DID A MEMBER OF THE VANESSA INDICA COMPLEX (NYMPHALIDAE) FORMERLY OCCUR IN NORTH AMERICA?

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ABSTRACT. The North American Oligocene fossil Vanessa amerindica is thought to be most like V. indica. Based on an 18th century painting made by the English naturalist Henry Seymer Jr., the possible existence of a member of the indica complex that occurred in North America as late as circa 1770 is demonstrated. New information on the classification of the nine extant species currently included in Vanessa sensu stricto strongly suggests that this apparently undescribed species is most closely related to the Atlantic Islands endemic, V. vulcania. Three competing scenarios that attempt to explain the highly disjunct distribution of the species that make up the V. indica complex are discussed, and it is concluded that the genus Vanessa most probably originated in North America, and that V. vulcania represents a separate, Atlantic colonisation event, separate from the Pacific colonisation event that gave rise to the Asiatic V. indica-group. This implies that, contrary to earlier hypotheses that sought to explain the distributional gap between the Canaries and India, the indica complex may never have been established on the western Palaearctic mainland, or in the Eremic Zone (Morocco to Somalia and Tien Shan). An African species formerly placed in Antanartia is formally transferred to the genus Vanessa (Vanessa abyssinica, comb. nov.).

Additional key words: Tertiary, relict, introduction, biogeography, Newfoundland, Macaronesia, Henry Seymer.

According to Art Shapiro (1992a), “The most peculiar Palearctic butterfly distribution is that of the Indian Red Admiral, Vanessa indica (Herbst).” Although the taxonomy of this member of the Nymphalidae has since changed — V. indica (Herbst, 1794), in Shapiro’s sense, is now divided into three allopatric species — the enigma to which he referred remains: how can the 7000 km gap in distribution between the Indian red admirals found on Madeira and the Canary Islands, and those occupying the rest of the range, in the Oriental region and far eastern Palaearctic, be explained? No extant member of the species complex to which these butterflies belong is known from the rest of the western Palaearctic, North Africa, or North America.

Fresh interest in this problem has come from the recent discovery of an 18th century painting of a member of the Vanessa indica complex, supposedly based on a specimen collected in Newfoundland circa 1770. This illustration is one of some 300 surviving images of exotic butterflies and moths made by the little-known British naturalist Henry Seymour (1714–1785), together with his son, Henry Seymour Jr. The Seymers obtained their natural history specimens, notably of molluscs and insects, through dealers, travellers, military personnel and other contacts. Based on an extensive analysis of all the known Seymour Lepidoptera paintings, and their notes and records, it has been demonstrated that the vast bulk of their exotic material came from China, Java, India, West Africa, South Africa, South America, Jamaica, and the early British colonies in North America (Vane-Wright & Hughes, 2005: table 1, p. 254). Their Lepidoptera collection apparently totalled some 20,000 specimens, but it was dispersed immediately after Henry Sr.’s death, and nothing is yet known to have survived (Vane-Wright & Hughes, 2005; Barker & Vane-Wright, 2007).

The Seymour paintings, made during the period 1755–1783, appear to have been intended as a virtual record of the collection. If so, it is fortunate they had such foresight. The level of accuracy achieved ranges from good to outstanding. Minute detail is often finely rendered, and the coloring remains authentic in all but a few instances (Vane-Wright & Hughes, 2005). The lack of degradation of tint that might be expected in such old watercolors is no doubt a consequence of the fact that, through the intervening years, the pictures were rarely on show, and were evidently preserved in library conditions.

The idea that a member of the V. indica complex recently occurred in North America is so surprising that, without a specimen and independent verification, considerable doubt must be accepted—although we
believe the case for authenticity (presented below) is good. However, whatever the final conclusion regarding the painting, it has stimulated us to review the “Vanessa indica” problem and, in turn, challenge two previous hypotheses regarding the biogeography of these butterflies, and support instead an alternative hypothesis in which North America plays a key role.

Phylogenetic Relationships of the Red Admiral Butterflies

The type species of Vanessa Fabricius, 1807, *Papilio atalanta* Linnaeus, 1758, is the familiar Red Admiral butterfly. In his major revision, Field (1971) placed five species of red admirals in the genus: *V. atalanta* (L., 1758), *V. tameanea* Eschscholtz, 1821, *V. indica* (Herbst, 1794), *V. dejeanii* Godart, 1824, and *V. samani* (Hagen, 1895), but more species are now recognized (see below). The two other main species groups usually included within the genus are the painted ladies (placed by Field in the genus *Cynthia*; type species *Papilio cardui* and the antipodal admirals (placed by Field in *Bassaris*; type species *Papilio thea*).

DNA sequence data (Wahlberg et al., 2005) suggest that within *Vanessa* and contrary to earlier phylogenetic work based solely on morphology (e.g. Craw, 1989, Holloway & Nielsen, 1999), the red admirals (*Vanessa sensu stricto*) have a sister-group relationship with *Vanessa abyssinica* (Field & Felder, 1867), a montane butterfly from East Africa. Previously *V. abyssinica* was treated as a member of the endemic Afrotropical genus *Antanartia* Rothschild & Jordan, 1903 (e.g. Howarth, 1966; Ackery et al., 1995).

Superficial comparison indicates that this new arrangement is credible: all five remaining *Antanartia*, including the type species, *Papilio delius* Drury, 1782, have distinct hindwing tails at vein M3, whereas *V. abyssinica* does not, looking instead rather like a small and drab red admiral (Fig. 1a). The work of Nakanishi (1989) on the early stages of *abyssinica* is consistent with this placement, as it has a peculiar setal arrangement in the first larval instar otherwise known only from *Vanessa*, and it shares the habit, in later instars, of making a nest by tying both edges of a leaf together with silk. Nakanishi recorded that neither *Antanartia schaenia* nor A. *hippomene* exhibit these *Vanessa* characters.

However, as also pointed out to us by Thomas Dimock, adult *abyssinica* are highly distinctive compared with all other *Vanessa s.s.* Notably, at least two of the hindwing ocelli always have blue pupils (invariably black in other *Vanessa s.s.*); the hindwing marginal band widens at cell M1, lacks any black submarginal spots (as seen in an aberration of *V. atalanta*; Frohawk, 1938: p. 86), and continues anteriorly into cell R1 (unlike other *Vanessa s.s.*); and hindwing vein Sc+R1 is relatively elongate, giving the wing a unique, almost square aspect. All of these differences can be seen as autapomorphies, except the first, which may be a synapomorphy (e.g. this condition is frequent in subgenus *Cynthia*, in *V. (C.) cardui* for example, being referred to as form *V. indica indica*. Left halves show upperside, right halves corresponding underside.

All figures (with exception of b) have been brought to the same forewing length to facilitate comparison; information on actual size is included with each separate legend. With the exception of b and h, all images are based on specimens in the Natural History Museum, London (BMNH); fw-l. = forewing length. a, V. (Vanessa) abyssinica abyssinica (Fielder & Felder, 1867), male [Ethiopia: Mt Zuquála, over 9000 ft., 25–27x.1926, H. Scott; BM1927-127, fw-l. 21 mm] [Howarth, 1966: 31, indicates a range of 17–22 mm for male *V. abyssinica*, and 20–24 mm for female]; b, V. (Vanessa) sp. nov. (V. caledonia-group), female? [Newfoundland, ca 1770; from ‘profile’ image made by Henry Sneyer Jr, ca 1773; Vane-Wright & Hughes, 2005; fw-l. estimated at 35 mm — see text]; c, V. (Vanessa) caledonia Godart, 1819, female [Spain: Canary [Islands], iv.1885. Lecceh Collection, BM1901-173;fw-l. 34 mm] [Field, 1971: 24, gives male 26–32 mm, female 29–33 mm, but there are large and smaller examples in the BMNH collection — see text]; d, V. (Vanessa) indica indica (Herbst, 1794), male [China: Siao-Lou, 1900; Oberthür Collection, BM1927-3;fw-l. 33 mm] [Field, 1971: 21, gives male 25–34 mm, female 27–37 mm]; e, V. (Vanessa) indica phoebe (Fruhstorfer, 1912), male [SW India: Anamully Hills, 3000–4000 ft., Davson; Godman-Salvin Collection, BM1903-4;fw-l. 30 mm] [Field, 1971: 22, gives male 27–29 mm, female 29–30 mm]; f, V. (Vanessa) indica ubicola (Fruhstorfer, 1898), male [Sri Lanka: Nawara Eliya, vi.1921, W. Oronsoton; BM1922-315;fw-l. 27 mm] [Field, 1971: 22, gives male 26–31 mm, female 30–33 mm]; g, V. (Vanessa) ianua Fruhstorfer, 1898, male [Indonesia: S Sulawesi, Bonthain, 5–7000 ft., x.1895, A. Ecerett; Rothschild Bequest, BM1939-1;fw-l. 24 mm] [Field, 1971: 23, gives male 27.5 mm; assuming figures in Tsukada, 1985: 82, are life-size, females are ca 25–27 mm]; h, V. (Vanessa) dilecta Hanafusa, 1902, male [Indonesia: W Timor, Mt Mutis, 1992; Hanafusa Collection] [Hanafusa, 1992, gives male fw-l. 27.5–30.5 mm, female 30–31 mm]; i, V. (Vanessa) samami (Hagen, 1895), male [Indonesia: SW Sumatra, Danan Bento Morass, Ft. of Kortinji Peak, 5000 ft., xii.1921, C.F. & J. Pratt;7.22; Joicey Bequest, BM1034-120;fw-l. 23 mm] [Field, 1971: 27, gives male 25 mm, female 23 mm]; j, V. (Vanessa) dejeanii dejeanii Godart, 1824, male [Indonesia: E Java, H. Fruhstorfer; Fruhstorfer Collection, BM1937-285;fw-l. 24 mm] [Field, 1971: 26, gives male 23–26 mm, female 23–27 mm]; k, V. (Vanessa) dejeanii samabuna (Fruhstorfer, 1898), male [Indonesia: Lombok, Sambuhan, 4000 ft., 1896, H. Fruhstorfer; Oberthür Collection, BM1927-3;fw-l. 25 mm] [Field, 1971: 26, gives same size as d. dejeanii, including samabuna as a subjective synonym]; l, V. (Vanessa) dejeanii numosegi (Talbot, 1903), male [Philippines: Mindanao]; W. Dannatt Collection, BM1940-130;fw-l. 24 mm] [Field, 1971: 27, gives a value of 26 mm for a male]; m, V. (Vanessa) atalanta atalanta (Linnaeus, 1758), male [Germany: Berlin; Lecceh Collection, BM1901-173;fw-l. 30 mm] [Field, 1971: 14, gives male 27–31.5 mm, female 27–34 mm]; n, V. (Vanessa) atalanta rubrice (Fruhstorfer, 1909), male [Canada: Newfoundland, W. St. John, 39.9.25. 65 655m;fw-l. 29 mm] [Field, 1971: 16, gives male 25–34 mm, female 25–35 mm]; o, V. (Vanessa) tameanea Eschscholtz, 1821, female [USA: Hawaii, Kauai, Mt Wainee, 3000 ft., vii.1894, Perkins; BM1899-227;fw-l. 34 mm] [Field, 1971: 18/19; gives male 31–37, female 32–40 mm].
V. abyssinica (Fielder & Fielder, 1867) is the smallest species in the group, comprising three races restricted to mountainous regions of East Africa (Ackery et al., 1995). As foreshadowed by Nakashima (1989) and demonstrated by Wahlberg et al. (2005: 238), abyssinica belongs to Vanessa sensu stricto, but this has not been signalled as a formal recombination, now done here for the sake of clarity (Appendix I).

V. atalanta (Linnaeus, 1758) is widespread throughout North America south to Guatemala, Cuba, Hispaniola, the Atlantic Islands, North Africa, and Europe through Pakistan, Kashmir and north of the Himalayas to the Amur River (Field, 1971). The American and Old World populations are divisible as separate subspecies, but are very similar.

V. tameamea Eschscholtz, 1821, the largest species of the group, is endemic to the Hawaiian Islands (Field, 1971).

V. indica (Herbst, 1794), the third species of the red admiral group as dealt with by Field (1971), and accepted by Shapiro (1992a), has since been subdivided. As currently recognized, the very widely distributed nominotypical race is found in central and eastern Asia (Leestmans, 1978: fig.1), occurring from northern India through Nepal and Bhutan to China, Korea, Japan, Siberia (migrants reaching the region of Lake Baikal) and far eastern Russia (migrants reaching Kamchatka: Korshunov & Gorbunov, 1995), and south to Myanmar, Thailand, Laos, Vietnam, Taiwan and northern Philippines (Luzon, Mindoro and Palawan: Treadaway, 1995: 27). The two populations named as V. i. pholoe (southern India) and V. i. nubicola (Sri Lanka) are virtually indistinguishable on the basis of their male genitalia (Leestmans, 1978) and, given their minor differences in wing pattern, this provides justification for continuing to regard these three taxa as no more than subspecies. Tsukada (1985: 303) treated the populations from southern India and Sri Lanka as the same, under the senior name V. indica nubicola.

V. samani (Hagen, 1895) is restricted to western Sumatra, in western Indonesia (Field, 1971).

V. dejeanii Godart, 1824 occurs as three races, one on Java, a second (very doubtfully distinct) on Bali, Lombok and Sumbawa in central Indonesia, and the third on Mindanao and Samar in the southern Philippines (Field, 1971; Treadaway, 1995). Conceivably this last taxon, V. dejeanii mounseyi, will prove to be a separate species.

V. buana (Fruhstorfer, 1898) is restricted to the mountains of extreme southern Sulawesi, Indonesia (Vane-Wright & de Jong, 2003). Treated by Field (1971) as one of the subspecies of V. indica, the male genitalia of buana are very distinct from those of indica s.s., sufficient to justify species-level status (Leestmans, 1978).

V. dilecta Hanafusa, 1992, was described as a separate species from Mt Mutis (2427 m), the highest mountain in Indonesian West Timor. The molecular results of Otaki et al. (2006a) suggest that this taxon is very closely related to V. buana, and they conclude that dilecta should either be treated as a subspecies of V. buana, or that the whole indica group be regarded as a superspecies. With respect to the former, the occurrence of a species on southern Sulawesi and Timor only would be a unique biogeographical pattern among the butterflies (Vane-Wright & de Jong, 2003). Our examination of the male genitalia of a specimen of V. dilecta (made available to us by Dr Otaki) confirms that it is almost identical to that of V. buana, as illustrated by Leestmans (1978: pl. 5, fig. 4). However, it also demonstrates that, as observed by Leestmans (1978) and noted by Otaki et al. (2006a: 365), the male genitalia of V. nubicola, V. dejeanii, V. buana and V. dilecta are all very similar, and both morphology and molecules indicate that this group forms a terminal group within
the V. indica complex. This clade has a distribution pattern “(2+5+6)”, which is also virtually unique: only the doubtful collective danainae taxon Tirumala ishmoioides has a comparable range (Vane-Wright & de Jong, 2003: 219), and even this does not include Timor or Sumatra. Our knowledge of these relatively rare montane Vanessa taxa may still be incomplete. We suggest that, for the present at least, V. dilecta should continue to be regarded as a separate species.

V. vulcania Godart, 1819, is native to the Canary Islands and Madeira in the Atlantic Ocean. Treated by Field (1971) as a subspecies of V. indica, in his major papers addressing the question its origin, Shapiro (1990, 1992a; but see also 1992b) overlooked the important work of Leestmans (1978) demonstrating the clear separation between V. vulcania and V. indica. Despite comments to the contrary by Shapiro (1992a), V. vulcania is also found occasionally on the western European mainland (e.g. Opheim, 1960; Gerisch 1975, 1978; Reinhardt & Gerisch, 1982; Fernández-Vidal, 1989). However, there seems nothing to suggest that these mainland records represent anything other than occasional strays or individuals accidentally imported from the Atlantic Islands (Leestmans, 1978).

A Re-assessment of Taxonomic Affinities within Vanessa sensu stricto

Field (1971), Leestmans (1978) and Wahlberg et al. (2005; and pers. comm.) all agree that the red admirals (Vanessa s.s.) form a monophyletic group. However, in their independent molecular analysis, Otaki et al. (2006a) did not get consistent support for such a clade. Based on morphological evidence (Leestmans, 1978), V. atalanta + V. tameamea could form a sister species pair, and this has been corroborated by some molecular data (Niklas Wahlberg and Dan Rubinoff, pers. comm.) although, again, Otaki et al. (2006a,b) report only weak support for this pairing.

According to Field (1971: 20), the five subspecies of V. indica that he recognized “display no differences in the male genitalia.” However, Leestmans (1978) pointed to genital characters that link V. buana with the other taxa found in the Malay Archipelago: V. nubicola (Sumatra) and V. dejeanii (Java to Sumbawa and Mindanao) — to which assemblage the recently described V. dilecta (Timor) certainly belongs (Otaki et al., 2006a,b; morphological evidence reported above).

As again clearly demonstrated by Leestmans (1978), although V. vulcania is similar to V. indica, it can be separated reliably on a number of small features of the male genitalia, as well as aspects of coloration. On this basis, together with its persistently red rather than more fugitive red-orange color, Leestmans (1978) justified recognition of V. vulcania as another, separate species.

Niklas Wahlberg (pers. comm.) has as yet unpublished molecular data regarding interrelationships of five of the six members of the indica complex: V. vulcania, V. indica, V. nubicola, V. buana and V. dejeanii (to which V. dilecta must be added). The new work confirms this complex as the sister group of the atalanta-group. Furthermore, within the complex, V. vulcania appears as sister to all the Asiatic taxa. Throughout this paper we refer to (vulcania-group + indica-group) as the V. indica complex. Within the indica-group, Otaki et al. (2006a,b) found evidence that diletta is sister to buana, these two together are sister to dejeanii, these three are sister to samani, and that these four altogether form a distinctive group sister to V. indica.

Thus the relationships of the species of Vanessa s.s., based on the information outlined above, can best be summarized by the following indented table, although evidence for monophyly of the group as a whole, and the V. atalanta + V. tameamea pairing, may not be very robust:

<table>
<thead>
<tr>
<th>Abyssinica-group [Africa]</th>
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<tbody>
<tr>
<td>Atalanta-group (atalanta + tameamea) [northern hemisphere]</td>
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<tr>
<td>Vulcania-group (vulcania) [Atlantic Islands]</td>
</tr>
<tr>
<td>Indica-group (indica + (samanii + dejeanii + (buana + diletta)))</td>
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<tr>
<td>[Nepal east to Japan and south to Timor]</td>
</tr>
</tbody>
</table>

Possible Origins of the V. indica Complex in Macaronesia

As indicated, there is no record for any indica-like taxon in the vast area between northern India and the Canary Islands, except occasional strays in western Europe (V. vulcania in the Iberian Peninsula, Germany and elsewhere; remarkably, V. indica indica has also been recorded from central England; Bretherton, 1989). Field (1971: 24) suggested that what he treated as the disjunct Atlantic Ocean race, V. indica vulcania, “may have evolved from specimens accidentally introduced from India by early Portuguese traders” — but on the basis of his morphological findings, Leestmans (1978) dismissed this idea as implausible. As suggested to us by Thomas Dimock, this is also very unlikely in terms of Vanessa biology and its ability to remain alive on board ship for several months. Shapiro (1992a), at that point unaware of Leestmans’ work, drew attention to an earlier, alternative explanation. Kostrowicki (1969: 282) had suggested that the various
disjunct populations, notably those on the Atlantic Islands, could be relics of a former, much wider Tertiary range. Shapiro (1992a) commented that molecular genetics could surely distinguish between two such extreme hypotheses, one requiring these Macaronesian populations of V. indica to be only hundreds of years old and to have gone through an initial ‘bottleneck’, the other implying that V. vulcania must be hundreds of thousands or even millions of years old. We call the first of these ideas “Field’s Introduction Hypothesis” (FIH), and the second “Kostrowicki’s Tertiary Relict Hypothesis (KTRH).

While KTRH appeals as a more interesting explanation, the absence of the indica complex anywhere in northern Europe, North Africa and North America seems surprising. However, as pointed out to us by Thomas Dimock, it would not be necessary to have continuous suitable habitat from India across the whole of Iran and Africa to Macaronesia. Indeed, large areas of unsuitable land between marginal habitats in the Mediterranean region might have made it more likely that migratory butterflies would reach distant localities, such as the Canary Islands, as they would be obliged to continue their search.

Shapiro (1992a) noted that in Macaronesia the butterfly is tied to laurisilva forest, considered to be a relict of former Tertiary broadleaved forests (Kostrowicki, 1969: 285; “nemoral forests”: Pielou, 1979: 204–210; Miller & Miller, 1990). However, in the far east the V. indica-group does not seem to be confined to such habitats, ranging widely from montane areas in the tropics to a variety of cool temperate zones in the north, in the summer migrating as far as southern Siberia and Kamchatka (Korshunov & Gorbunov, 1995). If the Macaronesian populations of V. vulcania are genuine relics (which must, at least, have island-hopped: Shapiro, 1992b), given the rich and varied forest habitats of North America in particular, it seems curious that no member of the V. indica complex has ever been found there.

If V. vulcania is a Relict, from Where has the V. indica Complex Disappeared?

As already indicated, V. indica sensu Field (1971) has largely been dismembered. The remaining populations now assigned to V. indica are divisible into just two or at most three subspecies: V. indica indica in the main Russian-Indo-Chinese range, including Japan, V. i. pholoe (Fruhstorfer, 1912) in southern India, and the very similar V. i. nubicola (Fruhstorfer, 1898) in Sri Lanka. As noted above, V. vulcania and V. buana were separated by Leestmans (1978) as distinct species. These taxonomic changes were made on the basis of small differences in wing patterns and male genitalia. If correct, they offer support for KTRH rather than FIH, insofar as we generally think of species evolving over many thousands if not millions of years, rather than a few hundred generations as implied by FIH. For example, based on extensive allozyme data, Shapiro & Geiger (1989) calculated that the very similar-looking Vanessa annabella (North America south to Guatemala) and V. carye (Hübner, 1812; South America) diverged about 3 million years ago.

While according to FIH the 7000 km gap from the Atlantic islands to NE India requires no other explanation, KTRH raises the question from where else have populations of the Vanessa indica complex disappeared? Given the known distribution of V. indica sensu lato, there is little reason to suppose that the indica complex ever occurred in South America. On the other hand, it might seem self-evident that it must have been lost from the whole region extending from the Mediterranean to northern India, including the Alps, Balkans, Turkey, Iraq, Iran and Afghanistan (notwithstanding Dimock’s suggestion above regarding migration between marginal habitat patches). However, many biotopes in these areas appear suitable for the butterflies. If so, why would they have died out in this region?

Leestmans (1978) made the interesting suggestion that during glacial maxima the V. indica complex could have been represented throughout what is now the so-called eremic zone, the vast region of deserts and semi-deserts that runs across almost the whole of North Africa east to Somalia and the Arabian Peninsula, and from there to the Iran Plateau, Thar Desert and Tien Shan (Leestmans, 1978: fig. 1). From southern Morocco it would have been easy for a red admiral to reach both the Canaries and Madeira. With a return to interglacial conditions, the indica complex populations would have died out across this huge tract as it became desertified. In contrast, the laurisilva forests survived on the well-watered Atlantic islands, until largely destroyed by human activity in the past few hundred years.

A possible objection to such a scheme is that, as the ice retreated northwards, what would prevent the butterflies entering the Mediterranean region? Kostrowicki (1969: 280) discussed the idea that North African mountains played an important role as refugia for butterflies, noting in particular that a number of “typical African subspecies penetrated the Iberian Peninsula.” Retreating higher and higher into the mountains, perhaps the Vanessa populations became trapped and died out in situ, unable to escape northwards. However, if we set this doubt aside, under
Leestman’s scenario we might expect that *V. vulcania* and *V. indica* would prove to be sister taxa. Leestmans further suggested that the time since *V. vulcania* became separated from the main range of what is now *V. indica* would be about 1 million years. This variant of KTRH we can call “Leestmans’ Eremitic Zone Hypothesis” (LEZH). A similar scenario is also entertained by Pittaway (1993: 35–36) in an effort to understand the distribution of western Palaearctic hawkmoths, and he notes inter alia that “by the end of the Tertiary … most eastern Asiatic species [of plants] had vanished from Europe (c. 1 million years BP).”

There is, however, a major alternative possibility: a North American origin (Vane-Wright, in Shapiro, 1990: 222) and subsequent loss (“American Origin Hypothesis”: AOH). Given the likelihood that the genus *Vanessa* is fundamentally American (stem group position of *V. annabella*; sister group relationship with *Hypanartia*), and given that *V. atalanta* actually occurs as two subspecies, one in the New World and one in the Old, we should consider the idea that *ur-indica* originated in the Neartic. Could the *indica* complex, in the form of *V. vulcania*, have reached the Atlantic Islands from eastern North America, rather than North Africa, while the Asian *indica*-group species reached Asia from western North America via Beringia? *V. indica* actually occurs in Beringia during the summer months, reaching to more than 50°N in Kamchatka.

Under AOH, one might expect *V. vulcania* to be the (relatively ancient) sister group of a clade comprising all the eastern *indica*-group taxa, and this is supported by the most recent molecular findings, as summarized in the indented table above. As already noted, under LEZH we might expect *vulcania* and *indica indica* to be (more recent) sister taxa. Under FH, if Portuguese traders were responsible, perhaps a Goanese population (*V. i. pholoe*) would be the most likely sister to *vulcania*, with a separation time of only a few hundred years. These alternatives are not supported by the current systematic arrangement (see table above).

While AOH would explain away the 7000 km gap between Macaronesia and India (under this scheme there is no compelling reason to suppose the *indica* complex ever occurred in this intervening region), it does so by substituting an even larger 10,000 km gap between Kanchatka and Madeira. Thus a choice between these two scenarios could be affected by any evidence of former presence of the *Vanessa indica* complex in either North America or the western Palaearctic/North Africa. Before turning to this issue, it is worth noting that there appears to be virtually no evidence of exclusive biogeographical connections between Macaronesia and the Indo-Australian region.

Increasing knowledge of the phylogenetic relationships of Macaronesian plants reveals that the great majority have their closest relatives in Europe and North Africa, although there do appear to be some links to East Africa, South Africa and, most notably in this context, the Americas (Carine et al., 2004).

A Fossil Member of the *Vanessa indica* Complex

There is one known fossil clearly relevant to this debate, the early Oligocene butterfly *Vanessa anerindica* Miller & Brown, 1989. This was described from the Florissant formation of Colorado (dated at ca 35 million years BP), and the authors considered it to be most like *Vanessa indica* amongst the recent fauna (Miller & Brown, 1989). Taken at face value this is consistent with AOH, and could be another example of marked stasis coupled with local extinction that may be emerging as characteristic of butterfly evolution during the middle to late Tertiary (e.g. Hall et al., 2004; Vane-Wright, 2004). Even so, this is not evidence enough to suggest that the modern distribution of *Vanessa* is somehow directly linked to the tectonic break up of the North Atlantic. This would only be plausible if the *V. indica* complex could be demonstrated to be at least 70 million years old (cf. Miller & Miller, 1990). Given the great rarity of butterfly fossils, the existence of *V. anerindica* dated at 35 mya is, however, both suggestive and challenging.

An 18th Century Record of an Apparently New Member of the *V. indica* Complex from North America

As indicated in the introduction, while researching a set of previously unpublished 18th century paintings of world Lepidoptera made by the British naturalists Henry Seymer (1714–1785) and Henry Seymour Jr, (1745–1800), we came across an image of what is undoubtedly a member of the *Vanessa indica* complex (Fig. 1b; Vane-Wright & Hughes, 2005: 165). The Seymers indicated that their painting was based on a specimen sent to them from Newfoundland, but gave no further details of date or collector. What credibility can be given to this seemingly very unlikely record?

Among hundreds of images of Lepidoptera made from the Americas, Europe, Africa, Asia and even Australia, the Seymers illustrated just three other species purportedly from Newfoundland (Fig. 1b). Neither can it be matched to *V. amerindica*,

Figs 1c–l).
as the fossil does not permit detailed evaluation based on wing patterns.

The other species the Seymers illustrated from Newfoundland were two swallowtails and a ghost moth: *Papilio brevicauda brevicauda* Saunders, 1869; *Papilio canadensis* Rothschild & Jordan, 1906; and *Sthenopis purpurascens* (Packard, 1863) (Vane-Wright & Hughes, 2005). *P. brevicauda* is quite narrowly restricted to parts of Quebec and the Maritime provinces of eastern Canada, where it is “widespread and commonly encountered in Newfoundland” (Layberry et al., 1998: 83). *P. canadensis* is well-known from almost all parts of Canada, including Newfoundland (Layberry et al., 1998: 87–88).

*S. purpurascens* (Hepialidae) is one of four species belonging to the exclusively North American genus *Sthenopis* Packard, 1865, known from USA and Canada (Nielsen et al., 2000: 850). Newfoundland records for *Sthenopis purpurascens* (Packard, 1863) are based on material housed in collections of the Canadian Forest Service (Corner Brook, NL; and Edmonton, Alberta), and Agriculture Canada Research Station (St. John’s, NL). The identifications of this material (under the synonymous name *Sthenopis quadriguttatus* (Grote, 1864)) were made by Canada Agriculture personnel in Ottawa (David Larson, pers. comm., September 2007; see also Bowers & Pardy, 1996). Currently, this is the only *Sthenopis* known from Newfoundland.

The dates for the four paintings on which these images appear are: *V. indica* complex ca 1773, *P. brevicauda* February 1776, *P. canadensis* 1772, and *S. purpurascens* ca 1773. The reason for uncertainty over the date for the *Vanessa* image is that the Seymer paintings were cropped at some point in the past to fit into a binding, and in some cases the dates have been cut off, in part or whole (Vane-Wright & Hughes, 2005: 53). In most cases other clues are available to give approximate dates, and we think that 1773 (not earlier than 1772, and unlikely to be later than 1776) is a good estimate for the date of the painting on which the *Vanessa* appears.

The Seymers misidentified the two swallowtails, but were aware that the other two insects represented undescribed species: the ghost moth they compared to *Hepialus humuli* (L.), and the *Vanessa* they noted as “Simillima *Atalanta* nostrae.” These illustrations are probably the first known for all four taxa. However, at the same time Pieter Cramer (1775: 132, Pl. 84, figs E,F) presented images of a “vulcaín” (Red Admiral) from China, under the name *Papilio atalanta*. His discussion indicates that he was aware of differences between his specimen and the familiar European insect. The paintings in Cramer clearly show true *Vanessa indica*, and demonstrate that by the 1770s Chinese material of this species was already reaching European collectors.

The Seymers had a great deal of material from China, and therefore it is conceivable they accidentally mislabelled a Chinese specimen of *V. indica*, and then made a slightly inaccurate picture of it. While not error-free, the Seymer paintings are, in general, precise (Vane-Wright & Hughes, 2005: 268). In several ways the Seymer image fits *V. vulcania* far better than true *V. indica* (see below). So an alternative possibility might be that the Seymers obtained a specimen of *V. vulcania* from the Canaries or Madeira, and then made a slightly inaccurate picture of that. Plants used in horticulture were certainly available from the Canary Islands by the mid 18th century, and probably much earlier (e.g. the endemic *Isoplexis canariensis*, named by Linnaeus in 1753; Vane-Wright & Hughes, 2005: 212). However, *V. vulcania* was not described until 1819, and very few other endemic Atlantic island Lepidoptera were named before that time: *Pararge xiphia* (Fabricius, 1775), endemic to Madeira, is a rare example (Weingartner et al., 2006). There is absolutely nothing to suggest that the Seymers ever received any insect material from the Atlantic Islands (Vane-Wright & Hughes, 2005: 254, table 1), whereas they undoubtedly did obtain a considerable number of insects from Newfoundland and China.

If we assume that all four taxa stated by the Seymers to have come from Newfoundland originated from a single source, then these specimens must have been collected before 1772. We found no further information concerning their possible origin (Vane-Wright & Hughes, 2005: 260), although we speculated that Joseph Banks might have collected this material during his visit to the island in 1766 (see Lysaght, 1971). By about 1775 the Seymers were also receiving specimens from Newfoundland collected by a Mr Top, an island resident. There is nothing to suggest that Banks visited China during this period, nor Top either.

As there is no reason to doubt the provenance of the other Lepidoptera reported by the Seymers from Newfoundland, this putative record for the *Vanessa indica* complex in Canada should be given credence. The evidence of *Papilio brevicauda* is significant, as it is a narrowly distributed species found only in northeastern Canada. We are thus confident that the *Vanessa* image must be based on one or more specimens that came into the Seymers’ possession ca 1770, and we see no particular reason to doubt the given provenance of Newfoundland, and some reasons to accept it. This includes our conviction that the image (Fig. 1b), which is detailed, cannot be matched precisely to any of the
old world taxa that make up the V. indica-group, including V. indica indica, or to V. vulcania (Figs 1c–l).

However, Thomas Dinock (in litt., 2007) has pointed out six peculiarities of the Seymer image which do give rise to questions regarding its accuracy—were it to be assumed that it is based on either V. indica or V. vulcania with incorrect provenance. We comment on each of these points, in turn:

1. “First is the extent and intensity of the blue markings on the HW underside, much bluer than any known Vanessa today.” As reproduced there is a blue cast. The original paintings are no longer readily available to us for re-examination. They were photographed as large format transparencies in 1992, scanned in 2004, and the resultant “tif” file was transformed in Adobe Photoshop to make the images presented here, in 2006. If you take a flash photograph of the underside of a V. vulcania specimen you will not see a blue cast, but you will see a very strong blue area at the end of the forewing discal cell, and a complete series of post-ocellar blue marks in cells R1–CuA2, as in the Seymer image.

2. “No living species of Vanessa has such a gigantic white costal bar extending into cell M3 . . . when measured along its greatest length, [it] reaches 7/15 (46.7%), or nearly half of the way to the wing margin near the tornus . . . The white bar in V. vulcania (Fig. 1c) reaches only 4/15 (26.7%), of the distance to the tornus.” Using the large white submarginal spot in cell M2 as a marker, we suggest that the Seymer image does not show this bar extending into cell M3, but crossing cell M2 to end at vein M3. Measured on a full-size photograph of the Seymer image, we make the extent 42.5%, not 46.7%. The extent of this mark in V. indica and V. vulcania can often exceed 30%, but undoubtedly this does represent a major difference to these species. Is such an extent impossible? Frohawk (1938: plate 20, p. 86) illustrates an aberration (‘albo-punctura’) of V. atalanta from Erith, England (now preserved in the BMNH), in which the outer half of forewing cells M2 and M3 are largely filled with white. In cell M2 it appears to consist of an extension of the white bar that has fused with the main submarginal white spot. Measuring on the underside from the costa, where the bar elements commence, to the margin of white area at vein M3 gives a value of 41% for the ratio in this atalanta. Making these measurements to vein M3 in V. vulcania and V. indica typically gives 38–40%. In subgenus Cynthia the white bar often extends back to vein M3. Field (1971: fig. 158) illustrates a specimen of V. (C.) annabella in which this is so; it has a value of 38.5%. We conclude that the Seymer figure is not so extreme as Dimock suggests, and is not implausible.

3. “No living species has the small posterior extension of this bar extending from the distal side of the bar, as the painting has.” It is certainly true that in the great majority of Vanessa (Vanessa) specimens that have this small extension (not all do), it arises from the proximal side of the bar. However, in such cases this extension occurs in the anterior half of cell M3, whereas the Seymer image shows this area filled with white and contiguous with the element of the bar in cell M3. The extension in the Seymer image occurs in the posterior half of cell M3, reaching vein M3, as already discussed. So in this case we are not comparing like with like. We have searched for Vanessa (Vanessa) with the posterior half of cell M3 filled with white but, apart from the Frohawk example described above, which is too extreme, we have not found anything really comparable. However, in Vanessa (Cynthia), the bar often crosses the whole of M3, and where it does so, the extension into the posterior half of the cell can be distal. Field (1971: figs 133,134) illustrates a specimen on V. (C.) terpsichore in which the configuration of the whole bar approaches that of the Seymer image. We conclude that if the Seymer image does represent a Vanessa in which the bar reaches across the whole of cell M3, the distal extension is entirely plausible.

4. “In the painting, the hindwing ocelli are all longitudinally flattened, equal in size, and the anterior four are in a very straight line, unlike all other Vanessa.” We agree that this configuration looks odd. The most complete ocellus on the hindwing underside in most V. indica and V. vulcania is the most posterior one, in cell CuA, and the Seymer image conforms in this regard. In V. indica and V. vulcania, however, as in other Vanessa, the more anterior border ocelli vary in size and shape, but have their centers located on a smooth arc, parallel to the curve of the wing margin.

5. “The painting shows a total of six ocelli or ocelli without pupils. Vanessa have only five, never a sixth ocellus in cell Sc + R1 .” We also agree that all Vanessa have examined have only five border ocelli on the hindwing, occurring in cells R3 to CuA, inclusive. We have not seen any Vanessa with a clear ocellus in cell R1, although this is part of the nymphalid groundplan, and can be seen very clearly in some species (e.g. Charaxes analava: Nijhout & Wray, 1986). According to Beldade & Brakefield (2003: 176), all marginal wing cells appear to have the potential to produce eyespots, and laboratory selection experiments rapidly reveal the capacity of species to produce ocelli in cells that do not normally exhibit them. “Eyespot number is not a very fixed trait even within a species” (Antónia Monteiro, in litt., July 2007). In conclusion on this point, we agree that the configuration of the hindwing ocelli in the
Seymer image are uncharacteristic of known Vanessa species, and could either reflect the fact that, as we suggest, this is a new species, or that the Seymer image is inaccurate in this respect. The hindwing underside pattern of Vanessa is very complex, and is a considerable challenge for any artist. Another possibility is that the Seymers’ specimen had the apex of the hindwing missing, and Henry Jr. simply interpolated what he thought it should look like. There is ample evidence that the Seymers ‘perfected’ incomplete specimens based on their general knowledge of similar species.

6. “Finally, look at the hindwing on the painting and notice how far distally from the dark discal spot that vein $M_3$ branches from $Cu_1$. It should arise from the posterior end of the discal spot, not 3 mm distally. Differences this great have been used to distinguish genera.” There seems no doubt that the hindwing venation has been misinterpreted in the Seymer image—and the forewing venation is also incorrect. Very few illustrators at this date produced accurate images of Lepidoptera wing venation. It was not until William Jones (1794) published his ground-breaking comparative work, some 20 years later, that lepidopterists regularly started to render accurate wing-vein schemes.

In conclusion, Dimock comments “Of course, all of these “inaccuracies” support the authors’ hypothesis [see below] that the painting is of an extinct species.” With respect to points 1–6 raised by Dimock above, on reflection we consider that 1–3 are consistent with our view that the Seymer image does represent an extinct species, while 4–6 probably do reflect genuine inaccuracies.

Shapiro says that V. vulcania is more like far-eastern V. indica than SE Asian, and that it also varies in the direction of Holarctic atalanta. However, as pointed out by Bascombe et al. (1999), V. indica indica is a migrant, and it hardly varies over its extensive range. John Tennent (2005, and pers. comm.) has related how he remembers “seeing indica occasionally in Hong Kong … it’s a small pale shadow of the brilliant, whopping thing that occurs on Madeira and the Canaries.” The Seymer paintings were executed life size (Vane-Wright & Hughes, 2005), and the forewing length of the supposed Newfoundland specimen, as figured, measures 35 mm — quite large for any red admiral except V. tameamea. While examination of a long series of V. indica from China and a considerable number of V. vulcania in the Rothschild Collection (at the Natural History Museum, London) confirms that the latter is undoubtedly “redder” in some sense than the more orange eastern taxon, any impression of larger size must be an illusion or a sampling artefact. A few female specimens from China equal or slightly exceed a forewing length of 35 mm, which is also about the maximum found among material from the Canaries. In this context it is notable that the forewing lengths of the two original specimens of V. amerindicata are given as 24 mm and 27 mm (Miller & Brown, 1989: 1). Some individuals of both V. indica and V. vulcania have a forewing length as short as 25 mm, or even less.

The persistent red coloration of V. vulcania appears to be a specific feature (fresh V. indica may be almost as red, but invariably fade to orange during life, or post-mortem). From this it would seem that, on the basis of its more orange color, Seymer’s image (Fig. 1b) does not represent V. vulcania (Fig. 3), but this cannot be given much weight. Assuming the postdiscal white patterning of the forewing has been rendered accurately (see discussion if Dimock’s points 2 and 3, above), it is not V. indica either (Figs 1d–f). As Higgins & Riley (1980: 102) point out, in the Canary Red Admiral “the short band of three white spots runs from the costa at a right angle”, whereas in V. indica this band is oblique. This reliable difference is most readily appreciated by extending an imaginary line along the distal margin of this short band. In V. indica this imaginary line will always enter (at the very least touch) the large white submarginal spot in cell $M_2$, whereas in V. vulcania such a line is always proximal to the smaller $M_2$ white spot, and never runs through it.

As examination of Field (1971: figs 33–80), Tsukada (1985: plate 49) and Figs 1a–o will confirm, the condition of this character in V. indica is shared with all other known Vanessa s.s., including V. abyssinica — V. vulcania being the only exception. This feature thus represents an apomorphy for the V. vulcania-group, and on this basis we suggest that the Seymer image, which shows exactly the same configuration (despite the very large submarginal spot shown in cell $M_2$), represents an undescribed and recently extinct member of the V. vulcania species group from North America. This previously unknown species differs from V. vulcania in having the principal forewing band orange rather than bright red; in having the short preapical forewing band composed of four elements (in cells C, R, $M_1$ and $M_2$), in which the white element in the anterior half of $M_1$ is the same width as in $M_2$, with a small distal extension into the posterior half of $M_2$ instead of small proximal extension to the white mark in $M_1$ that is confined to the anterior half of $M_2$; and in having the submarginal white spot in forewing cell $M_1$ large (ca 2 mm diameter), not small as in V. vulcania (usually about 1 mm diameter, although it can be larger).

Finally, regarding the plausibility of this apparent record, it is necessary to consider environmental
conditions in Newfoundland. Being unable to survive harsh winters, Vanessa species only occur in far northern areas, such as Lake Baikal (V. indica) and Newfoundland (V. atalanta), by annual remigration from the south. If, as pointed out to us by as Thomas Dimock, we accept the Seymer record as genuine, then his material must have been collected in the summer or autumn months, and been derived, directly or indirectly, from spring or early summer migrants from the far south. In which case one would expect that early collectors would have obtained this species from source colonies in the USA — as in the case of Vanessa (Cynthia) virginensis (Drury, 1773), first discovered in the USA, and which only reaches Newfoundland during the summer months (Layberry et al., 1998). If it is assumed that such a butterfly would have been common and abundant, like most familiar Vanessa species, then this is puzzling and must add to the uncertainties regarding the Seymer record. On the other hand, most genera do include genuinely rare species, often including some that appear close to extinction.

Given the various doubts indicated above, and that this insect is known only from a painting which could be inaccurate in details of pattern and provenance, we do not propose to give it a formal name. However, should the existence of such a Vanessa in North America ever be independently confirmed, we urge that it be named in honor of Henry Seymer.

CONCLUSIONS

While Wahlberg et al. (2005) conclude that the Palaeartic region and subsequent dispersal played a crucial role in the diversification of the Nymphalis-group sensu lato, we suggest here that North America could have been the origin for Vanessa, including not only the painted ladies, but also the red admirals. Were this to be the case, it would be plausible that offshoots of the group reached the Old World during the summer months (Layberry et al., 1998). If it is assumed that such a butterfly would have been common and abundant, like most familiar Vanessa species, then this is puzzling and must add to the uncertainties regarding the Seymer record. On the other hand, most genera do include genuinely rare species, often including some that appear close to extinction.

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Newfoundland Hesperioidea. Arthur Bydron kindly answered our queries regarding the biology of Pyemia, and James Hogan gave us access to the Oxford University Museum Vanessa collection. Roger Vila (MCZ) and Niklas Wahlberg (Stockholm) offered constructive criticism of an earlier version of the MS, and NW together with Dan Rotholz (Hawaii) also generously shared new, unpublished information. Thomas Dimock and Art Shapiro provided detailed criticisms of our first submitted draft, and we have revised the final version in light of their most valuable comments. The first author also wishes to thank Art Shapiro for engaging discussions on these insects in the past, and to acknowledge the National Endowment for Science, Technology and the Arts (NESTA), and the Natural History Museum (NHM), London, for continuing support.

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APPENDIX I

Checklist of the nine extant species of the subgenus Vanessa (Vanessa) currently recognized, and their accepted subspecies. Pyrameis abyssinica Felder & Felder, 1867, is here formally transferred to Vanessa, based on the results of Nakanishi (1989) and Wahlberg et al. (2005), and the discussion presented above. In addition, we include the fossil taxon V. amerindica Miller & Brown, and note the unnamed indica-complex taxon reported ca 1773 by Henry Seymer and Henry Seymer Jr. (see text). Among recently described Vanessa taxa, V. pulchra Chou, Yuan, Yin, Zhang & Chen, 2002, appears to be an aberration of V. (Cynthia) cardui (L.), and is not included here.

| Vanessa (Vanessa) Fabricius, 1807 (type species: Papilio atalanta Linnaeus, 1758) |
|---------------------------------|--------------------------------------------------|
| (Lepidoptera: Papilionoidea: Nymphalidae: Nymphalinae: Nymphalini: Nymphalina) |

1. V. (Vanessa) amerindica Miller & Brown, 1989 [USA (Florissant formation, Colorado; Oligocene fossil)], incertae sedis
2. V. (Vanessa) abysinica (Felder & Felder, 1867), **comb. nov.**
   - abysinica abysinica (Felder & Felder, 1867) [Ethiopia]
   - abysinica jacksoni (Howarth, 1966) [Kenya, northern Tanzania], **comb. nov.**
   - abysinica tansonereni (Howarth, 1966) [western Uganda, Rwanda, Democratic Republic of the Congo (Kivu, Ituri)], **comb. nov.**
3. V. (Vanessa) indica (Herbst, 1794)
   - indica indica (Herbst, 1794) [northern India, Nepal, Myanmar, Thailand, Laos, Cambodia, Vietnam, China, Korea, Russia (Siberia, Kamchatka, Sakhalin), Japan (including Ryukyu Islands), Taiwan, Philippines (Luzon, Mindoro, Palawan)]
   - indica pholoe (Fruhstorfer, 1912) [southern India (western Ghats)]
   - indica nubicola (Fruhstorfer, 1898) [Sri Lanka]
4. V. (Vanessa) samani (Hagen, 1895) [Indonesia (Sumatra)]
5. V. (Vanessa) dejeannii Godart, 1824
   - dejeannii dejeannii Godart, 1824 [Indonesia (Java)]
   - dejeannii samabana (Fruhstorfer, 1898) [Indonesia (Bali, Lombok, Sumbawa)] [synonymized with dejeannii dejeannii by Field, 1971, but maintained as distinct by Tsukada, 1985]
   - dejeannii movensegi (Talbot, 1936) [Philippines (Mindanao, Samar)] [possibly a distinct species]
6. V. (Vanessa) buana Fruhstorfer, 1898 [Indonesia (southern Sulawesi)]
7. V. (Vanessa) dilecta Hanafusa, 1992 [Timor] (Otaki et al., 2006a, suggest that this may be a subspecies of buana, but provisionally maintained here as a full species—see text]
8. V. (Vanessa) atalanta (Linnaeus, 1758)
   - atalanta atalanta (Linnaeus, 1758) [Atlantic islands, North Africa (south to northern Chad), Europe and temperate Eurasia eastwards to Pakistan, Kashmir, northern Himalayas and the Amur River]
   - atalanta rubria (Fruhstorfer, 1909) [Canada, USA, Mexico, Guatemala, Cuba, Haiti, Dominican Republic]
9. V. (Vanessa) tameamea Eschscholtz, 1821 [USA (Hawaii)]