduction in *Stefania* at the summit does not seem to be synchronous with that of *Stefania* on the slopes. This may be because the bromeliad microhabitat provides water and shelter from the summit winds, and it may provide *S. ayangannae* with suitable reproductive habitat throughout the year.

Habitat

Specimens collected at 1234–1411 m on Wokomung were in medium montane forest habitat, whereas the 1490–1550 m sites on Ayanganna supported wet low evergreen high-tepui forest (Huber *et al.* 1995). *Stefania ackawaio* and *S. roraimae* were more abundant on Wokomung than on Ayanganna; habitat may be a contributing factor to this difference. However, *Stefania ayangannae* was abundant on both mountains. It was most commonly collected in both high- and low-canopy forest, from 1234–1698 m elevation, but it was also collected in summit bog habitat on Wokomung, at 1698 m. Perhaps *S. ayangannae* can be viewed as an opportunistic colonizer, a common slope species which has been able to survive the harsh summit habitat by using the microhabitat within bromeliads.

Stefania coxi, collected in high-tepui forest at Ayanganna, was found only in tepui bog habitat on the summit of Wokomung, at 1698 m, despite intensive collecting effort at lower elevations. This species may not occur in medium montane forests; it is a member of the *S. goini* group, whose members seem to prefer high-tepui habitat rather than the taller-canopy habitat often found on tepui slopes (Señaris *et al.* “1996” [1997]). *Stefania coxi* and *S. ayangannae* were the only amphibians collected in tepui bog habitat at the summit, although

several individuals of an unknown species of *Colostethus* were heard calling there.

Stefania evansi and *S. woodleyi* were collected in submontane forest at Wokomung, at about 700 m. This habitat is similar to that in which these species have been collected elsewhere (MacCulloch and Lathrop 2002).

Zoogeography

The specimens of *Stefania ackawaio*, *S. ayangannae* and *S. coxi* from Mount Wokomung extend the range of these species, previously known only from their type locality on Mount Ayanganna, 37 km north of Wokomung. These three species were collected at 1490–1550 m on Ayanganna, in low-canopy high-tepui forest. At Wokomung *S. ackawaio* and *S. ayangannae* were abundant at both 1234 and 1411 m, in medium montane forest. At the summit of Wokomung, in tepui bog habitat, *S. ayangannae* and *S. coxi* were collected.

Stefania roraimae was known from both Ayanganna and Roraima, where it was collected at 1400–1550 m. At Wokomung it was abundant at 1234 and 1411 m.


Stefania evansi and *S. woodleyi* have been recorded from other nearby locations (MacCulloch and Lathrop 2002); both species occur in lowland, submontane or lower montane forest in western Guyana, below 900 m.

There was no overlap between the high- and low-elevation species of *Stefania* at Wokomung. *Stefania ackawaio*, *S. ayangannae*, *S. coxi* and *S. roraimae* were collected only at or above 1234 m, while *S. evansi* and *S. woodleyi* were collected only at 600–700 m. The lower elevation limits of the former species, and the upper limits of the latter, are not known. Nor is it known whether there is a point at which the high- and low-elevation species are sympatric.

The unprecedented diversity of *Stefania* at Mount Ayanganna led MacCulloch and Lathrop (2002) to speculate that it might be a centre of dispersal for the genus. The discovery of six species on Mount Wokomung shows that the

phenomenon of high diversity in *Stefania* is not limited to a single location. It is anticipated that further investigations in the Guiana highlands will yield other incidences of high diversity in *Stefania*.

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Appendix I - Specimens Examined

Stefania ackawaio – GUYANA: *District 8*: Mount Wokomung (ROM 42804–42831, CSBD Field # 15441–2, 15454, 15456); *District 7*: Mount Ayanganna (ROM 39473–39476).

Stefania ayangannae – GUYANA: *District 8*: Mount Wokomung (ROM 42893–42952, CSBD Field # 15494); *District 7*: Mount Ayanganna (ROM 39501–39551).

Stefania coxi – GUYANA: *District 8*: Mount Wokomung (ROM 42856–42860); *District 7*: Mount Ayanganna (ROM 39477–39480).

Stefania evansi – GUYANA: *District 8*: Mount Wokomung (ROM 42861–42892); Tukeit (ROM 20555, 20559); *District 7*: Mount Ayanganna (ROM 39450–39463).

Stefania roraimae – GUYANA: *District 8*: Mount Wokomung (ROM 42836–42855, CSBD Field # 15438–40, 15445, 15452); *District 7*: Mount Ayanganna (ROM 39466–39469).

Stefania woodleyi – GUYANA: *District 8*: Mount Wokomung (ROM 42832–42835); Tukeit (ROM 20570); Paramakatoi (ROM 28425–28426); *District 7*: Mount Ayanganna (ROM 39465).