DIVERSITY AND EVOLUTION OF TONGUE LENGTH IN HAWKMOTHS (SPHINGIDAE)

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ABSTRACT. Hawkmoths are best known as long-tongued nectar foragers, but as many as one-fifth of hawkmoth species have drastically shortened tongues and do not seek flower nectar. Clues to tongue-length diversity and evolution have not previously been sought in any hawkmoth stage but the adult. Using comparative methodology, and investigating some 150 species of New and Old World hawkmoths, I uncover correlations between tongue length and latitude of distribution, and between tongue length and growth form of larval foodplants. Through north latitudes ranging from 0 to 40 or 50°, mean tongue length declines worldwide from more than 40 mm to 15 mm or less. Through larval foodplant growth-form indexes ranging from 2 (herbs) to 6 (trees), mean tongue-length similarly declines from more than 40 to less than 15 mm. I speculate for extratropical regions that tongues have lengthened in hawkmoths that must imbibe large amounts of nectar as flight fuel to find inconspicuous, nonpersistent larval foodplants such as herbs, whereas tongues have shortened in hawkmoths that have the easier task of finding conspicuous, persistent larval foodplants such as trees. Residual tongue-length variation could reflect miscellaneous factors operating at smaller than continental geographic scales.

Additional key words: growth form, pollination, geographic variation, phylogenetic analysis.

The long proboscis or tongue is a hallmark of Sphingidae. The tongue of the neotropical *Amphimoeca walkeri* (Bdv.), whose length can reach 280 mm (Amsel 1938), is thought to be the longest haustellum in all Insecta. Also contributing to sphingid tongue lore is the story of the Madagascan hawkmoth *Xanthopan morgani praedicta* R. & J. (Kritsky 1991). Charles Darwin observed in 1862 that the nectar of the Madagascan star orchid, *Angraecum sesquipedale* Thouars (Orchidaceae), is hidden some 290 mm deep in the blossom. A hawkmoth pollinator with so long a tongue was then unknown, but Darwin predicted that one would be found. Four decades later, Rothschild and Jordan (1903) described the predicted hawkmoth. According to Kritsky (1991), yet another species of *Angraecum* orchid with still deeper nectar has surfaced, and yet another hawkmoth with a still longer tongue has been predicted! Although pollination literature often focuses on comparative lengths of tongues and nectar tubes, which makes one think of coevolution, no general mechanism has been advanced to explain the diversity and evolution of hawkmoth tongue length.

Hawkmoth visitors at flowers are often known by plant taxa because so much knowledge of nectar foraging comes from pollination studies. Hawkmoths insert their tongues, sometimes more of their bodies, into blossoms for nectar. In the process, they touch pollen-bearing anthers and pollen-receiving stigmas, accidentally transferring pollen within or among blossoms. The extensive foraging range (Linhart & Mendenhall

1977), swift, darting flight, and nocturnal activity of many hawkmoths makes it more practical for an investigator to remain near flowers and observe arrivals, rather than follow such fleeting matchmakers to see what flowers they visit. Fluorescent powders, dyes, devices that enhance night vision, and palynological analysis of tongues and faces of captures have enhanced hawkmoth investigations of interest in the present study (Eisikowitch & Galil 1971, Kislev et al. 1972, Linhart & Mendenhall 1977, Haber & Frankie 1989). Some of the pollinator lists by plant taxa that include hawkmoths are those for *Angraecum* spp. (Nilsson et al. 1985), *Lavandula* sp. (Labiatae) (Herrera 1989), *Luehea* spp. (Tiliaceae) (Haber & Frankie 1982), *Pancratium maritimum* L. (Amaryllidaceae) (Eisikowitch & Galil 1971), and Polemoniaceae spp. (Grant & Grant 1965). Conversely, lists by hawkmoth species of plant taxa visited or pollinated (Fleming 1970, Kislev et al. 1972) are less common.

From lists of pollinators by plant taxa, seven pollinator syndromes—flower types favoring different animal pollinator groups—have been characterized, one being the syndrome of sphingophilous or hawkmoth flowers (Baker & Hurd 1968, Faegri & van der Pijl 1979). Sphingophilous flowers have the following traits: nocturnal anthesis or opening, white or pale coloration, sweet fragrance, horizontal to pendant posture, abundant sucrose-rich nectar, and long nectar tube (Baker & Hurd 1968, Faegri & van der Pijl 1979, Cruden et al. 1983, Haber & Frankie 1989). The nectar tube may be formed by various flower parts such as corolla, calyx, petal spur, hypanthium, or consist of a false tube formed by stamens and petals (Grant 1983). Hawkmoth flowers belong to the evolutionarily advanced stereomorphic and zygomorphic types of angiosperm flowers (Leppik 1968, Crepet 1979).

A shorter tongue than tube usually prevents nectar extraction; a longer tongue than tube lessens pollen removal and pollination effectiveness. Most hawkmoths use a range of available tube lengths, and many hawkmoth flowers are pollinated by a range of pollinator types. Nevertheless, comparative lengths of hawkmoth tongues and nectar tubes of hawkmoth flowers still interest investigators (Gregory 1963–64, Grant & Grant 1965, 1983a, 1983b, R. B. Miller 1978, 1981, 1985, Haber & Frankie 1982, 1989, Herrera 1989, Grant 1983, Martinez del Rio & Búrquez 1986, Nilsson et al. 1985, Nilsson 1988, and others). Tube lengths of North American hawkmoth flowers range from nil to 175 mm, and tongue lengths of associated hawkmoth pollinators, from 23 to 138 mm, averaging 53 and 60 mm, respectively (Grant 1983). Corresponding statistics in a Costa Rican community are nil to 190 mm, and 10 to 200 mm, averaging 51 and 49 mm, respectively (Haber & Frankie 1989). The resulting tube-to-tongue ratios of 0.88 and 1.04 approximate those experimentally implicating current interactions as maintaining

long tubes and long tongues (Nilsson 1988). Relations between hawk-moth pollinators and plants range from strong one-to-one tongue- and tube-length mutualisms (Nilsson et al. 1985) to more general matches (Leppik 1968, Proctor 1978, Feinsinger 1983, Howe 1984, Bawa 1990).

Contrary to the popular image of long-tongued hawkmoths, several sphingid lineages have vestigial tongues and head musculature. Rudimentary tongues were well known by the time of Rothschild and Jordan (1903), and documented further by Hättich (1907), Mell (1922, 1940), Kernbach (1962), and Fleming (1968). Sphingidae are members of the suborder Glossata. One of the classical defining traits of Glossata is the presence of a functional proboscis (Kristensen 1984). Thus the hawk-moth ancestor had a functional tongue, and vestigial tongues in modern hawkmoths must be the result of reduction. Tongue shortening to 10 mm or less renders hawkmoths incapable of nectar foraging (Fleming 1968), but does not necessarily prevent them from drinking water (Kernbach 1962; Pittaway 1993:106). Although as many as one-fifth of hawkmoth species have shortened tongues and do not forage for nectar, interest in nonfeeding has been dwarfed by interest in nectar foraging. It seems unlikely that a coevolutionary hypothesis of tongue and tube lengths could account for tongue reduction and the order-of-magnitude range in tongue lengths from 2.5 mm in *Laothoe juglandis* (J. E. Smith) (Fleming 1968) to 280 mm in *Amphimoeca walkeri*.

Life-system investigations of sphingids often involve either adult or immature stages, seldom both. One reason is that foodplants of the adult and immature stages usually differ. Comparison of larval and adult foodplant records shows that only 3 to 5 percent of hawkmoth species are known to use even one foodplant genus in both stages (Fleming 1970, Hodges 1971, Grant 1983, Pittaway 1993). Clues to hawkmoth tongue-length diversity and evolution have never been sought in any but the adult stage, nor at broader than local geographic scales.

Here I investigate tongue length on a continental spatial scale using large samples of both New World and Old World hawkmoth species. I explore correlations of tongue length with three variables: midrange latitude of hawkmoth distributions, growth-form of larval foodplants, and percentage of eggs that are mature at adult eclosion. I compare tongue length and tube length of hawkmoth flowers on a latitudinal gradient. Using comparative methodology, I test statistical significance of correlations of tongue length with larval-foodplant growth form, and chart the evolution of both traits as well as that of their correlation.

MATERIALS AND METHODS

In comparative studies, conventional parametric methods may inflate degrees of freedom in significance testing. The reason is that traits of interest may have been inherited from a common ancestor rather than evolved independently by each sample taxon. This

problem is addressed by phylogenetic nested analysis of variance and covariance (Bell 1989, Harvey & Pagel 1991). In nested analysis, values for a given trait are nested heirarchically. Here, for a trait like tongue length, populations are nested within species, species within genera, genera within tribes, and tribes within subfamilies. In nesting by taxonomic level, species represent population ancestors, genera represent species ancestors, tribes represent genus ancestors, and subfamilies represent tribe ancestors. Nested groups are not weighted here by number of subtaxa. I use conventional parametric statistics to introduce and describe correlations, and nested analysis to estimate independent evolution and test statistical significance.

Three kinds of correlation are involved in this study. First is conventional product-moment correlation, r estimating degree of association between a dependent variable and one independent variable, R when there are two independent variables. Product-moment correlation coefficients are usually not tested for significance here because of the degrees-of-freedom problem. The second kind of correlation is intrinsic correlation (Bell 1989), which is identical to variance-component correlation in the output of nested analysis. The intrinsic correlation coefficient estimates degree of association between two variables at various taxonomic levels, and resolves the degrees-of-freedom problem in significance testing. The third kind of correlation is intra- and interclass correlation. Intraclass correlation is the cumulative percentage of total variance at successively lower taxonomic or nesting levels. It is readily derived from variance components in the output of nested analysis. The intraclass correlation coefficient is used in this study to estimate independent evolution of a trait at a given taxonomic or nesting level, and to trace the geologic history of variation in the trait (Bell 1989). Finally, interclass correlation is the cumulative covariance or joint variation between two traits at successively lower taxonomic or nesting levels standardized by the geometric mean of cumulative variances for each trait (Bell 1989). The interclass correlation coefficient is used in this study to trace the geologic history of covariation between two traits (Bell 1989). Coefficients of product-moment correlation range strictly between 0 and 1, those of intrinsic, intra- and interclass correlation nominally between 0 and 1. I used the NESTED procedure of SAS (1988) to perform nested analyses.

My use of hawkmoth classification rather than phylogeny for nesting is necessary because a cladistic or modern hawkmoth phylogeny is not available. Classifications and phylogenies are not necessarily isomorphic, and nesting based on classification may obscure phylogenetic divergences intermediate between taxonomic levels (Harvey & Pagel 1991). The importance of obscured divergences, if any, will only be revealed when a modern phylogeny can be used in place of the classification. Hawkmoth classification has long been stable, which makes it a suitable surrogate for phylogeny. The classification dates from Rothschild and Jordan's (1903) landmark revision of the world fauna which has not been appreciably altered except at the subgeneric level, a level I omit in nesting. Tribes Choerocampini and Macroglossini have been synonymized under the latter name (Hodges 1971, Pittaway 1993), and I follow the resulting arrangement. For New World hawkmoths, nomenclature follows Hodges (1983) and D'Abrera (1986), in that order of preference. For Old World hawkmoths, nomenclature follows Pittaway (1993) and D'Abrera (1986), in that order of preference. I do not distinguish named infraspecific forms in this study except as populations. My geological time scale (Fig. 5) depicts taxonomic divergence in Sphingidae as very slow. Although inspired by Wilson (1978a, 1978b), the scaling is but a guess. Even if wrong in absolute time, however, it is accurate in relative time.

Population tongue length refers to different tongue measurements for a species from different parts of its range. Multiple reports of tongue length are available for 41% (29/70) of the New World sample of hawkmoth species (Appendix 1), and for 11% (9/81) of the Old World sample (Appendix 2). With one exception, species tongue lengths refer to single reports or arithmetic means of population values including both sexes; genus tongue lengths refer to arithmetic means of the means of constituent species; and tribe tongue lengths refer to arithmetic means of the means of constituent genera. The exception concerning species tongue lengths involves the correlation between percentage of eggs that are mature at adult eclosion and tongue length. In this correlation, species tongue lengths are from females only. Sexual dimorphism in hawkmoth tongue lengths is minor, and is

usually related to sexual dimorphism in body size. In the sample where only female tongue lengths are used, females average 2.0 mm longer tongues than males, ranging in individual species up to 5.9 mm longer (n = 18; species with tongue length >4.0 mm; Mell 1922).

New World tongue lengths (Appendix 1) are taken from Gregory (1963–64), Fleming (1968, 1970), Hodges (1971), R. B. Miller (1978, 1981, 1985), Bullock and Pescador (1983), Grant (1983), Grant and Grant (1983a, 1983b), Martinez del Rio and Búrquez (1986), and Haber and Frankie (1989). Old World tongue lengths (Appendix 2) are taken from Hättich (1907), Künckel d'Herculais (1916), Mell (1922, 1940), Kernbach (1961), Kislev et al. (1972), Nilsson (1983, 1988), Herrera (1989), and Pettersson (1991).

All published tongue lengths known to me for hawkmoths with midrange latitudes of 0° or greater northward are included in this study, except one set from Costa Rica (Young 1972). These appear discrepant. For example, tongue lengths reported for species of *Xylophanes* are about twice those for the same species elsewhere in Costa Rica and in western Mexico (Bullock & Pescador 1983, Haber & Frankie 1989). Similar differences occur in *Manduca*, *Eumorpha*, *Cocytius*, *Erinnys*, *Pachylia,* and others.

Tongue length takes two forms in this study: arithmetic and natural logarithmic (ln). I use ln values in the nested analyses to homogenize variance (Bullock & Pescador 1983), and to place differences through a wide range on one scale. Arithmetic values appear in scattergrams, but are plotted on logarithmic scales. Scattergram trend lines are ordinary least-squares fits of the exponential function $y = a$ (10^x). I add 1 to latitudes and oogenesis percentages in some scattergrams and analyses to avoid computational and display problems associated with zero values. Flower-tube length also takes arithmetic form in description, and ln form in analysis.

I use forewing length as a surrogate for body size. Live body-weight increases as the square of forewing length, which makes forewing length a sensitive index of body size (W. E. Miller 1997). Forewing lengths of sample New World hawkmoths are taken from Bullock and Pescador (1983); D'Abrera (1986), whose life-size illustrations of spread specimens I measured; and Haber and Frankie (1989). Forewing lengths of sample Old World hawkmoths are taken from Mell (1922) and D'Abrera (1986). In checking for body-size influence on tongue length, I examine the correlation between tongue length and forewing length at the genus rather than species level. Many hawkmoth species have common ancestry, which, as mentioned, may reduce the validity of significance testing at the species level. In checking for body-size influence on correlations between tongue length and larval foodplant growth-form, I divide sample species by forewing length into small, medium, and large aliquots. The respective forewing-length class limits for the New World sample are 17–35, 36–50, and 51–88 mm; and for the Old World, 14–29, 30–39, and 40–71 mm.

Midrange latitudes serve here as comparative indexes of hawkmoth distributions. Midrange latitude for a species is the latitude midway on a polar axis between north and south extremes of the breeding distribution of combined infraspecifics, excluding erratic records. For a genus, midrange latitude is the arithmetic mean of midrange latitudes of constituent species, and for a tribe midrange latitude is the arithmetic mean of mean midrange latitudes of constituent genera. Midranges of New World species (Appendix 1) are based on Schreiber (1978). Midranges of Old World species (Appendix 2) are based mostly on Mell (1922) and Pittaway (1993), sometimes on D'Abrera (1986).

Larval foodplant records for New World sample hawkmoths are from Hodges (1971), one source cited therein, and Janzen (1984); those for the Old World, from Mell (1922), Lin (1987), Pittaway (1993), and Chen (1994). Foodplants are truncated to genus, and non-native foodplant genera are excluded.

Larval foodplant growth-form index (Appendices 1, 2) refers to the typical height of mature plants and their associated size and tendency to dominate sites. Of several available growth-form classifications, I use a simple one similar to that in Janzen (1984), which recognizes five classes: tree, 25 m high; treelet, 10 to 25 m high; large-shrub, 5 to 10 m high; small-shrub, 3 to 5 m high; and herb (Grime 1979, Collinson 1988). Except for climbing foodplants, I numerically score growth forms according to Box (1981): 2 for herbs, 3 for small shrubs, 4 for large shrubs, 5 for treelets, and 6 for trees. Climbers are usually considered to have a growth-form value of zero, but here they receive values rang-

TABLE 1.   Nested analysis of variance and covariance for tongue length (ln) and larval foodplant growth-form index. The subfamily level is omitted because of only two taxa at that level. Double asterisks indicate significance at P < 0.01.

Taxonomic (nesting) level	n	df	Tongue length	Growth form	Covariance	Intrinsic correlation
New World						
Tribe	5	3	0.580	0.667	−0.389	−0.63
Genus	34	29	0.474	0.707	−0.363	−0.63°°
Species	70	36	0.083	1.282	−0.148	−0.45°°
Population	124	54	0.008	0.000	0.000	0.00
Total	—	123	1.145	2.656	−0.519	−0.39°°
Old World						
Tribe	4	2	0.467	0.420	−0.489	−1.10
Genus	38	35	0.380	0.352	−0.082	−0.22
Species	81	42	0.062	0.294	−0.037	−0.28
Total	—	80	0.909	2.212	−0.987	−0.70°°

The "Variance" header spans the Tongue length, Growth form columns.

ing from 2 to 4 depending on size, whether woody or herbaceous, and whether annual or perennial, because they may be nearly as high and large as their plant supports (Janzen 1975). I obtained growth-form information from standard botanical compendia: for New World foodplants from Fernald (1950), Croat (1978), SCS (1982), and Janzen (1984); for Old World foodplants from Li (1935), Tutin et al. (1964, 1968), and Keng et al. (1993). Because many hawkmoth species use larval foodplants in several genera, foodplant growth-form values for species are usually means. The range of values underlying the mean growth-form for a hawkmoth is usually narrow, such as in Costa Rican hawkmoths (Janzen 1984). For a hawkmoth genus, foodplant growth-form index is the arithmetic mean of growth-form indexes of constituent species, and for a tribe, the arithmetic mean of growth-form indexes of constituent genera.

Data concerning percentage of eggs that are mature at adult eclosion are taken from Mell (1922, 1940). He recorded tongue length and numbers of mature and immature eggs and oocytes in 4 to 46 newly eclosed females per species in Old World hawkmoths (Appendix 2). He verbally described the resulting relation. I elaborate his observations with product-moment correlation analysis at species, genus, and tribe levels.

RESULTS

The assembled New World tongue-length sample consists of 124 observations on 70 species in 34 genera, 5 tribes, and 2 subfamilies, with multiple observations on 24 species (Table 1, Appendix 1). Although nesting extended to subfamily, no subfamily results are given for any variable because of only two taxa at that level. Tongue length in the New World sample varies inversely with latitude of midrange distribution at species, genus, and tribe levels, with product-moment correlation coefficients ranging between −0.44 and −0.57 (Fig. 1). Although these correlation coefficients were not tested for significance, they are judged to reflect a real relation because of similar signs and values at the different taxonomic levels. At the species level, mean tongue lengths at north latitudes of 0° (northern Brazil), 20° (southern Mexico), and 40° (central U. S.) are 50, 25, and 15 mm, respectively.
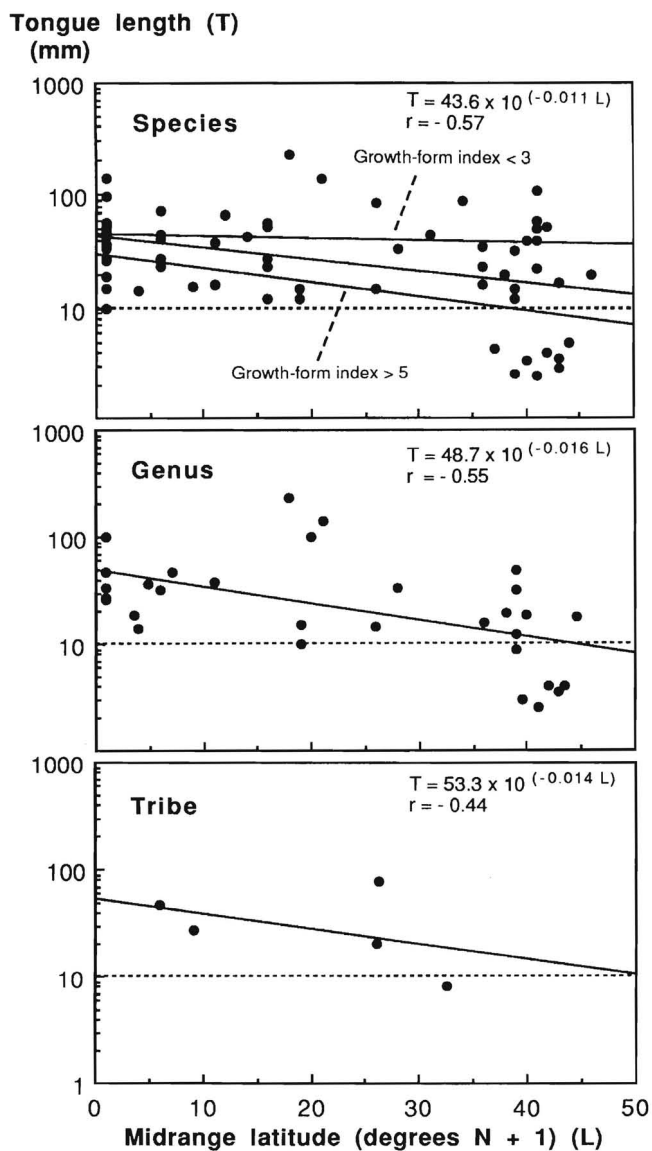
Tongue length (T)
(mm)

FIG. 1. Relation of tongue length to midrange latitude in New World hawkmoths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation describes the center trend line and encompasses all species points. Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

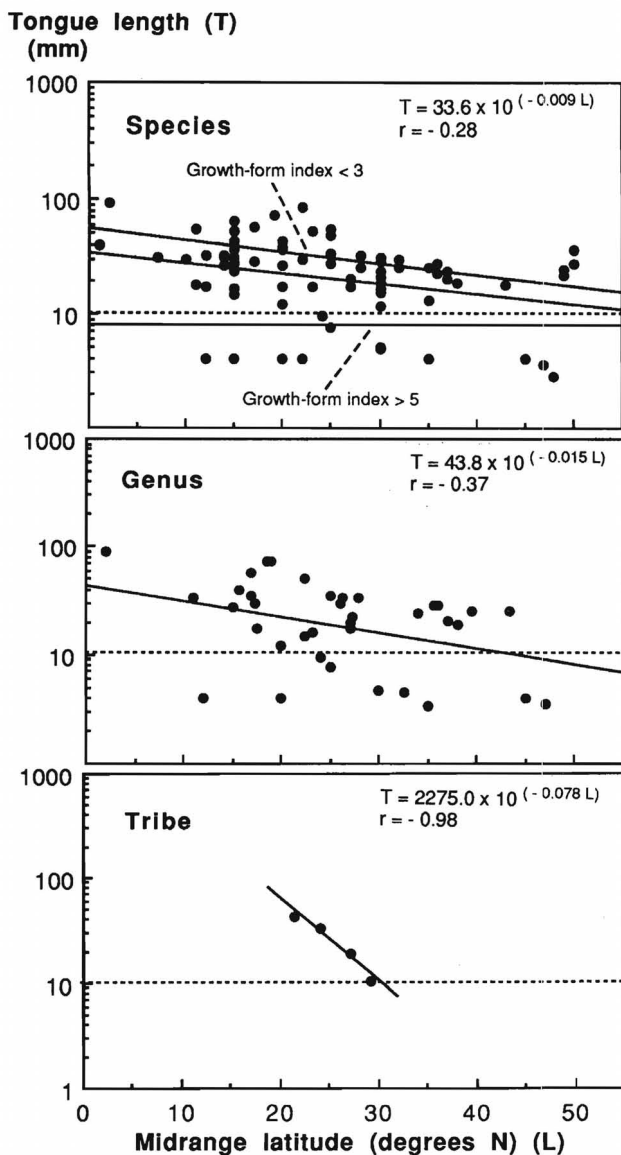**Tongue length (T)**
(mm)

FIG. 2.   Relation of tongue length to midrange latitude in Old World hawkmoths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation describes the center trend line and encompasses all species points. Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

The assembled Old World tongue-length sample consists of 92 observations on 81 species in 38 genera, 4 tribes, and 2 subfamilies, with multiple observations on 9 species (Table 1, Appendix 2). Although nesting extended to subfamily, no subfamily results are given for any variable because of only two taxa at that level. Old World tongue lengths also vary inversely with latitude of midrange distribution at species, genus, and tribe levels, with product-moment correlation coefficients ranging between –0.28 and –0.98 (Fig. 2). At the species level, mean tongue lengths at north latitudes of 0° (Borneo), 25° (southern China), and 50° (central Eurasia) are 42, 26, and 12 mm, respectively. The correlation here is also judged to reflect a real relation for the same reasons given above for the New World sample. New and Old World sample species represent 14% (151/1050) of the world hawkmoth fauna (D'Abrera 1986).

In both New and Old World tongue-length correlations with latitude, the trend lines for larval foodplant growth-form indexes <3 and >5 reveal a tendency for tongue lengths in these narrow index ranges to shorten as latitude increases (Figs. 1, 2). Thus the effect of latitude seems to operate regardless of foodplant growth-form.

Unlike tongue length, nectar-tube length appears to remain constant rather than shorten with increasing north latitude. In a community of hawkmoth flowers in Costa Rica (about 10° north latitude), mean tube length is 50 mm (n = 30; Haber & Frankie 1989), and in all known U. S. hawkmoth flowers (centering at 40° north latitude), mean tube length is 55 mm (n = 124; Grant 1983). The difference, 5 mm, is not significant (P = 0.23, Student t-test of difference in tube lengths [ln]).

Tongue length is inversely correlated also with larval foodplant growth-form index at species, genus, and tribe levels. In the New World sample, the product-moment correlation coefficients range between –0.43 and –0.51 (Fig. 3). At the species level, mean tongue lengths at foodplant growth-form indexes of 2 (herbs), 4 (large shrubs), and 6 (trees) are 53, 27, and 14 mm, respectively. In the Old World sample, product-moment correlation coefficients range between –0.59 and –0.84 (Fig. 4). At the species level, tongue lengths at foodplant growth-form indexes of 2, 4, and 6 are 41, 17, and 8 mm, respectively. As before, these correlation coefficients were not tested for significance, but they are judged to reflect a real relation because of similar signs and values at the different taxonomic levels. The mean tongue lengths for a given growth-form index vary some between New and Old World samples, but the relations are similar in form.

Previous authors report significant correlations between tongue length and body size in local hawkmoth assemblages (Bullock & Pescador 1983, Haber & Frankie 1989). Investigation here reveals that positive correlations between tongue length (T) and body size (F) are

Tongue length (T)
(mm)

Species

$T = 102.5 \times 10^{(-0.144\,I)}$
$r = -0.48$

Large-bodied   Medium-bodied

Small-bodied

1000
100
10

Genus

$T = 86.2 \times 10^{(-0.143\,I)}$
$r = -0.43$

1000
100
10

Tribe

$T = 128.9 \times 10^{(-0.163\,I)}$
$r = -0.51$

1000
100
10
1

2   3   4   5   6
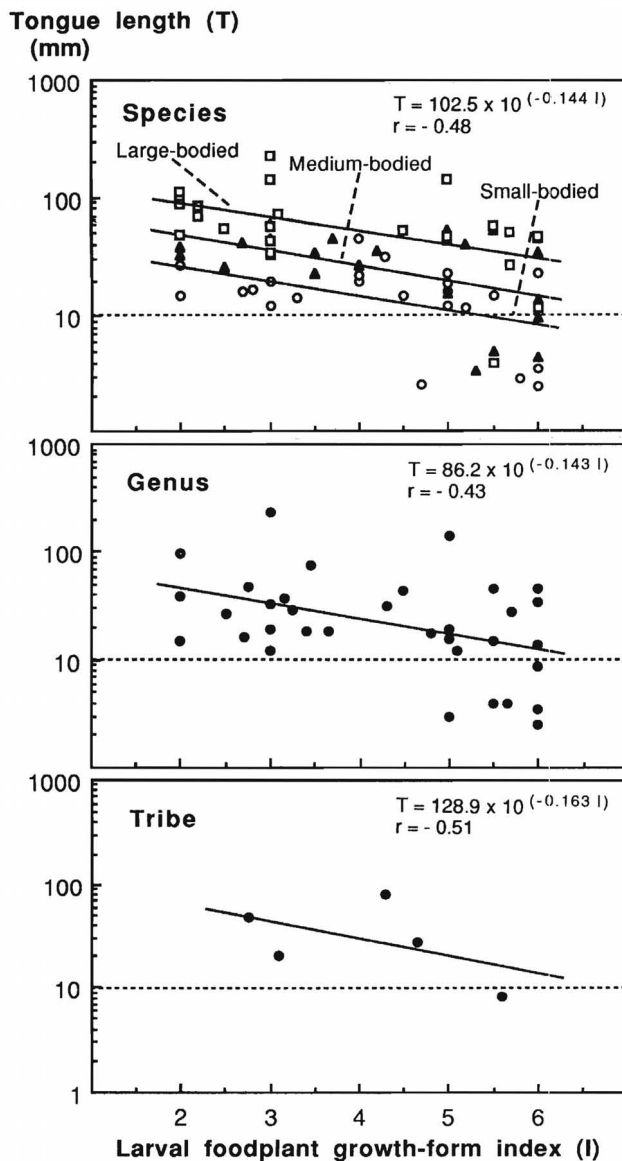
Larval foodplant growth-form index (I)

FIG. 3. Relation of tongue length to larval foodplant growth-form in New World hawkmoths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation represents all body sizes. Small, medium, and large body-size classes are defined, respectively, by forewing lengths of 17–31 mm (open circles), 32–46 mm (triangles), and 50–88 mm (open squares). Respective equations and product-moment correlation coefficients are $T = 45.0 \times 10^{-0.123I}$ ($r = -0.45$), $T = 86.0 \times 10^{-0.128I}$ ($r = -0.51$), and $T = 152.2 \times 10^{-0.117I}$ ($r = -0.51$). Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.
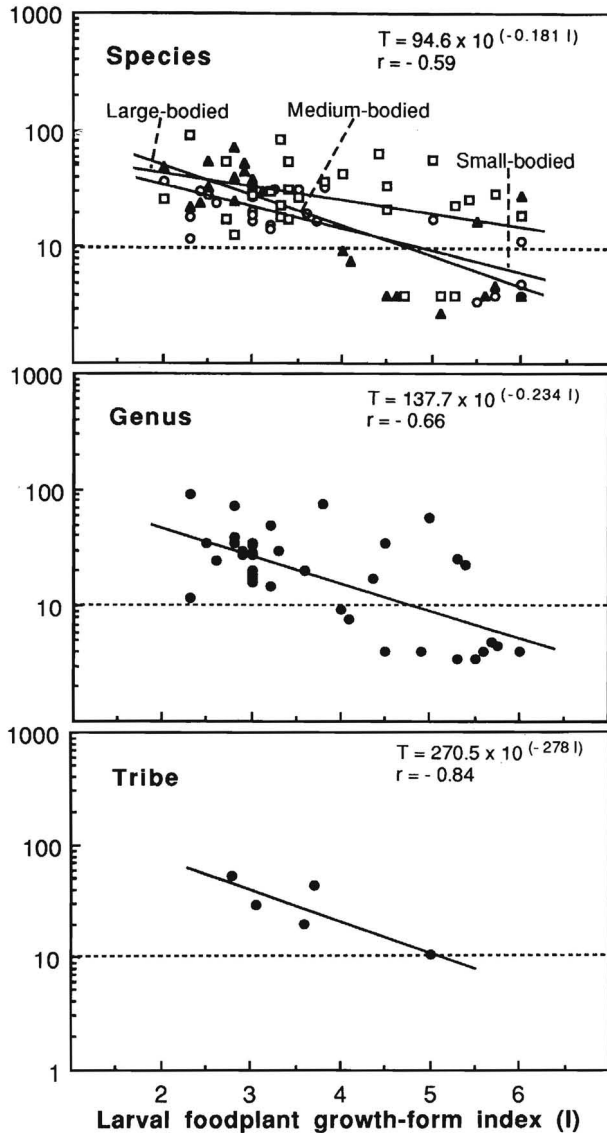
FIG. 4. Relation of tongue length to larval foodplant growth-form in Old World hawk-moths at species, genus, and tribe levels. Points are means except where only one tongue-length value is available. The species equation represents all body sizes. Small, medium, and large body-size classes are defined, respectively, by forewing lengths of 14–29 mm (open circles), 30–39 mm (triangles), and 40–71 mm (open squares). Respective equations and product-moment correlation coefficients are $T = 79.8 \times 10^{-0.186I}$ ($r = -0.78$), $T = 165.0 \times 10^{-0.258I}$ ($r = -0.76$), and $T = 69.1 \times 10^{-0.112I}$ ($r = -0.34$). Significance values are omitted because of problematic degrees of freedom as explained in text. Dotted lines at 10 mm represent length below which tongues are believed to be nonfunctional.

pervasive both above the species level and at broader geographic scales. For genera, the New World sample yields $T = 4.52 \times 10^{0.018F}$ ($r = 0.61$, $n = 34$); the Old World sample, $T = 7.53 \times 10^{0.011F}$ ($r = 0.32$, $n = 38$). If the degrees-of-freedom problem is assumed to be small at the genus level, then the significance values for these product-moment correlations are $P < 0.01$ and 0.05, respectively.

Despite the influence of body size on tongue length, the tongue-length correlations with foodplant growth-form are not merely an outcome of different hawkmoth body sizes. Tongue length decreases in all body-size ranges as foodplant growth-form index increases. In the three body-size aliquots of New World species, product-moment correlations range between -0.49 and -0.58, compared with -0.48 for all New World species (Fig. 3); in the three body-size aliquots of Old World species, they range between -0.34 and -0.78, compared with -0.59 for all Old World species (Fig. 4). The most telling evidence that growth form operates in all body-size ranges is that regression slopes in all six New and Old World aliquots are negative. Multiple regression analysis echoes this conclusion in its standardized slope coefficients, which reveal the relative influence of independent variables (SYSTAT 1992). These coefficients for foodplant growth-form and body size in New World species are -0.44 and 0.61, respectively ($r = 0.77$); and in Old World species -0.65 and 0.32, respectively, ($r = 0.67$).

Similarity of tongue-length change with latitude and larval foodplant growth-form index at three taxonomic levels (Figs. 1–4) suggests not only real relations, but relations with a long history. Both suggestions are confirmed for growth-form index by nested analyses (Table 1, Fig. 5), and for latitude by extension and inference. Overall intrinsic correlations between tongue length and growth-form index for New and Old World hawkmoth samples are -0.39 and -0.70, respectively ($P < 0.001$) (Table 1). Similar intrinsic correlations appear at the tribe level, which represents truly ancient ancestors. The respective New and Old World tribe covariances of -0.389 and -0.489 are the highest of any taxonomic level (Table 1). The histories of variation in tongue length and foodplant growth-from, as well as that of their covariation, show little change since genera diverged perhaps 15 million years before present (Fig. 5). Despite tongue-length relations with latitude and larval foodplant growth-form, it must be acknowledged that significant tongue-length variation remains unexplained (Figs. 1–4, Table 1).

The sample concerning percentage of eggs that are mature at adult eclosion in relation to tongue length consists of 26 Old World species in 14 genera, 2 tribes, and 1 subfamily (Appendix 2). Mell (1940) concluded from this sample that oogenesis at adult eclosion is more advanced the shorter the tongue. Mell's conclusion also applies at the
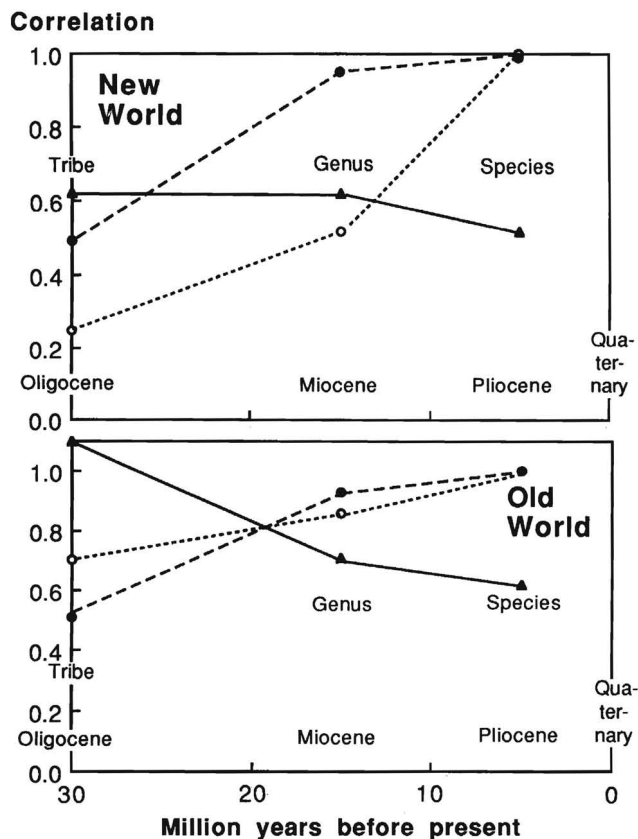
FIG. 5. Evolution of tongue length (solid circles, dashed lines), larval-foodplant growth-form (open circles, dotted lines), and their covariation (triangles, solid lines) at different taxonomic levels. Points for tongue length and foodplant growth-form represent intraclass correlations, and points for covariation represent interclass correlations, as explained in text. The geologic time scale is a best guess based on Wilson (1978a, b).

genus level, and, as far as the data go, at the tribe level (Fig. 6). These results point to another ancient relation. At the species level, mean percentage of eggs mature at eclosion for tongue lengths of 20, 50, and 80 mm, are 30, 15, and 7, respectively. If total egg production were known and incorporated, it would probably intensify the relation. That is, in long-tongued individuals, oocytes undetected at adult eclosion, or formed afterwards, would likely grow and mature from resources gained by nectar foraging. The link between tongue length and reproductive readiness at adult eclosion confirms that tongue length is intimately involved in hawkmoth life-system evolution.
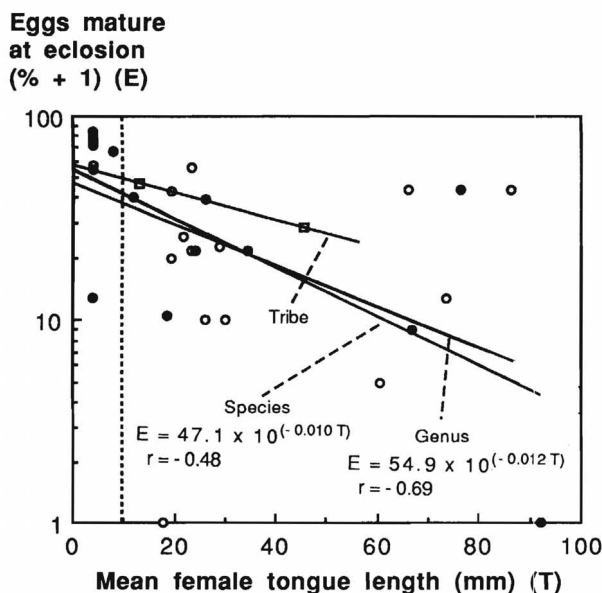
FIG. 6.   Relation of egg maturity at eclosion to tongue length in Old World hawk-moths. Points are means for females. Closed circles represent species, open circles genera, and open squares tribes. Data from Mell (1922, 1940). Dotted line at 10 mm represents length below which tongues are believed to be nonfunctional.

DISCUSSION

A hypothesis of hawkmoth tongue-length diversity and evolution must account for both tongue lengthening and shortening as well as for the new findings in this study. I summarize these findings as follows. Mean tongue length decreases with increasing north latitude worldwide (Figs. 1, 2), whereas tube length of hawkmoth flowers appears to remain constant. Mean tongue length decreases with increasing larval food-plant growth-form index worldwide (Figs. 3, 4, Table 1). Further, the shorter the tongue, the greater the percentage of eggs that are mature at adult eclosion (Fig. 6). These relations are ancient, their trends having formed before the divergence of genera, postulated as occurring in middle Miocene time, some 15 million years before present (Fig. 5).

At least three-quarters of the 25 tree genera used as larval foodplants by hawkmoths in this study are recorded as fossils from the middle Miocene or earlier (Leopold & MacGinitie 1972, Tanai 1972, Vakhrameev 1991). Also, plants with stereomorphic flowers, or still more advanced zygomorphic flowers with long nectar tubes, existed by the middle Miocene also (Leppik 1968, Proctor 1978, Crepet 1979). Thus the
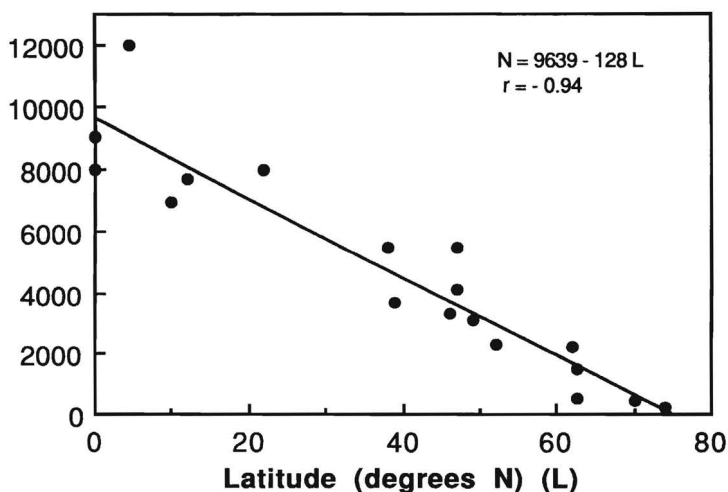
No. phanerogam species locally (N)

FIG. 7.   Species richness of local seed-plant floras in the northern hemisphere as related to latitude. Data from Rejmánek (1976).

potential for larval foodplants of high growth-form index, and adult foodplants with long-tubed flowers, to influence tongue length seems easily coextensive with the history of tongue-length variation on the postulated geologic time scale (Fig. 5). The latitudinal gradient in tongue length is equally or more ancient; the position of the continents relative to the equator has not changed greatly since the Paleocene, some 60 million years before present (Smith & Briden 1977).

No doubt many plausible hypotheses of tongue length diversity and evolution could be given. I favor an admittedly anthropocentric possibility, which focuses on larval foodplant finding, a process that remains to be studied. Especially in extratropical landscapes, herb foodplants (growth-form index 2) may be harder to find than tree foodplants (growth-form index 6). Moreover, foodplants of any growth-form index may be easier to find at higher north latitudes today because there is little doubt that patch size increases with increasing north latitude. This increase in patch size is as yet poorly quantified, and can best be visualized as a function of the polar-equatorial gradient of species richness in plants (Fig. 7). In this gradient, the number of seedplant species in local floras decreases at higher latitudes worldwide (Rejmánek 1976, Currie & Paquin 1987). As floras diminish in species richness toward polar regions—from near 10,000 species at the equator to one-fifth that num-

ber in central North America and central Eurasia (Fig. 7)—woody plants, and probably vascular plants in general, may occur in larger stands or patches (Dobzhansky 1950, Bourgeron 1983, Longman & Jeník 1987). Tropical forests often contain 60 to 1000 tree species per ha. In such forests, it seems physically impossible for very many individuals of one kind of tree to occur contiguously. Although unclear whether patch size of all plant growth-forms in the tropics would be similarly affected, small patch size for trees seems likely to prevail. In contrast, temperate forests often have only one or a few tree species per ha, rarely more than 10, and large patch sizes for trees and other plant growth-forms prevail.

Most hawkmoth adults are heavy bodied, and their energy expenditure in flight is enormous, with hovering consuming about 1 mg of sugar g^{-1} body weight min^{-1} (Heinrich 1983). For hawkmoths that must find nonpersistent, inconspicuous foodplants of low growth form in small patches (Figs. 2, 4, 7), and whose eggs are mostly immature at eclosion (Fig. 6), long tongues and nectar foraging are essential. The longer the tongue, the greater and faster the access to nectar in flowers of different depths, and the greater the chances of mutualistic specialization (Nilsson 1988, Haber & Frankie 1989, Herrera 1989). Also, the deeper the nectar, the more of it plants produce (Haber & Frankie 1989). In contrast, long tongues and nectar foraging may be superfluous for hawkmoths that have the easy task of finding persistent, conspicuous larval foodplants of high growth form in large patches (Figs. 2, 4, 7), and whose eggs are mostly mature at eclosion (Fig. 6).

The association of tongue shortening and larval feeding on trees in Glossata is not unique to hawkmoths (W. E. Miller 1996). Larvae of Lymantriidae and Saturniidae feed almost exclusively on trees or other woody plants, and their adults do not feed (Ferguson 1971–72, 1978, Janzen 1984, Schaefer 1989, Stone 1991). The same is true for many subgroups in other families such as Geometridae. Another trait associated with larval tree-feeding and loss of adult feeding capability in some Glossata is reduction in female flight capability. Flightless females dramatically demonstrate that flight is not essential when larval foodplants are trees occurring in large stands or patches (Gohrbandt 1940, Barbosa et al. 1989, Sattler 1991).

Although the foregoing speculative hypothesis involves mechanisms operating at continental geographic scales, it does not rule out other mechanisms of tongue-length adjustment operating at local scales.

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APPENDIX 1.   Taxa and variable values for sample New World hawkmoths. Sources are given in the Methods section. For mean tongue length, values without decimals are single observations in a single report; values with decimals are means of multiple observations at one location; values with decimals and SD are means of observations at multiple locations enumerated by (n).

Species	Mean tongue length ± SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Sphinginae: Sphingini			
Agrius cingulata (F.)	99.2 ± 4.6 (4)	0	2.0
Cocytius antaeus (Drury)	139	20	5.0
Ceratomia amyntor (Gey.)	12.0	38	6.0
C. catalpae (Bdv.)	4.4	36	6.0
C. undulosa (Wlk.)	9.8	40	6.0
Dolba hyloeus (Drury)	32	38	4.3
Lapara bombycoides Wlk.	3.5	42	6.0
Manduca barnesi (Clark)	52.0	15	4.5
M. corallina (Drc.)	56.8 ± 1.6 (2)	15	5.5
M. dilucida (Hy. Edw.)	43.2 ± 0.4 (2)	13	5.0
M. florestan (Cram.)	72.0 ± 15.6 (3)	5	3.1
M. lefeburei (Guér.)	51.8 ± 1.2 (2)	0	5.0
M. muscosa (R. & J.)	86.0	25	2.2
M. quinquemaculata (Haw.)	110.0 ± 14.9 (4)	40	2.0
M. occulta (R. & J.)	68.0	11	2.2
M. rustica (F.)	138.3 ± 5.1 (3)	0	3.0
M. sexta (L.)	89.0 ± 6.4 (4)	33	2.0
Neococytius cluentius (Cram.)	228.5 ± 37.5 (2)	17	3.0
Sphinx chersis (Hbn.)	50.4 ± 7.6 (5)	40	5.7
S. drupiferarum J. E. Sm.	52.0 ± 11.3 (2)	41	5.5
S. eremitoides Stkr.	39.0	40	2.0
S. kalmiae J. E. Sm.	40	39	5.2
S. libocedrus Hy. Edw.	45	30	4.0
S. sequoiae Bdv.	23.0	35	6.0
S. vashti Stkr.	60.0 ± 2.6 (3)	40	3.0
Sphinginae: Smerinthini			
Laothoe juglandis (J. E. Sm.)	2.5	40	6.0
Pachysphinx modesta (Harr.)	4.0	41	5.5

APPENDIX 1.   Continued.

Species	Mean tongue length ± SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Paonias excaecatus (J. E. Sm.)	3.4	39	5.3
P. myops (J. E. Sm.)	2.6	38	4.0
Protambulyx strigilis (L.)	27.5 ± 0.7 (2)	0	5.7
Smerinthus cerisyi Kirby	5	43	5.5
S. jamaicensis (Drury)	2.9	42	5.8
Macroglossinae: Dilophonotini			
Aellopos clavipes (R. & J.)	16.0	10	5.0
A. fadus (Cram.)	15.0	0	4.5
A. titan (Cram.)	23.0	5	5.0
Callionima falcifera (Gehl.)	15.5 ± 0.7 (2)	8	5.0
Erinnyis alope (Drury)	44.8 ± 0.2 (2)	5	3.7
E. ello (L.)	36.0 ± 1.0 (3)	0	4.2
E. lassauxii (Bdv.)	40.8 ± 1.6 (2)	5	2.7
E. obscura (F.)	27.0 ± 1.4 (2)	5	2.0
Eupyrrhoglossum sagra (Poey)	19.0	0	5.0
Hemaris diffinis (Bdv.)	17.0	42	2.8
H. thysbe (F.)	19.4	45	4.0
Isognathus rimosus (Grt.)	34.2 ± 1.1 (2)	27	6.0
Nyceryx coffeae (Wlk.)	14	3	6.0
Pachylia ficus (L.)	46.5 ± 0.7 (2)	0	5.0
P. syces (Hbn.)	45.0 ± 0.0 (2)	0	6.0
Pachylioides resumens (Wlk.)	26.5 ± 0.7 (2)	0	2.5
Perigonia lusca (F.)	15.0	18	5.5
Phryxus caicus (Cram.)	33	0	3.0
Pseudosphinx tetrio (L.)	46.5 ± 3.5 (2)	0	6.0
Macroglossinae: Phillampelini			
Eumorpha achemon (Drury)	45.7 ± 3.8 (3)	0	3.0
E. anchemola (Cram.)	58.0	0	3.0
E. fasciata (Sulz.)	48.0	0	2.0
E. labruscae (L.)	55.0	0	2.5
E. pandorus (Hbn.)	34.5	35	3.0
E. vitis (L.)	42.9 ± 0.1 (2)	0	3.0
Macroglossinae: Macroglossini			
Amphion floridensis Clark	16.0	35	2.7
Cautethia spuria (Bdv.)	12.0	18	5.2
C. yucatana Clark	12.3	15	5.0
Darapsa myron (Cram.)	14.7	38	3.3
D. pholus (Cram.)	22	40	4.0
Deidamia inscripta (Harr.)	12.2	38	3.0
Hyles lineata (L.)	38.3 ± 1.5 (11)	10	2.0
Proserpinus terlooii Hy. Edw.	14.8	25	2.0
Sphecodina abbottii (Swain.)	19.5	37	3.0
Xylophanes pluto (F.)	34.5 ± 0.7 (2)	0	3.5
X. porcus (Hbn.)	27.5 ± 0.7 (2)	15	4.0
X. tersa (L.)	33.5 ± 2.1 (2)	0	2.0
X. turbata (Hy. Edw.)	23.0 ± 1.4 (2)	15	3.5

APPENDIX 2.   Taxa and variable values for sample Old World hawkmoths. Sources are given in the Methods section. For mean tongue length, values with decimals are means of multiple observations from one location; values with decimals and SD's are means of observations from multiple locations enumerated by (n). Superscript b = species used here in the correlation between percentage of eggs that are mature at adult eclosion and tongue length (Fig. 6). Superscript c = tongue so short as to be nonfunctional according to Mell (1922, 1940); mean of all nonfunctional tongues measured by him was assigned.

Species	Mean tongue length ± SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Sphinginae: Sphingini			
Acherontia atropos (L.)	13.0	35	2.8
A. lachesis (F.)[b]	17.6 ± 1.8 (2)	12	3.4
A. styx (Westw.)[b]	17.7 ± 1.1 (2)	23	2.7
Agrius convolvuli (L.)[b]	90.9	2	2.3
Dolbina inexacta (Wlk.)[b]	7.6	25	4.1
Meganoton analis (Fldr.)[b]	56.5	17	5.0
M. rufescens Btlr.[b]	72.5	—	—
Psilogramma increta (Wlk.)[b]	63.7	15	4.4
P. menephron (Cram.)[b]	84.6	22	3.3
Sphinx calligineus Btlr.[b]	11.6	30	6.0
S. ligustri L.	36.6	50	3.8
S. pinastri L.	28.5 ± 1.4 (2)	50	6.0
Sphinginae: Smerinthini			
Ambulyx kuangtungensis (Mell)	17.0	30	5.5
A. liturata Btlr.[b]	29.7	30	5.7
A. ochracea Btlr.[b]	21.6	30	4.5
A. schauffelbergeri B. & G.[b]	19.0	30	6.0
A. sericeippenis Btlr.[b]	25.8	28	5.4
A. subocellata Fldr.[b]	23.5	15	5.2
Amplypterus panopus (Cram.)[b]	34.6	12	4.5
Clanis bilineata (Wlk.)[b]	22.9	36	3.3
C. undulosa Moore[b]	26.2	32	2.0
Cypa decolor Wlkr.[b]	4.0[c]	12	6.0
Laothoe populi (L.)	4.0 ± 1.4 (2)	45	5.6
Leucophlebia lineata Westw.	9.5	24	4.0
Marumba cristata (Btlr.)[b]	4.0[c]	15	5.2
M. dyras (Wlk.)[b]	4.0[c]	15	4.7
M. gaschkewitschi (B. & G.)[b]	4.0[c]	35	4.6
M. spectabilis (Btlr.)[b]	4.0[c]	15	5.1
Mimas tiliae (L.)	3.5 ± 0.7 (2)	47	5.5
Parum colligata (Wlk.)[b]	4.8	30	5.7
Polyptychus trilineatus Moore[b]	4.0[c]	20	4.5
Smerinthulus chinensis R. & J.[b]	4.0[c]	22	5.7
S. pallidus Mell	5.0	30	6.0
Smerinthus ocellatus (L.)	2.8 ± 0.4 (2)	48	5.1
S. planus Wlk.[b]	4.0[c]	35	6.0
Macroglossinae: Dilophonotini			
Cephonodes hylas (L.)	20.1	27	3.6
Hemaris staudingeri (Leech)	20.6	37	3.0
Sataspes infernalis (Westw.)	16.9	15	3.7
S. tagalica Bdv.	17.5	20	5.0

APPENDIX 2.   Continued.

Species	Mean tongue length ± SD (mm)	Midrange latitude (°N)	Mean larval foodplant growth form index
Macroglossinae: Macroglossini			
Acosmerycoides leucocraspis (Hamp.)	27.9	15	3.0
Acosmeryx castanea R. & J.	30.4	32	3.1
A. naga (Moore)	32.0	30	3.4
A. pseudomissa Mell	27.5	20	3.5
A. sericeus (Wlk.)	30.2	22	3.2
Ampelophaga rubiginosa B. & G.	28.2	36	3.0
Aspledon himachala (Btlr.)	15.4	30	3.2
A. hyas (Wlk.)	14.6	15	3.2
Cechenena lineosa (Wlk.)	55.3	25	3.4
C. minor (Btlr.)	44.2	20	2.9
Daphnis hypothous (Cram.)	43.5	15	4.0
Deilephila elpenor (L.)	21.9 ± 0.6 (3)	49	2.3
D. porcellus (L.)	18.5 ± 0.3 (2)	43	2.3
Hayesiana triopus (Westw.)	33.0	28	3.0
Hippotion boerhaviae (F.)	31.4	7	3.5
H. rafflesi (Btlr.)	37.0	15	2.0
Hyles gallii (Rtmbg.)	25.4 ± 0.6 (3)	49	2.8
H. livornica (Esper)	24.4	30	2.4
Macroglossum bombylans (Bdv.)	28.0	25	2.5
M. corythus Wlk.	33.3	14	3.0
M. passalus (Drury)	32.3	12	3.8
M. pyrrhostictum (Btlr.)	31.4	15	3.0
M. sitiene (Wlk.)	31.8	7	3.2
M. stellatarum (L.)	26.4	35	2.0
M. troglodytus (Bdv.)	26.9	14	3.0
Micracosmeryx macroglossoides Mell	17.2	27	3.0
Panacra busiris Wlk.	38.4	20	3.0
P. mydon Wlk.	32.0	14	3.0
Pergesa actea (Cram.)	73.5	19	2.8
Rhagastis albomarginatus (Roths.)	29.2	17	3.0
R. mongoliana (Btlr.)	24.0	37	2.6
R. olivaceae (Moore)	49.5	25	2.0
Sphingonaepiopsis pumilio (Bdv.)	12.0	20	2.3
Sphecodina caudata (B. & G.)	18.9	38	3.0
Theretra alecto (L.)	52.7	23	2.9
T. clotho (Drury)	18.5	11	3.3
T. japonica (Orza)	27.7	36	3.0
T. latreillei (MacLeay)	40.2	1	2.8
T. nessus (Drury)	55.5	11	2.7
T. oldenlandiae (F.)	32.8	14	2.5
T. pallicosta (Wlk.)	37.2	20	3.0
T. silhetensis (Wlk.)	30.5	10	2.4
T. suffusa Wlk.	53.9	15	2.5