

**THE NEW WORLD HAIRSTREAK GENUS *ARAWACUS* KAYE
(LEPIDOPTERA: LYCAENIDAE: THECLINAE: EUMAEINI)**

ROBERT K. ROBBINS

Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0127 U.S.A. (e-mail robbins.robert@nmnh.si.edu)

Abstract.—Even though *Arawacus* Kaye is widely used in works on North American butterflies, its characterization has been inconsistent and its included species have not been listed. Subterminally constricted tips of the papillae anales are proposed to be the best way to characterize *Arawacus*. They are consistent with the higher classification of the *Thereus* Section of the Eumaeini, to which *Arawacus* belongs. They are consistent with patterns of oviposition specificity. This characterization re-confirms that *Polyniphes* Kaye and *Dolymorpha* Holland are junior synonyms of *Arawacus*. *Tigrinota* Johnson is synonymized with *Arawacus*, **new synonym**. All nomenclaturally available specific names that belong to *Arawacus* are listed.

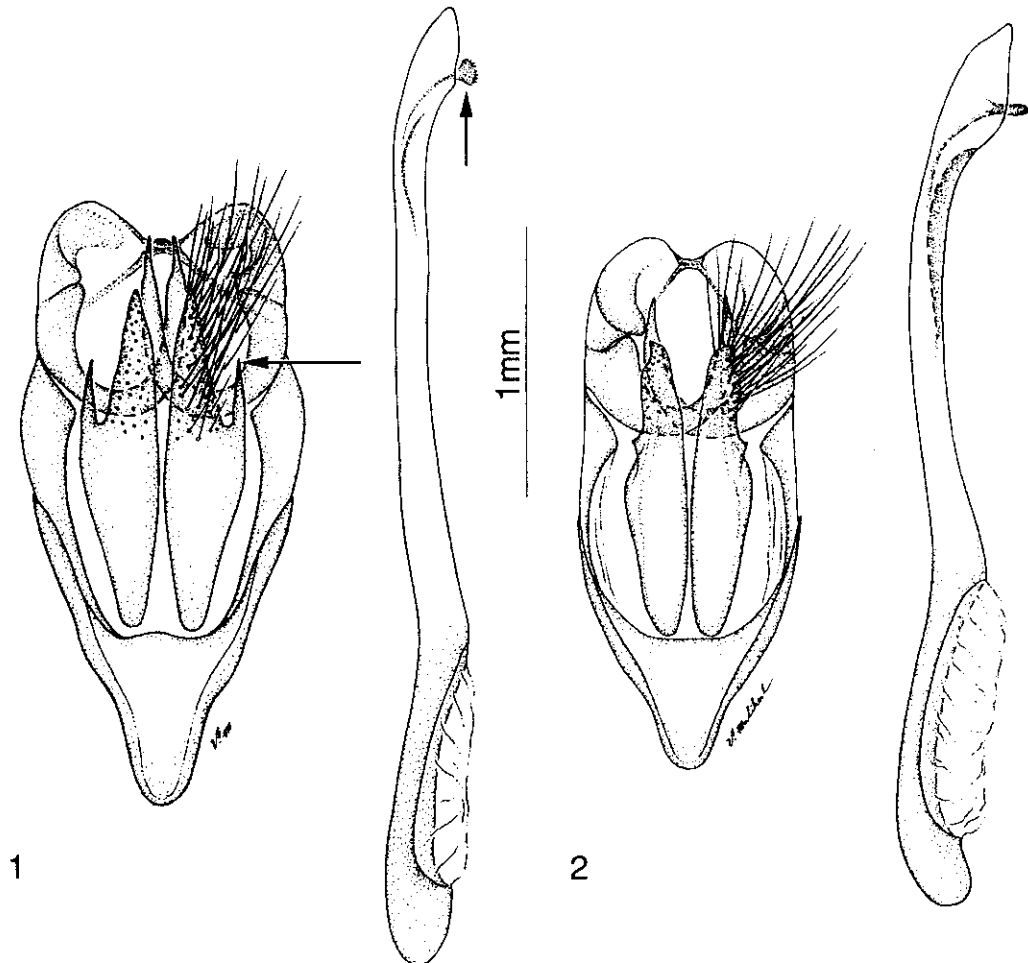
Key Words: *Thereus*, *Rekoa*, *Contrafacia*, *Dolymorpha*, *Polyniphes*, *Tigrinota*, Solanaeae

The generic name *Arawacus* Kaye was rarely used until 1981. The original description was based on superficial wing pattern elements of the South American type species, *A. aetolus* (Sulzer) (Kaye 1904). As a result, besides being cited in nomenclatural lists (e.g., Comstock and Huntington 1959–1964, Eliot 1973), *Arawacus* was used only for species with wing patterns similar to the type (Brown and Mielke 1967; Robbins 1980, 1981). But after Miller and Brown (1981) made *Arawacus* a senior synonym of *Dolymorpha* Holland, whose type species ranges into the United States, the use of *Arawacus* in general butterfly works mushroomed (e.g., Scott 1986, Bailowitz and Brock 1991, Stanford and Opler 1993, Cassie et al. 1995).

Arawacus was characterized by morphology of its male genitalia. Clench (1961: 212) had delimited *Dolymorpha* primarily by a “ventro-lateral conical, acuminate process at middle” of the valves and by the

two terminal cornuti, “one of which has an abrupt, larger disc-like terminal expansion with peripheral teeth” (Fig. 1). He later made *Dolymorpha* a junior synonym of *Arawacus* using the same two character states (an unpublished manuscript that is being deposited in the Archives of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.). Miller and Brown (1981), who received a copy of the manuscript after Clench’s death, published this synonymy in their catalog without explanation.

Arawacus has been characterized in different ways since 1991. Because Clench mistakenly lumped five distinct species in the *A. aetolus* complex (Robbins, Hudson, and Clench, in preparation), he did not realize that the type species of *Arawacus* lacks both male genitalia traits that he had proposed (Fig. 2). Consequently, when Robbins (1991: 3) briefly treated *Arawacus* as an outgroup of *Rekoa* Kaye, he provi-



Figs. 1–2. Male genitalia in ventral aspect with penis in lateral aspect, posterior end towards top of the page. 1, *Arawacus jada*, with arrows pointing to the posterior pointing processes on the valves and to the flattened cornutus with terminal teeth. 2, *A. aetolus*, which lacks the posterior pointing processes and has an arrowhead shaped cornutus.

sionally re-characterized it by “(1) papillae anales constricted subterminally, and (2) larvae that feed on the foliage of *Solanum* (Solanaceae),” but did not illustrate the first character or list the included species. He confirmed the synonymy with *Dolymorpha*, added *Polyniphes* Kaye as a second junior synonym of *Arawacus*, and placed *Arawacus* in the *Thereus* Section of the Eumaeini.

Johnson (1992, 1993) described and revised *Tigrinota* for species that possess both traits that Robbins had proposed for characterizing *Arawacus*, but Johnson did

not note either trait or mention that *Tigrinota* might be closely related to *Arawacus*. Further, he treated *Dolymorpha* as a distinct genus without mentioning the previous synonymy with *Arawacus*. (Note: Some copies of Johnson [1993] have Johnson and Kroenlein listed as the authors. I follow the citation in Lamas et al. [1995] with Johnson as the sole author).

The purpose of this paper is to stabilize usage of *Arawacus* and to provide a generic taxonomy for revision at the species level. Specifically, this paper shows that the con-

stricted papillae anales occur in the type species of *Arawacus*, *Dolymorpha*, *Polyniphes*, and *Tigrinota*, but not in other genera of the *Thereus* Section, to which *Arawacus* belongs. It is further shown that *Tigrinota* was delimited by characters that are incorrectly described or that occur in other genera of the *Thereus* Section. Finally, the specific taxa that belong to *Arawacus* are listed for the first time.

MATERIALS AND METHODS

This study was based upon the approximately 3,250 specimens belonging to the *Thereus* Section genera *Arawacus*, *Rekoa*, *Thereus* Hübner, *Contrafacia* Johnson, and the "*Thecla*" *ligurina* species group (an undescribed genus whose species are placed, following convention, in *Thecla* F., a genus that does not belong to the Eumaeini, Eliot 1973) in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM). Included were all species that belong to these genera as delimited by Robbins (1991). Preparation of genitalia for examination using light and scanning electron microscopes follows the procedures in Robbins (1991). The male and female genitalia of all species in the *Thereus* Section were dissected (except for those few species known from only one sex), including more than 120 genitalic dissections of those species placed in *Arawacus* in this paper.

PREVIOUS RESULTS

The *Thereus* section.—Robbins (1991) proposed two phylogenetic hypotheses involving *Arawacus*. First, *Arawacus*, *Rekoa*, *Thereus*, *Contrafacia*, and the "*Thecla*" *ligurina* group form the *Thereus* Section of the Eumaeini because they share a unique process of the vinculum abutting the brush organs, when present (illustrated in Robbins 1991). Second, the first three genera form a monophyletic group. The ductus seminalis arises from a pouch of the posterior corpus bursae. This pouch is dorsal of the ductus bursae, sclerotized laterally, and

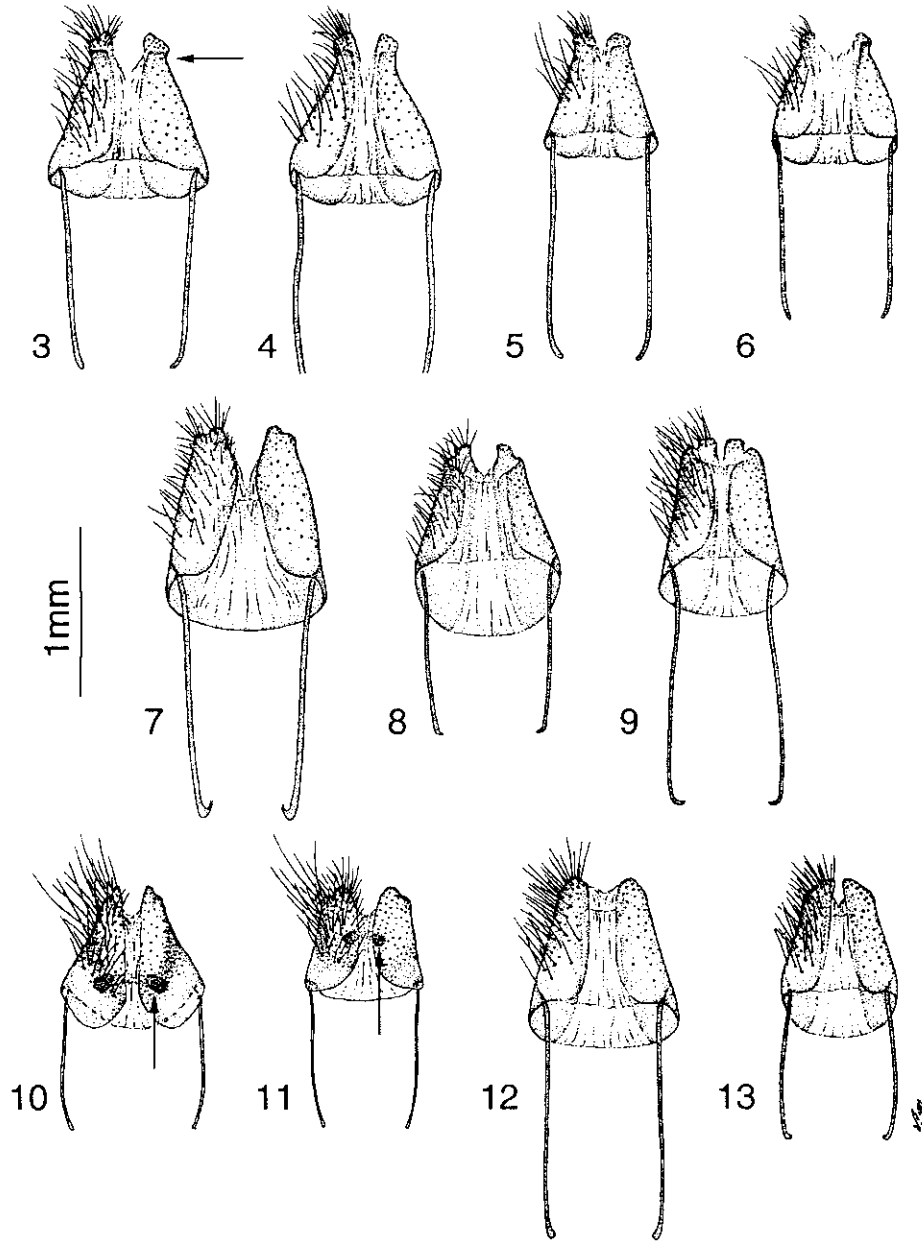
membranous dorsally (again illustrated in Robbins 1991). This classification is a framework within which the monophyly of *Arawacus* can be assessed.

Type species nomenclature.—Synonymy of the type species of *Arawacus*, *Contrafacia*, and *Tigrinota* is a bit confused. The type of *Arawacus* is *Papilio linus* Fabricius, which is a junior synonym of *P. aetolus* Sulzer (Comstock and Huntington 1959–1964). The type of *Contrafacia* is *C. mexicana* Johnson 1989, a species that is indistinguishable from *C. imma* (Prittwitz 1865) (Robbins 1991). The type of *Tigrinota* is *Thecla ellida* Hewitson, which occurs from northern Venezuela to central Argentina. Its wing pattern varies slightly over this wide range with virtually no geographical variation in genitalic structures (Robbins, in prep.), contrary to the treatments in Johnson (1992, 1993).

RESULTS

Monophyly and *Arawacus*.—The papillae anales ("ovipositor valves") were examined for 57 of the approximately 63 species that belong to the *Thereus* Section. Females are not known for the other 6 species. The tips of the papillae anales (ventral aspect) for the type species of *Arawacus* (Fig. 3), *Dolymorpha* (Fig. 4), *Tigrinota* (Fig. 5), and *Polyniphes* (Fig. 6) have a subterminal constriction, which might alternately be described as terminally expanded. The tips of the papillae anales of *Rekoa* (Figs. 7–9) are notched, not subterminally constricted. The papillae anales of *Thereus* (Figs. 10–11) are similar to those of *Rekoa*, but contain a sclerotized patch that is otherwise unreported in the Eumaeini (Robbins 1991). The tips of the papillae anales of *Contrafacia* (Fig. 12) and the "*Thecla*" *ligurina* group (Fig. 13) are regularly tapered. Although the papillae anales in the *Thereus* Section vary in shape, only those of *Arawacus* have a conspicuous subterminal constriction.

Larval food plant specificity.—Among the eumaeine genera, larval feeding on the



Figs. 3-13. Papillae anales in ventral aspect, posterior end towards top of the page. 3, *Arawacus aetolus*; arrow points to the subterminal constriction. 4, *A. jada*. 5, *A. ellida*. 6, *A. dumenilii*. 7, *Rekoa meton*. 8, *R. palegon*. 9, *R. marius*. 10, *Thereus lausus*; arrow points to sclerotized patch. 11, *T. praxis*; arrow points to sclerotized patch. 12, *Contrafacia imma*. 13, "*Thecla*" *lyde*.

leaves of *Solanum* (as opposed to flowers) occurs only in *Arawacus*, but the larvae of three *Arawacus* species have recently been reported to eat plants in the Compositae and

Leguminosae (Robbins, in press). Leaf feeding on *Solanum* has been recorded for 11 of the 17 *Arawacus* species (noted in the list at the end of this paper), including the

type species of *Arawacus*, *Dolymorpha*, *Tigrinota*, and *Polyniphes* (Guppy 1904, 1914; Bourquin 1945; Kendall 1975; Robbins, in press). However, larvae of *A. ellida* (Hewitson), which have been reared repeatedly from the leaves of *Solanum*, and *A. binangula* (Schaus) were both recently recorded eating flowers of Compositae—a larval food plant used in the related genus *Rekoa*—and the larvae of *A. tarania* were recorded on legumes (Brown 1993). Consequently, although larval feeding on the leaves of *Solanum* is widespread in *Arawacus* and is unreported in other Eumaeini, it cannot be used to delimit the genus.

The larvae of other *Thereus* Section species primarily use plants in families other than the Solanaceae as larval food (Robbins 1991, in press). *Rekoa* larvae are extremely polyphagous on buds, flowers, and shoots of plants in 16 families, including Solanaceae, but most records are in the Compositae, Leguminosae, and Malvaceae. In contrast, larvae of *Thereus* specialize on Loranthaceae, with one species eating Malpighiaceae and Chrysobalanaceae. *Contrafacia* larvae are recorded eating plants in the Compositae and Leguminosae, and the only food plant record in the "*Thecla*" *ligurina* group is in the Erythroxylaceae.

Monophyly and *Tigrinota*.—The only alternative to the proposed classification in this paper is that of Johnson (1992, 1993). It is the purpose of this section to assess the evidence supporting the monophyly of *Tigrinota*.

The diagnosis of *Tigrinota* (Johnson 1992, 1993) is similar in both works, but difficult to interpret. The diagnosis of the wings refers to the hindwing "with concentric bands," but bands on the wings of these species are not concentric. It refers to the "ovate brand," but the type species lacks an ovate brand or other scent patch. It mentions alternating bands on the hindwing, but these also occur in *Rekoa palegon* (Cramer) and *R. malina* (Hewitson). Since *Rekoa* is a close relative of *Arawacus* (Robbins



Fig. 14. Scanning electron micrograph of the valves of *Arawacus ellida* in ventral aspect, posterior end towards the top of the page. Note the lack of rims, microtrichia, and "caudo-lateral sculptures."

1991), these bands would appear to be a symplesiomorphy and are questionably diagnostic.

The diagnosis of the male genitalia of *Tigrinota* in Johnson (1992: 186) is cited in its entirety because it is confusing. "Ventrally, valvae appearing as paired and rather smoothly sclerotized oblongate lobes separated by a thin transparent fissure which at each end, shows sclerotized ridges forming (1) prominent rims about the bilobed area and (2) caudo-lateral sculptures of the valval terminus from which emerge clusters of robust microtrichia." The valves of the type species of *Tigrinota* are illustrated in ventral aspect (Fig. 14). There are no rims. There are no microtrichia, robust or not. Perhaps setae were mistaken for microtrichia, but if so, their occurrence on the ventral valves is true for virtually all eumaeines (e.g., Clench [1961] characterized *Callo-*

phrys Westwood by the unusual lack of setae on the valve tips). It is unclear to what the "caudo-lateral sculptures" refer (Fig. 14). Johnson (1993: 2) repeats these characters and adds "brush organ occurrences differential (sic)", but it is unclear what this means or how it might be diagnostic. As best I can tell, those parts of this diagnosis that are accurate do not differentiate *Tigrinota* from most eumacines.

The diagnosis of the female genitalia is similarly confusing (Johnson 1992, 1993). The description (I presume of the ductus bursae) with a "transparent neck" refers to the ductus bursae of most *Rekoa* and *Arawacus* (Robbins 1991; Robbins, Hudson, and Clench, in preparation) and is not diagnostic. The description of a simple "subcordate incised posterior cavity (abbreviated sipc in the diagnosis) of the 8th tergite" (probably referring to the shape of the 8th abdominal tergum) is difficult to interpret. However, the shape of this tergum is similar in *Tigrinota* and some *Rekoa*, such as *R. zebina* (Hewitson), so it is unlikely to be diagnostic.

DISCUSSION

Taxonomy.—The genus *Arawacus* appears to be monophyletic, characterized by the shape of the papillae anales. Although it is not desirable to delimit *Arawacus* by only one character, this classification is consistent with the hierarchical classification of the *Thereus* Section, and other morphological traits support the monophyly of *Thereus* and *Rekoa* (Robbins 1991). These characterizations of *Arawacus*, *Thereus*, and *Rekoa* are reasonably consistent with patterns of larval plant use. For these reasons, this classification appears to be the best option for promoting a stable generic nomenclature in the *Thereus* Section.

Recognition of *Tigrinota* is unlikely to be a reasonable alternative. Its use leaves *Arawacus* and *Polyniphes* uncharacterized and would consequently destabilize the generic taxonomy of the *Thereus* Section. There is little, if any, evidence to support the mono-

phyly of *Tigrinota*. Either its diagnostic traits are incorrect, such as the concentric hindwing bands and rims on the valves, or appear to be symplesiomorphic, such as the alternating hindwing bands and "transparent neck" of the ductus bursae.

Provisional classification of *Arawacus*.—The status of *Polyniphes* as a synonym (Robbins 1991) is confirmed. The status of *Dolymorpha* as a synonym (Miller and Brown 1981), which was not recognized in Johnson (1992), is also confirmed. *Tigrinota* is synonymized with *Arawacus*, **new synonym**.

Johnson (1992, 1993) presented a classification of almost half the specific names listed below. He did not assess intraspecific geographical variation and reported "diagnostic" morphological traits, such as concentric hindwing bands and rims on the valves, that do not exist. Further, my examination of more than 120 genitalic dissections and detailed comparison of androconia and wing patterns from throughout the range of each species failed to confirm most of his conclusions. Rather than await detailed species level revisions, I present an alternate classification below that is intended to be a working hypothesis for species level revisions. Although it is unusual to present a tentative classification, such as this one, the extensive reporting of characters that do not exist (Johnson 1992, 1993) is perhaps a more unusual circumstance that creates the need for a more reasonable working classification.

As characterized in this paper, *Arawacus* contains 39 available specific names representing 17 biological species. There is also one undescribed species (Robbins, Hudson, and Clench, in preparation). The female genitalia of all have been examined except for *A. euptychia*, for which no females are known. However, *A. euptychia* is placed in *Arawacus* because its male genitalia are barely distinguishable from those of *A. dumilii* and *A. tadita*.

Those species that have been reared from plants in the Solanaceae, Compositae, or

Leguminosae are designated respectively in bold with S, C, or L.

1. *Arawacus togarna* (Hewitson, 1867)
2. *Arawacus lincoides* (Draudt, 1917)—S
3. *Arawacus aetolus* (Sulzer, 1776)—S
Papilio linus Fabricius, 1776
Papilio amelia Herbst, 1804
4. *Arawacus separata* (Lathy, 1926)—S
Thecla paraguayensis Lathy, 1926
5. *Arawacus aethesa* (Hewitson, 1867)
6. *Arawacus sito* (Boisduval, 1836)—S
Thecla phaenna Godman and Salvin, 1887
Arawacus mexicana D'Abbrera, 1995
7. *Arawacus leucogyna* (Felder and Felder, 1865)—S
Thecla phaea Godman and Salvin, 1887
8. *Arawacus meliboeus* (Fabricius, 1793)—S
Jolaus eurisides Hübner, 1823
Thecla barrensis Rosa, 1936
9. *Arawacus jada* (Hewitson, 1867)—S
10. *Arawacus ellida* (Hewitson, 1867)—S,C
Thecla toba Hayward, 1949
Tigrinota perinota Johnson, 1992
Tigrinota jennifera Johnson, 1992
Tigrinota catamarciiana Johnson, 1993
Tigrinota chaosa Johnson, 1993
11. *Arawacus hypocrita* (Schaus, 1913)
12. *Arawacus dolyllas* (Cramer, 1777)—S
Pseudolycaena spurius Felder and Felder, 1865
Thecla dolosa Staudinger, 1888
Thecla pallida Lathy, 1930,
13. *Arawacus dumenilii* (Godart, 1824)—S
Thecla argiva Hewitson, 1877
Thecla obscura Staudinger, 1888
Thecla carteri Weeks, 1906
14. *Arawacus euptychia* (Draudt, 1921)
15. *Arawacus tadita* (Hewitson, 1877)—S
Thecla datitia Jones, 1912
16. *Arawacus binangula* (Schaus, 1902)—C
Thecla bolima Schaus, 1902
17. *Arawacus tarania* (Hewitson, 1868)—L
Thecla atrana Schaus, 1902.

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