

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

Gregory W. Courtney



SMITHSONIAN INSTITUTION PRESS

Washington, D.C.

1994



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 dolichozeza*, 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* + *rohndendorfi*)); and (2) *walkeri* group ((*walkeri* + *dolichozeza*) + (*brundini* + *holoptica*)). Several compelling characters help define the eastern Palearctic *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 *dolichozeza*) 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.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging-in-Publication Data

Courtney, Gregory W.

Biosystematics of the Nymphomyiidae (Insecta: Diptera): life history, morphology, and phylogenetic relationships /

Gregory W. Courtney.

p. cm. — (Smithsonian contributions to zoology ; no. 550)

Includes bibliographic references.

1. Nymphomyiidae. 2. Nymphomyiidae—Classification. I. Title. II. Series.

QL1.S54 no. 550 [QL537.N94] 591 s—dc20 [595.77'1] 93-40217

∞ The paper used in this publication meets the minimum requirements of the American National Standard for Permanence of Paper for Printed Library Materials Z39.48—1984.

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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 nematoceros 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. levanidovae* Rohdendorf and Kalugina, and *N. rohdendorfi* Makarchenko) and one each from the Himalaya's (*N. (= Felicitomyia) brundini* (Kevan)) and eastern North America (*N. (= Palaeodipteron) walkeri* (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 nematoceros 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.

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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



providing information on and representatives of the three species of *Nymphomyia* from far eastern Russia, without which I could not have completed the descriptive and phylogenetic components of this research.

The following individuals provided valuable information on nymphomyiid collection localities and natural history: P.H. Adler, Clemson University; K.L. Manuel, Duke Power Company; J.B. Wallace, University of Georgia; D.M. Wood, Canadian National Collection; and A. Huryn. I am grateful to W.T. Swank and the staff at Coweeta Hydrologic Laboratory for permission to use their forest and laboratory facilities. I thank K.E. Marsden for assistance on several collecting trips, and B.V. Brown, J.M. Burns, G.W. Byers, J.K. Gelhaus, W.N. Mathis, M.A. Solis, and F.C. Thompson for reviewing preliminary drafts of this paper. This research was supported by a Postdoctoral Fellowship through the Office of Fellowships and Grants, Smithsonian Institution. Additional funds for field work were provided by the Theodore Roosevelt Memorial Fund, American Museum of Natural History. I am particularly indebted to W.N. Mathis, (NMNH), and F.C. Thompson, Systematic Entomology Laboratory (United States Department of Agriculture), for their support and guidance in this research, and to the Department of Entomology, National Museum of Natural History, for providing facilities, supplies, and outstanding general support. Finally, I thank the following NMNH colleagues for assistance with various technical aspects of this research: S.G. Braden, W.R. Brown, E.R.S. Hodges, Y.T. Sohn, and H.B. Williams.

METHODS.—Collection Methods: Collection of nymphomyiid larvae and, at some sites, pupae and adults was accomplished primarily by rock-wash methods (Back and Wood, 1979; Courtney, 1991a). Because nymphomyiids readily detach from the substrate and remain adrift in the water column, wash solutions consisting of water alone worked nearly as well as those containing alcohol. Rocks supporting dense clumps of moss often were simply submerged and "shaken" in the wash solution, whereas rocks with less growth usually were scrubbed with a camel-hair (or comparable) shaving brush (Courtney, 1991a). Wash solutions were poured through a series of two sieves, the first of coarse mesh (pore size ~5 mm) and the second of fine mesh (~140 μ m). The former removed larger debris and organisms, whereas the fine sieve retained the smaller fraction (including nymphomyiids). The mesh size of the latter was sufficiently fine to collect all nymphomyiid instars, including newly hatched larvae. Most samples were fixed in 95% ethanol (EtOH) and stored in Whirl-Pak™ bags until sorted in the laboratory. Samples were sorted at a magnification of $\times 12$, or $\times 25$ if detection and removal of all first-instar larvae was desired. Nymphomyiids are extremely small, typically less than 1.5 mm in length, and live larvae, immature pupae, and pharate adults are transparent, which makes them difficult to detect without the aid of a hand lens or microscope. Dead larvae, which typically are brilliant white in color, are much more noticeable, but still require a hand lens for detection.

Drift nets were used occasionally to collect nymphomyiids, 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. dolichozeza* 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 (Huryn, 1991, pers. comm.). In my study, Malaise traps were placed at a North Carolina site during late spring and early summer, 1991, but no nymphomyiids 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. walkeri* and *N. dolichozeza*. 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. walkeri* than for *N. dolichozeza*, which may have been an artifact of the higher number of *N. walkeri* pupae collected or of the more destructive collection methods for *N. dolichozeza* (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 decticious. 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; *Pex*, 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 (Watrous 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 groundplan 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 nymphomyiids held an archaic and isolated systematic position within the Diptera. In contrast, Crampton (1942) used adult characters to place nymphomyiids in the Culicoidea, one of three superfamilies in the section Psychodomorpha. 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 Diplopolyneuromorpha. These fossil groups were based on single specimens of six species, placed in four extinct families. In recent studies of Triassic and Jurassic Diptera, Kovalev (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 Väisänen, 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 nymphomyiids 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 nematoceros flies: Tipulomorpha, Psychodomorpha, Culicomorpha, and Bibionomorpha. Based on an admittedly tenuous character—coalescence of the mesomeron and mesoepimeron—the Nymphomyiidae (as the monobasic superfamily Nymphomyioidea) were placed in the infraorder Psychodomorpha.

Other cladistic interpretations (Hackman and Väisänen, 1982; Griffiths, 1987, 1990) returned to the Rohdendorf system of placing nymphomyiids 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 nematoceros flies, Wood and Borkent (1989) provided the cladistic basis for the classification of McAlpine et al. and proposed that nymphomyiids 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 nymphomyiids 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 nematoceros 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 + (Ptychopteromorpha + 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 epicondyle 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 homoplastic. 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 Psychodomorpha, 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 Ptychopteromorpha 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. levanidovae* (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

1a

Frequency
40
30
20
10
0

b

Total length (mm)

2a

Frequency
50
40
30
20
10
0

b

Total length (mm)

FIGURE 1.—
postocciput to
FIGURE 2.—
scattergram of

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.

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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. dolichozeza* 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

Nymphomyia Tokunaga, 1932:560; 1935a:44; 1935b:127; 1936:189.—Rohdendorf and Kalugina, 1974:687.—Makarchenko, 1979:1070.—Makarchenko and Makarchenko, 1983:92.—Makarchenko et al., 1989:15 [type species: *Nymphomyia alba* Tokunaga, 1932, by monotypy].

Palaeodipteron Ide, 1965:497.—Cutten and Kevan, 1970:1.—Kevan and Cutten-Ali-Khan, 1975:853.—Kevan and Cutten, 1981:203 [type species: *Palaeodipteron walkeri* Ide, 1965, by monotypy.] [New synonymy.]
Archidipteron Ide, 1965:496. [Nomen nudum.]
Felicitomyia Kevan, in Cutten and Kevan, 1970:17 [type species: *Felicitomyia brundini* Kevan, 1970, by original designation.] [New synonymy.]

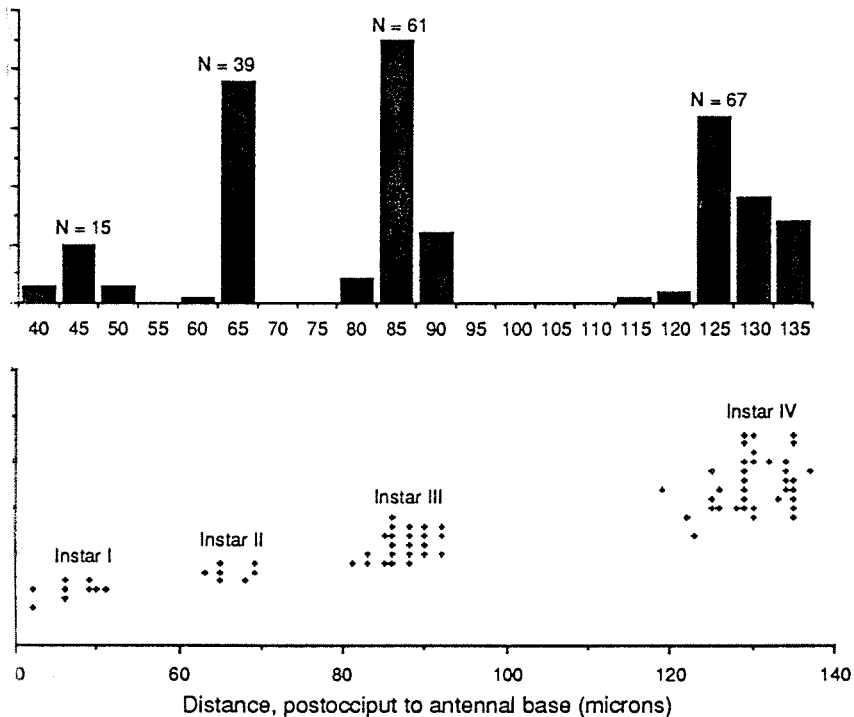
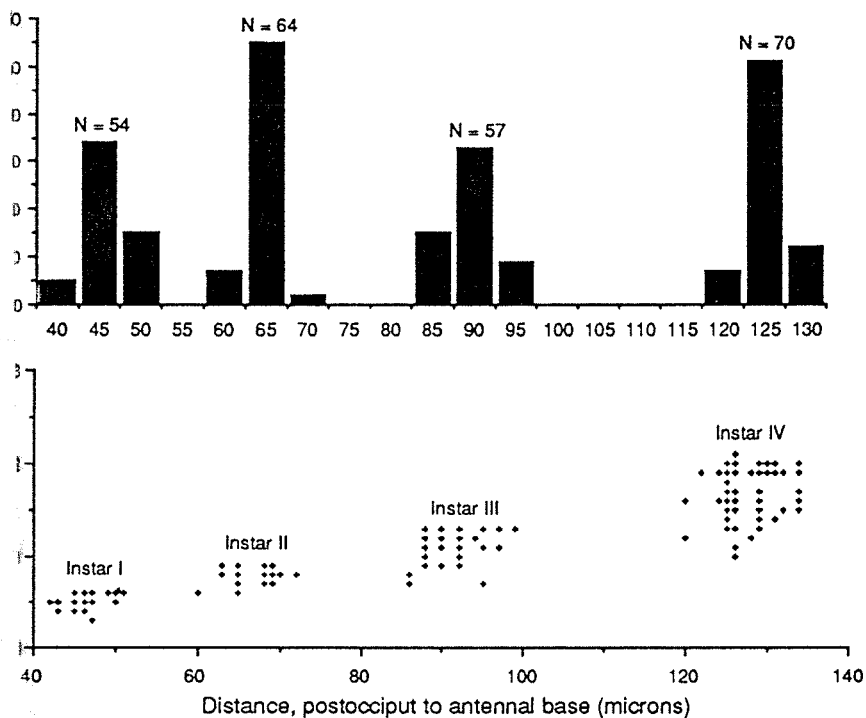
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2. *levanidovae* Rohdendorf and Kalugina, 1974
3. *rohndendorfi* Makarchenko, 1979
4. *walkeri* (Ide, 1965) [new combination]
5. *dolichozeza* new species
6. *brundini* (Kevan, 1970) [new combination]
7. *holoptica* new species

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 ecdysial 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 condyles indistinct. Anterior tentorial pits small, in depression anterior to antennal base; tentorial arms and posterior pits vestigial. Larval eyes (stemmata) 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. walkeri*: a, histogram of postocciput to antennal-base length; b, scattergram of antennal-base length vs. total length.

Instar data, *N. dolichozepeza*, new species: a, histogram of postocciput to antennal-base length; b, postocciput to antennal-base length vs. total length.

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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. Messors (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. Prosthema 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. Posteromedial (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. Prementohypopharyngeal 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); crochets dimorphic (multi-toothed and simple) on segments I–VII (Figure 65), monomorphic (multi-toothed) on segment IX (Figure 66). Segment IX with distinct posterodorsal 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 III (Figure 10): Similar to instar IV; length typically about 1 mm.

Instar II (Figure 9): Similar to instar III; length typically about 0.8 mm.

Instar I (Figure 8): Similar to instar II; length typically about 0.5 mm. Cranium posterodorsally 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 stemmatic bullae (lateral ocelli); cuticle slightly granulose over compound eyes, rather smooth and hyaline over stemmatic 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 posteromedial 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 sensilla 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 tubercle 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 ♂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, prognathous, 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. Stemmatic 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 posteroventral 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 μm), 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; propleuron 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 halteres, 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 R₁ 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. Acropod (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

¹Tokunaga (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 posteromedially 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 LARVAE²

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*
- Postmentum with first and second lateral teeth united basally, second tooth extended anteriorly beyond apices of others [Figure 48] *N. levanidovae*
- 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. dolichozeza*, new species
- *N. holoptica*, new species
- Postmentum with notch between lateral teeth I and II shallower than notches separating other teeth; second, third, and fourth lateral teeth with lateral serrations [Figures 22, 55] *N. walkeri*, new combination

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. dolichozeza*, new species
- Abdominal sternites with first pair of hooks on segment II
- *N. levanidovae*
- *N. rohdendorfi*
- 3(1). Abdominal tergites without spine rows; rostral hooks parallel [Figures 21, 67]
- *N. walkeri*, new combination
- Abdominal tergites with spine rows on at least segments II-VI; rostral hooks divergent anteriorly [as in Figure 6] 4

²Larvae of *N. brundini* unknown; larvae of *N. alba* are undescribed.

- 4(3). Abdominal tergites with spine row on segments II–VIII
 *N. brundini*, new combination
 Abdominal tergites without spine row on segment VIII 5
- 5(4). Abdominal tergites with spine row on segments II–VII
 *N. holoptica*, new species
 Abdominal tergites without spine row on segment VII *N. alba*

KEY TO ADULT MALES³

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 2
 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 5
- 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] 3
 Abdominal segment VIII not invested with setiform sensilla; gonocoxites
 reduced, extended posteriorly or medially for only a short distance; gonostylus
 variable [Figures 17–19, 27, 89, 91] 4
- 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. holoptica*, new species
 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. brundini*, 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 exerted, extended anteriorly to
 abdominal segment V *N. walkeri*, 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 exerted, extended anteriorly only to abdominal
 segment VIII [Figures 17–19] *N. dolichozepea*, new species
- 5(1). Gonocoxites not extended posteriorly beyond apex of cercus; gonostylus short,
 blunt, extended posteriorly *N. rohdendorfi*
 Gonocoxites extended posteriorly to near or beyond apex of cercus; gonostylus
 elongate, tapered, curved anteroventrally 6
- 6(5). Dorsal and ventral paratergal projections distinct, of approximately equal length

³Male *N. rohdendorfi* not available for examination; key characteristics based on Makarchenko, 1979.

[Figures 37, 46] *N. alba*
 Dorsal paratergal projections poorly developed [Figure 38]
 *N. levanidovae*

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 VIII with lateral flap bearing several
 thick, elongate, ventrally projecting, hair-like processes [Figures 28, 94]
 *N. walkeri*, 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 laterally with complex, glabrous receptacle for male gonostylus
 [Figures 19, 95] *N. dolichozeza*, 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, 1992:2.

DIAGNOSIS.—Pupa: rostral hooks divergent, abdominal sternites 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. rohdendorfi* 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 relatively 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 between tergites VIII and IX without setiform sensilla. Gonocoxites and cerci readily separable, at least distally; gonocoxites 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].

MATERIAL EXAMINED.—“Soviet Far East, Sahalinskaja oblast, Kunashir Island, Filatovka River, 19 June 1989, leg. T. Tiunova,” 14 ♂, 5 ♀.

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* from Shikoku (Shima, 1992) and Hokkaido (Okazaki, 1992, pers. comm.).

Nymphomyia levanidovae Rohdendorf and Kalugina

FIGURES 38, 45, 48, 96

Nymphomyia levanidovae Rohdendorf and Kalugina, 1974:687.—Makarchenko and Makarchenko, 1983:92.—Makarchenko et al., 1989:15.

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: Rostral hooks elongate, divergent anteriorly; antennal sheath more or less straight. Microsculpture: abdominal sternites II–VII with one pair of posteriorly directed hooks, tergites II–VIII with posterior spine rows. Anal hooks elongate, without serrations. Segment IX sexually dimorphic: male with two large, ventral lobes, each bearing a stout ventral spine; female with ill-defined lobes.

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 (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 sensillum, 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].

MATERIAL EXAMINED.—RUSSIA: PRIMORYE PROVINCE: Kedrovaja Pad' Nature Reserve, Kedrovaja R, 16 Aug 1991, E.A. Makarchenko, 4 ♂, 1 ♀; same data but 27 Jul 1975, pupae 3 ♂, 2 ♀, 1?.

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

Nymphomyia rohdendorfi Makarchenko, 1979:1070.—Makarchenko et al., 1989:15.

DIAGNOSIS⁵.—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 gonostyli; 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 two large, ventral lobes, each bearing a stout ventral spine; female with ill-defined lobes.

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. Terminal sensilla of antenna apical.

Terminalia: Sternites V and VI simple. Tergite VIII with one pair of large, elongate, posteriorly directed, lateral processes (paratergal projections); process with blunt apex; dorsal paratergal projection absent, but homologous area with large setiform sensillum. Gonocoxites and cerci readily separable, at least distally; gonocoxites broad, shorter than cercus. Gonostylus simple, short, blunt, invested with microtrichia. Aedeagus short; aedeagal sheath broad, with sinuate lateral margins and truncated apex.

Adult ♀: Similar to male. *Terminalia*: Tergite VIII with anterolateral tubercle (vestigial spiracle?) and narrow lateral lobe extending to tergite IX. Cerci broad, directed posteroventrally.

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

⁵Diagnoses and descriptions of pupae and adults based solely on Makarchenko (1979). Note that adult descriptions were based on teneral specimens dissected from pupae; thus, certain structures may not have been fully developed.

Russia, Magadan Province, Anuradat Basin, Kolyma R (upper flow), 3 Jul 1977, E. Makarchenko and S. Kocharina. Specimen deposited in Far Eastern Branch, Russian Academy of Sciences, Vladivostok (Makarchenko, 1979) [type not examined].

MATERIAL EXAMINED.—RUSSIA: SAKHALIN PROVINCE: Sakhalin Island, Belaja R, 29 Mar 1987, E.A. Makarchenko, ~25 larvae (mostly instar IV).

DISTRIBUTION (Figure 96).—Widespread in eastern Asia; recorded from northern Magadan Province, southward to Sakhalin and Primorye Provinces (Makarchenko et al., 1989).

Nymphomyia walkeri (Ide), new combination

FIGURES 20–28, 51–55, 58, 60, 65–70, 81–88, 91, 94, 97

Palaeodipteron walkeri Ide, 1965:497.—Cutten and Kevan, 1970:1.—Kevan and Cutten-Ali-Kahn, 1975:853.—Mingo and Gibbs, 1976:184.—Back and Wood, 1979:1287.—Kevan and Cutten, 1981:203.—Adler et al., 1985:211.—Harper and Lauzon, 1989:603.—Smith et al., 1989:122.

DIAGNOSIS.—Larva: median tooth of postmentum 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 sensilla of antenna subapical; male with elongate processes on abdominal sternites V and VI, simple, short gonostyli, 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 lateral teeth. Measurements (specimens from Pennsylvania and Vermont; values = range (mean ± standard deviation)):

Instar	Sample size	Total length (mm)	Postocciput to antennal base length (μm)
I	54	0.3–0.6 (0.5 ± 0.1)	42–51 (46.7 ± 2.3)
II	64	0.6–0.9 (0.8 ± 0.1)	60–72 (66.4 ± 2.3)
III	57	0.7–1.3 (1.1 ± 0.2)	86–99 (91.3 ± 2.9)
IV	70	1.0–2.1 (1.8 ± 0.3)	120–134 (127.1 ± 3.1)

Pupa (Figures 20, 21, 67–70): Rostral hooks short, parallel; antennal sheath straight, not elbowed. Microsculpture: abdominal sternites without hooks, tergites without spine rows. Anal hooks elongate, with small ventral serrations. Segments VIII and IX sexually dimorphic (Figures 23–25): male segment IX with elongate, posteroventral lobe and small lobe at inner

base of each anal hook; female segment VIII with circular posteroventral lobe.

Adult ♂: Rostrum apically round (Figures 26, 82). Cranium densely set with microtrichia dorsally and posteroventrally. Ommatidia of compound eyes contiguous ventrally, contact between two pairs of facets; microtrichia 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): Sternites V and VI each with one pair of elongate, apparently flexible, processes. Tergite VIII simple, without paratergal projections. Membrane between tergites VIII and IX without setiform sensilla. Gonocoxites reduced, fused broadly to cerci, surface generally invested with fine microtrichia, 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 exerted); 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): Sternites V and VI without elongate processes. Tergite VIII with broad lateral flap bearing several elongate, ventrally projecting, flexible, hair-like processes. Sternite VIII membranous, generally lacking microtrichia but with enlarged, spinose protuberance posteriorly. Cerci (?) broad, directed posteriorly.

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

OTHER MATERIAL EXAMINED.—CANADA: NEW BRUNSWICK: McCallum Bk, 46°17'N, 66°30'W, 1 Jun 1981 [L, P, A]; Middle Bk (Nashwauk R system), 3–6 Jun 1974 [A], Aug 1974 [L, P, (reared)A]. QUEBEC: Loon Bay Ck nr Harrington, 1967 [P]; Gaspé, Russeue Bonaventure Ouest, 16 May 1977 [L]; Gaspé, St Anne de Monts, 24 Jun 1977 [L]; Gagnon Ville, 51°45'N, 69°10'W, 21 Jul 1979, GN 142 [L]; Sakami, Lac Pipeau, 53°40'N, 76°05'W, 15 Jun 1977 [L, P, A], 17 Jun 1977 [A].

UNITED STATES. ALABAMA [tentatively identified as *N. walkeri*]: Cleburne Co: Talladega NF: Choccolocco Ck at FS Rd 540 Xing, 21 Apr 1990 [L], 21 Dec 1992 [L]. MAINE: Oxford Co: White Mountain NF: Evans Bk above Hwy 113 Xing, 44°18'N, 70°58'W, 20 Jun 1991 [L]; Little Lary Bk above FS Rd 8 Xing, 44°21'N, 70°58'W, 20 Jun 1991 [L]; Morrison Bk above Hwy 113 Xing, 44°20'N, 70°58'W, 20

Jun 1991 [L]; Mud Bk above Hwy 113 Xing, 44°19'N, 70°58'W, 20 Jun 1991 [L]; Stony Bk above Hwy 113 Xing, 44°18'N, 70°58'W, 20 Jun 1991 [L]. WASHINGTON Co: Narraguagus R at Hwy 9 Xing, 44°50'N, 68°04'W, elev. 270', 5 Jun 1987 [L]. NEW HAMPSHIRE: Carroll Co: White Mountain NF: Charles Bk, 44°14'N, 71°01'W, 21 Jun 1991 [L]. Coos Co: White Mountain NF: Ammonoosuc R at FS Rd 4 Xing, 44°16'N, 71°22'W, 20 Jun 1991 [Pex, A]; Blue Bk at FS Rd 12 Xing, 44°19'N, 71°01'W, 20 Jun 1991 [L]; Burnt Mill Bk at FS Rd 12 Xing, 44°19'N, 71°01'W, 20 Jun 1991 [L]; Jefferson Bk at upper Xing, FS Rd 4, 44°17'N, 71°21'W, 20 Jun 1991 [L, P]; Mount Pleasant Bk at FS Rd 4 Xing, 44°15'N, 71°23'W, 20 Jun 1991 [P, Pex, A]; Sebois Bk at FS Rd 4 Xing, 44°14'N, 71°24'W, 20 Jun 1991 [L]; S Br Israel R ~1 mi N Jefferson Notch, 44°19'N, 71°22'W, 20 Jun 1991 [Pex]; Twin Bk at FS Rd 12 Xing, 44°19'N, 71°03'W, 20 Jun 1991 [L]. Grafton Co: White Mountain NF: Drake Bk at Hwy 49 Xing, 43°56'N, 71°30'W, 19 Jun 1991 [L, Pex]; E Pond Bk at FS Rd 30 Xing, 43°59'N, 71°35'W, 19 Jun 1991 [L]; High Bk above Hwy 49 Xing, 43°55'N, 71°32'W, 19 Jun 1991 [L]; Scarface Bk at FS Rd 92 Xing, 44°13'N, 71°38'W, 19 Jun 1991 [L, P, Pex]; trib, Eman Bk at FS Rd 30 Xing, 43°59'N, 71°34'W, 19 Jun 1991 [L]; W Br Mad R at FS Rd 30 Xing, 43°58'N, 71°32'W, 19 Jun 1991 [Pex, A]. NEW YORK: Essex Co: Adirondack Forest Park: Schroon R at Sharp Bridge CG, elev. 400', 17 Jun 1991 [L]; "Owen Pond Br" nr confl W Br Ausable R, elev. 1600', 17 Jun 1991 [L]. Hamilton Co: Adirondack Forest Park: Bear Bk at Hwy 28 Xing, elev. 1840', 17 Jun 1991 [L]. PENNSYLVANIA: Centre Co: Black Moshannon State Forest: "Rattlesnake" trib, Benner Run, 40°55'N, 78°00'W, elev. 2000', 19 Apr 1991 [L, P], 15 Jun 1991 [L]; Smays Run, 40°54'N, 78°02'W, elev. 1900', 31 May 1985 [L], 2–3 Oct 1990 [L, P], 18 Nov 1990 [L], 27 Dec 1990 [L], 18–19 Apr 1991 [Pex, A], 15 Jun 1991 [P]. Clinton Co: Sproul State Forest: Middle Br at Penrose Rd, 41°12'N, 77°12'W, elev. 1900', 16 Jun 1991 [L, P]. VERMONT: Addison Co: Green Mountain NF: small Ck on FS Rd 59 (~2.5 mi N of Hwy 125), 43°58'N, 72°58'W, 18 Jun 1991 [L]; small Ck on FS Rd 59 (~3.5 mi N of Hwy 125), 43°59'N, 72°58'W, 18 Jun 1991 [L, Pex]; S Br Middlebury R at FS Rd 32 Xing, 43°56'N, 72°59'W, 18 Jun 1991 [L]; Sparks Bk at FS Rd 54 Xing, 44°00'N, 72°58'W, 18 Jun 1991 [L]. Rutland Co: Green Mountain NF: Black Bk at FS Rd 10 Xing, 43°22'N, 72°57'W, 21 Jun 1991 [L, P]; Little Black Bk at FS Rd 10 Xing, 43°22'N, 72°57'W, 21 Jun 1991 [L, P]; Ten Kilns Bk at FS Rd 10 Xing, 43°21'N, 72°54'W, 21 Jun 1991 [L, P]; small Ck ~2 mi E of AT/LT Trail (above FS Rd 10), 43°21'N, 72°55'W, 21 Jun 1991 [L, A]. Windham Co: Green Mountain NF: Ck at Junction FS Rd's FH-6 and 71, 43°03'N, 72°59'W, 21 Jun 1991 [L]. Windsor Co: Green Mountain NF: Greendale Bk at CG, 43°21'N, 72°49'W, 21 Jun 1991 [L]. VIRGINIA [tentatively identified as *N. walkeri*]: Giles Co: Jefferson NF: upper Stony Ck above confl White Rocks Br, 37°26'N, 80°31'W, elev. 2650', 26 May 1990 [L], 28 Apr 1991 [L]; White Rocks

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

DISTRIBUTION (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 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 III–VII with hooks, tergites II–VII with spine rows. Adult: ommatidia of compound eyes (two pair) contiguous 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)):

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

Pupa (Figures 4–6, 71, 72): Rostral hooks elongate, divergent; antennal sheath elbowed. Microsculpture: abdominal sternites III–VII with one pair of posteriorly directed hooks; tergites II–VII with posterior spine rows. Anal hooks elongate, with small dorsal serrations. Segment IX sexually dimorphic: male with circular, posteroventral lobes; female without lobes.

Adult ♂: Rostrum apically truncate (Figures 16, 74, 75). Cranium glabrous anterodorsally, 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. Gonocoxites 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.

TYPE MATERIAL.—*Holotype* ♂: United States, North Carolina, Macon Co, Nantahala NF, Coweeta Hydrologic Laboratory (hereafter, indicated by "CHL"), WS18 (Grady Br), 35°03'N, 83°26'W, elev. 2400', 19 Mar 1991, coll. G.W. Courtney. Specimen in Canada balsam on slide [USNM]. *Allotype* ♀: same data as holotype; on slide [USNM]. *Paratypes*: same data as holotype, 20 Oct 1990, 8 larvae, instar IV; 10 Dec 1990, 15 larvae [3, 3, 3, 6 of instars I–IV, respectively]; 18 Mar 1991, 4 larvae [1 each instars I–IV], 2 pupae ♀, 4 pupal exuviae [2 ♂, 2 ♀], 2 adults [1 ♂, 1 ♀]; 19 Mar 1991, 4 larvae [1 each instars I–IV], 1 pupae ♂, 3 pupal exuviae [2 ♂, 1 ♀], 1 adult ♂, 2 mating pairs; 20 Apr 1991, 2 adults ♂, 1 mating pair; 22 Apr 1991, 3 adults [2 ♂, 1 ♀], 2 mating pairs; May 92, 17 adults [5 ♂, 12 ♀]. Paratypes on slides, deposited in AMNH, CNC, GWC, and USNM.

OTHER MATERIAL EXAMINED.—UNITED STATES: GEORGIA: Rabun Co: Chattahoochee NF: Metcalf Ck nr Hale Church, 34°52'N, 83°15'W, 19 Oct 1990 [L]; Rock Mountain Ck nr confl Martin Ck, 34°48'N, 83°20'W, 19 Oct 1990 [L]; Warwoman Ck at picnic area, 34°48'N, 83°21'W, 19 Oct 1990 [L]. NORTH CAROLINA: Clay Co: Nantahala NF: trib, Park Ck at FS Rd 71 Xing, 35°03'N, 83°34'W, 22 Apr 1991 [L]. Macon Co: Nantahala NF: CHL, WS1 (Copper Br), 35°03'N, 83°26'W, elev. 2350', 20 Oct 1990 [L], 10 Dec 1990 [L, Pex], 1 Feb 1991 [L, Pex]; CHL, WS2 (Shope Br), 35°03'N, 83°26'W, elev. 2350', 20 Oct 1990 [L]; CHL, WS13 (Carpenter Br), 35°03'N, 83°26'W, elev. 2350', 20 Oct 1990 [L]; CHL, WS14 (Hugh White Ck), 35°03'N, 83°25'W, elev. 2350–

2600', 20 Oct 1990 [L], 19 Mar 1991 [L, P, Pex, A], 2 May 1991 [L, Pex]; CHL, WS17 (Hertzler Br), 35°02'N, 83°26'W, elev. 2450', 10 Dec 1990 [L, Pex]; CHL, WS18 (Grady Br), 35°03'N, 83°26'W, elev. 2400', 20 Oct 1990 [L, P], 28 Nov 1990 [L, Pex], 10 Dec 1990 [L, Pex], 1 Feb 1991 [L], 7 Mar 1991 [L], 18–19 Mar 1991 [L, P, Pex, A], 20 Apr 1991 [L, P, Pex, A], 2 May 1991 [L, P, Pex, A], 30 Jul 1991 [L]; CHL, WS19 (Snake Den Br), 35°02'N, 83°26'W, elev. 2650', 10 Dec 1990 [L, A]; CHL, WS34 (Bee Br), 35°03'N, 83°27'W, elev. 2850', 10 Dec 1990 [L, Pex]; lower Ball Ck, 35°03'N, 83°26'W, elev. 2350', 20 Oct 1990 [L]; CHL, upper Ball Ck, 35°02'N, 83°27'W, elev. 3450', 20 Oct 1990 [L], 18 Mar 1991 [L]; CHL, Henson Ck nr confl Ball Ck, 35°03'N, 83°26'W, elev. 2325', 20 Oct 1990 [L]; CHL, Lick Ck nr confl Ball Ck, 35°02'N, 83°26'W, elev. 2775', 20 Oct 1990 [L]; CHL, trib, Reynolds Br, 35°02'N, 83°26'W, elev. 2850', 20 Oct 1990 [L], 10 Dec 1990 [L, Pex], 18 Mar 1991 [L], 21 Apr 1991 [L, Pex]; CHL, upper Reynolds Br, 35°02'N, 83°27'W, elev. 3050', 20 Oct 1990 [L], 18 Mar 1991 [L]; small Ck S of Highlands (Hwy 28), 35°01'N, 83°11'W, 24 Oct 1990 [L]; small Ck nr Cliffside Lake, 35°03'N, 83°14'W, 24 Oct 1990 [L]; small Ck 0.4mi S of Hurricane Ck CG, 35°03'N, 83°30'W, 1 May 1991 [L]; small Ck 0.7 mi S of Bearpen Ck Xing (FS Rd 67), 35°01'N, 83°30'W, 1 May 1991 [L]. *McDowell Co*: Pisgah NF: trib, Slick Rock Br, 35°41'N, 82°12'W, 17 Mar 1991 [L]. *Jackson Co*: Nantahala NF: trib, E Fk Chattooga R nr Ellicott Mountain, 35°01'N, 83°03'W, 23 Oct 1990 [L].

DISTRIBUTION (Figure 97).—*Nymphomyia dolichozeza* 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 abundant insects in streams at Coweeta 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*, for long and *peza*, foot, in reference to the elongate empodium of the male foretarsus.

Nymphomyia brundini (Kevan), new combination

FIGURES 49, 50, 96

Felicitomyia brundini Kevan in Cutten and Kevan, 1970:18.

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 pair) 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.

Pupa: Rostral hooks short, parallel; antennal sheath straight. Microsculpture: abdominal sternites without hooks; tergites II–VIII with posterior spine rows. Anal hooks short, with small dorsal serrations. Segment IX sexually dimorphic: male with single enlarged, posteroventral lobe; female without lobe, segment somewhat shortened.

Adult ♂: 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 toward 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 ♀: Unknown.

TYPE MATERIAL.—*Holotype* ♂: "India, West Bengal, Darjeeling District; Teesta River; 24 Nov 1961; L. Brundin." Specimen in Hoyer's medium on slide [NRS]. "*Allotype*" ♂ and *paratypes* [pupal exuviae]: "India, West Bengal, Darjeeling District; 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 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.

Pupa: Rostral hooks elongate, divergent; antennal sheath elbowed. Microsculpture: abdominal sternites without hooks; tergites II–VII with posterior spine rows. Anal hooks short, with small dorsal serrations. Segment IX sexually dimorphic: male with single enlarged, posteroventral lobe; female without lobe, segment somewhat shortened (Figures 32, 34).

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 of foretarsus short, not extending beyond apex of tarsal claws; claws with prominent basal tooth (Figure 39).

Terminalia (Figures 35, 36): 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, elongate, projecting anteriorly to just beyond posterior margin of sternite VIII, invested with microtrichia, curved medially and tapered toward apex, with setiform sensilla along inner margin. Gonostylus bifurcate, of two glabrous, similarly shaped, curved lobes; anterior lobe relatively more tapered in apical half than posterior lobe, not overlapping posterior lobe from opposite side; anterior lobe relatively more curved, acute apically (Figure 35). Aedeagus short, thick, broadest at base; when not exerted, extending anteriorly to abdominal segment VII.

Adult ♀: Similar to male. Terminalia (Figure 33): Tergite VIII with large dorsolateral patch of setiform sensilla, glabrous anterolateral tubercle (vestigial spiracle?), and elongate, ventrally projected lobe. Sternite VIII membranous, microtrichia generally sparse. Cerci (?) broad, directed posteroventrally.

TYPE MATERIAL.—*Holotype* ♂: "Loc: Tai Po Kau Forest stream, Hong Kong, China [New Territories, southwestern shore of Tolo Harbour, ~140 m] Date: —1981, coll: David Dudgeon." Specimen in Canada balsam on slide [CNC]. *Allotype* ♀: same data as holotype; in Canada balsam on slide [CNC]. *Paratypes*: "HONG KONG, New Territories, southwestern shore of Tolo Harbour, Tai Po Kau Forest stream, ~140 m, 22 Jul 1983 [coll. David Dudgeon]" [2 larvae, instar IV; 2 pupae ♂, ♀]. Paratypes in Canada balsam on slides [USNM].

DISTRIBUTION (Figure 96).—Known only from Hong Kong. ETYMOLOGY.—Species name from the Greek *holos*, for entire, and *optikos*, sight, in reference to the extensively fused compound eyes of the adult.

Phylogenetics

INTERSPECIFIC RELATIONSHIPS.—Previous investigations have not explicitly discussed relationships within the Nymphomyiidae, yet phylogeny and classification have been implicit in recognition of three genera, two of which were monobasic. Ide (1965), by describing the Nearctic species *Palaeodipteron walkeri* as a new genus, initiated this trend toward monobasic genera. Criteria for placing this nymphomyiid in a genus other than *Nymphomyia* included "annulate" antennal flagellum (vs. "entire"), empodia "with stout spines" (vs. "brush-like"), and wing a "small scale" (vs. "large, triangular with long fringing setae"). I do not consider the former two differences particularly convincing, and even Ide correctly predicted that the wings of his specimens were in "a de-alated condition." For these reasons and others (see below) I have synonymized *Palaeodipteron* under the type genus *Nymphomyia*. The terminalia of *N. walkeri* and *N. alba*, the only other species known at that time of Ide's description, are quite different and might justify ranking these taxa as separate genera; however, most terminalia differences reflect autapomorphies of individual species, which are of little use for delimiting higher taxa.

The Himalayan genus *Felicitomyia* was said to be "somewhat less specialized" than *Nymphomyia* and *Palaeodipteron*, but with certain attributes of both (Cutten and Kevan, 1970). Generic rank was based on adult *Felicitomyia*, which were purportedly "sexually dimorphic" in head structure, yet both known adults are males (i.e., the allotype "female" is actually a male (personal observation)). Consequently, stated differences between the females of *Felicitomyia* and other nymphomyiids are untenable. Cutten and Kevan described minor differences in the shape of the antenna, tibia, and other structures, but these characters are variable and insignificant. Cutten and Kevan also mentioned differences between the male terminalia of *Felicitomyia* and those of other nymphomyiids; e.g., abdominal segments V and VI without ventral appendages (present in *Palaeodipteron*), abdominal segment VII without paratergal projections (present in *Nymphomyia*). Again, one could argue that terminalia differences justify recognition of three genera, but as was true regarding *Palaeodipteron*, most differences reflect autapomorphies. In contrast to earlier analyses, the present study considers both morphology and phylogeny as a basis for formal classification (see below).

The present analysis evaluated 20 characters and eight taxa (Tables 2, 3; Figure 3), including a generalized outgroup based largely on the Culicomorpha, Tipulidae, and Ptychopteromorpha. Autapomorphies, including certain features of the male terminalia (e.g., appendages on abdominal segments V and VI

TABLE 2.—Characters and alternate states used in cladistic analysis of *Nymphomyia*.

LARVA	
1. median postmental tooth	0. one pair of lateral tines 1. two pairs of lateral tines
2. anterior margin postmentum	0. median tooth to level of lateral teeth 1. trilobed, median tooth recessed
PUPA	
3. rostral sheath	0. elongate, slender 1. short, triangular
4. antennal sheath	0. straight 1. elbowed
5. abdominal sternites	0. without recurved hooks 1. with pair of recurved hooks
6. gonocoxite sheath	0. glabrous, without distinctive spine 1. with pair of sharp spines
7. gonostylus sheath	0. bilobed 1. enlarged, bilobed form lost
8. anal hooks	0. large, elongate 1. short, triangular
ADULT	
9. eye vestiture	0. without microtrichia between facets 1. microtrichia between dorsal facets 2. microtrichia between all facets
10. ventral eye bridge	0. absent 1. present, but facets not contiguous 2. contact between two pairs of facets 3. contact between three pairs of facets
11. tarsal claw	0. basal tooth present 1. basal tooth absent
12. paratergal projections	0. absent 1. one pair (ventral) present 2. two pairs (ventral and dorsal) present
13. abdominal segment VII	0. with dorsolateral patch of setiform sensilla 1. without dorsolateral patch of setiform sensilla
14. abdominal segment VII	0. setiform sensilla generally distributed on tergite 1. setiform sensilla clustered above ventral paratergal projection
15. gonocoxites and cerci	0. distinctly separable 1. indistinguishably fused
16. gonocoxites	0. extend posteriorly 1. extend anteriorly
17. gonostyli	0. simple 1. bifurcate
18. aedeagus (at rest)	0. short, extending (internally) anteriorly to segment VIII 1. elongate, extending anteriorly to segment VII 2. markedly elongate, extending to segment V
19. aedeagal sheath	0. tube-like, broad basally, gradually tapering to apex 1. markedly broad, sinuate laterally, truncate apically
20. ♀ abdominal segment VII	0. without ventrally directed, lateral processes or flaps 1. with narrow, lateral flap near posterior margin 2. with broad, lateral flap

TABLE 3.—Matrix of characters and alternate states used in cladistic analysis of *Nymphomyia* (0 = plesiomorphic; 1, 2, 3 = apomorphic; ? = character state unknown).

Taxon/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>N. alba</i>	?	?	0	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	1	1
<i>N. levanidovae</i>	1	1	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	2
<i>N. rohdendorfi</i>	1	1	0	1	1	1	0	0	?	1	?	1	0	1	0	0	0	0	1	?
<i>N. brundini</i>	?	?	1	0	0	0	1	1	1	2	?	0	0	0	1	1	1	1	0	?
<i>N. holoptica</i>	0	0	0	0	0	0	1	1	1	3	0	0	0	0	1	1	1	1	0	1
<i>N. walkeri</i>	0	0	1	0	0	0	0	0	2	2	1	0	1	0	1	0	0	2	0	2
<i>N. dolichozeza</i>	0	0	0	1	1	0	0	0	1	2	1	0	1	0	1	0	1	0	0	0
semaphoront	L	L	P	P	P	P	P	P	P	A	A	A	A	A	A	A	A	A	A	A

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* + *dolichozeza*) + (*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 *dolichozeza*) is mono-

phyletic, 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. dolichozeza* 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* + *dolichozeza* 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

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 relictual; i.e., nymphomyiids were previously more widespread, and the disjunct pattern seen today reflects local extinction through much of their historical range.

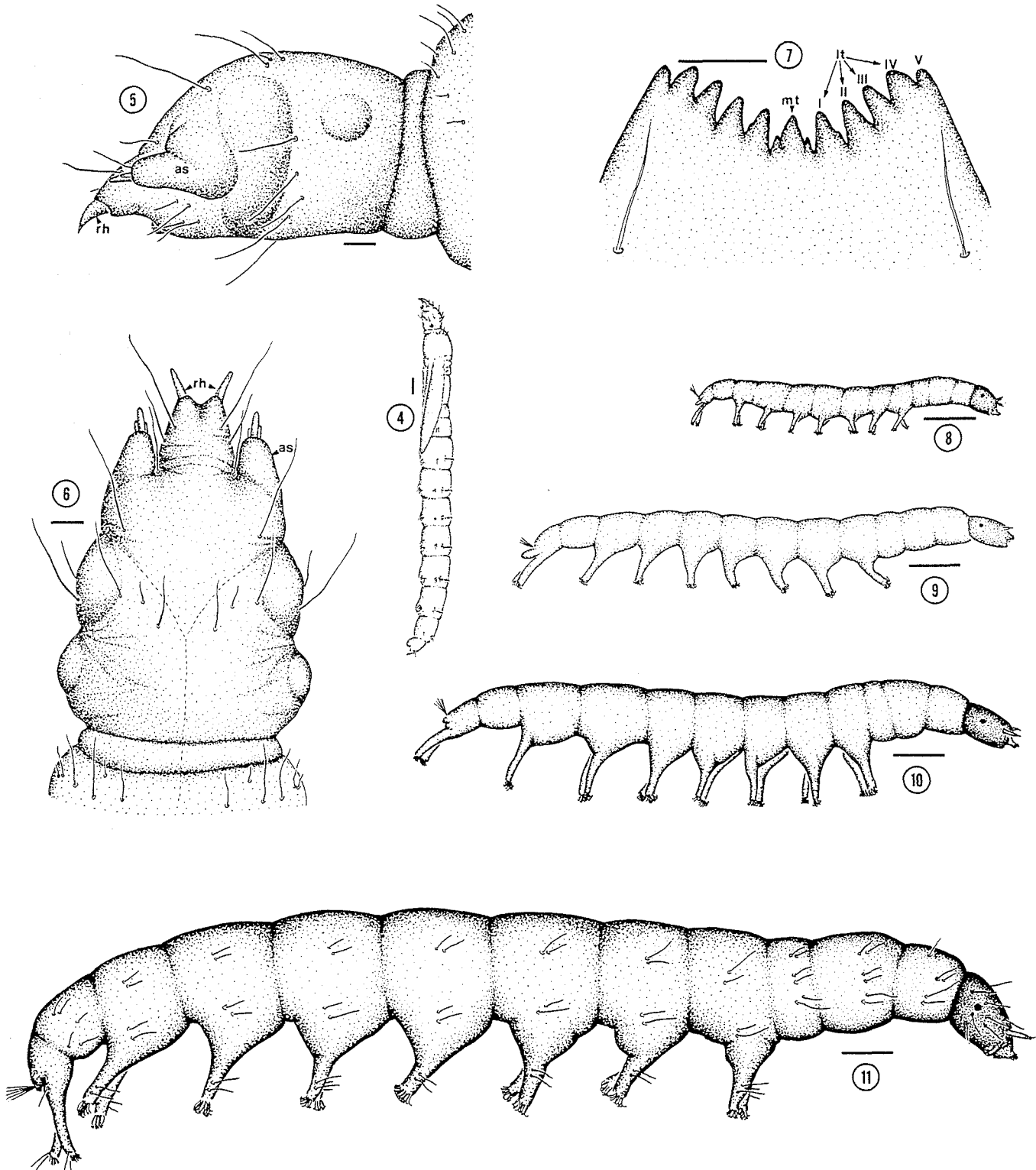
Whether or not this extinction was caused by natural (e.g., post-glacial warming of streams) or anthropogenic (e.g., water pollution) phenomena is unclear. Pesticide studies at Coweeta Hydrologic Laboratory have shown that nymphomyiids can recolonize impacted streams after just a few years (J.B. Wallace, 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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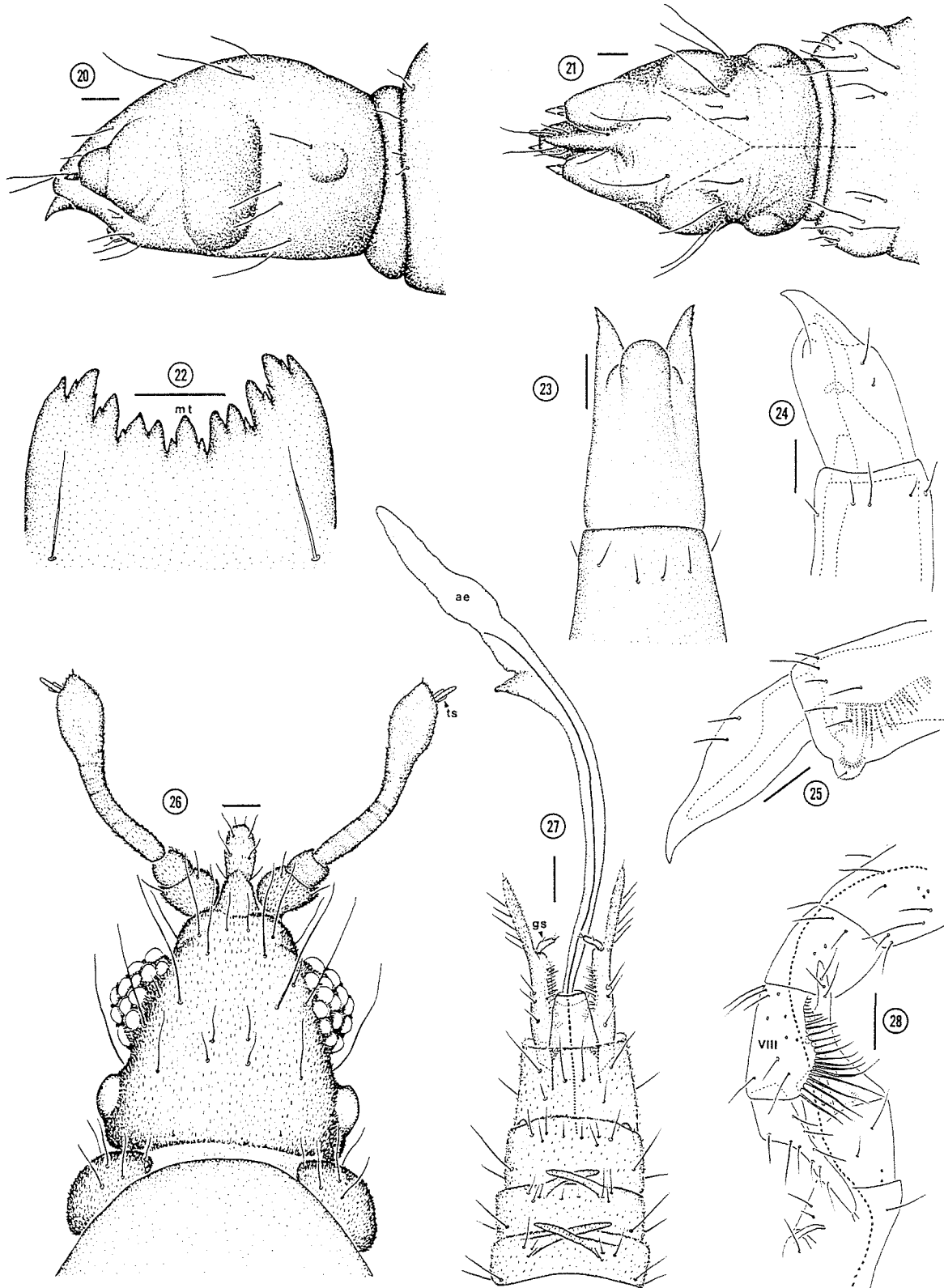
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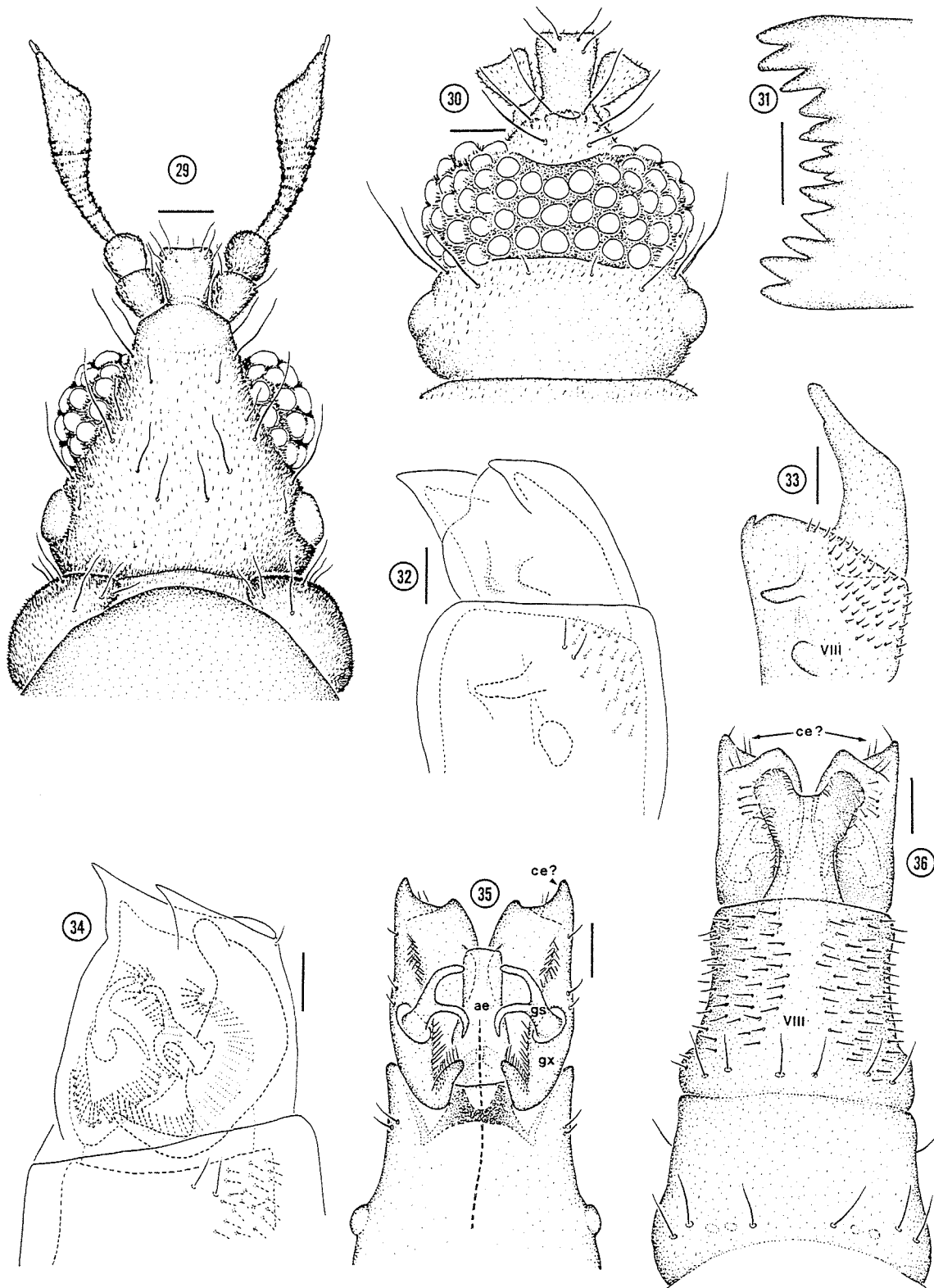
FIGURES 4-11.—*Nymphomyia dolichozeza*, new species: 4, habitus, male pupa; 5, pupal head, lateral; 6, pupal head, dorsal; 7, larval postmentum, anterior margin; 8, habitus, instar I; 9, habitus, instar II; 10, habitus, instar III; 11, habitus, instar IV. (Scale bars = 20 μ m (Figures 5, 6); 10 μ m (Figure 7); 0.1 mm (Figures 4, 8-11). Abbreviations: as = antennal sheath; mt = median tooth; lt = lateral teeth; rh = rostral hooks.)



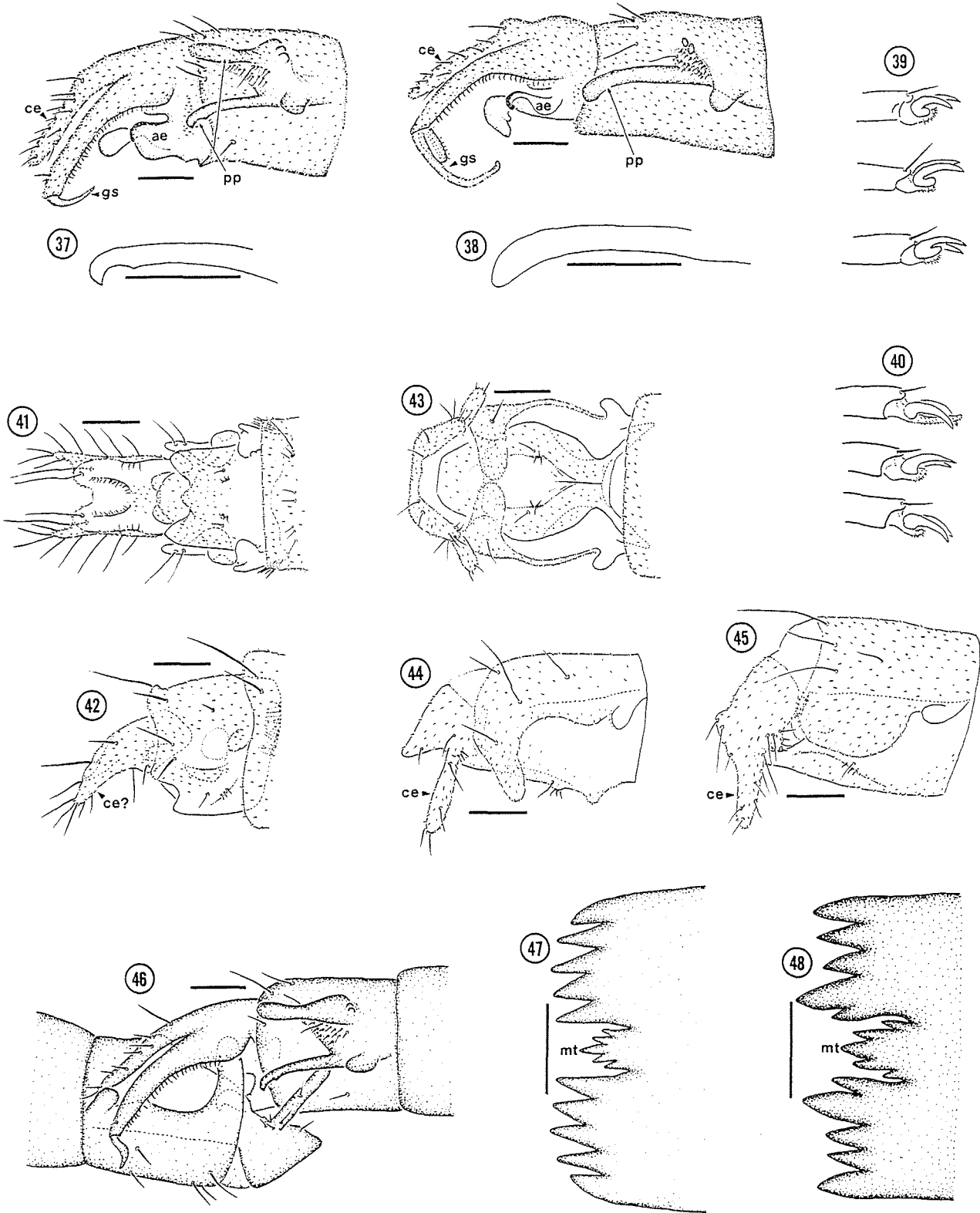
FIGURES 12-19.—*Nymphomyia dolichozeza*, new species: 12, female pupa, terminal abdominal segments, ventral; 13, female pupa, terminal abdominal segments, lateral; 14, male pupa, terminal abdominal segments, ventral; 15, male pupa, terminal abdominal segments, lateral; 16, adult head, dorsal; 17, male 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, dorsal; 26, adult head, terminalia, ventral; 27, male terminalia, ventral; 28, terminalia of copulating adults (male below). (Scale bars = 50 μ m (Figures 23-25, 27, 28); 20 μ m (Figures 20, 21, 26); 10 μ m (Figure 22). Abbreviations: ae = aedeagus; gs = gonostylus; mt = median tooth; ts = terminal antennal sensilla.)

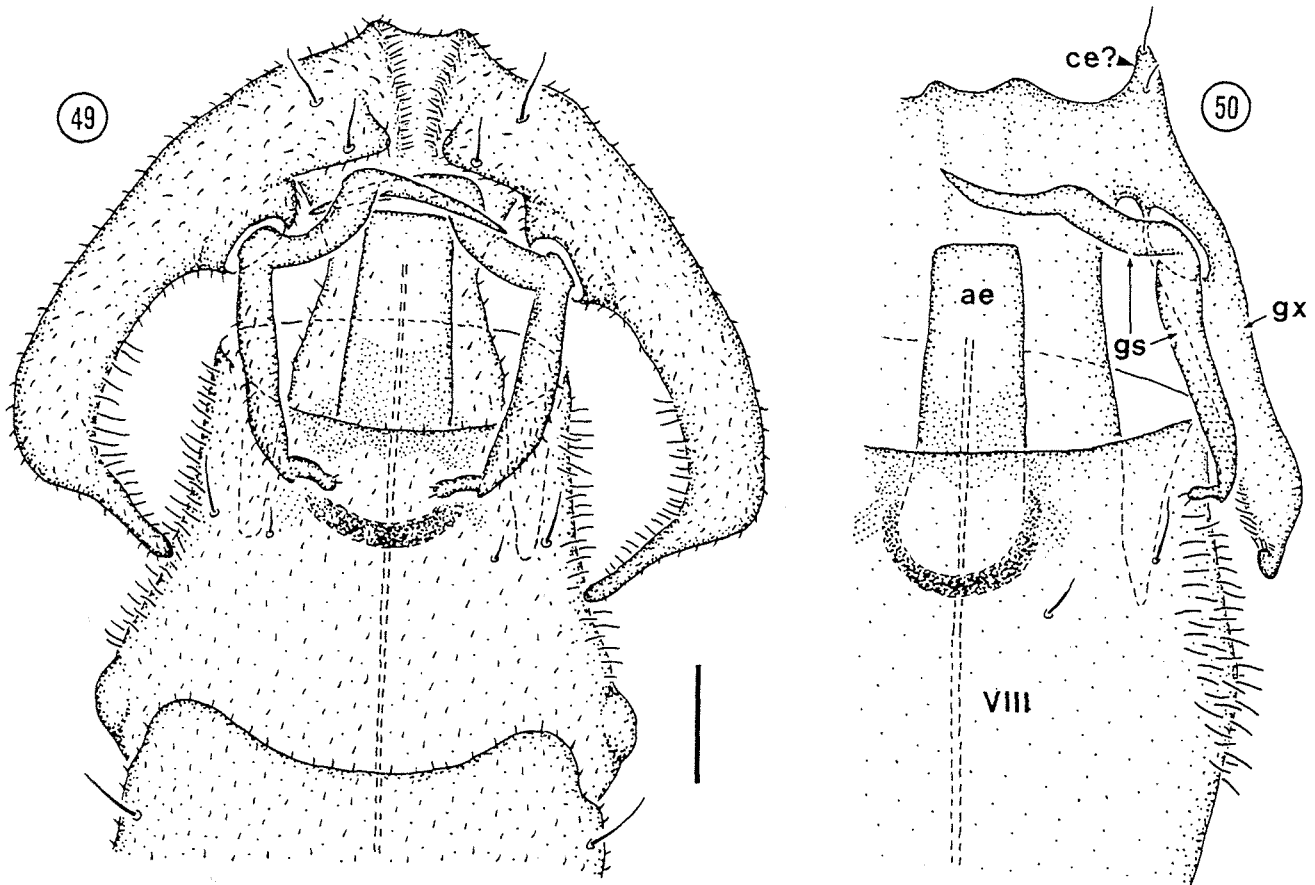


FIGURES 29-36.—*Nymphomyia holoptica*, new species: 29, adult head, dorsal; 30, adult head, ventral; 31, larval postmentum, anterior margin; 32, female pupa, terminal abdominal segments, lateral-oblique; 33, female terminalia, lateral; 34, male pupa, terminal abdominal segments, lateral-oblique; 35, male terminalia, ventral; 36, male terminalia, dorsal. (Scale bars = 25 μ m (Figures 29, 30, 32-36); 10 μ m (Figure 31). Abbreviations: ae = aedeagus; ce = cerci; gs = gonostylus; gx = gonocoxite.)

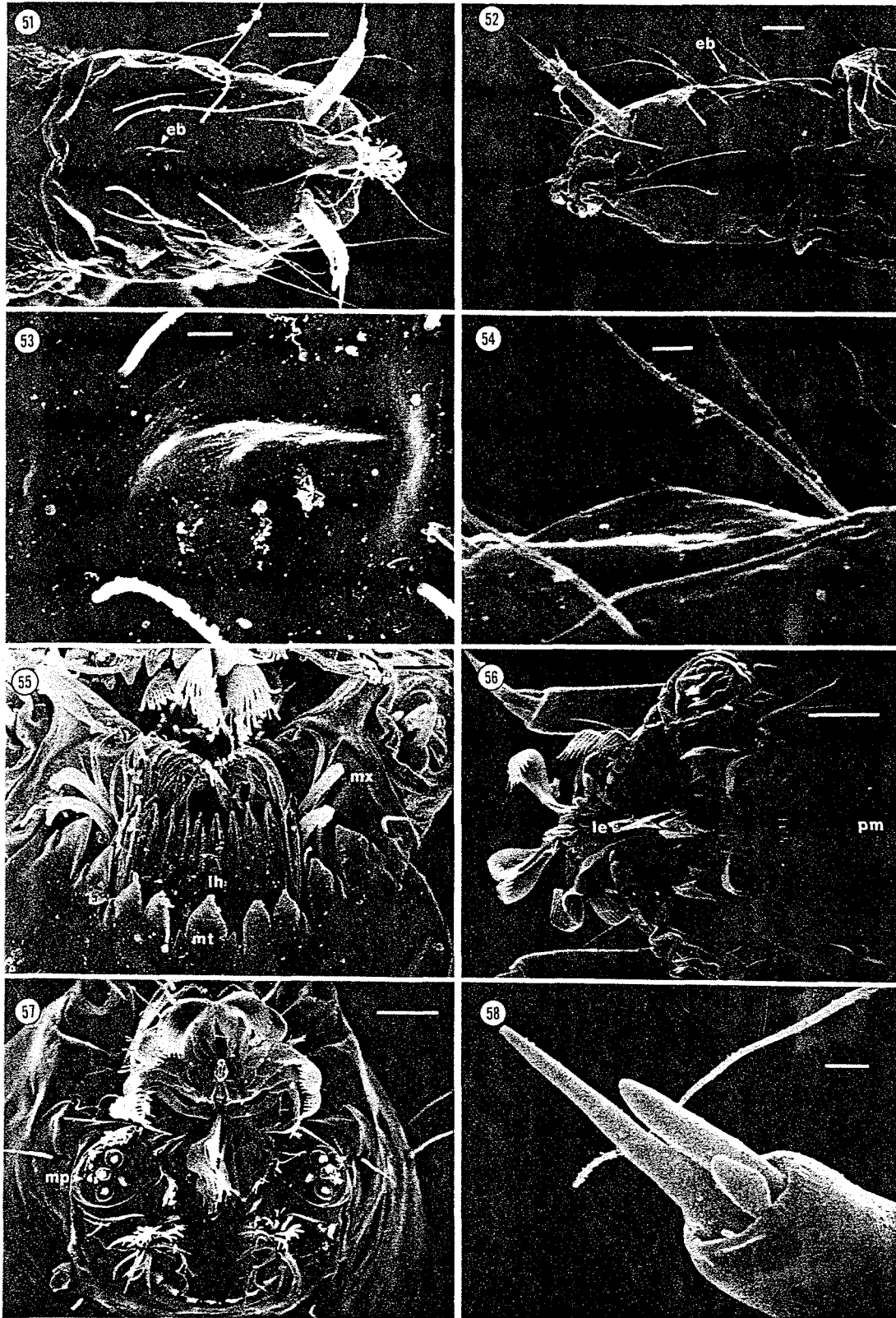


FIGURES 37-48.—*Nymphomyia*: 37, *N. alba*, male terminalia, lateral with detail of ventral paratergal projection; 38, *N. levanidovae*, male terminalia, lateral with detail of ventral paratergal projection; 39, *N. holoptica*, fore-, mid-, and hind-tarsal claws of male; 40, *N. dolichozeza*, fore-, mid-, and hind-tarsal claws of male; 41, *N. dolichozeza*, female terminalia, ventral; 42, *N. dolichozeza*, 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 μ m (Figures 37, 38, 41-46); 10 μ m (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.)



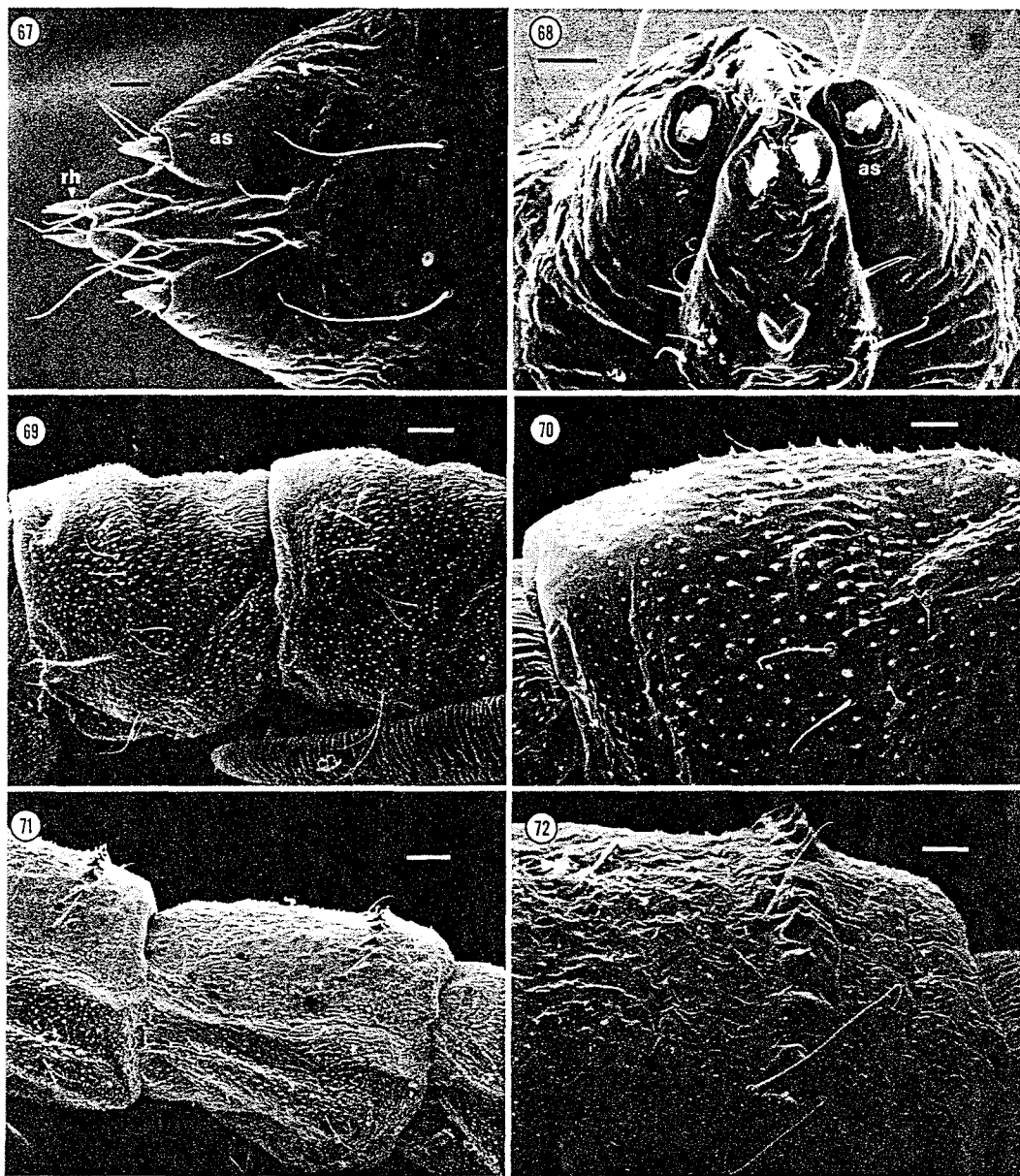
FIGURES 49-50.—*Nymphomyia brundini*: 49, male terminalia, ventral; 50, male terminalia, ventral, left gonopod removed. (Scale bar = 25 μ m. Abbreviations: ae = aedeagus; ce = cerci; gs = gonostylus; gx = gonocoxite.)



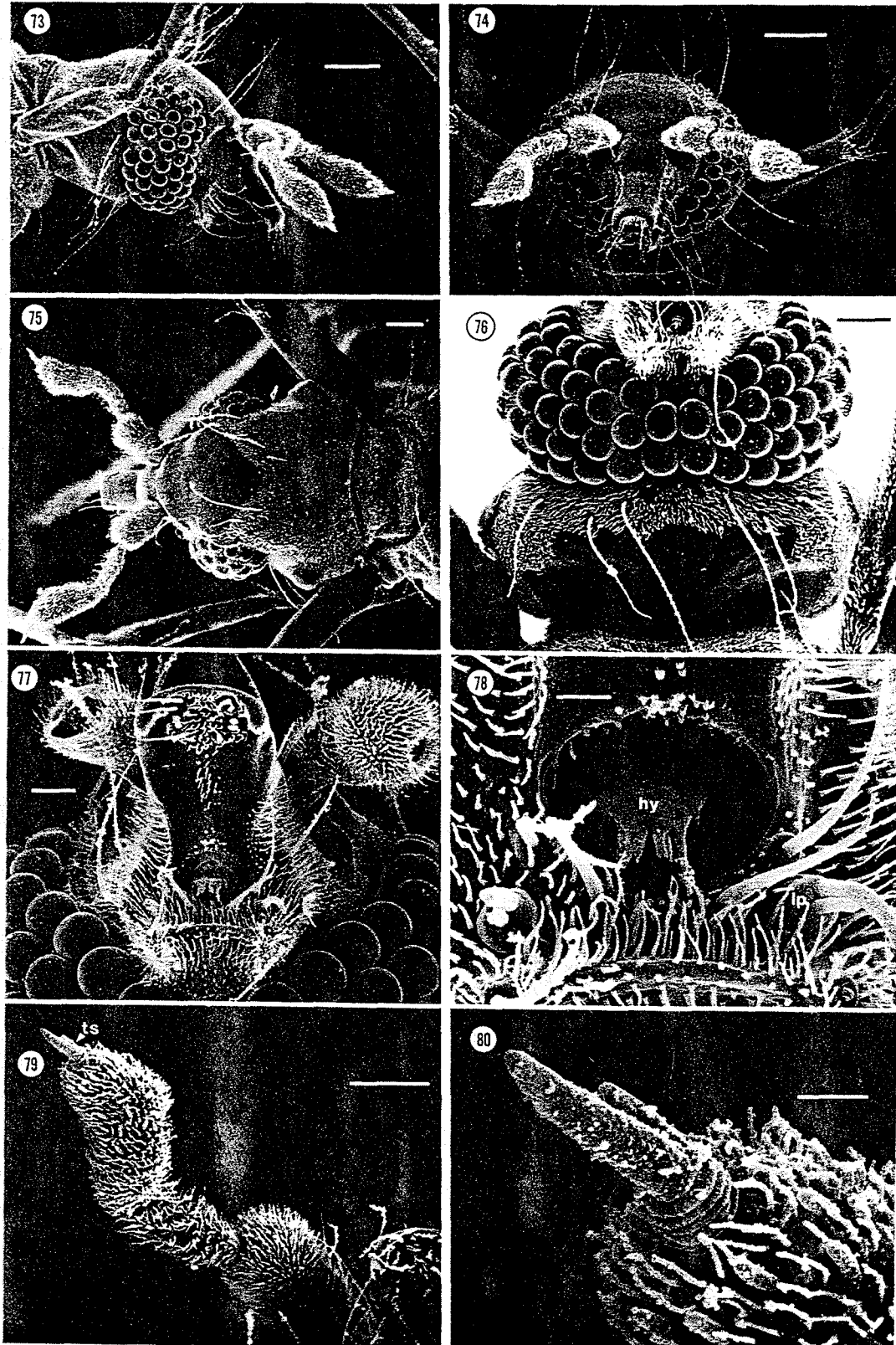
FIGURES 51–58.—*Nymphomyia* larvae: 51, *N. walkeri*, instar I head capsule, dorsal; 52, *N. walkeri*, instar I head capsule, lateral; 53, *N. walkeri*, egg burster, dorsal; 54, *N. walkeri*, egg burster, lateral; 55, *N. walkeri*, instar IV mouthparts, ventral; 56, *N. dolichozeza*, new species, instar IV mouthparts, ventral; 57, *N. dolichozeza*, new species, instar IV mouthparts, frontal; 58, *N. walkeri*, instar IV, apex of antenna. (Scale bars = 10 μ m (Figures 51, 52, 56, 57); 4 μ m (Figure 55); 2 μ m (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.)



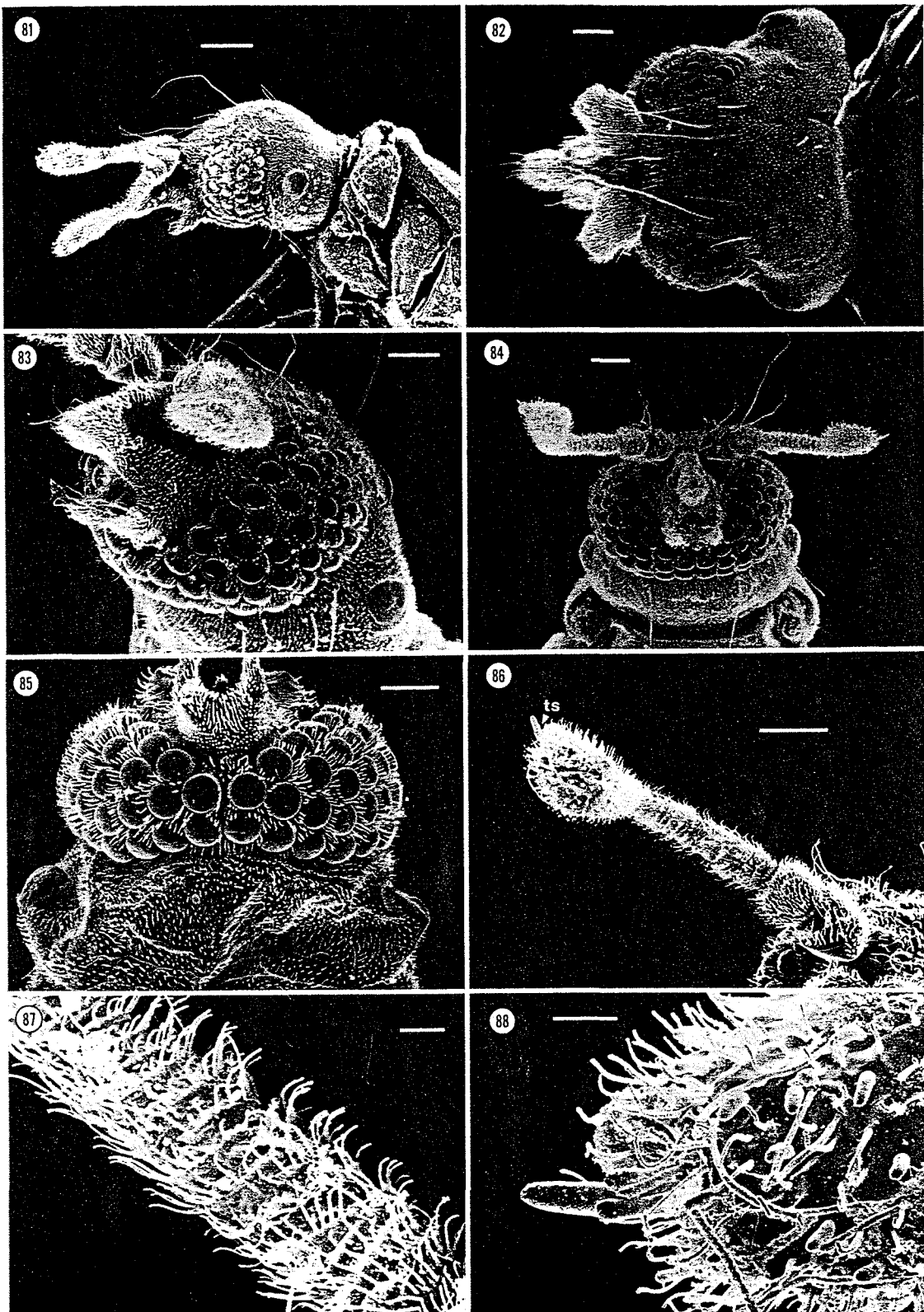
FIGURES 59-66.—*Nymphomyia* larvae, instar IV: 59, *N. dolichozepe*, new species, epipharyngeal surface; 60, *N. walkeri*, apex of mandible, adoral; 61, *N. dolichozepe*, new species, mandible, aboral; 62, *N. dolichozepe*, new species, apex of mandible, aboral; 63, *N. dolichozepe*, new species, maxilla; 64, *N. dolichozepe*, new species, maxillary palp; 65, *N. walkeri*, abdominal proleg, apical crochets; 66, *N. walkeri*, anal proleg, apical crochets. (Scale bars = 5 μ m (Figures 59, 61, 63, 65); 2 μ m (Figures 60, 62, 64, 66). Abbreviations: bl = basal mandibular lobe; mp = maxillary palp; pm = postmentum; pr = prostheca.)



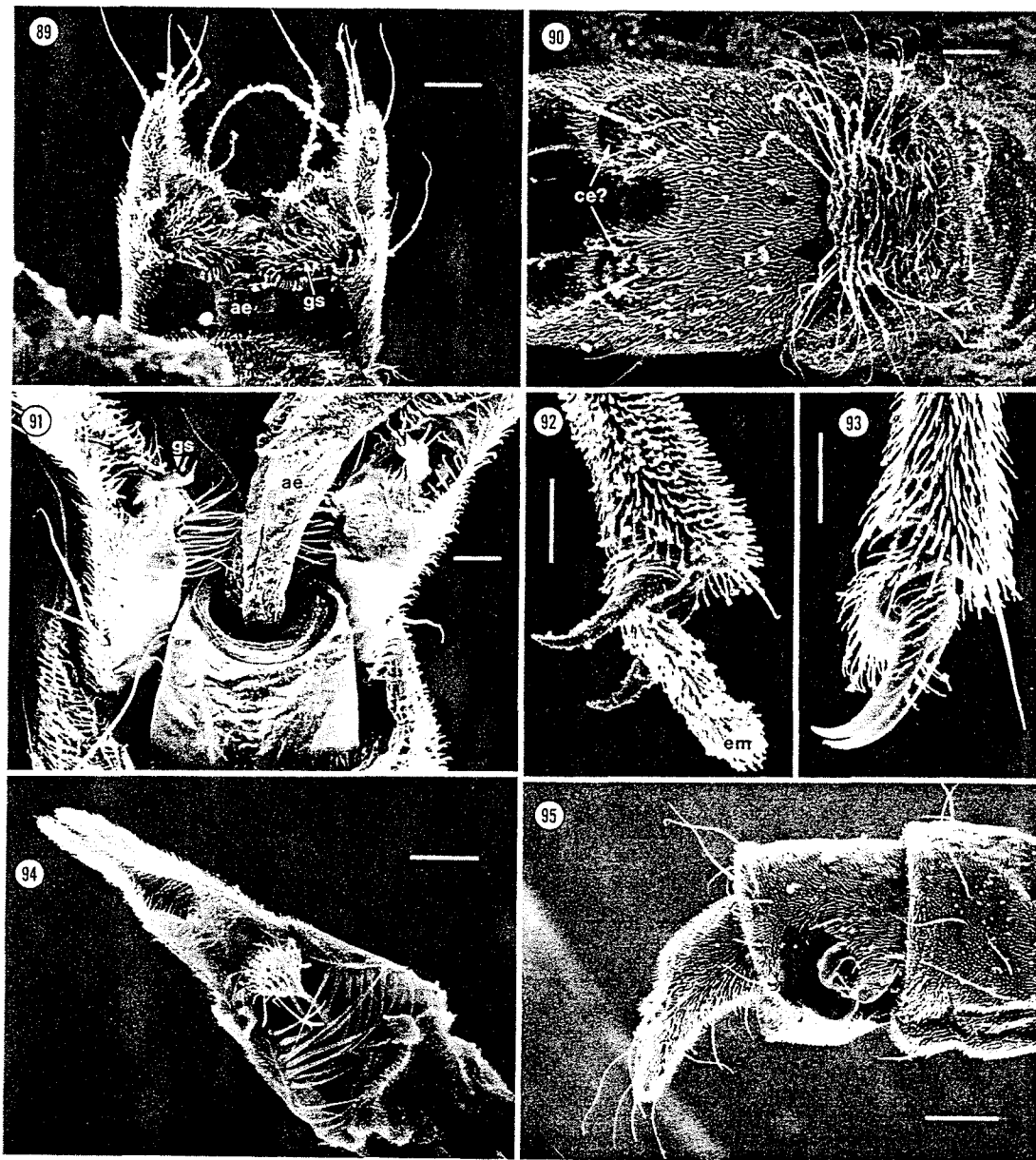
FIGURES 67-72.—*Nymphomyia* pupae: 67, *N. walkeri*, anterior margin of head, dorsal; 68, *N. walkeri*, anterior margin of head, frontal; 69, *N. walkeri*, abdominal segments II-IV (anterior = right); 70, *N. walkeri*, cuticle, abdominal segment IV; 71, *N. dolichozeza*, new species, abdominal segments IV-VI (anterior = left); 72, *N. dolichozeza*, new species, cuticle, abdominal segment V. (Scale bars = 25 μ m (Figures 69, 71); 10 μ m (Figures 67, 68, 70, 72). Abbreviations: as = antennal sheath; rh = rostral hooks.)



FIGURES 73-80.—*Nymphomyia dolichozeza*, 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 μ m (Figures 73, 74); 25 μ m (Figure 75); 20 μ m (Figures 76, 79); 10 μ m (Figure 77); 4 μ m (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, ventral; 85, head, frontal; 86, antenna, showing terminal sensilla (ts); 87, base of flagellomere; 88, terminal antennal sensilla. (Scale bars = 40 μ m (Figure 81); 20 μ m (Figures 82, 84-86); 10 μ m (Figure 83); 4 μ m (Figures 87, 88).)



FIGURES 89-95.—*Nymphomyia* adults: 89, *N. dolichozepe*, new species, male terminalia, ventral; 90, *N. dolichozepe*, new species, male terminalia, dorsal; 91, *N. walkeri*, male terminalia, ventral; 92, *N. dolichozepe*, new species, acropod of male foretarsus; 93, *N. dolichozepe*, new species, acropod of male midtarsus; 94, *N. walkeri* female terminalia, ventral; 95, *N. dolichozepe*, 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.)

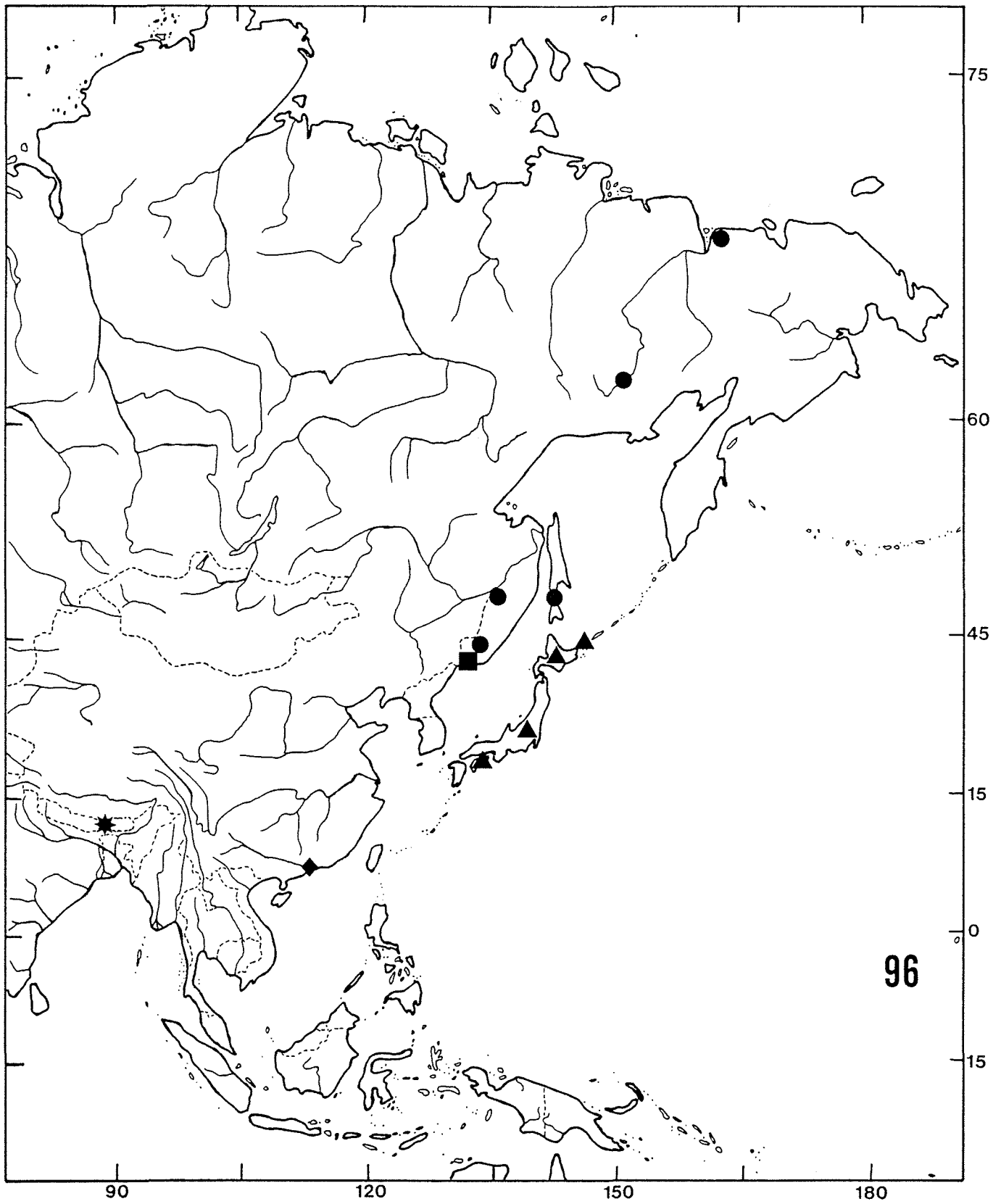
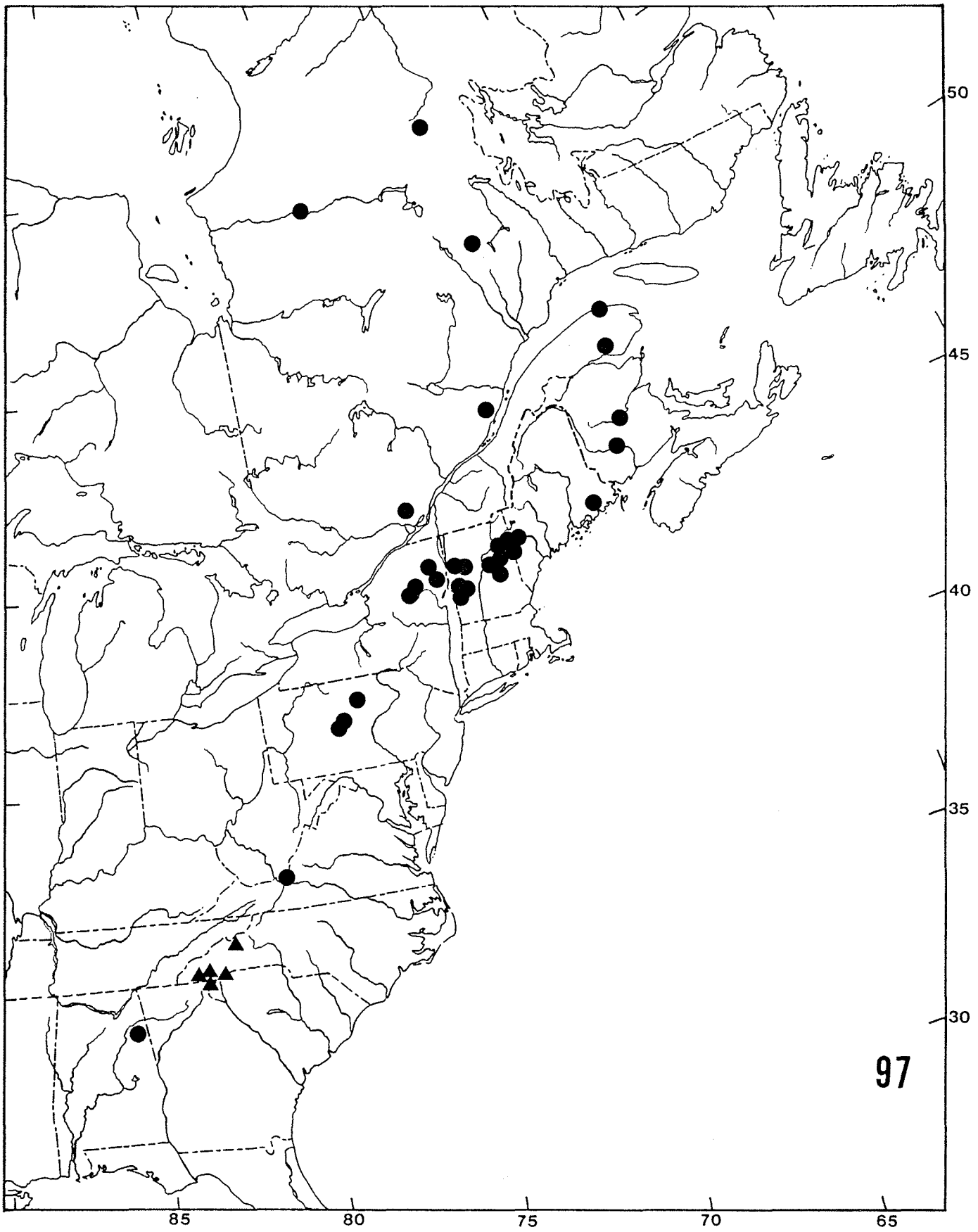


FIGURE 96.—Distributions of Palearctic and Oriental *Nymphomyia*: *N. alba* (triangles); *N. levanidovae* (square); *N. rohdendorfi* (circles); *N. brundini* (star); *N. holoptica* (diamond).



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FIGURE 97.—Distributions of Nearctic *Nymphomyia*: *N. walkeri* (circles); *N. dolichozepe* (triangles).

FIGURE 98.—Area cladogram for world species of *Nymphomyia*: *N. alba* (a); *N. levanidovae* (l); *N. rohdendorfii* (r); *N. brindini* (b); *N. holoptica* (h); *N. walkeri* (w); *N. dolichopeza* (d).

