Christopher Columbus and *Culicoides*: was *C. jamaicensis* Edwards, 1922 introduced into the Mediterranean 500 years ago and later re-named *C. paolae* Boorman 1996?

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Summary

The biting midge, *Culicoides paolae* Boorman, described from specimens collected in the extreme south of Italy in 1996, belongs in the subgenus *Drymodesmyia*. This subgenus was erected by Vargas in 1960 for the so-called Copiosus species group, an assemblage of 22 species endemic to the tropical regions of the New World and, where known, breed in vegetative materials including the decaying leaves (cladodes) and fruits of Central American cacti. The Mexican peoples have utilised these cacti for over 9 000 years; one of these, *Opuntia ficus-indica* Linnaeus, was brought to Europe by Christopher Columbus following his voyages of discovery. As a taxon *C. paolae* is very similar to the Central American *C. jamaicensis* Edwards, 1922 raising the possibility that it (or a closely related species of *Drymodesmyia*) was introduced into the Mediterranean Region at the time of Columbus, but was (perplexingly) discovered only 500 years later and named *C. paolae*. The comparison of Sardinian specimens of *C. paolae* with Panamanian material of *C. jamaicensis* (housed in the Natural History Museum in London) confirmed the two species to be very similar but unusual differences were noted around the precise distribution of the sensilla coeloconica on the female flagellum. Until it is understood whether these differences represent either intra- or interspecific variation, the question of the possible synonymy of *C. paolae* must be held in abeyance.

Keywords

Culicoides – *Culicoides jamaicensis* – *Culicoides paolae* – Taxonomy.

Introduction

In 1994 an apparently new species of *Culicoides* was captured at a horse stable in Pellaro, southern Italy. It was described subsequently and named *C. paolae* Boorman, 1996 (after its discoverer Paola Scaramozzino). Based upon similarities in the wing pattern *C. paolae* was first thought to belong in the Old World Schultzei Complex (= subgenus *Remmia* Glukhova, 1977) but closer scrutiny confirmed it to differ in many other taxonomic features. Despite these differences, the superficial resemblance between *C. paolae* and species of the Schultzei Complex was emphasised. This led to it being labelled a potential vector of livestock orbiviruses, firstly because it had been collected around horses and, secondly, because epizootic haemorrhagic disease of deer virus (EHDV) had previously been isolated in the Sudan from *C. kingi* Austen, 1912, a species of the Schultzei Complex.

Following the incursion of bluetongue (BT) virus (BTV) into Italy in August 2000, a national survey was implemented and *Culicoides* collected countrywide. Onderstepoort blacklight traps were deployed throughout the islands of Sardinia and Sicily and on the southern peninsula of mainland Italy. These soon revealed *C. paolae* to be widespread, and also that it could, on occasion, be captured in 100s (but never in 1 000s).

In 2001, it was noticed adventitiously that the wing of *C. paolae* closely resembled that of *C. jamaicensis* Edwards, 1922. However, this resemblance was initially ascribed to congruence as many species of world *Culicoides* share similar wing patterns. Also, the fact that *C. jamaicensis* was a Central American (New World) species seemed to weigh too heavily against its dispersal across such a wide expanse of ocean into the Mediterranean Basin (Old World). However, doubts persisted, firstly, because perusal of the published descriptions of the two species indicated that they were very similar indeed, and, secondly, because *C. paolae* seemed unrelated taxonomically to any other Old World species of *Culicoides*. These two facts heightened the likelihood of *C. paolae* being alien to the Mediterranean, and so it was decided to investigate the congruence in greater depth.

Materials and methods

Males and females of *C. paolae* captured in light traps on the island of Sardinia were slide-mounted. These were then compared in detail to the original descriptions (and re-descriptions) of *C. jamaicensis* (Fig. 1) and *C. paolae*; two slide-mounted specimens of *C. jamaicensis* from Panama, stored in the Natural History Museum in London, were also examined. Information on the biology of *C. jamaicensis* (and of related species) was also collated. All the taxonomic data were also compared against those obtained from the study of hundreds of afrotropical specimens of eight species of the Schultzei Complex. Two attempts were made in the field (in Italy) to harvest the immature stages of *C. paolae*.

Results and discussion

The taxonomic data on *C. jamaicensis* from various studies (1, 6, 9, 10) were compared with those presented in the original description of *C. paolae* (3) and with those gleaned from six specimens (three males and three females) collected in Sardinia. Based upon these published data, the two species seemed inseparable, and suggested *C. paolae* to be a junior homonym of *C. jamaicensis*. However, published descriptions of world *Culicoides* nearly always lack important species-specific details, and for this reason it was decided to also study New World material of identified *C. jamaicensis*. Two female specimens from two localities in Panama were located in the holdings of the Natural History Museum in London, and were examined in detail. At first, there seemed little doubt that *C. paolae* and *C. jamaicensis* were one and the same species. However, upon closer examination, the Panamanian specimens displayed an unusual conformation in the distribution of the sensilla coeloconica on the female flagellum in that they were found to occur on both faces of each of flagellomeres IV-VII. For example, on all four flagella examined, the four coeloconica

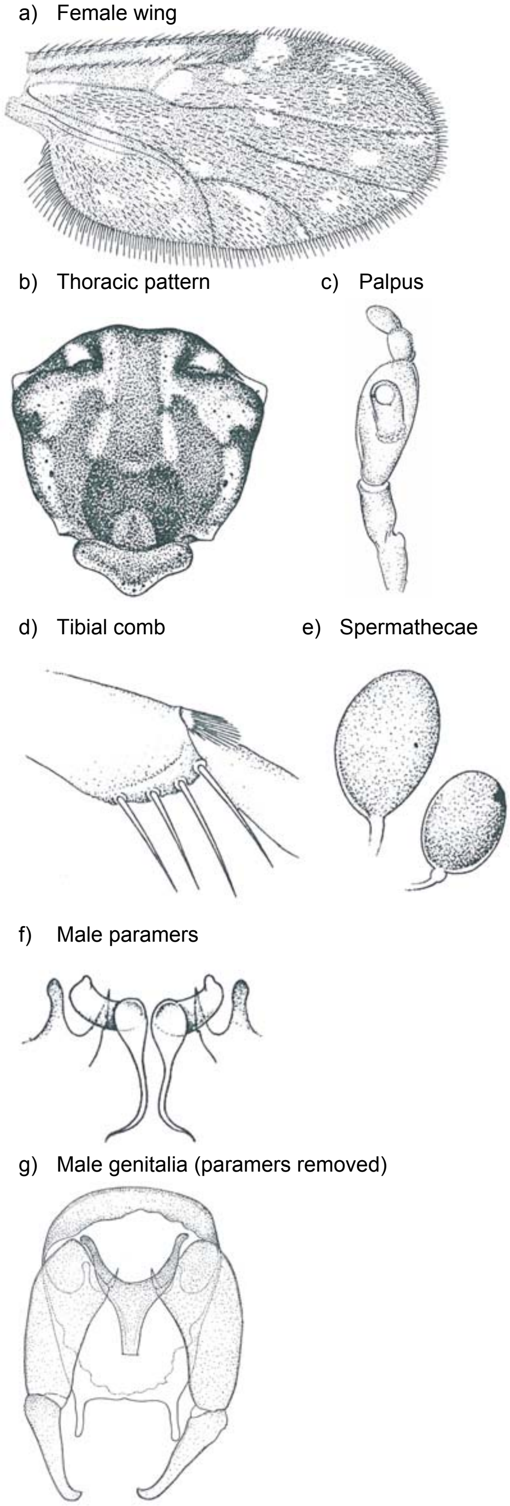

Figure 1
Culicoides jamaicens Edwards
Adapted from Wirth and Blanton (9)

found on flagellomere IV were always split into two distinct groups (of two sensilla each), and were positioned (in direct apposition to each other) on the dorsad and ventrad faces of this flagellomere. There are many species of world *Culicoides* that have multiple sensilla coeloconica on one or more of the basal flagellomeres but even where these may number up to 16 they are always found on one face of the flagellomere and are tightly grouped. Thus, it is highly unusual to find a species of *Culicoides* in which the coeloconica are split into two widely separate groups on a single flagellomere. This splitting of the coeloconica into two groups was not seen in the three Sardinian females (i.e. six antennae) of *C. paolae* examined. At this stage, it is not possible to decide the taxonomic importance of this difference. The study of further material of the subgenus *Drymodesmyia* from across a wider New World range is required to answer this question. We thus refrain from declaring *C. paolae* a junior homonym of *C. jamaicensis*.

In 1960, Vargas created the subgenus *Drymodesmyia* for those species of *Culicoides* that belong to the Copiosus group, which included *C. jamaicensis* (8). This fairly large subgenus of 22 species (4) is endemic to the New World, where some of its member species have been found to breed in the rotting parts of Central American cacti (10). No species of *Drymodesmyia* has ever before been reported from anywhere in the Palaearctic Region (nor from Africa), and so would support the contention that *C. paolae* is an introduced species and thus alien to the Old World (which includes the Mediterranean Basin). This, in turn, suggests that it may therefore be a synonym of a previously described New World species. However, it is possible also that still other species of *Drymodesmyia* remain to be discovered in Central America and that one of them could well prove to be *C. paolae*. In such an event, *C. paolae* would remain a valid taxon with the unusual distinction of having been described from well beyond its faunal 'home range'. The clarification of this issue requires the morphological study of all species of *Drymodesmyia* and, ideally, should be coupled to the sequencing of targeted gene regions.

In regard to the question of *C. paolae* having been introduced into the Mediterranean, it is pertinent to recall that another Central American species of *Drymodesmyia* was unexpectedly discovered in Australia (5). The species is *C. loughnani* Edwards, 1922, and most likely arrived there after boatloads of parasite-laden rotting cacti stems had been introduced from Central America to Australia in the 1920s as part of a biological control effort against the spread of jointed cactus (*Opuntia* sp.). *Culicoides loughnani* was subsequently found to breed in the rot pockets that formed in cacti stems in Australia just as the closely related *C. jamaicensis* has been found to do in Mexico. Ad hoc efforts to rear *C. paolae* from *Opuntia* in Italy have thus far failed and are discussed further below.

The prickly pear *Opuntia ficus-indica* Linnaeus apparently took its name from its alleged morphological similarity to the Mediterranean fig and from its geographical origin (the West Indies). It was introduced by Christopher Columbus into Spain in around 1500 to be cultivated in the gardens of the nobles (2); its strangely odd form led Oviedo to refer to it as the '…monster among trees'. It subsequently was spread throughout the hotter areas of the Mediterranean Basin by sailors who used it as a vegetable against scurvy. In these new locations in Europe, the spined and spineless forms of *Opuntia* were described subsequently (and erroneously) by botanists as 'new' species. Apparently the domestication of *O. ficus-indica* dates back some 9 000 years to the ancient Mexicans who referred to it as the 'sweet song plant' due to the sound made through the leaves by the blowing wind; it is also known as the 'bone fixing tree' as the leaves (more correctly cladodes) are used in poultices to treat bone fractures. The distribution of *C. paolae* in Italy has yet to be mapped thoroughly but current indications are that it, like *Opuntia*, is restricted to hotter climes, being found widely on the islands of Sardinia, Sicily and Malta (7), and on the southern third of peninsular Italy (which includes Pellaro the type locality of *C. paolae*). Whilst a number of species of *Drymodesmyia* have been shown to breed in cacti in Central America, two attempts to breed *C. paolae* from the ripe fruits, and from the rotting cladodes, of *Opuntia* in Italy, have failed. Thus the reputed association between the insect and this plant in the Mediterranean has still to be demonstrated.

In the original description of *C. paolae*, it was noted that because of its resemblance to species of the Schultzei Complex, and because it had been captured in abundance at a horse stable, it deserved consideration as a potential vector of orbiviruses to livestock. However, the adult female of *C. paolae* possesses three remarkable features that would seem to mitigate against this supposition, as follows:

a) the third palpal segment, which bears the host-seeking sensory pit, is extremely inflated
b) all basal flagellomeres III-X bear two long and two short sensilla trichodea that are not slender but inflated
c) multiple sensilla coeloconica occur on each of flagellomeres III-XV.

Although the host preferences of *C. paolae* are unknown, these three features suggest it to be ornithophilic in its bloodsucking habits. If this is the case, the original specimens of *C. paolae* captured at Pellaro may have been feeding on birds (or chickens) roosting in the vicinity of the light trap and not upon the stabled horses.

Finally, *C. paolae* is taxonomically quite dissimilar from eight species of the Schultzei Complex (= subgenus *Remmia*) that were studied. They also have little in common in terms of biology. Indeed, based upon the morphological data, their evolutionary links are, at best, tenuous, as the subgenus *Drymodesmyia* is restricted to the New World and *Remmia* to the Old World. Also, and contrary to a widespread belief amongst culicoidologists, the subgenus *Remmia* is not a synonym of the New World subgenus *Oecacta*.

Conclusions

This 'story' of *C. paolae* (and of *C. loughnani* in Australia) demonstrates clearly that species of *Culicoides* can be introduced by man into new localities and from across wide expanses of ocean. However, their successful establishment would depend upon a suitable larval habitat being available. In the case of *C. paolae* (and *C. loughnani*), it would seem that they could establish themselves because the larval host plants (cacti) were introduced simultaneously. Their establishment, and subsequent maintenance, would require at least one adaptive step, i.e. a switch to sucking blood from new hosts. In the case of these two taxa, their hosts are likely avian. It is also possible that species of *Drymodesmyia* are autogenous (i.e. do not require a blood-meal to lay their first batch of eggs) and, if so, would aid further in their ability to survive and persist in their new 'homes'. The fact that hundreds of specimens of *C. paolae* can be captured in a given locale, and over a considerable area in the central Mediterranean, would seem to attest to the apparent 'success' of *C. paolae*, but does make it difficult to explain why the presence of this species has been discovered only very recently. Is this due simply to a paucity of studies on the biting midge fauna of the Mediterranean or is there another explanation?

If indeed *C. paolae* was introduced from the West Indies some 500 years ago, it would be interesting to establish the degree of genetic drift that has occurred since. Such a study may provide molecular markers for dating the arrival and movement of taxa into new regions. A pertinent example is that of the BT vector *C. imicola*, which is believed by some to have arrived recently in the Mediterranean and is spreading rapidly northwards into Europe.

On the taxonomic level this 'case' of possible mistaken identity is not easily resolved. As noted above, small (but unusual) differences were found between *C. paolae* from the Mediterranean and *C. jamaicensis* from Panama. If these represent intraspecific variation, they would be highly unusual for the genus *Culicoides*. On another level, it is possible also that the Panamanian specimens in the National History Museum have been misidentified, which is not unlikely when many species complexes remain entirely hidden from view because inter- and intraspecific variation is consistently being confused. The onus is upon taxonomists to explore these variations in greater detail, through larger series of specimens collected over a wider geographic range. It is an inescapable fact that many species of *Culicoides* remain undiscovered because often their distinctness as genetic entities is not reflected by glaringly obvious changes in the phenotype. The elucidation of the true identity of *C. paolae* will require that it be more intensively compared against each of the 22 species currently deemed to comprise the subgenus *Drymodesmyia*, and that such a study be conducted on both morphological and molecular levels.

The wing pattern of *C. paolae* resembles that found in species of the Schultzei Complex; all share an hourglass-shaped pale spot in the centre of wing cell R5. Given the fact that the viruses of EHD and BT had previously been isolated from *Remmia* in Africa, *C. paolae* was implicated as a potential new vector. This deduction, based upon the tenuous taxonomic link between *C. paolae* and species of *Remmia*, is weakened further by the apparent vast differences in their respective biologies (which includes the possibility that *C. paolae* feeds preferentially on birds). However, these evidences should not be construed as mitigating unequivocally against the vector potential of *C. paolae*; rather they serve to illustrate that too little is known about the host preferences and breeding habitats of the 100 or more species of *Culicoides* that occur across the Mediterranean Basin. It is important for us to appreciate that our current reliance upon the light trap as the sole surveillance tool, though being of great value in determining the seasonal and geographic distribution and adult densities of *Culicoides* vectors, will contribute little towards elucidating the oft unusual life-cycles of these small blood-sucking insects.

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