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A revision of the Palaearctic species of *Lampromyia* Macquart (Diptera, Vermileonidae), with the description of a new Iberian species and a cladogram for the genus

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Abstract. The Palaearctic species of *Lampromyia* Macquart are revised; nine species are recognised. Previous identifications of the two European species are found to be incorrect. *L. cylindrica* (Fabricius) proves to be an African species; *L. funebris* Dufour is retrieved from synonymy for the species occurring in Iberia and France previously known as *cylindrica*. *L. pallida* Macquart also is exclusively an African species; specimens from Spain formerly identified as *pallida* are described as *L. iberica* sp.n. New keys and descriptions are given for all the species, and a neotype is designated for *cylindrica*. Apomorphies establishing the monophyly of *Lampromyia* are discussed. A cladistic analysis reveals three species-groups: the *pilosula* group of Southern Africa, the *canariensis* group of the Canary Islands, and the *cylindrica* group of NW Africa + Iberia/France. The cladogram is fully resolved, and biogeographical conclusions are drawn. An interesting distribution pattern in the Canary Islands is noted: the cladistic age of the species is incongruent with the geological ages of the islands. Two cases of vicariance are identified which evidently involved the dispersal of ancestral stocks from Africa into Iberia and their subsequent isolation.

Key words. Vermileonidae, Palaearctic Region, *Lampromyia*, systematics, cladistics, biogeography.

Introduction

Wormlion flies of the family Vermileonidae in the western Palaearctic fauna are classified into two genera, *Vermileo* Macquart, 1834 and *Lampromyia* Macquart, 1835. *Vermileo* is the more familiar genus in Europe, as it is quite widely distributed in the countries bordering the Mediterranean, and it has been the subject of a considerable literature devoted to the remarkable larval stages which make pitfall traps in fine sand and dust for catching their insect prey. *Lampromyia* is less familiar, being essentially an African genus with a limited extension into the Iberian Peninsula and adjacent parts of France.

In the literature of Palaearctic dipterology, these flies were traditionally considered to constitute a subfamily of the Rhagionidae. This classification gradually lost credibility, partly because of the lack of any suite of apomorphies by which the family Rhagionidae could be defined (Hennig 1967, Woodley 1989). After various authors had queried affinities between vermilionines and rhagionids, the wormlion flies eventually were given family status by Nagatomi (1977), although their relationships could not be clarified. Despite attempts in more recent years to refine the classification of the Lower Brachycera, the affinities of the Vermileonidae are still uncertain and disputed (Griffiths 1994, Stuckenberg 1995a, Nagatomi 1996). The family was segregated by Griffiths (1994) in an infraorder Vermileonomorpha, along with the fossil families Eremochaetidae and Protobrachycerontidae.

This study extends a series directed at a revision of all the Afrotropical Vermileonidae. Earlier contributions were the description of the new genus *Vermilynx* Stuckenberg (1995a), a revision of the genus *Vermipardus* Stuckenberg (1995b), the description of a second species of *Vermilynx* (Stuckenberg 1996a), and a revised generic classification of the Southern African vermilionids (Stuckenberg 1996b). The scope of this revision of the Palaearctic species of *Lampromyia* has been defined by the new generic classification of Southern African species, most of which were described originally in *Lampromyia*. It was established that a large majority of these species are generically distinct, and that *Lampromyia* is represented in Southern Africa only by a clade of three eastern montane species; the main centre of diversity of *Lampromyia* is now seen to be in the Canary Islands, north-western Africa, and south-western Europe, where nine species are known.

It has been an enduring biogeographical enigma that a vast geographical gap exists between the Southern African and Palaearctic wormlion faunas; both Wheeler (1930) and Hennig (1967) drew attention to this peculiarity. Progress in understanding factors behind the pattern was retarded by a lack of knowledge of the phylogenetic relationships between the members of these faunas. The problem now is more sharply focused: it remains to elucidate affinities only between the species of *Lampromyia*, using the more restricted definition now applied to this genus. In the cladistic study presented below, a clear pattern of relationships is revealed; the resulting cladogram for *Lampromyia* is robust and translates into an informative area cladogram of considerable interest.

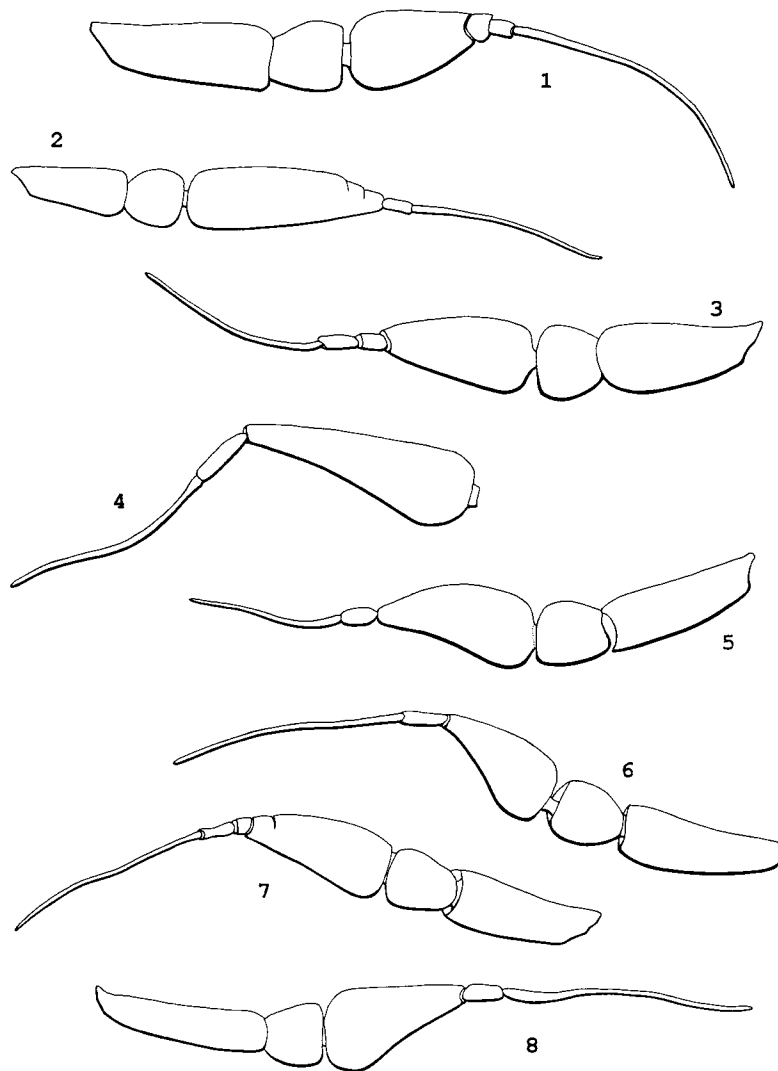
The early literature on Palaearctic wormlion biology was reviewed in detail by Wheeler (1930). Later studies were published by Buchner (1940), Hafez & El-Moursy (1956a, 1956b, 1964), Le Fauchaux (1961), Hemmingsen (1963, 1968, 1977), Hemmingsen & Regner Nielsen (1971), and Frederiksen & Hemmingsen (1972). The larval mouthparts of *Vermileo vermileo* (L.) were examined recently by Ludwig, Smola & Melzer (1996).

Material, methods and antennal segmentation

Specimens used in this study are pinned flies in the following collections: Natal Museum, Pietermaritzburg (NMSA); Muséum National d'Histoire Naturelle, Paris (MNHN); Institut Royal des Sciences Naturelles de Belgique, Brussels (IRSN); Naturhistorisches Museum, Vienna (NHMV); Institut voor Taxonomische Zoölogie, Universiteit van Amsterdam (ITZA). Label data are cited as originally given; a slash (/) indicates the end of a line of data, and two (//) indicate data either on a second label or on the reverse side of a label.

Terminology used for male genitalic structures follows that in previous publications (Stuckenberg 1995b, 1996b), and is largely standard. The following abbreviations are used in the illustrations: ae, aedeagus; ag, apical guides, paired distal ventromedian extensions of the synsternite, one on each side of the ventral aperture; cd, mediodorsal projections on upper margins of synsternite; db, dorsal bridge, a transverse sclerotisation across the dorsobasal edges of the gonocoxites, to which the aedeagus is attached dorsobasally; ea, ejaculatory apodeme; gs, gonostyle; p, lateral projections of aedeagus; pr, male proctiger; sn, synsternite, the compound structure formed by fusion of the gonocoxites and (apparently) the hypandrium; va, ventral aperture, a distal ventromedian aperture in the synsternite, partly closed distally by the apical guides. T=tergite, S=sternite.

Reduction of antennal segmentation in Southern African vermilionids was discussed previously (Stuckenberg 1996b). It was shown that the primitive brachycerous condition of a scape and pedicel followed by a tapering series of eight segments, was modified in various



Figs 1—8: Antennae of *Lampromyia* species. 1) *L. canariensis*; 2) *L. fortunata*; 3) *L. hemmingseni*; 4) *L. iberica* sp. n. (scape and pedicel missing); 5) *L. funebris*; 6) *L. cylindrica*; 7) *L. lecerfi*; 8) *L. pallida*. Not to scale.

clades as follows: a) segment 10 becomes more slender and elongate, and segment 9 shorter and narrower, both losing the trichoid sensilla and evolving into a two-segmented stylus; b) segments 3—8 become compacted and undergo fusion in a progressive distal sequence, beginning with fusion of 3 and 4, and proceeding to the condition in some species in which only a composite unit comprising 3—8 exists between the stylus and the pedicel. The stylus thus comprises morphologically segments 9+10 in all species; it evolved to fulfil a tactile function, while the intermediate segments are the carriers of chemoreceptors. To ensure morphological correctness, the scape and pedicel are numbered 1 and 2 respectively, and the stylus segments are numbered 9 and 10; numbering of intermediate segments indicates which are still unfused. For example, in some Palearctic species the formula 1+2+3—7+8+9+10 applies (figs 1, 3); 3—7 indicates fusion of five segments. If a segment is partially fused, it is counted as present.

Inventory of species

Growth of taxonomic knowledge of the Palaearctic *Lampromyia* fauna has been prejudiced by misidentifications of the two species in Europe, to which the names *L. cylindrica* (Fabricius) and *L. pallida* Macquart were applied. Confusion also surrounded the identity of vermilionids in the Canary Islands.

The oldest species, *Lampromyia cylindrica* (Fabricius, 1794), was very briefly described, with reference to coloration only. The source of the material nevertheless was clearly stated to be north-western Africa ('Habitat in Barbaria'), but few authors considered the possible implications of this. Subsequently, a species with similar coloring, named as *Lampromyia funebris* Dufour, was described in 1850 from specimens collected in Madrid ('*Hispaniae campo Matritense*'). It was listed by Osten Sacken (1883) as a synonym of *cylindrica*, and Becker (1908) concurred, stating that he had the 'echte' *cylindrica* from Spain; all subsequent authors accepted and perpetuated this synonymy. In fact, *cylindrica* is exclusively an African species, for which a neotype and restricted Algerian type locality are designated below. *L. funebris*, though closely similar and related, is not conspecific; it is retrieved from synonymy, and this name is applied to the dark-winged *Lampromyia* occurring in Iberia and France.

The second-oldest species and type of the genus, *Lampromyia pallida* Macquart (1835), was described on specimens from Oran on the Algerian coast. Material from Tunis, including the immature stages, was described and named as *L. miki* Marchal (1897), but this species was soon synonymised with *pallida* (Becker 1900). In "Die Fliegen", Lindner (1924) listed three species: *L. canariensis* Macquart of the Canary Islands; *L. cylindrica* (Fabr.), with *funebris* as a synonym, of North Africa and Spain; and *L. pallida* Macquart (with synonym *miki*) not only of North Africa but also of Southern France. Wheeler (1930) noted this and observed that Lindner's record of *pallida* from France was unsupported by definite data. A French record for any *Lampromyia* species first became available when Séguy (1926) stated that *cylindrica* occurs in the Drôme District. Lindner seems to have been the first author to record *pallida* in both Africa and Europe. Séguy (1926), however, considered *pallida* to be distributed in North Africa and the south of Spain, and subsequently (Séguy 1934) he published two Spanish records for *pallida*. A description of the hypopygium of a Spanish specimen identified as *pallida* was published by me (Stuckenberg 1960). During the 1960s, however, I was able to examine *Lampromyia* flies reared by the late Dr A. M. Hemmingsen from larvae he had collected in Tunisia, and also specimens from Spain, identified as *pallida*, in European museums. It was apparent that Spanish specimens were not conspecific with *pallida*. Dr Hemmingsen was informed of my findings and mentioned them in two publications (Hemmingsen 1968; Hemmingsen & Regner Nielsen 1971), thus anticipating the following results.

It turns out that no species occurs on both sides of the Mediterranean: *pallida* is a species of north-western Africa; the closely similar species in Spain is undescribed and is named below as *Lampromyia iberica* sp. n. There is no evidence that any species other than *funebris* occurs in France. The inventories of species by Kertész (1908), Becker (1921), Lindner (1924), Séguy (1926, 1930, 1934), Szilády (1934) and Stuckenberg (1960) are thus defective, and all published keys to the Palaearctic species are invalid.

The most recent catalogue of Palearctic Vermileonidae was published by Majer (1988). It suffers from so many errors and omissions that its scientific value is greatly impaired. Inexplicably, Majer included the South African species *Lampromyia sericea* (Westwood), wrongly stating that its type locality is 'North Africa'.

The following species are recognised in this study:

Lampromyia cylindrica (Fabricius, 1794); NW Africa

Lampromyia pallida Macquart, 1835; NW Africa

Lampromyia canariensis Macquart, 1839; Canary Islands

Lampromyia funebris Dufour, 1850; Iberia, France

Lampromyia lecerfi Séguy, 1928; NW Africa

Lampromyia nigripennis Séguy, 1930; NW Africa

Lampromyia fortunata Stuckenberg, 1971; Canary Islands

Lampromyia hemmingseni Stuckenberg, 1971; Canary Islands

Lampromyia iberica sp.n.; Iberia.

Cladistic analysis

In the cladistic analysis presented below, it emerges that *Lampromyia* comprises three distinctive, monophyletic, allopatric species-groups: the *pilosula* group of Southern Africa (3 species), the *canariensis* group of the Canary Islands (3 species), and the *cylindrica* group of north-western Africa, Iberia and France (6 species). A cladistic demarcation of *Lampromyia* that spans the gaps between these groups, in a manner confirming the monophyly of the genus, proves to be based on limited evidence.

General exoskeletal morphology of *Lampromyia* and related afrotropical genera is notably constant and appears plesiomorphic. The main modifications involve a suite of specialisations linked to anthophily and to diversification of male genital structures. Morphological diversification during cladogenesis was associated particularly with mouthpart evolution (rostral elongation and labellar modifications), antennal specialisations (evolution of a style and fusion of segments), and changes to the form of components of the hypopygium. The terrestrial larval habit, specialised predatory behaviour based on pitfall-trapping, and associated larval morphology, are constant and plesiomorphic for the entire family. This may be associated with a uniform, distinctive female genital and postabdominal morphology, possibly linked to a consistent oviposition behaviour (for data on oviposition, see Hemmingsen & Regner Nielsen 1971).

In the Afrotropical vermilionid fauna, *Vermipardus* of South Africa has several primitive features (Stuckenberg 1995b, 1996b). The other genera constitute a monophyletic sister-group to *Vermipardus*; this comprises *Vermilynix* Stuckenberg, *Leptynoma* Westwood (with subgenera *Leptynoma* s. str. and *Perianthomyia* Stuckenberg) and *Lampromyia*. Adaptations possibly associated with hovering flight during flower visiting characterise *Leptynoma*; the species have a slender body, a more petiolate and narrower wing form, unique specialisations of the radial venation, marked development of strongly reflective silvery pruinescence on the male abdomen (possibly a conspicuous sexual signal in arid habitats and montane shrublands), and apical thickening of the hind tibia.

Lampromyia is now defined mainly by plesiomorphies which involve body habitus, wing form and venation, and hind tibial form (Stuckenberg 1996b). The very

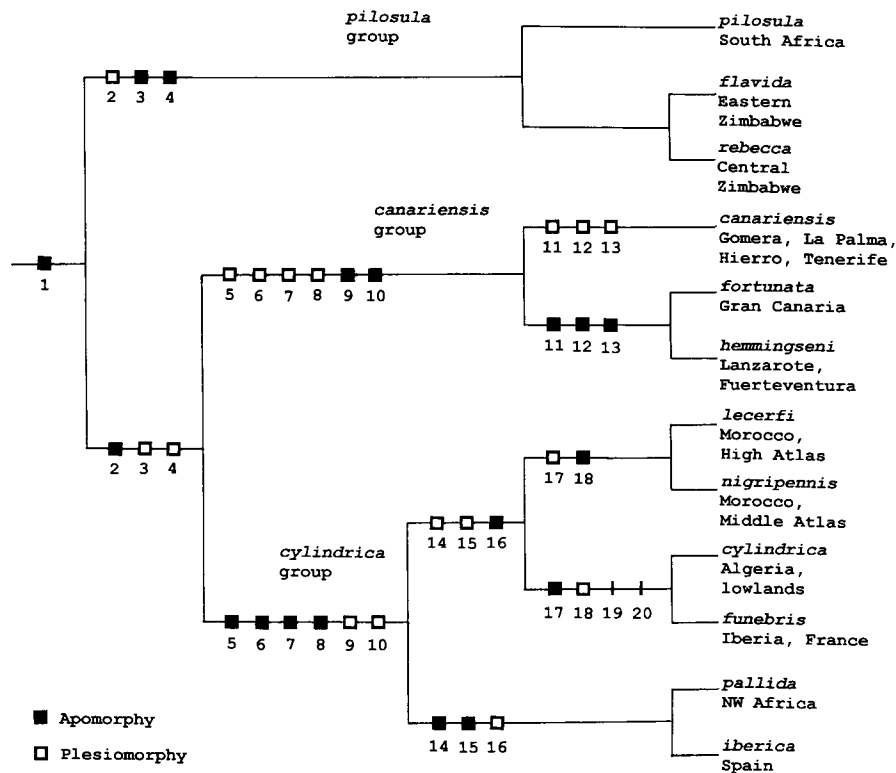


Fig. 9: Cladogram proposed for *Lampromyia*; characters 19 and 20 are treated provisionally as synapomorphies of *L. cylindrica* and *L. funebris*, and are predicted to occur also in *L. lecerfi* and *L. nigripennis* (see text). Relationships within the *pilosula* group are established by Stuckenberg (1996b).

elongate proboscis is a striking apomorphy but also occurs in *Leptynoma*, probably as a homoplasy. The possibility of homoplasy was revealed by the discovery of a difference in the pattern of reduction of the pseudotracheae in the labellum: in *Lampromyia* there is only a single, bifid pseudotrachea in each labellum, whereas in *Vermilynx* + *Leptynoma* the pseudotrachea is trifid (Stuckenberg 1996b). Moreover, the proboscis of *Vermilynx* is of intermediate length, and represents a precursor state to the one in *Leptynoma*. It has been suggested that *Lampromyia* may have evolved from a *Vermilynx*-like form elsewhere in Africa (Stuckenberg 1996b).

Monophyly of *Lampromyia* is demonstrated by this specialisation of the pseudotracheae, in conjunction with the greatly elongate proboscis, but no other apomorphy has been detected for the genus as a whole. However, monophyly of the *cyindrica* + *canariensis* groups (involving 75 % of the species of *Lampromyia*) is proved by a highly apomorphic modification of T8 in the male (character 2 below). The only clade lacking this modification (the *pilosula* group) is clearly monophyletic, and is biogeographically distinctive in its isolation in Southern Africa. Given the geographically fragmented and relictual condition of *Lampromyia*, a scarcity of synapomorphies shared between the *pilosula* group and the distant northern species-groups is not unexpected.

In this cladistic analysis, paragraph numbers correspond to numbers in the cladogram (fig. 9), and the italicized opening statement of each paragraph specifies the apomorphic state. Reference was made to *Vermileo*, *Vermipardus*, *Leptynoma* and *Vermilynx* for outgroup comparison. No male specimens are known for *nigripennis* and *lecerfi*, but two female apomorphies (characters 5 and 6) were found that convincingly place these species in the cladogram. Characters 19 and 20 had to be treated provisionally as synapomorphies of male *cylindrica* and *funnebris*. It is predicted that hypopygial characters 7, 8, 19 and 20 will all prove to exist in *nigripennis* and *lecerfi*; if this prediction is fulfilled, the cladogram should be irrefutable.

1. *A single, bifid pseudotrachea present in each labellum.* The most plesiomorphic state is in *Vermileo* which has many pseudotracheae in each labellum in a common brachycerous arrangement; in *Vermipardus* the labella are more specialised, being smaller with the pseudotracheae reduced to a cluster of 6–7 in each labellum; in *Vermilynx* + *Leptynoma* there is a single, trifid pseudotrachea (Stuckenberg 1996b, Figs 10, 11).

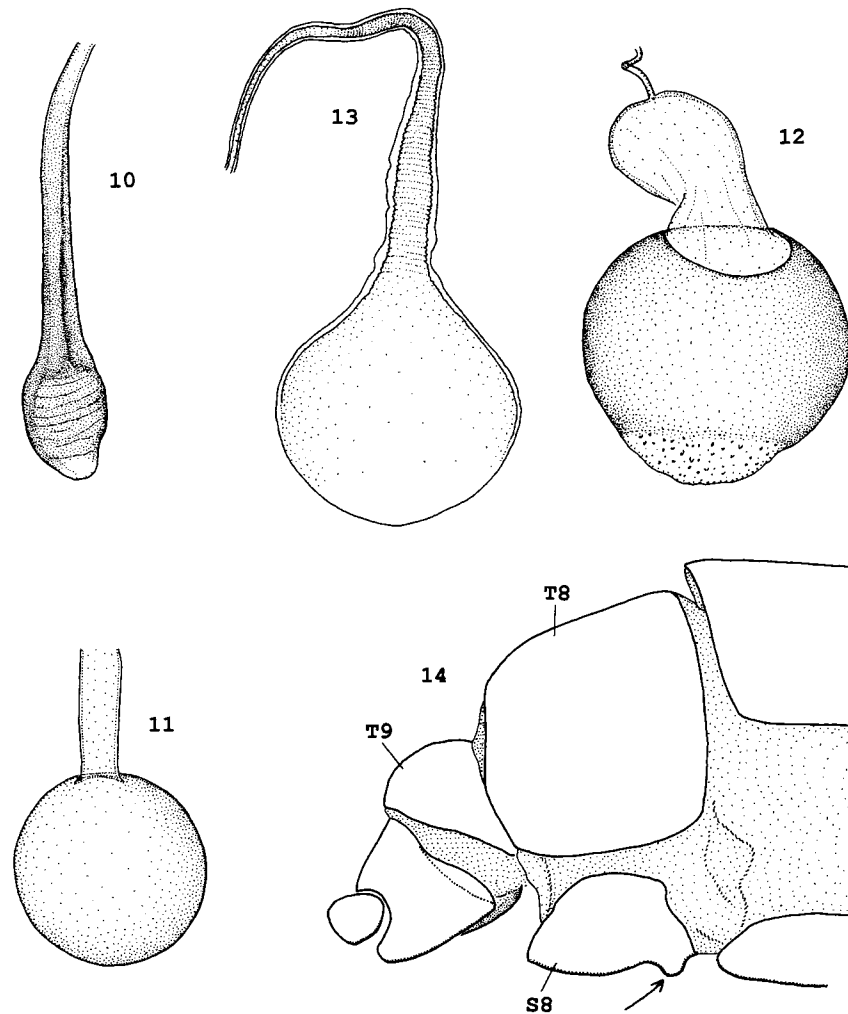
2. *T8 of ♂ deeply concave on posterior margin, much shortened over most of its width and withdrawn under T7, exposed and setose only laterally (figs 21–24, 34).* T8 is completely reflexed beneath T7 except for a small, triangular lateral section which is exposed on each side; the posterior edge of T7 is thus adjacent to the basal border of the epandrium; T8 would be exposed only during mating, when the infolded intersegmental membranes would be extended. Associated with this feature is a characteristic posture in which the hypopygium is flexed dorsad relative to the longitudinal axis of the abdomen, found in the Palaearctic species except those in the Canary Islands. The very large size of the epandrium is made more conspicuous by this posture (figs 24, 34). Character 2 occurs in the Palaearctic species of *Lampromyia* and is assumed for *nigripennis* and *lecerfi*; in the Southern African species, T8 is exposed and of normal, plesiomorphic form. The least modified form of T8 among the Palaearctic species occurs in *hemmingseni* (fig. 18).

3. *Spermathecae small, gradually and irregularly swollen terminally, and darkly sclerotised (fig. 10).* This condition occurs in the Southern African species only; all Palaearctic species have subspherical, less thickly sclerotised, relatively larger spermathecae (figs 11–13), and the same general form occurs in the outgroups. Spermathecal form varies greatly in the Orthorrhaphous Brachycera, but the spherical condition occurs frequently and is probably plesiomorphic. The *canariensis* group and both subgroups of the *cylindrica* group may each be characterised by modifications of the spherical form: all species of the *canariensis* group have the same, least specialised spermatheca (fig. 11); in the *cylindrica* group, material was inadequate for all the species to be examined, but probably in the *cylindrica* subgroup the form in fig. 12 is characteristic, in which a membranous sac arises from a relatively large aperture in the spermathecal wall and gives rise to the duct; in the *pallida* subgroup, the almost colorless spermatheca with long tapering extension and rugose inner surface as found in *pallida* (fig. 13) probably occurs also in *iberica*.

4. *Dorsal bridge extended posteriorly in a symmetrical, apically rounded lobe.* Found only in the Southern African species (Stuckenberg 1960, Fig.11; 1996b, Fig.33). This is a more elaborate state; usually the dorsal bridge is transversely rectangular or arched.

5. *T9 of ♀ extended posteriorly as a short hood with a broad, shallow excision in posterior margin (fig. 15).* The ♀ terminal tergite of all *cylindrica*-group species has this form. What is visible in pinned flies depends on postmortem drying; T9 may become rather flattened dorsoventrally, which has the effect of straightening out the apical emargination, but relaxation by maceration of the postabdomen will reveal its true form. In the *canariensis* group T9 has other forms.

6. *Cerci of ♀ with apical segment short, largely hidden beneath basal segment.* In females of the *cylindrica* group, only the basal cercal segment is clearly exposed in dorsal view (fig. 16). In the *canariensis*-group species, the apical cercal segment is longer and clearly exposed (fig. 14).

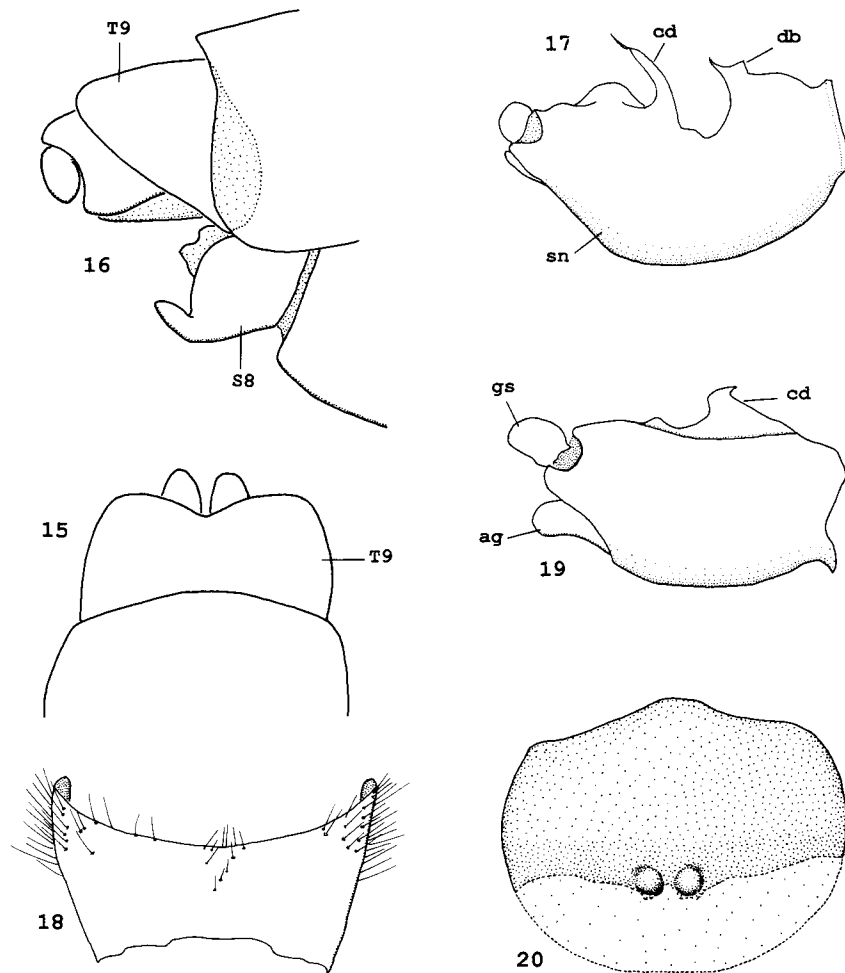


Figs 10—14: 10—13 Spermathecae. 10) *L. flavida*; 11) *L. canariensis*; 12) *L. lecerfi*; 13) *L. pallida*. 14) *L. hemmingseni*, ♀ abdomen, lateral, showing shape of cercus; position of median swellings on S8 indicated by arrow.

7. *Epandrium elongate*, projecting well beyond apex of synsternite (figs 24, 34). This condition contributes to the characteristic appearance of ♂♂ of the *cylindrica* group, which seemingly have a disproportionately large hypopygium. A relatively much shorter epandrium occurs in the *pilosula* and *canariensis* groups, and in other afrotropical genera, except, but less markedly, in *Perianthomyia* (Stuckenberg 1996b, Figs 21, 22).

8. *Aedeagus lacking lateral projections*. In *Vermipardus* the aedeagus is a curved tube, this evidently being the plesiomorphic form. In species of *Leptynoma*, *Vermilynx*, the *pilosula* group, and the *canariensis* group (figs 51, 55, 59, p), the aedeagus appears trifold because of two lateral extensions or arms; these do not include the lumen of the aedeagus. In species of the *cylindrica* group, only *funnebris* and *pallida* have any structural development which may be comparable, in the form of dorsally directed flanges on each side of the aedeagus (figs 31, 41, p). As the trifold condition is so widespread, the lack of these lateral arms must be a reversal.

9. *Mediodorsal projection present on upper margins of synsternite*. This structural elaboration is apomorphically developed only in the species of the *canariensis* group (Stuckenberg 1960,



Figs 15–20: Structural details. 15–16 *L. lecerfi*; 15) ♀ terminal tergites, showing apical emargination of T9; 16) ♀ abdomen, lateral, terminal segments, showing shape of cercus; 17) *L. fortunata* synsternite, lateral, showing form of mediodorsal projection (cd) (character 9). 18–20 *L. hemmingseni*; 18) ♂ T8, basal margin below; 19) synsternite, lateral, showing form of mediodorsal projection (cd); 20) ♀ S8, showing position of paired median swellings.

Fig. 32 cd; 1971, Figs. 7, 8, 12, cd). It varies in form specifically, as illustrated below (figs 17, 19, 48, 50, 52, 58, cd).

10. *Aedeagus almost straight* (figs 51, 55, 59). A character of the Canary Islands species. In all other species of *Lampromyia*, and in other afrotropical genera, the aedeagus is strongly curved upwards.

11. *S8 of ♀ with two closely adjacent, median, basal swellings* (figs 14, 20). An exceptional apomorphy in *fortunata* and *hemmingseni* of the Canary Islands.

12. *Epandrium with two deep dorsal invaginations* (figs 54, 56, 57). In *fortunata* and *hemmingseni* these invaginations in the dorsal surface appear ventrally as internal projections; in *fortunata* they are pits with an internal space, but in *hemmingseni* the walls have fused. This is a unique apomorphy.

13. *Aedeagus partly desclerotised apico-dorsally* (figs 58, 59). An exceptional condition found only in *fortunata* and *hemmingseni*.

14. *Dense silvery-grey pruinosity developed on head and thorax*. The characteristic and unique appearance of *pallida* and *iberica* is due to this feature.

15. *Oblique apruinose mark on thoracic pleura.* A bare, shining brown mark descends obliquely forwards from before the wing to the fore coxa, in *pallida* and *iberica*; not seen in any other species of *Lampromyia*.

16. *Wings dark or obviously patterned.* Unusually dark wings without clearcut pattern are a feature of *cylindrica*, *funnebris* and *nigripennis*; in *lecerfi* an intermediate state occurs, with staining of the membrane more constrained into a pattern. In *pallida* and *iberica* the wings are clear with only a limited, weak pattern.

17. *Hind leg unicolorous.* In *cylindrica* and *funnebris* the hind femur and tibia are not darkened apically as in *nigripennis*, *lecerfi*, and the great majority of African vermilionids. The only other Palaearctic species with this feature is *Lampromyia canariensis*.

18. *Mesonotum with only a median vitta* (fig. 36). Both *nigripennis* and *lecerfi* have a simplified mesonotal pattern featuring orange-brown or yellowish-brown general coloring and a single broad, brownish median vitta that does not extend onto the scutellum. In *cylindrica* and *funnebris* the mesonotum is trivittate and the scutellum is darkened on the disc, a common condition in afrotropical vermilionids.

19. ♂ *Cerci massive, dark, with form as in figs 25, 29, pr.* This unusual condition, often visible without dissection, occurs in *cylindrica* and *funnebris*; it is treated as a synapomorphy of this pair, but is probably also synapomorphous in *lecerfi* and *nigripennis*.

20. *Epandrium with complex dorsal form* (fig. 21). In *cylindrica* and *funnebris* the epandrium has a median basal depression enclosed by the arms of a Y-shaped elevation that extends posteriorly to the truncated apical margin; the median arm of the elevation is bordered by flattened, rim-like surfaces extending to the posterior margin on each side.

The following preliminary biogeographical conclusions are drawn regarding these palaeogenic flies:

1. The primary division of the genus into the three species-groups, *pilosula* gp + (*canariensis* gp + *cylindrica* gp), is congruent with their interrupted pattern of distribution. The area cladogram thus is: Southern Africa + (Canaries + NW Africa/SW Europe). The great gap separating the *pilosula* group from the others is commensurate with the morphological gap between them.

2. *Lampromyia* appears to be a relict genus of the original African fauna as it used to exist before aridification of the Saharan area and faunal exchange with the Palaearctic Region established the present features of the Afrotropical Region.

3. Although close affinities between the Canarian insect fauna and that of north-western Africa have been noted by various authors, in the case of *Lampromyia* affinities are not so close. The *canariensis* group clearly is a monophyletic clade with a separate history.

4. There is convincing evidence that the Canarian species are related as follows: *canariensis* + (*fortunata* + *hemmingseni*). This results in the unexpected and anomalous discovery that the oldest species (*canariensis*) occupies the geologically younger islands. Moreover, these islands (the western ones — La Palma, Gomera, Hierro, Tenerife) are furthest from the presumed African mainland source of the ancestral vermilionid stock.

5. The *cylindrica* group is deeply cleft into the *cylindrica* and *pallida* subgroups; in turn, the *cylindrica* subgroup separates into two species-pairs each biogeographically different. Elements of both subgroups evidently participated in dispersal events, probably coeval, from Africa into Iberia during a period of dry-land connection between them. Subsequent vicariance produced the two pairs of closely similar species: *pallida* + *iberica*, and *cylindrica* + *funnebris*.

6. The *lecerfi* + *nigripennis* pair is associated with the Atlas orogeny which dates from the Oligocene onwards.

A fuller examination of African vermilionid biogeography is planned for a later publication.

Keys

The southern boundary of the Palearctic Region in China is placed at 30°N latitude (Soós & Papp 1988), so the genus *Vermiophis* Yang, with six Chinese species and one in Tibet, is entirely Palearctic (Yang 1979; Yang & Chen 1986, 1987, 1993). However, *Vermiophis* is unlikely to occur in Europe or Africa.

Key to western Palearctic genera

1. Proboscis elongate, labium more than twice length of mesonotum; labella narrow, dorsoventrally compressed, held closely together; face protruding prominently, subtriangular in profile *Lampromyia*
— Labium very short; labella relatively large and close to ventral surface of head; face curving ventrally and following profile of eye, not visible in lateral view *Vermileo*

Key to species of the Canary Islands

1. Median vitta of mesonotum broad, dark, mat, not divided longitudinally by a pale midline stripe; costal cell conspicuously dark smoky brown; hind tibia and femur uniformly brownish, not obviously darker apically. [Dark species with conspicuous greyish pruinose bands on abdomen; Tenerife, La Palma, Gomera, Hierro] *canariensis*
— Mesonotum with two narrow, dark, median vittae separated by a conspicuous pale midline stripe; costal cell weakly colored, not much darker than rest of wing; hind femur and tibia contrastingly dark brown over short apical section 2
2. Brownish, hairy flies, with bright reddish-yellow pruinescence and obvious hairs on head and thorax; no greyish pruinescence on abdominal tergites of either sex; male abdomen uniformly wide and abundantly clothed with dark, erect hairs; wing shining smoky brown; R_{2+3} usually with moderate posterior recurvature apically. [Lanzarote, Fuerteventura] *hemmingseni*
— Head and thorax silvery-grey pruinose; tergites with basal bands of silvery pruinescence in both sexes; male abdomen slightly petiolate, without conspicuous hairs; wing greyish-hyaline, costal cell pale brownish; R_{2+3} without apical recurvature, strongly flexed forwards to costa. [Gran Canaria] *fortunata*

Key to species of north-west Africa

1. Face, frons, occiput and thorax extensively and densely silvery-grey pruinose; mesonotum with conspicuous marks posteriorly (fig. 35); pleura with oblique, shining brown band; R_{2+3} with abrupt or angular apical bend. [Coastal Tunisia and Algeria, probably also Morocco] *pallida*
— Not conspicuously silvery-grey flies with such markings; R_{2+3} not abruptly bent forwards apically 2
2. Hind legs almost unicolorous; median mesonotal vitta extending onto scutellum which is intensely dark on disc. [Abdomen blackish or brownish-black; Algerian coastal hinterland] *cylindrica*
— Hind tibia and femur both contrastingly darker apically; median vitta of mesonotum not extending onto scutellum [Atlas ranges] 3
3. Conspicuously bicolorous species, thorax orange-brown, abdomen intensely dark blackish-brown; wing almost uniformly intense smoky-brown, costal cell not distinctly darker than adjacent cells; cell r_1 without a clear subtriangular area basally; fork of R_4 and R_5 longer and narrower (fig. 33). [Middle Atlas] *nigripennis*

— Almost uniformly yellowish-brown or orange-brown species; female abdomen irregularly darker apically in more mature specimens, but no strong colour contrast between thorax and abdomen; wing not uniformly colored, greyish with weak smoky-brown tinge which is stronger in anterior cells, or greyish with brownish staining bordering veins, but costal cell always more strongly colored and a conspicuous pale area present in base of cell r_1 ; radial fork as in fig. 32. [High Atlas] *lecerfi*

Key to European species

1. Pale species, wing clear with only sparse, weak, brown staining around some veins; mesonotum with three similar dark vittae heavily overlain with greyish pruinescence; abdomen mostly orange, with dark brown markings across T1 and T2; hind femur and tibia contrastingly dark brown apically. [Pleura greyish pruinose, with bare shining brown band obliquely between wing and fore coxa; Iberia] *iberica* sp. n.
- Dark species, wing macroscopically entirely dark brown; mesonotum with a single, very dark brown median vitta; abdomen uniformly dark chocolate-brown or blackish-brown; legs uniformly yellowish-brown [Iberia, southern France] *funnebris*

Taxonomy

cylindrica group

Synapomorphies defining this group: characters 2 and 5—8 above.

cylindrica subgroup: *cylindrica* + *funnebris*

Species with dark wings and body; antennae bicolorous; hind femur and tibia unicolorous; thorax dark brown with dark chocolate-brown median vitta and somewhat fugitive lateral vittae; scutellum dark on disc; abdomen uniformly blackish or brownish-black, hypopygium paler; epandrium (figs 21, 24, 28) very large, its dorsal surface with Y-shaped form, obliquely flexed dorsally relative to longitudinal axis of abdomen; aedeagus (figs 27, 31) strongly curved, lacking ventral keel and lateral arms (possibly represented in *funnebris* by the flanges marked p in fig. 31); ventral aperture large (fig. 26, va); gonostyles short, truncate; male cerci (figs 25, 29) large, dark, enlarged apically and protruding; dorsal bridge (fig. 30, db) arched, concave posteriorly. Spermathecal form like that in *lecerfi* (fig. 12), opening in spermathecal wall relatively smaller than illustrated for that species.

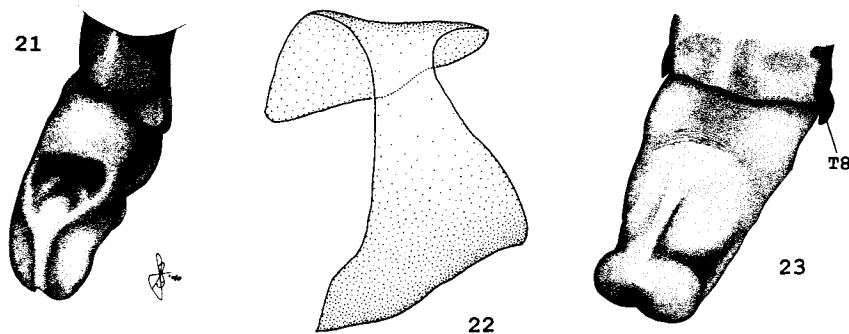
Separated by many hypopygial characters (compare figs 24—27 and 28—31): shape of aedeagus, male cerci, and gonostyli notable; *funnebris* has a short antennal stylus (fig. 5) with apical segment about equal to length of scape; in *cylindrica* (fig. 6) stylus longer, scape about $\frac{3}{4}$ length of apical stylus segment; frons silvery-grey pruinose in *cylindrica*, greyish with warm yellowish overtinting in *funnebris*.

Lampromyia cylindrica (Fabricius, 1794)

Empis cylindrica Fabricius, 1794: 403.

All published references to this species as a member of the European fauna are misidentifications and refer to *L. funnebris* Dufour.

Fabricius described this species on an unknown number of specimens in the collection of R. L. Desfontaines. According to Zimsen (1964), Desfontaines travelled in Tunisia and Algeria around 1790, where he collected plants and insects. His collection of insects was placed in the Paris Museum in 1828, but now appears to be lost. A series from Algeria, identified as *cylindrica* by J. Villeneuve, is in the IRSN; it matches the description by Fabricius and is here accepted as of his species. Designation of a neotype from this series is warranted. All the



Figs 21–23: 21) *L. funebris* apex of ♂ abdomen, showing form of epandrium — T8 is largely withdrawn beneath T7 and only its postero-lateral corners are exposed (see fig. 24). 22–23 *L. pallida*; 22) ♂ T8, oblique dorso-lateral, posterior margin on left; 23) apex of ♂ abdomen, showing form of epandrium in postero-dorsal view, posterior margin of T7 adjacent to basal margin of T9, only the postero-lateral corners of T8 visible.

specimens were collected at Mascara, in a district between the Algerian coast and the interior high plateau that has long been settled, and is on a route that travellers such as Desfontaines would probably have used.

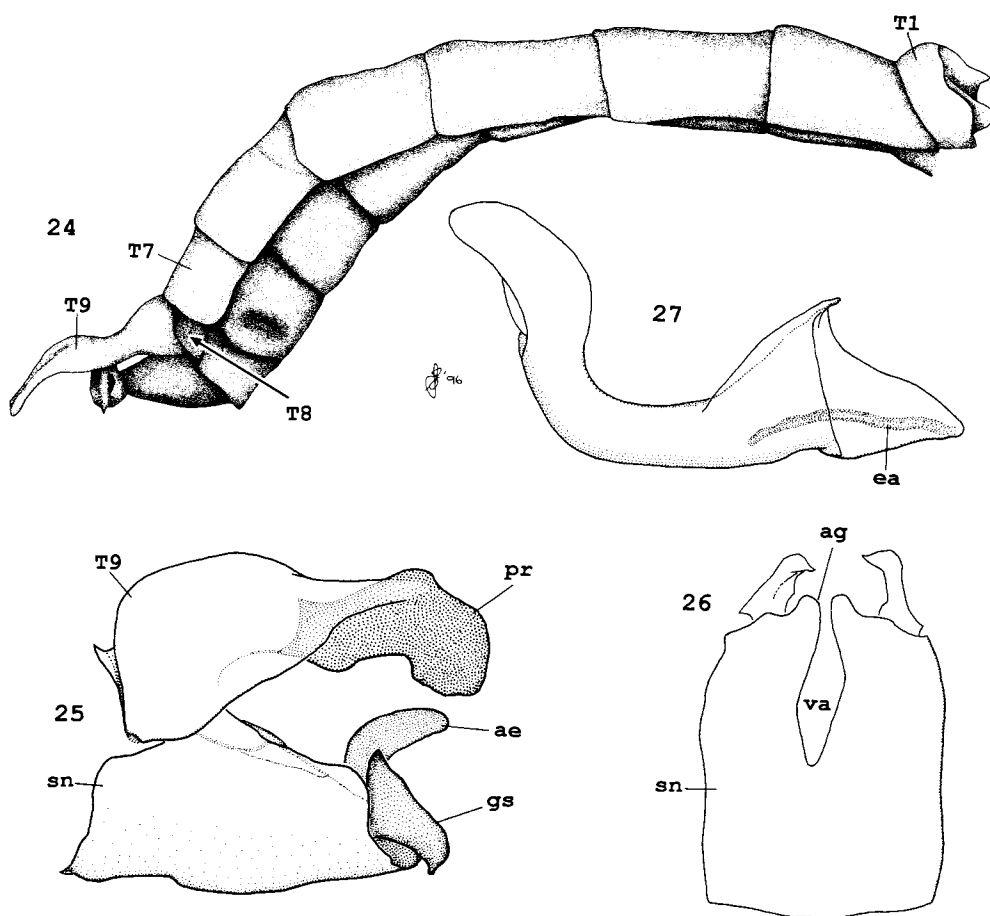
Neotype designation: ♂, Mascara/ (Algeria)/ [illegible hand-written date] (IRSN). Other specimens seen are as follows: 1♂, Mascara, Algeria/ Dr J. Bequaert. 1♂, labelled like Neotype. 2♀ ♀. labelled like Neotype, date '26 Juni 1910'. 1♀, Mascara/ (Algerie)/ [date illegible except year 1908]/ *Lampromyia/ cylindrica/* F. All specimens bear the following printed label: Coll. J. Villeneuve/ *Lampromyia/ cylindrica* F./ R.M.N.H.Belg.15.392. Part of this series was not seen by me.

Male

Head: Antenna (fig. 6) light brown, 1+2+3—8+9+10, 3–8 short, subpyriform; proboscis about 2.7x mesonotal length; face and proboscis dark brown, face bare and shining on sides, thickly brownish pruinose medially, silvery-grey above; frons as wide as long, slightly narrowed apically, shifting shining greyish pruinose over dark brown ground colour; ocellar tubercle shining blackish-brown; occiput with narrow median stripe of dark velvety brown from ocellar tubercle to cervix; remainder of occiput with fugitive, shining, brown-tinged greyish pruinescence.

Thorax: Pronotum dark brown with velvety pruinescence that changes colour with position, in some views silvery-greyish, pale golden in others; mesonotum darkish brown (most evident laterally), with a broad, median, dark chocolate-brown vitta which narrows posteriorly; in dorsolateral view a dark brown sublateral vitta appears adjacent to median vitta, extending from just behind level of humeral callus, in other views these sublateral vittae obscured by shifting colour of mesonotal pruinescence which is warm pale brownish changing to shining greyish; a small, quite intensely dark brown, subtriangular mark postsuturally on lateral declivity above wing; scutellum brown on sides, darkened on disc; pleura mostly strongly brownish with silvery or pale golden pruinescence; posterior pleura and coxae strong yellowish-brown, legs almost uniformly yellowish-brown; metanotum yellowish-brown with narrow brown median stripe in neotype, golden pruinose in more mature specimens.

Wing: Membrane with extensive brownish diffusion around all veins, with weakly developed greyish areas within most cells, these not apparent macroscopically; a conspicuous, uncolored, subtriangular area in base of cell r_1 , and a clear streak in cell sc above it; R_{2+3} gently curved at base, strongly curved forwards to costa apically where there is also a gentle posterior



Figs 24–27: *L. cylindrica*. 24) ♂ abdomen; 25) hypopygium, epandrium incomplete (see T9 in fig. 24); 26) synsternite, ventral; 27) aedeagus, lateral.

recurvature; fork of R_4 and R_5 widely divergent, R_4 a little more curved than R_5 , enclosing wingtip almost symmetrically; cell m_3 closed and stalked, anal cell open.

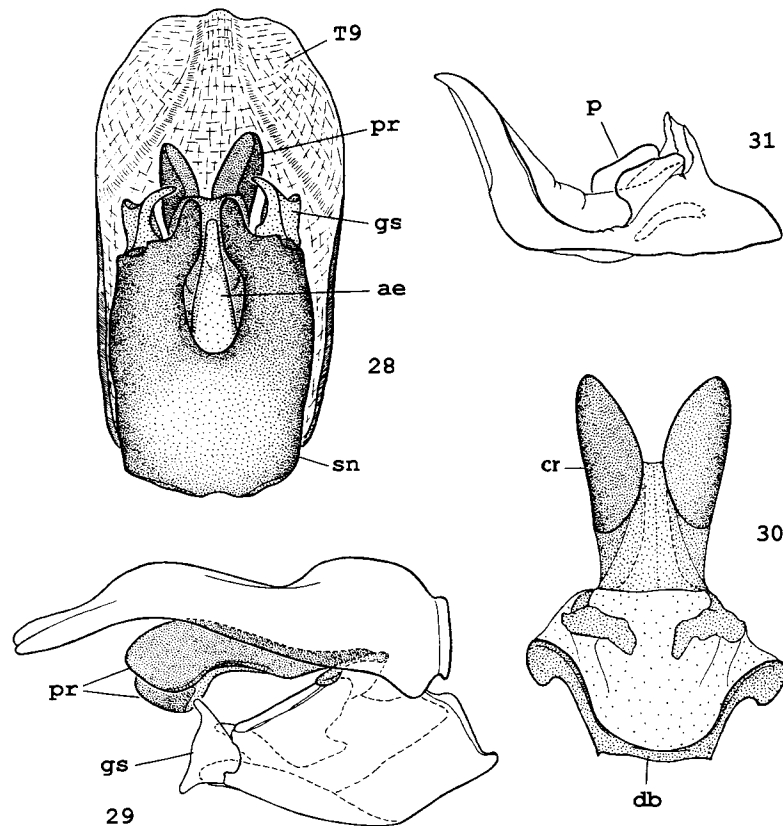
Abdomen (fig. 24): Mostly black, T1 brownish-black laterally, hind margins of T2 and T3 narrowly dark brown; vestiture usually inconspicuous, in anterodorsal view most tergites are seen to have narrow basal bands of fugitive pruinescence fluctuating in colour from greyish to reddish-aureous, elsewhere the tergites with small, fine, recumbent, dark reddish-brown hairs; hypopygium contrasting reddish-brown in mature specimens, yellowish-brown in neotype.

Wing length: Neotype 8.0 mm, other ♂♂ 8.0–8.6 mm.

Female

Closely resembling ♂; abdomen shining dark brown to brownish-black, depending on maturity; proboscis length 2.5–3.0 x mesonotal length; three subspherical, pale brown spermathecae in segment 7, like those in *lecerfi*.

Wing length: 7.0–8.4 mm.



Figs 28–31: *L. funebris*. 28) hypopygium, ventral; 29) hypopygium, lateral; 30) ♂ proctiger and dorsal bridge, dorsal; 31) aedeagus, lateral. (From Stuckenberg 1960.)

***Lampromyia funebris* Dufour, 1850 stat. rev.**

Lampromyia funebris Dufour, 1850, p. 152, pl. vi, fig. 14; Hemmingsen & Regner Nielsen, 1971, pp. 177–8, 201. Not *Lampromyia cylindrica* (Fabricius, 1794) of other authors.

The taxonomic history of this species is described above. It was wrongly synonymised with *cylindrica* by Osten Sacken (1883), and this was accepted by subsequent authors.

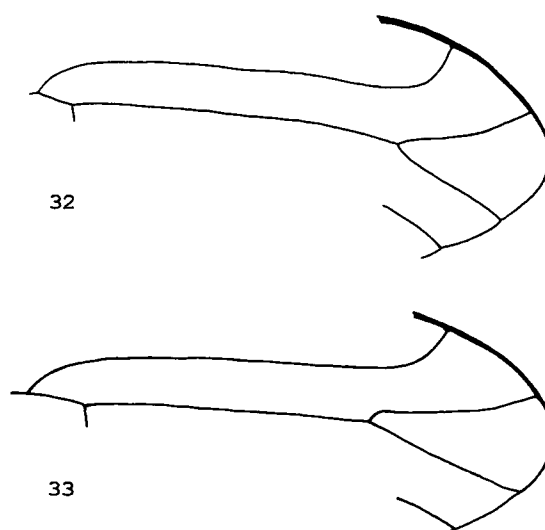
Séguy (1926, 1934) provided a drawing of a fly of this species, captioned as '♂' *cylindrica*; the drawing in fact shows a ♀.

Type locality: Madrid, Spain; no extant type material known.

Previous records (as *cylindrica*): SPAIN: Ribera (Lérida) (Séguy 1934); Barcelona (Séguy 1926). FRANCE: Drôme District (Séguy 1926); Pyrenees, Ax. (Stuckenberg 1960).

New records: SPAIN: 1♂. Aragon, Albarracín (NHMV); ♂♂ ♀♀. Valle de Puerto de Santa Maria, and Camino de la Nieve, Arcos da Frontera, numerous specimens reared from larvae by A. M. Hemmingsen (NMSA and Zoological Museum, Copenhagen). Dr Hemmingsen (in litt.) found this species to be common at the localities in southern Spain cited above. It still occurs in the Barcelona area from where I have seen specimens collected recently by Dr Miguel Carles-Tolrà.

Diagnostic characters: The few external characters distinguishing *funebris* from *cylindrica* are given under that species. Hypopygial characters (figs 21, 28–31): aedeagus,



Figs 32—33: Radial venation, showing shape of radial fork and relative length of R_{4+5} . 32) *L. lecerfi*; 33) *L. nigripennis*.

male cerci and gonostyli obviously of different shape. Spermathecae like those in *lecerfi* (fig. 12).

cylindrica subgroup: *lecerfi* + *nigripennis*

Two fairly large species with orange or orange-brown thorax, mesonotum with a single broad, chocolate-brown median vitta, a small dark brown lateral spot postsuturally on supra-alar declivity, scutellum not darkened on disc, face sinuous in profile, antennal segmentation $1+2+3-6+7+8+9+10$ (*lecerfi*, fig. 7, assumed for *nigripennis*), hind femur and tibia darkened apically, and apical part of R_{2+3} only gently curved (figs 32, 33).

***Lampromyia lecerfi* Séguy, 1928**

Lampromyia lecerfi Séguy, 1928: 45; Séguy 1930: 67–8, fig. 60.

The original description was scanty and unillustrated; Séguy (1930) subsequently published another description, with a drawing of the fly.

Type material: Conflicting information was given by Séguy; originally he cited only one specimen, a female, for which he gave the following data: 'Maroc: Grand-Atlas: Timmel (F. Le Cerf)'. In the second description he amended the data: 'Tinnel (Goundafa), 17–24. v. 27 (F. Le Cerf & Talbot) [Type]'; but he also recorded another specimen as 'Cotype', labelled: 'Asni, 3. v. 1928 (R. Benoist)'. The specimen from Tinnel must be accepted as the holotype; the 'Cotype' from Asni has no status as a type as it was not part of the original material. Both specimens are in the MNHN and have been examined by me. Holotype ♀: labelled 'TYPE' in red, with four other labels: 1) Museum Paris; 2) Tinnel/ G. Atlas (Goundafa)/ 17. 24. v. 1927; 3) Miss. Le Cerf/ & Talbot/ Grand Atlas/ 28. iv a 9. vi. 1927; 4) Lampromyia/ Le Cerfi/ Type Seguy/ E. Séguy det. 1928. 1 ♀: labelled 'COTYPE' in red; three other labels: 1) Museum Paris/ Asni/ 31. v. 1928/ R. Benoist 1928; 2) Museum Paris/ Maroc/ R. Benoist 1919; 3) Lampromyia/ Le Cerfi/ Cotype Seguy/ E. Séguy det. 1928. No locality called 'Tinnel' could be found in gazeteers; the closest is Tinnelrit (30°47'N, 8°01'W); Goundafa is a tribal area at about 31°00'N, 8°05'W. Asni is at 31°17'N, 7°58'W.

New records: MOROCCO: 4 ♀♀. Oukaïmeden/ 2500–2800 m/ 12-22-vii-1977// Maroc Ht Atlas/ Massif Toubkal/ v.Oorschof, Houkes & Oosterbroek (ITZA). This species is known only from the western end of the High Atlas Range, in the region of the Toubkal Massif (31°03'N, 7°57'W).

♀ Holotype

Head: Face projecting strongly, sinuous in profile, brown with shifting golden pruinescence; proboscis dark brown, about 2.5x mesonotal length; frons dark brown with greyish pruinescence laterally ('Cotype' frons greyish with yellowish overtinting, medially shifting where dark brown in some positions); ocellar tubercle shining blackish; occiput with dark brown, median, linear mark to cervix; antennae bicolorous, scape and pedicel orange-brown, remainder dark brown; segments 3–8 form an elongate subovoid unit.

Thorax: Orange-brown, with broad chocolate-brown median vitta that extends anteriorly onto pronotum, fading out posteriorly; a small, dark brown, somewhat fugitive mark, surrounded by golden pruinescence, on upper part of lateral declivity above wing attachment.

Wing: Greyish-hyaline with brownish tinge irregularly developed beneath stigmal area and in first basal cell; a characteristic colourless area in base of cell r_1 ; fork of R_4 and R_5 as in fig. 32, R_{4+5} measured from r-m crossvein to start of fork about 2.4 times length of R_5 .

Abdomen: Yellowish-brown, lateral tergal margins narrowly darkened, apically the abdomen darkened, possibly partly by postmortem changes ('Cotype' with only weak apical darkening).

Wing length: Holotype 9.8 mm, 'Cotype' 10.8 mm.

♀ Oukaïmeden series: More recently collected and evidently fully mature. Wing greyish-hyaline with brownish suffusion along all veins and throughout costal cell, anteriorly in first basal cell, and in and below stigmal area; clear subtriangular area in base of cell r_1 present but not as large as in Holotype. Slide-mounted antenna reveals an incomplete dorsal suture between 7 and 3–6 (fig. 7). Three subspherical, pale brown spermathecae in segment 7, subcylindrical, apical end pale with small, highly refractive surface irregularities; a large circular opening basally from which a membranous sac emerges, a very slender duct arising from this sac (fig. 12).

Lampromyia nigripennis Séguy, 1930

Lampromyia nigripennis Séguy, 1930: 68.

This species is inappropriately named: the wings are strongly smoky brown.

Type material: Séguy referred to only one specimen, sex not stated, for which he gave the following data: 'Moyen Atlas: Berkine [Morocco, 33°46'N, 3°51'W], 1350–1400 m., jardins dans le Tlet n'Rhor, 10. vi. 29 (F. Le Cerf)? However, the specimen labelled as 'TYPE' of this species (MNHN) has different locality data; it bears two original labels: 1) Ras el Ksar [33°58'N, 3°50'W]/ 900m/ 12–13. vi. 29/ F. Le Cerf// Museum Paris/ Meudon. 2) *Lampromyia nigripennis* Séguy/ Type/ E. Séguy det. 1929. Dr L. Tsacas (in litt.) informed me that he has not been able to find the specimen from Berkine, and he has no explanation for this discrepancy. As Berkine and Ras el Ksar are close together and were visited almost on consecutive days by the collector, I accept this unique specimen as the Holotype and have labelled it as such. It is in quite good condition, except that only the left fore and hind legs are present and both antennae are broken. This species is known only from its type locality at the north-eastern end of the Middle Atlas Range.

♀ Holotype

Head: Face strongly protruding, front edge sinuous in profile, brownish with thin, pale aureous pruinescence, bare on sides; proboscis black, slender, about 2.6x mesonotal length; frons broader than long, with slightly curved, linear impression on each side, these demarcating a slightly raised median area; frons and occiput greyish pruinose with slight sepia overtint; ocellar tubercle shining blackish; occiput with dark brown median stripe from tubercle

to cervix, narrowing posteriorly, clearly visible in dorsal view but disappearing under pruinescence in posterior view; only scape and pedicel present, pale brown.

Thorax: Entirely orange, fore and hind coxae translucent yellowish; a narrow, dark brown stripe before anterior spiracle; mesonotum with broad, brownish median vitta which encloses a narrow, paler midline stripe; median vitta extending onto pronotum, posteriorly fading away in an apruinose prescutellar area; a small, somewhat fugitive, postsutural dark brown spot on each supra-alar declivity; mesonotal pruinescence fine, shifting pale silvery yellow; scutellum and metanotum clear dull orange. Fore leg uniformly clear yellowish; hind femur and tibia yellowish with poorly defined dark brown apical section; hind tarsus dark brown; trochanters edged with black.

Wing: Uniformly dark smoky brown; no colorless area in base of cell r_1 ; R_{2+3} with gentle forward curvature apically; fork of R_4 and R_5 quite long, almost symmetrical (fig. 33), R_{4+5} measured from r-m crossvein to start of fork about 1.7 times length of R_5 ; cell m_3 closed at wing margin, anal cell open.

Abdomen: Relatively broad, slightly petiolate at junction of T2 and T3; shining blackish, in some views with obscure brownish tinge.

Wing length: 11.2 mm.

pallida subgroup: *pallida* + *iberica*

Two quite large species; face, frons, occiput and thorax thickly greyish or silvery pruinose; ocellar tubercle contrastingly very dark; antenna 1+2+3—8+9+10; upper pleura with conspicuous apruinose shining strip descending obliquely forwards between wing and fore coxa; abdomen largely apruinose, shining pale orange-brown, with dark lateral markings on tergites; wing clear with weak pattern of small brownish marks; R_{2+3} apically bent abruptly towards costa; spermathecae (*pallida*) round, pale, extended into elongate, narrow, internally rugose necks to which ducts are attached (fig. 13); hypopygium prominent, epandrium large (figs 34, 37, 43), proctiger elongate (fig. 37); aedeagus (figs 45, 46) strongly flexed near base, lacking definite lateral extensions or these possibly represented by undulant flanges in *pallida* (fig. 41, p), lacking ventral keel (fig. 41) or a small one present (fig. 45); dorsal bridge (fig. 44, db) arched, convex posteriorly; ventral aperture small (fig. 43) or absent (fig. 38); apical guides rounded (figs 38, 42, ag); gonostyli narrow (figs 40, 42, gs); ejaculatory apodeme (fig. 41, ea) slender, slightly curved.

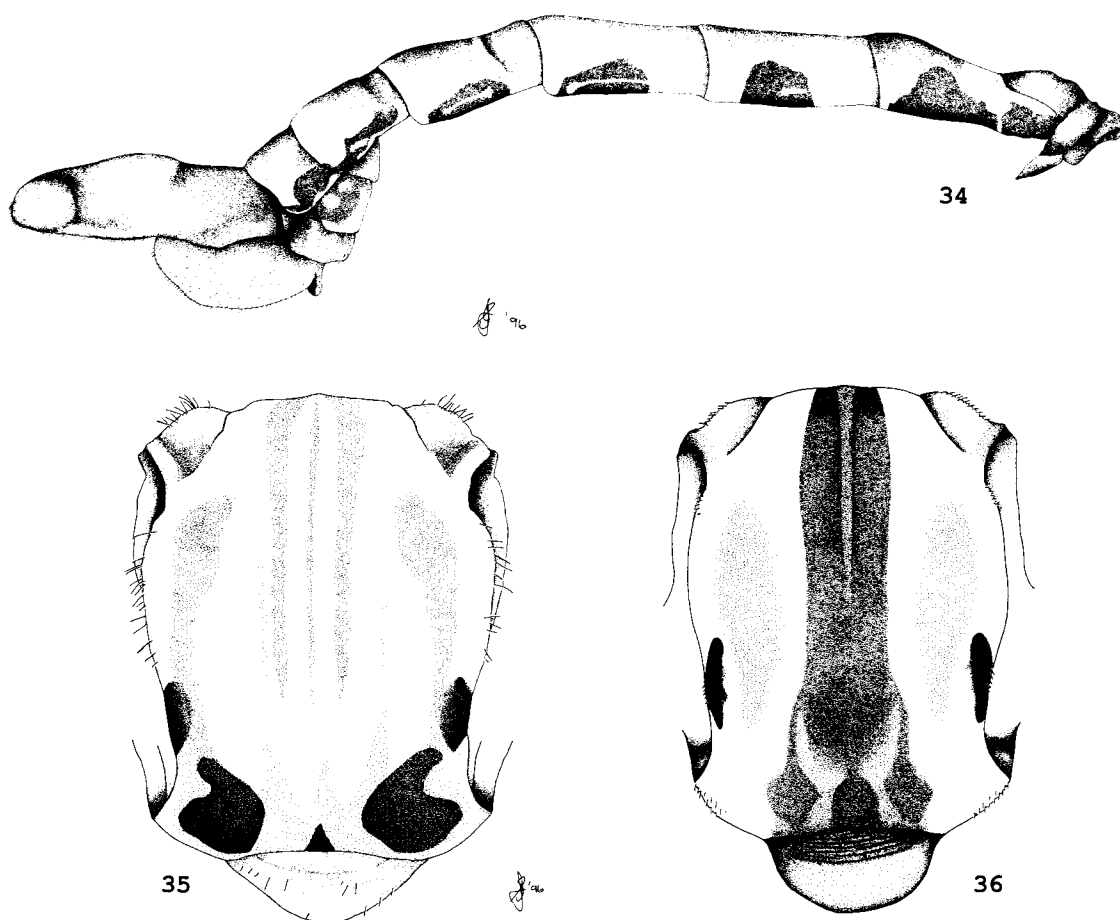
Key to these species:

1. Humeri apruinose, shining, contrasting with pruinose mesonotum; antennal segments 3—8 shorter (fig. 8); T1 narrowly dark on sides only; T2 with lateral dark markings subtriangular and not coalescent medially; mesonotal spots conspicuous (fig. 35). [Africa] *pallida* — Humeri pruinose, not shining; antennal segments 3—8 longer (fig. 4); T1 mostly dark brown; T2 continuously dark brown across midline; mesonotal spotting inconspicuous. [Iberia]. *iberica* sp. n.

In *pallida* the anal cell is open, and cell m_3 is closed with a short stalk; in *iberica* the anal cell is closed, and m_3 is closed with a longer stalk (about equal to base of m_2). These features may prove to be variable in long series.

***Lampromyia pallida* Macquart, 1835**

Lampromyia pallida Macquart, 1835: 662, pl. 24, fig. 18; Becker 1900: 7; 1908: 22; 1921: 42; Bequaert 1922: 278; Séguy 1930: 68; Szilády 1934: 231; Hemmingsen 1968: 290—2, 298—300; Hemmingsen & Regner Nielsen 1971: 160—5, 201, figs 4—9. Not *Lampromyia pallida* Macquart sensu Lindner 1924:



Figs 34–36: 34–35 *L. pallida*; 34) ♂ abdomen, T8 visible only as a small, triangular sclerite at base of epandrium; 35) ♂ mesonotal pattern. 36) *L. lecerfi* ♀ mesonotal pattern.

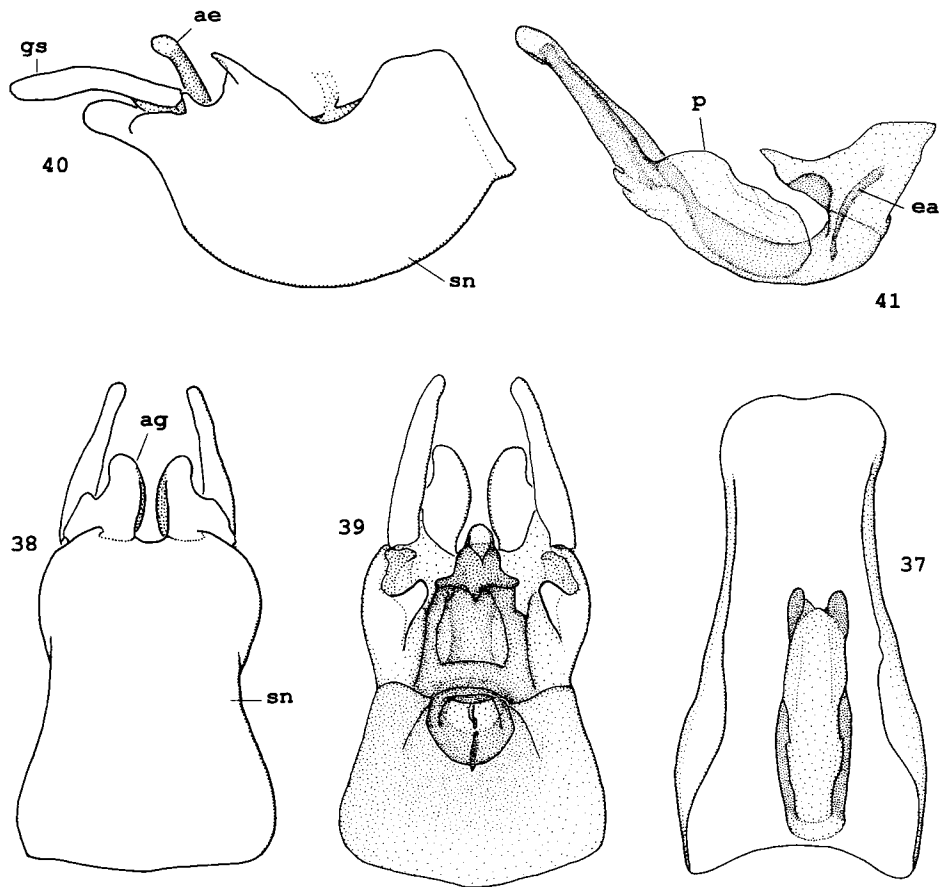
6, 7; Séguy 1926: 93; 1934: 20; Stuckenberg 1960: 250–2, figs 42–45. (Misidentifications of *L. iberica* sp.n.)

Lampromyia miki Marchal, 1897: 6–13, pl. 1, figs 1–14; Becker 1900: 7 (synonymy).

Lampromyia mikii, invalid emendation; Kertész 1908, Séguy 1926, Stuckenberg 1960.

Type locality: Oran, Algeria; no extant type material known.

Previous records: Marchal (1897) found larval colonies between Tunis and Bardo, at an ancient Turkish fort. Becker (1906) visited the same locality and collected larvae which he reared in Germany. Bequaert (1922) found numerous larval colonies and flies in suburban Algiers during June 1910. Hemmingsen (1968) located the site (Fort des Andalouses) where Marchal and Becker collected, and found larvae still ‘in abundance’; he also discovered *pallida* colonies at Carthago and Qued El Abid, and south of Tunis at an old Roman aqueduct between Mohammedia and Oudna. From larvae taken to Denmark, Hemmingsen reared many flies; specimens from the Tunisian localities were donated to the NMSA, and are the basis of the following description; other specimens are in the Zoological Museum, Copenhagen. The species is thus known from coastal and hinterland districts of Tunisia and Algeria, from Tunis to Oran; it probably also occurs westward in Morocco.



Figs 37—41: *L. pallida*; 37) epandrium and proctiger, ventral; 38) synsternite, ventral; 39) synsternite, dorsal; 40) synsternite, lateral; 41) aedeagus, lateral.

Male

Head: Face nasute, projecting prominently, leading edge almost straight, shining silver pruinose, bare glossy brown laterally; proboscis about 2.8x mesonotal length, when folded posteriorly reaching middle of S4, blackish-brown, palp pale yellowish-brown; frons and occiput thickly ashy-grey pruinose, occiput with pale silvery-yellow hairs; ocellar tubercle shining black; antennae (fig. 8) relatively short, segments 3—8 asymmetrically pyriform.

Thorax: Pronotum pale amber-yellow, thinly silvery pruinose; mesonotum thickly silvery-grey pruinose, posteriorly with conspicuous array of spots (fig. 35), two large, apruinose, glossy dark brown dorsolateral spots, a smaller, median subovoid mark of same colour and gloss, and a pruinose, velvety dark brown spot on lateral declivity above wing base; anterior mesonotal pattern of dark vittae subdued by pruinescence, consisting of narrowly separated median pair which coalesce anteriorly and taper posteriorly to disappear between transverse sutures, and indefinite sublateral vittae which are more intense on their outside margins; humeral calli bare, shining, pale waxy yellow, narrowly bordered by dark brown. Scutellum pale, apruinose yellowish-brown. Metanotum contrastingly shining silvery-grey pruinose on upper half, glossy apruinose brown on lower half. Pleura finely silvery-grey pruinose; glossy apruinose brown stripe obliquely on mesopleuron, a paler brown shining area on pteropleuron beneath wing; prominent dark marks before anterior spiracle and before basicosta; hypopleuron and anterior sternopleuron with brown areas showing through shifting pruinescence.

Legs pale yellowish-brown, coxae silvery pruinose; hind femur and tibia narrowly darkened apically.

Wing: Glossy hyaline, costal cell faintly brown, veins mostly pale brown, darker where adjacent membrane is patterned; weak pattern of brownish area in apex of first basal cell, brownish cloud around apical section of R_{2+3} and faintly around apex of discal cell and base of fork of R_4 and R_5 ; petiole about one-fifth of total wing length; apical flexure of R_{2+3} abrupt, forming almost a right-angle to costa.

Abdomen: Weakly petiolate between T3 and T4; extensively yellowish-brown with bold, narrow, dark brown lateral marks on T1–5; T6–7 narrowly and irregularly darkened along entire lateral margins; T2–6 with narrow, transverse bands of silvery pruinescence basally. Hypopygium (figs 34, 37–41) massive, epandrium projecting conspicuously; distinguished from *iberica* by more elongate gonostylus (gs), swollen apex of epandrium (fig. 23), flanges on aedeagus (p), deeply concave dorsal margin of synsternite (fig. 40, sn), absence of ventral aperture, no ventral keel on aedeagus.

Wing length: Conspicuously shorter than body, 9.6–10.0 mm.

Female

Head, thorax, legs and wings as in ♂, hind coxae brownish laterally; abdomen bicolorous, bright yellowish-brown with strongly contrasting shining dark brown lateral markings, these usually subtriangular, narrowly separated medially on T2–4, coalescent medially on T5–6, in some specimens separated medially on all tergites; T2–6 transversely silvery-grey pruinose basally. Spermathecae (fig. 13), three in segment 6.

Wing length: 11.0–11.4 mm.

Lampromyia iberica sp. n.

Not *Lampromyia pallida* Macquart, sensu Lindner (1924), Séguy (1926, 1934), Szilády (1934), Stuckenberg (1960).

Etymology: Based on Iberia, an ancient name for the peninsula now comprising Spain and Portugal.

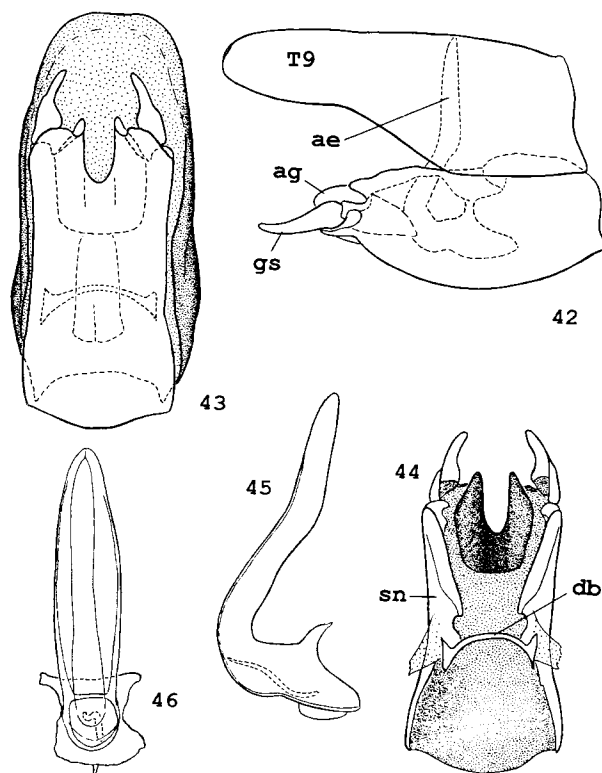
Type material: Holotype ♂ (NHMV): SPAIN: Zaragoza, 21-vi-[190-]3 (handwritten label); it bears a determination label of L. Czerny, 'Lampromyia pallida Macq.' Labelled by me 'Holotype *Lampromyia iberica* Stuckenberg', rectangular label with red border. Paratype 1 ♀ (MNHN): SPAIN: Zaragoza, 27.iv.[19-]27; the locality labels on both type specimens are in the same handwriting.

Previous records (as *pallida*): SPAIN: Barcelona (Stuckenberg 1960); Sena and Zaragoza (Séguy 1934). Rare in collections, the specimens available date from more than half a century ago. On present evidence, *iberica* seems confined to north-eastern Spain; there are no records supporting the statement by Séguy (1926) that it occurs in the south. It may be significant that most specimens come from the Zaragoza region; this includes the Monegros, '... one of the most desert-like areas in the Iberian peninsula ... its vegetation often resembles that of the North African steppes' (Merz & Blasco-Zumeta 1995). The coloring of *iberica* and its African sister-species *pallida* is of a sort often seen in Diptera of arid biomes.

Male Holotype

Head: Similar to *pallida*; antennal segments 3–8 form a more elongate and tapering unit (fig. 4), style short, about as long as 3–8; colouring and vestiture as in *pallida*; proboscis brownish, 2.7x mesonotal length.

Thorax: Resembling *pallida* but immediately distinguished by lack of dark mesonotal spots; mesonotum densely greyish pruinose, with dark underlying vittae showing through pruinescence quite strongly, comprising a median pair which coalesce anteriorly and terminate posteriorly between wings, and on each side a sublateral vitta starting behind level of humeral callus and terminating posteriorly above postalar callus; declivous postsutural sides of mesonotum entirely pale brownish. Pleura as in *pallida*, but humeri pruinose, not shining; an



Figs 42—46: *L. iberica* sp. n.; 42) hypopygium, lateral; 43) hypopygium, ventral; 44) synsternite, dorsal; 45—46) aedeagus. (From Stuckenberg 1960, as *pallida*.)

oblique band of apruinose, shining reddish-brown across lower part of mesopleuron to upper sternopleuron; lower sternopleuron, hypopleuron and coxae dark brown. Legs pale yellowish-brown, unlike ♂ *pallida* in lacking definite dark brown apical bands on hind tibia and femur.

Wing: Generally as in *pallida*, membrane mostly greyish-hyaline; weakly patterned, brownish in apex of first basal cell, along all of R_{2+3} , around R_4 and R_5 , and apex of discal cell; R_{2+3} more strongly curved basally than in *pallida*, with abrupt forward curvature to costa apically; fork of R_4 and R_5 almost symmetrical about wing tip; in left wing an abnormal vein creates a spurious subtriangular cell in apex of m_3 .

Abdomen: T1 yellowish-brown, dark brown laterally; T2 with large lateral, dark brown markings that narrow subtriangularly medially in posterior half of this tergite; T3—7 pale orange-brown with conspicuous dark brown lateral markings; hypopygium yellowish-brown. Genitalia (figs 42—46) as described and illustrated by Stuckenberg (1960, as *pallida*); dorsal margin of synsternite gently curved, lacking strong curvature of *pallida*; epandrium simpler, more uniform over dorsal surface, lacking terminal swellings of *pallida*; aedeagus simple, lacking flanges.

Wing length: 9.0 mm (body about 13.4 mm).

Female Paratype

Resembling ♂, coloring more intense; proboscis elongate, about 3.3x mesonotal length; antennal segments 3—8 bright yellowish, stylus dark; frons and occiput greyish-pruinose, face silvery; ocellar tubercle dark brown; mesonotum as in ♂, ground colour darker brown, and a small, intensely dark brown spot at posterior end of each sublateral vitta; legs brighter

yellowish-brown, hind coxae dark brown with this coppery pruinescence; hind femur dark brown over about apical one-fifth, hind tibia narrowly dark brown apically. Abdomen apruinose, shining, mostly orange-brown, T2–5 with narrow, silvery pruinose transverse basal bands, T1 and most of T2 dark brown, T2 dark orange-brown medially on posterior half and narrowly along hind margin; T3–6 narrowly dark brown laterally.

Wing length: 10.0 mm.

canariensis group

Synapomorphies defining this group: see characters 2, 9, 10 above. Spermathecal form (fig. 11) distinctive, though unspecialised.

The taxonomic history of the Canarian vermilionid fauna was reviewed by Wheeler (1930), Hemmingsen (1963) and Stuckenberg (1971). *L. canariensis* Macquart was described in 1839 from Tenerife specimens and remained the only species definitely known for many years; it was redescribed and illustrated by Becker (1908) and Wheeler (1930). Becker (1921) later confusingly stated of *canariensis*, *cylindrica* and *pallida*: 'Alle 3 Arten fand ich auf den Kanarischen Inseln.' He gave no supporting data, and his statement may merely have been a lapsus calami. A possible occurrence of *Vermileo* arose from an old record based on larvae by Brauer (1883). Understanding of the fauna emerged only after Axel Hemmingsen discovered worm-lions on all seven of the major islands. He reared many specimens of *Lampromyia*, revealing that three endemic, allopatric species are present (Stuckenberg 1971). No specimens of *Vermileo* were found; Brauer's record of the genus was surely a misidentification.

The material reared by Hemmingsen is mostly now in NMSA. The flies were generally dirty and in poor condition, and this presented problems when I wrote descriptions of the species in 1971. I can now redescribe *canariensis* and *hemmingseni* from clean field-caught specimens.

canariensis subgroup

♀ S8 without basal swellings externally; aedeagus rigidly sclerotised throughout; epandrium without two dorsal invaginations; ventral aperture very large, exposing most of aedeagus.

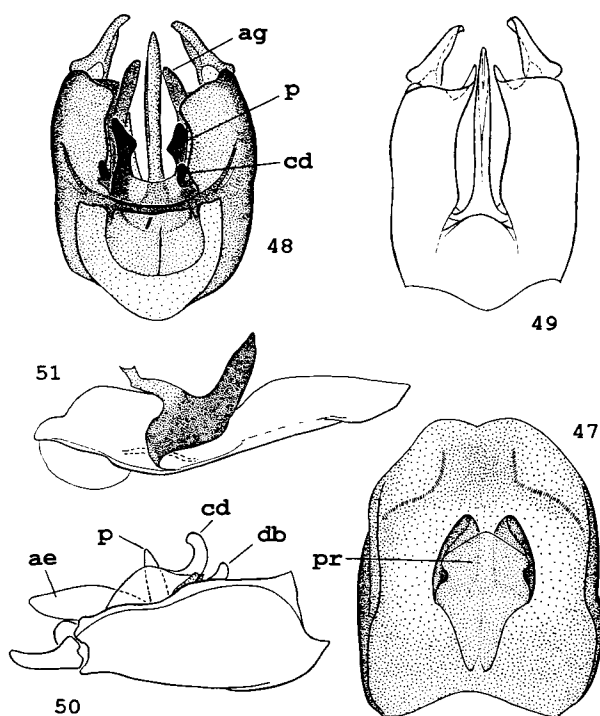
Lampromyia canariensis Macquart, 1839

Lampromyia canariensis Macquart, 1839: 105, pl. 4, figs 7, 7b; Macquart 1840: 29, pl. 3, figs 1, 1a–d; Becker 1908: fig. 4; Becker 1921; Lindner 1924: 7; Séguy 1930: 63; Wheeler 1930: 248–53, fig. 45; Szilády 1934: 231; Frey 1936: 43, fig. 9; Fernandez 1952: figs 1–5; Stuckenberg 1960: 247–50, figs 32–6; Stuckenberg 1971: 81–2, fig. 2; Hemmingsen & Regner Nielsen 1971; Frederiksen & Hemmingsen 1972. Not *Lampromyia canariensis* Macq., sensu Hemmingsen 1963: 237–67.

Material examined: CANARY ISLANDS: 1♂. España/ Islas Canarias/ La Palma/ AC & WN Ellis// Los Tilos/ 3 km SW Los Sauces/ 55 m/ 20.vii.1985 (ITZA). 1♀. Isl. Canarias/ Tenerife/ B. van Aartsen// Guimar/ 2.iv.1968 (ITZA).

Male

Head: Face blackish-brown, shining ashy-grey pruinose; proboscis blackish, about 3.4x mesonotal length; frons ashy-grey, ocellar tubercle shining blackish; occiput with dark brown hairs and fugitive pruinescence, dark velvety black to greyish with golden-brown overtinting; antenna (fig. 1) 1+2+3–7+8+9+10, separation of 3–7 and 8 incomplete.



Figs 47—51: *L. canariensis*; 47) epandrium and proctiger, ventral; 48) synsternite and aedeagus, dorsal; 49) synsternite, ventral; 50) synsternite, lateral; 51) aedeagus, lateral. (From Stuckenberg 1960.)

Thorax: Mesonotum with strong, broad, very dark brown median vitta of uniform coloring, not enclosing any pale midline stripe, this vitta bordered by stripes of shining brown pruinescence which widen anteriorly, humeral calli and declivous lateral areas shining silvery-grey; pronotum greyish laterally, medially with dark mark bordered by shining brown pruinescence; dark lateral mesonotal vittae dulled by overlying shifting greyish pruinescence; scutellum dark on disc, borders obscurely paler, with silvery pruinescence. Pleura dark, apruinose, shining brown over much of mesopleuron and hypopleuron, appearing paler elsewhere because of overlying silvery-grey pruinescence. Coxae brownish-yellow with poorly defined dark brown areas, all with shifting silvery pruinescence. Fore and middle legs dull orange-brown; hind femur darkish brown, narrowly paler at base, hind tibia uniformly medium brown, tarsus concolorous.

Wing: Pattern distinct (Stuckenberg 1971, fig. 2), membrane greyish-hyaline, veins dark, costal cell dark smoky-brown, apex of cell *sc* and stigmal area beneath similar, also an irregular dark area in apex of first basal cell and along *R*₅; some indefinite brown staining bordering costa in cells *r*₁ and *r*₂, in base of discal cell, base of *m*₁, around *R*₂₊₃ and *R*₄₊₅; cell *m*₃ closed with short stalk, anal cell narrowly open.

Abdomen: Slender, moderately petiolate between T2 and T3; tergites shining brownish-black, T2—6 with conspicuous silvery-grey pruinose basal bands; T7 with very narrow basal pruinose band and testaceous infusion which is also on epandrium. Hypopygium (figs 47—51) distinctive in form of aedeagus, mediodorsal extensions of synsternite (figs 48, 50, *cd*), and very large ventral aperture which exposes most of aedeagus in ventral view.

Wing length: 8.6 mm.

Female

Closely resembling ♂ in coloring and pruinescence; proboscis 2.9x mesonotal length; abdomen conspicuously banded due to densely pruinose basal grey bands on T2–6, occupying about one-third of tergal length, tergites elsewhere bare, shining dark brown; spermathecae (fig. 11), three in segment 6, pale brown, almost spherical, with relatively broad duct arising directly from aperture in wall.

Wing length: 8.4 mm.

fortunata + *hemmingseni* subgroup

♀ S8 with a median pair of external basal swellings (figs 14, 20); aedeagus partly desclerotised apico-dorsally; epandrium with dorsal invaginations (character 12 above); ventral aperture small; proctiger elongate.

Lampromyia fortunata Stuckenberg, 1971

Lampromyia fortunata Stuckenberg, 1971: 82–5, figs 3, 5–9; Hemmingsen & Regner Nielsen 1971: 168–75, 190–3; Frederiksen & Hemmingsen 1972.

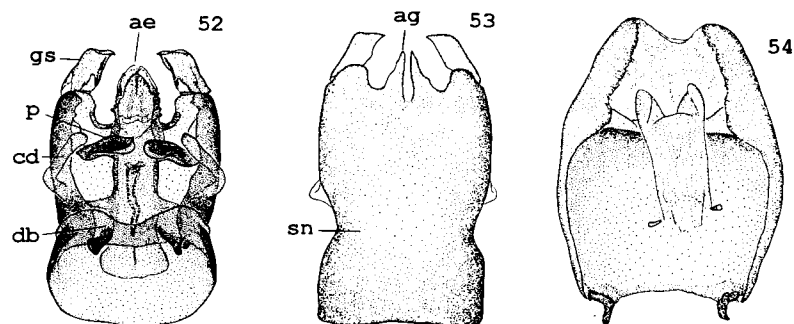
Not *Lampromyia canariensis* Macq., sensu Hemmingsen 1963: 237–67.

Additional description from long series reared from larvae collected on Gran Canaria by Hemmingsen (for collecting data, see Stuckenberg 1971: 85).

Male

Head: Face densely shining silvery-grey pruinose; proboscis black, 2.6–3.5x mesonotal length (in one specimen reaching backwards to midlength of S6); frons greyish pruinose; ocellar tubercle shining blackish; antenna (fig. 2) 1+2+3–7+8+9+10, bicolorous, scape and pedicel pale yellowish-brown, remainder dark sepia brown; occiput with fine, pale hairs, densely pruinose, shining silvery-grey laterally, shifting warm sepia brown dorsally except in median depression below ocellar tubercle which is greyish.

Thorax: Mesonotal pattern complex; a dull golden midline stripe, separating two dark brown stripes which coalesce postsuturally into a paler brown median vitta that extends onto scutellum; these dark stripes narrowly bordered by dull golden pruinescence which in turn is bordered by shining silvery-grey pruinescence that also occurs on sides of mesonotum and on humeral calli; dark sublateral vittae also present, covered with shifting brownish-aureous pruinescence; a dark velvety brown mark on declivity above wing attachment. Pronotum pruinose, silvery-grey laterally, dark brown medially. Pleura mostly brown, shining greyish pruinose. Fore coxae pale yellowish-brown; other coxae brownish like pleura; legs pale yellowish brown, hind femur and tibia both dark brown apically. Scutellum dark brown, thinly



Figs 52–54: *L. fortunata*; 52) synsternite and aedeagus, dorsal; 53) synsternite, ventral; 54) epandrium and proctiger, ventral. (From Stuckenberg 1976.)

greyish pruinose. Postnotum shining brown on lower half, densely silvery pruinose on upper half.

Wing: Greyish-hyaline with dark veins; costal cell only slightly brownish; stigmal area and an irregular strip along posterior side of radial-sector and a short adjacent section of R_1 irregularly brownish; R_{2+3} strongly arched basally, apical portion abruptly curved forwards to costa; cell m_3 closed, usually with short stalk, fork of R_4 and R_5 almost symmetrical about wingtip, these veins almost straight.

Abdomen: Variably colored, mature specimens dark brown on T1, T2 dark brown over most of apical two-thirds, basal third brownish-orange, T3 and T4 irregularly dark brown medially, brownish-orange elsewhere, T4–6 more extensively brownish-orange, centrally with dark blotching; T2–6 silvery pruinose basally, with sparse, small, dark, recumbent hairs elsewhere. Hypopygium (figs 17, 52–55) with all components of different form from those of *hemmingseni* (figs 19, 56–59), especially shape of aedeagus, synsternite, gonostylus, and mediodorsal extensions (md).

Wing length: 6.8–9.4 mm.

Female

Abdomen mostly brownish-orange, with poorly defined dark brown markings laterally on T2–6, some irregular dark blotching also present; silvery pruinescence in basal bands on most tergites, but inconspicuous. Spermathecae three, subspherical, pale brown, in segment 6.

Lampromyia hemmingseni Stuckenberg, 1971

Lampromyia hemmingseni Stuckenberg, 1971: 85–8, figs 4, 10–3; Hemmingsen & Regner Nielsen 1971: 176–7.

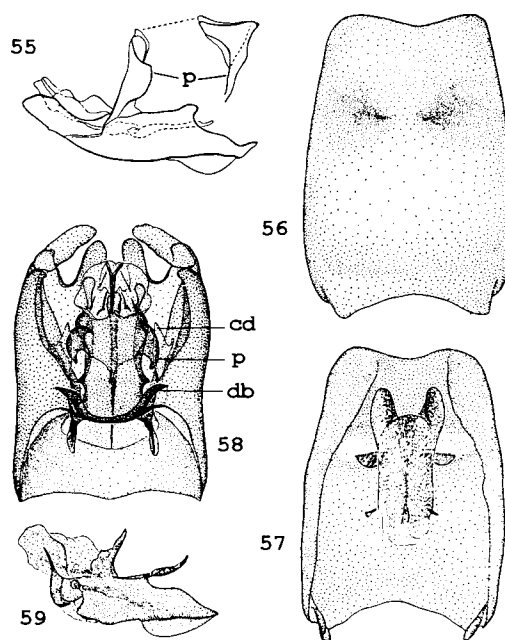
Material examined: CANARY ISLANDS: 1♂ 1♀. Espana/ Islas Canarias/ Fuerteventura/ Corralejo/ W. N. & A. C. Ellis-Adam// on *Cakile/ maritima/* 21.11.1992 (ITZA). 1♀. Islas Canarias/ Fuerteventura/ 3–20.11.1990/ AC & WN Ellis// Corralejo/ 12–18.11.1990 (ITZA).

Male

Head: Face protruding strongly, slightly concave in profile, brownish medially, yellowish-brown laterally, pruinescence shifting from dark velvety brown to shining reddish-yellow; proboscis blackish, 2.4–2.6x mesonotal length; antenna (fig. 3) 1+2+3–7+8+9+10, yellowish-orange on scape and pedicel, brownish elsewhere; frons thickly ginger pruinose; ocellar tubercle shining blackish; occiput ginger pruinose with numerous long, pale brown hairs.

Thorax: Pronotum and mesonotum thickly orange-brown pruinose, with abundant erect brown hairs; mesonotum with two narrow, blackish-brown stripes bordering orange-brown midline stripe, dark stripes coalescent anteriorly, disappearing posteriorly so that there is a clear orange-brown prescutellar area; a fugitive lateral vitta on each side of upper mesonotal surface, most visible in postero-lateral view, running into an intensely blackish mark above postalar callus. Scutellum orange-brown laterally and around hind rim, shining dark brown centrally. Pleura dark yellowish-brown, obscurely dark brown in shining apruinose area in meso-, sterno- and hypo-pleura, elsewhere pleura thinly pale ginger pruinose. Postnotum bare, shining brownish on lower half, orange-brown with golden pruinescence on upper half. Fore coxae clear yellowish-orange, other coxae yellow-brown, with underlying strong brown tinge on outer surface; fore and middle legs yellowish-orange; hind legs darker, femur and tibia darkened apically.

Wing: Macroscopically appearing smoky brown as a result of shining microtrichia on membrane and veins, these microtrichia fugitively colored pale reddish-golden in reflected light; microscopically membrane is weakly diffused with brown along veins, leaving pale greyish hyaline areas centrally or medially in cells; an almost colorless subtriangular area in base of cell r_1 ; R_{2+3} evenly curved at base, apically with a distinct though moderate, variably



Figs 55—59: 55) *L. fortunata*; aedeagus, lateral. 56—59 *L. hemmingseni*; 56) epandrium, dorsal; 57) epandrium and proctiger, ventral; 58) synsternite and aedeagus, dorsal; 59) aedeagus, lateral. (From Stuckenberg 1976.)

developed, posterior recurvature before turning forwards to costa, sometimes R_{2+3} weakly undulant in this section; fork of R_4 and R_5 almost symmetrical about wingtip, both almost straight, cell m_3 closed at margin.

Abdomen: Not petiolate, uniformly wide over most of length, tapering moderately from segment 6 posteriorly; mostly orange-brown, T1 obscurely dark brown on anterior corners and medially on posterior margin; T2 with two dark brown anterior marks narrowly separated medially; T3—6 without markings; T1 with long, dark hairs; T2—6 each with bare transverse areas across basal third, elsewhere with conspicuous, erect dark hairs; T7, S7 and S8 thickly haired, T8 as in fig 18; hypopygium (figs 19, 56—59) distinctive (see *fortunata* above).

Wing length: 8.2—8.4 mm.

Female

Resembling ♂; this specimen darker orange-brown beneath pruinescence on head and thorax; abdomen reddish-orange, T2 with two small, narrowly separated, subquadrangular brown marks basally, as in ♂; T2—6 each with bare depressed basal section and more elevated posterior section with dark, erect hairs. Spermathecae three, subspherical, pale brown, in segment 6.

Wing length: 8.0 mm.

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Zusammenfassung

Im Rahmen einer Revision der Gattung *Lampromyia* Macquart für die paläarktische Region werden neun Arten unterschieden. Frühere Vorstellungen über die Identität der beiden europäischen Arten erweisen sich als falsch. *L. cylindrica* (Fabricius) ist eine afrikanische Art; *L. funebris* Dufour ist dazu nicht synonym, sondern eine Art der Iberischen Halbinsel und Frankreichs, die bisher als *L. cylindrica* mißverstanden wurde. *L. pallida* Macquart ist ebenfalls auf Afrika beschränkt; als *pallida* bestimmte Stücke aus Spanien werden als *Lampromyia iberica* sp.n. beschrieben. Für alle Arten werden neue Bestimmungsschlüssel und Beschreibungen gegeben; für *L. cylindrica* wird ein Neotypus festgelegt. Apomorphien, die die Monophylie der Gattung begründen können, werden erörtert. Eine phylogenetische Analyse stellt drei Artengruppen heraus: die *pilosula*-Gruppe im südlichen Afrika, die *canariensis*-Gruppe auf den Kanarischen Inseln und die *cylindrica*-Gruppe in Nordwestafrika, der Iberischen Halbinsel und Frankreich. Ein Stammbaum gibt die wahrscheinliche Phylogenese der Gattung wieder und läßt Schlüsse zur Biogeographie zu. Das Verbreitungsmuster der drei Arten der Kanarischen Inseln weicht vom gewohnten Bild ab, indem die älteste Art die jüngere westliche Inselgruppe besetzt, während die jüngeren, durch Synapomorphien verbundenen Arten über die ältere östliche Inselgruppe verteilt sind. Zwei Fälle von Vikarianz sind zu beobachten; sie können mit der Ausbreitung der Stammarten von Afrika auf die Iberische Halbinsel und nachfolgender Isolation der europäischen von der afrikanischen Population erklärt werden.

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