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Unveiling one of the rarest ‘butterflies’ ever (Lepidoptera: HesperIIDae, Noctuidae)

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Abstract

Many insect species named by the Danish entomologist J.C. Fabricius remain enigmatic due to loss of the original type specimens, sketchy descriptions and lack of illustrations, but even some well-illustrated taxa remain unrecognized. This is the case for *Hesperia busiris*, a ‘butterfly’ illustrated by W.J. Jones, the identity of which has puzzled experts for 225 years. Here we argue that the description and illustrations of this species are a perfect fit to a colourful moth later described by F. Walker as *Eusemia contigua*. Furthermore, we present evidence that Walker unwittingly based his name on the same specimen as Fabricius, and that this is the only known example of this species. An extraordinary sequence of misconceptions led the geographic origin of this specimen to become thoroughly confused, so that it is currently unknown where on Earth this species may occur (although a substantial body of evidence points to West Africa) and if it is even still extant.

Introduction

Carolus Linnaeus’s student, Johann(es) C. Fabricius (1745–1808), was one of the most fecund entomologists ever, naming about 10 000 insect species (Tuxen, 1967). Among these, in volume 3.1 of the *Entomologia Systematica* (Fabricius, 1793), he described a butterfly, *Hesperia (Urbicola) busiris*, based on specimen(s) in Dru Drury’s collection and figured by William Jones of Chelsea ([1745]–1818) in his unpublished work of Lepidoptera illustrations known as the ‘Jones’ Icones’ (Vane-Wright, 2010). This item is now in the Archives and Library of the Oxford University Museum of Natural History (Smith, 1986; Santry, 2014), and for some time has been accessible at Jones’ Icones Online (2015). *Hesperia busiris* was placed by Fabricius as species number 310 in the family HesperIIDae (‘skippers’), preceded by *H. (U.) aracinthus* (Fabricius) [= *Heteropterus morpheus* (Pallas), Palearctic] and followed by *H. (U.) pisistratus* Fabricius (now *Coeliades pisistratus*, South African). It is not to be confused with other hesperiids with similar epithets, namely the Neotropical *Achlyodes busirus* (Cramer) and *Epargyreus barisses* var. *busiris* Mabille, as its

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description *Hesperia busiris* has been retained in catalogues and revisions of the Hesperidae (e.g. Donovan, 1800–1804; Mielke, 2005). However, due to a failure to collect anything similar since its description, and the fact that the current whereabouts of the type specimen(s) are unknown, its identity has remained in doubt. Despite the description by Fabricius and illustrations by Jones (Fig. 1A–E), both being sufficiently detailed, and the pattern of *Hesperia busiris* appearing very distinct, promising easy association with extant specimens, no such recognition has ever been made.

The antennae shown in Jones's ([1785-1787]) illustrations are a perfect match for those of Hesperidae, due to the presence of a well-developed club and reflexed tip (cf. Ackery et al., 1998). No subsequent author who treated *Hesperia busiris* recorded additional specimens, nor did they shed light on its identity. They did not question its position within the Hesperidae either, evidently as a consequence of its original placement in the genus *Hesperia* and the features of its antenna. However, its wing shape and wing and body pattern are not like those of any known hesperiid, being instead reminiscent of the Agaristinae, a group of colourful day-flying moths within the family Noctuidae. Nevertheless, this cannot simply be assumed, as pattern mimicry is common among butterflies and moths. For example, some Hesperidae from the genera *Entheus* Hübner and *Cabirus* Hübner look exceedingly similar to moths from several families, such as species of *Cylopora* Dalman (Geometridae: Sterrhinae), *Seirocastnia* Grote (Noctuidae: Agaristinae) and *Erbessa* Walker (Notodontidae: Dioprinae). Therefore, it is not inconceivable that a mimetic hesperiid may share a wing pattern with an agaristine moth.

Here, we detail our argumentation leading us to conclude that this rarest 'butterfly' is actually an agaristine moth, the geographic origin of which is unknown and which has so far been collected only once.

Materials and methods

This work derives from an integration of all information pertaining to the taxa under consideration collated from a critical examination and evaluation of relevant literature, archival documentation, historical reconstruction of personal connections among contemporary authors, direct examination of museum holdings, study of specimens, and inquiries at various institutions.

Abbreviations for repository institutions are as follows: BM, British Museum, London (subsequently BMNH and NHMUK); BMNH, British Museum (Natural History), London (previously BM, subsequently NHMUK); CMNH, Carnegie Museum of Natural History, Pittsburgh; MfNB, Museum für Naturkunde, Berlin; MMUS, Macleay Museum, University of Sydney; NHMUK, Natural History Museum, London (formerly BM and BMNH); OUMNH, University Museum of Natural History, Oxford; ZMUC, Zoological Museum, University of Copenhagen; ZMUK, Zoological Museum, University of Kiel. This work was supported in part by NIH grant GM127390 to NVG.

Results

The original description of *Hesperia busiris* and Jones's illustrations

Fabricius's (1793: 345) description of *Hesperia busiris*, reproduced here as Fig. 1A, consists of four sections: a brief diagnosis, a bibliographic reference, indication of geographic origin and repository, and a description proper. It can be translated from Latin as follows (interpolations within brackets):

310. H[esperia] U[rbicola] with elongated, fully entire [= not crenulated] black wings: forewings with two yellow spots and two yellow dots, hindwings with yellow [tawny – see comments below] disc.

Papilio Busiris. Jones' painted figures ["Icones" vol.] 6, plate 23, Figure 1.

Inhabits Indies Housed by [= in collection] Drury.

Body black with white-dotted thorax, and ringed abdomen. Forewings black with two transverse spots, and between these with two yellow dots. Apex of wing greyish. Hind-wings tawny with black margin, underside similarly coloured.

A translation of the first sentence was also published by Donovan (1800–1804). It is worth noting that while Jones's volume 6 is mentioned in the description, the relevant illustrations are currently bound into volume 5 of the work due to a rebinding that combined the original volumes 2 and 3 into one (Waterhouse, 1938). This volume is undated, although all the evidence points to it being produced between 1785, the latest estimated date for a volume of Jones' *Icones* (viz. the current no. 3), and 1787, when Fabricius is thought to have examined Jones's work during a visit to England (Vane-Wright, 2010).

The description is in good agreement with Jones's illustrations (Fig. 1B–E), except for one minor internal inconsistency. In the diagnosis, the colour of the hindwing disc is stated to be yellow ('disco flavo', the same word used to describe forewing spots). In the extended description, the hindwings are referred to as tawny ('fulvae'), but this confusion between, and even equivalence of, the Latin terms 'flavus' and 'fulvus' has always been historically frequent (cf. Eco, 1985; Biggam, 2006; Jones, 2013). It is clear that Fabricius and Jones coordinated their efforts, as they frequently cross-referenced each other in their respective works despite the discrepancy in relative dates. So, it is most likely that Fabricius simply did not pay sufficient attention and introduced a *lapsus calami*. In fact, they both used the same wording for their diagnoses of *busiris*, but the handwritten version included by Jones below his drawings of 'Fabricius ES 310 – Busiris – Drury' (where 'ES' stands for *Entomologia Systematica*), states 'disco fulvo' rather than 'disco flavo'.

Jones's illustrations of the dorsal and ventral sides of the insect are more detailed than Fabricius's written description. Importantly, they show faint but definite stripes of metallic-blue scales on the forewing upper side between the yellow spots, forming a 'V' that outlines the small yellow spot in the discal cell (Fig. 1E), a similar line of metallic blue along the vein 1A + 2A, white highlighting of the veins in the black distal band of the hindwing underside, and a conspicuously ringed abdomen.

Subsequent literature

According to Mielke (2005), only seven publications refer to *busiris* following its description: Donovan (1800–1804), Latreille ([1824]), Westwood (1852), Butler ([1870]), Kirby (1871), Mabilite & Boulet (1919), and Zimsen (1964). To these, citations by Westwood (1842) and Scudder (1874–1875), and that of Mielke (2004, 2005) himself, should be added. None of these sheds much additional light on the identity of the nominal taxon. Donovan (1800–1804) illustrated the dorsal aspect of the species (Fig. 1F), but the figure appears less detailed than Jones's originals and looks like an amalgamation of Jones's dorsal and ventral views, i.e. it shows pale-lined veins in the distal band of the hindwing. The greyish tinge along the forewing apex is also broader and the apex of the antennae is less reflexed. It is unclear whether this illustration was made from a specimen or is a copy of Jones's illustration, but it could have been based on either, for Donovan (1800–1804) acknowledged Drury in the introduction for allowing inspection of his collection, whereas he referred to Jones as a 'worthy friend' (Donovan, 1805) and is known to have described species directly from his paintings (Vane-Wright, 2010). It should be noted that the identical position of the wings in Donovan's illustration and Jones's painting strongly supports the interpretation that the former was based on either the original specimen(s) or its 'iconotype', and not on any additional subsequent material. Inconsistencies in the antennal apices and patterns between the two illustrations are minor and can be ascribed to the poor reliability by Donovan, who reputedly introduced many errors into his artwork (R.I. Vane-Wright, personal communication, 2018).

Donovan's illustration was subsequently reissued in the revised edition of his work by Westwood (1842), who added an indication of the size of the species. This was evidently taken from the plate itself, as contrary to other species for which he had supplementary materials, Westwood simply recorded the same basic information previously given by Fabricius and, subsequently, Latreille ([1824]).

Interestingly, all the authors treated the taxon within the Hesperidae and most of them assigned it to one of the gaudy-patterned genera of Neotropical skippers presently placed in the subfamily Eudaminae (Butler, [1870]; Kirby, 1871; Mielke, 2004, 2005). Westwood (1852) and Butler ([1870]) used *Phareas busiris*, and Kirby (1871), followed by Mabilite & Boulet (1919, misspelled as *busirus*), used *Entheus busiris*. Butler ([1870]) likened *busiris* to the species currently known as *Cabirus procas* (Cramer), misspelling it as '*phorcas*'. Species of *Entheus* Hübner (formerly placed in *Phareas* Westwood) and *Cabirus* Hübner (formerly placed in *Entheus*, and before that in *Phareas*) are characterized by white, yellow and orange spotting on black wings, with hindwings being mostly orange with black margins in several species, matching Jones's illustrations well (Warren et al., 2018). However, the forewing pattern of *Hesperia busiris* is significantly different from that of any known *Entheus* or other Hesperidae (cf. Warren et al., 2018).

Strangely, Mabilite & Boulet (1919) admitted to not having seen any specimens, but stressed that the species was known only on the basis of the male sex, evidently by analogy with other *Entheus*, in which only the males have yellow bands on forewings. They also mentioned the elongated wings, unusual for the Hesperidae, and which are, following a

suggestion by Latreille ([1824]), more typical of *Heliconius* Kluk (Nymphalidae: Heliconiinae).

On the early fate of the type of *Hesperia busiris*

As clearly stated by Jones ([1785–1787]) and Fabricius (1793), the type(s) of *Hesperia busiris* belonged to Dru Drury (1725–1803, or –1804), a London silversmith and jeweller who established a collection of over 11 000 insect specimens ‘from all the various parts of the World where we have any intercourse as Englishmen’ (Drury, 1778), mostly in short series and in 1788 including exactly 2148 Lepidoptera species (Smith, 1842; Chalmers-Hunt, 1976). The accession date of the *busiris* specimen(s) into Drury’s collection should not necessarily be assumed to be after 1782 solely on grounds that otherwise he would have described such a gaily patterned species himself (Drury, 1770–1782). In fact, a review of the catalogue of his collection of exotic Lepidoptera, dated 1784 on the frontispiece but updated to 1789 (Drury, 1784[–1789]a,b), reveals that he described only a minority of the species he owned, many of which remained unidentified. On the other hand, *Hesperia busiris* should have been illustrated by 1787, the date inferred for Fabricius’s visit to Jones, a fond admirer of Drury (Salmon, 2000), to see the plates that had made been from his material (Vane-Wright, 2010). In fact, in that year the Dane visited England once again with all his family, whereas up to 1782 he had not mentioned Jones in his correspondence despite thoroughly reporting on all the people and places he had seen during his numerous stays in London (Fabricius, 1784; Hope, 1845; Armitage, 1958).

There is no indication that the type(s) of *Hesperia busiris* may have been retained by Fabricius following its description. In fact, Zimsen (1964: 565) specifies for *Hesperia busiris*: ‘»in Indiis Dom. Drury« – ‘ with no mention of specimen(s) location after the dash. In contrast, for ‘*Hesperia Pisiistratus*’, the species described next by Fabricius (1793), Zimsen lists ‘Dom Drury«, – Kiel 2 specimens.’ The Fabrician collection of Lepidoptera belonging to ZMUK has long been united with that of ZMUC, where indeed there are presently two specimens presumed to be *H. pisiistratus* types, but nothing referable to *Hesperia busiris* is present in either of the two holdings (cf. ZMUC, 2015). In fact, it is known that rather than borrowing specimens from Drury, Fabricius spent long visits with him to work with his collection, as recalled by Drury himself (‘He is now in London, and very busy in making descriptions from Mr. Banks’ and my Collections, where he will have employment for some months’; Smith, 1842). Fabricius himself admits he simply examined and described Drury’s material (Fabricius, 1784: ‘Die mehrsten derselben habe ich bei den Banks und bei den Drury gesehen, beschrieben’).

Considering the extreme rarity of a species that, despite its outstanding pattern, remained unrecognized and was never subsequently collected following its description (see later for a discussion on its distribution), it is very unlikely that, by the end of 1787, Drury owned more than one specimen, by which time *busiris* had already been portrayed by Jones. Although Drury’s collection was considered by a contemporary evaluator as ‘la plus parfaite Collection au Monde’ (Anonymous, 1780), it was not that large according to modern standards, if we consider that in 1788 it contained 2462 Lepidoptera specimens belonging to 2148 species (Smith, 1842), thus averaging 1.15 specimens per species. Although the

possibility that the original series consisted of multiple syntypes cannot be ruled out with certainty, we will nevertheless, for convenience and brevity, refer subsequently to only a single type specimen of *Hesperia busiris*. Furthermore, the available information is fully consistent with this specimen being retained by Drury, and eventually auctioned with the sale of Drury's collection (Anonymous, 1805).

Heraclia contigua* is a perfect match for *Hesperia busiris

Stripes and spots of metallic-blue scales between yellow bands and spots on forewings are not present in any known Hesperidae but are characteristic of many Agaristinae (Noctuidae). The conspicuously ringed abdomen also closely corresponds with that seen in many agaristine taxa. Wide diagonal yellow bands and spots on the forewings are typical of African agaristine species, in particular in the genus *Heraclia* Hübner, which also has clubbed antennae with a reflexed tip (Jordan, 1913–1934; Kiriakoff, 1977a). However, the wing and body patterns of most common and widespread species of *Heraclia* do not correspond to those of *Hesperia busiris*. Thus, we searched the Agaristinae holdings at NHMUK for specimens that agree closely with Jones's illustrations. We found a single specimen, the holotype of *Eusemia contigua* Walker (now in *Heraclia*), which is a perfect match (Fig. 1G–J). The agreement in pattern is so close that it is far more parsimonious to conclude that *busiris* is an agaristine moth than to envisage the existence of a mimetic hesperiid that has yet to be rediscovered since Fabricius's time. According to provisions of ICZN (1999), the valid name for this species thus becomes *Heraclia busiris* (Fabricius, 1793) **comb.n.** (= *Eusemia contigua* Walker, 1854, **syn.n.**). In fact, conditions for reversal of precedence between names and considering *busiris* as an unused senior synonym are not met (ICZN 1999: art. 23.9.1), because *Entheus busiris* has been used as a valid name after 1899. Furthermore, the junior name has not been used frequently enough to be considered in 'prevailing usage' and therefore it does not warrant referral of the case to the International Commission on Zoological Nomenclature for suppression of precedence.

The reasons for the long-standing failure to recognize the close similarity between *Hesperia busiris* and *E. contigua* probably reside in various circumstances, but the main one possibly arises because Jones's work was unpublished. Despite being in the OUMNH since at least 1933 (Vane-Wright, 2010), the work was made freely available only recently (Jones' Icones Online, 2015). In addition, as noted earlier, the only subsequent illustration of *busiris* was quite different from the original (Donovan, 1800–1804; Westwood, 1842). Walker's *contigua* is itself, in turn, a poorly known taxon. Only the male holotype is so far known (Mabille, 1890; Kirby, 1891; Jordan, 1913–1934; Kiriakoff, 1977a) and was illustrated only once by Butler (1877) (Fig. 1G,H). Although Jordan (1913–1934: 8) claimed to have included a new illustration of *contigua* on plate 5 of his extensive work on the group, he eventually failed to do so.

Systematic position of *Heraclia busiris* within Agaristinae

Regarding its systematic position and affinities, Kirby (1891) tentatively placed the species (as *contigua*) in the endemic African genus *Xanthospilopteryx* Wallengren, 1858 (currently a junior synonym of *Heraclia*), stating that it was an unmistakable species probably allied to *Polacanthopoda tigrina* (Druce, 1882) (cited under *Xanthospilopteryx*). Later, he assigned it

fully to *Xanthospilopteryx* (Kirby, 1892). Karsch (1895), reporting an observation by Hermann Dewitz, suggested an association with his *Mitrophrys fabricata* Karsch, 1895, which is still, however, a name relating to Druce's (1882) *tigrina*, either as a race or a form (Kiriakoff, 1977a; Poole, 1989). By contrast, Hampson (1901) placed *contigua* in *Rothia* Westwood, 1877, another African agaristine genus, his concept of which included species that are currently placed in other genera, such as *Heraclia*. Strangely enough, Hampson dismissed any similarity between *fabricata* and *tigrina*, considering the former as a synonym of *contigua* and the latter as the type species of his new monotypic genus, *Polacanthopoda* Hampson, 1901. Strand (1912) echoed Hampson (1901) by placing *contigua* in *Rothia* and considering *fabricata* to be an aberration of *contigua*.

Jordan (1913–1934) and Kiriakoff (1977a) conclusively placed *contigua* in *Heraclia* (= *Xanthospilopteryx*) and *fabricata* as infraspecific within *P. tigrina*. The two species do not show any particularly stronger resemblance than they do with a number of other agaristine taxa (cf. Jordan, 1913–1934; Kiriakoff, 1977a), and exhibit clear differences, including the orientation of inner yellow band(s) of the forewing, the abdominal pattern (Figs 1I,J, 2A–D), the configuration of labial palps, the tibial spining and features of the genitalia (Fig. 3A,B).

The systematic position of *contigua* within *Heraclia* has never seriously been questioned. In this context, we should draw attention both to its placement in another agaristine genus, namely *Aegocera* Latreille, 1809, and to the synonymy of *Polacanthopoda* with this genus, as seen in some web sources. Neither of these taxonomic acts has been substantiated in any publications, so that the taxonomic arrangement recorded by Poole (1989) remains in force. Nevertheless, it should be noted that many genera of Agaristinae, including *Heraclia*, are only imperfectly characterized, essentially on features of the wing venation alone, and other structural characters, such as those of the genitalia, have been stated to be quite variable within species, even in formal diagnoses (cf. Kiriakoff, 1977a: 13). However, even though the holotype of *contigua* matches the general wing venation of *Heraclia*, the fine details of the forewing radial system place this species somewhat aside from the main assemblage of the genus. So Jordan (1913–1934: 7–8) associated *contigua* with a small group of deviant species characterized by vein Rs_1 ('2. Subcostalast' in his unusual terminology, cf. Miller, 1970) arising from the areole, whereas the condition of Rs_1 stalked with Rs_2 and arising from beyond the areole is considered to be diagnostic for *Heraclia* s.s. (Jordan, 1913–1934: 1; Kiriakoff, 1977a: 3, 12). Other features, such as mouthparts, appear in agreement with *Heraclia*, but the male genitalia (Fig. 3A) again show several discrepancies with respect to most congeners. These, including the type species, *Phalaena euphemia* Stoll, 1781 [currently a junior synonym of *Heraclia geryon* (Fabricius, 1781)], generally show a very tall tegumen and broadly axe-shaped valvae (Fig. 3C), whereas, at least in the general shape of the valvae and saccus, the male genitalia of *Heraclia busiris* (= *contigua*) resemble those of *P. tigrina* (Fig. 3B).

The distribution of Heraclia busiris: everywhere and nowhere

Although the identity of Fabricius' *busiris* has now been clarified, the actual distribution of the species remains a mystery. The original type locality of *Hesperia busiris* was stated to be 'Indiis' (Indies), a notation that, during Fabricius's time, was inconsistently used in

reference to both the Oriental Indies (East Indies), with particular reference to east side of the Indian subcontinent, and the West Indies.

Based on data provided in ZMUC (2015), a comparison of citations of ‘Indian’ localities for Lepidoptera in Fabricius (1793) yielded the following results: (in) Indiis (81), India (35), India orientalis (21), Tranquebariae (7), India occidentalis (1), Bengalia (1), Coromandel (1), Madras (1), Malabar (1), and nova Hollandia [= W. Australia, cf. Scott, 1914] (1). Thus, being fully aware of the distinctions (or lack thereof) among India, East Indies, West Indies and Australia, one can really only assume a general region stretching from Indochina to Malesia. Of course, Fabricius could only rely on the information associated with the specimens or supplied by the various owners of the material that he was describing. In addition, the actual provenance of specimens described as being from ‘Indiis’ may have been other areas, due to imperfect recording of localities in early lepidopterology. For example, several Fabrician species from ‘Indiis’ were later found to originate from other regions; for example, *Hesperia nerva* Fabricius (Hesperiidae, presently in the genus *Kedestes* Watson) is South African, and *Hesperia aemulius* Fabricius (Riodinidae, presently in the genus *Catocyclotis* Stichel) is South American.

Donovan (1800–1804) included *busiris* in his work on Lepidoptera from India and islands of the Indian seas. Latreille ([1824]) maintained ‘Indies’, whereas Westwood (1842) narrowed down its provenance specifically to India, but, as noted earlier, most authors associated the species with Neotropical eudamine hesperiids. In particular, Mabille & Boulet (1919) explicitly gave ‘Amérique méridionale’ as the type locality. Since then, *busiris* has been included in lists of Neotropical Hesperiidae (Mielke, 2004, 2005).

The original locality of *E. contigua* was clearly unknown to Walker (1854), who simply described it as coming from G. [George] Milne’s (aka Mylne) collection, without stating the provenance of the type specimen. Butler (1877), Kirby (1891, 1892), Hampson (1901) and all subsequent authors did likewise. Nonetheless, the taxon was very early considered to be African (e.g. Butler, 1877: ‘this and the following are doubtless African species’) or associated with African genera of the Agaristinae (e.g. Kirby, 1891, 1892). It was eventually included in synopses of African species of this subfamily (e.g. Jordan, 1913–1934; Kiriakoff, 1977a).

Hampson (1901) was the only author to mention a possible second specimen of *contigua*, and one of known origin, by listing a ‘record’ from West Africa, Lower Guinea, in addition to the holotype. However, Hampson did not state the sex of this ‘specimen’, as he did for all the other species that he treated in his account, and there is no other specimen of this species from Lower Guinea in the NHMUK collections under *contigua*, *fabricata* or *tigrina*. Therefore, we surmise that there was no second specimen and that he simply appended information taken from Karsch’s (1895) description of *Mitrophrys fabricata*, which Hampson wrongly listed as a synonym of *contigua*. The type locality of *fabricata* is indeed ‘Nieder-Guinea’. Two decades later, Jordan (p. 7, dated 1913, in 1913–1934), who had access to the then BMNH collections, clearly reconfirmed that *contigua* was known from ‘Nur 1 Exemplar ohne Vaterland’. Strand (1912) then took the next step, explicitly stating

‘Westafrica (Nieder-guinea)’ as the locality for *contigua*, evidently referring to the locality of *fabricata*, a taxon that he incorrectly considered to be an aberration of *contigua*.

The type of *contigua* has been repinned, reset and possibly partly damaged since it was illustrated by Butler (1877). Its genitalia have been dissected and mounted with the abdomen on slide ‘BMNH Noct. 8601’ by M.L. (Maureen Lane) in 1973 (Fig. 3A). The moth bears a label with the following data: ‘Africa | 39.6.19 | 899.’ (Fig. 1I,J), where the numbers refer to an entry in the museum’s Accessions Register. Examination of the Accessions Register in the NHMUK (BM, 1837–1839) showed that this code associated exactly with specimen no. 899, registered on 19 June 1839, in a large lot of insects bought at the sale of the late Mr Milne’s collection, and that it was entered as a species of *Agarista*.

We are now left with an intriguing situation: a species seemingly with only two known individuals, viz. those of Drury and Milne (only the latter extant), which had variously been recorded or mentioned as being of American (Neotropical), African (Afrotropical) or Oriental (Indoaustralian) origin. The absence of subsequent records under either the hesperiid or the agaristid name has so far prevented resolution of the species’ distribution.

Even though there is an extant specimen, which led the species to be reassigned subsequently to the exclusively African genus *Heraclia*, it seems that rediagnosis of this and other related agaristine genera, including reassessment of the taxonomic value of the characters so far employed, should be undertaken within a broader phylogenetic context. As shown earlier, *Heraclia busiris* is a fairly aberrant member of the genus, sharing some characters with *P. tigrina* (Fig. 2A–D), so that its African origin is likely, although corroboration would require new material. However, a search of other museums with large holdings of African Agaristinae, namely MfNB and CMNH, yielded no further specimens of *Hesperia busiris*.

From his correspondence (Drury, 1768a,b,c; Cockerell, 1922; Sherborn, 1937), it is evident that to obtain specimens for his entomological collection, Drury liaised with so many ships’ crews travelling around the globe that unambiguously tracking down the provenance of *busiris* from his writings is unfeasible. However, he did consider that ‘The Brazills & Africa have yielded a very considerable number more than half the Collection’ (Drury, 1778).

Finally, it is difficult to ascertain when the label stating ‘Africa’ was added to the holotype of *E. contigua*. The specimen was not considered to bear any indication of locality by Hampson (1901) and, as late as 1977, Kiriakoff (1977a), explicitly stating: ‘The single specimen in British Museum does not bear any indication.’ On the other hand, the label appears to be quite old and yellowed. Moreover, pinned near to the specimen, is a black-and-white version of Butler’s (1877) illustration onto which someone has annotated in pencil ‘W. Africa’ (Fig. 1H). Finally, Mrs Maureen Lane, who prepared dissections for Kiriakoff’s revision (Kiriakoff, 1977b: 2), recorded the specimen as being from Africa, both on the genitalia slide label and in the BMNH slide register. Whether she did this by implication because the taxon was being treated in an exclusively African genus, or after directly reading that particular specimen label, we are unable to determine. If the latter is true, she appears to have failed to inform Kiriakoff that an indication of a locality was present. Nevertheless, this

apparently puzzling situation could be easily explained if we consider that the concept of 'locality' can be interpreted in a broader or narrower sense by different persons. The handwritten label bearing the indication 'Africa' matches those that were added during recuration of BMNH specimens in the second half of 19th century, and was probably added following Butler's (1877) suggestion that *E. contigua* had to be African. As all subsequent authors treating *contigua* took it for granted that this taxon was African, their comments that no locality was present may simply relate to the fact that a more restricted locality or region was unknown.

The original specimens of Hesperia busiris and Eusemia contigua are the same individual

Curatorial practices in natural history museums require that collecting data are not only associated with specimens but also with information about their lawful acquisition. This is true for the original specimen of *E. contigua*, which, as noted earlier, bears a label with a code recording the circumstances of its accession by the then BM following the sale of Milne's collection (BM, 1837–1839). This collection was sold at auction on 18–19 June 1839, when the BM secured 1749 of his insects, almost all butterflies and moths (BM, 1837–1839; Anonymous, 1839; Authors' Team, 1906). Importantly, in the auction booklet we find mention that Milne owned specimens from Drury (Anonymous, 1839), which he had in turn bought at the auction of Drury's collection held on 23 May 1805 (Anonymous, 1805). The results of the sale of each individual lot at the auction of Drury's collection were duly annotated in pencil on a copy of the 1805 auction booklet by Donovan himself (Chalmers-Hunt, 1976; Hayek, 1985), with an indication of the starting price, the purchaser and the price paid. Examination of this copy reveals that Milne was indeed one of the most important and recurrent buyers of Drury's Lepidoptera. In total, Milne purchased 19 lots, which included over 442 specimens (the absolute figure is not known, as the number included in lot 137 was not specified). Unfortunately, only some species names are recorded from the total number of specimens that comprised each lot (e.g. '*Papilio Pasithoe* – *Genutia*, and 48 other. [£] 50'), and the name *busiris* was not among those mentioned in full, so from Donovan's annotations we cannot trace who was its actual purchaser.

Nevertheless, we would argue that the original specimen of *Hesperia busiris* held in Drury collection, illustrated by Jones and described by Fabricius in 1793, was auctioned with Drury's collection in 1805 and purchased by Milne. It was subsequently auctioned at the sale of Milne's collection in 1839, whereby it eventually entered the BM collections and was correctly recognized as an agaristine moth. The Agaristinae holdings at the BM were then revised in 1852 by Walker (Authors' Team, 1906), who eventually redescribed the species as *E. contigua*. He clearly mentioned that the singleton present originated from Milne's collection (Walker, 1854), but made no reference to any previous provenance. The argumentation supporting this conclusion can be summarized as follows:

- The type of *Hesperia busiris* belonged to Drury (Jones, [1785–1787]; Fabricius, 1793).
- The holotype of *Eusemia contigua* originated from Milne (Walker, 1854).
- Milne's purchase of many of Drury's Lepidoptera has been determined (Anonymous, 1805).

- The BM then purchased Milne's collection (BM, 1837–1839; Authors' Team, 1906). It should be noted that a first auction of Milne's material contained only specimens regarded as duplicates (Anonymous, 1824).
- Milne was interested in Agaristinae, as no fewer than 15 specimens of this subfamily were obtained by the BM at the auction of his collection (BM, 1837–1839). It is thus likely that he chose lots with this moth group when bidding at the sale of Drury's collection (Anonymous, 1805).
- A search of all surviving holdings of other main purchasers of Drury's Lepidoptera did not lead to the discovery of any specimen matching with *Heracleia busiris*. In particular, analysis of the annotated copy of Drury's sale (Anonymous, 1805), cross-checked with available information about the lepidopterists and general natural historians active in England at that time (Hagen, 1862; Horn & Kahle, 1935–1937; Chalmers-Hunt, 1976; Gilbert, 1977; Salmon, 2000; Cooper, 2001; Gordh & Headrick, 2011; Jackson et al., 2013), identified Alexander Macleay (as McLeay), John Francillon, Adrian Hardy Haworth, Edward Donovan, George Humphrey and [John and/or Ann] Latham as bidders who secured a few lots, in addition to a handful of others. Extant material from the first four are preserved in MMUS (Macleay), NHMUK and OUMNH (Francillon, Haworth and Donovan) (Horn & Kahle, 1935–1937; Salmon, 2000; The University of Sydney, 2015), where extensive searches, via curators (Robert Blackburn, MMUS), online type catalogues (OUMNH, 2015) or direct examination (NHMUK), did not yield any results. Regarding the Macleay collection, some specimens went missing over time (Horning, 1983), but some of Drury's types have recently been rediscovered in it (e.g. Brosch et al., 2001).
- Although speculative, it should be noted that in lot 229 of Milne's sale a '*Hesperia Busirus*' was included (Anonymous, 1839), but in the absence of evidence to the contrary we must parsimoniously conclude that it was Cramer's *busirus* that was meant. That this name has been repeatedly misspelled as *busiris* (e.g. Hübner, 1816[–1826]; Ménétriés, 1829; Kaye, 1914; Miller & Brown, 1981; Koçak & Kemal, 2015), and Fabricius's *busiris* as *busirus* (e.g. Mabilie & Boulet, 1919), clearly does not help in this respect, but examination of the NHMUK holdings of *Achlyodes busirus* did not lead to the discovery of any specimen of this species derived from Milne.
- Other Drury Lepidoptera types have been subsequently recovered in Milne's material at the BM (Authors' Team, 1906; Horn & Kahle, 1935–1937).
- The holotype of *E. contigua* perfectly matches illustrations of *Hesperia busiris* made by Jones from Drury's original specimen. In addition to the dorsal and ventral sides of wings, the abdominal pattern also agrees, which can be assessed from the illustration of the *contigua* holotype in Butler (1877) made before this was dissected.
- A difference in the coloration of the forewing apices and hindwing margins, white in the specimen and grey in Jones's illustrations, partly so in Donovan's,

corresponds to what is observed in many of the white-coloured parts of other butterflies portrayed by Jones (R.I. Vane-Wright, personal communication), a phenomenon known as lead ‘white darkening’, which commonly affects old paintings in which lead was used as a component of white dyes (Lussier & Smith, 2007). The fact that Fabricius (1793) mentions grey apices too gives a hint that he may have based his description on Jones’s artwork rather than on the original specimen, so Donovan (1800–1804) should have so done for his picture. In fact, lead white deterioration can develop according to several pathways such as exposure to hydrogen sulphide released after burning of coal (Goltz et al., 2003), at that time already extensively used in English houses for heating (Braudel, 1992).

- The position of the wings of the holotype of *contigua* are today very different from those of Jones’s illustration, but it has clearly been repinned and reset from its original position, as is evident from an old hole visible in the thorax (Fig. 1I). By contrast, the position of the wings of the specimen when it was illustrated by Butler (1877) strictly matches that of Jones’s illustration of the dorsal aspect. A missing antenna today is of no relevance, as that may have been lost over time, possibly when the specimen was handled for resetting or examined for the wing venation by Jordan (1913–1934). Alternatively, it may have been introduced into the illustrations as an embellishment, a common practice in the past (cf. Vane-Wright & Hughes, 2005, 2007; Hancock et al., 2008).
- Any alternative hypothesis that presumes the specimen is not the one illustrated by Jones would imply that Drury’s was either lost or bought by somebody other than Milne, and that another example of this rarest of species was to hand for the latter. For an agaristine species that has not been recorded since Milne’s singleton was auctioned (1839), this is very unlikely, especially given that *Heracleia busiris* is a conspicuous member of a group of moths with predominantly day-flying habits (Kitching & Rawlins, 1998), and would have been easily spotted during field surveys since that time.

Conclusion

During the undertaking of this work, which was originally aimed at resolving the identity of *Hesperia busiris*, a clear thread appeared that linked Drury’s specimen, as described by Fabricius and portrayed by Jones, with that described by Walker as *E. contigua*, via the purchases by Milne at the sale of Drury’s collection, and the subsequent purchase of Milne’s material by the BM. Supporting evidence, such as a complete agreement between the *busiris* ‘iconotype’ and the holotype of *contigua*, the specimen accession code, archival documentation, links established among contemporary lepidopterists, the fate of the respective collections, and the extraordinary rarity of the species, has led us to conclude that the original name-bearing specimens of *Hesperia busiris* and *E. contigua* are one and the same, and the only one known specimen of an agaristine moth, the nomenclaturally valid name of which is thus *Heracleia busiris* (Fabricius, 1793). Butler’s ([1870]) statement that *Phareas busiris* was ‘not in the collection of the British Museum’ proved to be wrong, as the

original specimen was in the then BM, albeit in the Agaristinae. Although the holotype of *contigua* could be considered an extant syntype from an original series of *busiris* of an unknown number of specimens, for the reasons discussed earlier we consider it is most unlikely that Drury had more than one specimen available. In either case, the two names were based on the same primary types, which makes their synonymy objective. This demonstrated synonymy resolves the enigma of a mysterious hesperiid yet to be rediscovered since at least 1787.

Hesperia busiris, one of the ‘rarest butterflies ever’, eventually proved to be a moth, although no less a rare one, entering the ranks of moth species known only from unique specimens. Its systematic relationships as a member of the African genus *Heraclia* are sufficiently, albeit not fully, clear. Although the species is likely African, over the centuries its provenance has also been recorded as American and Oriental. Its similarities with the Afrotropical genus *Polacanthopoda*, and the somewhat stronger focus of Drury’s collection on African insects with a prevalence of samples from the Gulf of Guinea (Drury, 1768a,b,c, 1778; Fabricius, 1784; Smith, 1842), all point to the coast of West Africa as the most probable origin for *Heraclia busiris*.

This line of reasoning allows us to narrow down further the putative range of *busiris* thanks to Drury’s entries in his collection catalogue, where, until 1789, he recorded places of origin, collectors and years of accession (or collection) of his specimens. His Lepidoptera list follows the Linnaean system, with the butterflies being arranged into Papiliones – Equites (Troiani and Achivi), Heliconii, Danai (Candidi and Festivi), Nymphales (Phalerati and Gemmati) and Plebeji (Rurales and Urbicolae) – followed by the moths in Sphinges and Phalaenae (Drury, 1784[–1789]a,b). Recalling that *busiris* was placed within the Plebeji Urbicolae (Fabricius, 1793), corresponding to the present-day Hesperidae, Drury had only 143 specimens of this group, the vast majority unidentified. Their verbatim places of origin were as follows: Rio Janeiro (42), Georgia [USA] (20), Sierra Leon (16), Madras (13), New York (12), St. Kitts [Caribbean] (6), Cape Good Hope (5), Bay of Honduras (4), Surinam (4), Brazills (3), Gold Coast [Ghana] (2), Smyrna [Turkey] (2), Lima in Peru (2), Antigua (1), Callabar [Nigeria] (1), China (1), India (1), Jamaica (1), Muskito Shore [Honduras/Nicaragua] (1), Virginia (1) and five without data. Thus, for purely probabilistic reasons, the original locality of *Heraclia busiris* has the greatest chance of being Sierra Leone, from where the type would then have been collected by Henry Smeathman (cf. Cockerell, 1922; Griffin, 1942; Noblett, 1985; Douglas, 2008). Between 1773 and 1776, this correspondent sent 16 Urbicolae to Drury (1784[–1789]a,b). If so, then the holotype would be at least 242 years old. However, Drury’s catalogue still leaves open a possible Indian origin for *busiris* in view of the 13 specimens from Madras (= Chennai), the Coromandel Coast, and another Indian singleton. The first of these were collected by [S.O.] Sheene, possibly a surgeon (Drury, 1768a), and accessioned in 1772, but as he collected Urbicolae in the Cape of Good Hope too, the possibility of mixing African and Indian localities by this and other Drury’s collectors when ships were calling at various ports cannot be ruled out. Considering the lack of any further records of the species since it was independently described twice, and the past and current rates of deforestation in both West Africa (83.3% loss during the 20th century; Aleman et al., 2018) and the Coromandel Coast (over 95% of original coverage lost; Rawat et al., 2002), it is possible that this species has already become extinct.

Although we hope that our concern will be soon refuted by further study, we wish to draw attention to the role of natural history museums in preserving essential vouchers for our future understanding of biodiversity. By raising the issue of the roles and fate of natural history collections, several contributions have more or less implicitly revealed growing concern for the destiny of major repository institutions (e.g. Krishtalka & Humphrey, 2000; Suarez & Tsutsui, 2004; Winker, 2004; Wandeler et al., 2007; Wen et al., 2015), with much debate among governing bodies over whether their maintenance costs are justifiable in the light of modern research trends. In this paper, we have presented a case study demonstrating that a long-standing issue involving the identity of a long unrecognized ‘butterfly’ could only be resolved because of the preservation of a historical specimen and associated documentation that is guaranteed by such institutions.

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Fig. 1.

Documentation regarding *Hesperia busiris* and *Heraclia contigua*. (A) Original description of *Hesperia busiris* from Fabricius (1793: 345). (B–E) Illustrations of *Hesperia busiris* by W. Jones: (B) top portion of the plate 23 from volume 5; (C, D) dorsal and ventral aspects, respectively; (E) magnified view of the forewing discal area showing stripes of metallic scales. (F) Illustration of *Hesperia busiris* from Donovan (1800–1804). (G) Illustration of *Heraclia contigua* from Butler (1877: pl. 4, fig. 8, under *Eusemia*). (H) Black-and-white version of the illustration by Butler pinned in the NHMUK (formerly BMNH) collection near the holotype. (I, J) Dorsal and ventral aspects, respectively, of the *Heraclia contigua* holotype, no. BMNH[E] 1377146, herein considered to be same specimen as holotype of *Hesperia busiris* (labels are shown around the specimen images; scale bar on the left refers to

the specimen, that on the right to the labels). Illustrations are scaled approximately. Images (B)–(E) are copyright of the University Museum of Natural History, Oxford (used with permission); (I) and (J) are copyright of the Trustees of the Natural History Museum, London (used with permission). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)].

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Fig. 2.

Polacanthopoda tigrina. (A) Original illustration of *Mitrophrys fabricata* (a junior subjective synonym of *Polacanthopoda tigrina*) by Karsch (1895: pl. 2, f. 4). (B) Original illustration of *P. tigrina* by Druce (1882: pl. 60, fig. 4, under *Hespagarista*). (C, D) Dorsal and ventral aspects, respectively, of a male with wing pattern intermediate between f. *fabricata* and typical *tigrina* [Congo, Katanga, Kafakumba, specimen no. BMNH(E) 1377147, in NHMUK]. Images (C) and (D) are copyright of the Trustees of the Natural History Museum, London (used with permission). [Colour figure can be viewed at wileyonlinelibrary.com].

Fig. 3. Male genitalia of Noctuidae Agaristinae. (A) Same as Fig. 1 (I, J), BMNH Noct. slide 8601. (B) *Polacanthopoda tigrina*, holotype, Nigeria, Akwa Akpa ('Old Calabar'), BMNH Noct. slide 8562. (C) *Heraclia geryon*, type species of genus *Heraclia* (as *Phalaena euphemia*), Sierra Leone, BMNH Noct. slide 8597. Aedeagi are shown on the right. All specimens are in the NHMUK collection and their photographs are copyright of the Trustees of the Natural History Museum, London (used with permission).