REVIEWS

Dermatobia, The Neotropical Warble Fly

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The neotropical warble fly, Dermatobia hominis *(Fig. 1), has plagued neotropical America since preColombian times, and has become an economically important pest causing substantial losses to the meat, milk and leather industries from northern Mexico down to northern Argentina. Its life cycle (Box 1) is astonishingly complex, requiring another insect as a phoretic carrier of its eggs to the skin of its mammal hosts. Here Eugenio Sancho discusses factors that contribute to the current economic and public health importance of this myiasis-causing fly.*

Knowledge of *Dermatobia hominis* in neotropical America dates back to preColombian cultures before the 16th century. The Mayan, Nahuatl and Guarani amerindians of Mexico, Central and South America, called it '*suglacuru*', '*colmoyote*' and '*mbusura*' in the descriptions they gave to the Spaniards. Other local names since applied include '*berne*', '*nuche*' and '*tórsalo*'.

Larvae of *D. hominis* develop within a painful subdermal swelling – often at areas inaccessible to host grooming behaviour (Fig. 2). Larval development is completed in 5–10 weeks, after which the larvae escape and pupate below the surface of the ground. Adult flies emerge some weeks later. They mate, but do not feed – relying instead on nutrition accumulated during the larval stages. When the adult female is ready to oviposit she captures another insect – usually a mosquito or other blood-sucking fly – and glues her eggs to the captured insect's abdomen (Fig. 3). When the carrier insect then alights on a warm-blooded host, the *D. hominis* eggs hatch (Fig. 4) and young larvae burrow into the host skin to continue their development (see Box 1). A wide range of warm-blooded hosts appear suitable, including most mammals (and man) and several species of birds.

It seems clear that *Dermatobia* exploited a wide range of hosts in preColombian America, but the introduction of cattle ranching since European colonization has greatly increased its geographical distribution and the size of the susceptible host population. Systematic study of the pest began with Spanish and Portuguese missionaries, explorers and naturalists, who described the wounds caused by *D. hominis* larvae in the skin and hides of men and of cattle. The incidence of such studies increased in the late 19th century as cattle ranching became a dominant economic factor in Latin America[1–7], but it was not until 1911 that the full complexity of the fly's life cycle was clarified[8,9]. Even then, the great body of accumulated literature about the fly was often confusing[1–14].

Box 1. The Life Cycle of *Dermatobia hominis*

Dermatobia hominis is a cuterebrid fly, related to the oestrid flies such as *Hypoderma bovis* and *H. lineatum* – the cattle warble flies of the northern hemisphere (see *Parasitology Today* 2,111–116). *D. hominis* is known only from Latin America, from northern Mexico to northern Argentina, where it is a common cause of myiasis in cattle, but parasitizes other mammals, birds and sometimes humans.

Adult *Dermatobia* are handsome metallic blue flies, about 12–17 mm long, with a dark brown head. Adults have atrophied mouthparts and do not feed, relying instead on food reserves accumulated during the larval stage. They can survive for 8–19 days in laboratory colonies with controlled temperature and humidity, but probably survive for less time in nature. Survival is much reduced at temperatures below 18°C or above 30°C[16,23].

When ready for oviposition, the female *Dermatobia* captures another insect on which to lay her eggs. A wide range of insects appear suitable as egg carriers, especially mosquitoes such as *Psorophora* and other blood-sucking insects, although several non-biting flies may also be used (see Table 1). The opaque white eggs, about 1 mm long, are laid in batches of 30–40 on the abdomen of the captive insect, which is then released. Egg survival is dependent on a high local humidity, and hatching is stimulated by the warmth of a mammalian or avian host on which the carrier insect alights. The L1 larva, about 1–1.5 mm long, is very active and migrates over the surface of the vertebrate host for distances up to 19 cm[45]. It then penetrates the host skin to develop inside a subdermal cavity. For respiration, it maintains its entrance hole open to the external air, and the presence of swellings with a small central hole is thus indicative of infestation. Inside the cavity the larva feeds and moults twice, burrowing out of the host skin when it reaches the L3 stage, usually after about 5–10 weeks. The mature larva is about 25 mm long, and it is this exit phase, which leaves a substantial hole in the host's skin, that is responsible for most damage to the hide.

The L3 larvae leave their host during the night or early morning, never during the afternoon – presumably to avoid risk of desiccation. They fall to the ground, into which they burrow, and pupate. Adults emerge 3–5 weeks later, depending on climate[1,5].

Table 1. Known carrier insects of *Dermatobia hominis* eggs[5,7]

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Aedes angustivitattus
Asilidae
Callitroga macellaria
Coenosia spp
Culicidae
Cyrtoneuropsis spp
Dolichopudidae
Drosophilidae
Ephydridae
Fanninae
Larvaevoridae (Tachinidae)
Limnophora sp.
Morellia scapulata
Musca domestica
Otitidae
Psorophora sp.
Sarcophagidae
Sarcopromusca arcuata
Siphona irritans
Stomoxys calcitrans
Stratiomyidae
Synthesiomyia nudiseta
Syrphidae
Tabanidae
Tipulidae
Trupaneidae
Tylidae (calobatidae)

Some authors emphasized the importance of phoretic insect carriers[8,9], while others – such as Arthur Neiva[14] – doubted that other insects carried out this function, attributing the spread of *Dermatobia* to other mechanisms such as eggs on the leaves of trees or on the hair of the cattle.

By 1910, Neiva concluded that the distribution of *D. hominis* extended from about latitude 25° N to 32° S, encompassing all of neotropical America from Taumalipas, Mexico (bordering southern Texas) to southern Brazil[2]. The fly is now known from all countries of Latin America except Chile. It was first reported from northern provinces of Argentina in 1984, where its spread appears to have followed the opening of new lands for cattle ranching[15].

The life cycle of *D. hominis* is so complex – exploiting a wide range of carrier insects and hosts – that it is difficult to believe that climatic or geographical factors exercise direct control over the fly populations. Many authors consider that relative humidity is a key factor controlling the life cycle[2,5,7,13,16–20]. For example, Neiva and Gomez[3] concluded that in NE Brazil, the dry season was unfavourable to *Dermatobia*, but not the rainy season. Similarly Zeledon and Jiron[7] indicated that a damp environment was necessary for survival of the fly's eggs and larvae, while Lobo and Zeledon[21] reported that a low relative humidity would reduce pupal survival. In Costa Rica however, where *Dermatobia* is found over a very wide range of climatic and geographical variables, we found that association of these variables could predict the frequency of infection, but no single climatic or geographical variable could do so (E. Sancho and C. Boschini, unpublished) (Box 2).

Nevertheless, some authorities insist that *Dermatobia* requires special conditions for its development. Some argue, for example, that carrier insects are absolutely necessary because they provide the humid microenvironment required to maintain viability of the fly's eggs[7,17]. Others believe that the key factor involves the conditions for pupal development in the soil, noting that pupae require conditions similar to those needed in Latin America for certain agricultural crops such as coffee and eucalyptus[5,15,22–25]. In general, these crops require soft moist soil, rich in organic matter, with shade and warmth – characteristic of the tropical forest areas. However, in some regions, the destruction of tropical forest to plant crops such as cotton, rice and sugar cane, has been associated with a decrease in the prevalence of *Dermatobia*.

There is no evidence of specific predators or parasites of adult *Dermatobia* that might exercise some controlling influence on fly abundance, although larvae and pupae have occasionally been reported to be parasitized by the microhymenopteran *Megaselia scalaris*[6]. Moreover, since such

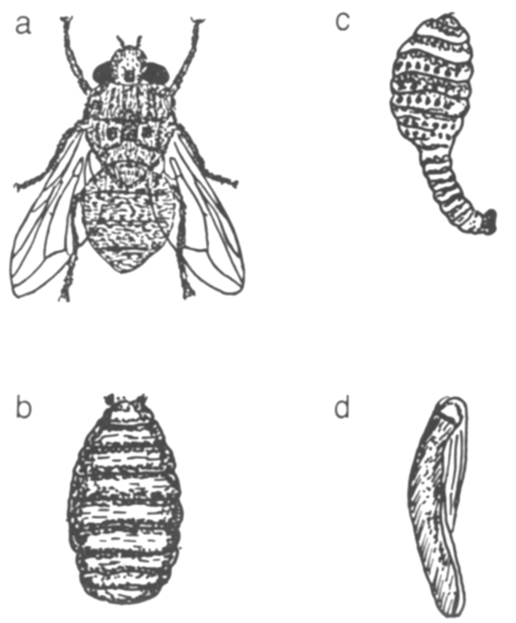

Fig. 1. Stages in the life cycle of Dermatobia hominis. *(a) Adult. (b) Pupa. (c) Mature larva. (d) Egg.*

Box 2. Distribution of *Dermatobia hominis*

Dermatobia hominis is known from the northern provinces of Mexico (Taumalipas, bordering southern Texas) to the northern Argentine provinces of Misiones, Tres Rios, Corrientes and Formosa – roughly between latitudes 25° N and 32° S. All Latin American countries are affected, with the exception of Chile, and infected cattle have been found at altitudes from sea level to above 3000 m in Peru and Bolivia[3]. The fly's distribution appears to relate primarily to the abundance of suitable mammalian hosts, of which cattle are now the most important. *D. hominis* will also parasitize other large mammals, small rodents and man, and has sometimes been found on birds. It is possible that its distribution was more limited prior to the great expansion in cattle ranching since the 18th and 19th centuries.

Climatic and geographical factors also influence the distribution of *D. hominis*, because it requires an adequate humidity for egg survival, and soft, moist soil for pupation. Moreover, adult survival is significantly reduced at temperatures below 18°C or above 30°C. However, studies in Costa Rica, where *D. hominis* is widespread throughout the broad range of climatic variables at all altitudes from sea level to over 1400 m (Fig. 6), showed that no single variable was an adequate predictor of the proportion of cattle infected. The following multiple regression shows the relative influence of each climatic and geographical factor on the proportion of cattle parasitized:

$$y = -178.3286K + 6.246885T + 0.740154R - 0.2739741A - 0.0237065TR + 0.0205699TA - 0.0003906AR$$

(y = proportion of cattle parasitized; T = temperature (°C); R = annual rainfall (mm); A = altitude (m); TR = interaction of temperature and rainfall; TA = interaction of temperature and altitude; AR = interaction of altitude and rainfall.)

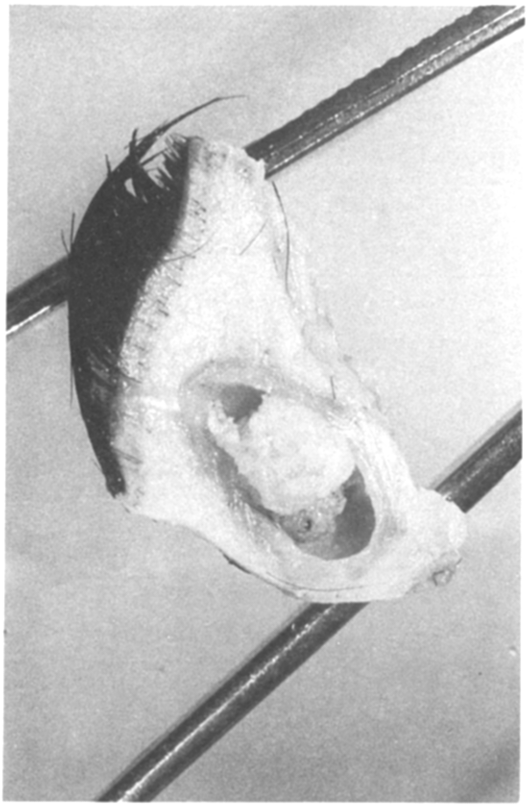

Fig. 2. Section of cow skin showing a Dermatobia *larva inside its cavity.*

Dermatobia is now known from all countries of Latin America except Chile. Because of the Andean mountains to the east, and the dry Atacama desert to the north, Chile is biogeographically rather isolated from the rest of Latin America, and generally displays a much smaller spectrum of pest species than its neighbouring countries.

a wide range of carrier insects are known to be exploited by *D. hominis* (see Table 1), it seems unlikely that availability of carrier insects would impose limits to the fly's abundance. It seems likely that the range of insect carriers will depend on the local distribution of potential carriers, which will vary from region to region[22].

Given that neither predators, parasites nor carrier insects appear to exercise a controlling influence on the development of *Dermatobia* populations, and that the fly has a very wide geographical and climatic range, it may be that the abundance of this pest is primarily regulated by the availability of hosts for the larvae.

Fig. 3. Eggs of Dermatobia hominis *glued to the abdomen of a carrier insect.*

There is little evidence for natural immunity to *Dermatobia* infestation[26]. Antibodies can be induced by inoculating mammals with extracts of the internal organs of larvae[27], but under normal conditions these organs would have no direct contact with the host. An inflammatory reaction does occur around the penetrating larvae (see Fig. 2), but this does not seem to inhibit larval development nor to result in any acquired resistance of the host to subsequent reinfestation. A stratified, non-keratinized epithelium lines the cavity where the larva lodges and presumably acts as a barrier between larva and host.

The likelihood of *Dermatobia* infestation, and the distribution of parasites over the body of the host, are affected by host characteristics of appearance and behaviour that influence the attack by blood-sucking insect carriers of *Dermatobia* eggs. Several authors now agree that dark-haired animals are more susceptible than those with lighter-coloured coats[10,15,16,28,29]; this is interpreted as showing that darker animals are more attractive to blood-sucking insects. Darker animals absorb more heat into the skin, and also radiate more. An unpublished study of Zebu cattle in Brazil (cited in Ref. 28) found the skin temperature of dark-coloured cattle averaged 3–4°C higher than that of light-coloured cattle during the hottest part of the day. This elevated temperature may be more attractive to blood-sucking insects. Also, in hotter climates, dark-coloured animals tend to seek shade more often and so increase their exposure to biting insects in shaded areas.

Host behaviour is also important in determining the distribution of *Dermatobia* lesions. In one study in Costa Rica, we found that cattle that lay more frequently on their left sides were more heavily parasitized[30]. This seems to be because while lying on the left side, the mechanical 'shooing' action of the tail is diminished over the posterior part of the animal; in contrast, animals resting on their right side have a more efficient tail action supplemented by head movements and ear flicks that help discourage biting and non-biting flies. In beef cattle allowed to roam freely in pasture, we found a different distribution of *Dermatobia*, with more lesions on the anterior quarters than on the left side[31].

Economic impact of *Dermatobia*

As the *Dermatobia* larva develops under the skin of its host, it produces a swelling with a central hole through which the larva breathes. These swellings are painful and, in dairy cattle, heavy infestations are associated with reduced milk yields. When the adult fly emerges from the lesion it leaves a clearly visible hole that can markedly reduce the value of the animal's hide. In addition, the *Dermatobia* lesions may become exploited by other myiasis-causing flies – including screwworm (*Cochliomyia hominivorax*).

In 1959, economic losses in meat, milk and leather production due to *D. hominis* in Central America alone were estimated at US$4 million[10]. This estimate excluded the cost of importing insecticides for *Dermatobia* control – mainly using organochlorines and organophosphates[32–36]. In 1966, losses were estimated as US$3.25 million in meat, US$450 000 in milk, and US$1 million in leather and hides[19]. Earlier estimates of losses in other parts of South America indicate an average loss equivalent to US$10 per hide, with milk production reduced by 25% as a consequence of *D. hominis* infection[16]. In Costa Rica and Honduras, meat production is believed to be reduced by 30% as a result of *Dermatobia*[6], while overall hide losses due to fly damage, poor skinning and hide preservation in Costa Rica are now put at 18–67% – with a cash loss averaging US$17 000 per month (F. Brenes and A. de Mezerville, unpublished).

Available data do not allow precise estimates of the economic losses attributable to *Dermatobia* throughout Latin America, but these have been put as high as US$200 million annually[37]. In many areas, infestation rates are high and increasing. Lombardero[15] estimates that 1.6 million cattle are affected by *D. hominis* in the northern Argentine provinces of Misiones, Tres Rios, Corrientes and Formosa, and believes that the problem is spreading with the expansion of the cattle industry – a condition mirrored in other parts of Latin America. Moreover, even the available estimates of losses probably underestimate the damage by a substantial amount[16], partly because costs of current control methods are rarely taken into account, and partly because the use of chemical control methods masks much of the damage caused by this myiasis. In Costa Rica, the cost of organophosphate insecticides imported for control of cattle myiasis is estimated at US$12 000 per year[31]. But the use of such insecticides does not completely eliminate hide damage due to *Dermatobia* because although holes left by emerging adult flies can be avoided, the death of a larva inside the subdermal cavity initiates a fibrotic reaction that can also mar the hide and reduce its value.

***Dermatobia* and public health**

Dermatobia infections in man are most common among cattle workers and among children under five years old[15,38–44] (E. Sancho and C. Boschini, unpublished). The relatively high prevalence in infants may be because they tend to be less aware of insects on their skin, they often wear less clothing than adults, and their soiled diapers may particularly attract insect carriers of *Dermatobia* eggs. In cattle areas where control methods have been widely applied against *Dermatobia*, outbreaks of infection have been noted among children and other domestic animals, possibly because the application of insecticides to cattle has encouraged some insect species to switch to other hosts.

In children, the most frequent sites of *Dermatobia* lesions are on the most

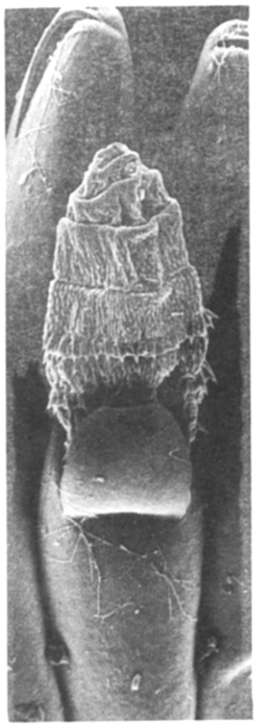

Fig. 4. Young larva of Dermatobia hominis *hatching from egg batch.*

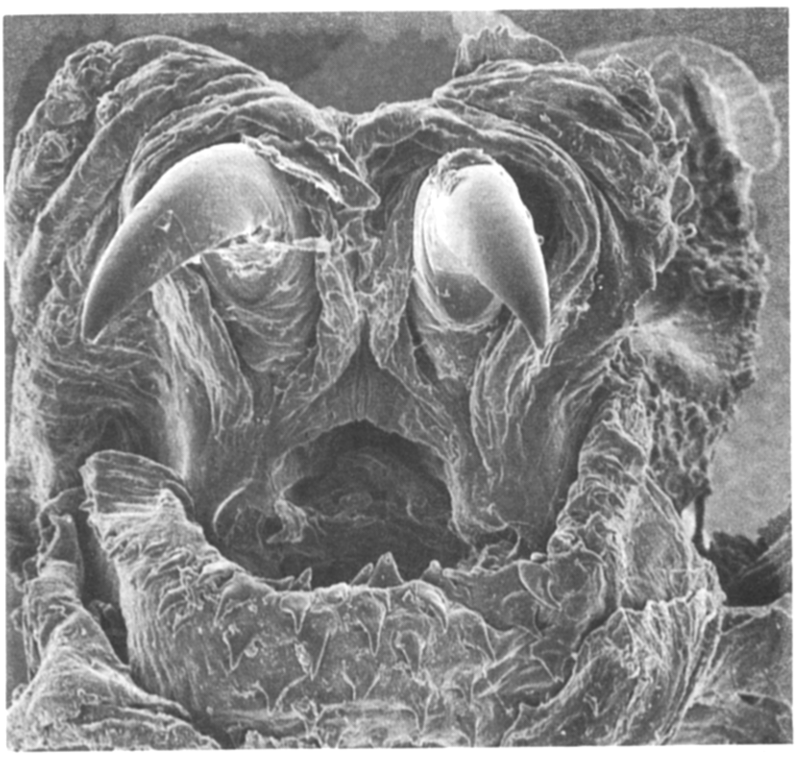

Fig. 5. Mature larva of Dermatobia hominis *showing anterior hooks.*

Fig. 6. Distribution of Dermatobia hominis *in Costa Rica. (Adapted from Ref. 30.)*

exposed parts of the body – particularly the head, face, arms and legs[41]. Larvae in the scalp may produce a scar resulting in baldness of that area. Larvae lodging under the eyelid can provoke serious ophthalmic problems resulting in loss of the eye[42]. Infant mortality due to *Dermatobia* is infrequent, but can occur if the larvae penetrate deeper under the skin and into young bones. Three such cases are known (in Costa Rica, Panama and Brazil), where the larvae penetrated the child's scalp and lodged in the brain[18, 43, 44]. In such cases, neurological symptoms including convulsions and vomiting were noted, with a clinical picture similar to bacterial meningoencephalitis observed through changes in the cerebrospinal fluid. In general, the presence of one or more superficial painful swellings with a central opening would be suggestive of *Dermatobia* infection, but specific diagnosis can only be made after surgical extraction of the larvae. Secondary bacterial infection can result if the larva is not removed but killed within its cavity.

Available data probably underestimate the losses due to Dermatobia. *Reductions in milk and meat yields are very hard to quantify in rural areas of Latin America, and even direct estimates of losses to the leather industry based on numbers of damaged hides do not usually take account of the costs of control measures already applied. Moreover, the public health importance of* Dermatobia *is rarely considered.*

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