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Fine-Scale Morphology of Nymphomyiidae: A Relict Lineage of Diptera

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Abstract: *The relict flies (family Nymphomyiidae) are among the most peculiar and little-known groups of true flies. they belong to a lineage that dates back to the Jurassic period and currently only found in a few areas of East Asia and North America. Unlike most flies, relict flies are extremely small, delicate, and short-lived as adults, while their larvae develop in clear, fast-flowing streams. This study examines the external form and structural features of both larval and adult stages, mainly focused on their wings, antennae, mouthparts, and body form. We demonstrate how these characteristics reflect the family's long evolutionary history and are associated with aquatic habitat survival. By comparing relict flies with other groups of flies, this work highlights their importance for understanding the early evolution of Diptera and the need to conserve these rare insects as living representatives of a very old branch of fly diversity.*

Keywords: Nymphomyiidae, Relict flies, Diptera, Morphology, Evolution, Aquatic insects

I. INTRODUCTION

Nymphomyiidea is a family of tiny, slender, delicate flies belongs to order Diptera (Insecta). Larvae are found among aquatic mosses in small, rapid streams in northern regions of the world. Many fossil species and a few extent species are known. Under an alternative classification, they are considered the only living representative of a separate, archaic suborder called "Archidiptera"

The Nymphomyiidae are one of the most socialized and distinctive, yet least-studied families of Nematocerous Diptera. These flies, which typically colonize small, cool, pristine, mountain streams, are currently known from only five described species, including three from Asia (Nymphomyia alba Tokunaga, N. levanidovae Rohdendorf and kalungina, and N. rohdendrofi Makarchenko) and one each from the Himalaya's (N.(Felicitomya 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

Nymphomyiidea are neotenic retaining various larval features. The flies have strap like wings with a much-reduced venation and the wing margins have long fringes like those of Thysanoptera. The wings are shed after mating. The antennae are much reduced. Species in the genus Nymphomyia have atrophied mouthpart. In the other genus and subfamily Oreadolyia adults have mouthparts. Oreadolyia are virtually apterous.

Like most of other nematocerous flies, nymphomyiids pass through four larval instars, each of which can be distinguished by grazers or collector-gatherers (Cutten and Kevan 1970; Courtney 1994) feeding on diatoms, bacteria, and fine organic material.

Pupation usually occurs in the larval microhabitat, example some species will pupate within the coarse gravels of the streams bed (Courtney 1994). Although seemingly uncommon, pupation in chironomid tubes and other retreats has also been observed in some species (Courtney 1994).

Adults of all species possess wings at emergence, but few details of flight behaviour exist. Data on several species suggest that adults mate soon after emergence, crawl beneath the water in copula; shed their wings, and female oviposits around the coupled bodies. Adults of at least some species die in copula.

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This behaviour has been recorded for at least Nymphomyia alba Tokunaga. N. dolichopeza Courtney, and N. walker (Ide). Because adults possess vestigial mouthparts and a poorly developed digestive tract, it is assumed that they survive for only a few days.

Many streams at higher latitude presumably freeze of the substratum during winter months, and resident nymphomyiids probably survive these conditions in an egg diapauses. However, in most areas, the larva is the overwintering stage (Harper and Lauzon 1989; Smith et al. 1989; Courtney 1994) Most Nymphomyia populations appear to be multivoltine, but usually with one generation that is relatively synchronous and involves more individuals. Tokunaga's (1932,1935a) original collections of N. alba suggest a bivoltine pattern, with emergence in March and October, the latter involving more individuals. Phonological data on N. levanidovae Rohdendorf and Kalugina also indicate a bivoltine life history (Makarchenko and Makarchenko 1983), with emergence in spring and fall. Data for N. rohdendorfi Makarchenko suggest a univoltine life history (Makarchenko et al. 1989) with adult emergence in late summer and early fall. Phenological characteristics of Nearctic species may very latitudinally and between years (Courtney 1994), and the same is probably typical of Eurasian species.

II. METHODOLOGY

Collection of nymphomyiid larvae and, at some sites, pupae and imagoes were accomplished primarily by rock-wash methods (Back and Wood, 1979; Courtney, 1991a) because nymphomyiids readily detach from the subsrate and remain drifted in the water column, wash solution 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 solution was poured through a series of two sieves, the first of coarse mesh (pore size-5mm) and the second of fine mesh (-140mm). The former removed larger debris and organism, whereas the fine sieve retained the smaller fraction (Including nymphomyiids). The mesh size of the letter was sufficiently fine to collect all nymphomyiids instars, including newly hatched larvae.

Most samples were fixed in 95% ethanol (EtOH) and stored in bags until sorted in the laboratory. Samples were sorted at a magnification of x 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 of 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 of larvae and pupae is infrequent under normal streams 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 if collecting pupae and adults, particularly at sites where rocks lacked a dense coating of moss At several sites in Himalayan Mountains, kick samples yielded far more pupae and

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adults of N dolichopeza than did rock wash samples. This pattern may indicate differences in pupation and perhaps oviposition behavior at sites with and without mossy substrates.

Samples were stored in bags in a chilled container and stored on the same day, usually less than six hours after collection. Mortaility 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 TM tissue culture plate) that was stored in a refrigerator (<15°C and checked at least per day. Samples maintaining at higher temperatures (e.g. rooms temperatures) showed substantially greater mortality.

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 by removing soft tissue with lactic acid or dilute (approximately 10%) potassiumhydroxide (KOH) Specimens treated in KOH were either permanently mounted in Canada balsam or converted to temporary slide mounts in glycerin.

Specimens were examined using a Motic Digital dissecting Microscope and a Motic Digital M-320 microscope, and drawing were rendered with the aid of the Nikon Drawing Tube.

III. MORPHOLOGY

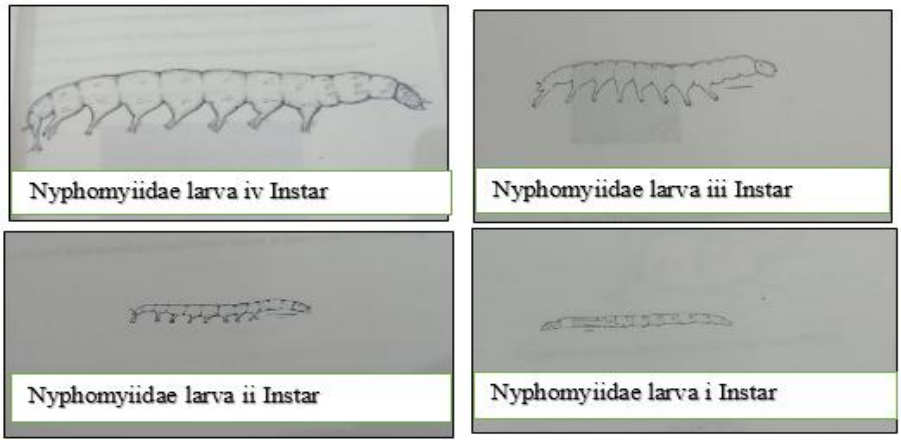
Morphological investigation were based mostly on representative of Himalayan species. Terms for structures: Morphological terms are based largely Courtney, 1990,1991b) or from comprehensive reviews in the literature (e.g., Henning, 1973; McAlpine et al., 1981a; Wood and Borkent, 1989). Description of larval structures are based mostly on 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.

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 projection (Tokunaga, 1935a) the proboscis case (Rohdendorf and Kalugina 1974) and mandibles (Cutten and Kevan 1970).

Comparative information on adult nymphomyiids comes partly from the detailed studies of Tokunaga (1935b, 1936) and terms of structures are based largely on thsese investigation. However, We adopt the terms of McAlpine (1981) and Wood (1991) regarding features of the adults terminalia.

MORPHOLOGY OF IMAGOES AND IMMATURE STAGES

Diagnostic characters OF Larvae



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Nyphomyiidae larva iv Instar

Larva compressed laterally, eucephalous; postgenital 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.

Taxonomic description

Larval instar IV: 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, steose; 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 nature. Antenna one-segmented, elongate, approximately five times longer than broad, glabrous, with four apical sensilla (Figure): one large, narrow, tapered apically, two blunt, broadened distally, and one thick, striated, tapered distally.

Apex of Antenna of Nymphomyia

Labrum-epipharynx complex predominantly membranous, with band of enlarged, apical, posterio-ventrally curved, spatulate macrotrichia, cluster of posteroventrally curved, brush-like macrotrichia and row of large, thick, simple microtrichia adjacent to U-shaped epipharyngeal bar. A pair of large, blunt sensilla just anterior to row of simple macrotrichia. Messors (premandibles) absent.

Hypopharynx and prementum of Nymphomyia

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

Maxilla reduced lacinial, palpal, and galeal lobes fused, not readily separable. Postermedial (lacinia) and anteromedial (galea) regions with clusters of elongate macrotrichia. Maxillary paip on small, subcircular prominence (stipes), with 8 apical sensilla

Maxilla of Nymphomyia

Labium with broad, flat, sclerotized postmentum (hypostoma) and complex, mostly hidden prementum Postmentum serrate anteriorly fused with postgena laterally and posteriorly. Prementohypo pharyngeal apparatus present

Labium of IV instar larva of Nymphomyia

Thorax cylindrical, glabrous except for a few setiform sesilla; 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 prologs (pseudopods); crochets dimorphic (multi-toothed and simple) on segments I-VII, monomorphic (multi-toothed) on segment IX Segments IX with distinct posterodorsal tubercle bearings several large setiform sensilla on each side of midline. Anal papillae four, thick, evertile, digitiform lobes between procercus and anal prologs; dorsal pair markedly larger than ventral pair.

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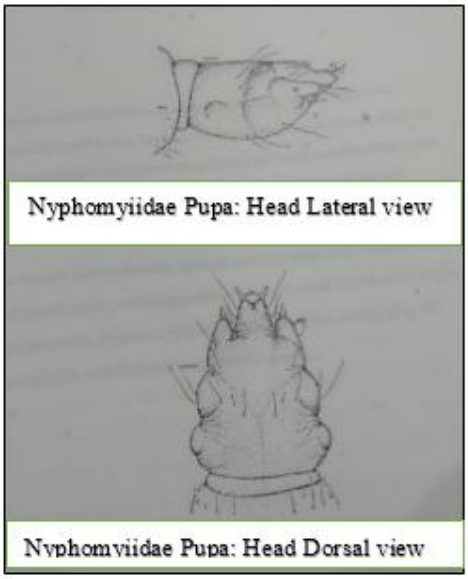
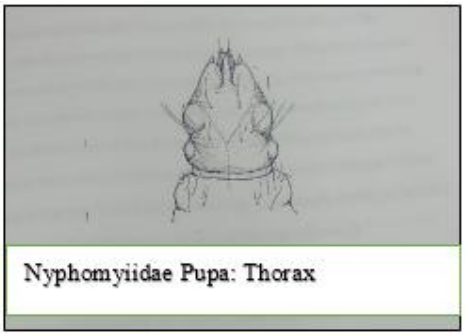
Instar III : Similar to instar IV; length typically about 1 mm.
Instar 1: Similar to instar II; length typically about 0.5 min.
Cranium posterodorsally with prominent egg burster, egg burster nearly three times longer than broad in lateral view broad at base with tooth-like apex

Diagnostic characters of pupae

Pupa slender, elongate, without respiratory organs; apneustic, head prognathous, antennal and rostral sheaths paired, projecting anteriorly as conical lobes.
Pupa: Body typically 2-2.5 mm in length, slender, cylindrical. Curticle thin, semihyaline to light brown, glaboraous except for a few setiform and et actiform serisilla
Head : distinct prognathous convex dorsally, somewhat flattened ventrally, with prominent lateral bulges corresponding to regions of developing compound eyes and stemmatic bulae (lateral ocelli) cuticle slightly granulose 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 hooks.
Antennal sheath on lateral margin of head, simple or L-shaped extended anteriorly, terminating in three prominent sensillae. Oral region with shallow concavity bordered posteriorly by irregularly shaped lobes and several setiform sensilla. Cervical region constricted.


Nyphomyiidae Pupa: Head Lateral view

Nyphomyiidae Pupa: Head Dorsal view


Nyphomyiidae Pupa: Thorax

Thorax : elongate, convex dorsally, flattened ventrally, respiratory oragans absent.
Ecdysial suture straight, extending posteriorly through thorax to abdominal tergite
Pronotum narrow, setigerous, with several setiform lateral sensilla (Fig. 15)
prosternum broad, with U-shaped posteromedial groove,
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, postnatal region large glabrous, with shallow lateral furrows, possibly separating region of medeotergite and laterotergites; mesostenum 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.

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Wing sheath narrow, elongate extending posteriorly to abdominal segments II. Halter sheath extending posteriorly from lateral margin of postnatal region along dorsal margin of wing sheath. Leg sheaths more or less S-shaped, with sharp bands corresponding to membranous, basal zones of femora and tibia, leg sheaths terminating as follows: prothoracic sheath near base of metathoracic leg. Mesotheracic sheath just anterior to tip of wing sheath, metathoracic sheath to abdominal segment II.

Abdomen narrow, elongate, apparently nine-segmented. Seginents comprised of tergal and sterna plats separated by narrow, pleural folds. Segment I typically longer that other segments, with 5 to 6 setiform sensilla dorsolatterally. Tergites II-VI with setiform sensilla near pleural membrance (two per side) and dorsolaterally (2 to 3 per side); in most species a row of 10-15 small spines posteriorly; sternites with 2 10 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; segments IX with 2 to 3 pair setiform sensilla and pairs or terminal, posteroventrally directed, thorn-like spines.

Diagnostic characters of imagoes

Adult slender, delicate, mouthparts vestigial; compund eyes contiguous ventrally, stemmatic bullae districs, dorsal ocelli absent; tentorioum vestigial; antenna short, clavate, apparently three segmented; thorax elongate, cylindrical, spiracles vestigial; wings elongate, fringed with long macrotrichila, primary veins reduced; legs elongate, femur and tibia superficially bisegmented; acropod with well-developed claws and setiform empodium, pulvilli absent; absent abdomen without spiracles; male terminalia directed ventrally, aedeagus sheathed, eversible, with thin internal aedeagal rod; female with vestigial spermathecae.

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

Head small prognathous, broad pesteriorly, narrowing anteriorly toward rostrum. Cranial sclerites fused solidaly, dorsal sutures indistinct, cranium largely invested with fine microtrichia. Occipital foramen large, slightly smaller that maximum width of head; occipital condyles indistinct. Tentorium vestigial. Compound eyes large, contiguous ventrally, widely separated dorsally, each eye with about 35-40 facets. Stemmetic 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. Mouthpart vestigial. 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). Hypopharnyx small, multi-lobed, papilliform, projected from within cibarial opening.

Antenna short (length to about 150 um.) clavate, of three apparent segments (Figu 16) 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 miocrotrichia, broadly articulated to scape: Flagellum longer than preceding segments, clavate, uniformly but less densely covered with microtrichia; microtrichia arranged in circular or spinral rows, especially on narrow, proximial part of flagellum distal part with numerous small, blunt, peg-like sensilla among microtrichia; flagellum terminating in cluster of four sensilla: one large elongate, peg-like one thick, longitudinally grooved, and twe claviform.

Thorax markedly elongate, cylindrical, generally glabroun, with few setiform sensilla. Cervix broad, nearly as wide as head, membranpus. Prothorax small, consisting of two pairs of notal (an unpaired sterna, and a pair of plecural sclerites); antepronotum of two lobes separated medialy by anteriorly projecting mesonotum and wide membranous zone, each lobe invested with fine microtrichia, typically with five setiforms sensilla postpronotum subtriangular, between antepronotum and mesonotum. Prosternuin large, broad, subquadrate undivided, with a pair of setiform sensilla laterally; anterolateral margin slightly excised near foreleg base; propleuron small, subtriangilar, in membrane between antepronotum and prosternum.

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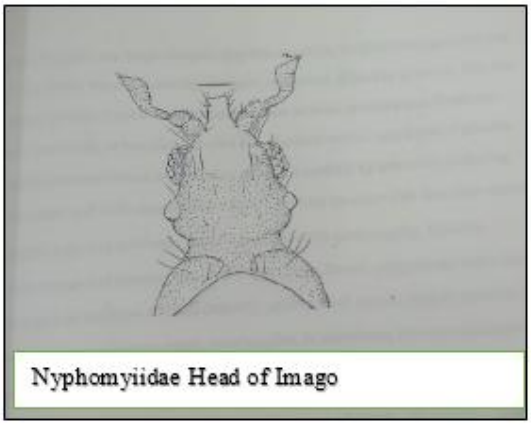

Mesothorax markedly enlarged, occupying most of thorax. Mesonotum divided into long scuto-prescutum, small scutellum, and large postnotum. Scuto-prescutum separable anteriorly by weak prescutal sutures; scuto-prescutum predominantly glabrous, except small, setiform supra-alar sensilum posterolaterally and sparse microtrichia posteromedialy 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 medialy. Postnotum mostly exposed, markedly enlarged broader than scutellum; mediotergite with straight anterior margin, widest Just anterior to level of halters. Extended posteriorly into abdominal segment 11. posterior margine round laterotergite shield-like, broadly rectangular anteriorly (anatergite) pentagonal posteroirly (katatergite) Mesopleuron small, membranous, mostly below anatergite, sutures indistinet. 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 2mm in length; membrance 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 ½ 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; articulation of three pairs of legs widely separated. Foreleg's 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 sensila along margin and distally. Tibia cylindrical, slender, superficially bisegmented as in femur, distal potion with several setiform sensilla along margin and distally, spurs absent. Tarsus five-segmented; 11 (tarsomere 1) and 15 longer that 12, 13, or t4 with ti the longest. Acropod with two well-developed claws. Midleg similar to foreleg. but shorter, tibia rather swollen distally; t1 length subequal to or shorter 15 in some species. Hindleg similar to other legs of intermediate length in most species.

Abdomen cylindrical slender, extremely elongate, weakly sclerotized, with nine apparent segments. Segments invested with abundant microtrichia and several setiform sensilla. Spiracles absent most species with small tubercles (possibly vestigial spiracles) near anterior, dorsolateral margin of abdominal segments.

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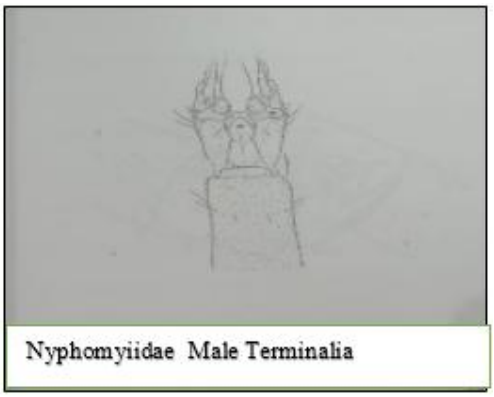
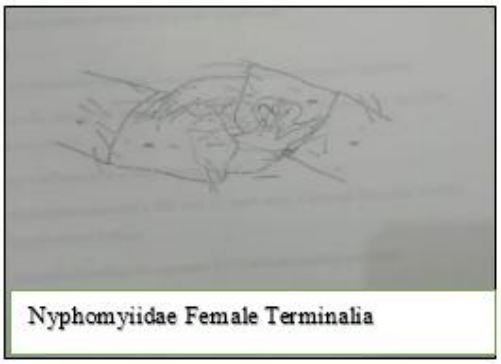


Nyphomyiidae Male Terminalia

Terminalia : Male terminalia of Nymphomyia

some directed ventrally. segments V,VI and/or modified some species. Tergites IX and X, gonocoxites and cerci fused, demarcation between the, not readily apparent, Gonocoxites typically large, elongate densely with lateral microtrichia and elongate patch of setiform sensilla; shape of gonocoxites and gonostyl, varies lobe, sternites IX and X vestigial, ventral sur occupied mostly by aedeagal sheath. Aedeagus large, membranous, glabrous, eversible in most species; aedegal sheath tube-like, originating at inner base o gonocoxites, shape variable.



Nyphomyiidae Female Terminalia

Adult female: Similar to male in most features.

Terminalia **:** 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.

PECULIAR TAXONOMIC CHARACTERS

Important characters of various stages of Nymphomyia

LARVA

Larval tentorium vestigial, arms and posterior tentorial pits not apparent.

Ventral surface of labrum-epipharynx with rows of pectinate or spatulate macrotrichia.

Apex of Mandible a multi-toothed comb.

Abdominal segments I-VII and IX each with a pair of elongate, crochet-tipped ventral prolegs.

Adbominal prolegs on segments I-VII with dimorphic crochets.

Apneustic Malpighian tubules two in number, both borne on common stalk on ventral surface of gut

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PUPA

Prognathous

Antennal sheath directed anterioly

ADULT

Adult with compound eyes contiguous ventrally
Primary ocelli absent
Mouthparts and digestive tract vestigial
Tentorium vestigial
Antenna short, with clavate flagellum of three apparent flagellomeres.
Wing narrow, with marginal fringe of elongate macrotrichia and slightly developed anal lobe.
Wing with posterior veins reduced and anterior veins concentrated along costel margin.
Wings deciduous, shed after and/or during oviposition
Femur and tibia subdivided by membranous cuticle into short, basal zone and elongate, distal zone.
Tibial spurs absent.
Anterolateral angle of abdominal tergite VIII with prominent tubercle
Abdominal spiracles absent
Spermathecae absent
Imago neotenic, retaining several larval characterstics (Courtney. 1991)
Oviposition behaviour in which the male and female re-enter the water in coupla and eggs are deposited in a rosette around the coupled bodies.

II. CONCLUSION

The study of Nymphomyiidae morphology provides critical insights into the evolutionary, functional, and ecological adaptations of this rare and enigmatic family of Diptera. Their highly specialized external morphology—including miniaturized body size, delicate wings, and unique cuticular structures—reflects adaptations to their aquatic larval environment and ephemeral adult stage. Detailed morphological analyses not only aid in clarifying their systematic position within Diptera but also highlight the significance of structural reductions and modifications associated with extreme life history strategies. Continued investigation of their fine-scale morphology, particularly using modern imaging and comparative approaches, will deepen our understanding of their phylogenetic relationships, functional anatomy, and the broader evolutionary trends shaping dipteran diversity.

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