



Taxonomic revision of the tribe Acraeini Boisduval, 1833 (Papilionoidea: Nymphalidae: Heliconiinae)

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Abstract: The systematic and taxonomic history of the tribe Acraeini is reviewed. Using a robust dated molecular phylogeny published in 2021, and combining this with morphological and ecological data-sets, we divided the clearly paraphyletic genus *Acraea* (*sensu lato*) into five genera. We raised the subgenera *Rubraea* Henning, 1992, *Stephenia* Henning, 1992 to genera and reinstate *Bematistes* Hemming, 1935 and *Telchinia* Hübner, [1819] as valid genera. The genus *Tildia* **gen. nov.** is erected for a monophyletic clade of *Acraea* (*sensu lato*), and we treat the Neotropical *Actinote* and the Afrotropical *Telchinia* as separate genera. Because of the relatively low sampling of 'Telchinia' species in the dated molecular phylogeny we suggest that the possibly paraphyletic *Telchinia* be further investigated using more complete sampling. We furthermore present an updated alpha taxonomy for the six Afrotropical genera in the tribe – *Acraea*, *Rubraea* **stat. nov.**, *Stephenia* **stat. nov.**, *Tildia* **gen. nov.**, *Bematistes* **stat. rev.** and *Telchinia* **stat. rev.** The current alpha taxonomy of the New World genus *Actinote* and the Old World genus *Cethosia* is given.

Key words: Systematics, phylogeny, paraphyletic, subgenus, alpha taxonomy.

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Peer reviewed

INTRODUCTION

The tribe Acraeini Boisduval, 1833 is one of four tribes currently placed in the nymphalid subfamily Heliconiinae Swainson, 1822 (Penz & Peggie, 2003). The systematics and taxonomy of the tribe has been investigated by Pierre (1985a & b; 1986; 1987; 2020), Henning (1986, 1992; 1993a & b), Penz & Peggie (2003), Silva-Brandão *et al.* (2008), Henning & Williams (2010), Müller & Beheregary (2010), Pierre & Bernaud (2014), Timmermans *et al.* (2016), Williams & Henning, 2020 and Carvalho *et al.* (2021).

Pierre (1987) proposed an arrangement which divided the genus *Acraea* into two subgenera, *Acraea* and *Actinote*, synonymised the genus *Bematistes* and downgraded the status of genus *Actinote* to that of a subgenus. Within these subgenera he further divided them into five super-groups under subgenus *Acraea* and six super-groups under subgenus *Actinote*.

Henning, (1992) raised *Bematistes* and *Actinote* to genus level and divided *Acraea* into three subgenera (*Acraea*, *Rubraea* and *Stephenia*). *Hyalites* was raised to generic status and was divided into four subgenera (*Hyalites*, *Pareba*, *Aurora* and *Alacria*). The monobasic *Pardopsis* was placed in the tribe Pardopsidini.

Penz & Peggie (2003) produced a phylogeny of the Heliconiinae based on morphology and placed *Pardopsis*,

Acraea and *Actinote* in the tribe Acraeini and *Cethosia* in the tribe Heliconiini.

Silva-Brandão *et al.* (2008) cite Pierre (1985a, b; 1986) but were apparently unaware of Henning (1992). According to their molecular phylogenetic hypothesis for the tribe Acraeini, *Pardopsis* is not part of the tribe Acraeini, but appears, with weak support, in the Argynnini clade (tribe Argynnini). In their topology the genus *Cethosia* is the sister group of Heliconiini, and both tribes are sister to Acraeini (excluding *Pardopsis*). They found that the genus *Acraea* is paraphyletic, and includes *Bematistes* and the monophyletic "Old World *Actinote*" (*Hyalites* of Henning, 1992); this clade is the sister group to all Neotropical species (*Actinote* of Henning, 1992). The monophyletic *Bematistes* appears as sister group of the tribe Acraeini (*sensu stricto*), while *Acraea* is paraphyletic. The Neotropical *Actinote* appears as a monophyletic group with very short branches separating the species. Taxonomic suggestions arising from their results were: (1) *Acraea* should be used temporarily at generic level for the mainly Passifloraceae-feeding African *Acraea*, until further sampling defines the natural groups in this paraphyletic genus, (2) *Telchinia* Hübner, [1819] (type species: *Papilio serena* Fabricius 1775) (syn. *Hyalites* Doubleday, 1848) should be revived at generic level for the mainly Urticaceae feeding series included by Pierre in his subgenus *Actinote* ("Old World *Actinote*" in this paper), and (3) *Actinote* Hübner, [1819] should be expanded to include all Neotropical Acraeini.

Henning & Williams (2010) noted that the raising of *Acraea serena* by Silva-Brandão *et al.* (2008) made the genus name *Telchinia* Hübner, [1819] available as it had previously been synonymised with *Acraea*. *Telchinia* pre-dates *Hyalites* Doubleday, 1848 and therefore takes precedence over *Hyalites*, which had been used by

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Henning (1992; 1993a, b). In the present paper all species hitherto placed in *Hyalites* are transferred to *Telchinia*, where applicable. *Bematistes* Hemming, which was retained as a genus name by Henning (1992), is accorded subgeneric rank within *Acraea*, largely due to their shared host-plants (Passifloraceae).

Despite the above publications, Pierre & Bernaud (2014), as Pierre (1987) had done, persisted in using *Acraea* (*Acraea*) and *Acraea* (*Actinote*) for all the species in the tribe Acraeini in the Afrotropical and Neotropical regions.

Timmermans *et al.* (2016) sequenced the full mitochondrial genomes of 19 African species of Acraeini. They confirmed a monophyletic *Telchinia* to include the Asiatic *Pareba* with a complicated paraphylum, traditional (sub)genus *Acraea*, toward the base. They suggest that several proposed subgenera and some species groups within *Telchinia* are not monophyletic, while two other (sub)genera could possibly be combined. *Telchinia* was recovered without strong support as sister to the potentially interesting system of distasteful model butterflies known as *Bematistes*. They found that the latter genus has remarkably divergent mitogenomes and unexpected synapomorphic tRNA rearrangements. The fact that these gene order changes, combined with evidence for deviating dN/dS ratios and evidence for episodal diversifying selection, suggested that the ancestral *Bematistes* mitogenome has had a turbulent past. Their study adds genetic support for treating this clade as a distinct genus, while the alternative option, adopted by some authors, of *Acraea* being equivalent to Acraeini merely promotes redundancy. They state that it would appear at present a minimum of five genera with available names (*Rubraea/Stephenia*, *Acraea*, *Bematistes*, *Telchinia*, *Actinote*) might be required, even if *Stephenia* were to be synonymised with *Rubraea* or vice-versa. Also, *A. zetes* (and probably its entire species group) might require an additional genus according to its isolated position in both Silva-Brandão *et al.* (2008) results and theirs. Their results support the view that the Asian (sub)genus *Pareba* Doubleday, 1848 really belongs in *Telchinia* (it was sister to the other *Telchinia* in Silva-Brandão *et al.* (2008)), but they also clearly suggest that further subdivision as suggested by Henning and Williams (2010) should probably be abandoned. They state that key questions for future resolution regarding the “*Acraea* paraphylum” is where in the tree the type species of *Acraea*, *A. horta* and the Oriental *Miyana* Fruhstorfer, 1914 (type species *Papilio moluccana* Cramer) fall.

Recently, Carvalho *et al.* (2021) investigated whether sexual conflict is a driver of speciation in the tribe Acraeini. In order to do this they generated the most robust and comprehensive dated molecular phylogenetic hypothesis for the tribe to date. The data set comprised 160 Acraeini species (52% of the described diversity of the tribe) and 48 outgroups for a total of 208 species. The included species represented two valid Acraeini genera, *Acraea* and *Cethosia*, and all *Acraea* species-groups (*sensu* Pierre & Bernaud (2014)). The BUTTERFLY2.0 probe set used captured up to 13 loci including the barcoding mitochondrial gene cytochrome c oxidase subunit I (COI). These authors state: “Within Acraeini six well-supported clades were recovered, one supporting the monophyly of *Cethosia* and five major clades within *Acraea*, which

represent previously valid genera or subgenera of *Acraea* (*sensu lato*): *Acraea* (*sensu stricto*), *Actinote*, *Bematistes*, *Rubraea/Stephenia*, and *Telchinia*. Within each of these clades, however, nodal support varied significantly, and support was generally higher in groups for which more loci were present.”

Using the phylogeny published by Carvalho *et al.* (2021), and combining this with morphological and ecological data-sets, we divide the clearly paraphyletic genus *Acraea* into five genera and recognize *Cethosia*, *Actinote* and *Telchinia* as distinct genera. We furthermore present an updated alpha taxonomy for the six Afrotropical genera in the tribe (excluding the New World genus *Actinote* and the Old World genus *Cethosia*).

METHODS AND MATERIALS

From the dated molecular phylogeny of the tribe Acraeini published by Carvalho *et al.* (2021) we identified eight monophyletic lineages that arose between 16 and more than 30 million years ago (Mya). Using published taxonomic work on the tribe, genus names were assigned to each lineage of the Carvalho *et al.* phylogeny: *A. egina* to *A. kraka* (*Rubraea*), *A. aglaonice* to *A. natalica* (*Stephenia*), *A. rabbaiae* to *A. zetes* (*Tildia* gen. nov.), *A. ranavalona* to *A. neobule* (*Acraea*), *A. schubotzi* to *A. leopoldina* (*Bematistes*), *A. eresia* to *A. pellenea* (*Actinote*) and *A. anacreon* to *A. melanoxantha* (*Telchinia*). Morphological synapomorphies were determined for each of the six Afrotropical genera. A data-set of ecological parameters was generated for each of the Afrotropical species using information in Williams (2022). These ecological parameters included the early stages, larval host plant genera and families, habitat (biome) and geographical range. The ecological data-set was then examined to determine if there were patterns common to the species within each of the genera.

RESULTS

Family Nymphalidae Rafinesque, 1815

Subfamily Heliconiinae Swainson, 1822

Tribe Acraeini Boisduval, 1833

Genus *Cethosia* Fabricius, 1807

Type species *Papilio cydippe* Linnaeus, 1763

Synonyms: *Alazonia* Hübner, 1819; *Eugramma* Billberg, 1820.

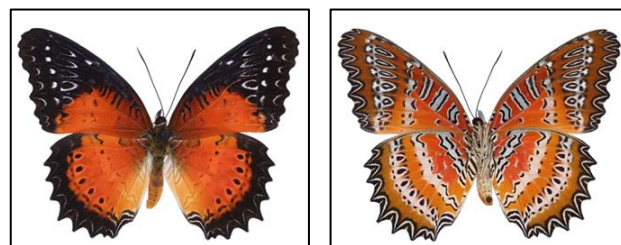


Figure 1 – *Cethosia biblis perakana* (male), a typical member of the genus. Left – upper side. Right – underside. Wingspan: 67 mm. Chaweng Beach, Ko Samui, Thailand. 19 March 2019. J.C.H. Dobson.

This genus of 17 species is found mainly in the Oriental Region but also extends into the Australian Region.

The list of species given here is based on Müller & Beheregaray, 2010.

Species list

Cethosia biblis (Drury, [1773])
Cethosia cyane (Drury, [1773])
Cethosia cydippe (Linnaeus, 1763)
Cethosia gabinia Weymer, 1883
Cethosia hypsea Doubleday, [1847]
Cethosia lamarcki Godart, 1819
Cethosia leschenault Godart, [1824]
Cethosia luzonica C. & R. Felder, 1863
Cethosia methypsea Butler, 1879
Cethosia mindanensis C. & R. Felder, 1863
Cethosia moesta C. & R. Felder, [1867]
Cethosia myrina C. & R. Felder, [1867]
Cethosia nietneri C. & R. Felder, [1867]
Cethosia obscura Guérin-Méneville, [1830]
Cethosia penthesilea (Cramer, [1777])
Cethosia tambora Doherty, 1891
Cethosia vasilina Müller, 1999

Genus *Acraea* Fabricius, 1807

Type-species *Papilio horta* Linnaeus, 1764

Synonyms: *Aphanopeltis* Mabille, 1887; *Phanopeltis* Mabille, 1887; *Solenites* Mabille, 1887; *Miyana* Fruhstorfer, 1914.

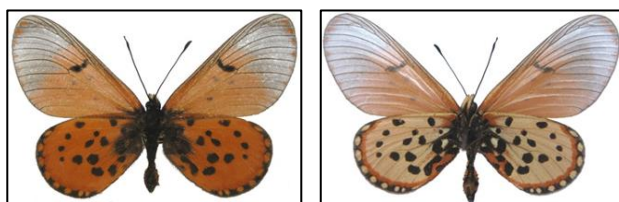


Figure 2 – *Acraea horta* (male), the type species of the genus. Left – upper side. Right – underside. Wingspan: 52 mm. Golden Gate Highlands National Park, Free State Province, South Africa. 9 January 2001. M.C. Williams.

This is a predominantly Afrotropical genus of 31 medium- to large-sized species, four of which occur in the Oriental and Australian Regions. The lineage arose ~ 16 Mya.

Body: Head large, broad and hairy. Antennae shorter than half length of forewing, averaging 45% (41–48%) of forewing for both sexes. Palpi 1st joint twice as long as broad, 2nd joint three times longer than first joint and terminal joint minute, oval. All joints hairy. Thorax short, compressed laterally, hairy and scaly. Abdomen long, extending just beyond outer edge of hindwings, laterally compressed, broader distally. **Legs:** Anterior legs slender and less than half length of pterothoracic legs; tarsi of male single joint without spines, female tarsi five jointed with spines on each except last, no terminal spine. Pterothoracic legs robust, external claw of male furrowed on inner surface, terminal claws asymmetrical. **Wing venation:** Radial veins of forewing not stalked; R1 branching off from cell rather than stalked. Cell of hindwing slightly more than half of total wing length. **Markings:** Hindwing with a row of four spots below the apex, three across the centre and two across mid-cell (4-3-2 configuration). These spots may be absent or coalesced into a single patch or into two patches. Hyaline areas and hyaline patches present. There are no marginal markings or spots on forewing upper side. **Male genitalia:** Uncus beak-shaped and elongate,

acute or bifid at tip; aedeagus long, narrow and needle like; sclerotized and modified 8th sternite present, distally lobed velum, may have distal tooth; valves subtriangular, pronounced dorsally; juxta elongate, triangular, weakly sclerotized; vinculum fairly broad; saccus small. **Female genitalia:** Anal lobes small, posterior apophyses slightly longer than lobes; sterigma usually taking the form of a large plate; ostium centrally or posteriorly placed; ductus short and sclerotized; bursa ovoid or spherical; single pair of signa, very small or absent. Sphragis present except in *A. satis* species group.

Early stages: Egg ovoid; almost as broad as high, sometimes taller; laid in clusters. Larvae gregarious. Pupa often extensively marked with black. **Host plant genera:** *Rinorea* (7 records), *Passiflora* (3 records), *Corchorus*, *Turnera*, *Kiggelaria* and *Adenia* (2 records each). There are single records for *Gymnosporia*, *Lauridia*, *Rawsonia*, *Premna*, *Smeathmannia*, *Ceratosicyos*, *Guthriea*, *Camellia*, *Gossypium*, *Vitis*, *Barteria*, *Basananthe*, *Hibiscus*, *Hybanthus*, *Ipomoea*, *Nicotiana*, *Tricliceras*, *Drypetes*, *Tylophora* and *Scepocarpus*. **Host plant families:** Violaceae (7 records), Passifloraceae (4 records), Turneraceae and Achariaceae (3 records each), Malvaceae (2 records). Single records for Celastraceae, Flacourtiaceae, Verbenaceae, Theaceae, Vitaceae, Convolvulaceae, Solanaceae, Euphorbiaceae, Apocynaceae and Urticaceae. **Habitats (biomes):** Predominantly a forest genus, with one species in arid savanna. Wet forest (10 spp.), submontane and montane forest (4 spp.), coastal forest (3 spp.), dry forest (4 spp.), woodland (4 spp.), savanna (*A. neobule*) and very dry savanna (*A. brainei*). **Geographical range:** The genus occurs throughout the Afrotropical Region and there are four species in the Oriental and Australian regions. On the mainland the genus is best represented in east-central Africa (Tanzania, southern and eastern DRC, Uganda and Kenya) and west-central Africa (Nigeria, Cameroon, Gabon and Angola).

Diagnosis

Facies: In the genus *Acraea* the hindwing has a row of four spots below the apex, three across the centre and two across mid-cell (4-3-2 configuration). In the other African genera the spots in the row below the apex are joined to the central row creating a discontinuous arrangement of spots (7:2 configuration). These spots may be coalesced into a single patch or into two patches. Hyaline areas and hyaline patches present on fore- and hindwings. There are no marginal markings or spots on forewing upper side.

It would be pertinent to mention here that as the *Acraeini* are both models and mimics, and in particular they mimic themselves, various patterns can be found repeated across several of the genera. Examples would be *Acraea quirina*, *Rubraea cerasa* and *Telchinia orestia*; also *Tildia zetes*, *Rubraea egina*, *Stephenia rogersi* and *Telchinia pharsalus*. These Müllerian mimicry rings are found throughout all the genera of *Acraeini* and could lead to some confusion with regard to the use of facies in establishing a diagnosis.

Genitalia: The male genitalia in all *Acraea* have extra modifications. In the *horta* species group the 8th sternite is modified to form a protective plate called a velum. In the *machequena* species group the valves are strongly

incurved, forming a claw. In the *satis* species group the 8th tergite is produced into a pseudouncus, with the rest reduced in size. In the *admatha* species group the juxta is articulated by a transtilla and connected by an elongate sclerite. In the *quirina* species group the uncus is divided into two hooks as large as the valves. The female genitalia have the sterigma usually taking the form of a large plate.

Species list

- Acraea admatha* Hewitson, [1865]
Acraea andromacha (Fabricius, 1775) – Extralimital
Acraea boopis Wichgraf, 1914
Acraea boopis boopis Wichgraf, 1914
Acraea boopis ama Pierre, 1979
Acraea boopis choloui Pierre, 1979
Acraea brainei Henning, 1986
Acraea camaena (Drury, 1773)
Acraea cuva Grose-Smith, 1889
Acraea dammii van Vollenhoven, 1869
Acraea eltringhami Joicey & Talbot, 1921
Acraea endoscota Le Doux, 1928
Acraea eugenia Karsch, 1893
Acraea hamata Joicey & Talbot, 1922
Acraea hamata hamata Joicey & Talbot, 1922
Acraea hamata batangi Bernaud, Ducarme & Pierre, 2017
Acraea horta (Linnaeus, 1764)
Acraea hova Boisduval, 1833
Acraea igati Boisduval, 1833
Acraea insignis Distant, 1880
Acraea kappa Pierre, 1979
Acraea kia Pierre, 1990
Acraea kinduana Pierre, 1979
Acraea leucographa Ribbe, 1889
Acraea leucographa leucographa Ribbe, 1889
Acraea leucographa jolyi Pierre, 2009
Acraea machequena Grose-Smith, 1887
Acraea mahela Boisduval, 1833
Acraea meyeri Kirsch, 1877 – Extralimital
Acraea matuapa Grose-Smith, 1889
Acraea moluccana Felder, 1860 – Extralimital
Acraea neobule Doubleday, [1847]
Acraea punctimarginea Pinhey, 1956
Acraea quirina (Fabricius, 1781)
Acraea ranavalona Boisduval, 1833
Acraea satis Ward, 1871
Acraea terpsichore (Linnaeus, 1758) – Extralimital
Acraea turlini Pierre, 1979

Species groups of *Acraea* (based on male genitalia)

- A. horta species-group:** the 8th sternite is modified to form a protective plate called a velum.
Acraea brainei Henning, 1986, *Acraea camaena* (Drury, 1773), *Acraea cuva* Grose-Smith, 1889, *Acraea dammii* van Vollenhoven, 1869, *Acraea eltringhami* Joicey & Talbot, 1921, *Acraea eugenia* Karsch, 1893, *Acraea hamata* Joicey & Talbot, 1922, *Acraea horta* (Linnaeus, 1764), *Acraea igati* Boisduval, 1833, *Acraea insignis* Distant, 1880, *Acraea mahela* Boisduval, 1833, *Acraea matuapa* Grose-Smith, 1889, *Acraea neobule* Doubleday, [1847], *Acraea punctimarginea* Pinhey, 1956, *Acraea turlini* Pierre, 1979.
A. machequena species-group: the valves are strongly incurved forming a claw.

Acraea machequena Grose-Smith, 1887, *Acraea ranavalona* Boisduval, 1833.

A. satis species-group; the 8th tergite is produced into a pseudouncus with the rest reduced in size.

Acraea satis Ward, 1871.

A. admatha species-group: the juxta is articulated by a transtilla and connected by an elongate sclerite.

Acraea admatha Hewitson, [1865], *Acraea boopis* Wichgraf, 1914, *Acraea endoscota* Le Doux, 1928, *Acraea hova* Boisduval, 1833, *Acraea kappa* Pierre, 1979, *Acraea kinduana* Pierre, 1979, *Acraea leucographa* Ribbe, 1889.

A. quirina species-group: the uncus is divided into two hooks as large as the valves.

Acraea quirina (Fabricius, 1781), *Acraea kia* Pierre, 1990.

Genus *Rubraea* Henning, 1992 stat. nov.

Type species *Papilio egina* Cramer, [1775]

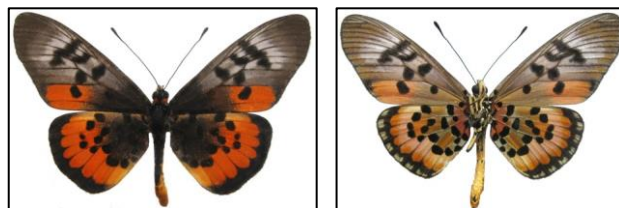


Figure 3 – *Rubraea egina* (male), the type species of the genus. Left – upper side. Right – underside. Wingspan: 62 mm. Mabira Forest, Uganda. 14 June 2009. J.C.H. Dobson.

This is a purely Afrotropical genus of 39 medium- to large-sized species. The lineage arose ~ 18 Mya.

Body: Head large, broad and hairy. Antennae shorter than half length of forewing, averaging 47% (42-52%) of forewing for both sexes. Palpi 1st joint twice as long as broad, 2nd joint three times longer than first joint and terminal joint minute, oval. All joints hairy. Thorax short, compressed laterally, hairy and scaly. Abdomen long, extending beyond outer edge of hindwings, laterally compressed, broader distally. **Legs:** Anterior legs slender and less than half length of pterothoracic legs; tarsi of male single joint without spines, female tarsi five jointed with spines on each except last, no terminal spine. Pterothoracic legs, robust, external claw of male furrowed on inner surface, terminal claws asymmetrical. **Wing venation:** Radial veins of forewing not stalked; R1 branching off from cell rather than stalked. Cell of hindwing about half of total wing length. Markings: Hindwing has the spots in the row below the apex joined to the central row creating a discontinuous arrangement of spots (7:2 configuration). Hyaline areas and hyaline patches not present. There are no marginal markings or spots on forewing upper side. **Male genitalia:** Uncus short, acute or bifid at tip; aedeagus long, narrow but not needle like, distally thin in one species group with broad truncate base, all basally bifid into two prongs; sclerotized and modified 8th tergite present; valves large, distally obtuse or elongate with distal processes; juxta elongate, triangular, weakly sclerotized; vinculum fairly broad; saccus very broad. **Female genitalia:** Anal lobes small, evenly rounded, posterior apophyses as long or longer than the lobes; sterigma convex, U-shaped; ostium centrally or anteriorly placed; ductus very short; bursa spherical; single pair of signa very small or absent. Sphragis present except in *A. acrita* species group.

Early stages: Egg elongate; laid in clusters, sometimes singly (*R. nohara*). Larvae gregarious; dorsal spines on segments 3–6 sometimes longer and thicker. Pupa with wing covers finely lined by black on wing veins. **Host plant genera:** *Triliceras* and *Basananthe* (4 records each), *Adenia* and *Oncoba* (3 records each), *Rawsonia* (2 records). One record each for *Triumfetta*, *Drypetes*, *Rinorea*, *Caloncoba* and *Xylothea*. **Host plant families:** Passifloraceae (6 records), Salicaceae, Turneraceae and Achariaceae (3 records each), Malvaceae, Euphorbiaceae, Violaceae and Flacourtiaceae (1 record each). **Habitats (biomes):** Predominantly a woodland genus, with five species in grassland. Woodland (14 spp.), forest (7 spp.), grassland (5 spp.), submontane forest (1 sp.) and coastal forest (1 sp.). **Geographical range:** *Rubraea* is confined to the sub-Saharan African mainland, with a few species in the Gulf of Guinea islands. The genus is concentrated in east-central Africa (eastern and southern DRC, Tanzania, Zambia and Angola).

Diagnosis

Facies: Rufous to ochreous with black spots. Hyaline areas or patches are absent. The genus *Rubraea* can be distinguished from *Stephenia* by their generally less acute forewings.

Genitalia: The male genitalia in *Rubraea* have the aedeagus long, narrow but not needle-like; distally thin in one species group with broad truncate base, all basally bifid into two prongs; sclerotized and modified 8th tergite present; valves large, distally obtuse or elongate with distal processes. In the female genitalia the sterigma is convex, U-shaped, with the ductus very short.

Species list

- Rubraea abdera* (Hewitson, [1852]) **comb. nov.**
Rubraea abdera abdera (Hewitson, [1852])
Rubraea abdera eginopsis (Aurivillius, [1899]) **comb. nov.**
- Rubraea acrita* (Hewitson, [1865]) **comb. nov.**
Rubraea annonae (Pierre, 1987) **comb. nov.**
Rubraea asema (Hewitson, 1877) **comb. nov.**
Rubraea atolmis (Westwood, 1881) **comb. nov.**
Rubraea bailundensis (Wichgraf, 1918) **comb. nov.**
Rubraea bellona (Weymer, 1908) **comb. nov.**
Rubraea cepheus (Linnaeus, 1758) **comb. nov.**
Rubraea cepheus cepheus (Linnaeus, 1758)
Rubraea cepheus bergeriana (Pierre, 1979) **comb. nov.**
- Rubraea cerasa* (Hewitson, [1861]) **comb. nov.**
Rubraea cerasa cerasa (Hewitson, [1861])
Rubraea cerasa cerita (Sharpe, 1906) **comb. nov.**
- Rubraea chaeribula* (Oberthür, 1893) **comb. nov.**
Rubraea chambezi (Neave, 1910) **comb. nov.**
Rubraea diogenes (Suffert, 1904) **comb. nov.**
Rubraea egina (Cramer, [1775]) **comb. nov.**
Rubraea egina egina (Cramer, [1775])
Rubraea egina bellehui (Carcasson, 1961) **comb. nov.**
- Rubraea eltringhamiana* (Le Doux, 1932) **comb. nov.**
Rubraea guillemei (Oberthür, 1893) **comb. nov.**
Rubraea guluensis (Le Doux, 1932) **comb. nov.**
Rubraea kraka (Aurivillius, 1893) **comb. nov.**
Rubraea lapidorum (Pierre, 1988) **comb. nov.**

- Rubraea lofua* (Eltringham, 1911) **comb. nov.**
Rubraea loranae (Pierre, 1987) **comb. nov.**
Rubraea lualabae (Neave, 1910) **comb. nov.**
Rubraea manca (Thurau, 1904) **comb. nov.**
Rubraea mansya (Eltringham, 1911) **comb. nov.**
Rubraea medea (Cramer, [1775]) **comb. nov.**
Rubraea niobe (Sharpe, 1893) **comb. nov.**
Rubraea nohara (Boisduval, 1847) **comb. nov.**
Rubraea nohara nohara (Boisduval, 1847)
Rubraea nohara halali (Marshall, 1896) **comb. nov.**
Rubraea nohara dondoensis (Stevenson, 1934) **comb. nov.**
- Rubraea omrora* (Trimen, 1894) **comb. nov.**
Rubraea omrora omrora (Trimen, 1894)
Rubraea omrora umbraetae (Pierre, 1988) **comb. nov.**
- Rubraea onerata* (Trimen, 1891) **comb. nov.**
Rubraea overlaeti (Pierre, 1988) **comb. nov.**
Rubraea peetersi (Pierre, 1992) **comb. nov.**
Rubraea periphanes (Oberthür, 1893) **comb. nov.**
Rubraea petraea (Boisduval, 1847) **comb. nov.**
Rubraea pseudatolmis (Eltringham, 1912) **comb. nov.**
Rubraea pudorina (Staudinger, [1885]) **comb. nov.**
Rubraea punctellata (Eltringham, 1912) **comb. nov.**
Rubraea rohlfsi (Suffert, 1904) **comb. nov.**
Rubraea unimaculata (Grose-Smith, 1898) **comb. nov.**
Rubraea utengulensis (Thurau, 1903) **comb. nov.**
Rubraea violarum (Boisduval, 1847) **comb. nov.**
Rubraea violarum violarum (Boisduval, 1847)
Rubraea violarum gracilis (Wichgraf, 1909) **comb. nov.**
Rubraea violarum anchietai (Mendes & Bivar-de-Sousa, 2017) **comb. nov.**

Species groups of *Rubraea* (based on male genitalia)

***R. acrita* species-group:** the 8th tergite is modified; aedeagus short, distally thin and acute, anteriorly broad and truncate, bifid; uncus short; valve large obtuse with distal processes.

Rubraea acrita (Hewitson, [1865]), *Rubraea annonae* (Pierre, 1987), *Rubraea bailundensis* (Wichgraf, 1918), *Rubraea bellona* (Weymer, 1908), *Rubraea chaeribula* (Oberthür, 1893), *Rubraea diogenes* (Suffert, 1904), *Rubraea eltringhamiana* (Le Doux, 1932), *Rubraea guillemei* (Oberthür, 1893), *Rubraea guluensis* (Le Doux, 1932), *Rubraea loranae* (Pierre, 1987), *Rubraea lualabae* (Neave, 1910), *Rubraea manca* (Thurau, 1904), *Rubraea periphanes* (Oberthür, 1893), *Rubraea pudorina* (Staudinger, [1885]), *Rubraea utengulensis* (Thurau, 1903).

***R. egina* species-group:** aedeagus moderately long; uncus short, basally broad; valve large, elongate, not narrowing distally.

Rubraea egina (Cramer, [1775]), *Rubraea medea* (Cramer, [1775]), *Rubraea niobe* (Sharpe, 1893).

***R. nohara* species-group:** valves elongate, basally obtuse narrowing centrally, apically truncate with distal process in some species.

Rubraea atolmis (Westwood, 1881), *Rubraea cerasa* (Hewitson, [1861]), *Rubraea dondoensis* (Stevenson, [1934]), *Rubraea chambezi* (Neave, 1910), *Rubraea kraka* (Aurivillius, 1893), *Rubraea lapidorum* (Pierre, 1988), *Rubraea lofua* (Eltringham, 1911), *Rubraea mansya* (Eltringham, 1911), *Rubraea nohara* (Boisduval, 1847),

Rubraea onerata (Trimen, 1891), *Rubraea peetersi* (Pierre, 1992), *Rubraea pseudatolmis* (Eltringham, 1912), *Rubraea punctellata* (Eltringham, 1912), *Rubraea unimaculata* (Grose-Smith, 1898).

R. violarum species-group: valves short and broad, uncus bifid.

Rubraea asema (Hewitson, 1877), *Rubraea omrora* (Trimen, 1894), *Rubraea overlaeti* (Pierre, 1988), *Rubraea violarum* (Boisduval, 1847).

R. cepheus species-group: uncus straight and acute; vinculum broad.

Rubraea abdera (Hewitson, [1852]), *Rubraea cepheus* (Linnaeus, 1758), *Rubraea petraea* (Boisduval, 1847), *Rubraea rohlfsi* (Suffert, 1904).

Genus *Stephenia* Henning, 1992 stat. nov.

Type species *Papilio caecilia* Fabricius, 1781

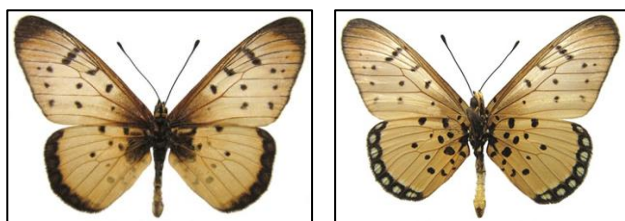


Figure 4 – *Stephenia caecilia* (male), the type species of the genus. Left – upper side. Right – underside. Wingspan: 48 mm. Zamaye, Cameroon. July 1993. Ex Henning Collection.

This is a purely Afrotropical genus of 29 medium- to large-sized species. The lineage arose ~ 17 Mya.

Body: Head large, broad and hairy. Antennae shorter than half length of forewing, averaging 47% (43–50%) of forewing for both sexes. Palpi 1st joint twice as long as broad, 2nd joint three times longer than first joint and terminal joint minute, oval. All joints hairy. Thorax short, compressed laterally, hairy and scaly. Abdomen long, extending beyond outer edge of hindwings, laterally compressed, broader distally. **Legs:** Anterior legs slender and less than half length of pterothoracic legs; tarsi of male single joint without spines, female tarsi five jointed with spines on each except last, no terminal spine. Pterothoracic legs, robust, external claw of male furrowed on inner surface, terminal claws asymmetrical. **Wing venation:** Radial veins of forewing not stalked; R1 branching off from cell rather than stalked. Cell of hindwing about half of total wing length. Markings: Hindwing has the spots in the row below the apex joined to the central row creating a discontinuous arrangement of spots (7:2 configuration). Hyaline areas and hyaline patches restricted to subapical area of forewing. There are no marginal markings or spots on forewing upperside. **Male genitalia:** Uncus short, acute or slightly bifid tip; aedeagus long to very long, narrow but not needle like, basally bulbous but not bifid; sclerotized and modified 8th tergite or sternite not present; valves comparatively short and angular, distally broad; juxta small, subangular to elongated, gutter like, weakly sclerotized; vinculum fairly broad; saccus pronounced, broad to very elongate. **Female genitalia:** Anal lobes short and broad, posterior apophyses as long or longer than the lobes; sterigma broad and lobed; ostium anteriorly or posteriorly placed; ductus long to very long; bursa spherical to ovoid; single pair of small signa, may be widely separated. Sphragis may be present or absent

depending on the species group.

Early stages: Egg conical, flat topped; laid in clusters but in some species singly. Larvae gregarious. Pupa with wing veins delicately outlined in black. **Host plant genera:** *Adenia* (12 records), *Tricliceras* (6 records), *Passiflora* (5 records), *Vitis* and *Oncoba* (3 records each). One record each for *Basananthe*, *Paropsia*, *Malva*, *Loewia*, *Streptopetalum*, *Wormskioldia* and *Xylothea*. **Host plant families:** Passifloraceae (14 records), Turneraceae (7 records), Vitaceae, Salicaceae and Malvaceae (3 records each). One record for Achariaceae. **Habitats (biomes):** *Stephenia* is a genus largely of woodland and savanna biomes. Savanna (12 spp.), Woodland (11 spp.), forest (2 spp.) **Geographical range:** The genus is centred in east-central Africa, extending to Angola in the west. Found predominantly in Uganda, Kenya, Tanzania, eastern and southern DRC, Zambia and Angola.

Diagnosis

Facies: Rufous to ochreous with black spots. Hyaline patches are present but are restricted to the subapical area of the forewing. The genus *Stephenia* can be distinguished from *Rubraea* by the generally more acute forewings.

Genitalia: The male aedeagus is long to very long, narrow but not needle-like; basally bulbous but not bifid; sclerotized and modified 8th tergite or sternite not present; valves comparatively short and angular. The female genitalia have the sterigma broad and lobed, with the ductus long to very long.

Species list

Stephenia aglaonice (Westwood, 1881) **comb. nov.**

Stephenia asboloplintha (Karsch, 1894) **comb. nov.**

Stephenia asboloplintha asboloplintha (Westwood, 1881)

Stephenia asboloplintha rubescens (Trimen, 1909) **comb. nov.**

Stephenia atatis (Pierre, 2004) **comb. nov.**

Stephenia atergatis (Westwood, 1881) **comb. nov.**

Stephenia axina (Westwood, 1881) **comb. nov.**

Stephenia braesia (Godman, 1885) **comb. nov.**

Stephenia buettneri (Rogenhofer, 1890) **comb. nov.**

Stephenia caecilia (Fabricius, 1781) **comb. nov.**

Stephenia caldarena (Hewitson, 1877) **comb. nov.**

Stephenia caldarena caldarena (Hewitson, 1877)

Stephenia caldarena neluska (Oberthür, 1878) **comb. nov.**

Stephenia doubledayi (Guérin-Méneville, 1849) **comb. nov.**

Stephenia doubledayi doubledayi (Guérin-Méneville, 1849)

Stephenia doubledayi azvaki (d'Abbrera, 1980) **comb. nov.**

Stephenia ella (Eltringham, 1911) **comb. nov.**

Stephenia equatorialis (Neave, 1904) **comb. nov.**

Stephenia equatorialis equatorialis (Neave, 1904)

Stephenia equatorialis caoncius (Suffert, 1904) **comb. nov.**

Stephenia intermediodes (Ackery, 1995) **comb. nov.**

Stephenia leucopyga (Aurivillius, 1904) **comb. nov.**

Stephenia lyci (Pierre, 2006) **comb. nov.**

Stephania lygus (Druce, 1875) **comb. nov.**
Stephania mirabilis (Butler, 1886) **comb. nov.**
Stephania miranda (Riley, 1920) **comb. nov.**
Stephania natalica (Boisduval, 1847) **comb. nov.**
Stephania oncaea (Hopffer, 1855) **comb. nov.**

Stephania oncaea oncaea (Hopffer, 1855)
Stephania oncaea shimba (Bernaud & Collins, 2021) **comb. nov.**
Stephania oncaea idjwi (Bernaud & Collins, 2021) **comb. nov.**

Stephania pseudogina (Westwood, [1852]) **comb. nov.**
Stephania pudora (Aurivillius, 1910) **comb. nov.**
Stephania pudorella (Aurivillius, [1899]) **comb. nov.**
Stephania pudorella pudorella (Aurivillius, 1899)
Stephania pudorella detecta (Neave, 1910) **comb. nov.**

Stephania regalis (Oberthür, 1893) **comb. nov.**
Stephania rhodesiana (Wichgraf, 1909) **comb. nov.**
Stephania rogersi (Hewitson, 1873) **comb. nov.**
Stephania stenobea (Wallengren, 1860) **comb. nov.**
Stephania sykesi (Sharpe, 1902) **comb. nov.**
Stephania zoumi (Pierre, 1995) **comb. nov.**

Species groups of *Stephania* (based on wing markings; male genitalia; female sphragis)

***S. caecilia* species-group:** the aedeagus and saccus are elongated to very elongated; sphragis mostly absent.

Stephania asboloplintha (Karsch, 1894), *Stephania atatis* (Pierre, 2004), *Stephania atergatis* (Westwood, 1881), *Stephania axina* (Westwood, 1881), *Stephania braesia* (Godman, 1885), *Stephania buettneri* (Rogenhofer, 1890), *Stephania caecilia* (Fabricius, 1781), *Stephania caldarena* (Hewitson, 1877), *Stephania doubledayi* (Guérin-Méneville, 1849), *Stephania ella* (Eltringham, 1911), *Stephania equatorialis* (Neave, 1904), *Stephania intermediodes* (Ackery, 1995), *Stephania leucopyga* (Aurivillius, 1904), *Stephania lyci* (Pierre, 2006), *Stephania lygus* (Druce, 1875), *Stephania natalica* (Boisduval, 1847), *Stephania oncaea* (Hopffer, 1855), *Stephania pseudogina* (Westwood, [1852]), *Stephania pudora* (Aurivillius, 1910), *Stephania pudorella* (Aurivillius, [1899]), *Stephania regalis* (Oberthür, 1893), *Stephania rhodesiana* (Wichgraf, 1909), *Stephania stenobea* (Wallengren, 1860), *Stephania sykesi* (Sharpe, 1902), *Stephania zoumi* (Pierre, 1995).

***S. rogersi* species-group:** hindwing with a complete or partial row of submarginal spots and the aedeagus has a large distinctly oval shaped anterior plate.

Stephania rogersi (Hewitson, 1873).

***S. aglaonice* species-group:** valve has a long process on the basal half, uncus bifid; sphragis present.

Stephania aglaonice (Westwood, 1881), *Stephania mirabilis* (Butler, 1886), *Stephania miranda* (Riley, 1920).

Genus *Tildia* Williams & Henning, 2023 **gen. nov.**

Type species *Papilio zetes* Linnaeus, 1758

This is a purely Afrotropical genus of 13 fairly large to large species. The lineage arose ~ 17 Mya.

Body: Head large, broad and hairy. Antennae shorter than half length of forewing, averaging 42.5% (37–46%) of forewing for both sexes. Palpi 1st joint twice as long as broad, 2nd joint three times longer than first joint and terminal joint minute, oval. All joints hairy. Thorax short,



Figure 5 – *Tildia zetes* (male), the type species of the genus. Left – upper side. Right – underside. Wingspan: 65 mm. Kakum Forest, Ghana. 20 November 2011. J.C.H. Dobson.

compressed laterally, hairy and scaly. Abdomen long, extending beyond outer edge of hindwings, laterally compressed, broader distally. **Legs:** Anterior legs slender and less than half length of pterothoracic legs; tarsi of male single joint without spines, female tarsi five jointed with spines on each except last, no terminal spines. Pterothoracic legs, robust, external claw of male furrowed on inner surface, terminal claws asymmetrical. **Wing venation:** Radial veins of forewing not stalked; R1 branching off from cell rather than stalked. Cell of hind wing more than half of total wing length. Markings: Similar in placement to *Acraea* but with marginal markings or spots on forewing upper side in both species groups. **Male genitalia:** Uncus beak-shaped and elongate, as long, or longer, than tegumen, arched, acute at tip; aedeagus thin, needle like, curved; sclerotized and modified 8th tergite or sternite not present; valves very elongated, not triangulate basally and have inward projections, not fused basally, more than twice length of uncus; juxta extremely narrow, elongated and strongly sclerotized; vinculum broad and almost filling the saccus. **Female genitalia:** Anal lobes short, produced ventrad, posterior apophyses longer than lobes and supporting sclerites combined. Sterigma usually taking the form of a large U-shaped plate; ostium anteriorly placed; ductus short and sclerotized; bursa elongate or spherical; two signa, very small or absent. Sphragis present.

Early stages: Egg squat, ovoid, almost as broad as high; laid in small batches. The larvae are gregarious. Pupa white to creamy, with black lines marking the nervules on the wing covers. **Host plant genera:** *Adenia* (6 records), *Passiflora* (2 records) and *Basananthe* (2 records). The following plant genera have been recorded only for *T. zetes*: *Vitis*, *Barteria*, *Deidama*, *Hydnocarpus*, *Phyllobotryum*, *Smeathmannia* and *Tacsonia*. **Host plant families:** Passifloraceae (7 records), Flacourtiaceae (1 record), Vitiaceae (1 record). **Habitats (biomes):** A predominantly woodland and savanna genus, with a single species in the Namib desert. Woodland (5 spp.), savanna (4 spp.); coastal forest (2 spp.); Namib Desert (*T. hypoleuca*). **Geographical range:** Kenya and Tanzania have the most species (7 each), with six species in southern DRC and five species in Angola, Zambia, Mozambique, South Africa and Namibia. There are four species in Malawi, Zimbabwe, Botswana and Ethiopia, and three in Southern Sudan, Uganda, Somalia and Swaziland. One species (*T. zetes*) is widespread in the Afrotropical Region and there is a single species in Madagascar (*T. turna*).

Diagnosis

Facies: The genus *Tildia* can be distinguished from *Acraea* by the presence of marginal spots on the forewing upper side in species from each species group. The genus

Cethosia has marginal spots on the forewing upperside as has *anacreon*, the earliest offshoot of *Telchinia* (Carvalho *et. al.*, 2021) and as do other tribes in the Subfamily Heliconiinae. Some species of *Tildia* have normal markings entirely absent on the upper side.

Genitalia: The male genitalia in *Tildia* are fairly simple in comparison to the adaptations in *Acraea* genitalia. In *Acraea horta* species-group the 8th sternite is modified to form a protective plate called a velum, in the *machequena* species-group the valves are strongly incurved forming a claw, in the *satis* species-group the 8th tergite is produced into a pseudouncus with the rest reduced in size, in the *admatha* species-group the juxta is articulated by a transtilla and connected by an elongate sclerite, in the *quirina* species-group the uncus is divided into two hooks as large as the valves. In comparison the male genitalia of *Tildia* are simple with the valves greatly elongated and not subtriangular and the juxta narrow, elongated and strongly sclerotized. The vinculum is also largely enclosed within the saccus. In the female genitalia the ostium is anteriorly placed as compared to *Acraea* which are central or posteriorly placed in the species examined.

Species list

- Tildia acara* (Hewitson, [1865]) **comb. nov.**
Tildia anemosa (Hewitson, [1865]) **comb. nov.**
Tildia barberi (Trimen, 1881) **comb. nov.**
Tildia chilo (Godman, 1880) **comb. nov.**
Tildia chilo chilo (Godman, 1880)
Tildia chilo crystallina (Grose-Smith, 1890) **comb. nov.**
Tildia hypoleuca (Trimen, 1898) **comb. nov.**
Tildia oscar (Rothschild, 1902) **comb. nov.**
Tildia pseudolycia (Butler, 1874) **comb. nov.**
Tildia pseudolycia pseudolycia (Butler, 1874)
Tildia pseudolycia astrigera (Butler, 1899) **comb. nov.**
Tildia rabbaiae (Ward, 1873) **comb. nov.**
Tildia rabbaiae rabbaiae (Ward, 1873)
Tildia rabbaiae perlucida (Henning & Henning, 1996) **comb. nov.**
Tildia trimeni (Aurivillius, [1899]) **comb. nov.**
Tildia turna (Mabille, 1877) **comb. nov.**
Tildia welwitschii (Rogenhofer, 1893) **comb. nov.**
Tildia zetes (Linnaeus, 1758) **comb. nov.**
Tildia zetes zetes (Linnaeus, 1758)
Tildia zetes sidamona (Rothschild & Jordan, 1905) **comb. nov.**
Tildia zetes annobona (d'Abbrera, 1980) **comb. nov.**
Tildia zonata (Hewitson, 1877) **comb. nov.**

Species groups of *Tildia* (based on male genitalia)

***T. zetes* species-group:** valves elongate and sharply truncate or rounded distally with juxta large, narrow and elongated.

Tildia acara (Hewitson, [1865]), *Tildia barberi* (Trimen, 1881), *Tildia chilo* (Godman, 1880), *Tildia hypoleuca* (Trimen, 1898), *Tildia oscar* (Rothschild, 1902), *Tildia trimeni* (Aurivillius, [1899]), *Tildia turna* (Mabille, 1877), *Tildia zetes* (Linnaeus, 1758), *Tildia anemosa* (Hewitson, [1865]), *Tildia pseudolycia* (Butler, 1874), *Tildia welwitschii* (Rogenhofer, 1893).

***T. rabbaiae* species-group:** valves with projection on inner margin with juxta elongate triangular.

Tildia rabbaiae (Ward, 1873), *Tildia zonata* (Hewitson, 1877).

Genus *Bematistes* Hemming, 1935 **stat. rev.**

Type species *Papilio epaea* Felder, 1779



Figure 6 – *Bematistes epaea* (male), the type species of the genus. Left – upper side. Right – underside. Wingspan: 60 mm. Biakpa Mountain Paradise, Ghana. 24 November 2011. J.C.H. Dobson.

This is a purely Afrotropical genus of 35 fairly large to large species. The lineage arose ~ 27 Mya.

Body: Head moderately large, hairy. Antennae broad and abrupt, shorter than half length of forewing, averaging 42% (38-46%) of forewing for both sexes. Palpi 1st joint four times as long as broad, 2nd joint twice as long as first joint and terminal joint minute, oval. Black with lateral white line. All joints hairy. Thorax elongate; compressed laterally, hairy and scaly. Abdomen long, extending beyond outer edge of hindwings, laterally compressed, broader distally. **Legs:** Anterior legs slender and less than half length of pterothoracic legs; tarsi of male single joint with terminal spine, female tarsi five jointed with spines on each except last, with a terminal spine. Pterothoracic legs robust, external claw of male furrowed on inner surface, two terminal claws asymmetrical in male, symmetrical in female. **Wing venation:** Radial veins of forewing stalked; R1 branching off from R2-R5 well beyond the upper angle of cell. Cell of hindwing slightly more than one third of total wing length. Markings: Hindwing has no spots or coalesced, forming a tight grouping. Hyaline areas and hyaline patches absent. There are no marginal markings or spots on forewing or hindwing. **Male genitalia:** Uncus very short with bifid tip; aedeagus long, straight and narrow but not needle like, basally narrow and not bifid; sclerotized and modified 8th tergite or sternite not present; valves comparatively short and angular, incurved and broadly claw-like; juxta small, U-shaped, weakly sclerotized; vinculum large and broad; saccus elongate. **Female genitalia:** Anal lobes short and broad, posterior apophyses as long, or longer, than the lobes; two sub-pupillary glands; sterigma broad and U-shaped; ostium posteriorly placed; ductus short and sclerotized; bursa spherical to ovoid; two pairs of prominent spinose signa. Sphragis present.

Early stages: Egg cylindrical, twice as high as wide, evenly domed on top; laid in batches. Pupa with four pairs of long dorsal processes on the first four abdominal segments. **Host plant genera:** *Adenia* (13 records), *Barteria* (3 records), *Oncoba* and *Vitis* (2 records each). One record for each of *Basananthe*, *Passiflora* and *Trypsohemma*. **Host plant families:** Passifloraceae (15 records), Salicaceae and Vitaceae (2 records each). **Habitats (biomes):** *Bematistes* is predominantly a forest genus. Forest (19 spp.), submontane forest (3 species),

montane forest (2 species). Two species are found in moist woodland. There are no savanna species. **Geographical range:** A genus of the Guineo-Congolian forest block. Best represented in the Democratic Republic of Congo (23 spp.), Cameroon (19 spp.), Uganda (18 spp.), Tanzania (16 spp.), Gabon (13 spp.) and Nigeria (11 spp.).

Diagnosis

Facies: Forewing radials stalked (not stalked in other African genera in the tribe). Generally large butterflies; wings dark with coloured patches; limited spotting restricted towards base of wings. The genus *Bematistes* has no hindwing marginal spots and no hyaline areas on the wings. The cell of the hindwing is comparatively short compared to the other genera. Anterior legs of male with terminal spine present; not present in the other African genera. Pupa with four pairs of long dorsal processes not found in other African genera. Some mimics found in *Telchinia*.

Genitalia: In the male genitalia the uncus is very short; aedeagus long, straight and narrow but not needle-like, basally narrow and not bifid; sclerotized and modified 8th tergite or sternite absent, valves claw-shaped. In the female genitalia the sterigma is broadly U-shaped; there are two pairs of signa (only one pair in other African genera).

Species list

- Bematistes adrasta* (Weymer, 1892) **comb. rev.**
Bematistes aganice (Hewitson, [1852]) **comb. rev.**
Bematistes aganice aganice (Hewitson, [1852])
Bematistes aganice montana (Butler, 1888) **comb. rev.**
Bematistes aganice orientalis (Ungemach, 1932) **comb. rev.**
Bematistes alcinoe (Felder & Felder, [1865]) **comb. rev.**
Bematistes alcinoe alcinoe (Felder & Felder, [1865])
Bematistes alcinoe nado (Ungemach, 1932) **comb. rev.**
Bematistes bakundu (Bernaud, 2021) **comb. rev.**
Bematistes bana (Pierre & Bernaud, 2012) **comb. rev.**
Bematistes consanguinea (Aurivillius, 1893) **comb. rev.**
Bematistes consanguinea consanguinea (Aurivillius, 1893)
Bematistes consanguinea albicolor (Karsch, 1895) **comb. rev.**
Bematistes dewitzi (Staudinger, 1896) **comb. rev.**
Bematistes dimonika (Bernaud, 2021) **comb. rev.**
Bematistes ducarmeii (Bernaud & Pierre, 2012) **comb. rev.**
Bematistes elongata (Butler, 1874) **comb. rev.**
Bematistes epaea (Cramer, [1779]) **comb. rev.**
Bematistes epiprotea (Butler, 1874) **comb. rev.**
Bematistes epitellus (Staudinger, 1896) **comb. rev.**
Bematistes excisa (Butler, 1874) **comb. rev.**
Bematistes formosa (Butler, 1874) **comb. rev.**
Bematistes indentata (Butler, 1895) **comb. rev.**
Bematistes kivuana (Jordan, 1910) **comb. rev.**
Bematistes kivuensis (Joicey & Talbot, 1927) **comb. rev.**
Bematistes kivuensis kivuensis (Joicey & Talbot, 1927)
Bematistes kivuensis elgonense (Poulton, 1927) **comb. rev.**
Bematistes leopoldina (Aurivillius, 1895) **comb. rev.**

- Bematistes lequeuxi* (Bernaud & Pierre, 2012) **comb. rev.**
Bematistes macaria (Fabricius, 1793) **comb. rev.**
Bematistes macaria macaria (Fabricius, 1793)
Bematistes macaria macaroides (Aurivillius, 1893) **comb. rev.**
Bematistes macaria hemileuca (Jordan, 1914) **comb. rev.**
Bematistes macarista (Sharpe, 1906) **comb. rev.**
Bematistes melina (Thurau, 1903) **comb. rev.**
Bematistes obliqua (Aurivillius, [1913]) **comb. rev.**
Bematistes parageum (Grose-Smith, 1900) **comb. rev.**
Bematistes parageum parageum (Grose-Smith, 1900)
Bematistes parageum homochroa (Rothschild & Jordan, 1905) **comb. rev.**
Bematistes parageum insulana (Achery, 1995) **comb. rev.**
Bematistes persanguinea (Rebel, 1914) **comb. rev.**
Bematistes poggei (Dewitz, 1879) **comb. rev.**
Bematistes poggei poggei (Dewitz, 1879)
Bematistes poggei ras (Ungemach, 1932) **comb. rev.**
Bematistes pseudeuryta (Godman & Salvin, 1890) **comb. rev.**
Bematistes quadricolor (Rogenhofer, 1891) **comb. rev.**
Bematistes sartina (Jordan, 1910) **comb. rev.**
Bematistes scalivittata (Butler, 1896) **comb. rev.**
Bematistes schubotzi (Grünberg, 1911) **comb. rev.**
Bematistes tellus (Aurivillius, 1893) **comb. rev.**
Bematistes tellus tellus (Aurivillius, 1893)
Bematistes tellus eumelis (Jordan, 1910) **comb. rev.**
Bematistes umbra (Drury, 1782) **comb. rev.**
Bematistes vestalis (Felder & Felder, [1865]) **comb. rev.**
Bematistes vestalis vestalis (Felder & Felder, [1865])
Bematistes vestalis congoensis (Le Doux, 1937) **comb. rev.**

Species groups of *Bematistes*. This genus is homogeneous, with no identifiable species groups.

Genus *Actinote* Hübner, [1819]

Type species *Papilio thalia* Linnaeus, 1758

Synonyms: *Calornis* Billberg, 1820; *Abananote* Potts, 1943; *Altinote* Potts, 1943.

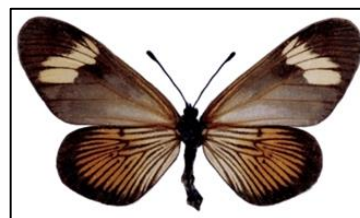


Figure 7 – *Actinote parapheles* (male upper side), a typical member of the genus. Wingspan: 55 mm. Credit: Wikipedia images.

This is a Neotropical genus of 59 species. The lineage arose ~ 23 Mya.

Species list

- Actinote abana* (Hewitson, 1868)
Actinote alalia (C. & R. Felder, 1860)
Actinote alberti Neild & Romero, 2008

Actinote alcione (Hewitson, 1852)
Actinote anaxo (Hopffer, 1874)
Actinote anteas (Doubleday, 1847)
Actinote ballettae Neild & Romero, 2008
Actinote bonita Penz, 1996
Actinote brylla Oberthür, 1917
Actinote callianthe (C. & R. Felder, 1862)
Actinote canutia (Hopffer, 1874)
Actinote catarina Penz, 1996
Actinote carycina Jordan, 1913
Actinote conspicua Jordan, 1913
Actinote dalmeidai Francini, 1996
Actinote dicaeus (Latreille, [1817])
Actinote discrepans d'Almeida, 1958
Actinote eberti Francini, Freitas & Penz, 2004
Actinote eresia (C. & R. Felder, 1862)
Actinote erinome (C. & R. Felder, 1861)
Actinote euryleuca Jordan, 1910
Actinote furtadoi Paluch, Casagrande & Mielke, 2006
Actinote genitrix d'Almeida, 1922
Actinote griseata Butler, 1873
Actinote guatemalena (Bates, 1864)
Actinote hiliaris Jordan, 1910
Actinote hylonome (Doubleday, 1844)
Actinote intensa (Jordan, 1910)
Actinote johncoulsoni Willmott, Lamas & Hall, 2017
Actinote kennethi Freitas, Willmott & Hall, 2009
Actinote lapitha (Staudinger, 1885)
Actinote latior Jordan, 1913
Actinote mamita (Burmeister, 1861)
Actinote mantiqueira Freitas *et al.*, 2018
Actinote melampepos Godman & Salvin, [1881]
Actinote melanisans Oberthür, 1917
Actinote mielkei Paluch & Casagrande, 2006
Actinote mirnae Paluch & Mielke, 2006
Actinote momina Jordan, 1910
Actinote morio Oberthür, 1917
Actinote negra (C. & R. Felder, 1862)
Actinote neleus (Latreille, [1813])
Actinote ozomene (Godart, 1819)
Actinote pallescens Jordan, 1913
Actinote paraphelus Jordan, 1913
Actinote pellenea Hübner, [1819]
Actinote pratensis Francini, Freitas & Penz, 2004
Actinote pyrrha (Fabricius, 1775)
Actinote quadra (Schaus, 1902)
Actinote rhodope d'Almeida, 1923
Actinote romeroi Neil & Costa, 2008
Actinote rubrocellulata Hayward, 1960
Actinote rufina Oberthür, 1917
Actinote stratonice (Latreille, [1813])
Actinote surima (Schaus, 1902)
Actinote tenebrosa (Hewitson, 1868)
Actinote thalia (Linnaeus, 1758)
Actinote trinacria (C. & R. Felder, 1862)
Actinote zikani d'Almeida, 1951

Genus *Telchinia* Hübner, [1819] **stat. rev.**

Type species *Papilio serena* Fabricius, 1775
 Synonyms: *Gnesia* Doubleday, 1848; *Hyalites* Doubleday, 1848; *Pareba* Doubleday, 1848; *Planema* Doubleday, 1848; *Alacria* Henning, 1992; *Aurora* Henning, 1992; *Auracraea* Henning, 1993

This is an almost exclusively Afrotropical genus of 102 small to fairly large species. One species (*T. issoria*) is found in the Oriental Region. The lineage arose ~ 23 Mya.



Figure 8 – *Telchinia serena* (male), the type species of the genus. Left – upper side. Right – underside. Wingspan: 40 mm. Madikwe Nature Reserve, North West Province, South Africa. June 1998. M.C. Williams.

Body: Head large, broad and hairy. Antennae shorter than half length of forewing, averaging 43% (38–48%) of forewing for both sexes. Palpi 1st joint twice as long as broad, 2nd joint three times longer than first joint and terminal joint minute, oval. All joints hairy. Thorax short, compressed laterally, hairy and scaly. Abdomen long, extending just beyond outer edge of hindwings, laterally compressed, broader distally. **Legs:** Anterior legs slender and less than half length of pterothoracic legs; tarsi of male single joint without spines, female tarsi five jointed with spines on each except last, no terminal spine. Pterothoracic legs, fairly robust, external claw of male without furrow on inner surface, terminal claws symmetrical or asymmetrical. **Wing venation:** Radial veins of forewing not stalked; R1 branching off from cell rather than stalked. Cell of hindwing about half of total wing length. The *anacreon* species group has a rudimentary vein between the second cubital and second anal vein, as found in the South American genus *Actinote*. Markings: Hindwing has the spots in the row below the apex joined to the central row creating a discontinuous arrangement of spots (7:2 configuration) forming a curved row of spots or spots may be restricted to basal area. Hyaline areas and hyaline patches present. There are no marginal markings or spots on forewing upper side in most species except *anacreon* species group and *serena* species sub-group. **Male genitalia:** Uncus beak-shaped, short or half the length of the tegumen, tip acute; aedeagus short, not narrow and not needle like, may be stout, distally truncate or acute, basally bulbous but not bifid; sclerotized and modified 8th tergite or sternite not present; valves may be long and elongated to short and broad, distally broad but tapering and rounded; juxta small, subtriangular, weakly sclerotized; vinculum fairly broad; saccus, short to pronounced. **Female genitalia:** Anal lobes short and broad, posterior apophyses shorter than the lobes; sterigma forms a pouch-like vestibulum with a posterior projection; ostium anteriorly or posteriorly placed; ductus short; bursa large, elongate to ovoid; single pair of signa, large patch, ovoid to elongated; sub-pupillary gland developed anteriorly; one terminal gland. Sphragis may be present or absent depending on the species group.

Early stages: Egg conical to barrel shaped, may be rounded or flat topped; usually laid in untidy clusters but in some species in a neat single layer. Larvae gregarious; often spin silk to form untidy shelters of dead leaves and entrapped larval frass. Pupa with wing cases usually lined in black. **Host plant genera:** *Scepocarpus* (23 records), *Triumfetta* (10 records), *Pouzolzia* (9 records), *Laportea* (8

records), *Boehmeria* (7 records), *Fleurya* (6 records), *Adenia*, *Aeschynomene* and *Hibiscus* (5 records each), *Urtica* and *Musanga* (4 records each), *Myrianthus* (3 records), *Obetia*, *Commelina*, *Desmodium*, *Cephaloma*, *Clappertonia*, *Hermannia*, *Alchemilla*, *Tectona* and *Sparmannia* (2 records each). One record each for *Bridelia*, *Kolobopetalum*, *Mikania*, *Dioscorea*, *Ficus*, *Murdannia*, *Aneleima*, *Phaseolus*, *Corchorus*, *Cordia*, *Dombeya*, *Gmelina*, *Melochia*, *Nicotiana*, *Sida*, *Tilia*, *Waltheria*, *Chaemacrista*, *Lythrum*, *Nesaea*, *Rotola*, *Ipomoea*, *Lepistemom*, *Merremia*, *Passiflora*, *Solanum*, *Vernonia*, *Ancistrocarpus*, *Grewia*, *Lamium*, *Cliffortia*, *Wormskioldia*, *Cassia*, *Kotschya*, *Erigeron* and *Persicaria*. **Host plant families:** Urticaceae (32 records), Malvaceae (11 records), Fabaceae (8 records), Moraceae (5 records), Passifloraceae (4 records), Asteraceae, Commelinaceae and Rosaceae (3 records each), Menispermaceae, Verbenaceae, Lamiaceae and Solanaceae (2 records each). One record each for Phyllanthaceae, Dioscoraceae, Boraginaceae, Lythraceae, Convolvulaceae, Turneraceae and Polygonaceae. **Habitats (biomes):** *Telchinia* is predominantly a forest genus. It is distributed as follows: Forest (42 spp.), submontane forest (9 spp.), montane forest (10 spp.), coastal forest (1 sp.), woodland (16 spp.), savanna (1 sp.) and grassland (6 spp.). Ten species are found in marshy areas in a range of biomes. **Geographical range:** The genus occurs throughout the Afrotropical Region, with a single extralimital species in the Oriental Region. The greatest number of species occurs in the forests stretching from Nigeria and Angola in the west to Kenya and Tanzania in the east, and south to Zambia.

Diagnosis

Facies: In the genus *Telchinia* the *anacreon* species-group has a rudimentary vein between the second cubital and second anal vein, as found in the Neotropical genus *Actinote*. Wings rufous to ochreous, spotted or with colour patches. Hyaline areas and hyaline patches present. There are no marginal markings or spots on forewing upper side in most species except the *anacreon* species-group and *serena* species-subgroup. Hindwing marginal spots absent in many species. The external claw of the pterothoracic legs is without a furrow on the inner surface, which is present in the other African genera; terminal claws may be symmetrical.

Genitalia: The male genitalia in *Telchinia* have the aedeagus short, not narrow and not needle-like, may be stout, distally truncate or acute, basally bulbous but not bifid; sclerotized and modified 8th tergite or sternite not present. In the female genitalia the sterigma forms a pouch-like vestibulum with a posterior projection and the signa are a large patch, ovoid to elongated; in other genera they are small, rounded and spinose.

Species list

Telchinia bergeri (Gaede, 1915) is regarded to be a **nomen nudem**.

Telchinia acerata (Hewitson, 1874) **comb. rev.**
Telchinia actinotina (Lathy, 1903) **comb. rev.**
Telchinia acuta (Howarth, 1969) **comb. rev.**
Telchinia alalonga (Henning & Henning, 1996) **comb. rev.**
Telchinia alberta (Eltringham, 1911) **comb. rev.**

Telchinia alciope (Hewitson, [1852]) **comb. rev.**
Telchinia alcioipoides (Joicey & Talbot, 1921) **comb. rev.**
Telchinia althoffi (Dewitz, 1889) **comb. rev.**
Telchinia amicitiae (Heron, 1909) **comb. rev.**
Telchinia anacreon (Trimen, 1868) **comb. rev.**
Telchinia anacreontica (Grose-Smith, 1898) **comb. rev.**
Telchinia anacreontica anacreontica (Grose-Smith, 1898)
Telchinia anacreontica chyulu (van Someren, 1939) **comb. rev.**
Telchinia ansorgei (Grose-Smith, 1898) **comb. rev.**
Telchinia aubyni (Eltringham, 1912) **comb. rev.**
Telchinia aurivillii (Staudinger, 1896) **comb. rev.**
Telchinia aurivillii aurivillii (Staudinger, 1896)
Telchinia aurivillii schecana (Rothschild & Jordan, 1905) **comb. rev.**
Telchinia bankoides (Collins & Larsen, 2021) **comb. rev.**
Telchinia baxteri (Sharpe, 1902) **comb. rev.**
Telchinia baxteri baxteri (Sharpe, 1902)
Telchinia baxteri oldeani (Kielland, 1990) **comb. rev.**
Telchinia bomba (Grose-Smith, 1889) **comb. rev.**
Telchinia bonasia (Fabricius, 1775) **comb. rev.**
Telchinia burgessi (Jackson, 1956) **comb. rev.**
Telchinia burni (Butler, 1896) **comb. rev.**
Telchinia buschbecki (Dewitz, 1889) **comb. rev.**
Telchinia cabira (Hopffer, 1855) **comb. rev.**
Telchinia calida (Butler, 1878) **comb. rev.**
Telchinia cinerea (Neave, 1904) **comb. rev.**
Telchinia circeis (Drury, 1782) **comb. rev.**
Telchinia comor (Pierre, 1992) **comb. rev.**
Telchinia conradti (Oberthür, 1893) **comb. rev.**
Telchinia conradti conradti (Oberthür, 1893)
Telchinia conradti kuekenthalie (Le Doux, 1922) **comb. rev.**
Telchinia disjuncta (Grose-Smith, 1898) **comb. rev.**
Telchinia encedana (Pierre, 1976) **comb. rev.**
Telchinia encedon (Linnaeus, 1758) **comb. rev.**
Telchinia encedon encedon (Linnaeus, 1758)
Telchinia encedon rathjensi (Le Doux, 1933) **comb. rev.**
Telchinia encoda (Pierre, 1981) **comb. rev.**
Telchinia esebria (Hewitson, [1861]) **comb. rev.**
Telchinia excelsior (Sharpe, 1891) **comb. rev.**
Telchinia excelsior excelsior (Sharpe, 1891)
Telchinia excelsior usambarae (Jackson, 1951) **comb. rev.**
Telchinia fornax (Butler, 1879) **comb. rev.**
Telchinia goetzei (Thurau, 1903) **comb. rev.**
Telchinia grosvenori (Eltringham, 1912) **comb. rev.**
Telchinia guichardi (Gabriel, 1949) **comb. rev.**
Telchinia hecqui (Berger, 1981) **comb. rev.**
Telchinia humilis (Sharpe, 1897) **comb. rev.**
Telchinia igola (Trimen, 1889) **comb. rev.**
Telchinia induna (Trimen, 1895) **comb. rev.**
Telchinia induna induna (Trimen, 1895)
Telchinia induna salmontana (Henning & Henning, 1996) **comb. rev.**
Telchinia insularis (Sharpe, 1893) **comb. rev.**
Telchinia issoria (Hübner, [1819]) **comb. rev.** – Extralimital (Oriental)
Telchinia iturina (Grose-Smith, 1890) **comb. rev.**
Telchinia jodutta (Fabricius, 1793) **comb. rev.**
Telchinia jodutta jodutta (Fabricius, 1793)

- Telchinia jodutta aethiops* (Rothschild & Jordan, 1905) **comb. rev.**
- Telchinia johnstoni* (Godman, 1885) **comb. rev.**
- Telchinia kaduna* (Pierre, 1993) **comb. rev.**
- Telchinia kakana* (Eltringham, 1911) **comb. rev.**
- Telchinia kalinzu* (Carpenter, 1936) **comb. rev.**
- Telchinia lia* (Mabille, 1879) **comb. rev.**
- Telchinia lumiri* (Bethune-Baker, 1908) **comb. rev.**
- Telchinia lusinga* (Overlaet, 1955) **comb. rev.**
- Telchinia lycoa* (Godart, [1819]) **comb. rev.**
- Telchinia lycoa lycoa* (Godart, [1819])
- Telchinia lycoa aequalis* (Rothschild & Jordan, 1905) **comb. rev.**
- Telchinia lycoa fallax* (Rogenhofer, 1891) **comb. rev.**
- Telchinia lycoa kenia* (Eltringham, 1911) **comb. rev.**
- Telchinia masamba* (Ward, 1872) **comb. rev.**
- Telchinia masaris* (Oberthür, 1893) **comb. rev.**
- Telchinia masaris masaris* (Oberthür, 1893)
- Telchinia masaris jodina* (Pierre, 1992) **comb. rev.**
- Telchinia melanoxantha* (Sharpe, 1891) **comb. rev.**
- Telchinia mirifica* (Lathy, 1906) **comb. rev.**
- Telchinia necoda* (Hewitson, [1861]) **comb. rev.**
- Telchinia newtoni* (Sharpe, 1893) **comb. rev.**
- Telchinia ntebiae* (Sharpe, 1897) **comb. rev.**
- Telchinia ntebiae ntebiae* (Sharpe, 1897)
- Telchinia ntebiae nyongana* (d'Abreu, 1980) **comb. rev.**
- Telchinia obeira* (Hewitson, 1863) **comb. rev.**
- Telchinia oberthueri* (Butler, 1895) **comb. rev.**
- Telchinia oberthueri oberthueri* (Butler, 1895)
- Telchinia oberthueri laetopicta* (Rebel, 1914) **comb. rev.**
- Telchinia ochrascens* (Sharpe, 1902) **comb. rev.**
- Telchinia odzala* (Collins, 1997) **comb. rev.**
- Telchinia oreas* (Sharpe, 1891) **comb. rev.**
- Telchinia oreas oreas* (Sharpe, 1891)
- Telchinia oreas oboti* (Collins & Larsen, 2000) **comb. rev.**
- Telchinia orestia* (Hewitson, 1874) **comb. rev.**
- Telchinia orina* (Hewitson, 1874) **comb. rev.**
- Telchinia orinata* (Oberthür, 1893) **comb. rev.**
- Telchinia parei* (Henning & Henning, 1996) **comb. rev.**
- Telchinia parei parei* (Henning & Henning, 1996)
- Telchinia parei orangica* (Henning & Henning, 1996) **comb. rev.**
- Telchinia parrhasia* (Fabricius, 1793) **comb. rev.**
- Telchinia parrhasia parrhasia* (Fabricius, 1793)
- Telchinia parrhasia servona* (Godart, [1819]) **comb. rev.**
- Telchinia pelopeia* (Staudinger, 1896) **comb. rev.**
- Telchinia peneleos* (Ward, 1871) **comb. rev.**
- Telchinia peneleos peneleos* (Ward, 1871)
- Telchinia peneleos gelonica* (Rothschild & Jordan, 1905) **comb. rev.**
- Telchinia penelope* (Staudinger, 1896) **comb. rev.**
- Telchinia penelope penelope* (Staudinger, 1896)
- Telchinia penelope derubescens* (Eltringham, 1912) **comb. rev.**
- Telchinia pentapolis* (Ward, 1871) **comb. rev.**
- Telchinia pentapolis pentapolis* (Ward, 1871)
- Telchinia pentapolis epidica* (Oberthür, 1893) **comb. rev.**
- Telchinia perenna* (Doubleday, [1847]) **comb. rev.**
- Telchinia perenna perenna* (Doubleday, [1847])
- Telchinia perenna kaffana* (Rothschild, 1902) **comb. rev.**
- Telchinia pharsalus* (Ward, 1871) **comb. rev.**
- Telchinia pierrei* (Berger, 1981) **comb. rev.**
- Telchinia polis* (Pierre, 1999) **comb. rev.**
- Telchinia pseudepaea* (Dudgeon, 1909) **comb. rev.**
- Telchinia pseudepaea pseudepaea* (Dudgeon, 1909)
- Telchinia pseudepaea ziama* (Belcastro, Boireau & Safian, 2020) **comb. rev.**
- Telchinia quirinalis* (Grose-Smith, 1900) **comb. rev.**
- Telchinia rahira* (Boisduval, 1833) **comb. rev.**
- Telchinia rahira rahira* (Boisduval, 1833)
- Telchinia rahira mufindi* (Kielland, 1990) **comb. rev.**
- Telchinia rangatana* (Eltringham, 1912) **comb. rev.**
- Telchinia rangatana rangatana* (Eltringham, 1912)
- Telchinia rangatana basilewskyi* (Berger, 1956) **comb. rev.**
- Telchinia rangatana bettiana* (Eltringham, 1912) **comb. rev.**
- Telchinia rangatana ecketti* (Jackson, 1951) **comb. rev.**
- Telchinia rangatana maji* (Carpenter, 1935) **comb. rev.**
- Telchinia rileyi* (Le Doux, 1931) **comb. rev.**
- Telchinia rupicola* (Schultze, 1912) **comb. rev.**
- Telchinia safie* (Felder & Felder, [1865]) **comb. rev.**
- Telchinia sambavae* (Ward, 1873) **comb. rev.**
- Telchinia semivitrea* (Aurivillius, 1895) **comb. rev.**
- Telchinia serena* (Fabricius, 1775) **comb. rev.**
- Telchinia silia* (Mabille, [1885]) **comb. rev.**
- Telchinia sotikensis* (Sharpe, 1892) **comb. rev.**
- Telchinia sotikensis sotikensis* (Sharpe, 1892)
- Telchinia sotikensis karschi* (Aurivillius, [1899]) **comb. rev.**
- Telchinia speciosa* (Wichgraf, 1909) **comb. rev.**
- Telchinia strattipocles* (Oberthür, 1893) **comb. rev.**
- Telchinia supponina* (Staudinger, 1896) **comb. rev.**
- Telchinia toruna* (Grose-Smith, 1900) **comb. rev.**
- Telchinia ungemachi* (Le Cerf, 1927) **comb. rev.**
- Telchinia uvui* (Grose-Smith, 1890) **comb. rev.**
- Telchinia uvui uvui* (Grose-Smith, 1890)
- Telchinia uvui balina* (Karsch, 1892) **comb. rev.**
- Telchinia ventura* (Hewitson, 1877) **comb. rev.**
- Telchinia vesperalis* (Grose-Smith, 1890) **comb. rev.**
- Telchinia vesperalis vesperalis* (Grose-Smith, 1890)
- Telchinia vesperalis catori* (Bethune-Baker, 1904) **comb. rev.**
- Telchinia viviana* (Staudinger, 1896) **comb. rev.**
- Telchinia vuilloti* (Mabille, 1889) **comb. rev.**
- Telchinia wigginsii* (Neave, 1904) **comb. rev.**
- Telchinia wigginsii wigginsii* (Neave, 1904)
- Telchinia wigginsii occidentalis* (Bethune-Baker, 1926) **comb. rev.**
- Telchinia zitja* (Boisduval, 1833) **comb. rev.**

Species groups of *Telchinia* (based on wing venation; wing markings; male genitalia; female sphragis)

***T. anacreon* species-group:** hindwing with a rudimentary vein between the second cubital and second anal vein; forewing with marginal markings; no hyaline patches; aedeagus elongate, distally acute; sphragis present.

Telchinia alalonga (Henning & Henning, 1996), *Telchinia anacreon* (Trimen, 1868), *Telchinia anacreontica* (Grose-Smith, 1898), *Telchinia bomba* (Grose-Smith, 1889), *Telchinia induna* (Trimen, 1895), *Telchinia kaduna* (Pierre, 1993), *Telchinia lusinga* (Overlaet, 1955), *Telchinia parei* (Henning & Henning, 1996), *Telchinia speciosa* (Wichgraf, 1909), *Telchinia wigginsii* (Neave, 1904), *Telchinia mirifica* (Lathy, 1906), *Telchinia odzalea* (Collins, 1997).

***T. encedon* species-group:** forewing without marginal markings; rudimentary vein between the second cubital and second anal vein absent; hyaline patches present; aedeagus elongate, distally acute; sphragis present or absent.

Telchinia acuta (Howarth, 1969), *Telchinia alciope* (Hewitson, [1852]), *Telchinia alciopeoides* (Joicey & Talbot, 1921), *Telchinia ansorgei* (Grose-Smith, 1898), *Telchinia aurivillii* (Staudinger, 1896), *Telchinia comor* (Pierre, 1992), *Telchinia disjuncta* (Grose-Smith, 1898), *Telchinia encedana* (Pierre, 1976), *Telchinia encedon* (Linnaeus, 1758), *Telchinia encoda* (Pierre, 1981), *Telchinia esebria* (Hewitson, [1861]), *Telchinia insularis* (Sharpe, 1893), *Telchinia jodutta* (Fabricius, 1793), *Telchinia johnstoni* (Godman, 1885), *Telchinia lycoa* (Godart, [1819]), *Telchinia masaris* (Oberthür, 1893), *Telchinia necoda* (Hewitson, [1861]), *Telchinia pharsalus* (Ward, 1871), *Telchinia toruna* (Grose-Smith, 1900), *Telchinia vuilloti* (Mabille, 1889).

***T. serena* species-group:** forewing without marginal markings except in *serena* sub-group; rudimentary vein between the second cubital and second anal vein absent; hyaline patches absent; aedeagus elongate, not narrow, distally acute; sphragis present.

Telchinia acerata (Hewitson, 1874), *Telchinia althoffi* (Dewitz, 1889), *Telchinia bankoides* (Collins & Larsen, 2021), *Telchinia bonasia* (Fabricius, 1775), *Telchinia burgessi* (Jackson, 1956), *Telchinia cabira* (Hopffer, 1855), *Telchinia calida* (Butler, 1878), *Telchinia excelsior* (Sharpe, 1891), *Telchinia formax* (Butler, 1879), *Telchinia goetzei* (Thurau, 1903), *Telchinia guichardi* (Gabriel, 1949), *Telchinia hecqui* (Berger, 1981), *Telchinia lumiri* (Bethune-Baker, 1908), *Telchinia oberthueri* (Butler, 1895), *Telchinia ochrascens* (Sharpe, 1902), *Telchinia pierreii* (Berger, 1981), *Telchinia pseudopaea* (Dudgeon, 1909), *Telchinia rahira* (Boisduval, 1833), *Telchinia rangatana* (Eltringham, 1912), *Telchinia rupicola* (Schultze, 1912), *Telchinia serena* (Fabricius, 1775), *Telchinia sotikensis* (Sharpe, 1892), *Telchinia supponina* (Staudinger, 1896), *Telchinia uvui* (Grose-Smith, 1890), *Telchinia ventura* (Hewitson, 1877), *Telchinia viviana* (Staudinger, 1896), *Telchinia zitja* (Boisduval, 1833).

***T. circeis* species-group:** pterothoracic claws equal in both sexes in some subgroups; forewing without marginal markings; rudimentary vein between the second cubital and second anal vein absent; hyaline patches present; aedeagus short and broad, often distally obtuse; sphragis mostly absent.

Telchinia actinotina (Lathy, 1903), *Telchinia alberta* (Eltringham, 1911), *Telchinia amicitiae* (Heron, 1909),

Telchinia aubyni (Eltringham, 1912), *Telchinia baxteri* (Sharpe, 1902), *Telchinia burni* (Butler, 1896), *Telchinia buschbecki* (Dewitz, 1889), *Telchinia cinerea* (Neave, 1904), *Telchinia circeis* (Drury, 1782), *Telchinia conradti* (Oberthür, 1893), *Telchinia grosvenori* (Eltringham, 1912), *Telchinia humilis* (Sharpe, 1897), *Telchinia igola* (Trimen, 1889), *Telchinia iturina* (Grose-Smith, 1890), *Telchinia kakana* (Eltringham, 1911), *Telchinia kalinzu* (Carpenter, 1936), *Telchinia lia* (Mabille, 1879), *Telchinia masamba* (Ward, 1872), *Telchinia melanoxantha* (Sharpe, 1891), *Telchinia newtoni* (Sharpe, 1893), *Telchinia ntebiae* (Sharpe, 1897), *Telchinia obeira* (Hewitson, 1863), *Telchinia oreas* (Sharpe, 1891), *Telchinia orestia* (Hewitson, 1874), *Telchinia orina* (Hewitson, 1874), *Telchinia orinata* (Oberthür, 1893), *Telchinia parrhasia* (Fabricius, 1793), *Telchinia pelopeia* (Staudinger, 1896), *Telchinia peneleos* (Ward, 1871), *Telchinia penelope* (Staudinger, 1896), *Telchinia pentapolis* (Ward, 1871), *Telchinia perenna* (Doubleday, [1847]), *Telchinia polis* (Pierre, 1999), *Telchinia quirinalis* (Grose-Smith, 1900), *Telchinia rileyi* (Le Doux, 1931), *Telchinia safie* (Felder & Felder, [1865]), *Telchinia sambavae* (Ward, 1873), *Telchinia semivitrea* (Aurivillius, 1895), *Telchinia silia* (Mabille, [1885]), *Telchinia strattipocles* (Oberthür, 1893), *Telchinia ungemachi* (Le Cerf, 1927), *Telchinia vesperalis* (Grose-Smith, 1890).

DISCUSSION

Summary of findings

The taxonomy of the tribe Acraeini presented here is largely based on the robust dated phylogeny published by Carvalho *et al.* (2021). They recovered six well supported clades in the Acraeini, one supporting the monophyly of *Cethosia* and five major clades within *Acraea*. Combining this data with the phylogenetic hypothesis proposed by Henning (1992), which was largely based on genitalic morphology, we have determined that there are eight valid genera within the tribe Acraeini. We present an updated alpha taxonomy for the six Afrotropical genera in the tribe – *Acraea*, *Rubraea* **stat. nov.**, *Stephenia* **stat. nov.**, *Tildia* **gen. nov.**, *Bematistes* **stat. rev.** and *Telchinia* **stat. rev.** We also list, as best we can, the species in the New World genus *Actinote* and the Old World genus *Cethosia*. The new genus *Tildia* has been created to accommodate the monophyletic *zetes* species-group and is named for the spouse of the first author (MCW) in appreciation for her moral support.

Comparative natural history of the six genera of Afrotropical Acraeini

Early stages: The eggs are mostly ovoid in *Acraea* and *Telchinia*, ovoid and squat in *Tildia*, conical and flat-topped in *Stephenia*, elongate in *Rubraea*, and tall and cylindrical in *Bematistes*. They are laid in batches in all six genera, but sometimes singly in species of *Rubraea* and *Stephenia*. Batches are small in *Tildia*, while batches are often laid in untidy clusters in *Telchinia*. The larvae are gregarious in all genera. In *Rubraea* the dorsal spines on segments 3–6 are sometimes more prominent. The larvae of *Telchinia* often live in silken nests. Generally, the pupae in all the genera have the veins on the wing covers outlined in black. Uniquely, the pupae of *Bematistes* have pairs of dorsal processes on the first four abdominal segments.

Plant families used: Nine plant families are mainly utilised by the larvae. Passifloraceae is used by all six genera; Turneraceae by *Acraea*, *Rubraea* and *Stephenia*; Salicaceae by *Rubraea*, *Stephenia* and *Bematistes*; Achariaceae by *Acraea* and *Rubraea*; Vitaceae by *Stephenia* and *Bematistes*, and Malvaceae by *Stephenia* and *Telchinia*. Violaceae is used almost exclusively by *Acraea*, while Urticaceae, Fabaceae and Moraceae are used almost exclusively by *Telchinia*.

Biomes inhabited: All six genera have both forest and woodland species. *Bematistes*, *Acraea* and *Telchinia* are predominantly forest genera. *Rubraea* is found mainly in forest and woodland, while *Stephenia* and *Tildia* occur mainly in woodland and savanna. At least five species of *Rubraea* and six species of *Telchinia* are found in grasslands. Ten species of *Telchinia* are restricted to marshy habitats. One species of *Acraea* (*brainei*) occurs in semi-desert and one species of *Tildia* (*hypoleuca*) is a Namib Desert endemic.

Comparative ranges: Four of the six genera are pan-Afrotropical (*Acraea*, *Rubraea*, *Stephenia* and *Telchinia*). The genus *Acraea* is found mainly in east and west central Africa, with six species in Madagascar, five of them endemics. A further four species are found in the Oriental and Australasian Regions. *Rubraea* and *Stephenia* are mainly east-central African. *Tildia* is predominantly in eastern and southern Africa and is centred on east central Africa. One species (*turna*) is a Madagascan endemic. *Bematistes* is centred on the Guineo-Congolian forest block. *Telchinia* is centred on the central African forest zone but eleven species, nine of them endemics, are found in Madagascar and there is a single Oriental species (*issorina*).

Future research

It is hoped that the delimitation of genera in the tribe Acraeini here published will have laid a foundation for further hypotheses and research on the systematics, evolution and ecology of the tribe. Carvalho *et al.* (2021) sampled just less than 50% (160/325) of the described species in the tribe. For each genus the sampling rates were: *Cethosia* 82% (14/17), *Acraea* 48% (15/31), *Rubraea* 23% (9/39), *Stephenia* 38% (11/29), *Tildia* 54% (7/13), *Bematistes* 71% (25/35), *Actinote* 63% (37/59) and *Telchinia* 41% (42/102). In order to further our understanding of the taxonomic and evolutionary relationships of the species and subspecies of each genus more intensive intrageneric sampling is needed, particularly in the genera *Rubraea*, *Stephenia* and *Telchinia*.

Knowledge about the larval host-plants and early stages of the Afrotropical species of Acraeini is currently poor (Williams, 2022). Host-plants have only been recorded for 51% (124/244) species and the early stages are (often poorly) known for 43% (106/244). Much more data is desirable before evolutionary and ecological aspects of the tribe can be reliably examined in the light of their natural history.

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