Euploea dorippus Klug, 1845: species, semispecies, subspecies, junior subjective synonym of *Danaus chrysippus chrysippus* (Linnaeus), and/or form – what does Klug's *dorippus* represent? (Lepidoptera: Nymphalidae, Danainae)

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Abstract. The type material of the available name *Euploea dorippus* Klug, 1845, originated from northern Sudan, an area that lies beyond the core zone of the semispecies or subspecies currently known as *Danaus chrysippus dorippus*, and the description did not include examples of the phenotype currently referred to as *Danaus chrysippus* f. 'dorippus'. Possible consequences for nomenclature of the infraspecific species group taxa and form names of *Danaus chrysippus* are discussed.

Introduction

> "Mr. Butler has pointed out to me that Klug's type of *L. dorippus* has white hind wings, a fact which appears to have been entirely overlooked ..."
> Swinhoe 1885 page 126.

> "None of these specimens have [sic] any white on the secondaries, and agree best with fig. 5 of Klug's plate."
> Godman 1885 page 537.

> "ab. infumata n. nom. — … *dorippus* var. Klug, Symb. Phys., t. 48 f. 5."
> Aurivillius 1899 page 33

> "*dorippus* Klug … FW unpatterned, orange; HW orange."
> Smith et al. 1997 page 57, table 2

During recent work addressing *Danaus chrysippus* (Linnaeus, 1758) in the eastern Mediterranean and Egypt (John and Vane-Wright 2019; Vane-Wright and John 2019), a taxonomic problem came to light concerning use and application of the available binomen *Euploea dorippus* Klug, 1845. As with some other available names subsumed within *Danaus chrysippus* sensu lato (e.g. *Papilio alcippus* Cramer, 1777; *Danaida chrysippus* var. *orientis* Aurivillius, 1909), the epithet *dorippus* is used today in two fundamentally different ways – first, as the trinomen for a semispecies or subspecies considered to have its 'heartland', in the sense of Smith et al. (2019), in the Horn of Africa;

second, as the name of a form (phenotype) of *Danaus chrysippus* found more widely in Africa, and also in parts of the Indian region, including Sri Lanka (Donahue 1962).

There are at least two different problems relating to these two uses. The first, with respect to the application of *dorippus* to a species group taxon in the sense of the International Code of Zoological Nomenclature (ICZN 1999), depends on whether subspecies are considered geographically exclusive (non-overlapping, allopatric) or not – and, even if geographical segregation is insisted on for subspecies, and is usually expected for allospecies (Amadon 1966; Short 1969; Helbig et al. 2002), is this necessarily the case with respect to semispecies, the main populations of which are usually connected by a hybrid zone? The second problem relates to the fact that the ICZN regulations simply do not apply to form names, or any other taxon or appellation considered to be infra-subspecific (Masters 1972; Vinarski 2015b).

The interaction of these two uses of available names, as contended by John & Vane-Wright (2019), creates a further problem – that of confusion in communication. Thus in this case, if I use the name *Danaus dorippus*, am I referring to a taxon of the species group (species, superspecies, allospecies, semispecies, subspecies – Helbig et al. 2002), or to a phenotype that can transcend the boundaries of geographically circumscribed taxa, and thus be regarded as a form found in two or more species group taxa due to gene flow, shared descent (trans-species polymorphism in the sense of Ségurel et al. 2012), or convergent evolution? Moreover, does it matter if the type locality falls outside the area to which any such species group taxon is considered to be restricted or characteristic? – in other words, beyond its core range, or 'heartland'. And does it matter if the phenotype currently referred to when the name is used as a 'form' does not correspond to any of the phenotypes originally described under that name? Before endeavouring to address these problems, it is first necessary to assess the material basis on which Klug's name rests – and then explore the various ways in which it has been used in the past, and how it is being used now.

Throughout this paper I use, as normal, italic font for generic and species group names (e.g. *Anosia*, *Danaus chrysippus alcippus*), but non-italic font within single quotes when referring to named phenotypes (e.g. *Danaus chrysippus* 'albinus'). This convention, derived from Masters (1972), was employed by Vane-Wright (1975) and in many publications since, including Ackery & Vane-Wright (1984). The reasons for doing this are re-stated by John & Vane-Wright (2019, page 142/43) – where, in addition, the phenotype names are all prefixed with f. (for form) – thus *Danaus chrysippus* f. 'albinus'. Although the problems discussed in this paper go far deeper than mere typographical distinction, this convention if applied consistently does remove one source of confusion.

Genera, subgenera and combinations

Before presenting synoptic information on the original combination, type material and subsequent combinations and uses for Klug's *dorippus*, it is helpful to note the various generic names that, since 1845, have been applied to butterflies now placed in the genus *Danaus* Kluk, 1780, sensu Ackery & Vane-Wright (1984) and Smith (2014). These include four objective synonyms of *Danaus*, one of which is also a homonym: *Danaida* Latreille, 1804; *Danais* Latreille, 1807; *Danaus* Latreille, 1809; and *Festivus* Crotch, 1872. Subjective synonyms at generic level are *Limnas* Hübner, 1806 [this name, first published in Hübner's *Tentamen*, is nomenclatorially invalid]; *Anosia* Hübner, 1816; *Salatura* Moore, 1880; *Nasuma* Moore, 1883; *Tasitia* Moore, 1883; *Danaomorpha* Kremky, 1925; *Panlymnas* Bryk, 1937; and *Diogas* d'Almeida, 1938. For completeness, it should be noted

that at the time of Klug's description it was frequent practice to include species now assigned to *Danaus* within *Euploea* Fabricius, 1807, due to a lack of agreement regarding the type species of the latter – a problem not finally resolved until publication of Opinion 163 (ICZN 1945) – see below.

In recent decades *Anosia* (type species *Papilio gilippus* Cramer) and *Salatura* (type species *Papilio genutia* Cramer) have been used by a few authors for genera separate from *Danaus* (type species *Papilio plexippus* Linnaeus), or more frequently as subgenera of *Danaus*. In rejecting all subgeneric divisions of *Danaus*, Smith (2014: 120) stated that *Salatura* and *Anosia* were "resurrected" by Ackery & Vane-Wright (1984) as subgenera. Their three-fold division was however identical to that recognised by D'Almeida (1939): *Diogas* (subjective synonym of *Danaus* s.s.), "*Danaus*" (equivalent to *Salatura*, based on a misidentified type species in the current sense), and *Anosia*. Under the influence of Takashi Shirôzu (e.g. 1960) the same division into three full genera, *Danaus*, *Salatura* and *Anosia*, was for a period employed by Japanese lepidopterists (e.g. Kawazoé and Wakabayashi 1979). Brower et al. (2010) also recognised all three, but as subgenera, with the hierarchical or cladistic relationship ((*Danaus*) (*Anosia* + *Salatura*)) – as proposed by Ackery & Vane-Wright (1984). Others (e.g. Morishita 1981) placed *Salatura* as a subjective synonym of *Anosia*, recognising the latter together with *Danaus* as two separate genera. Morishita's arrangement is supported by data derived from cardenolide resistant Na+/K+-ATPases (Petschenka et al. 2013). However, the most recent statement remains that of Smith (2014) who, based in part on evidence of conflict among haplotypes, rejected all subgeneric divisions of *Danaus*.

Euploea dorippus Klug, 1845

Euploea dorippus Klug, 1845: text (signature h[iii]), pl. 48, figs 1–5. Male and female syntypes, Sudan: [New] Dongola, Dunqulah, 19°10'N, 30°29'E, and Ambikol, 18°03'N, 31°31'E, leg. C.G. Ehrenberg & W.F. Hemprich (Baker 1997: 194) (material apparently lost – not in Museum für Naturkunde, Berlin: Olivier and Nekrutenko 2000).

Limnas dorippus (Klug): Butler, 1886: 758. Butler acted as first reviser, restricting application of the name *Euploea dorippus* to Klug 1845: pl. 48, figs 1–4 (see also Swinhoe 1885: 126). [In this paper Butler excluded the specimen represented by Klug 1845: pl. 48, fig. 5, to become part of the type series of a new nominal taxon, *Limnas klugii* (Butler, 1886: 758 – type locality currently accepted to be Somalia: inland south of Berbera).

Type material. Klug's (1845) description of *Euploea dorippus* was based on at least two males and one female collected by Ehrenberg and Hemprich at two localities on the banks of the Nile in northern Sudan, *ca* 150 km apart, in May and July 1822 ("Habitat ad Dongalae novae castra Aethiopiae in Echii floribus Maio; ad Ambukohl Iulio."). The precise locations, as noted above, have been given by Baker (1997); a very helpful map is presented by Chester Bradley (1968). Their approximate location is plotted on Fig. 1.

Klug's original description was in Latin: "Euploea *alis testaceis, nigro-limbatis, limbo, subtus praesertim, albo-punctato, posticis maculis, subtus albo-notatis, in disco nigris. Mas. Fem. .... Magnitudine* E. Chrysippi*, cui valde affinis. Caput et thorax nigra, albo-punctata. Antennae nigrae. Alae fulvo-testaceae, supra margine omni, sparsim albo-punctato, nigro; anticae macula insuper triangulari costali media, posticae maculis discoidalibus quatuor (in femina tribus) nigris; subtus alae basi fulvae, limbo maculisque discoidalibus nigris ubique maculis albis ornatis. Pedes nigri. Abdomen fulvo-testaceum, subtus album. Variat uterque sexus alis posticis medio albis.*"

This has kindly been translated by Tony Galsworthy as follows: "A *Euploea* [now *Danaus*] with orange wings, bordered with black, the border, particularly below, spotted with white, hind wings

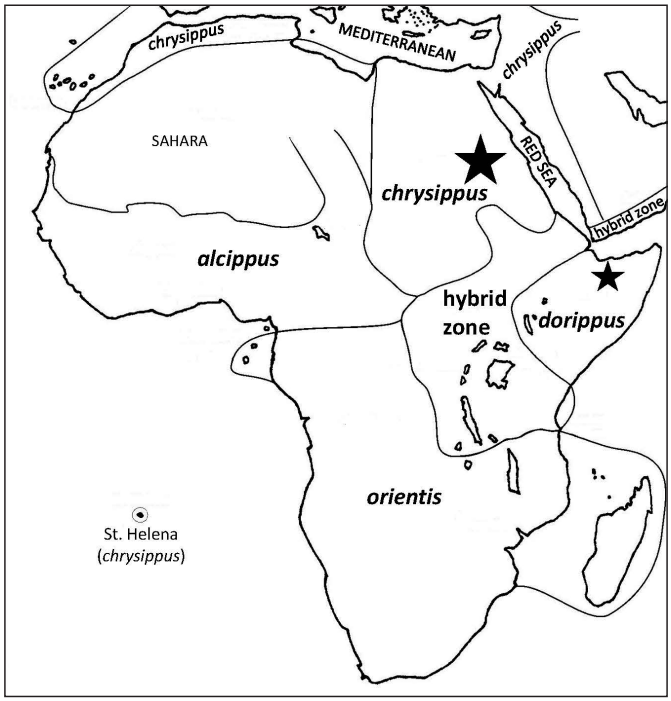

Figure 1. Outline distribution map for the four subspecies or semispecies of *Danaus chrysippus* in mainland Africa, as recognised by David Smith and co-workers (e.g. Smith et al. 2010 fig.1). This map is based on Lushai et al. 2003 fig. 1 (for which the original caption reads: 'geographical distribution of the subspecies of *D. chrysippus* in the Afrotropical region, showing the approximate boundaries of the hybrid zone … '). Note this extensive 'hybrid zone' in eastern Africa. The large five-pointed star in northern Sudan is centred on the type localities of *D. dorippus* (Klug), in an area supposedly occupied by subspecies *D. c. chrysippus* or semispecies *D.* [*c.*] *chrysippus*. Not one of the three phenotypes exhibited by the type material of *D. dorippus* (Fig. 2) corresponds to the phenotype regarded as typical of the Horn of Africa subspecies *D. c. dorippus* or semispecies *D.* [*c.*] *dorippus* (as currently named). The small five-pointed star in northern Somalia is centred on the approximate type locality of *D. klugii* (Butler) (See text).

black on the disc marked below with white. Male. Female. …. Size as *E. chrysippus*, to which it is certainly related. Head and thorax black, spotted with white. Antennae black. Wings fulvo-testaceous, upperside with the margin completely black, sparsely spotted with white; fore wing upperside with a triangular costal marking, hind wings with four black discal marks (three in female); underside wings fulvous at base, with black border and discal marks, everywhere ornamented with white markings. Legs black. Abdomen fulvo-testaceous, white below. Both sexes vary in the white in the middle of the hind wings."

Given the three different phenotypes originally illustrated by Klug (Fig. 2), it might be considered desirable to select a lectotype. This, however, is not possible in terms of an actual specimen as it appears all the original material is lost (Olivier and Nekrutenko 2000). Moreover, with respect to the taxonomic application of the name, unless we insist that Klug was working from a mixed series of two or more species (possibly the case based on the conclusions of Smith et al. 2005), the type localities are accurately known and sufficiently close together (*ca* 150 km) that any application

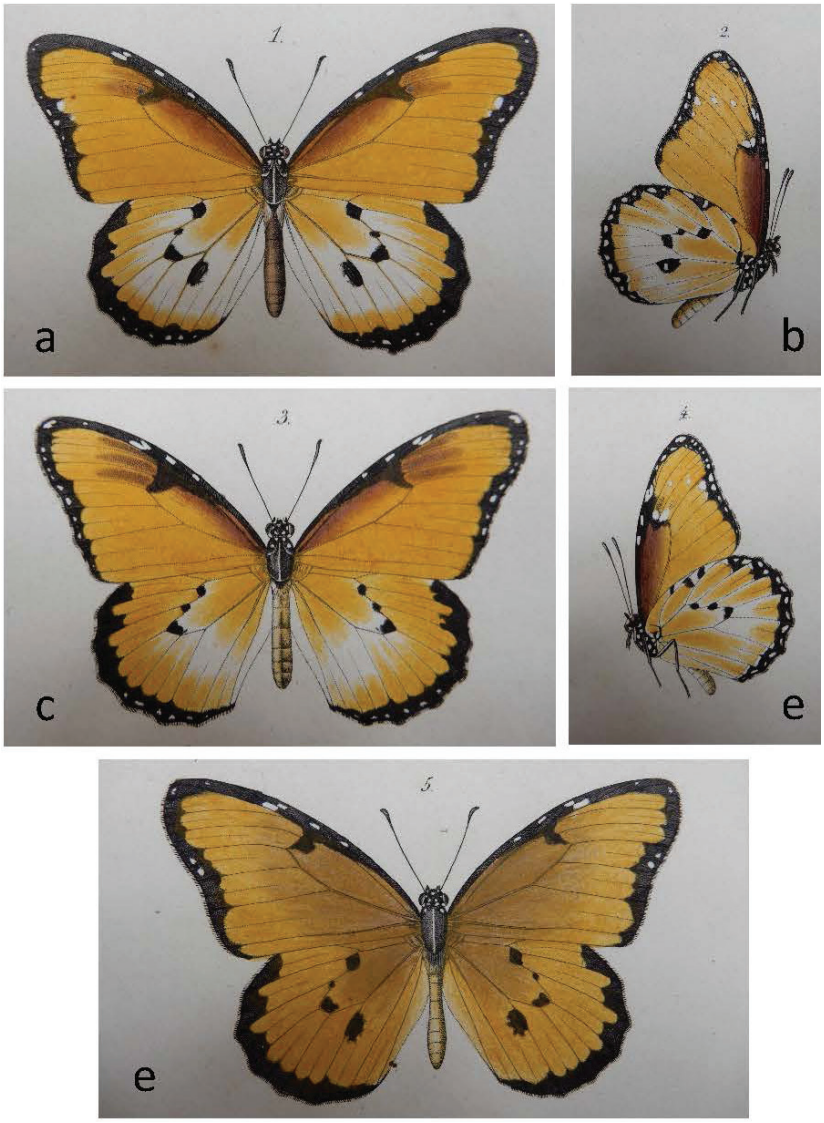

Figure 2. The five images published by Klug (1845, plate 48) to illustrate his original description of *Euploea dorippus*. **a, b** – pl. 48 figs 1,2 ("*E. dorippus* mas."); **c, d** – pl. 48 figs 3, 4 ("*E. dorippus* fem."); **e** – pl. 48 fig. 5 ("*E. dorippus* mar. var." – this "variety" was later included as part of *Limnas klugii* Butler, 1886, and subsequently given the infra-subspecific name *Danais dorippus* ab. 'infumata' (Aurivillius 1899)). See text.

dependent on geo-location is not likely to be equivocal. Thus I consider making a lectotype (or neotype) designation unnecessary (even undesirable) *at the present time* with respect to application of *Euploea dorippus* as an available name (see Discussion).

Before considering these matters further, the various ways in which the name *dorippus* has been applied over the past 175 years are enumerated and exemplified.

Previous applications of the name *Euploea dorippus*. Ignoring differing generic combinations, there are at least nine ways in which the available name *Euploea dorippus* has been employed since it was first proposed as a new species: 1) separate monotypic species (*Danaus dorippus*); 2) separate polytypic species; 3) form of a polymorphic *D. dorippus*; 4) subspecies of a polytypic *D. dorippus*; 5) semispecies of superspecies *Danaus* [*chrysippus*]; 6) subspecies of species *D. chrysippus*; 7) form of a monotypic but polymorphic *D. chrysippus*; 8) form of *D. chrysippus* subspecies *chrysippus*; and 9), form of *D. chrysippus* subspecies *aegyptius* (Schreber, 1759). It could also have been used as a form of subspecies *D. chrysippus dorippus* or of semispecies *D.* [*chrysippus*] *dorippus*, but I have not seen this done explicitly – and insofar as David Smith and his co-workers have regarded the 'dorippus' forewing pattern to be fixed in semispecies or subspecies *dorippus* in its core area (Smith 2014, page 188; Smith et al. 2016 – but see Discussion), it would be an unlikely previous usage. Instances of all nine uses that I have found are listed sequentially below (ciphers in square brackets refer to the usages listed above).

Literary synonymy of *Euploea dorippus*.

Euploea dorippus – Klug 1845: text (signature h[iii]), pl. 48, figs 1–5. [1]

Danais dorippus – Peters 1862: 371; Godman 1885: 537; Marshall & de Nicéville 1882: 52; Pagenstecher 1902: 129. [1]

Limnas dorippus – Moore 1883: 238; Swinhoe 1885: 126. [1]

Danaida dorippus – Aurivillius 1910a: 2, 1910b: 72 [1]

Danaus dorippus – Smith et al. 2005. [1]

Danaus dorippus bataviana (Moore, 1883) – Smith et al. 2005. [2]

Danais dorippus var. *klugii* – Holt White 1894: 49. [2 or 3]

Danaus dorippus f. dorippus – Suffert 1900: 116. [3]

Danaus dorippus dorippus – Smith et al 2005. [4]

Danaus [*chrysippus*] *dorippus* – Smith et al. 2010; Smith 2014; Gordon et al. 2014, 2015. [Note – square brackets around *chrysippus* used here indicate that *dorippus* is a member of a superspecies of which *Danaus chrysippus* is the first-named taxon, in accordance with the proposals of Amadon (1966; see also Helbig et al. 2002).] [5]

Danaus chrysippus dorippus – Bryk, 1937: 66; ?Talbot 1943: 121; Gordon 1984; Smith et al. 1997, 1998, 2002, 2016, 2019; Lushai et al. 2003a, 2003b, 2005; Herren et al. 2007; Traut et al. 2017; Williams 2018; Duplouy and Hornett 2018; Martin et al. 2019. [6]

Limnas chrysippus var. *dorippus* – Butler 1897: 923. [6 or 7]

Danais chrysippus var. *dorippus* – Kirby 1871: 7; Trimen 1887: 53. [6 or 7]

Salatura chrysippus var. *dorippus* – Ormiston 1918: 5. [6 or 7]

Danaida chrysippus var. *dorippus* – Ormiston 1924: 3. [6 or 7]

Danaida chrysippus f. dorippus – Fruhstorfer 1910: 194; Hulstaert 1931: 27. [7]

Danais chrysippus f. dorippus – Manders 1912; Woodhouse and Henry 1942: 39, pl. 2 fig. 3. [7]

Danaus chrysippus f. dorippus – Woodhouse 1952; Donahue 1962; Gifford 1965; Owen 1971; Dickson and Kroon 1978; Kielland 1990; Idris and Hassan 2012; Idris 2013; Hassan et al. 2013. [7]

Danaus chrysippus chrysippus f. dorippus – Carcasson 1963: 21; Larsen 1990, 1991; Gillett 1998; ?Braby et al. 2015; van der Poorten & van der Poorten 2016. [8]

Danaus chrysippus aegyptius f. dorippus – ?Talbot 1943: 120; Pierre 1974; Rothschild et al. 1975; D'Abrera 1980; Ackery & Vane-Wright 1984; Smith et al. 1988; Ackery et al. 1995; d'Abrera 1997. [9]

Danaus dorippus

This usage reflects its original, species-level status – having first been introduced by Klug (1845) as a species of *Euploea* Fabricius, 1807. Fabricius included three nominal species in *Euploea*, one being *Papilio plexippus* L., the type species of *Danaus* Kluk, 1780. The current usage of *Euploea* was not finally stabilised until publication of Opinion 163 (ICZN 1945), which fixed *Papilio corus* Fabricius, 1793, as its type species. *Papilio corus* is now used as the name for a subspecies of the butterfly currently known as *Euploea phaenareta* (Schaller, 1785).

Species level status for *dorippus* was maintained by Aurivillius in several publications, notably the very influential 'Seitz' (Aurivillius 1911, as *Danaida dorippus*). In that work he states that the forewing apex is brown-yellow without any subapical white band, and "the hindwing is not white [sic]". He does acknowledge that it is often only regarded as a form of *D. chrysippus*, "but of this there is no sufficient evidence" (Aurivillius, 1911: 12). From Aurivillius (1899: 32/33) it is evident that he regarded Butler's *Limnas klugii* as a synonym of *dorippus*, but recognised *Danais dorippus* ab. 'albinus' Lanz, 1896, as a variety, and gave Klug's 1845: pl. 48 fig. 5 "var." the infra-subspecific name *Danais dorippus* ab. 'infumata'. This suggests that Aurivillius (see also Suffert 1900) conflated Klug's *dorippus* with the all-orange ground colour morph that also lacks all trace of the forewing pre-apical transverse white spots ('transiens') as well as hindwing discal white – a morph which, as shown above, Klug did not describe or illustrate. Thus regardless of Swinhoe's (1885, p. 126) earlier stricture "Klug's type of *L. dorippus* has white hind wings, a fact which appears to have been entirely overlooked", this misapplication of Klug's name to the all-orange phenotype has continued ever since.

Despite Aurivillius's great authority, during most of the rest of the 20th century *dorippus* was generally regarded as a form and/or subspecies of *D. chrysippus*, not a separate species. Particularly important in this shift was Poulton's (1924) short paper entitled "*Danaida chrysippus* L. and *D. dorippus* Klug, proved by breeding to be forms of the same species". However, separate species status was accorded once more by Smith et al. (2005). Following a series of complex analyses based on mitochondrial 12S rRNA and COI sequences, the authors concluded that "*dorippus* … is the basal clade of the genus and is reinstated as the species *D. dorippus*" (Smith et al. 2005: 1291). Furthermore, the authors regarded it as composed of two subspecies: *D. dorippus dorippus* (range: Somalia, Kenya, Tanzania, Uganda, Sudan, Ethiopia, Arabia, Iran, Pakistan (Baluchistan), India (Sind, Kutch), and *D. dorippus bataviana* (Moore, 1883) from SE Asia.

Compared with all other interpretations of this group, these were unexpected and radical findings. Five years later Smith et al. (2010) announced "we wish to renounce our decision to restore *dorippus* to full species status, based solely on the evidence of mtDNA-based phylogenies …. and designate *D. c. dorippus* (stat. rev.) as its fourth African semispecies". This is so despite the fact that fig. 3.3. in Smith (2014, p. 129, p. 153) shows *D. chrysippus dorippus* twice – once (*dorippus-NB* haplotype) as the sister clade to all other taxa of *Danaus* (including *D. plexippus*), and second (*dorippus-DP* haplotype) as sister to *Danaus chrysippus bataviana*. In contrast, as pointed out by Brower (2016) "A recent molecular systematic paper by Braby et al. (2015) does not support Smith's results and shows a monophyletic *D. chrysippus* including African and Asian forms with very low levels of sequence divergence."

David Smith's research group has not been consistent with application of semispecies/subspecies rank. In recent publications (e.g. Smith et al. 2016, 2019; Traut et al. 2017; Martin 2019) they have reverted to calling *dorippus* a subspecies of *D. chrysippus*.

Danaus [*chrysippus*] semispecies *dorippus*
Smith and his associates (Smith et al. 2010, summarised in Smith 2014: fig. 2.34) developed a classification of *Danaus chrysippus* in the Afrotropical Region based on a hypothesis of past incipient geographical speciation in Africa during the late Pleistocene. They recognised a superspecies with four semispecies in the Afrotropics, for which they applied the following names (without the use of square brackets, a convention adopted here based on Amadon 1966):

- *D.* [*c.*] *chrysippus* in the north-east, to include North Africa, Egypt, northern Sudan (including the type localities for *Euploea dorippus*), the Canary Islands and Mediterranean eastwards to China etc.);
- *D.* [*c.*] *alcippus* (Cramer) in West Africa north of the Equator and south of the Sahara;
- *D.* [*c.*] *dorippus* in the Horn of Africa region (including the type localities for *Limnas klugii*); and
- *D.* [*c.*] *orientis* (Aurivillius) in most of Africa south of the Equator, including the Malagasy region.

However, according to the Smith scheme, all these populations are now in contact within a very extensive east African 'Hybrid Zone' covering much of Uganda, Tanzania, Kenya, Ethiopia and north of the Horn through Eritrea to Yemen. Although genetically compatible only to varying degrees involving several complex factors (e.g. localised infections with male-killing bacteria – Jiggins et al. 2000), due to the migratory nature of these butterflies, extensive gene flow nonetheless occurs. As a result, all of the various phenotypes can be found well beyond their core zones, including those of the other semispecies (within Africa, most notably the case with semispecies *orientis* – Smith et al. 2019, fig. 2). Within the Hybrid Zone, Smith (2014) has recognised many forms and genotypes as the result of hybridization between the semispecies, where they apparently coexist, in some sense, as sympatric taxa. Thus although the core area for supposedly 'pure' *D.* [*chrysippus*] semispecies *dorippus* is Somalia, eastern Ethiopia and north-eastern Kenya, Smith (2014: fig. 4.1) describes the polymorphism at Dar es Salaam, some 600 km south of this core area, as the result of hybridization between all four semispecies.

Danaus chrysippus subspecies *dorippus*
Talbot (1943: 121) stated "The form *dorippus* appears dominant in Abyssinia, Somaliland, Kenya and Tanganyika Territory; it may be considered almost as an eastern race." Subsequently *dorippus* has quite often been used for the name of a subspecies of *D. chrysippus* centred on the Horn region (e.g. Gordon 1984; Herren et al. 2007; Lushai et al. 2003a; Smith et al. 1997, 2002). As noted above, Smith et al. (2016, 2019) have recently reverted to this usage.

Danaus chrysippus in Sudan – the *dorippus* type localities and Khartoum

During the first two weeks of February 1909 the indefatigable traveller, naturalist and 'butterfly-hunter' George Longstaff was in Khartoum. He reported finding "typical *chrysippus*", *chrysippus* "with the veins of the hind-wing dusted with white" "f. *alcippoides*", "f. *alcippus*", and "f. *dorippus*, Klug, var. *albinus*". He also noted that "Of the total specimens seen, I estimated at the time that at least three-fourths were either *alcippus* or *alcippoides*" (Longstaff 1912, page 406).

Under the superpecies scheme, this strongly suggests that in 1912 at least three of the semispecies were present: *D.* [c.] *chrysippus*, *D.* [c.] *alcippus*, and *D.* [c.] *dorippus* – in other words, Khartoum was within the hybrid zone. Some 90 years earlier, it would seem on the evidence of the Hemprich

and Ehrenberg material described by Klug as *Euploea dorippus*, that the hybrid zone extended further north, perhaps as far as the Egyptian border. If we were to accept Longstaff's (1912, page 395) suggestion that the butterflies depicted on a tomb at Thebes are 'mid-way in colouring between the type [*D. chrysippus*] and the variety [var. *dorippus*]', then we could speculate that at *ca* 1400 BCE the hybrid zone extended as far north as Luxor. And why not? The 'dorippus' forewing phenotype extends east to India and south to Sri Lanka (van der Poorten & van der Poorten 2016) – where, on the face of it, and making the assumption that the same alleles express as the same phenotypes, then the same three semispecies may also co-occur (this is in fact David Smith's current view: in litt., August 2019).

The limitation is that we can only observe the phenotypes of the vast majority of specimens on which these observations are based – we have far less knowledge of the supposedly fundamental genetic distinctions between them. Observed differences in nuclear gene Elongation Factor 1-α and haplotypes for mitochondrial genes 12S rDNA and COI were summarised by Smith et al. (2010, table 1). These are:

- *D.* [*c.*] *chrysippus EF1*-α–1, haplotype ST1;
- *D.* [*c.*] *orientis EF1*-α–2, haplotype ST2;
- *D.* [*c.*] *alcippus EF1*-α unstated, haplotype GH;
- *D.* [*c.*] *dorippus EF1*-α–3, haplotype NB/DP.

It would be very interesting to have comparable data for the three forms of *D. chrysippus* found on Sri Lanka. In this context it may be relevant to note that Singh et al. (2018) have recently reported six haplotypes from 30 individuals of *D. chrysippus chrysippus* obtained from six sites in the western Himalayan state of Uttarakhand – and, by analysing 54 additional *D. chrysippus* sequences obtained from the National Center for Biotechnology Information database (samples spanning Africa to Korea), they arrived at a total of 24 *D. chrysippus* haplotypes.

According to the map of Smith et al. (1998, fig. 3), and those later derived from it (e.g. Smith 2014, fig. 1.13.1; Smith et al. 2019, fig. 2a), Khartoum lies within the range of *D. c. chrysippus*, beyond that of *D. c. dorippus*. However, Idris & Hassan (2012) report that the same morphs noted by Longstaff (2012) co-occur at Khartoum today (with 'albinus' and 'dorippus' still relatively rare) – and they conclude, in contrast to Smith et al. (1998), that Khartoum lies within the hybrid zone.

The type material of *Limnas klugii*

Butler (1886, page 758) based his new species *Limnas klugii* – which he distinguished from *Limnas dorippus* (Klug) – on the following material:

- The "variety" of *Euploea dorippus* from northern Sudan represented by Klug (1845, pl. 48, fig. 5) – reproduced here as Fig. 2e;
- A male collected by J.W. Yerbury "on the Somali coast" (Butler 1886, page 756), "2nd April, 1884." [on evidence of specimen label, *lapsus calami* for 22.iv.1884] – Fig. 3a;
- One or more males and females collected by J.G. Thrupp "southwards into the interior of Somali from Berbera … Inland south of Berbera" – Fig. 3b–d).

As already noted above, the Ehrenberg/Hemprich "variety" of *Euploea dorippus* from northern Sudan illustrated by Klug (1845, pl. 48, fig. 5) was subsequently named *Danais dorippus* ab. 'in-

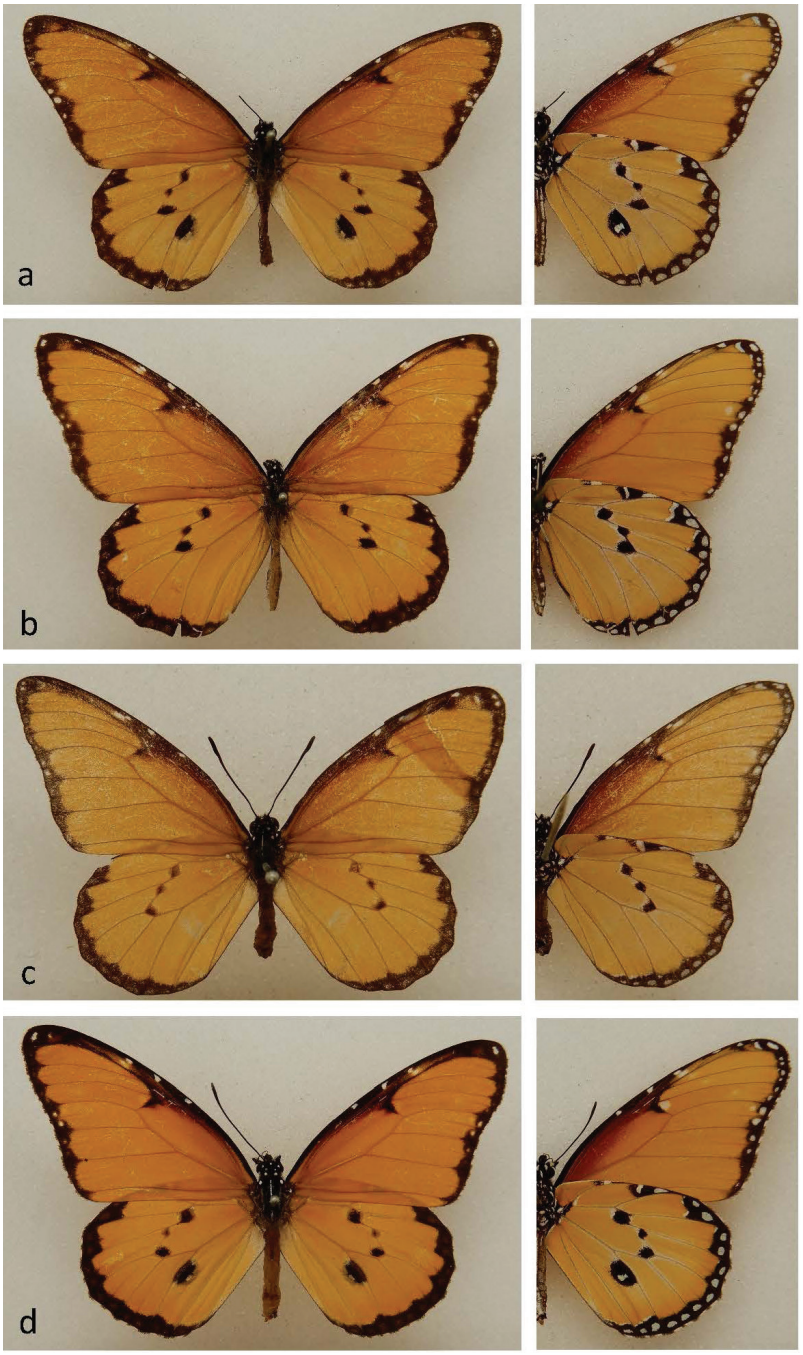

Figure 3. Four syntypes of *Limnas klugii* Butler, 1886, from northern Somalia (NHMUK, London). Upperside left; halved underside right. **a** – male "Somali 84.83 22.4.84" [Somali coast, *J.W. Yerbury*; NHMUK010241714]; **b** – female "Somali 85.38 Dec. 23" [inland, south of Berbera, *J.G. Thrupp*; NHMUK010241716]; **c** – female "Somali 85.38" [inland, south of Berbera, *J.G. Thrupp*; NHMUK010241717]; note – this specimen appears to be have been 'repaired']; **d** – male "Somali 85.38" [inland, south of Berbera, *J.G. Thrupp*; NHMUK010241715].

fumata' by Aurivillius (1899). Butler's (1886) paper is devoted to butterflies of Somalia and, in his description of *L. klugii*, he makes no mention of northern Sudan (or Nubia as this region was then referred to), despite his inclusion of Klug's "var.". Somalia south of Berbera is currently accepted as the (restricted) type locality for *L. klugii* (Ackery et al. 1995).

The Natural History Museum London (NHMUK) has two male and two female specimens from Somalia identified in 1971 by Phillip Ackery as syntypes of *E. klugii* Butler. All four are illustrated in Fig. 3. Applying current terminology, three of them (Fig. 3a–c) would be referred to f. 'dorippus' (cf Smith 2014 fig. 4.1.2/3); the fourth (Fig. 3d) to f. 'transiens' (cf Smith 2014 fig. 3.20.9).

Discussion

Vane-Wright & John (2019, page 152) stated: "In passing, we note that … there is a nomenclatural problem regarding application of the name *Euploea dorippus* Klug, 1845, to a semispecies or subspecies of *Danaus chrysippus* restricted to the Horn of Africa." In this paper the focus is on the nomenclature affecting *dorippus*; there are also issues of classification that require an extensive overview of the whole species complex, including discussion of the superspecies and subspecies concepts in both theory and application (see e.g. Helbig et al 2002; Vinarski 2015a,b), which I am unable to undertake at this time. Even so, some account of classificatory differences cannot be entirely avoided.

With respect to the classification of *Danaus chrysippus* in mainland Africa, Vane-Wright & John (2019, page 147) stated "There are now two different, rival systems … the 'Larsen classification', which includes all populations in a greatly expanded ssp. *chrysippus*, and the 'Smith classification', which divides African *D. chrysippus* into four named semispecies together with a large 'hybrid zone'." However, there is a third system, also due to Smith and his co-workers, and currently apparently favoured by them (e.g. Smith et al. 2019). This corresponds to the 'Smith classification', but treats the four segregates as subspecies. The difference, even if at first sight merely semantic, or simply an issue of assigned rank, can have consequences for nomenclature. Below I will refer to these three systems for *D. chrysippus* in Africa as:

- C1 (one polymorphic subspecies – Larsen 1991)
- C2 (four subspecies – Smith et al. 1998)
- C3 (a superspecies comprising four semispecies – Smith et al. 2010).

Potential consequences for form names

Based on the nomenclature of Smith (2014), the three phenotypes illustrated by Klug (1845 pl. 84 – see Fig. 2 a–e) are:

- male f. 'albinus' (with 'transiens') (Klug 1845 pl. 84 fig. 2: 1,2; cf Smith 2014: fig. 4.1.11);
- female f. 'semialbinus' (with 'transiens') (Klug 1845 pl. 84 fig. 2: 3,4; cf Smith 2014: fig. 4.1.12);
- male f. 'klugii' ('transiens' not apparent) (Klug 1845 pl. 84 fig. 2: 5; cf Smith 2014: fig. 4.1.1).

Smith et al. (2019, table 1) consider all three to be of hybrid origin: f. 'albinus' = *alcippus* × *dorippus* F2 hybrid; f. 'semialbinus' = *alcippus* × *dorippus* F1 hybrid; and f. 'klugii' = *orientis* × *dorippus* F1 hybrid.

The ground colour of the first two specimens represented in Klug (1845: pl. 48, figs 1–4) appears to be plain orange (Fig. 2a–d). Butler (1886), acting as first reviser, restricted application of the name *Euploea dorippus* to these 'albinus' / 'semialbinus' morphs. The third specimen, the "variety" (Klug 1845: pl. 48, fig. 5), which appears to be brown/orange, he included in the type material of his new taxon, *Limnas klugii*.

The primary problem is then that not one of the phenotypes described and illustrated in the original description of *Euploea dorippus* corresponds to the all-orange-without-'transiens' phenotype currently designated in almost all relevant literature on *Danaus chrysippus* as f. 'dorippus' (including Smith's 2014 summary volume). Moreover, were we to apply the rules of nomenclature to form names as if we were dealing with available names (and both *E. dorippus* and *L. klugii* are available), then we would have to consider treating either f. 'albinus' or f. 'semialbinus' as a junior synonym of f. 'dorippus' (Table 1). A lectotype has yet to be designated for Butler's *Limnas klugii* – three of the Somalia syntypes appear to be the "dorippus" phenotype (Fig. 3a–c) as that name is currently applied.

Potential consequences for names of species-group taxa

Classification C1. Under C1, all African mainland *D. chrysippus* are referred to the nominotypical subspecies, *D. c. chrysippus*. This is taken to extend eastwards across Asia to China, including India, Sri Lanka and the Malay Peninsula (Braby et al. 2015). Within Africa, the near East, India, Sri Lanka and the Malay Peninsula, *D. c. chrysippus* is considered to be polymorphic, particular forms being fixed (or almost so) in some areas, while two, three or four forms, with various transitional phenotypes, occur elsewhere. Under this classification *Euploea dorippus*, as an available name, is considered to be a subjective synonym of *D. c. chrysippus*. With respect to forms, if the changes proposed in Table 1 were to be accepted, then the form name nomenclature for several morphs of *D. chrysippus chrysippus* would be expected to change in the ways discussed above.

Classification C2. According to C2, African mainland *D. chrysippus* are referred to four extensively allopatric subspecies that also coexist and exchange genes in a very extensive hybrid zone centred on but extending well beyond Uganda. The available name *Euploea dorippus* is currently applied to the subspecies which occupies the Horn of Africa east of the hybrid zone (Fig. 1), as *Danaus chrysippus dorippus*. According to Smith et al. (2016), in this core or heartland area, the

Table 1. Names for forms or phenotypes relating to *Danaus dorippus* (Klug), if usage were determined by appeal to type specimens in a way comparable to the regulation of available names under the ICZN International Code of Zoological Nomenclature (see text).

Current name	'Correct' name suggested by present analysis
f. 'dorippus'	f. 'klugii' (subject to fitting lectotype designation for *Limnas klugii* Butler)
f. 'klugii'	f. 'infumata' (Aurivillius) – which is based on Klug 1845, pl. 48, fig. 5
f. 'albinus'	f. 'dorippus' (*if* Klug 1845, pl. 48, figs 1,2 is accepted as type of *dorippus*)
f. 'albinus'	f. 'albinus' (*if* Klug 1845, pl. 48, figs 3,4 is accepted as type of *dorippus*)
f. 'semialbinus'	f. 'semialbinus' (*if* Klug 1845, pl. 48, figs 1,2 is accepted as type of *dorippus*)
f. 'semialbinus'	f. 'dorippus' (*if* Klug 1845, pl. 48, figs 3,4 is accepted type of *dorippus*)
f. 'transiens'	unaltered – refers to heterozygous C-locus individuals detectable by inspection

colour-pattern genotype of this butterfly is *AAbbCC* (but see below). None of the three specimens described and illustrated by Klug (1845) could have had this genotype. In addition, the type locality of *E. dorippus* lies well to the north of the heartland area, in northern Sudan – an area considered by Smith et al. (2019, fig. 2) to be occupied by *D. c. chrysippus*. Given that the subspecies category requires allopatry or parapatry (Short 1969; Vinarski 2015b, table 2), then it cannot technically be correct to refer to a core zone *AAbbCC* population by the name *dorippus*.

The oldest available name for the populations currently included under C2 within the core range of subspecies (or semispecies) "*D. c. dorippus*" appears to be *Limnas klugii* Butler (see above). The correct name for the Horn of Africa subspecies recognised by Smith and co-workers would thus most likely become *D. chrysippus klugii* Butler – subject to an appropriate lectotype designation.

Classification C3. If we consider ff. 'albinus' and 'semialbinus' to be species hybrids under the superspecies hypothesis (classification C3) then the name *Euploea dorippus*, insofar as it denotes the same phenotype, although available for the purposes of homonymy, being a "species-group name established for an animal **later found** to be a hybrid … **must not be used** as the valid name for either of the parental species" (ICZN 1999 Art. 23.8, 'Application to species-group names established on hybrids', page 27, emphases added). Thus on the *Danaus* [*chrysippus*] superspecies (C3) hypothesis it might appear, for nomenclatorial reasons alone, that *dorippus* could not be used for any of the semispecies. However, this is arguably only the case if semispecies are, for the purposes of nomenclature, ranked as separate (biological or phylogenetic) species – as seemingly intended by Mayr (1963, page 672) when he defined superspecies as "a monophyletic group of entirely or essentially allopatric species [semispecies] that are too distinct to be included in a single species".

However, as pointed out by Amadon (1966), under the influence of Lorković (1958), Mayr had given an additional definition of semispecies on the previous page (Mayr 1963, page 671): "populations that have acquired some, but not yet all, attributes of species' rank; borderline cases between species and subspecies". Amadon (1966) proposed to restrict the use of the term 'semispecies' to this second, "borderline" rank. For the components of a superspecies that have achieved full species status (Mayr 1963, page 672), Amadon proposed the term allospecies.

This then raises the issue of what name can be applied to the Horn of Africa population under C3. Here it seems relevant to consider that, according to Sharpe (1896), Mrs E. [Ethelbert] Lort-Phillips [née Louisa Gunnis] collected "*Limnas chrysippus*, *Limnas dorippus* and *Limnas klugii*" all on the same day, 4th February 1895, in the Golis Mountains [9°52'0"N, 44°55'0"E], northern Somalia – an area seemingly close to the type locality of *D. klugii*. [The introduction to the earlier paper of Butler (1886) strongly suggests that Thrupp's material, on which Butler's *Limnas klugii* was in part based, was from the same range.]

In 1929 M. [Malcolm] Portal Hyatt collected a series of *Danaus chrysippus* in northern Somalia in the general area of the Golis Mountains, now preserved in the NHMUK. Four of these specimens are illustrated (Fig. 4), representing ff. 'transiens', 'albinus', 'chrysippus' and 'dorippus' (as currently named). The museum also has a female f. 'albinus' collected by Frederick Gillett (later Frederick Lort-Phillips) on 22.i.1897, at Beichen, Somalia (Butler 1897).

These observations appear to challenge the idea that the Horn of Africa population of *D. chrysippus* is fixed at the *A* and *C* loci, as stated by Smith (2014, page 188) and Smith et al. (2016). Although the genetic composition of the Somalia population could have changed over the past century, it could still be considered 'borderline' with respect to species rank. On this basis one can agree with Smith et al. (2010) that this is a semispecies in Amadon's (1966) restricted sense. If it is argued that

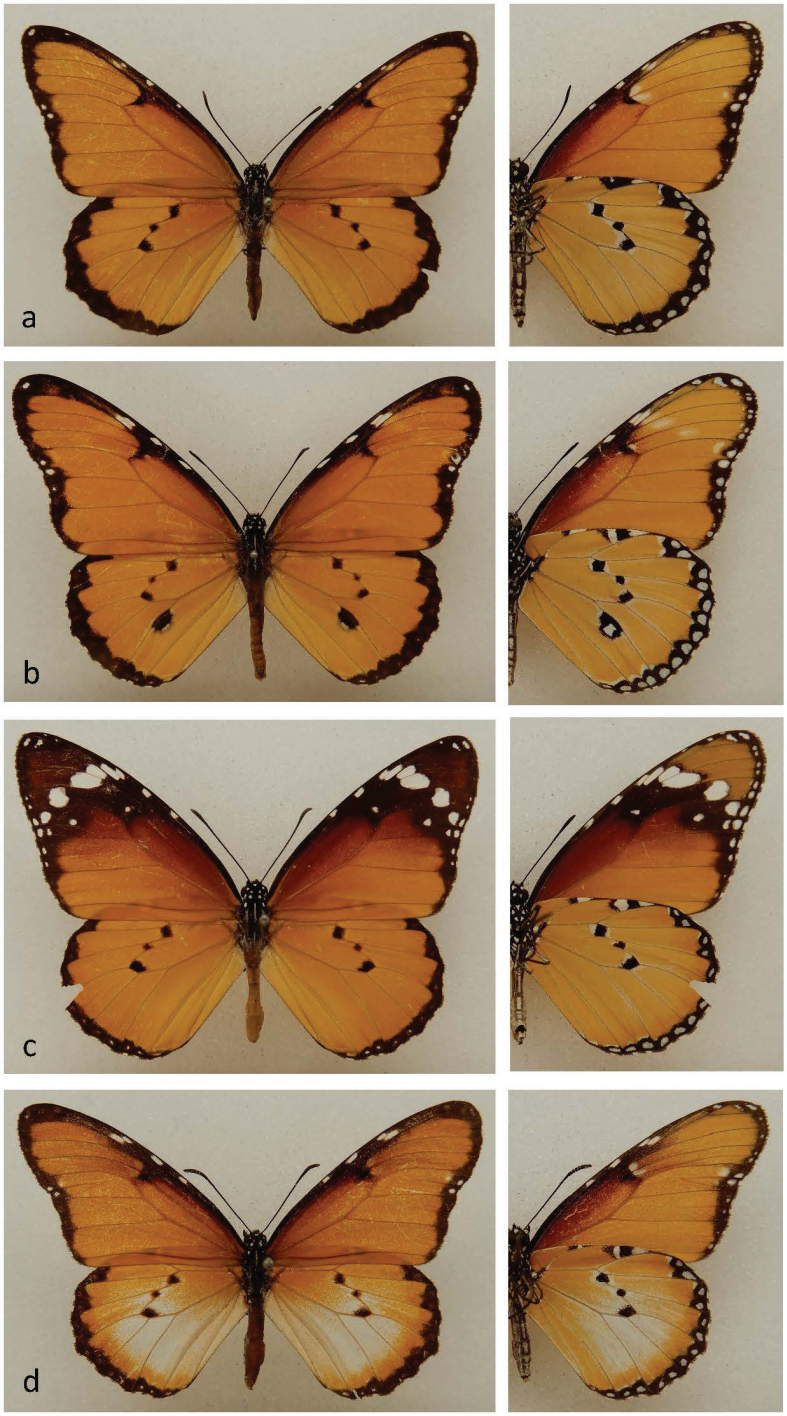

Figure 4. Four specimens of *Danaus chrysippus* collected during 1929 in NW Somalia by *M. Portal Hyatt* (NHMUK, London, BM 1929-534). Upperside left; halved underside right. **a** – female "10.10N, 45.45E, ca 1500 ft, Jan." [NHMUK010241712]; **b** – male, same data as (a) [NHMUK010241710]; **c** – female, same data as (a) [NHMUK010241713]; **d** – female, "9.30N, 44.30E, 4000 ft, May." [NHMUK010241711].

borderline status does not preclude the use of *Euploea dorippus* as an available name because it is not therefore a species hybrid, then its treatment must revert to that of a subspecies – and as already discussed above, application of *dorippus* to the Horn of Africa population conceived as a subspecies is ruled out on account of its north Sudan type locality. Both lines of argument converge on the conclusion that, supposing an appropriate lectotype selection can be made (consider Fig. 3a–c), and if a Horn of Africa subspecies or semispecies is to be recognised, *Limnas klugii* could be a substitute name, as either *Danaus chrysippus klugii* (subspecies), or *Danaus* [*chrysippus*] *klugii* (semispecies).

In conclusion: should any of these changes be implemented now?

Despite the various issues presented above, I would not lightly recommend implementation of any changes that might appear to be called for *at the present time*. There are several reasons:

Despite the evident regret expressed by Vinarski (2015b), unlike available names, form names are currently unregulated. I can call a black butterfly f. 'alba' if I wish; I can call an all-orange phenotype of *Danaus chrysippus* f. 'dorippus' if I wish, even though that form was not among those included by Klug under the available name *Euploea dorippus*. Of course, naming a black butterfly 'white' in Latin would be perverse – and the same could be said, as Swinhoe (1885) was surely trying to indicate, of the application of *dorippus* to a phenotype that Klug did not describe. But both *can* be done – form names are not regulated.

With respect to the three infraspecific classifications applied to African *Danaus chrysippus*, there are at least two issues: 1) much work on the butterfly in Africa and elsewhere is in progress, including increasingly complex molecular studies; and 2) there are many other issues affecting the classification of *D. chrysippus* as a whole, throughout the Old World tropics and subtropics (see e.g. Braby et al. 2015). To give just one example, as discussed above, what do the three forms of *chrysippus* found on the island of Sri Lanka really represent? Also, from a more theoretical perspective, I have avoided discussion here of different species concepts. A curiosity is that, following the initial criticisms of Wilson & Brown (1953; see also e.g. Zink 2006; Vinarski 2015a, 2015b), the subspecies category remains so widely used in butterfly systematics when in most other animal groups, apart from birds and mammals, it has largely been abandoned. But lepidopterists need not necessarily repent. To quote Gippoliti & Amori (2007) "while the taxonomic validity of many described subspecies is regularly questioned … there is mounting evidence that an astounding amount of taxonomic diversity among mammals has been overlooked; many recognised subspecies may deserve to be considered full species according to evolutionary species concepts … and many clearly distinct taxa remain undescribed". This often seems to be the case for butterflies too. However, in-depth genomic investigations can reveal excessive taxonomic splitting, as recently shown for the hawkmoth *Hyles euphorbiae* (L.) by Hundsdoerfer et al. (2019). Each case has to be taken on its own merits.

These issues aside, to introduce a few name changes at this point risks adding to the confusion. The infraspecific taxonomy of *Danaus chrysippus* across its entire range is very much still a work in progress. Until consensus and greater stability emerge, name changes are generally better resisted unless literally unavoidable (e.g. objective synonymy). After all, unlike genus and species, subspecies is (fortunately!) not a mandatory category in animal taxonomy, and forms names are still unregulated.

Thus the problems revealed here, and the possible solutions proposed, should perhaps be 'stored' for appropriate action once a clearer picture has emerged. This investigation also serves to remind that for taxonomic nomenclature there is still a great need for scholarly research – taxonomists themselves, and those who have to make use of taxonomic works and acts, can never rely solely on

secondary sources, as these are invariably interpretations. Over time, as our taxonomic concepts change with the growth of biological knowledge, failing to check and reinterpret primary sources can be a recipe for cumulative error and/or confusion. At the same time, when the classificatory framework is itself in flux, piecemeal and premature name changes rarely help. "There is a time to be silent, and a time to speak." The time to make changes regarding the application of *Euploea dorippus* has arguably not yet arrived.

However, one of the reviewers of this paper asked that I be encouraged "to 'stick [my] neck out' and recommend whether C1, C2 or C3 should preferably be used." Given the huge amount of work already lavished on *Danaus chrysippus* in Africa, when compared to the relative poverty of investigations to date in Asia and the Malay Archipelago, and for all the reasons given above, there is to me currently no objective basis for choosing between C1, C2 or C3. Moreover, the assumption that we should always strive for a single, preferred 'unitary' classification has been challenged. Thus Scoble (2004) cogently observed that "in reality multiple classifications of the same taxon exist, since different taxonomists often hold different concepts of their taxa", and argued instead for a *unifying* rather than unitary approach, whereby the richness and value of maintaining "multiple taxonomies" could be acknowledged and made accessible.

Larsen's simple system (C1), to record Mediterranean, Afrotropical and Indian subregion Queen butterflies as *Danaus chrysippus chrysippus*, if given together with form name, phenotype and/or genotype plus locality, is sufficient for most if not all individuals to be 'translated' into the current C2 or C3 classifications if those are preferred. However, having been pressed to be more assertive, I am willing to offer four provisional recommendations at this juncture regarding the use of names. Taken together these would result in making one change to species-group nomenclature (under C2 or C3; none under C1), and one change to form nomenclature:

1. Anyone wishing to signify a subordinate taxon of *Danaus chrysippus* that encompasses the populations of northwest Somalia should in future be encouraged to call this *D. chrysippus klugii* or *D.* [*chrysippus*] *klugii*, not (respectively) subspecies or semispecies *dorippus*.
2. The name *Euploea dorippus* Klug, under C3 arguably based on hybrids, should not be used to indicate a species-group taxon but should, instead, be included in the synonymy of *Danaus chrysippus chrysippus* (or *D. chrysippus aegyptius*, if that name is ever resurrected from synonymy).
3. Anyone wishing to use a form name for the 'all-orange' phenotype of *Danaus chrysippus* should continue to apply 'dorippus', but in so doing explicitly state (or accept) that they are using the name as a form in the sense of Aurivillius, not Klug. This is perfectly permissible in my view, and avoids confusion so long as *dorippus* Klug is not used for a taxon of the species group (recommendation 2). [While I greatly regret that butterfly workers ever started to use available names in a two-fold way, the practice is so deeply engrained that no resolution of this awkward case will wash away the many 'sins of the past'.]
4. Anyone wishing to refer to 'all orange' *D. chrysippus* phenotypes that have the basal upperside coloration of both wings darkened (infumed) should in future be encouraged to refer to these as f. 'infumata', not f. 'klugii'. This is perfectly permissible, and removes ambiguity with *klugii* as a species group name.

If these four recommendations are followed, then there is no current threat to other named 'dorippus'-like forms in common use, notably 'transiens', 'albinus' and 'semialbinus'.

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References

Ackery PR,Vane-Wright RI (1984) Milkweed Butterflies. Cornell University Press, NY, ix + 425 pp.

Ackery PR, Smith CR, Vane-Wright RI (1995) Carcasson's African butterflies: an annotated catalogue of the Papilionoidea and Hesperioidea of the Afrotropical Region. CSIRO, East Melbourne, pp. xi + 803 pp. https://doi.org/10.1071/9780643100787

Amadon D (1966) The superspecies concept. Systematic Zoology 15: 246–249. https://doi.org/10.2307/sysbio/15.3.245

Aurivillius [PO]C (1899) Rhopalocera Aethiopica. Kongliga Svenska Vetenskaps-Akademiens Handlingar 31(5):1–561. [+6 pls] [Publication date of 1899, not 1898 as printed: Cowan CF, Annotationes Rhopalocerogicae 1970. Privately published, Berkhamsted, UK, 70 pp.]

Aurivillius [PO]C (1910a) Lepidoptera. In: Sjöstedt Y (Ed.) Wissenschaftliche Ergebnisse der Schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaisteppen Deutsch-Ost Afrikas 1905–1906 2(9): 56 pp, 2 tabs. Königlich Schwedischen Akademie der Wissenschaften, Stockholm.

Aurivillius POC (1910b–1911) Family: Danaididae. The Macrolepidoptera of the World (2)13. In: Seitz A (Ed.) The African Rhopalocera, Alfred Kernen, Stuttgart, 71–79. [pls. 23–25] [English translation]

Baker DB (1997) C.G. Ehrenberg and W.F. Hemprich's travels, 1820–1825, and the Insecta of the Symbolae Physicae. Deutsche Entomologische Zeitschrift 44(2): 165–202. https://doi.org/10.1002/mmnd.19970440208

Braby MF, Farias Quipildor GE, Vane-Wright RI, Lohman DJ (2015) Morphological and molecular evidence supports recognition of *Danaus petilia* (Stoll, 1790) (Lepidoptera: Nymphalidae) as a species distinct from *D. chrysippus* (Linnaeus, 1758). Systematics and Biodiversity 13(4): 386–402. https://doi.org/10.1080/14772000.2014.992378

Brower AVZ (2016) [review of] David A. S. Smith. 2014. African Queens and their Kin. News of The Lepidopterists' Society 58(2): 86–87.

Brower AVZ, Wahlberg N, Ogawa JR, Boppré M, Vane-Wright RI (2010) Phylogenetic relationships among genera of danaine butterflies (Lepidoptera: Nymphalidae) as implied by morphology and DNA sequences. Systematics and Biodiversity 8(1): 75–89. https://doi.org/10.1080/14772001003626814

Bryk F (1937) Danaidae I: Subfamilia: Danainae. In: Bryk F (Ed.) Lepidopterorum Catalogus 28(78): 432 pp. W. Junk, 's-Gravenhage.

Butler AG (1886) An account of two collections of Lepidoptera recently received from Somali-land. Proceedings of the Zoological Society of London 1885: 756–776. [1 pl.]

Butler AG (1897) On a small collection of Lepidoptera made by Mr. F. Gillett in Somali-land. Proceedings of the Zoological Society of London 1897: 923–925. https://doi.org/10.1111/j.1096-3642.1898.tb01396.x

Carcasson RH (1963) The milkweed butterflies of East Africa (Lepidoptera, Danaidae). Journal of the East African Natural History Society 24(2): 19–32.

Chester Bradley J (1968) The Hemprich-Ehrenberg expedition to Egypt and Asia Minor of 1820–25. Deutsche Entomologische Zeitschrift NF 15(1/3): 107–109. https://doi.org/10.1002/mmnd.4810150107

D'Abrera B (1980) Butterflies of the Afrotropical Region. Based on Synonymic catalogue of the butterflies of the Ethiopian Region by R.H. Carcasson. Lansdowne, East Melbourne, xx + 593 pp.

d'Abrera B (1997) Butterflies of the Afrotropical Region (2nd edn). Part I. Papilionidae, Pieridae, Acraeidae, Danaidae & Satyridae. Hill House, Melbourne, xiv + 263 pp.

d'Almeida RF (1939) Revisão das espécies americanas da superfamilia Danaoidea (Lepid.: Pieridae) [sic]. Parte 1. Familia Danaidae, subfam. Danainae. Memorias do Instituto Oswaldo Cruz Rio de Janeiro 34(1): 1–113. [30 pls] https://doi.org/10.1590/S0074-02761939000100001

Dickson CGC, Kroon DM (1978) Pennington's Butterflies of Southern Africa. Donker, Johannesburg, [iv] + 670 pp. [1 map]

Donahue JP (1962) *Danaus chrysippus* form *dorippus* in Rajasthan. Journal of the Bombay Natural History Society 59: 311–312.

Duplouy A, Hornett EA (2018) Uncovering the hidden players in Lepidoptera biology: the heritable microbial endosymbionts. PeerJ, 6: e4629. https://doi.org/10.7717/peerj.4629

Fruhstorfer H (1910) Genus: *Danaida* Latr. The Macrolepidoptera of the World, (2)9. In: Seitz A (Ed.) The Indo-Australian Rhopalocera. Alfred Kernen, Stuttgart, 192–215. [English translation]

Gifford D (1965) A list of the butterflies of Malawi. The Society of Malawi, Blantyre, [vi] + vi + 151 pp. [9 pls]

Gillett MPT (1998) Butterflies of the UAE and neighbouring areas of northern Oman – the polymorphic status and phyto-chemical associations of the Plain Tiger, *Danaus chrysippus chrysippus* (Linnaeus), in the region (Lepidoptera: Rhopalocera). Tribulus 8(1): 8–13.

Gippoliti S, Amori G (2007) The problem of subspecies and biased taxonomy in conservation lists: the case of mammals. Folia Zoologica 56(2): 113–117.

Godman FD (1885) A list of the Lepidoptera collected by Mr. H.H. Johnston during his recent expedition to Kilima-njaro. Proceedings of the Zoological Society of London 1885: 537–541. https://doi.org/10.1111/j.1469-7998.1885.tb07860.x

Gordon IJ (1984) Polymorphism of the tropical butterfly, *Danaus chrysippus* L., in Africa. Heredity 53(3): 583–593. https://doi.org/10.1038/hdy.1984.116

Gordon IJ, Ireri P, Smith DAS (2014) Hologenomic speciation: synergy between a male killing bacterium and sex-linkage creates a 'magic trait' in a butterfly hybrid zone. Biological Journal of the Linnean Society 110: 92–109. https://doi.org/10.1111/bij.12185

Gordon IJ, Ireri P, Smith DAS (2015) Preference for isolated host plants facilitates invasion of *Danaus chrysippus* (Linnaeus, 1758) (Lepidoptera: Nymphalidae) by a bacterial male-killer *Spiroplasma*. Austral Entomology 54(2): 210–216. https://doi.org/10.1111/aen.12113

Hassan SSM, Idris E, Majerus MEN (2013) Is it just a coincidence that aposematic polymorphism and sex ratio distortion co-occur in a tropical butterfly? Evolutionary Ecology Research 15: 93–102.

Helbig AJ, Knox AG, Parkin DT, Sangster G, Collinson M (2002) Guidelines for assigning species rank. Ibis 144: 518–525. https://doi.org/10.1046/j.1474-919X.2002.00091.x

Herren JK, Gordon IJ, Holland PWH, Smith DAS (2007) The butterfly *Danaus chrysippus* (Lepidoptera: Nymphalidae) in Kenya is variably infected with respect to genotype and body size by a maternally transmitted male-killing endosymbiont (*Spiroplasma*). International Journal of Tropical Insect Science 27: 62–69. https://doi.org/10.1017/S1742758407818327

Holt White AE (1894) The butterflies and moths of Teneriffe. Reeve & Co., London, xii + 108 pp. [4 pls]

Hundsdoerfer AK, Lee KM, Kitching IJ, Mutanen M (2019) Genome-wide SNP data reveal an overestimation of species diversity in a group of hawkmoths. Genome Biology and Evolution 11(8): 2136–2150. https://doi.org/10.1093/gbe/evz113

Hulstaert RPG (1931) Lepidoptera Rhopalocera: Fam. Danaididae: Subfam. Danaidinae & Tellervinae. Genera Insectorum, Bruxelles 193: 1–215. [6 pls]

ICZN (1999) International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature, London, xxix + 306 pp.

Idris E (2013) Aposematic polymorphism in the tropical butterfly *Danaus chrysippus*: A review. Egyptian Academy Journal of Biological Science 6(1): 67–78. https://doi.org/10.21608/eajbsa.2013.13820

Idris E, Hassan SSM (2012) The queen butterfly, *Danaus chrysippus* (L.) (Lepidoptera: Nymphalidae) at Khartoum, Sudan. Egyptian Academy Journal of Biological Science 5: 95–102. https://doi.org/10.21608/eajbsa.2012.14812

Jiggins FM, Hurst GDD, Jiggins CD, Schulenburg JHG vd, Majerus MEN (2000) The butterfly *Danaus chrysippus* is infected with a male-killing Spiroplasma bacterium. Parasitology 120(5): 439–446. https://doi.org/10.1017/S0031182099005867

John E, Vane-Wright RI (2019) *Danaus chrysippus chrysippus* (Linnaeus, 1758) ff. 'alcippus' and 'alcippoides' (Lepidoptera: Nymphalidae, Danainae) from Cyprus. Entomologist's Gazette 70(3): 135–146. https://doi.org/10.31184/G00138894.703.1723

Kawazoé A, Wakabayashi M (1979) Coloured Illustrations of the Butterflies of Japan (revised edn). Hoikusha Publishing, Osaka, viii + 423 pp. [72 pls]

Kielland J (1990) Butterflies of Tanzania. Hill House, Melbourne, 363 pp.

Kirby WF (1871) A Synonymic Catalogue of Diurnal Lepidoptera. John Van Voorst, London, vii + 883 pp. https://doi.org/10.5962/bhl.title.11905

Klug F (1845) Symbolae Physicae seu Icones et Descriptiones Insectorum quae ex Itinere per Africam borealem et Asiam occidentalem Friderici Guilelmi Hemprich et Christiani Godofredi Ehrenberg. Decas Quinta [41 unnumbered pp., pls. 41–50.]. Officina Academica, Berlin.

Larsen TB (1990) The Butterflies of Egypt. Apollo Books, Svendborg, Dk, 112 pp. [8 pls]

Larsen TB (1991) The Butterflies of Kenya and their natural history. Oxford University Press, New York, xxii + 490 pp. [64 pls]

Longstaff GB (1912) Butterfly-hunting in many lands. Longmans, Green, and Co., London, xx + 729 pp. [frontispiece + 6 + 9 pls]

Lorković Z (1958) Die Merkmale der unvollständigen Speziationsstufe und die Frage der Einführung der Semispezies in die Systematik. Uppsala Universitets Årsskrift 1958(6): 159–168.

Lushai G, Smith DAS, Gordon IJ, Goulson D, Allen JA, Maclean N (2003a) Incomplete sexual isolation in sympatry between subspecies of the butterfly *Danaus chrysippus* (L.) and the creation of a hybrid zone. Heredity 90: 236–246. https://doi.org/10.1038/sj.hdy.6800219

Lushai G, Smith DAS, Goulson D, Allen JA, Maclean N (2003b) Mitochondrial DNA clocks and the phylogeny of *Danaus* butterflies. Insect Science and its Application 23: 309–315. https://doi.org/10.1017/S1742758400012376

Lushai G, Zalucki MP, Smith DAS, Goulson D, Daniels G (2005) The lesser wanderer butterfly, *Danaus petilia* (Stoll 1790) stat. rev. (Lepidoptera: Danainae), reinstated as a species. Australian Journal of Entomology 44: 6–14. https://doi.org/10.1111/j.1440-6055.2005.00423.x

Manders N (1912) The study of mimicry (Batesian and Müllerian) by temperature experiments on two tropical butterflies. Transactions of the Entomological Society of London 1912: 445–469. [1 pl.] https://doi.org/10.1111/j.1365-2311.1912.tb03103.x

Marshall GFL, de Nicéville L (1882–1883) The Butterflies of India, Burmah and Ceylon. Vol. 1. Nymphalidae. Danainae, Satyrinae, Elymniinae, Morphinae, Acraeinae. Central Press, Calcutta, frontispiece, [v] + vii + 327 pp, 17 pls.

Martin SH, Singh KS, Gordon IJ, Omufwoko KS, Collins S, Warren IA, Mumby H, Brattström O, Traut W, Martins DJ, Smith DAS, Jiggins CD, Bass C, ffrench-Constant RH (2019) Whole-chromosome hitchhiking driven by a male-killing endosymbiont. bioRxiv preprint. https://doi.org/10.1101/703421

Masters JH (1972) A proposal for the uniform treatment of infrasubspecific variation by lepidopterists. Journal of the Lepidopterists' Society 26(4): 249–260.

Mayr E (1963) Animal species and evolution. Harvard UP, Cambridge, Mass, xv + 797 pp. https://doi.org/10.4159/harvard.9780674865327

Moore F (1883) A monograph of Limnainae and Euploeina, two groups of diurnal Lepidoptera belonging to the subfamily Euploeinae, with descriptions of new genera and species. Proceedings of the Zoological Society of London 1883: 201–324, 4 pls. https://doi.org/10.1111/j.1469-7998.1883.tb06651.x

Morishita K (1981) Danaidae. In: Tsukada E (Ed.) Butterflies of the South-East Asian Islands, 2, Pieridae, Danaidae. Plapac, Tokyo, 439–628.

Olivier A, Nekrutenko YP (2000) The butterflies described by Johann Christoph Friedrich Klug (1775–1856) in his Symbolae Physicae, Insecta (Lepidoptera, Pieridae, Lycaenidae, Nymphalidae): an annotated review, with a catalogue of the existing types. Deutsche Entomologische Zeitschrift 47(1): 95–104. https://doi.org/10.1002/mmnd.4800470109

Opinion 163 (1945) Suspension of the rules for *Euploea* Fabricius, 1807 (Class Insecta, Order Lepidoptera). Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature 2(33): 335–346.

Ormiston W (1918) Notes on Ceylon butterflies. Spolia Zeylanica, Colombo 11: 1–69.

Ormiston W (1924) The Butterflies of Ceylon. H.W. Cave, Colombo, xi + 143 + [20] pp. [8 pls]

Owen DF (1971) Tropical Butterflies. Oxford University Press, Oxford, xiv + 214 pp. [40 pls]

Pagenstecher A (1902) Wissenschaftliche Resultate der Reise des Freiherrn Carlo von Erlanger durch Süd-Schoa, die Galla und Somalilander in 1900 und 1901. Tagfalter. Jahrbuch des Nassauischen Vereins für Naturkunde 55:113–204. [1 pl.]

Peters WCH (1862) Naturwissenschaftliche Reise nach Mossambique. Zoologie 5. Insecten und Myriopoden. Georg Reimer, Berlin.

Petschenka G, Fandrich S, Wagschal V, Boppré M, Dobler S (2013) Stepwise evolution of resistance to toxic cardenolides via genetic substitutions in the Na+/K+-ATPase of milkweed butterflies (Lepidoptera: Danaini). Evolution 67(9): 2753–2761. https://doi.org/10.1111/evo.12152

Pierre J (1974) Polymorphisme et coupes infraspécifiques africaines dans l'espéce *Danaus chrysippus* L. (Lepidoptera: Danaidae). Bulletin of the Museum d'Histoire Naturelle, Paris 149: 601–638. [1 pl.]

Poulton EB (1924) *Danaida chrysippus* L. and *D. dorippus* Klug, proved by breeding to be forms of the same species. Proceedings of the Entomological Society of London 1924: cxix–cxxiii.

Rothschild M, Von Euw J, Reichstein T, Smith DAS, Pierre J (1975) Cardenolide storage in *Danaus chrysippus* (L.) with additional notes on *D. plexippus* (L.). Proceedings of the Royal Society of London (B) 190: 1–31. https://doi.org/10.1098/rspb.1975.0076

Scoble M (2004) Unitary or unified taxonomy? Philosophical Transactions of the Royal Society of London B 359: 699–710. https://doi.org/10.1098/rstb.2003.1456

Ségurel L, Thompson E, Flutre T, Lovstad J, Venkat A, Margulis SW, Moyse J, Ross S, Gamble K, Sella G, Ober C, Przeworski M (2012) The ABO blood group is a trans-species polymorphism in primates. PNAS 109(45): 18493–18498. https://doi.org/10.1073/pnas.1210603109

Sharpe EM (1896) List of Lepidoptera collected in Somali-land by Mrs. E. Lort-Phillips. Proceedings of the Zoological Society of London 1896: 523–529. https://doi.org/10.1111/j.1096-3642.1896.tb03058.x

Short LL (1969) Taxonomic aspects of avian hybridization. The Auk 86: 84–105. https://doi.org/10.2307/4083543

Shirôzu T (1960) Butterflies of Formosa in colour. Hoikusha Publishing, Osaka, viii + 481 pp.

Singh VK, Joshi PC, Joshi BD (2018) Molecular data suggest population expansion and high level of gene flow in the Plain Tiger (*Danaus chrysippus*; Nymphalidae: Danainae). Mitochondrial DNA(B) 3: 2, 707–712. https://doi.org/10.1080/23802359.2018.1483751

Smith DAS (2014) African queens and their kin – a Darwinian odyssey. Brambleby Books, Taunton, UK, xxxiii + 810 pp. [77 pls]

Smith DAS, Shoesmith E, Smith A (1988) Pupal polymorphism in the butterfly *Danaus chrysippus* L.: environmental, seasonal and genetic influences. Biological Journal of the Linnaean Society 33: 17–50. https://doi.org/10.1111/j.1095-8312.1988.tb00444.x

Smith DAS, Owen DF, Gordon IJ, Lowis NK (1997) The butterfly *Danaus chrysippus* (L.) in East Africa: polymorphism and morph-ratio clines within a complex, extensive and dynamic hybrid zone. Zoological Journal of the Linnean Society 120(1): 51–78. https://doi.org/10.1111/j.1096-3642.1997.tb01272.x

Smith DAS, Gordon IJ, Depew LA, Owen DF (1998) Genetics of the butterfly *Danaus chrysippus* (L.) in a broad hybrid zone, with special reference to sex ratio, polymorphism and intragenomic conflict. Biological Journal of the Linnean Society 65(1), 1–40. https://doi.org/10.1111/j.1095-8312.1998.tb00349.x

Smith DAS, Gordon IJ, Lushai G, Goulson D, Allen JA, Maclean N (2002) Hybrid queen butterflies from the cross Danaus chrysippus (L.) × D. gilippus (Cramer): confirmation of species status for the parents and further support for Haldane's Rule. Biological Journal of the Linnean Society 76: 535–544. https://doi.org/10.1046/j.1095-8312.2002.00073.x

Smith DAS, Lushai G, Allen JA (2005) A classification of Danaus butterflies (Lepidoptera: Nymphalidae) based upon data from morphology and DNA. Zoological Journal of the Linnean Society 144: 191–212. https://doi.org/10.1111/j.1096-3642.2005.00169.x

Smith DAS, Gordon IJ, Allen JA (2010) Reinforcement in hybrids among once isolated semispecies of Danaus chrysippus (L.) and evidence for sex chromosome evolution. Ecological Entomology 35: 77–89. https://doi.org/10.1111/j.1365-2311.2009.01143.x

Smith DAS, Gordon IJ, Traut W, Herren J, Collins S, Martins DJ, Saitoti K, Ireri P, ffrench-Constant R (2016) A neo-W chromosome in a tropical butterfly links colour pattern, male-killing, and speciation. Proceedings of the Royal Society (B) 283: 20160821 (9 pp.). https://doi.org/10.1098/rspb.2016.0821

Smith DAS, Traut W, Martin SH, Ireri P, Omufwoko KS, ffrench-Constant R, Gordon IJ (2019) Neo sex chromosomes, colour polymorphism and male-killing in the African Queen butterfly, *Danaus chrysippus* (L.). Insects 10: 291. https://doi.org/10.3390/insects10090291

Suffert E (1900) Eine neue Aberration des *Danaus dorippus* Klug, aus Deutsch-Ostafrica. Berliner Entomologische Zeitschrift 45: 115–116. https://doi.org/10.1002/mmnd.47919000109

Swinhoe C (1885) On the Lepidoptera of Bombay and the Deccan. Proceedings of the Zoological Society of London 1885: 124–148. [1 pl.] https://doi.org/10.1111/j.1096-3642.1885.tb02888.x

Talbot G (1943) Revisional notes on the genus *Danaus* Kluk (Lep. Rhop. Danaidae). Transactions of the Royal Entomological Society 93(1): 115–148. https://doi.org/10.1111/j.1365-2311.1943.tb00432.x

Traut W, Ahola V, Smith DAS, Gordon IJ, ffrench-Constant RH (2017) Karyotypes versus genomes: the nymphalid butterflies *Melitaea cinxia*, *Danaus plexippus*, and *D. chrysippus*. Cytogenetic and Genome Research 153: 46–53. https://doi.org/10.1159/000484032

Trimen R (1887) South-african butterflies. Vol. 1. Nymphalidae. Trübner, London, xv + 355 pp. [6 pls]

van der Poorten GM, van der Poorten NE (2016) The Butterfly Fauna of Sri Lanka. Lepodon Books, Toronto, vi + 418 pp.

Vane-Wright RI (1975) An integrated classification for polymorphism and sexual dimorphism in butterflies. Journal of Zoology (London) 177: 329–337. https://doi.org/10.1111/j.1469-7998.1975.tb02236.x

Vane-Wright RI, John E (2019) A note on *Papilio aegyptius* Schreber, 1759, and its synonymy with *Danaus chrysippus chrysippus* (Linnaeus, 1758) (Lepidoptera: Nymphalidae, Danainae). Entomologist's Gazette 70(3): 147–154. https://doi.org/10.31184/G00138894.703.1729

Vinarski MV (2015a) The fate of subspecies category in zoological systematics. 1. The history. Biology Bulletin Reviews 5(5): 395–404. https://doi.org/10.1134/S2079086415050060

Vinarski MV (2015b) The fate of subspecies category in zoological systematics. 2. The present. Biology Bulletin Reviews 5(5): 405–414. https://doi.org/10.1134/S2079086415050072

Williams MC (2018) Genus *Danaus* Kluk, [1780]. Afrotropical butterflies 17th ed., 14 pp. http://www.metamorphosis.org.za/articlesPDF/1073/116%20Genus%20Danaus%20Kluk.pdf [accessed 19th June 2019]

Wilson EO, Brown WL (1953) The subspecies concept and its taxonomic application. Systematic Zoology 2: 97–111. https://doi.org/10.2307/2411818

Woodhouse LGO (1952) The butterfly fauna of Ceylon. Second complete edition. Colombo Apothecaries' Co., Colombo, xxxii + 231 pp.

Woodhouse LGO, Henry GMR (1942) The Butterfly Fauna of Ceylon. Ceylon Government Press, Colombo, xiv + 153 pp. [50 pls]

Zink RM (2006) Rigor and species concepts. The Auk 123(3): 887–891. https://doi.org/10.1093/auk/123.3.887