Biosystematics of the
Nymphomyiidae (Insecta: Diptera):
Life History, Morphology, and
Phylogenetic Relationships

Gregory W. Courtney
ABSTRACT

Courtney, Gregory W. Biosystematics of the Nymphomyiidae (Insecta: Diptera): Life History, Morphology, and Phylogenetic Relationships. Smithsonian Contributions to Zoology, number 550, 41 pages, 98 figures, 3 tables, 1994.—Previously undescribed characters are evaluated and incorporated in a redescription of the Nymphomyiidae (Diptera). The revised family includes seven species, two of which are new. Nymphomyia dolichopeza, new species, is widespread and locally abundant in streams of the southern Blue Ridge Mountains, primarily in North Carolina and Georgia, U.S.A.; and N. holoptica, new species, is recorded from Hong Kong. Based on structural and phylogenetic criteria, the monobasic genera Palaeodipteron Ide and Felicitomyia Kevan are new synonyms of Nymphomyia Tokunaga. Larval, pupal, and adult characters were used to reconstruct the phylogenetic and biogeographic relationships of world species of Nymphomyia. Based primarily on adult features, Nymphomyia is divided into two species groups with the following phylogenetic relationship: (1) alba group (alba + (levanidovae + rohdendorfi)); and (2) walkeri group ((walkeri + dolichopeza) + (brundini + holoptica)). Several compelling characters help define the eastern Palaearctic alba group, and others provide strong evidence that the Oriental species brundini and holoptica are monophyletic. Although data suggest that the Nearctic fauna (walkeri and dolichopeza) is monophyletic, the cladistic basis for this hypothesis is relatively weak (two reductive characters). Keys to larvae, pupae, and adults and a discussion of collection techniques, ecological data, and distributions are provided.

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Biosystematics of the Nymphomyiidae (Insecta: Diptera): Life History, Morphology, and Phylogenetic Relationships

Gregory W. Courtney

Introduction

The Nymphomyiidae are one of the most specialized and distinctive, yet least-studied families of nematocerous Diptera. These flies, which typically colonize small, cool, pristine, mountain streams, are currently known from only five described species, including three from northeastern Asia (Nymphomyia alba Tokunaga, N. levandovae Rohdendorf and Kalugina, and N. rohdendorfi Makarchenko) and each one from the Himalaya's (N. (= Felicitomyia) brundini (Kevan)) and eastern North America (N. (= Palaeodipteron) walkeriana (Ide)). Nymphomyiid larvae are considered grazers, feeding on the periphytic film on riffle substrates, and adults appear to be short-lived and non-feeding. The phylogenetic position of the Nymphomyiidae has been one of the most important questions of dipterology, yet few studies have critically evaluated the group's phylogenetic affinities. Our ignorance about nymphomyiids stems largely from the dearth of biological information and material for examination, which in turn may reflect the minute size (<2 mm), cryptic habits, and typically scattered distributions of these flies.

The major objectives of this research were to (1) provide detailed morphological data on larval Nymphomyiidae; (2) determine the phylogenetic relationship between the Nymphomyiidae and other Diptera; (3) revise the world species of Nymphomyiidae, including descriptions of new species; (4)

evaluate the phylogenetic and biogeographic relationships between species of Nymphomyiidae. The second objective will be discussed in a companion paper on the higher phylogeny of all families of nematocerous Diptera, while the remaining topics are addressed here. Collection techniques, habitat characteristics, and basic life-histories are also discussed.

ACKNOWLEDGMENTS.—This study was based largely on examination of larvae, pupae, and adults of Nearctic species collected during 1990–1992. Most of this material is housed in the National Museum of Natural History. Representatives of Palaearctic species and additional North American material were borrowed from, or are deposited with, the following institutions and individuals.

AMNH American Museum of Natural History, New York, New York (D. Grimaldi)
CNC Canadian National Collection, Ottawa, Canada (J.M. Cumming)
GWC Collection of author
NRS Naturhistoriska Riksmuseet, Stockholm, Sweden (H. Hippa)
ROM Royal Ontario Museum, Toronto, Canada (G.B. Wiggins)
USNM Collections of the United States National Museum, now deposited in the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, D.C.

Additional specimens (now in USNM or GWC) were provided by D.A. Craig, University of Alberta, Edmonton; D. Dudgeon, University of Hong Kong; and A. Huryn, University of Alabama, Tuscaloosa. To these institutions and individuals, I express my sincere gratitude. I am further indebted to E.A. Makarchenko, Russian Academy of Sciences, Vladivostok, for

Drift nets were used occasionally to collect nymphyiids, though resultant samples yielded few specimens. Adults (often pharate, alate specimens) and pupal exuviae were sometimes common in drift samples, though collections suggest that drift of larvae and pupae is infrequent under normal stream conditions. Exceptions to this pattern come from studies of the effects of pesticides on non-target organisms (Ide, 1964, 1965; Eidt and Weaver, 1983).

Kick sampling was sometimes an effective means of collecting pupae and adults, particularly at sites where rocks lacked a dense coating of moss. At several sites in the southern Appalachian Mountains, kick samples yielded far more pupae and adults of *N. dolichopeza* than did rock wash samples. This pattern may indicate differences in pupation and perhaps oviposition behavior at sites with and without mossy substrates (see under "Life History").

Emergence traps effectively capture adults at some sites (Back and Wood, 1979; personal observations), and Malaise traps occasionally collect them (Hurny, 1991, pers. comm.). In my study, Malaise traps were placed at a North Carolina site during late spring and early summer, 1991, but no nymphyiids were taken. However, because this period coincides with a rather small emergence, failure to collect adults may have reflected poor timing rather than an ineffectual collection technique.

**Rearing Techniques**: I attempted to rear pupae of the Nearctic species *N. walker* and *N. dolichopeza*. Samples for rearing were collected in the same manner as those to be preserved. Samples were stored in Whirl-Pak™ bags in a chilled container (e.g., cooler) and sorted on the same day, usually less than six hours after collection. Mortality in samples sorted on the day of collection was often limited to individuals damaged during sampling. The longest period between collection and sorting was nearly four days, after which at least some live pupae were found. Pupae were placed on damp filter paper or a natural substrate (e.g., wet leaf) in a loosely sealed container (e.g., Multiwell™ tissue culture plate) that was stored in a cooler or refrigerator (<15°C) and checked at least once per day. Samples maintained at higher temperatures (e.g., room temperature) showed substantially greater mortality. Rearing success was greater for pupae of *N. walker* than for *N. dolichopeza*, which may have been an artifact of the higher number of *N. walker* pupae collected or of the more destructive collection methods for *N. dolichopeza* (i.e., kick sampling).

**Morphology**: Morphological investigations were based mostly on representatives of Nearctic species collected during 1990–1992. Structural features were determined from whole-animal slide mounts, larval dissections, and scanning electron microscopy (SEM). Most slide-mounted material was cleared in cedarwood oil and mounted in Canada balsam, following procedures described elsewhere (Courtney, 1990). Additional material was prepared by removing soft tissues with lactic acid or dilute (approximately 10%) potassium hydroxide (KOH). Specimens treated in KOH were either permanently mounted in Euparal or converted to temporary slide mounts in glycerin.
Specimens were examined using a WILD M-5 dissecting microscope and a WILD M-20 compound microscope, and drawings were rendered with the aid of a camera lucida (on M-5) or drawing tube (on M-20). Material for SEM examination was prepared by critical-point drying and gold-coating in a sputter coater; some specimens were sonicated briefly (1 to 2 seconds) in EtOH or an EtOH-KOH mixture. Prepared material was examined with a Cambridge Stereoscan 250 SEM at 10-25 kv. Observations were recorded on either Tri-X Pan Professional or Plus-X film.

Terms for Structures: Morphological terms are based largely on my own studies of the structure and phylogeny of Diptera (Courtney, 1990, 1991b) or from comprehensive reviews in the literature (e.g., Hennig, 1973; McAlpine et al., 1981a; Wood and Borkent, 1989). Descriptions of larval structures are based mostly on last (fourth) instars, because of the size and relative development of structures, and because of the comparatively larger data base (i.e., in the literature) on this instar. Early-instar larvae of Nearctic species were also examined, and morphological variation from the final instar is mentioned for certain structures. Homologies were determined primarily by general resemblance of structure, spatial relationships, landmark features (e.g., primary sensilla), and post-hatching ontogenetic data (e.g., histoblast location). Except for differences discussed below, I adopt the descriptive terms of Teskey (1981) and Courtney (1990).

Cutten and Kevan (1970) presented the first and, until now, the most complete description of nymphomyiid larvae, and recent studies of related taxa (Courtney, 1990, 1991b) have provided additional details. I deviate from the former investigation in my interpretation of several structures. I found no evidence that the antenna is three-segmented or “biramous”; SEM examination of the antenna suggests that the two distal-most “segments” (sensu Cutten and Kevan) are a single structure, the largest of the four apical sensilla (Figure 58). This sensillum and the slightly smaller, stouter and grooved apical sensillum give the antenna a somewhat biramous appearance, but this arrangement clearly is not homologous to that in larval Deuterophlebiidae (whose distal antennal segment bears multiple and diverse sensilla and is truly biramous [Courtney, 1990]). I have also been unable to find “paralabial plates,” or structures that even remotely resemble those described by Cutten and Kevan (1970). Likewise, no structures seem to match what they describe as “thickened spines” on the medial surface of the maxilla. I follow my earlier interpretation (Courtney, 1990) that the “premandibular sclerites” (sensu Cutten and Kevan) are actually the tormae. A final point regarding larval mouthparts pertains to labial structure. There is considerable controversy about the homologies of the ventral cranial bridge and hypostoma, specifically whether these structures are of postgenal and/or labial origin. I have discussed elsewhere (Courtney, 1990, 1991b) evidence that the larval hypostoma is in fact a modified postmentum, and the present analysis accepts this interpretation. I interpret the nymphomyiid labium as consisting of an anteriorly serrated postmentum that is fused solidly to the postgenae, and a prementum that is complex, mostly internal, and fused with the hypopharynx. In accordance with Teskey (1981), I refer to the latter, including the “lingua of the hypopharynx” (sensu Cutten and Kevan), as the prementohypopharyngeal apparatus. Finally, I accept Wood and Borkent’s (1989) interpretation that nymphomyiid proleg “segments” (sensu Cutten and Kevan, 1970; Rohdendorf and Kalugina, 1974) are not homologous with true segments of thoracic legs in other insect larvae, but rather their structure is an artifact of proleg flexion and retractability of the apical hooks.

Terms for pupal structures are based primarily on the detailed description of N. alba (Tokunaga, 1935a). The apex of the pupal rostrum bears a pair of heavily sclerotized, anteriorly projecting lobes that have been variously termed snout-like projections (Tokunaga, 1935a), the proboscis case (Rohdendorf and Kalugina, 1974), and mandibles (Cutten and Kevan, 1970). Cutten and Kevan proposed that these structures are articulated, the implication being that pupae are decticous. The latter condition is unknown in Diptera, and its demonstration in nymphomyiids could have significant phylogenetic implications; however, I share Wood and Borkent’s (1989) doubt that Cutten and Kevan homologized these structures correctly. In fact, these thorn-like lobes house the developing adult rostrum (i.e., that part anterior and dorsal to the cibarium), which may be largely of labral origin; however, because the homologies of these structures are unclear, I adopt the non-committal term “rostral hooks” (Figures 5, 6, 67). Superficially similar structures occur in other groups (e.g., certain Tipulidae, Tanyderidae), though it is unclear if these structures are homologous.

Comparative information on adult nymphomyiids comes partly from the detailed studies of Tokunaga (1935b, 1936), and terms for structures are based largely on these investigations. However, I adopt the terms of McAlpine (1981) or Wood (1991) regarding features of the adult terminalia. I make special mention here of the reported “valvular ovipositor-like structure” in adult females of N. brundini (Cutten and Kevan, 1970: 22), a condition that, if present, could have significant phylogenetic implications. However, I have determined that the specimen to which Cutten and Kevan were referring (their allotype) is actually a male, and the structure in question appears to be the aedeagal sheath.

Descriptive Format: Relatively complete descriptions are given for new taxa and for Nearctic species; otherwise, I generally refer to the original description. The latter is supplemented by certain taxonomic information not described in the original reference (e.g., pupal microsculpture). Label data, if recorded exactly as they appear on the label, are placed in quotation marks; supplemental information is given in brackets. Latitude, longitude, and altitude were in most instances derived from maps published by the U.S. Geological Survey or the U.S. Forest Service.

Abbreviations for label and locality data include the following: Bk, Brook; Br, Branch; CG, Campground; ca,
approximately; Ck, Creek; Co, County; confl, confluence; E, East; FS, [United States] Forest Service; Fk, Fork; Hwy, Highway; M, Middle; mi, mile(s); N, North; NF, National Forest; NP, National Park; nr, near; R, River; Rd, Road; S, South; trib, tributary; W, West; Xing, crossing/bridge. Abbreviations for life stages are L, larvae; P, pupae; Pxx, pupal exuviae; A, adults. The classificatory arrangement is phyletic (i.e., relatively plesiomorphic species listed prior to more apomorphic species), as determined by the cladistic analysis.

**Phylogenetic Methods:** Phylogenetic relationships were evaluated according to cladistic principles (sensu Hennig, 1966, as modified by Wiley, 1981), a method in which common ancestry is determined on the basis of synapomorphies, or shared, derived, homologous character states. Decisions about character polarity (i.e., the direction of character-state evolution) were based on outgroup methods (Wattrous and Wheeler, 1981; Maddison et al., 1984); however, outgroup procedures were confounded by the inadequately resolved phylogenetic relationship between the Nymphomyiidae and other Diptera. Character polarities were also evaluated in the context of the presumed ground condition of Diptera (Hennig, 1973; Teskey, 1981), using Siphonaptera and Mecoptera as outgroups. Character matrices analyzed initially by character-by-character (“hand”) analysis were then tested with the computer program Hennig86 (Farris, 1988). For the latter, I assumed equal character weights and used the implicit enumeration (ie*) option.

**Phylogenetic and Taxonomic History**

**RELATIONSHIPS OF HIGHER TAXA.—** The phylogenetic position of the Nymphomyiidae is one of the least resolved yet most important questions of dipterology. Shortly after the family was discovered, Tokunaga (1935b, 1936) conducted a detailed morphological study of adult *Nymphomyia*, which was the basis for his proposal that nymphyiids held an archaic and isolated systematic position within the Diptera. In contrast, Crampton (1942) used adult characters to place nymphyiids in the Culicoidea, one of three superfamilies in the section Psychodormorpha. Rohdendorf (1964, 1974), in the first comprehensive classification of extant and fossil Diptera, recognized two suborders, Archidiptera and Eudiptera, and five extant infraorders—Nymphomyiomorpha, Deuterophlebiomorpha, Blephariceromorpha, Tipulomorpha, and Bibionomorpha. Rohdendorf’s Archidiptera (emended to Archaeodiptera by Kevan and Cutten-Ali-Kahn, 1975) contained the monobasic infraorder Nymphomyiomorpha and two fossil infraorders, the Dictyodipteromorpha and Diploplyneuromorpha. These fossil groups were based on single specimens of six species, placed in four extinct families. In recent studies of Triassic and Jurassic Diptera, Kovalov (1987) and Krzeminski (1992) examined fossils from Rohdendorf’s Archidiptera and demonstrated that most of these specimens can be placed in tipulomorph and bibionomorph groups. And one of the six fossils is apparently not even a dipteran, let alone related to the Nymphomyiidae.

Rohdendorf’s placement of the Nymphomyiidae as the most primitive Diptera was accepted by several authors (Ide, 1965; Cutten and Kevan, 1970; Hackman and Väisälänen, 1982), although “support” for this hypothesis came mostly from unique, derived character states (i.e., autapomorphies) or from features that are rather homoplastic (e.g., long larval antennae). Attempts to place the family in a phylogenetic framework have been confounded by the prevalence of autapomorphies, which has generally led to the conclusion that nymphyiids are primitive or “phylogenetically isolated” (Rohdendorf, 1964, 1974). Rohdendorf assumed that extreme specialization was correlated with early divergence and a long period of evolutionary isolation (i.e., aberrant = plesiomorphic).

Hennig (1973) provided one of the first cladistic hypotheses that incorporated data on all currently recognized extant families. Hennig recognized four infraorders of nematocerous flies: Tipulomorpha, Psychodomorpha, Culicomorpha, and Bibionomorpha. Based on an admittedly tenuous character—coalescence of the mesomer and mesoepimeron—the Nymphomyiidae (as the monobasic superfamily Nymphomyioidea) were placed in the infraorder Psychodomorpha.

Other cladistic interpretations (Hackman and Väisälänen, 1982; Griffiths, 1987, 1990) returned to the Rohdendorf system of placing nymphyiids as the most primitive dipteran, but none provided strong evidence to support this hypothesis. The most compelling argument (Griffiths, 1990) pertained to the central nervous system of adults—nymphomyiids have a full complement of eight abdominal ganglia, while all other Diptera show coalescence of at least the 7th and 8th ganglia. However, recent analyses have discussed the homoplastic nature of this character (Wood and Borkent, 1989) and presented other characters (Courtney, 1991b) that implicate neoteny, rather than plesiomorphic retention of an ancestral feature.

A classification by McAlpine et al. (1981b) implied that the Nymphomyiidae, Deuterophlebiidae, and Blephariceridae form a monophyletic taxon (infraorder Blephariceromorpha). In their comprehensive analysis of nematocerous flies, Wood and Borkent (1989) provided the cladistic basis for the classification of McAlpine et al. and proposed that nymphyiids were the sister-group of the Deuterophlebiidae + Blephariceridae. Wood and Borkent recognized seven infraorders—Tipulomorpha, Blephariceromorpha, Psychodomorpha, Ptychopteromorpha, Culicomorpha, Axymyiomorpha, and Bibionomorpha—but were unable to resolve the relationships among four major clades, one being the Blephariceromorpha. Monophyly of the Blephariceromorpha was based on the shared presence of larval abdominal prolegs, but their inclusion of nymphyiids in this clade was considered “somewhat tenuous” (Wood and Borkent, 1989: 1348).

Recent investigations of the Deuterophlebiidae have addressed problems with former classificatory systems, provided additional insights into interfamilial relationships of nematocerous flies, and identified areas of needed future research (Courtney, 1990, 1991b). My study of larval mountain midges (Courtney, 1990) provided resolution to the four-way polytomy
of Wood and Borkent (1989) and proposed four additional synapomorphic characters to support monophyly of the Blephariceromorpha. Other life stages provided an additional synapomorphy for the Blephariceromorpha (Courtney, 1991b). Both papers discussed apparent similarities between the larvae of nymphomyiids and certain Culicomorpha (e.g., anal prolegs, cranial structure) but acknowledged that the significance of these similarities was unclear. Both papers also emphasized that the paucity of data on nymphomyiids has greatly hindered phylogenetic hypothesis tests.

Definitive conclusions about the distribution and significance of certain characters in nymphomyiids required detailed analyses of all nematocerous Diptera, including observations of all larval stages and of material prepared and dissected using several techniques. My research on nymphomyiids has tested several phylogenetic hypotheses, particularly (1) Nymphomyiidae as the sister-group of all other Diptera (Rohdendorf, 1964, 1974; Hackman and Väisänen, 1982; Griffiths, 1990); (2) Nymphomyiidae as a member of the Blephariceromorpha (Wood and Borkent, 1989; Courtney, 1990, 1991b); and (3) Nymphomyiidae as a close relative of the Culicomorpha. Details of this comprehensive study on the higher phylogeny of all families of nematocerous Diptera will be published separately, but I will provide here a brief discussion of characters that help place the Nymphomyiidae.

I previously presented two alternative phylogenetic hypotheses, one proposing the monophyly of the Blephariceromorpha + Psychodomorpha and one with the Blephariceromorpha as sister-group to the Psychodomorpha + (Psychoderomorpha + Culicomorpha) (Courtney, 1991b). Both hypotheses were based partly on larval character-states that had not been evaluated for nymphomyiids (Courtney, 1991b): mandible superficially biarticled; mandibular epicoxyle on tentorial phragma; and membranous cardo. My recent analysis has shown that nymphomyiids lack these derived conditions and that the latter state (membranous cardo) is homoplastic in the Blephariceridae. The following derived states provide evidence for monophyly of the Blephariceromorpha (character numbers refer to Courtney, 1991b): apex of mandible a multi-toothed comb (9); abdominal segments I–VII with elongate, eversible, crochet-tipped prolegs (10); apneustic (11); and setiform empodium (13). However, the last two characters and perhaps the first are rather homoplasic. Furthermore, recent observations show that the anal papillae of nymphomyiid larvae are not permanently exserted (character 12 in Courtney, 1991b), thus eliminating this as evidence for including nymphomyiids in the Blephariceromorpha.

My earlier analyses dealt almost exclusively with the Blephariceromorpha and clades with Blephariceromorpha as a subordinate taxon, and I did not evaluate characters that help define other clades (e.g., Culicomorpha). However, my recent analysis required that I examine all characters used by Hennig (1973), Wood and Borkent (1989), Courtney (1990, 1991b), and others. These studies were the basis for several character matrices with 80–85 characters and 27 taxa. Although parsimony analysis supports the hypothesized sister-group relationship between Deuterophlebiidae and Blephariceridae and clusters this group with the Psychodromorpha, it suggests that the Blephariceromorpha (sensu Wood and Borkent, 1989; Courtney, 1990, 1991b) are polyphyletic. Several characters, most pertaining to structure of the larval cranium and mouthparts, are instead consistent with the hypothesis that the Nymphomyiidae and Culicomorpha are closely related, perhaps as sister-taxa.

Regardless of their interfamilial relationships, the Nymphomyiidae are clearly monophyletic. Derived character states, some of which were discussed by Courtney (1991b), are given in Table 1. Character 15 from my earlier paper (postmentum (= hypostoma) serrate anteriorly and fused solidly to a postgenal bridge) is a synapomorphy only if nymphomyiids are retained within the Blephariceromorpha. If, as my recent analysis suggests, the family is the sister-group of the Culicomorpha, this character helps define a more inclusive higher taxon, comprising not only the Nymphomyiidae and Culicomorpha but also the Tipulidae. If this arrangement is accepted, several other characters can be added as synapomorphies of the Nymphomyiidae: e.g., elongate, eversible, crochet-tipped, ventral prolegs on abdominal segments I–VII (and IX?)—prolegs on segment IX also occur in certain Psychodromorpha and Culicomorpha, and may, therefore, define a more inclusive, higher taxon (see Table 1).

TAXONOMIC HISTORY OF Nymphomyia.—The original description of the Nymphomyiidae was based on six adult flies from Kibune, a torrential stream near Kyoto, Japan (Tokunaga, 1932). Tokunaga subsequently collected additional specimens from this site, providing the basis for detailed descriptions of pupae (Tokunaga, 1935a) and adults (Tokunaga, 1935b, 1936). In spite of apparently high local abundance of pupae and adults, larvae were not found at Kibune. Ide (1964) reported the discovery of a second species of nymphomyiid from a small stream in eastern Canada; he later (Ide, 1965) described N. (= Palaeodipteron) walkeri, then known only from dealate adults and a single pupal exuvium. Shortly thereafter, Brundin (1966) collected nymphomyiid adults and pupal exuviae in India’s Darjeeling District. Cutten and Kevan (1970) subsequently described this Himalayan species, N. (= Felicitomyia) brundini, in a paper that also gave a historical summary of nymphomyiid research and, most importantly, reported on the first larval collections (N. walkeri from western Quebec).

Since the Cutten and Kevan publication, Russian entomologists have described two new species, N. levandovae (Rohdendorf and Kalugina, 1974) and N. rohdendorfi (Makarchenko, 1979), and presented data on the life histories and/or distributions of Nymphomyia from eastern Asia (Makarchenko and Makarchenko, 1983; Makarchenko et al., 1989). Recent publications on North American nymphomyiids include a general review (Kevan and Cutten, 1981) and papers on distributional, phenological, and/or habitat data (Kevan and...
but, as mentioned by Harper and Lauzon (1989), Back and Wood may have terminated sampling before the second (fall) generation emerged. Most populations of *N. walkeri* from southern Canada and New England are bivoltine (Cutten and Kevan, 1970; Kevan and Cutten-Ali-Kahn, 1975; Harper and Lauzon, 1989; this research) though, again, there appears to be some variation. Data from Smays Run in central Pennsylvania suggest two generations, with emergence in June to July and October (Adler et al., 1985), but 1990–1991 collections suggest a third (overwintering) generation that emerges early in the year (March). My data also indicate that phenological characteristics may vary between years; Smays Run yielded a large, relatively synchronous emergence in early-mid October, 1990, yet samples from the same period in 1991 (a drought year) contained almost no specimens. The low number of adults from fall 1991 does not appear to reflect poor timing, as larvae and pupal exuviae were also rare.

Data from Coweeta Hydrologic Laboratory, North Carolina, indicate that *N. dolichopeza* has a complex, variable, but probably multivoltine, life history. Collections from 1990 and 1991 suggest a large, highly synchronous emergence during late November to early December, a small, trickling of adults emerging from late December to early March, and a moderate but essentially continuous (asynchronous) emergence from mid-March to May. Samples from mid-summer (July 1991), when stream flow was minimal, yielded only a few, instar IV larvae. Data also suggest that, in contrast to *N. walkeri* populations from the northern Appalachians, most *N. dolichopeza* populations pass the summer in the egg stage. As mentioned for *N. walkeri*, this could reflect the apparent “drought” conditions of summer 1991.

Researchers have proposed that the overwintering stage of nymphomyiids is the egg (Back and Wood, 1979), larva (Rohdendorf and Kalugina, 1974; Makarchenko and Makarchenko, 1983), or pupa (Cutten and Kevan, 1970). Although regional variation is possible, data from the Appalachian Mountains (Harper and Lauzon, 1989; Smith et al., 1989; this research) provide strong evidence that nymphomyiids overwinter as larvae. November and December (1990–1991) samples for an *N. walkeri* site (Smays Run, Pennsylvania) contained only larval instars I and I–III, respectively. Data for the less synchronous *N. dolichopeza* populations from North Carolina are comparable, except that a small portion of the population may pupate and emerge during the winter months.

**Classification**

**Family NYMPHOMYIIDAE**

**Genus Nymphomyia Tokunaga, 1932**


Archidipter翁 Ide, 1965:496. [Nomen nudum.]


**INCLUDED SPECIES.—Nymphomyia Tokunaga, 1932:**

1. *alba* Tokunaga, 1932
2. *levanidovae* Rohdendorf and Kalugina, 1974
3. *rohdendorfi* Makarchenko, 1979
5. *dolichopeza* new species
6. *brundini* (Kevan, 1970) [new combination]
7. *holoptica* new species

**DIAGNOSIS.—Larva compressed laterally, euccehalous; postgenal bridge complete, fused with anteriorly serrate postmentum (hypostoma); antenna elongate, one-segmented; abdominal segments I–VII and IX with paired, eversible, crocheted-tipped ventral prolegs; apneustic. Pupa slender, elongate, without respiratory organs; head prognathous, antennal and rostral sheaths paired, projecting anteriorly as conical lobes. Adult slender, delicate, mouthparts vestigial; compound eyes contiguous ventrally, stemmatic bullae distinct, dorsal ocelli absent; tentorium vestigial; antenna short, clavate, apparently three-segmented; thorax elongated, cylindrical, spiracles vestigial; wings elongate, fringed with long macrotrichia, primary veins reduced; legs elongate, femur and tibia superficially bisegmented; acropod with well-developed claws and setiform empodium, pulvilli absent; abdomen without spiracles; male terminalia directed ventrad, aedegus sheathed, eversible, with thin, internal aedeagel rod; female with vestigial spermathecae.

**DESCRIPTION.—Larval Instar IV** (Figure 11): Body typically 1 to 2 mm in length, compressed laterally, lightly sclerotized except head capsule. Euccehalous. Antenna elongate, one-segmented. Thoracic segments distinct; appendages absent. Abdomen nine-segmented; segments I–VII and IX with paired, crocheted-tipped ventral prolegs. Anal papillae four in number. Apneustic. Body surface mostly glabrous, with few setiform sensilla.

Head ovate, with faint, Y-shaped, dorsal ecysial line. Clypeolabrum anteriorly produced, conical, setose; torma distinct, articulated dorsally with labral sclerite, extended ventrally toward epipharyngeal bar. Cranium sclerotized ventrally, postgenal bridge complete, fused with postmentum (hypostoma). Occipital conyles indistinguishable. Anterior tentorial pits small, in depression anterior to antennal base; tentorial arms and posterior pits vestigial. Larval eyes (stemma) on posterolateral part of head, darkly pigmented in mature larva. Antenna one-segmented, elongate, approximately five times longer than broad, glabrous, with four apical sensilla (Figure 58): one large, narrow, tapered apically, two blunt, broadened distally, and one thick, striated, tapered distally.
Instar data, *N. walkerii*: a, histogram of postoccipt to antennal-base length; b, scattergram of antennal-base length vs. total length.

Instar data, *N. dolichopeza*, new species: a, histogram of postocciput to antennal-base length; b, postocciput to antennal-base length vs. total length.
but, as mentioned by Harper and Lauzon (1989), Back and Wood may have terminated sampling before the second (fall) generation emerged. Most populations of *N. walkeri* from southern Canada and New England are bivoltine (Cutter and Kevan, 1970; Kevan and Cutter-Ali-Kahn, 1975; Harper and Lauzon, 1989; this research) though, again, there appears to be some variation. Data from Smays Run in central Pennsylvania suggest two generations, with emergence in June to July and October (Adler et al., 1985), but 1990–1991 collections suggest a third (overwintering) generation that emerges early in the year (March). My data also indicate that phenological characteristics may vary between years; Smays Run yielded a large, relatively synchronous emergence in early-mid October, 1990, yet samples from the same period in 1991 (a drought year) contained almost no specimens. The low number of adults from fall 1991 does not appear to reflect poor timing, as larvae and pupal eviscerate were also rare.

Data from Coweeta Hydrologic Laboratory, North Carolina, indicate that *N. dolichopeza* has a complex, variable, but probably multivoltine, life history. Collections from 1990 and 1991 suggest a large, highly synchronous emergence during late November to early December, a small, trickling of adults emerging from late December to early March, and a moderate but essentially continuous (asynchronous) emergence from mid-year) contained almost no specimens. The low number of *N. dolichopeza* from the northern Appalachians, most *N. walkeri* populations from North Carolina may pupate and emerge during the winter months.

Researchers have proposed that the overwintering stage of nymphomyiids is the egg (Back and Wood, 1979), larva (Rohdendorf and Kalugina, 1974; Makarchenko and Makarchenko, 1983), or pupa (Cutter and Kevan, 1970). Although regional variation is possible, data from the Appalachian Mountains (Harper and Lauzon, 1989; Smith et al., 1989; this research) provide strong evidence that nymphomyiids overwinter as larvae. November and December (1990–1991) samples for an *N. walkeri* site (Smays Run, Pennsylvania) contained only larval instars I and I–III, respectively. Data for the less synchronous *N. dolichopeza* populations from North Carolina are comparable, except that a small portion of the population may pupate and emerge during the winter months.

**Classification**

**Family NYPHOMYIIDAE**

**Genus Nymphomyia** Tokunaga, 1932


*Archidipteron* Ide, 1965:496. [Nomen nudum.]


**INCLUDED SPECIES.—** *Nymphomyia* Tokunaga, 1932:

1. *alba* Tokunaga, 1932
2. *levanidovae* Rohdendorf and Kalugina, 1974
3. *rohdendorfi* Makarchenko, 1979
4. *walkeri* (Ide, 1965) [new combination]
5. *dolichopeza* new species
6. *brundini* (Kevan, 1970) [new combination]
7. *holoptica* new species

**DIAGNOSIS.—** Larva compressed laterally, eucephalous; postgenal bridge complete, fused with anteriorly serrate postmentum (hypostoma); antenna elongate, one-segmented; abdominal segments I–VII and IX with paired, eversible, crochet-tipped ventral prolegs; apneustic. Pupa slender, elongate, without respiratory organs; head prognathous, antennal and rostral sheaths paired, projecting anteriorly as conical lobes. Adult slender, delicate, mouthparts vestigial; compound eyes contiguous ventrally, stemmatic bullae distinct, dorsal ocelli absent; tentorium vestigial; antenna short, clavate, apparently three-segmented; thorax elongated, cylindrical, spiracles vestigial; wings elongate, fringed with long macrotrichia, primary veins reduced; legs elongate, femur and tibia superficially bisegmented; acropod with well-developed claws and setiform empodium, pulvilli absent; abdomen without spiracles; male terminalia directed ventrad, aedeagus sheathed, eversible, with thin, internal aedeagal rod; female with vestigial spermathecae.

**DESCRIPTION.—** Larval Instar IV (Figure 11): Body typically 1 to 2 mm in length, compressed laterally, lightly sclerotized except head capsule. Eucephalic. Antenna elongate, one-segmented. Thoracic segments distinct; appendages absent. Abdomen nine-segmented; segments I–VII and IX with paired, crochet-tipped ventral prolegs. Anal papillae four in number. Apneustic. Body surface mostly glabrous, with few setiform sensilla.

Head ovate, with faint, Y-shaped, dorsal ec dysial line. Clypeolabrum anteriorly produced, conical, setose; torula distinct, articulated dorsally with labral sclerite, extended ventrally toward epipharyngeal bar. Cranium sclerotized ventrally, postgenal bridge complete, fused with postmentum (hypostoma). Occipital conodes indistinct. Anterior tentorial pits small, in depression anterior to antennal base; tentorial arms and posterior pits vestigial. Larval eyes (stemmata) on postero lateral part of head, darkly pigmented in mature larva. Antenna one-segmented, elongate, approximately five times longer than broad, glabrous, with four apical sensilla (Figure 58): one large, narrow, tapered apically, two blunt, broadened distally, and one thick, striated, tapered distally.
Labrum-epipharynx complex, predominantly membranous, with band of enlarged, apical, posteroventrally curved, spatulate macrotrichia, cluster of posteroventrally curved, brush-like macrotrichia, and row of large, thick, simple macrotrichia adjacent to U-shaped epipharyngeal bar (Figures 56, 57, 59). Pair of large, blunt sensilla just anterior to row of simple macrotrichia. Messori (premandibles) absent.

Mandible (Figures 60–62) darkly sclerotized, broad and flattened basally, constricted medially, expanded apically into multi-toothed comb. Basal mandibular lobe broad at base, terminated in two blunt, apically directed teeth and one blunt, medially directed tooth. Prostheca on medial margin of mandible beneath basal mandibular lobe, comprising several clusters of compound, basally united macrotrichia; second group of compound or simple macrotrichia lateral to basal mandibular lobe. Mandibular comb at apex of mandible comprising seven blunt, curved teeth; teeth of approximately equal length, progressively broader toward medial margin of mandible.

Maxilla (Figures 63, 64) reduced; lacinial, palpal, and galeal lobes fused, not readily separable. Postero medial (lacinia?) and anteromedial (galea?) regions with clusters of elongate macrotrichia. Maxillary palp on small, subcircular prominence (stipes), with 8 apical sensilla.

Labium with broad, flat, sclerotized postmentum (hypostoma) and complex, mostly hidden prementum (Figures 55, 56). Postmentum serrate anteriorly (Figures 7, 22, 31, 47, 48), fused with postgena laterally and posteriorly. Premontohypo- pharyngeal apparatus present.

Thorax cylindrical, glabrous except for a few setiform sensilla; segments distinct, subequal, without appendages.

Abdomen apparently nine-segmented, glabrous except for a few setiform sensilla. Segments I–VII and IX each with paired, elongate, eversible, crochet-tipped, ventral prolegs (pseudopods); coxets dimorphic (multi-toothed and simple) on segments I–VII (Figure 65), monomorphic (multi-toothed) on segment IX (Figure 66). Segment IX with distinct postero dorsal tubercle bearing several large setiform sensilla (procercus?) on each side of midline. Anal papillae of four thick, exsertile, digitiform lobes between procercus and anal prolegs; dorsal pair markedly larger than ventral pair.

**Instar I** (Figure 7): Similar to instar IV; length typically about 1 mm.

**Instar II** (Figure 8): Similar to instar III; length typically about 0.8 mm.

**Instar I** (Figure 9): Similar to instar III; length typically about 0.5 mm. Cranium postero dorsally with prominent egg burster; egg burster nearly three times longer than broad (Figures 51, 53), in lateral view broad at base with tooth-like apex (Figures 52, 54).

**Pupa** (Figure 4): Body typically 2–2.5 mm in length, slender, cylindrical. Cuticle thin, semihyaline to light brown, glabrous except for a few setiform and chaetiform sensilla.

Head (Figures 5, 6, 20, 21, 67, 68) distinct, prognathous, convex dorsally, somewhat flattened ventrally; with prominent lateral bulges corresponding to regions of developing compound eyes and stomatogastric bullae (lateral ocelli); cuticle slightly granulose over compound eyes, rather smooth and hyaline over stomatogastric bullae. Epicranial suture Y-shaped, branches extended toward anterior margins of compound eyes. Rostral sheath a pair of medial lobes, extended anteriorly, terminating in two, anteroventrally curved (possibly articulated) hooks. Antennal sheath on lateral margin of head, simple or L-shaped, extended anteriorly, terminating in three prominent sensilla. Oral region with shallow concavity bordered posteriorly by irregularly shaped lobes and several setiform sensilla. Cervical region constricted.

Thorax elongate, convex dorsally, flattened ventrally; respiratory organs absent. Ecdysial suture straight, extending posteriorly through thorax to abdominal tergite I. Pronotum narrow, setigerous, with several setiform lateral sensilla (Figures 6, 21); prosternum broad, with U-shaped postero medial groove and small, chaetiform sensillum near base of foreleg sheath. Prescutal region large, broadly triangular in dorsal view, bluntly pointed anteriorly, convex posteriorly; small, chaetiform sensillum on posterolateral margin and near base of wing sheath; scutal region triangular, slightly elevated near base of wing sheath; scutellar region ovoid, with two small, chaetiform sensilla and several small, campaniform sensilla on either side of midline; postnotal region large, glabrous, with shallow lateral furrows, possibly separating region of mediotergite and laterotergites; mesosternum large, with shallow, V-shaped medial furrow and small, chaetiform sensilla near base of mesothoracic leg. Metanotum hidden externally by postnotum and abdominal segment I; metasternum comparatively small, with shallow, V-shaped medial furrow and small, chaetiform sensilla near base of metathoracic leg. Sheaths of thoracic appendages closely appressed to body. Wing sheath narrow, elongate, extending posteriorly to abdominal segment II. Halter sheath extending posteriorly from lateral margin of postnotal region along dorsal margin of wing sheath. Leg sheaths more or less S-shaped, with sharp bends corresponding to membranous, basal zones of femora and tibiae; leg sheaths terminating as follows: prothoracic sheath near base of metathoracic leg; mesothoracic sheath just anterior to tip of wing sheath; metathoracic sheath to abdominal segment II.

Abdomen narrow, elongate, apparently nine-segmented. Segments comprised of large tergal and sternal plates separated by narrow, pleural folds. Segment I typically longer than other segments, with 5 to 6 setiform sensilla dorsolaterally. Tergites II–VI with setiform sensilla near pleural membrane (two per side) and dorsolaterally (2 to 3 per side); in most species a row of 10–15 small spines posteriorly; sternites with 2 to 3 pairs of large, setiform sensilla on raised tubercles or adjacent to ventral hooks. Segment VII similar to preceding segments except dorsal spine row absent. Segments VIII and IX sexually
dimorphic; segment IX with 2 to 3 pairs setiform sensilla and pair of terminal, posteroventrally directed, thorn-like spines.

Adult $\delta^1$: Small, delicate, elongate fly; length typically about 2 mm. Wings deciduous, narrow, fringed with long macrotrichia; venation reduced. Legs similar, long, thin; femur and tibia superficially bisegmented. Terminalia directed ventrad.

Head (Figures 16, 26, 29, 30, 73-75, 81-84) small, prothorax, broad posteriorly, narrowing anteriorly toward rostrum. Cranial sclerites fused solidly, dorsal sutures indistinct; cranium largely invested with fine microtrichia. Occipital foramen large, slightly smaller than maximum width of head; occipital condyles indistinct. Tentorium vestigial. Compound eyes large, contiguous ventrally, widely separated dorsally, each eye with about 35–40 facets. Stemmata bullae ("lateral ocelli") large, prominent, glabrous, on lateral margin of cranium, posterior to compound eyes. Dorsal ocelli absent. Rostrum with several prominent, setiform dorsolateral sensilla and two clusters of blunt, peg-like apicoventral sensilla. Mouthparts vestigial (Figures 77, 78, 84). Cibarium posterior to rostrum, ovoid, bordered posteriorly by bilobed structure (labium?) bearing several setiform sensilla and two clusters of blunt, peg-like sensilla (labial palps?). Hypopharynx central to rostrum, ovoid, bordered posteriorly by bilobed structure (labium?). Ocelli posterior to compound eyes. Dorsal ocelli absent. Rostrum with several prominent, setiform dorsolateral sensilla and two clusters of blunt, peg-like apicoventral sensilla. Mouthparts vestigial (Figures 77, 78, 84). Cibarium posterior to rostrum, ovoid, bordered posteriorly by bilobed structure (labium?) bearing several setiform sensilla and two clusters of blunt, peg-like sensilla (labial palps?). Hypopharynx small, multi-lobed, papilliform, projected from within cibarial opening.

Antenna short (length to about 150 $\mu$m), clavate, of three apparent segments (Figures 16, 26, 29, 79, 86). Socket small, ovoid, at lateral base of rostrum. Scape pyriform, with 3–5 setiform sensilla near distal margin, densely set with microtrichia; pedicel globular, slightly smaller than scape, densely set with microtrichia, broadly articulated to scape. Flagellum longer than preceding segments, clavate, uniformly but less densely covered with microtrichia; microtrichia arranged in circular or spiral rows, especially on narrow, proximal part of flagellum (Figure 87); distal part with numerous small, blunt, peg-like sensilla among microtrichia; flagellum terminating in cluster of four sensilla (Figure 88): one large, elongate, peg-like, one thick, longitudinally grooved, and two claviform.

Thorax markedly elongate, cylindrical, generally glabrous, with few setiform sensilla. Cervix broad, nearly as wide as head, membranous. Prothorax small, consisting of two pairs of notal-, an unpaired sternal-, and a pair of pleural sclerites; antepronotum of two lobes separated medially by anteriorly projecting mesonotum and wide membranous zone, each lobe invested with fine microtrichia, typically with five setiform sensilla; postpronotum subtriangular, between antepronotum and mesonotum. Prosternum large, broad, subquadrate, undivided, with a pair of setiform sensilla laterally; anterolateral margin slightly excised near foreleg base; pleuron small, subtriangular, in membrane between antepronotum and prosternum.

Mesothorax markedly enlarged, occupying most of thorax. Mesonotum divided into long scuto-prescutum, small scutellum, and large postnotum. Scuto-prescutum posteriorly concave, anteriorly rounded; scutum and prescutum separable anteriorly by weak prescutal sutures; scuto-prescutum predominantly glabrous, except small, setiform, supra-alar sensillum posterolaterally and sparse microtrichia posteromedially and along prescutal suture. Transverse and median scutal sutures absent. Scutellum small, broadly rectangular; anterior margin convex, posterior margin slightly sinuate; two pairs long, setiform sensilla laterally, one pair short, setiform sensilla medially. Postnotum mostly exposed, markedly enlarged, broader than scutellum; mediotergite with straight anterior margin, widest just anterior to level of halters, extended posteriorly into abdominal segment II, posterior margin round; laterotergite shield-like, broadly rectangular anteriorly (anatergite?), pentagonal posteriorly (katatergite?). Mesopleuron small, membranous, mostly below anatergite, sutures indistinct. Mesosternum large, exposed, elongate.

Metathorax greatly reduced; metanotum vestigial; pleuron mostly membranous. Metasternum relatively large, exposed posterior and medial to hindcoxa.

Wing elongate, typically about 2 mm in length; membrane mostly glabrous, but wing fringed with numerous, long macrotrichia; anal lobe poorly developed. Veins reduced: C thick anteriorly, extended around entire wing; Sc and R, short, each ending in C near base of wing; Rs evanescent basally, gradually curved anteriorly, ending in C in basal 1/3 of wing; other veins (M and Cu ?) poorly developed, evanescent basally, ending before wing margin.

Halter large, pubescent, with single, subapical, setiform sensillum on knob.

Legs delicate, slender, similar in structure and length; articulations of three pairs of legs widely separated. Foreleg: coxa elongate, superficially subdivided into short proximal and long distal article, with several (6–8) setiform sensilla. Trochanter barrel-shaped, with 2–4 setiform sensilla and several (3 to 4) campaniform sensilla. Femur superficially bisegmented; basal portion short, darkly pigmented, thinner than trochanter; membranous portion ventrally with two rows of three campaniform sensilla; distal portion pale, with several setiform sensilla along margin and distally. Tibia cylindrical, slender, superficially bisegmented as in femur; distal portion with several setiform sensilla along margin and distally; spurs absent. Tarsus five-segmented; t1 (tarsomere 1) and t5 longer than t2, t3, or t4, with t1 the longest. Acropleura (Figures 92, 93) with two well-developed claws. Midleg similar to foreleg, but shorter; tibia rather swollen distally; t1 length subequal to or shorter than t5 in some species. Hindleg similar to other legs, of intermediate length in most species (but see Tokunaga, 1935b).

Abdomen cylindrical, slender, extremely elongate, weakly sclerotized, with nine apparent segments. Segments invested

$^1$Tokunaga (1935b) provided a comprehensive description of adult N. alba, a typical nymphomyiid in most structural features; I therefore present a somewhat abbreviated description, and recommend consulting Tokunaga's paper for details about certain structures (e.g., thoracic sclerites).
with abundant microtrichia and several setiform sensilla. Spiracles absent; most species with small tubercles (possibly vestigial spiracles) near anterior, dorsolateral margin of abdominal segments. Terminalia (Figures 17–19, 27, 28, 35, 37, 38, 49, 50, 89, 91) directed ventrally. Segments V, VI, and/or VIII modified in some species. Tergites IX and X, gonocoxites, and cerci fused, demarcation between them not readily apparent. Gonocoxites typically large, elongate, densely set with lateral microtrichia and elongate medial patch of setiform sensilla; shape of gonocoxites and gonostyli varies with species; gonostylus typically bifurcate or with basal lobe. Sternites IX and X vestigial, ventral surface occupied mostly by aedeagal sheath. Aedeagus large, membranous, glabrous, eversible in most species; aedeagal sheath tube-like, originating at inner base of gonocoxites, shape variable. 

**Adult** 
Similar to male in most features. Terminalia (Figures 19, 28, 33, 41–46, 94, 95): Tergite VIII with anterolateral tubercles larger than on preceding segments, typically with folds or projections posterolaterally; other lateral modifications vary with species. Sternite VIII membranous, swollen medially, folded posteromedia!y around large genital chamber. Tergite IX broadly fused to base of cerci; sternite IX membranous. Spermathecae not apparent. 

**Keys to Species of Nymphomyia**

**KEY TO INSTAR IV LARVAE**

1. Postmentum trilobed anteriorly; median tooth shorter than adjacent lateral teeth; median tooth with two pairs of lateral serrations [Figures 47, 48] .... 2
   Postmentum not trilobed anteriorly; median tooth and lateral teeth extended anteriorly to about same level; median tooth with one pair of lateral serrations [Figures 7, 22, 31, 55, 56] .... 3

2(1). Postmentum with lateral teeth of more or less uniform size and shape [Figure 47] ....  
   N. rohdendorfi

3(1). Postmentum with notch between lateral teeth I and II as deep as notches separating other teeth; lateral teeth without lateral serrations [Figures 7, 31, 56] ....  
   N. dolichopeza, new species  
   N. holoptica, new species

**KEY TO PUPAE**

1. Abdominal sternites II or III to VII with a pair of posteriorly directed hooks .... 2
   Abdominal sternites without hooks, though two raised welts bearing setiform or chaetiform sensilla may be present .... 3

2(1). Abdominal sternites with first pair of hooks on segment III ....  
   N. dolichopeza, new species

3(1). Abdominal tergites without spine rows; rostral hooks parallel [Figures 21, 67] ....  
   N. walkeri, new combination

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2 Larvae of *N. hrundini* unknown; larvae of *N. alba* are undescribed.
4(3). Abdominal tergites with spine row on segments II–VIII

\[ N. \text{ brundini}, \text{ new combination} \]

Abdominal tergites without spine row on segment VIII

5(4). Abdominal tergites with spine row on segments II–VII

\[ N. \text{ holoptica}, \text{ new species} \]

Abdominal tergites without spine row on segment VII

\[ N. \text{ alba} \]

**KEY TO ADULT MALES**

1. Ommatidia of compound eyes contiguous ventrally [Figures 30, 76, 85]; abdominal segment VIII without elongate lateral processes [Figures 17–19, 27, 28, 35, 36, 49, 50]; gonocoxites and cerci fused indistinctly

\[ N. \text{ holoptica}, \text{ new species} \]

Ommatidia of compound eyes separated ventrally; abdominal segment VIII with elongate lateral processes [paratergal projections—Figures 37, 38]; gonocoxites and cerci readily separable, at least distally

2(1). Abdominal segment VIII dorsolaterally and/or laterally set with numerous setiform sensilla [Figures 36, 49, 50]; gonocoxites enlarged, extended anteroventrally to beyond posterior margin of abdominal segment VIII, tapered apically; gonostylus bifurcate [Figures 35, 49, 50]

\[ N. \text{ holoptica}, \text{ new species} \]

Abdominal segment VIII not invested with setiform sensilla; gonocoxites reduced, extended posteriorly or medially for only a short distance; gonostylus variable

3(2). Ventral eye bridge with contact between three pairs of ommatidia [Figure 30]; gonostylus of two similarly shaped, curved lobes, anterior lobe relatively more tapered apically than posterior lobe [Figure 35]

\[ N. \text{ brundini}, \text{ new combination} \]

Ventral eye bridge with contact between two pairs of ommatidia [as in Figures 76, 85]; gonostylus of two lobes, posterior lobe curved basally, bent abruptly at middle, narrowly tapered apically, anterior lobe thick, invested with microtrichia on outer margin, with short, blunt, medially directed apical lobe bearing short sensilla at tip [Figures 49, 50]

\[ N. \text{ brundini}, \text{ new combination} \]

4(2). Compound eyes with microtrichia between all facets [Figure 85]; cranium almost entirely covered with microtrichia [Figures 26, 82]; terminal sensilla of antenna subapical [Figure 26]; empodium of foretarsus not extended beyond tarsal claws [as in Figure 39]; abdominal sternites V and VI each with a pair of posteriorly or medially projected processes [Figure 27]; gonostylus simple; aedeagus markedly elongate, aedeagal rod, when not exserted, extended anteriorly to abdominal segment V

\[ N. \text{ walkeri}, \text{ new combination} \]

Compound eyes without microtrichia between ventral facets [Figure 76]; cranium glabrous anterodorsally [Figures 16, 75] and posteroventrally [behind eyes—Figure 76]; terminal sensilla of antenna apical [Figures 16, 79]; empodium of foretarsus elongate, extended beyond tarsal claws [Figure 40]; abdominal sternites V and VI without elongate processes; gonostylus bifurcate; aedeagus short, aedeagal rod, when not exserted, extended anteriorly only to abdominal segment VIII

\[ N. \text{ dolichopeza}, \text{ new species} \]

5(1). Gonocoxites not extended posteriorly beyond apex of cercus; gonostylus short, blunt, extended posteriorly

\[ N. \text{ rohdendorfi} \]

Gonocoxites extended posteriorly to near or beyond apex of cercus; gonostylus elongate, tapered, curved anteroventrally

6(5). Dorsal and ventral paratergal projections distinct, of approximately equal length

\[ N. \text{ rohdendorfi} \] not available for examination; key characteristics based on Makarchenko, 1979.
KEY TO ADULT FEMALES⁴

1. Ommatidia of compound eyes contiguous ventrally .......................... 2
   Ommatidia of compound eyes separated ventrally .......................... 4

2(1). Abdominal segment VIII dorsolaterally and/or laterally set with numerous 
      setiform sensilla [Figure 33]; ventral eye bridge with contact between three pairs 
      of ommatidia [Figure 30] ........................ N. holoptica, new species

   Abdominal segment VIII not invested with setiform sensilla; ventral eye bridge 
   with contact between two pairs of ommatidia [as in Figures 76, 85] .... 3

3(2). Compound eyes with microtrichia between all facets [Figure 85]; cranium almost 
      entirely covered with microtrichia [Figures 26, 82]; terminal sensilla of antenna 
      subapical [Figure 26]; abdominal segment VII with lateral flap bearing several 
      thick, elongate, ventrally projecting, hair-like processes [Figures 28, 94] ....

   ................................................................. N. walker, new combination

   Compound eyes without microtrichia between ventral facets [Figure 76]; cranium 
   glabrous anterodorsally [Figures 16, 75] and posteroventrally [behind eye— 
   Figure 76]; terminal sensilla of antenna apical [Figures 16, 75]; abdominal 
   segment VIII with complex, glabrous receptacle for male gonostylus 
   [Figures 19, 95] ........................ N. dolichoepiza, new species

4(1). Tergite VIII with broad, ventrally projected lobe that does not overlap with lobe 
      from opposite side; cerci broad [Figure 45] ........................ N. levanidovae

   Tergite VIII with narrow, ventrally projected lobe that overlaps with lobe from 
   opposite side; cerci thin [Figures 43, 44] ........................ N. alba

⁴Females of N. brundini unknown; female N. rohdendorfi not available for examination, not included 
   in the key.

Nymphomyia alba Tokunaga

Figures 37, 43, 44, 46, 96

Nymphomyia alba Tokunaga, 1932:561; 1935a:44; 1935b:127; 1936:189; 
1950:1567; 1959:649; 1965:184.—Makarchenko et al., 1989:15.—Shima, 

Diagnosis.—Pupa: rostral hooks divergent, abdominal 
stermites without hooks, tergites II–VI with spine rows. Adult: 
ommatidia of compound eyes not contiguous ventrally; male 
with two pairs of elongate paratergal projections and simple 
gonostyli; female with narrow, elongate lobe on posterolateral 
margin of tergite VIII and cylindrical, ventrally directed cerci.

Description.—Larva: Undescribed.

Pupa: See Tokunaga (1935a). Rostral hooks short, stout, 
divergent anteriorly; antennal sheath more or less elbow-
shaped. Microsculpture: abdominal sternites without hooks, 
tergites II–VI with posterior spine rows. Anal hooks short, with 
dorsal and lateral serrations. Segments VIII and IX sexually 
dimorphic: male with large, circular, ventral lobes on segment 
VIII; female with large, circular, ventral lobes on segment IX. 
(Because no pupal material was available for examination, I 
accept Tokunaga’s interpretation of sexual dimorphism in N. 
alba; however, observations of N. levanidovae and N. rohdendo-
rfi suggest that Tokunaga may have confused the sexes—see 
descriptions of latter species. I see no (adult) morphological 
reason for N. alba to differ from this arrangement.)

Adult ♂: Rostrum apically truncate. Cranium glabrous 
anterodorsally, from apex of rostrum to near anterior margins 
of eyes; microtrichia absent posteroventrally (behind eyes). 
Ommatidia of compound eyes separated ventrally; microtrichia 
absent between facets. Terminal sensilla of antenna apical. 
Empodium of foretarsus short, not extending beyond apex of 
tarsal claws; claws with prominent basal tooth.

Terminalia (Figures 37, 46): Sternites V and VI simple. 
Tergite VIII with two, large, elongate, posteriorly directed 
lateral processes (paratergal projections); dorsal process rela-
tively broad, invested with microtrichia, with large setiform 
lateral sensillum, thin, elongate ventral setae, and two, small 
glabrous basal tubercles; ventral process relatively narrow, 
glabrous, with ventrally directed apical hook and large, 
glabrous basal tubercle (vestigial spiracle?). Membrane be-
tween tergites VIII and IX without setiform sensilla. Gono-
ocxites and cerci readily separable, at least distally; gono-
ocxites elongate, broad basally, slightly tapered distally,
extending posteriorly to or beyond apex of cercus; entire surface invested with microtrichia, inner surface with rows of chaetiform sensilla, distal end with small, setiform, dorsal sensillum. Gonostylus simple, thick basally, curved and tapered apically, invested with fine microtrichia; base (articulation with gonocoxite) with blunt, pubescent lobe. Aedeagus short, membranous, glabrous; aedeagal sheath broad, with sinuate lateral margins and truncated apex; small hirsute lobe at base.

**Adult ♀:** Similar to male. Terminalia (Figures 43, 44, 46): Tergite VIII with glabrous anterolateral tubercle (vestigial spiracle?), narrow medial flap contiguous with elongate, ventrally projected lobe that overlaps with lobe from opposite side; ventral lobes with abundant microtrichia. Sternite VIII membranous, microtrichia sparse generally, but abundant anteromedially; two short, rounded, lateral lobes each with three chaetiform sensilla, one setiform sensillum. Cerci narrow, cylindrical, directed ventrally.

**Type Material.**—Holotype ♀: Japan, Kyoto Prefecture, Kibune, 10 Mar 1932, M. Tokunaga. Allotype ♀ and paratypes 2 ♀, 2 ♀: same data as holotype. Type material deposited in Entomology Laboratory, Kyoto Imperial University (Tokunaga, 1932) [types not available for examination].


**Distribution (Figure 96).**—Recorded from Japan and Kunashir Island (Makarchenko, 1991, pers. comm.). Japanese material includes pupae and adults from Kibune, Honshu (see Tokunaga papers) and larvae presumed to be N. alba (Tokunaga, 1932) [types not available for examination].

**Nymphomyia levanidovae** Rohdendorf and Kalugina

FiguREs 38, 45, 48, 96


**Diagnosis.**—Larva: median tooth of postmentum shorter than adjacent lateral teeth and with two pairs of lateral serrations; lateral teeth without lateral serrations, notch between lateral teeth I and II shallower than notches separating other teeth. Pupa: rostral hooks divergent, abdominal sternites II–VII with hooks, tergites II–VII with spine rows. Adult: ommatidia of compound eyes not contiguous ventrally; male with one pair of elongate paratergal projections and elongate, simple gonostyli; female with broad lobe on lateral margin of tergite VIII and broad, posteroventrally directed cerci.

**Description.**—Larva: Postmentum (Figure 48) trilobed anteriorly, median tooth shorter than adjacent lateral teeth and with two pairs of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II shallower than notches separating other teeth; second lateral tooth extended anteriorly beyond apices of other teeth.

**Pupa:** Rostrum apically truncate. Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally (behind eyes). Ommatidia of compound eyes separated ventrally; microtrichia absent between facets. Terminal sensilla of antenna apical. Empodium of foretarsus short, not extending beyond apex of tarsal claws; claws with prominent basal tooth.

Terminalia (Figure 38): Sternites V and VI simple. Tergite VIII with one pair of large, elongate, glabrous, posteriorly directed, lateral processes (paratergal projections); process with blunt apex and large, glabrous basal tubercle (vestigial spiracle?); dorsal paratergal projection absent, but homologous area with large setiform sensilla, thin, elongate ventral setae, and two, small, glabrous dorsal tubercles. Membrane between tergites VIII and IX without setiform sensilla. Gonocoxites and cerci readily separable, at least distally; gonocoxites elongate, broad basally, slightly tapered distally, extended posteriorly to or beyond apex of cercus; entire surface invested with microtrichia, inner surface with rows of chaetiform sensilla, distal end with small, setiform, dorsal sensillum. Gonostylus simple, elongate, slender, curved anteroventrally and tapered to slightly bulbous apex; surface generally invested with fine microtrichia; base (articulation with gonocoxite) with elongate, blunt, pubescent lobe. Aedeagus short, membranous, glabrous; aedeagal sheath broad, with sinuate lateral margins and truncate apex; small hirsute lobe at base.

**Adult ♀:** Similar to male. Terminalia (Figure 45): Tergite VIII with glabrous anterolateral tubercle (vestigial spiracle?) and broad, ventrally projected lobe that does not overlap with lobe from opposite side. Sternite VIII membranous, microtrichia sparse generally, abundant anteromedially; without lateral lobes, but with three chaetiform sensilla and one setiform sensillum anteriorly. Cerci broad, directed posteroventrally.

**Type Material.**—Holotype ♀ (dissected from pupa): Russia, Primorye Province, Suyfun R Basin, El’duga R, 28 May 1972, I.M. Levanidova. Paratypes (?) [pupae 8 ♀, 5 ♀; instar IV larva 1]: same data as holotype. Type material deposited in Zoological Institute, Academy of Sciences, St. Petersburg (Rohdendorf and Kalugina, 1974) [types not available for examination].


**Distribution (Figure 96).**—Recorded only from the Primo-
rye Province in far eastern Russia (Rohdendorf and Kalugina, 1974; Makarchenko et al., 1989).

_Nymphomyia rohdendorfi_ Makarchenko

_FIGURES 47, 96_


**DIAGNOSIS**.—_Larva:_ median tooth of postmentum shorter than adjacent lateral teeth and with two pairs of lateral serrations; lateral teeth without lateral serrations, notch between lateral teeth I and II as deep as notches separating other teeth. _Pupa:_ rostral hooks divergent, abdominal sternites II–VII with hooks, tergites II–VII with spine rows. _Adult:_ ommatidia of compound eyes not contiguous ventrally; male with one pair of elongate paratergal projections and short, blunt, simple gonostylus; female with narrow lobe on lateral margin of tergite VIII and broad, posteroventrally directed cerci.

**DESCRIPTION.**—_Larva:_ Postmentum (Figure 47) trilobed anteriorly, median tooth shorter than adjacent lateral teeth and with two pairs of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other teeth; lateral teeth of more or less uniform size and shape.

_Pupa:_ Microsculpture: abdominal sternites II–VII with one pair of posteriorly directed hooks, tergites II–VII with posterior spine rows. Anal hooks elongate, without serrations(?). Segment IX sexually dimorphic: male with one pair of posteriorly directed hooks, tergites II–VII with spine rows. _Adult:_ ommatidia of compound eyes two pairs of contiguous ventrally, male with one pair of elongate paratergal projections and short, blunt, simple gonostylus; female with narrow lobe on lateral margin of tergite VIII and broad, posteroventrally directed cerci.

**DESCRIPTION.**—_Larva:_ Postmentum (Figure 20) trilobed anteriorly, median tooth shorter than adjacent lateral teeth and with two pairs of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other teeth. _Pupa:_ rostral hooks short, parallel, abdominal sternites without hooks, tergites without spine rows. _Adult:_ ommatidia of compound eyes (two pair) contiguous ventrally, microtrichia between all facets; terminal sensillum of antenna subapical; male with elongate processes on abdominal sternites V and VI, simple, short gonostyly, and markedly elongate aedeagus; female abdominal segment VIII with lateral flap bearing several elongate, ventrally projecting, hair-like processes.

**DESCRIPTION.**—_Larva:_ Postmentum (Figures 22, 55) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth II–IV with lateral serrations, notch between lateral teeth I and II shallower than notches separating other teeth. _Pupa:_ rostral hooks short, parallel, abdominal sternites without hooks, tergites without spine rows. _Adult:_ ommatidia of compound eyes (two pair) contiguous ventrally, microtrichia between all facets; terminal sensillum of antenna subapical; male with elongate processes on abdominal sternites V and VI, simple, short gonostyly, and markedly elongate aedeagus; female abdominal segment VIII with lateral flap bearing several elongate, ventrally projecting, hair-like processes.

**TYPE MATERIAL.—** Holotype ♂ (dissected from pupa):

Diagnoses and descriptions of pupae and adults based solely on Makarchenko (1979). Note that adult descriptions were based on several specimens dissected from pupae; thus, certain structures may not have been fully developed.
base of each anal hook; female segment VIII with circular posteroventral lobe.

**Adult♂**: Rostrum apically round (Figures 26, 82). Cranium densely set with microtrichria dorsally and posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between two pairs of facets; microtrichria between all facets (Figure 85). Terminal sensilla of antenna subapical (Figure 26). Empodium of foretarsus short, not extending beyond apex of tarsal claws; claws without prominent basal tooth.

Terminalia (Figures 27, 28, 91): Stermites V and VI each with one pair of elongate, apparently flexible processes. Tergite VIII simple, without paratergal setae. Membrane between tergites VIII and IX without setiform sensilla. Gonocoxites reduced, fused broadly to cerci, surface generally invested with fine microtrichria, inner surface with rows of chaetiform sensilla. Gonostylus simple, glabrous, extending medially and/or ventrally, with 2 to 3 apical sensilla and two subapical sensilla, the latter borne on slight lateral protuberance. Aedeagus thin proximally and throughout most of length, slightly expanded distally, with membranous apical lobe and hook-like, subapical lobes; aedeagus markedly elongate, extending anteriorly to abdominal segment V (when not exserted); aedeagal rod darkly pigmented, extending from base of aedeagus to slightly beyond subapical lobes; aedeagal sheath tube-like, broad basally, tapered slightly distally.

**Adult♀**: Similar to male. Terminalia (Figures 28, 94): Stermites V and VI without elongate processes. Tergite VIII with broad lateral flap bearing several elongate, ventrally projecting, flexible, hair-like processes. Stermite VIII membranous, generally lacking microtrichria but with enlarged, spinose protuberance posteriorly. Cerci (?) broad, directed posteriorly.

**Type Material.—**Holotype♂: Canada, New Brunswick, Kent Co, Melus R, 11–12 Jun 1961, F. Ide. Specimen on slide [ROM]. Allotype♀: same data as holotype; on slide [ROM] or in EtOH [CNC].


Br above Rd 635 Xing, 37°26'N, 80°30'W, elev. 2650', 26 May 1990 [L].

**DISTRIATION.** (Figure 97).—Widespread eastern Nearctic, from northcentral Quebec southward in the Appalachian Mountains, possibly to northeastern Alabama. The species is most abundant in streams of the northern Appalachians but occurs in widely scattered, disjunct populations in the southern part of its range (Pennsylvania to Alabama). Because they are based solely on larval collections, the Alabama and Virginia records are only tentatively identified as **N. walkeri**.

**Nymphomyia dolichopeza,** new species

**FIGURES 4–19, 40, 56, 57, 59, 61–64, 71–80, 89, 90, 92, 93, 95, 97**

**DIAGNOSIS.**—Larva: median tooth of postmentum projecting anteriorly to level of lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations, notch between lateral teeth I and II as deep as notches separating other teeth. Pupa: rostral hooks divergent, abdominal sternites III–VII with hooks, tergites II–VII with spine rows. Adult: ommatidia of compound eyes contiguous ventrally, contact anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; notch between lateral teeth I and II as deep as notches separating other teeth. Pupa: rostral hooks divergent, abdominuous ventrally; male with empodium of foretarsus longer than tarsal claw and gonostylus bifurcate, anterior branch broader than posterior branch; female abdominal segment VIII without lateral flaps but anteriorly with circular zone of glabrous cuticle bearing curved lobes and depressions.

**DESCRIPTION.**—Larva: Postmentum (Figures 7, 56) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other lateral teeth. Measurements (specimens from Coweeta Hydrologic Laboratory; values = range (mean ± standard deviation)):

<table>
<thead>
<tr>
<th>Instar</th>
<th>Sample size</th>
<th>Total length (mm)</th>
<th>Postocciput to antennal base length (µm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>15</td>
<td>0.4–0.7 (0.6 ± 0.1)</td>
<td>42–51 (46.3 ± 2.9)</td>
</tr>
<tr>
<td>II</td>
<td>39</td>
<td>0.7–0.9 (0.8 ± 0.1)</td>
<td>63–69 (65.3 ± 1.2)</td>
</tr>
<tr>
<td>III</td>
<td>61</td>
<td>0.9–1.4 (1.1 ± 0.1)</td>
<td>81–92 (87.3 ± 2.3)</td>
</tr>
<tr>
<td>IV</td>
<td>67</td>
<td>1.2–2.3 (1.8 ± 0.3)</td>
<td>119–137 (129.9 ± 3.8)</td>
</tr>
</tbody>
</table>


Adult ♂: Rostrum apically truncate (Figures 16, 74, 75). Cranium glabrous anteriorly, from apex of rostrum to near posterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between two pairs of facets (Figure 76); microtrichia between dorsal facets only. Terminal sensilla of antenna apical (Figures 16, 79). Empodium of foretarsus elongate, extending beyond apex of tarsal claws; claws without prominent basal tooth (Figures 40, 92, 93).

Terminalia (Figures 17–19, 89, 90): Sternites V and VI and tergite VIII simple, without elongate processes. Membrane between tergites VIII and IX with clusters of setiform sensilla. Gonostylus reduced, fused broadly and indistinguishably to cerci, surface generally invested with fine microtrichia. Gonostylus bifurcate, anterior branch markedly broader than posterior branch, invested with microtrichia; posterior branch glabrous, with 2 to 3 apical sensilla. Aedeagus short, thick, broad basally, constricted subapically, thickened distally; when not exerted, extending anteriorly only to abdominal segment VIII; aedeagal rod extending from base of aedeagus to slightly beyond subapical constriction; aedeagal sheath short, broad basally, more or less continuous with base of aedeagus, sparsely set with lateral microtrichia.

Adult ♀: Similar to male. Terminalia (Figures 19, 41, 42, 95): Abdominal segment VIII without lateral flaps but anteriorly with circular zone of complex, glabrous cuticle bearing curved lobes and depressions (receptacle for male gonostylus—Figure 95). Abdominal segment IX with slightly developed lateral flaps; tergite densely set with microtrichia, sternite mostly glabrous except for pubescent medial depression. Cerci (?) broad, directed posteriorly.


DISTRIBUTION (Figure 97).—Nymphomyia dolichopeza is apparently confined to the southern Blue Ridge Mountains of eastern U.S.A., being most abundant in tributaries of the upper Tennessee River drainage. This species can be one of the most conspicuous in streams at Coweta Hydrologic Laboratory (personal observation; J.B. Wallace, pers. comm.). In addition to North Carolina and Georgia, the species evidently occurs in northwestern South Carolina, primarily in the Lake Jocassee drainage (K.L. Manuel, 1990, pers. comm.).

ETYMOLOGY.—Species name from the Greek dolichos, long and pesa, foot, in reference to the elongate empodium of the male foretarsus.

**Nymphomyia brundini (Kevan), new combination**

**FIGURES 49, 50, 96**


*Nymphomyia* sp.—Brundin, 1966:457.

DIAGNOSIS.—Pupa: rostral hooks parallel, abdominal sternites without hooks, tergites II–VIII with spine rows. Adult: ommatidia of compound eyes (two pairs) contiguous ventrally; male abdominal segment VIII set with setiform dorsolateral sensilla, gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with posterior lobe glabrous, bent abruptly at middle and tapered apically, and anterior lobe thick, invested with microtrichia on outer margin, and with short, blunt, medially directed lobe at tip.

DESCRIPTION.—*Larva*: Unknown.


**Adult male**: Rostrum apically truncate. Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between two pairs of facets, microtrichia between dorsal facets only. Terminal sensilla of antenna apical. Empodium of foretarsus short, not extending beyond apex of tarsal claws; claws with prominent basal tooth.

Terminalia (Figures 49, 50): Sternites V and VI and tergite VIII simple, without elongate processes; tergite VIII with large dorsolateral patch of setiform sensilla. Membrane between tergites VIII and IX without setiform sensilla. Gonocoxites fused broadly to cerci, markedly elongate, projecting anteriorly well beyond posterior margin of sternite VIII, invested with microtrichia throughout length, curved medially and tapered anteriorly to apex, with setiform sensilla along inner margin. Gonostylus bifurcate; posterior lobe glabrous, curved basally, bent abruptly at middle, tapered to acute apex, overlapping medially with posterior lobe from opposite side; anterior lobe thick, invested with microtrichia on outer margin, with short, blunt, medially directed apical lobe bearing short sensilla at tip (Figures 49, 50). Aedeagus short, thick, broadest at base; when not exerted, extending anteriorly to abdominal segment VII.

**Adult female**: Unknown.

TYPE MATERIAL.—Holotype ♂: “India, West Bengal, Darjeeling D[istrict]; Teesta River; 24 Nov 1961; L. Brundin.” Specimen in Hoyer’s medium on slide [NRS]. “Allotype” ♂ and paratypes (pupal exuviae): “India, West Bengal, Darjeeling D[istrict]; Rangeet River; 25 Nov 1961; L. Brundin.” “Allotype” transferred to Canada balsam, paratypes in Hoyer’s medium; all specimens on slides [NRS].

DISTRIBUTION (Figure 96).—Known only from the Darjeeling District of India.

**Nymphomyia holoptica, new species**

**FIGURES 29–36, 39, 96**

*Palaeodipteron* sp.—Dudgeon, 1989:193.

DIAGNOSIS.—*Larva*: median tooth of postmentum projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations, notch between lateral teeth I and II as deep as notches separating other teeth. *Pupa*: rostral hooks divergent, abdominal sternites without hooks, tergites II–VIII with spine rows.
Adult: ommatidia of compound eyes (three pair) contiguous ventrally, abdominal segment VIII set with setiform dorsolateral sensilla; male with gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with two similarly shaped, curved lobes; female with narrow, elongate lobe on posterolateral margin of tergite VIII, and posteroventrally directed cerci.

DESCRIPTION.—Larva: Postmentum (Figure 31) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other lateral teeth.


Adult ♀: Rostrum apically truncate (Figures 29, 30). Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between three pairs of facets; microtrichia between dorsal facets only. Terminal sensilla of antenna apical. Empodium between three pairs of facets; microtrichia between dorsal, ventrally, abdominal segment VIII set with setiform dorso-lateral sensilla; male with gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with two similarly shaped, curved lobes; female with narrow, elongate lobe on posterolateral margin of tergite VIII, and posteroventrally directed cerci.

DESCRIPTION.—Larva: Postmentum (Figure 31) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other lateral teeth.


Adult ♂: Rostrum apically truncate (Figures 29, 30). Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between three pairs of facets; microtrichia between dorsal facets only. Terminal sensilla of antenna apical. Empodium between three pairs of facets; microtrichia between dorsal, ventrally, abdominal segment VIII set with setiform dorso-lateral sensilla; male with gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with two similarly shaped, curved lobes; female with narrow, elongate lobe on posterolateral margin of tergite VIII, and posteroventrally directed cerci.

DESCRIPTION.—Larva: Postmentum (Figure 31) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other lateral teeth.


Adult ♂: Rostrum apically truncate (Figures 29, 30). Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between three pairs of facets; microtrichia between dorsal facets only. Terminal sensilla of antenna apical. Empodium between three pairs of facets; microtrichia between dorsal, ventrally, abdominal segment VIII set with setiform dorso-lateral sensilla; male with gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with two similarly shaped, curved lobes; female with narrow, elongate lobe on posterolateral margin of tergite VIII, and posteroventrally directed cerci.

DESCRIPTION.—Larva: Postmentum (Figure 31) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other lateral teeth.


Adult ♂: Rostrum apically truncate (Figures 29, 30). Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between three pairs of facets; microtrichia between dorsal facets only. Terminal sensilla of antenna apical. Empodium between three pairs of facets; microtrichia between dorsal, ventrally, abdominal segment VIII set with setiform dorso-lateral sensilla; male with gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with two similarly shaped, curved lobes; female with narrow, elongate lobe on posterolateral margin of tergite VIII, and posteroventrally directed cerci.

DESCRIPTION.—Larva: Postmentum (Figure 31) not trilobed anteriorly; median tooth projecting anteriorly to level of adjacent lateral teeth and with one pair of lateral serrations; lateral teeth without lateral serrations; notch between lateral teeth I and II as deep as notches separating other lateral teeth.


Adult ♂: Rostrum apically truncate (Figures 29, 30). Cranium glabrous anterodorsally, from apex of rostrum to near anterior margins of eyes; microtrichia absent posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between three pairs of facets; microtrichia between dorsal facets only. Terminal sensilla of antenna apical. Empodium between three pairs of facets; microtrichia between dorsal, ventrally, abdominal segment VIII set with setiform dorso-lateral sensilla; male with gonocoxites enlarged and extending anteroventrally to beyond margin of segment VIII, gonostylus bifurcate, with two similarly shaped, curved lobes; female with narrow, elongate lobe on posterolateral margin of tergite VIII, and posteroventrally directed cerci.
**TABLE 2.—Characters and alternate states used in cladistic analysis of Nymphomyia.**

<table>
<thead>
<tr>
<th>Larva</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. median postmental tooth</td>
<td>0. one pair of lateral tines</td>
<td>1. two pairs of lateral tines</td>
<td></td>
</tr>
<tr>
<td>2. anterior margin postmentum</td>
<td>0. median tooth to level of lateral teeth</td>
<td>1. trilobed, median tooth recessed</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Pupa</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>3. rostral sheath</td>
<td>0. elongate, slender</td>
<td>1. short, triangular</td>
<td></td>
</tr>
<tr>
<td>4. antennal sheath</td>
<td>0. straight</td>
<td>1. elbowed</td>
<td></td>
</tr>
<tr>
<td>5. abdominal sternites</td>
<td>0. without recurved hooks</td>
<td>1. with pair of recurved hooks</td>
<td></td>
</tr>
<tr>
<td>6. gonocoxite sheath</td>
<td>0. glabrous, without distinctive spine</td>
<td>1. with pair of sharp spines</td>
<td></td>
</tr>
<tr>
<td>7. gonostylus sheath</td>
<td>0. bilobed</td>
<td>1. enlarged, bilobed form lost</td>
<td></td>
</tr>
<tr>
<td>8. anal hooks</td>
<td>0. large, elongate</td>
<td>1. short, triangular</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Adult</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>9. eye vestiture</td>
<td>0. without microtrichia between facets</td>
<td>1. microtrichia between dorsal facets</td>
<td>2. microtrichia between all facets</td>
</tr>
<tr>
<td>10. ventral eye bridge</td>
<td>0. absent</td>
<td>1. present, but facets not contiguous</td>
<td>2. contact between two pairs of facets</td>
</tr>
<tr>
<td>11. tarsal claw</td>
<td>0. basal tooth present</td>
<td>1. basal tooth absent</td>
<td></td>
</tr>
<tr>
<td>12. paratergal projections</td>
<td>0. absent</td>
<td>1. one pair (ventral) present</td>
<td>2. two pairs (ventral and dorsal) present</td>
</tr>
<tr>
<td>13. abdominal segment VII</td>
<td>0. with dorsolateral patch of setiform sensilla</td>
<td>1. without dorsolateral patch of setiform sensilla</td>
<td></td>
</tr>
<tr>
<td>14. abdominal segment VII</td>
<td>0. setiform sensilla generally distributed on tergite</td>
<td>1. setiform sensilla clustered above ventral paratergal projection</td>
<td></td>
</tr>
<tr>
<td>15. gonocoxites and cerci</td>
<td>0. distinctly separable</td>
<td>1. indistinguishably fused</td>
<td></td>
</tr>
<tr>
<td>16. gonocoxites</td>
<td>0. extend posteriorly</td>
<td>1. extend anteriorly</td>
<td></td>
</tr>
<tr>
<td>17. gonostyli</td>
<td>0. simple</td>
<td>1. bifurcate</td>
<td></td>
</tr>
<tr>
<td>18. aedeagus (at rest)</td>
<td>0. short, extending (internally) anteriorly to segment VIII</td>
<td>1. elongate, extending anteriorly to segment VII</td>
<td>2. markedly elongate, extending to segment V</td>
</tr>
<tr>
<td>19. aedeagal sheath</td>
<td>0. tube-like, broad basally, gradually tapering to apex</td>
<td>1. markedly broad, sinuate laterally, truncate apically</td>
<td></td>
</tr>
<tr>
<td>20. ♂ abdominal segment VII</td>
<td>0. without ventrally directed, lateral processes or flaps</td>
<td>1. with narrow, lateral flap near posterior margin</td>
<td>2. with broad, lateral flap</td>
</tr>
</tbody>
</table>
TABLE 3.—Matrix of characters and alternate states used in cladistic analysis of Nymphomyia (0 = plesiomorphic; 1, 2, 3 = apomorphic; ? = character state unknown).

<table>
<thead>
<tr>
<th>Taxon/Character</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
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in N. walkeri), provide no information about relationships and were therefore excluded from the analysis. Most multistate characters (9, 10, 12) were coded as additive, as outgroup comparison permitted logical arrangement in linear transformation series. Character 20, however, was coded as non-additive, because there was no logical basis for polarizing alternative character states in a transformation series; this was confounded further by lack of data on two species. Character analysis resulted in a single tree (Figure 3) with a length of 33 steps, and consistency and retention indices of 78 and 78, respectively; this hypothesis accepts homoplasy in six characters (3, 4, 5, 17, 18, 20).

Cladistic analysis of larval, pupal, and adult characters suggests that the Nymphomyiidae comprise two species groups with the following phylogenetic relationship (Figure 3): (1) alba group (alba + (levanidovae + rohdendorfi)) and (2) walkeri group ((walkeri + dolichopeza) + (brundini + holoptica)). This hypothesis is based largely on features of the adult cranium and terminalia and, to a lesser extent, on pupal and larval characters. A transformation series involving the adult eye (character 10), ventral eye bridge absent—bridge present, but facets not contiguous—contact between two pairs of facets—touch between three pairs of facets) is one of the most compelling characters. The latter two steps, as well as two other characters—(9) microtrichia between eye facets and (15) gonocoxites and cerci indistinguishably fused—support the monophyly of the walkeri group. Characters that help define the alba group include: (12) paratergal projections; (14) cluster of setiform sensilla above ventral paratergal projection; (19) aedeagal sheath broad, sinuate laterally, truncate apically. Other characters provide evidence for the monophyly of the Oriental species brundini + holoptica: (7) gonostylus sheath enlarged, not bilobed; (8) pupal anal hooks short, triangular; and (16) gonocoxites extend anteriorly. Although data suggest that the Nearctic fauna (walkeri and dolichopeza) is monophyletic, the basis for this hypothesis is weak, consisting of two reductive characters: (11) basal tooth of tarsal claw lost; (13) setiform sensilla on abdominal segment VII of male lost. Nymphomyia walkeri is clearly very distinctive, possessing more unique features than any other species, yet N. dolichopeza does not share this distinctness. Because differences between currently recognized genera are minor or reflect autapomorphies, their separate taxonomic status is untenable. I therefore synonymize Palaeodipteron and Felicitomyia with Nymphomyia.

ZOOGEOGRAPHY.—Structural and phylogenetic criteria help separate species of Nymphomyia into two groups, the north-ern Palaearctic alba group (alba + (rohdendorfi + levanidovae)) and the walkeri group, with the latter subdivided further into two, geographically distinct, lineages: (1) brundini + holoptica in the Oriental Region and (2) walkeri + dolichopeza in the Nearctic Region. While little can be said about zoogeographic relationships within these regions, the relationship between the Palaearctic, Oriental, and Nearctic faunas deserves comment. Of particular interest is the direction and timing of origin of the Nearctic nymphomyiid fauna. Numerous studies in cladistic biogeography have examined the origins of the North American insect fauna, particularly the relationships between the Palaearctic, Oriental, and Nearctic faunas into two, geographically distinct, lineages: (1) alba group (alba + (levanidovae + rohdendorfi)) and (2) walkeri group ((walkeri + dolichopeza) + (brundini + holoptica)). This hypothesis is based largely on features of the adult cranium and terminalia and, to a lesser extent, on pupal and larval characters. A transformation series involving the adult eye (character 10), ventral eye bridge absent—bridge present, but facets not contiguous—contact between two pairs of facets—contact between three pairs of facets) is one of the most compelling characters. The latter two steps, as well as two other characters—(9) microtrichia between eye facets and (15) gonocoxites and cerci indistinguishably fused—support the monophyly of the walkeri group. Characters that help define the alba group include: (12) paratergal projections; (14) cluster of setiform sensilla above ventral paratergal projection; (19) aedeagal sheath broad, sinuate laterally, truncate apically. Other characters provide evidence for the monophyly of the Oriental species brundini + holoptica: (7) gonostylus sheath enlarged, not bilobed; (8) pupal anal hooks short, triangular; and (16) gonocoxites extend anteriorly. Although data suggest that the Nearctic fauna (walkeri and dolichopeza) is monophyletic, the basis for this hypothesis is weak, consisting of two reductive characters: (11) basal tooth of tarsal claw lost; (13) setiform sensilla on abdominal segment VII of male lost. Nymphomyia walkeri is clearly very distinctive, possessing more unique features than any other species, yet N. dolichopeza does not share this distinctness. Because differences between currently recognized genera are minor or reflect autapomorphies, their separate taxonomic status is untenable. I therefore synonymize Palaeodipteron and Felicitomyia with Nymphomyia.

ZOOGEOGRAPHY.—Structural and phylogenetic criteria help separate species of Nymphomyia into two groups, the northeastern Palaearctic alba group (alba + (rohdendorfi + levanidovae)) and the walkeri group, with the latter subdivided further into two, geographically distinct, lineages: (1) brundini + holoptica in the Oriental Region and (2) walkeri + dolichopeza in the Nearctic Region. While little can be said about zoogeographic relationships within these regions, the relationship between the Palaearctic, Oriental, and Nearctic faunas deserves comment. Of particular interest is the direction and timing of origin of the Nearctic nymphomyiid fauna. Numerous studies in cladistic biogeography have examined the origins of the North American insect fauna, particularly the relationships between eastern Nearctic groups and those from the western Nearctic or the Palaearctic (e.g., Allen, 1983; Noonan, 1986, 1988). Results of these studies have implications for the importance of Beringian vs. trans-Atlantic dispersal routes and, concomitantly, for the timing of faunal invasions. The Beringian land bridge existed periodically until recently, with its latest appearance during the Late Wisconsinan glaciation (ca. 18,000 years ago). Noonan (1988) posits that trans-Atlantic dispersal routes were severed approximately 20–35 million years ago, with more recent dates coinciding with the Thulean land bridge. Phylogenetic evidence suggests that the Nearctic nymphomyiid fauna is monophyletic and represents a single
FIGURE 3—Character state distribution and hypothesized phylogenetic relationships of Nymphomyia. Numbers refer to characters discussed in the text.
invasion of North America, yet the source of this invasion is unclear. The absence of nymphomyiids in either the western Nearctic or western Palaearctic is problematic. The sister-group of the Nearctic fauna is the Oriental clade brundini + holoptica (Figure 98), which could support the hypothesis of an ancient trans-Atlantic invasion; this requires that nymphomyiids later became extinct in the western Palaearctic. It is possible that the group has simply been overlooked in the western Nearctic or western Palaearctic and that appropriate collection methods will result in their discovery. However, because the Diptera fauna of Europe and western Asia is relatively well known, it is doubtful that nymphomyiids will be found in the western Palaearctic. Surveys of central and eastern Asian streams hold more promise. Further sampling in western North America, particularly the extreme northwest (e.g., Alaska), may lead to the discovery of nymphomyiids from the western Nearctic; however, I predict that nymphomyiids from this area will be more closely related to the alba group than to eastern Nearctic species. Nymphomyia rohdendorfi presently occurs in extreme northeastern Russia, and it is reasonable to predict that this or a related species could have invaded the arctic or subarctic regions of Alaska during the Pleistocene. The accepted phylogeny predicts that such an invasion would be more recent than and unrelated to that which established the eastern Nearctic fauna.

Although the range of nymphomyiids is fairly broad, including the Nearctic, Palaearctic, and Oriental regions, species distributions within these areas typically are restricted and disjunct. The Russian and North American faunas each contain one relatively widespread species (rohdendorfi and walkeri, respectively), but most nymphomyiids are known from one or a few localities. The present distribution of nymphomyiids, particularly in the Appalachian Mountains, can be interpreted as relicual; i.e., nymphomyiids were previously more widespread, and the disjunct pattern seen today reflects local extinction through much of their historical range. Whether or not this extinction was caused by natural (e.g., post-glacial warming of streams) or anthropogenic (e.g., water pollution) phenomena is unclear. Pesticide studies at Coweeta Hydrologic Laboratory have shown that nymphomyiids can recolonize impacted streams after just a few years (J.B. Wallace, 1990, pers. comm.). The mechanism of recolonization has not been established, but may depend on downstream drift of immature stages from tributary streams, or on colonization by adults from adjacent watersheds. Because of their presumably short life and limited flight abilities, adult nymphomyiids are thought to be poor dispersers. These presumptions may be largely justified; however, demonstration that adults can survive in the laboratory for up to four days suggests that their life span may be greater than predicted. Furthermore, our ignorance about nymphomyiid flight behavior precludes definitive conclusions about adult dispersal capabilities. Wing morphology suggests that nymphomyiids are poor "active" fliers, but may be adept at "passive" (e.g., wind-assisted) flight. If so, aerial plankton samples in the appropriate habitats may provide adult nymphomyiids. Such collections would demonstrate that these flies have a greater dispersal potential than previously expected, and would provide an alternative to the above (vicariance-based) explanation for their disjunct distributions.

Clearly many discoveries about nymphomyiid phylogeny, biogeography, and ecology remain for future dipterists and aquatic biologists. Recent collections confirm that nymphomyiids are more widespread and diverse than was previously thought, and records from Hong Kong indicate that the group is not restricted to boreal and temperate zones. It is, therefore, probable that new records and species will be found in other areas, including parts of southeastern Asia and perhaps even mountain streams of the Neotropics. However, as is the case for many small, specialized insects, the key to future discoveries will be to adopt collection methods that effectively sample their unusual habitats.
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FIGURES 4–11.—Nymphomyia dolichopeza, new species: 4, habitus, male pupa; 5, pupal head, lateral; 6, pupal head, dorsal; 7, larval postmentum, anterior margin; 8, habitus, instar I; 9, habitus, instar II; 10, habitus, instar III; 11, habitus, instar IV. (Scale bars = 20 μm (Figures 5, 6); 10 μm (Figure 7); 0.1 mm (Figures 4, 8–11). Abbreviations: as = antennal sheath; mt = median tooth; lt = lateral tooth; rh = rostral hooks.)
FIGURES 12–19.—Nymphomyia dolichopeza, new species: 12, female pupa, terminal abdominal segments, ventral; 13, female pupa, terminal abdominal segments, lateral; 14, male pupa, terminal abdominal segments, ventral; 15, male pupa, terminal abdominal segments, lateral; 16, adult head, dorsal; 17, male terminalia, ventral; 18, male terminalia, lateral; 19, terminalia of copulating adults (male on left). (Scale bars = 50 μm (Figures 12–15, 18); 45 μm (Figure 19); 25 μm (Figure 17); 20 μm (Figure 16). Abbreviations: ae = aedeagus; gs = gonostylus; ts = terminal antennal sensilla.)
FIGURES 20–28.—Nymphomyia walkeri: 20, pupal head, lateral; 21, pupal head, dorsal; 22, larval postmentum, anterior margin; 23, male pupa, terminal abdominal segments, ventral; 24, male pupa, terminal abdominal segments, lateral; 25, female pupa, terminal abdominal segments, lateral; 26, adult head, dorsal; 27, male terminalia, ventral; 28, terminalia of copulating adults (male below). (Scale bars = 50 μm (Figures 23–25, 27, 28); 20 μm (Figures 20, 21, 26); 10 μm (Figure 22). Abbreviations: ae = aedeagus; gs = gonostylus; mt = median tooth; ts = terminal antennal sensilla.)
FIGURES 29–36.—_Nymphomyia holoptica_, new species: 29, adult head, dorsal; 30, adult head, ventral; 31, larval postmentum, anterior margin; 32, female pupa, terminal abdominal segments, lateral-oblique; 33, female terminalia, lateral; 34, male pupa, terminal abdominal segments, lateral-oblique; 35, male terminalia, ventral; 36, male terminalia, dorsal. (Scale bars = 25 μm (Figures 29, 30, 32–36); 10 μm (Figure 31). Abbreviations: ae = aedeagus; ce = cerci; gs = gonostylus; gx = gonocoxite.)
Figures 37-48.—Nymphomyia: 37, N. alba, male terminalia, lateral with detail of ventral paratergal projection; 38, N. levanidovae, male terminalia, lateral with detail of ventral paratergal projection; 39, N. holopisca, fore-, mid-, and hind-tarsal claws of male; 40, N. dolichopeza, fore-, mid-, and hind-tarsal claws of male; 41, N. dolichopeza, female terminalia, ventral; 42, N. dolichopeza, female terminalia, lateral; 43, N. alba, female terminalia, ventral; 44, N. alba, female terminalia, lateral; 45, N. levanidovae, female terminalia, lateral; 46, N. alba, terminalia of copulating adults (male on right); 47, N. rohdendorfi, larval postmentum, anterior margin; 48, N. levanidovae, larval postmentum, anterior margin. (Scale bars = 50 μm (Figures 37, 38, 41-46); 10 μm (Figures 47, 48). Abbreviations: ae = aedeagus/aedeagal sheath; ce = cerci; gs = gonostylus; mt = median tooth; pp = paratergal projections.) (Figure 48 after Rohdendorf and Kalugina, 1974.)
FIGURES 49-50.—Nymphomyia brundini: 49, male terminalia, ventral; 50, male terminalia, ventral, left gonopod removed. (Scale bar = 25 μm. Abbreviations: ae = aedeagus; ce = cerci; gs = gonostylus; gx = gonocoxite.)
FIGURES 51–58.—*Nymphomyia* larvae: 51, *N. walkeri*, instar I head capsule, dorsal; 52, *N. walkeri*, instar I head capsule, lateral; 53, *N. walkeri*, egg burster, dorsal; 54, *N. walkeri*, egg burster, lateral; 55, *N. walkeri*, instar IV mouthparts, ventral; 56, *N. dolichopeza*, new species, instar IV mouthparts, ventral; 57, *N. dolichopeza*, new species, instar IV mouthparts, frontal; 58, *N. walkeri*, instar IV, apex of antenna. (Scale bars = 10 urn (Figures 51, 52, 56, 57); 4 urn (Figure 55); 2 urn (Figures 53, 54, 58). Abbreviations: eb = egg burster; le = labrum-epipharynx; lh = “lingua” of prementohypopharyngeal apparatus; mp = maxillary palp; mt = median tooth; mx = maxilla; pm = postmentum.)
FIGURES 59–66.—Nymphomyia larvae, instar IV: 59, N. dolichopeza, new species, epipharyngeal surface; 60, N. walkeri, apex of mandible, adoral; 61, N. dolichopeza, new species, mandible, aboral; 62, N. dolichopeza, new species, apex of mandible, aboral; 63, N. dolichopeza, new species, maxilla; 64, N. dolichopeza, new species, maxillary palp; 65, N. walkeri, abdominal proleg, apical crochets; 66, N. walkeri, anal proleg, apical crochets. (Scale bars = 5 um (Figures 59, 61, 63, 65); 2 um (Figures 60, 62, 64, 66). Abbreviations: bl = basal mandibular lobe; mp = maxillary palp; pm = postmentum; pr = prostheca.)
FIGURES 67–72.—Nymphomyia pupae: 67, *N. walkerii*, anterior margin of head, dorsal; 68, *N. walkerii*, anterior margin of head, frontal; 69, *N. walkerii*, abdominal segments II–IV (anterior = right); 70, *N. walkerii*, cuticle, abdominal segment IV; 71, *N. dolichopeza*, new species, abdominal segments IV–VI (anterior = left); 72, *N. dolichopeza*, new species, cuticle, abdominal segment V. (Scale bars = 25 μm (Figures 69, 71); 10 μm (Figures 67, 68, 70, 72). Abbreviations: as = antennal sheath; rh = rostral hooks.)
FIGURES 73–80.—Nymphomyia dolichopeza, new species, adults: 73, head, lateral; 74, head, frontal; 75, head, dorsal; 76, head, ventral; 77, rostrum, ventral; 78, cibarial region; 79, antenna; 80, terminal antennal sensilla.
(Scale bars = 40 μm (Figures 73, 74); 25 μm (Figure 75); 20 μm (Figures 76, 79); 10 μm (Figure 77); 4 μm (Figures 78, 80). Abbreviations: hy = hypopharynx; lp = labial palp; ts = terminal antennal sensilla.)
Figures 81–88. *Nymphomyia walkeri*, adults: 81, head, lateral; 82, head, dorsal; 83, head, lateroventral; 84, head, frontal; 85, head, ventral; 86, antenna, showing terminal sensilla (ts); 87, base of flagellomere; 88, terminal antennal sensilla. (Scale bars = 40 μm (Figure 81); 20 μm (Figures 82, 84–86); 10 μm (Figure 83); 4 μm (Figures 87, 88).)
FIGURES 89–95.—Nymphomyia adults: 89, *N. dolichopeza*, new species, male terminalia, ventral; 90, *N. dolichopeza*, new species, male terminalia, dorsal; 91, *N. walkeri*, male terminalia, ventral; 92, *N. dolichopeza*, new species, acropod of male foretarsus; 93, *N. dolichopeza*, new species, acropod of male midtarsus; 94, *N. walkeri* female terminalia, ventral; 95, *N. dolichopeza*, new species, female terminalia, lateral. (Scale bars = 40 μm (Figures 94, 95); 20 μm (Figures 89, 90); 10 μm (Figures 91–93). Abbreviations: ae = aedeagus; ce = cerci; em = empodium; gs = gonostylus.)
FIGURE 96.—Distributions of Palaearctic and Oriental Nymphomyia: *N. alba* (triangles); *N. levandovae* (square); *N. rohdendorfi* (circles); *N. brundini* (star); *N. holoptica* (diamond).
FIGURE 97.—Distributions of Nearctic Nymphomyia: *N. walkeri* (circles); *N. dolichopeza* (triangles).