

Male secondary sexual characters in Aphnaeinae wings (Lepidoptera: Lycaenidae)

ZS. BÁLINT¹, A. HEATH², G. KATONA³, K. KERTÉSZ⁴ & SZ. SÁFIÁN⁵

¹Zsolt Bálint, Department of Zoology, Hungarian Natural History Museum, Budapest, Baross u. 13, H-1088, Hungary. E-mail: balint.zsolt@nhmus.hu

²Alan Heath, Iziko South African Museum, Cape Town, South Africa. E-mail: alan.heath3@gmail.com

³Katona Gergely, Department of Zoology, Hungarian Natural History Museum, Budapest, Baross u. 13, -1088, Hungary. E-mail: katona.gergely@nhmus.hu

⁴Krisztián Kertész, Nanostructures Department, Institute of Technical Physics and Materials Sciences, Centre for Energy Research, Hungarian Academy of Sciences, Budapest, POB 49, H-1515 Hungary. E-mail: kerteszk@mfa.kfki.hu

⁵Szabolcs Sáfián, Faculty of Forestry, University of West Hungary, Bajcsy-Zsilinszky u. 4, Sopron H-9400, Hungary. E-mail: safian@bcghana.org

Abstract. Male secondary sexual characters have been discovered on the hindwing verso of genera *Aphnaeus* Hübner, [1819], *Cigaritis* Donzel, 1847, *Lipaphnaeus* Aurivillius, 1916 and *Pseudaletis* Druce, 1888 representing the Palaeotropical subfamily Aphnaeinae (Lycaenidae: Lepidoptera). Relevant wing parts are illustrated, described, and some observations on the organs are briefly annotated. With an appendix and 14 figures.

Keywords. Androconia, hair tuft, classification, Palaeotropics, scaling.

INTRODUCTION

One of the most characteristic features of Lepidoptera is the scaled membranous wing surface of the imagines. The scales covering the membrane have various functions often determined sexually, hence they show specialized structures. In the family Lycaenidae male secondary sexual characters in the wings are widely distributed and highly variable, hence they drew the attention of classical workers focused on the diversity, classification, and systematics of the family. In a world-wide review, John Nevill Eliot († 2003) mapped and discussed Lycaenidae male secondary sexual characters in great detail for his classification (see Eliot 1973).

The subfamily Aphnaeinae was recently the subject of important studies (Heath 1997, Boyle *et al.* 2015). These were inspired by Eliot who pointed out the peculiarity of this lycaenid assemblage and recorded morphological traits for his classification (Eliot 1973: 470 in footnote no. 11;

and Eliot 1990). However, Eliot did not indicate any male secondary sexual characters in this subfamily, nor did any of the previous or subsequent workers (*eg.* Stempffer 1954, Heath 1997, Libert 2013).

Whilst curating aphnaeine material in the Hungarian Natural History Museum one of us became aware of special scaling present on the hindwing underside of certain males (Figs. 1–2). This character was recorded and described in detail in the case of genera *Pseudaletis* and *Aphaneus* without using the expression that they may have a sexual role (*cf.* Libert 2007: 11; Libert 2013: 212–13). After studying additional material and conduct some microscopic studies it became obvious that hitherto unrecognized secondary male sexual characters in Aphnaeinae were discovered. The aim of this paper is to report on this discovery, to describe the characters, to present a brief overview of their generic distribution, and to comment our results in the light of recent knowledge regarding the subfamily.

MATERIAL AND METHODS

All material examined are listed in Appendix. Genus-level classification of the *Aphnaeinae* follows Boyle *et al.* (2015).

Specimens were first inspected using a hand magnifier, then relevant wing areas were digitised using a binocular stereo microscope Olympus SZX12 supplemented by camera DP70 in the Hungarian Natural History Museum (HNHM). In the Institute of Technical Physics and Materials Science (Centre for Energy Research, Hungarian Academy of Sciences) (CER-HAS) images of high magnification were taken using an optical microscope Zeiss Axio Imager A1.

Terminology of veins, wing regions and scales follows Ehrlich & Ehrlich (1961), Eliot (1973) and Scott (1990).

RESULTS

Examining the hind wing ventral surfaces of the *aphnaeinae* genera in the representatives of *Aphnaeus* Hübner, [1819] (type species: *Papilio orcas* Drury, [1782]), *Lipaphnaeus* Aurivillius, 1916 (type species: *Aphnaeus spindasoides* Aurivillius, 1916), *Pseudaletis* Druce, 1888 (type species: *Pseudaletis agrippina* H. H. Druce, 1888) and several taxa in *Cigaritis* Donzel, 1847) (type species: *Cigaritis zohra* Donzel, 1847) we have found male secondary sexual characters (Figs. 1–6), that we briefly describe below.

Aphnaeus, *Cigaritis* and *Lipahnaeus* (Figs. 1, 4–6, 7–8, 10, 12, 14): In the intervenial area of the cell formed by veins Cubitus 1–2 there is a “line” comprised of long plume scales erecting caudad from the wing membrane. These hair scales form a tuft that can be seen even under low magnification. The tuft forms a somewhat differently coloured (darker compared to the background) delicate line running from the submedian area to the postmedian region. The line never reaches the base nor the margin of the wing. The region

between the veins is often creased, especially in *Aphnaeus*.

The tuft is more easily seen in living individuals, because in set museum specimens the hair scales are often addressed to the level of the cover scales, hence they are difficult to detect. This may explain why this scaling has hitherto remained unnoticed. In living specimens the space involved is often creased, and this results in the tuft being exposed and clearly visible when the individual perches (Fig. 14).

Regarding *Aphnaeus* our material was limited (see Appendix), but consulting recent literature (d’Abrera 2009, Libert 2013) it seems that the presence of the tuft is not limited to the species of *A. orcas* and *A. argyrocyclus* as has been indicated but it is more widespread. This has been confirmed by our studies.

The representatives of *Cigaritis* are well documented in the folio books of d’Abrera (1986, 1993, 2009) also in (Kielland 1991, Larsen 1994, Weidenhoffer & Bozano 2007). We found that whilst Afrotropical and Oriental species probably all possess the tuft, species inhabiting the Palaearctic region do not. Although we could examine only two species of the less diverse genus *Lipaphnaeus* ($n = 4$, *sensu* Heath 1997), we presume that all the species possess the male secondary character discussed as the figures in d’Abrera (2009) suggest this is the case.

Pseudaletis (Figs 3, 9–10, 13): The wing membrane in the cell formed by the veins Cubitus 1–2 from the postbasal area to the outer margin is covered by long plume scales erecting caudad but they do not form any tuft. Along the veins Cubitus 2 there are androconia (presumably scent disseminating) mixed with ordinary cover- and ground-scales. The membrane of the intervenial area is creased.

According to the current literature (Libert 2007, d’Abrera 2009) There are 24 species in *Pseudaletis* divided into three species-groups. We recorded alar male sexual character only in the taxa representing the species group *P. leonis*.

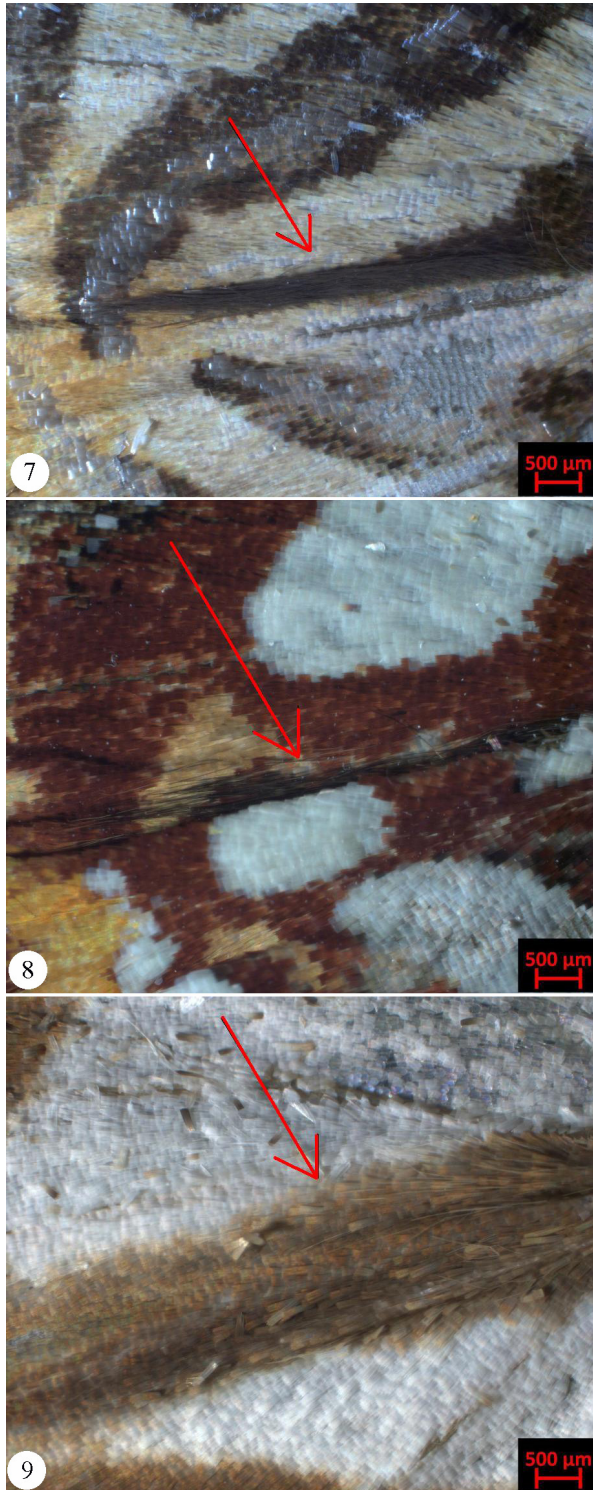


Figures 1-6. Imagines of Aphnaeinae, in ventral view. The arrows indicate the position of the alar male sexual character. 1 = *Cigaritis larseni* (Bouyer, 2012), male (Ghana), 2 = ditto, female (no brush organ); 3 = *Pseudaletis leonis* (Staudinger, [1888], male; 4 = *Cigaritis syama* (Horsfield, [1829]), male (Thailand); 5 = *Lipaphnaeus leonina* (Bethune-Baker, 1904), male (Iberia); 6 = *Aphnaeus orcas* (Drury, 1782), male (Ghana) (all at the same magnification, 1mm scale as indicated) (photos: G. Katona, HNHM).

DISCUSSION

It is curious that despite much of scientific attention, aphnaeine male secondary sexual characters remained overlooked for a long time, and it is surprising that classical workers paying great attention to special characters, missed them. Although it is not surprising that in lithographic

figures the delicate and hardly visible alar brush organ is never conspicuous (for example: Aurivillius 1925, Murray 1935), in more recent publications the figures produced using more advanced photography, we found the pattern formed by the specialized hair scales is often more clearly visible, or at least detectable with greater certainty (see d'Abrera 1986, Kielland 1991, Larsen 1991,



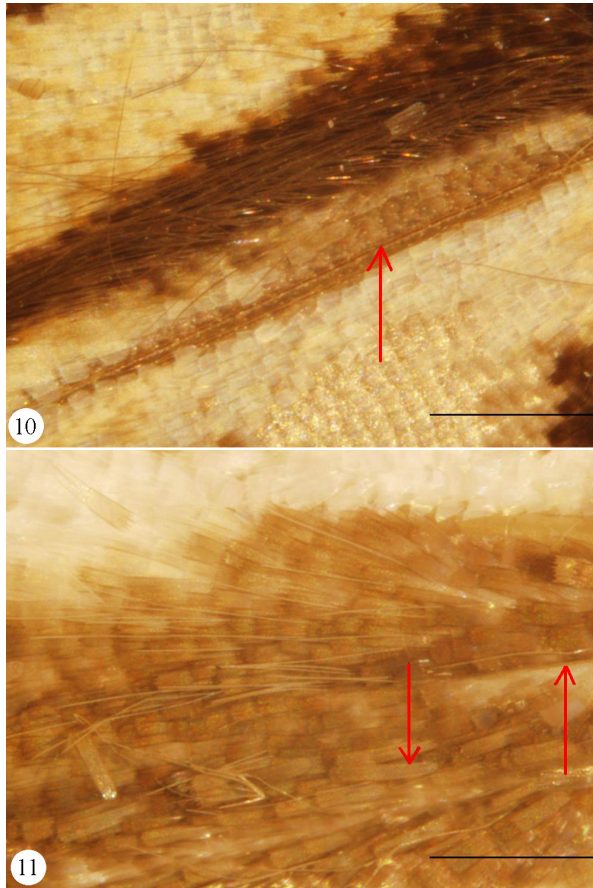
Figures 7-9. Male aphnaeine hindwing ventral surface sexual characters at high magnification, indicated by red arrows. 7 = *Aphnaeus orcas* (Drury, 1782); 8 = *Cigaritis lohita* (Horsfield, [1829]), 9 = *Pseudaletis leonis* Staudinger, [1888], (scales as indicated) (Photos: K. Kertész, CER-HAS).

1993, Weidenhoffer & Bozano 2016, Libert 2007, d’Abrera 2009; Libert, 2013 and Weidenhoffer *et al.*, 2016).

Because of the complex optical appearance of the *Aphnaeus* ventral wing surface, and that the space is often creased, it is sometimes difficult to detect the tuft in illustrations or even in actual specimens. Therefore careful examination of museum material is obligatory for mapping the distribution of the male secondary character in the genus.

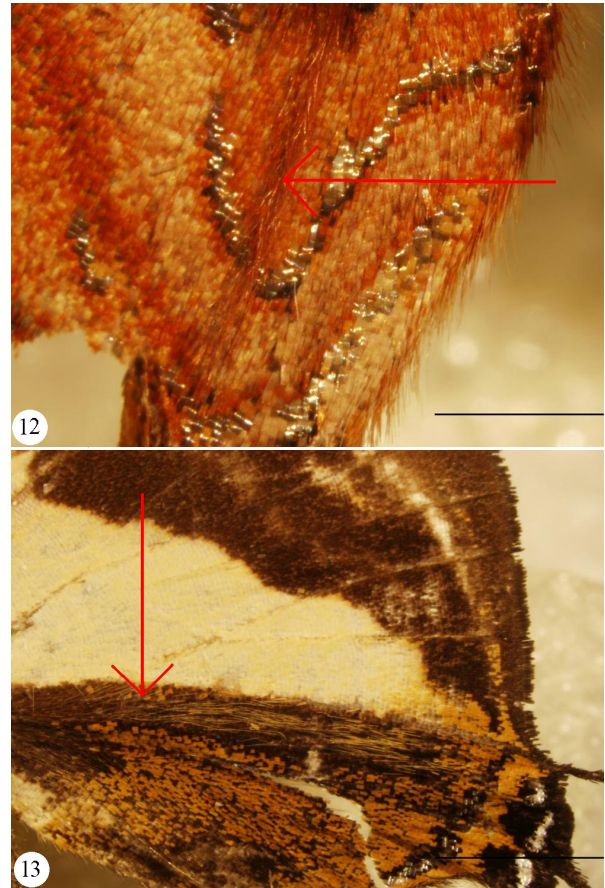
An interpretation of our findings in *Cigaritis* is problematic in regard to genus-level classification. According to Boyle *et al.* (2015) the genus *Cigaritis* includes all the taxa, which were formerly classified as *Spindasis* Wallengren, 1857 (type species: *Spindasis masilikazi* Wallengren, 1857) and *Apharitis* Riley, 1925 (type species: *Polyomantus epargyros* Eversmann, 1854). Taxa considered representing the genus *Spindasis* by some workers (*e.g.* Larsen 2005, d’Abrera 2009) all have the hair tuft, whilst *Cigaritis sensu str.* and *Apharitis* do not. This suggests that lumping *Apharitis* with *Cigaritis* may reflect the reality, but Palaeotropical *Cigaritis* might deserve the generic name *Spindasis* (having almost 60 species according to Bridges 1994) – if we take the hair tuft as an important character for classification. However, the uniform type of male genitalia as well as their facies mitigate against such splitting, and also there is a growing evidence that male secondary characters are not stable (see for example Robbins *et al.* 2012, 2015 and Martins *et al.* 2016). Nevertheless this needs a thorough analysis of all the taxa, as male secondary sexual characters are often difficult to interpret regarding phylogenetics.

The four aphnaeine genera (*Aphnaeus*, *Cigaritis*, *Lipaphnaeus* and *Pseudaletis*) possessing male secondary sexual character are paraphyletic in the hypothetical phylogenetic tree provided by the most recent paper on the subfamily (Boyle *et al.* 2015). We note that these genera represent both of the main aphnaeine lineages being sisters to each other, and in one of the lineages there is a basal genus with androconia (*Pseudaletis*).



Figures 10-11. Aphnaeinae scaling at high magnification. 10 = *Cigaritis formosanus* (Moore, 1877), the vein Cubitus 2 is well visible in the lower half of the image (indicated by arrow pointing up) and there are no androconia around or under the long plume scales. 11 = *Pseudaletis leonis* Staudinger, [1888], a small part of the naked vein Cubitus 2 is visible on the right side of the image (arrow pointing up), and androconial scales (indicated by arrow pointing down) mixed with hair scales, ordinary cover- and ground scales are detectable (Scale bars: 160 μ m) (photos: Zs. Bálint, HNHM).

Although the sister group of Aphnaeinae has not yet been identified, it is suggested that it is the sister of the lineage containing all the other subfamilies recognized in Lycaenidae (Boyle *et al.* 2015: 7). If so, *Pseudaletis* represents one of the most basal lineages of the family. What this might imply is that the presence of a ventral hindwing male sexual organ was once a general character, but it was subsequently lost and later regained several times independently.



Figures 12-13. Aphnaeinae male hindwing ventra with special scaling: 12 = *Lipaphnaeus aderna* (Plötz, 1880), red arrow indicates the long plume scales erecting caudad from the wing membrane in the cell formed by the veins Cubitus 1–2 and forming a tuft (scale bar: 2 mm); 13 = *Pseudaletis antimachus* (Staudinger, 1888), red arrow indicates the long plume scales dispersed on the wing membrane between the cell area formed by the veins Cubitus 1–2 (scale bar: 4 mm) (photos: Zs. Bálint, HNHM).

It is interesting, that Eumaeini, which can be considered as a “primitive” group in Lycaenidae (see Eliot 1973: 454), offers analogues for the aphnaeinae male secondary sexual characters (see Faynel & Bálint 2012). For example in the genus *Theritas* Hübner, [1818] and its relatives there is a ventral hindwing cubital pouch (see Bálint 2006 and Robbins *et al.* 2012). In the genus *Brangas* Hübner, [1819], there is a pouch with hairpencils between vannal veins 2 and 3 (Bálint & Faynel 2009). And in this context it is also interesting

that the character of a female abdominal tuft is also shared by aphnaeine (*Pseudaletis*, *Chloroselas* Butler, 1886 and *Trimenia* Tite & Dickson, 1973) and eumaeine lycaenids (for *Neolycaena* de Nicéville, 1890 and *Satyrium* Scudder, 1876 see in Weidenhoffer *et al.*, 2016).

Female abdominal tufts are also present in Riodinidae (eg. *Sarota* Westwood, [1851], see Hall 1998) and also in some hesperiid genera (eg. *Tagiades* Hübner, 1819, Alan Heath, unpublished), and even some moths in the Geometridae and Tortricidae (see Pellmyr 1980). Hence, the abdominal tufts also pose interesting questions regarding higher level classification in Lycaenidae, as well as in other Lepidoptera families (see for Hesperidae: Warren *et al.*, 2009).

What is the function of these aphnaeine organs *in vivo* we reported on? We do not know yet. For *Pseudaletis* probably it is a scent-disseminating organ, as we were able to detect androconia at the base of the hair scales, which supposedly contained aphrodites. The physiological role of a hair tuft in *Aphnaeus*, *Cigaritis* and *Lipaphnaeus* is a mystery to us as we were unable to find any androconia under the hair-scales, or on the hindwing dorsal surface of the female there is nothing unusual, merely the normal scaling. Is it an organ that has lost its function? These questions need to be answered in future studies.

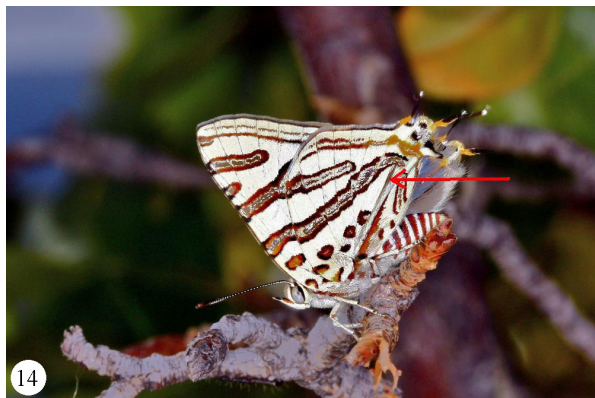


Figure 14. Perching male of *Cigaritis natalensis* (Westwood, 1852); the red arrow indicates the exposed hair tuft situated between the veins Cubitus 1–2 (Photo: A. Schutte).

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APPENDIX

Aphnaeinae material examined. All specimens are deposited in the HNHM Lepidoptera collection excluding 16 individuals which are in loan. These specimens are indicated with RCS (= research collection of Szabolcs Sáfián, Sopron, Hungary). Genus-level classification follows Boyle *et al.* (2015). Genera and species are listed in alphabetical order. Species given in bold possesses male secondary sexual character on their hindwing verso. Geographical Provenance of the specimens is given verbatim according to the labels; „?Patria?” means lack of geographical data.

ALOEIDES Hübner, [1819] – *A. aranda* (Wallengren, 1857): ♂, South Africa. *A. conradsii* Aurivillius, 1907: ♂, Kenya. *A. dentatis* (Swiestra, 1909): ♂, South Africa. *A. pallida* Tite & Dickson, 1968: ♂, South Africa. *A. pierus* (Cramer, 1777): ♂, South Africa.

APHNAEUS Hübner, [1819] – *A. gilloni* Stempffer, 1996: ♂, Ghana. *A. hutchinsoni* Trimen, 1887: ♂, South Africa. *A. jacksoni* Stempffer, 1954: ♂, Ghana (RCS). *A. nimbaensis* Sáfián & Libert, 2013: ♂, Liberia (RCS). *A. orcas* (Drury, 1782): 3 ♂♂, ♀, Ghana (♂, ♀: RCS). *A. zanzibarensis* Grose-Smith, 1889: 2 ♂♂, Kenya (♂: RCS).

ARGYROSPODES Tite & Dickson, 1973 – *A. argyraspsis* (Trimen, 1873): ♂, South Africa.

AXIOCERSES Hübner, [1819] – *A. amanga* (Westwood, 1881): ♀ Congo; ♂ Tanganyika. *A. coelescens* Heming & Hemming, 1996: ♂ South Africa. *A. harpax* (Fabricius, 1775): 4 ♂♂, Gambia; 2 ♂♂, 2 ♀♀, Ghana; 20 ♂♂, 2 ♀♀, Guinée; ♀ Kenya; ♂, South Africa; ♂, 2 ♀♀, Tanzania; ♂, 2 ♀♀, Togo; 11 ♂♂, 2 ♀♀, Yemen.

- CHLOROSELAS Butler, [1886] – *C. argentomaculata* (Pagenstecher, 1902): 4 ♂♂, ♀ Abyssinia. *C. pseudozeritis* (Trimen, 1873): ♂, South Africa.
- CHRYSORITIS Butler, [1898] – *C. aethon* (Trimen, 1887); ♂ South Africa. *C. beaufortius* (Dickson, 1966); ♂ South Africa. *C. felthami* (Trimen, 1904); ♂ South Africa. *C. palmus* (Stoll, 1781); ♂ South Africa. *C. penningtoni* (Riley, 1938); ♂ South Africa. *C. pyramus* (Pennington, 1953); ♂ South Africa. *C. zonarius* (Riley, 1938); 2 ♂ South Africa.
- CIGARITIS Donzel, 1847 – *C. acamas* (Klug, 1834): ♀, Afghanistan; ♂, ?Patria?; ♂, ♀ Syria (“Cupidopsis acamas dueldueli” syntypes). *C. crustaria* (Holland, 1890): ♂ Belgian-Congo. *C. elima* (Moore, 1877): ♂, ♀, Nepal; ♂ ?Patria?. *C. epargyros* (Eversmann, 1854): ♀ Caucasus; ♀ Kazakhstan; 4 ♂♂, 8 ♀♀, Mongolia; ♂, ♀, ?Patria?; ♂ Uzbekistan; 2 ♂♂, 3 ♀♀, Turkestan; 25 ♂♂, 10 ♀♀, Turkmenistan. *C. farsica* (Rose & Schurian, 1977): ♂ Mesopotamia; ♂, ♀, Syria. *C. formosanus* (Moore, [1877]): 24 ♂♂, 6 ♀♀, Taiwan. *C. homeyeri* (Dewitz, 1886): ♂, Zambia (RCS). *C. iza* (Hewitson, 1865): ♂, Zambia (RCS). *C. larseni* (Bouyer, 2012): ♂, 2 ♀♀, Gambia; ♀, Ghana; 2 ♂♂, Togo. *C. maxima* (Staudinger, 1901): ♀ Afghanistan; 9 ♂♂, Iran; 4 ♂♂, Syria. *C. natalensis* (Westwood, [1851]): ♂, South Africa. *C. lohita* Horsfield, [1829]: ♂, Indonesia; 3 ♂♂, 6 ♀♀, Thailand. *C. namanga* (Trimen, 1847): ♂, South Africa. *C. phanes* (Trimen, 1873): ♂ South Africa. *C. seliga* (Fruhstorfer, [1912]): ♂ Borneo; 3 ♂♂, China; ♂, Indonesia; ♂, Java; ♀, Nepal; ♀, ?Patria?; 5 ♂♂, 3 ♀♀, Philippines; 2 ♂♂, Thailand. *C. siphax* Lucas, 1849: 2 ♀♀, Algeria; 2 ♂♂, 5 ♀♀, Tunisia. *C. syama* (Horsfield, [1829]): ♂, Nepal; 2 ♂♂, 2 ♀♀ Vietnam. *C. takanonis* (Matsamura, 1906): ♂, ♀ North Korea. *C. trimeni* (Neave, 1910): ♂, Liberia (RCS). *Cigaritis zohra* Donzel, 1847: ♂, ♀, Algeria.
- CRUDARIA Wallengren, 1875 – *C. leroma* (Wallengren, 1879): ♂, South Africa.
- ERIKSSONIA Trimen, 1891 – *E. edgei* Gardiner & Terblanche, 2010: ♂, South Africa.
- LIPAPHNAEUS Aurivillius, 1916 – *L. aderna* (Plötz, 1880): ♂, ♀, Uganda (RCS). *L. leonina* (Sharpe, 1890): ♂, Ghana (RCS); ♂, ♀, Liberia (♀: RCS).
- PHASIS Hübner, [1819] – *P. clavum* Murray, 1935: ♂, South Afrika. *P. pringlei* Dickson, 1977: ♂, South Africa. *P. thero* (Linnaeus, 1764): ♂, 2 ♀♀, Süd Afrika.
- PSEUDALETIS H. H. Druce, 1888 – *P. antimachus* (Staudinger, [1888]): ♂, Cameroon (RCS). *P. jolyana* Libert, 2007: ♂, Liberia (RCS). *P. leonis* (Staudinger, [1888]): ♂, ♀, Ghana (♀: RCS); ♂, ♀, Liberia (RCS).
- TRIMENIA Tite & Dickson, 1973 – *T. malagrida* (Wallengren, 1857): ♂, South Africa. *T. wallengrenii* (Trimen, 1887): ♂, South Africa.
- TYLOPAEDIA Tite & Dickson, 1973 – *T. sardonys* (Trimen, 1868): ♂, South Africa.
- VANSOMERENIA Heath, 1997 – *V. rogersi* Riley, 1832: ♀, Tanzania.
- ZERITIS Boisduval, 1836 – *Z.* (Boisduval, 1836): 2 ♂♂, Guinée.

REFERENCES

- AURIVILLIUS, C. (1925): *Tagfalter*. In: SEITZ A. (Ed.) *Die Gross-Schmetterlinge des Afrikanischen Faunengebietes*. Stuttgart: Alfred Kernen Verlag, 613 pp, 80 pls.
- BOYLE, J.H., KALISZEWSKA, Z.A., ESPELAND, M., SUDERMAN, T., FLEMING, J., HEATH, A. & PIERCE N. (2015): Phylogeny of the Aphnaeinae: myrmecophilous African butterflies with carnivorous and herbivorous life histories. *Systematic Entomology* **40**: 169–182. doi: [10.1111/syen.12098](https://doi.org/10.1111/syen.12098)
- BRIDGES CH. (1994): *Catalogue of the Family-group, Genus-group and Species-group names of the Riodinidae & Lycaenidae (Lepidoptera) of the World*. Urbana, Illinois: Author's publication, 1204 pp. doi: [10.5962/bhl.title.15814](https://doi.org/10.5962/bhl.title.15814)
- D'ABRERA, B. (1986): *Butterflies of the Oriental Region. Part III Lycaenidae & Riodinidae*. Melbourne/London: Hill House, p. xv + 535–672.
- D'ABRERA, B. (1993): *Butterflies of the Holarctic Region. Part III Nymphalidae (concl.), Libytheidae, Riodinidae & Lycaenidae*. Melbourne/London: Hill House, p. i–vii + 335–524.
- D'ABRERA, B. (2009): *Butterflies of the Afrotropical Region. New and Revised Edition part III Lycaenidae & Riodinidae*. Melbourne/London: Hill House, p. i–xxvi + 531–884.
- EHRlich, P.R. & Ehrlich, A.H. (1961): *How to Know the Butterflies*. Dubuque, Iowa: W.M.C. Brown Company Publishers, 262 pp.
- ELIOT, J.N. (1973): The Higher Classification of the Lycaenidae (Lepidoptera): A Tentative Arrangement. *Bulletin of the British Museum (Natural History), Entomology*, 28(6): 371–505. doi: [10.5962/bhl.part.11171](https://doi.org/10.5962/bhl.part.11171)

- ELIOT, J. N. (1990): Notes on the genus *Curetis*. *Tyô ta Ga* 41: 201–225.
- FAYNEL, CH. & BÁLINT, ZS. (2012): An overview of alar organs in French Guiana hairstreaks (Lepidoptera: Lycaenidae: Theclinae, Eumaini). *Lépidoptères de Guyane*, 5: 46–54.
- HALL, J.P.W. (1998): A review of the genus *Sarota* (Lepidoptera: Riodinidae). *Tropical Lepidoptera*, 9(Suppl. 1): 1–21.
- HEATH, A. (1997): A Review of African Genera of the Tribe Aphnaeini (Lepidoptera: Lycaenidae). *Metamorphosis*, Supplement 2: 1–60.
- KIELLAND, J. (1991): *Butterflies of Tanzania*. Melbourne/London: Hill House, 363 pp.
- LARSEN, T.B. (1991): *The Butterflies of Kenya and Their Natural History*. Oxford: Oxford University Press, [xvii] + 490 pp. 64 pls.
- LARSEN, T.B. (2005): *Butterflies of West Africa*. Senstrup: Apollo Books, 595 (text volume) + 270 (plate volume) pp.
- LIBERT, M., 2007: *Révision du genre Pseudaletis Druce (Lepidoptera, Lycaenidae)*. Nairobi: African Butterfly Research Institute and Tervuren: Union des Entomologistes Belges, 61 pp. + 14 pls.
- LIBERT, M. (2013): *Révision du genre Aphnaeus Hübner (Lepidoptera, Lycaenidae)*. Nairobi: African Butterfly Research Institute, 99 pp + 13 pls.
- MARTINS, A.R.P., FAYNEL, C. & ROBBINS, R. (2016): Variation of Male Secondary Sexual Structures and the Taxonomy of *Theritas lisus* and Relatives (Lepidoptera, Lycaenidae, Eumaeini). *Proceedings of the Entomological Society of Washington* 118(4): 555–573. doi: [10.4289/0013-8797.118.4.555](https://doi.org/10.4289/0013-8797.118.4.555)
- MURRAY, D.P. (1935): *South African Butterflies. A Monograph of the Family Lycaenidae. With description and illustration of every species and figures of many of the larvae*. London: Staples Press, viii + 195 pp. xii + 144 figs.
- PELLMYR, O. (1980): Morphology of the genitalia of Scandinavian brachypterous female Geometridae (Lepidoptera). *Insect Systematics & Evolution* 11(4): 413–423. doi: [10.1163/187631280794709990](https://doi.org/10.1163/187631280794709990)
- ROBBINS, R.K., MARTINS, A.R.P., BUSBY, R.C. & DUARTE, M. (2012): Loss of male secondary sexual structures in allopatry in the Neotropical butterfly genus *Arcas* (Lycaenidae: Theclinae: Eumaeini). *Insect Systematics & Evolution* 43: 35–65. doi: [10.1163/187631212X626195](https://doi.org/10.1163/187631212X626195)
- ROBBINS, K.R., HEREDIA, M.D. & BUSBY, R.C. (2015): Male secondary sexual structures and the systematics of the *Thereus oppia* species group (Lepidoptera, Lycaenidae, Eumaeini). *ZooKeys* 520: 109–130. doi: [10.3897/zookeys.520.10134](https://doi.org/10.3897/zookeys.520.10134)
- SCOTT, J.A. (1999): Adult structure and function, pp 108–151. In: KUDRNA, O. (Ed.) *Butterflies of Europe, Volume 2. Introduction to Lepidopterology*. Wiesbaden: Aula-Verlag, 557 pp.
- STEMPFER, H. (1954): A revision of the genus *Aphnaeus* Hübner (Rhopalocera: Lycaenidae). *Transactions of the Entomological Society, London* 105: 493–516, pls I–II. doi: [10.1111/j.1365-2311.1954.tb00775.x](https://doi.org/10.1111/j.1365-2311.1954.tb00775.x)
- WARREN, A.D., OGAWA, J.R. & BROWER, A.V.Z. (2009): Revised classification of the family Hesperioidea (Lepidoptera: Hesperioidea) based on combined molecular and morphological data. *Systematic Entomology* 34: 467–523. doi: [10.1111/j.1365-3113.2008.00463.x](https://doi.org/10.1111/j.1365-3113.2008.00463.x)
- WEIDENHOFFER, Z. & BOZANO, G. C. (2007): *Guide to the Butterflies of the Palearctic Region. Lycaenidae part III. Subfamily Theclinae, Tribes Tomarini, Aphnaeini and Theclini (partim)*. Milano: Omnes Artes, 97 pp.
- WEIDENHOFFER, Z., BOZANO, G.C., ZHDANKO, A. & CHURKIN, S. (2016): *Guide to the Butterflies of the Palearctic Region. Lycaenidae part II. Subfamily Theclinae, Tribe Eumaeini (partim)*. Milano: Omnes Artes, 106 pp.