

A REMARKABLE NEW RIODINID SPECIES, *STALACTIS HALLOWEENI* (RIODINIDAE:
STALACTINI), FROM MOUNT AYANGANNA, GUYANA

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ABSTRACT. A new riodinid species, *Stalactis halloweeni* Hall n. sp. (Stalactini), is described from Mount Ayanganna, a tepui in western Guyana. A preliminary hypothesis of phylogenetic inter-relationships within the small genus *Stalactis* Hübner is suggested, based on an informal study of external morphology and male genitalia. Three species groups are proposed, the *phlegia*, *calloipe* and *euterpe* groups, and *S. halloweeni* is hypothesized to be sister to the remaining members of the *euterpe* group.

Additional key words: endemism, montane forest, morphology, South America

Situated in the Pakaraima Mountain Range of western Guyana, Mount Ayanganna (2042m) is one of the easternmost tepuis in the Guiana Shield. Like the other tepuis in western Guyana and eastern Venezuela, Mount Ayanganna consists of eroded sandstone remnants of the Roraima Formation (MacCulloch & Lathrop 2001), and its isolated high-elevation habitats harbor significant numbers of endemic plants and animals. During the last five years alone, several new endemic species of frogs, snakes and lizards have been described from Mount Ayanganna (MacCulloch & Lathrop 2001, 2002, 2004).

During the last ten years, there have been numerous Lepidoptera expeditions to the upland regions of western and southern Guyana (Fratello 1996, 2001, 2003, 2005). In 1999, accompanied by several US and

Guyanese colleagues, S. Fratello led the first Lepidoptera collecting expedition to the upper slopes of Mount Ayanganna. Among the many new taxa of butterflies collected there were several new species of Riodinidae, including a new species of *Stalactis* Hübner, 1818 (Stalactini), although most of these species were represented by only a small number of female specimens. Fortunately, a second expedition to Mount Ayanganna in 2002, by a different team that included one of the 1999 Guyanese expedition members (R. Williams), produced additional *Stalactis* specimens, including males.

This new *Stalactis* species is remarkable in several respects. It is the first new species to be described in this small, essentially South American genus of aposematic species for over 150 years, since Westwood (1851) described *S. magdalena*; it is the first known *Stalactis* species to apparently occur exclusively in montane habitats; and its wing pattern differs substantially from that of its congeners. I herein describe this new *Stalactis* species and attempt to establish its phylogenetic position within the genus by informally constructing a preliminary hypothesis of phylogenetic relationships for *Stalactis* and proposing a new species-group classification.

***Stalactis halloweeni* Hall, new species**

(Figs. 1–2; 3; 4)

Description: MALE: Forewing length 29.5 mm. Forewing elongate, costal and distal margins approximately straight, four forewing radial veins, discal cell elongate; hindwing rounded and slightly elongate, hindwing veins R_s and M_1 stalked. **Dorsal surface:** Forewing ground color black, discal cell orange with some black scaling medially, broad orange rays in cells $2A$ and Cu_2 extending from (Cu_2) or near ($2A$) wing base to join submarginal band, orange rectangle at base of cell Cu_1 , small orange spot at base of cell M_3 , orange streaks in cells M_2 to R_{4+5} and R_2 immediately distal to discal cell end, decreasing in size from cell M_2 to cell R_2 , broad submarginal orange band extending from costa to tornus, with an enlarged rectangular orange patch nearly encircling a black spot in cells M_3 and Cu_2 , distal fringe black; hindwing ground color black, pale orange spot at wing base, a broad orange streak through discal cell and cells Cu_2 to M_1 , and along anal margin, those in cells Cu_1 and M_3 shorter than



FIGS. 1–2. *Stalactis halloweeni* adults (dorsal surface on left, ventral surface on right). 1. Holotype male, Mount Ayanganna, Guyana (USNM). 2. Paratype female, Mount Ayanganna, Guyana (USNM).

others and that in cell Cu_2 joining submarginal band, small distal orange spot in cell $Sc+R_1$, broad and uneven submarginal orange band extending from apex to tornus, distal fringe black. Ventral surface: Forewing differs from dorsal surface by having a small orange spot at costal wing base, only distal portion of orange streak present in cell 2A, orange streak in cell M_2 joining submarginal band, orange spot in cell R_5 replaced by a sparse scattering of whitish scales; hindwing differs by having a very narrow line of orange scaling at middle of costal margin, with a sparse scattering of whitish scales distally, a larger orange spot in cell $Sc+R_1$, a much larger and darker orange spot at wing base, and a sparse scattering of whitish scales along anal margin.

Head: First segment of labial palpi a mixture of black and white scaling, segment two black with a broad white lateral band and some white scaling ventrally, and third segment black; eyes bare and black, with a mixture of black and white scaling at margins; frons black, with white scaling laterally; antennae 60% of forewing length, segments black with white scaling at ventral base and narrow nudum region along inner ventral margin, clubs black.

Body: Dorsal surface of thorax black, tegula black with dark orange scaling at base, ventral surface of thorax black with a white band between legs and a large orange patch near base of forewing; abdomen black dorsally, with a broad orange band laterally, and white ventrally, with narrow black lines on either side (patterning virtually indiscernible in Fig. 1 due to a covering of mold), all legs black.

Genitalia (Fig. 3): Uncus in lateral view rectangular and vertically elongate, lateral "window" anterior to uncus very narrow, tegumen very narrow, with a triangular ventral margin; falces extremely long and ventrally directed, with a weakly bent "elbow"; vinculum narrow, anteriorly bowed, broadest medially and slightly posteriorly indented near ventral tip, with a posteriorly directed triangular section of sclerotized tissue at ventral margin and no anterior saccus; aedeagus narrow, convex and of medium length, gradually tapering to a slightly upturned and finely pointed tip, vesica exits along ventral margin of posterior third of aedeagus, cornutal patch consists of a short sclerotized rod with about six prominently curved and anteriorly directed spines densely positioned along all but its anterior tip, cornutal patch positioned about one third distance from posterior to anterior tip of aedeagus on unevverted vesica; pedicel in lateral view broad basally, becoming narrower in angular posterior section, pedicel joins aedeagus about one third distance from anterior to posterior tip; valvae in lateral view consist of a large rectangular basal section, a narrow, posteriorly elongate and round-tipped lower process, a slightly broader, more rectangular and posteriorly elongate upper process, with a posteriorly and upwardly curved, finely pointed terminal projection, a very broad and rounded inner process, slightly shorter than lower process, and a pointed transtilla of medium length extending posteriorly between pair of inner processes and across top of aedeagus; narrow tuft of long, posteriorly directed, pale brown setae around outer margin of genital capsule; eighth abdominal tergite and sternite rectangular.

FEMALE: Differs from male in following ways: Forewing length 28 mm. Distal forewing margin convex. **Wings:** Orange on both wings very slightly paler, medial black scaling in forewing discal cell more prominent, several forewing postdiscal orange spots do not extend as far proximally to cell bases, orange ray in ventral forewing cell M_2 does not distally join submarginal band.

Head: Second palpal segment slightly more elongate, third segment about twice as long; nudum region on antennal segments slightly larger.

Genitalia (Fig. 4): Corpus bursae somewhat narrow and elongate, with a pair of small, sclerotized, invaginated spine-like signa; ductus bursae consists of a large, creased, hardened swelling immediately posterior to corpus bursae containing about four pieces of rectangular sclerotization, a short membranous section posteriorly, then a long and twisted lightly sclerotized section, followed by a short, concave ventral section of sclerotization; membranous ductus seminalis exits ductus bursae dorsally immediately anterior to ventral section of sclerotization; ostium bursae in dorsal view consists of a small, round, sclerotized entrance hole, with a broad and prominently convex band

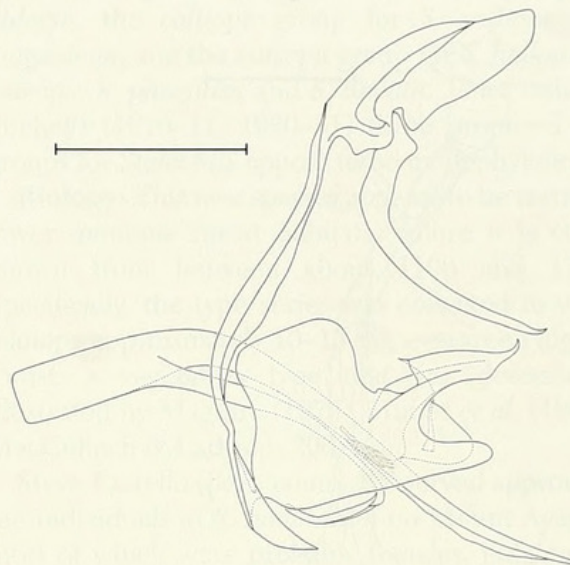


FIG. 3. Male genitalia of *Stalachtis halloweenii* holotype in lateral view. Scale bar = 1 mm.

of sclerotization dorsally curving anteriorly into an invaginated pouch below papillae anales that is membranous except for a broad, triangular, horizontal band of sclerotization along dorsal "roof" of pouch (perhaps a protected resting place for extremely long male genital falces during copulation); papillae anales proportionately small and round; very broad, semicircular tuft of long, posteriorly directed, pale brown setae around posterior margin of eighth tergite.

Types: *Holotype* ♂, GUYANA: *Cuyuni-Mazaruni*, Mount Ayanganna, 1120 m, 5°22.22'N 59°57.34'W, 12–16 Oct 2002 (R. Williams) (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA [USNM]).

Paratypes: 1♂, 1♀, same data as holotype. 3♀, GUYANA: *Cuyuni-Mazaruni*, Mount Ayanganna, 4500–5500 ft, 5°24.1'N 59°57.4'W, 13–18 Apr 1999 (S. Fratello *et al.*) (USNM).

No additional specimens have been located in the major museums of Europe and North America (as listed in Hall 1999, 2005).

Etymology: The name is derived from the middle English word halloween, in reference to the fact that the wing pattern is composed of the traditional orange and black colors of Halloween, and is reminiscent of a carved pumpkin.

Systematic placement and diagnosis: *Stalachtis* (= *Nerias* Boisduval, 1836) is the sole genus currently treated in the tribe Stalachtini. The family-group name was proposed by Bates (1861), as a subfamily, for an undefined number of genera whose species possessed a "pupa not flattened beneath, secured rigidly by the tail in an inclined position, without girdle", a set of characters quickly discovered by Bates (1868: 368) himself not to be phylogenetically informative in the context of the higher classification of the Riodinidae. Stichel (1910–11) used the Stalachtini as a tribal name for the first time (as the Stalachtidi), and followed Bates (1868) in including only *Stalachtis* within it. Most recently, Harvey (1987) defined the monotypic Stalachtini by the presence of a tuft of long setae around

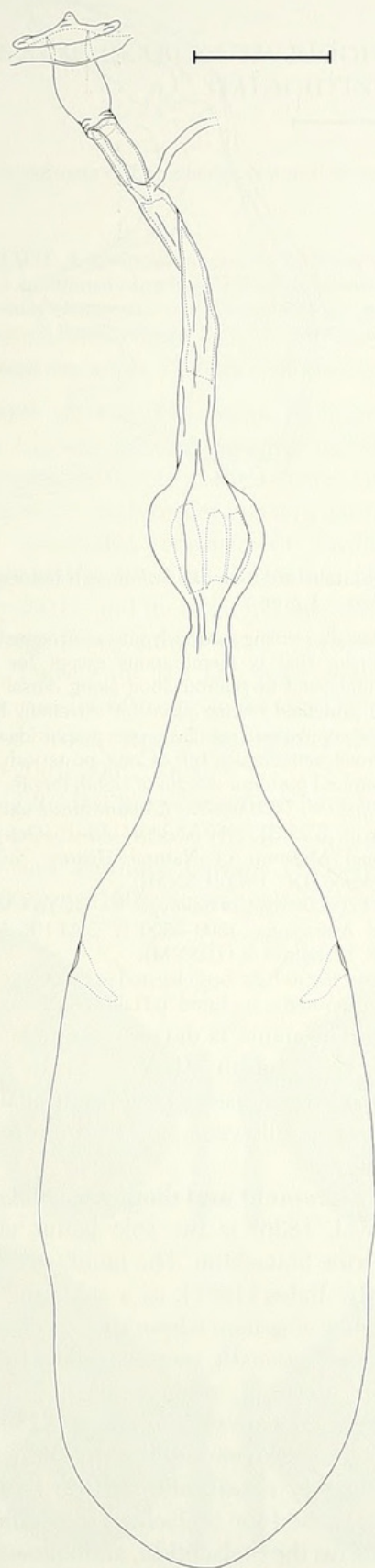


FIG. 4. Female genitalia of *Stalachtis halloweenii* paratype in dorsal view. Scale bar = 1 mm

the posterior margin of abdominal segment eight in males and, to a greater extent, females, and mentioned that its species are unusual in the Riodinidae in having hindwing veins Rs and M_1 stalked rather than arising separately from the discal cell end (Bates 1868; Stichel 1910–11). Additional unique characters that are universal within the Stalachtini include extremely long and weakly bent (i.e. ventrally directed) falces, a complex arrangement of inner valve processes, and a long straight comb of prominently curved, anteriorly directed spines on the aedeagal vesica in the male genitalia (Hall unpubl. data). The new *Stalachtis* species, *S. halloweenii*, possesses all of the above characters.

Traditionally, *Stalachtis* has been treated as containing eight species (e.g. Stichel 1910–11, 1930–31), although some authors have listed as many as ten species (D'Abrera 1994; Bridges 1994). However, the genus is now justifiably recognized to contain only six species (Callaghan & Lamas 2004). Hemming (1964, 1967) selected the type species of Hübner's (1818) *Stalachtis* to be *S. phaedusa* (Hübner, [1813]). It is worth mentioning that the name *Stalachtis funereus albulus* Lathy, 1958, which occasionally appears in the riodinid literature (e.g. Rebillard 1958; D'Abrera 1994; Bridges 1994), actually refers to a pericopine moth (Arctiidae) (Hall unpubl. data). Stichel (1910–11, 1930–31) divided *Stalachtis* into two sections, the "Adiorati" for *S. calliope* (Linnaeus, 1758) and *S. magdalena* Westwood, 1851, in one subgroup and *S. phlegia* (Cramer, 1779) (+ *S. susanna* (Fabricius, 1787)) and *S. euterpe* (Linnaeus, 1758) in another subgroup, and the "Diaphanes" for *S. phaedusa* (+ *S. zephyritis* (Dalman, 1823)) and *S. lineata* (Guérin-Ménéville, [1844]). Based on a study of wing pattern and male genitalia characters in all six *Stalachtis* species, an alternative species-group classification and preliminary hypothesis of phylogenetic relationships for the genus is proposed here.

As *S. calliope*, *S. magdalena*, *S. euterpe*, *S. phaedusa* and *S. lineata* all share a pair of large, rounded, inner valve processes, with an elongate, pointed transtilla extending posteriorly between them and across the top of the aedeagus, *S. phlegia* is hypothesized to be sister to the remaining species in the genus. *Stalachtis phlegia* has a much smaller pair of inner valve processes, without the intervening transtilla, and has the least derived wing pattern, with a full complement of white basal, postdiscal and submarginal spots. *Stalachtis calliope* and *S. magdalena*, like *S. phlegia*, but unlike any other *Stalachtis* species, have a complete row of submarginal white spots on the forewing, an orange patch at the base of the dorsal forewing and hindwing,

and an entirely checkered black and white hindwing fringe. Their similar wing patterns, with mottled orange markings at the base of the forewing and parallel orange bands on the hindwing, shared possession of an upper valve process that is broadest medially (instead of basally in *S. phlegia* and distally in the remaining three species), and parapatric geographic ranges strongly suggest that they are sister species. *Stalachtis euterpe*, *S. phaedusa* and *S. lineata* appear to form a monophyletic group, as all three species share similarly positioned white wing markings that are consistently formed into rays instead of spots, the absence of an orange patch at the base of the dorsal forewing and hindwing, the absence of a complete row of submarginal white spots on the forewing, largely black wing fringes, and an upper valve process that is broadest distally. As *Stalachtis phaedusa* and *S. lineata* both have elongate hyaline rays on both wings they are probably sister species.

Stalachtis halloweenii appears to exhibit external pattern characters that are somewhat intermediate between those of members in the *calliope* and *euterpe* groups. It shares with the two *calliope* group species the presence of orange markings at the base of the dorsal forewing, and with *S. magdalena* the absence of a lateral white line above as well as below the lateral orange band on the abdomen. It shares with the three *euterpe* group species a similar pattern of rays at the base of the forewing and particularly the hindwing, even if these are orange instead of white, the absence of a complete row of submarginal white spots on the forewing, and black wing fringes. Based on the above characters, and the fact that *S. halloweenii* has the full complement of inner valve processes and an upper valve process that is broadest distally, this new species is tentatively suggested to be the most basal member of the *euterpe* group. The male genitalia of *Stalachtis* species are rather homogeneous, with the most significant interspecific variation exhibited by the upper and, to a lesser extent, lower valve processes. Although *S. halloweenii* appears to be most closely related to *S. euterpe*, its male genital valvae are probably most similar to those of *S. phaedusa*, but its upper valve process does not have such a prominent ventral protrusion at the posterior tip, and the posterior margin extends at about a 45° angle instead of vertically. Elsewhere in the *euterpe* group, *S. euterpe* can be characterized by its dorsal as well as ventral swelling to the distal tip of the upper valve process and atypically small and straight terminal projection, and *S. lineata* can be characterized by its broadly triangular instead of narrower rod-shaped lower valve process.

In conclusion, *Stalachtis* seems to be best divided

into three species groups, the *phlegia* group for *S. phlegia*, the *calliope* group for *S. calliope* and *S. magdalena*, and the *euterpe* group for *S. halloweenii*, *S. euterpe*, *S. phaedusa* and *S. lineata*. Thus, only two of Stichel's (1910–11, 1930–31) three proposed species groups for *Stalachtis* appear to be monophyletic.

Biology: This new species appears to be restricted to lower montane forest habitats, where it is currently known from between about 1100 and 1700 m. Specifically, the type series was collected in wet, low (canopy approximately 10–15 m), evergreen high-tepui forest, a vegetation type that was described and illustrated by Maguire (1970), Huber *et al.* (1995) and MacCulloch & Lathrop (2001).

Steve Fratello (pers. comm.) observed approximately ten individuals of *S. halloweenii* on Mount Ayanganna, most of which were probably females, judging by the fact that all individuals captured were of that sex. Within the forest, these individuals consistently flew at about 5 to 7 m above the ground, although two individuals were observed flying only 2 to 3 m above the ground over a patch of low tepui scrub at 1700 m. Individuals were seen flying over a wide area from mid-morning to mid-afternoon, with a rather slow, steady flight, and were not observed alighting or resting. No other *Stalachtis* species were seen flying in the same habitats as *S. halloweenii*, but *S. phaedusa*, *S. calliope* and *S. euterpe* have been commonly collected in neighboring lowland areas of Guyana (Fratello pers. comm.).

Stalachtis is one of the most well known groups of aposematic riordinids (Seitz 1916–20; D'Abrera 1994). Given that the known caterpillars are gregarious and aposematic (Callaghan 1986), and members of at least some of the known foodplant families (e.g. Simaroubaceae) contain toxic phytochemicals (e.g. Moretti *et al.* 1982; Polonsky *et al.* 1984), it seems likely that some or all of the *Stalachtis* life stages are to some extent distasteful to predators, and adults may thus be predominantly Mullerian rather than Batesian mimics. However, I am not aware of any sympatric butterflies or moths that specifically closely resemble *S. halloweenii*.

Distribution: *Stalachtis halloweenii* is currently known only from the middle slopes of Mount Ayanganna, in the uplands of western Guyana. However, the geographic range of this species probably extends to neighboring highland areas in Guyana and extreme eastern Venezuela. There continues to be debate about whether most Guiana highland endemics are relicts of a widespread pantepui fauna or descendants of lowland ancestors (e.g. Myers & Donnelly 1996; MacCulloch & Lathrop 2001). Given that all six described *Stalachtis* species have entirely lowland distributions, the ancestor of *S. halloweenii*

presumably colonized Mount Ayanganna from the surrounding lowlands.

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