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Abstract. The genus *Manophylax* (Trichoptera:Apataniidae) contains 3 species from the Nearctic Region and 3 species from Japan. A 7th species of *Manophylax* new for science is described and illustrated from Alaska. Habitats of larvae and pupae of the different *Manophylax* species are either mostly hygropetric or mostly terrestrial. Phylogenetic analysis infers 3 principal species groups occurring in the eastern and western Nearctic and eastern Palearctic Biogeographic Regions. The habitat of the western Nearctic *M. annulatus* Species Group is mostly hygropetric and that of the eastern Nearctic *M. altus* and eastern Palearctic *M. futabae* Species Groups are mostly terrestrial. The phylogeny suggests that the mostly terrestrial habitat evolved through a mostly hygropetric habitat. The phylogeny also implies that the eastern Nearctic and eastern Palearctic species share a more recent common ancestor than they share with the western Nearctic species, a result further supporting a commonly observed historical biogeographic pattern for these regions. *Madeophylax* Huryn and Wallace is redefined as a subgenus of *Manophylax* Wiggins, including the species of the *M. altus* and *M. futabae* Species Groups. Keys to adult males, females, larvae, and pupae of the 4 North American species of *Manophylax* are included.

Key words: *Manophylax alascensis* n. sp., hygropetric habitat, terrestrial habitat, Nearctic, Palearctic, diagnostic characters, area cladogram.

Larvae of some caddisflies are observed occasionally above the surface water in which they normally reside (e.g., *Neophylax* spp., Vineyard et al. 2005), but consistently terrestrial habits have been reported only rarely for Trichoptera larvae. The 3 species of *Enoicyla* (Trichoptera:Limnephilidae), restricted to Europe, are terrestrial in all life-history stages and typically occur

on broad-leaved forest floors (Harding 1998). Larvae of some species of the eastern Asian genus *Nothopsyche* (Trichoptera:Limnephilidae) are adapted to temporary stream habitats and aestivate terrestrially before autumn pupation and adult emergence; one Japanese species is entirely terrestrial (Nozaki 1993, 1999, Nozaki et al. 2006). The evolution of this terrestrial habitat was described by Nozaki (2008). In North America and Japan, gill-less larvae of 5 species of *Manophylax* have been reported from generally terrestrial rock faces where they are most active and feed on epilithic algae and diatoms when the rock is moist. The single remaining known North American species of *Manophylax* has gills and lives in the thin film of water in hygropetric habitats.

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Invertebrates can live exclusively (eumadiculous species) or commonly, partly, or accidentally (tychomadiculous species) in hygropetric (on stones) and madicolous (e.g., on stones, mud, mosses) habitats (Vaillant 1955). Such habitats occur as thin films of moving water below springs and seeps, on surfaces wetted by spray from waterfalls, or as wet emergent rocks beside streams or rocky chutes (Hynes 1970). Species in these habitats are typically small or depressed clingers and scrapers that feed on periphyton or mosses and that have adaptations to move or aestivate in drying or flooding conditions (Vaillant 1955, 1961, Hynes 1970). Most madicolous Diptera are air breathers (Hynes 1970, Sinclair and Marshall 1986). Vaillant (1955) reported >400 species of invertebrates in madicolous habitats in France, Corsica, and northern Africa, and 83 of those species were eumadiculous. Sinclair and Marshall (1986) collected >70 madicolous species in southern Ontario, of which 13 were eumadiculous. The morphology and biology of eumadiculous Trichoptera species have been investigated in the hydroptilid genera *Stactobia* (Vaillant 1951, Danecker 1961), *Ochrotrichia* (Vaillant 1984), and *Uganda-trichia* (Vaillant 1984); the psychomyiid genus *Tinodes* (Vaillant 1954b, Danecker 1961); the beraeid genera *Ernodes* and *Beraea* (Vaillant 1953, 1954a); the odontocerid genus *Pseudogoera* (Wallace and Ross 1971); and the apataniid genus *Manophylax* (Huryn and Wallace 1984, Schuster 1997). Several tychomadiculous caddisflies were mentioned by Wiggins (1996) and Cummins et al. (2008) and references cited by them.

The genus *Manophylax* was created by Wiggins (1973) for a single species, *Manophylax annulatus* Wiggins, 1973 (Limnephilidae:Apataniinae), that he described from hygropetric habitat (with larvae on “flat rocks in a thin film of flowing water” and pupal cases, mostly empty, “on the damp surfaces of rocks along the edge of the stream”) in Idaho. A 2nd North American species was described from a minimally hygropetric rock face in North Carolina by Huryn and Wallace (1984), who erected a new genus, *Madeophylax*, to accommodate this species. Huryn and Wallace (1984) mentioned observations of specimens from West Virginia that were later described by Schuster (1997) as a 3rd North American species whose habitat was dry for all but a few weeks of the year. Meanwhile, Nishimoto (1997, 2002) described 3 species from mostly dry rock-face habitats in Japan, synthesized the current knowledge of the Japanese species, and provided distribution maps and keys for males, females, and larvae of those species. No similar synthesis has been published for the North American species, and no distributional records for those species apart from the type localities have been published.

The genus *Manophylax* is currently placed in the family Apataniidae. The family Apataniidae was erected and described by Wallengren (1884, 1886), but most authors until recently considered the group a subfamily of Limnephilidae (e.g., Schmid 1953, 1954). Gall (1994, 1997) returned the group to family status, but with a revised definition that accommodated *Manophylax* and 3 other genera that previously also had been classified as Limnephilidae genera *incertae sedis*. Gall (1994) also provided evidence that *Madeophylax* is a junior synonym of *Manophylax*, but that evidence has not been published formally. Furthermore, Gall (1994) recommended that subfamilies in his more broadly defined family Apataniidae not be recognized until a revision of the world genera was undertaken. Although a resolution of the phylogenetic relationships among the genera of Apataniidae is beyond the scope of our paper, we lay groundwork for such a study by inferring the relationships of the species of *Manophylax*.

The habitat and biological characteristics of larvae and pupae for all known species of *Manophylax*, including the one described here, are summarized in Table 1. All larvae seem to be scrapers of diatoms, algae, and cyanobacteria. Larvae and pupae occur on vertical rock faces that are usually hygropetric or dry. Other habitat characteristics, such as elevation, rock type, and forest cover, vary among the species.

The prefix *mano-* (Greek) means rare, indicating that species of *Manophylax* are “exceedingly localized” (Wiggins 1996) or infrequently encountered (Nishimoto 2002). The usually hygropetric or terrestrial habitat of the larvae and pupae (e.g., Wiggins 1996) might be another reason that benthologists seldom find them.

A new species of the genus was forwarded to SC and JCM by Richard Merritt upon its discovery by JL, MEB, and MW, who were graduate students or postdoctoral scientists in Merritt’s laboratory at that time. Additional specimens of the new species, including a female, were captured recently (by JH). We describe that new species here and infer a phylogeny for the world fauna of *Manophylax* species to observe any historical biogeographic patterns and to gain insight into the evolutionary pathway to the terrestrial habitat in this genus.

With the new species, the current classification of world species of *Manophylax*, with distributions, is as follows:

FAMILY Apataniidae Wallengren, 1884

SUBFAMILY placement uncertain in family Apataniidae

GENUS *Manophylax* Wiggins, 1973; type species: *Manophylax annulatus* Wiggins (original designation; described originally in family Limnephilidae)

Manophylax alascensis Chuluunbat and Morse, n. sp.: Alaska, USA

Manophylax altus (Huryn and Wallace, 1984), *Madeophylax*: North Carolina, USA

Manophylax annulatus Wiggins, 1973: Idaho, USA

Manophylax butleri Schuster, 1997: Kentucky and West Virginia, USA

Manophylax futabae Nishimoto, 1997: Japan

Manophylax kyushuensis Nishimoto, 2002: Japan

Manophylax omogoensis Nishimoto, 1997: Japan

Materials and Methods

Twenty-four larvae, 1 pupa, and 3 teneral adults of the new species were collected in June, July, and August 2002 and 2004, and 18 larvae, 1 pupa, 2 pupal exuviae, and 5 nonteneral adults were collected in August 2008 from hygropetric habitats near Juneau, Alaska.

Nugget Creek is located in the Northern Pacific Coastal Forests Ecoregion in the Tongass National Forest near Juneau, Alaska. The Creek originates about 9 km east of Mendenhall Lake as melt-water from Nugget Creek Glacier. Snowmelt from Bullard Mountain and Heintzelman Ridge (including Vista Creek, Fall Creek, Goat Creek, and Canyon Creek) and frequent rains during warmer months all contribute to Nugget Creek as it flows towards Nugget Falls. Leaking Glacier also might provide some flow to Nugget Creek. The watershed is composed generally of Mesozoic Era metamorphic rock and rock of sedimentary and volcanic origins. Local soils are generally <18,000 y old and are composed of bedrock detritus in the form of clay, silt, sand, gravel, and boulders intermixed during deposition by glacial, erosional, and fluvial action (Barnwell and Boning 1968).

The larvae and cases of this species were first discovered in late July 2002 in the splash zone on the south side of Nugget Creek Falls, ~700 m south of Mendenhall Glacier, Juneau, Alaska (lat 58.426958°N, long 134.537463°W; WGS84 Datum). The larvae were found on the vertical surface of bedrock near the bottom of the falls where Nugget Creek spills into Lake Mendenhall at an elevation of ~28 m. All larvae were found on steep hygropetric habitats (wetted vertical rock faces). The rock surface was smooth, but not slippery, and the larvae on this date were abundant but not dense (<3/m²). Unidentified algal or diatomaceous growth could be seen and felt in the thin water film of these rock faces. On this first sampling occasion, several

adult caddisflies were observed in the same location as the larvae and were collected as the presumptive adult of this species. All specimens were placed in labeled glass jars and preserved with 95% ethanol.

In 2004, additional specimens were collected from both Nugget Falls and a considerably smaller, unnamed seep ~500 m to the south located between Steep Creek and Nugget Falls. This smaller stream can be found on some topographic maps and is labeled simply as 'Falls.' The environments of the 2 collection sites were similar. Until recently (<150 y), these 2 sites had been covered by the Mendenhall Glacier whose most recent advance over the valley began ~1000 BCE with the onset of the cool and wet climate conditions of the Little Ice Age (Barnwell and Boning 1968), although the glacier again encroached close to the Falls in 1984/1985 (Molnia 2008).

Physical and chemical characteristics of Nugget Creek Waterfall are provided in Table 2. Temperature, dissolved O₂, and conductivity were measured in situ on 28 June 2004 with a YSI probe (Yellow Springs Instruments, Yellow Springs, Ohio). Analytical results for 7 other variables in water samples collected on 28 June and 26 July 2004 were provided by staff of the US Department of Agriculture Forest Service, Juneau Forestry Sciences Laboratory.

Hygropetric habitats in 6 other locations were investigated, but no *Manophylax* specimens were observed in them.

West Glacier Trail/Mt. McGinnis Trail.—Several hygropetric areas of snowmelt seeps located along the West Glacier Trail were examined.

Mendenhall Glacier/exposed schist ridge.—An unnamed stream originating from snowmelt on Mt. McGinnis was investigated as it flowed over a recently exposed schist ridge and beneath the Mendenhall Glacier.

Steep Creek/East Glacier Trail.—Steep Creek, along the East Glacier Trail, was investigated at a waterfall.

Shrine Creek.—A hygropetric area of Shrine Creek was investigated at km 37 of the Glacier Highway. Several other small seeps along the Glacier Highway also were investigated. Many of these hygropetric habitats are a result of the construction of the Glacier Highway.

Mt. Juneau Trail, Perseverance Trail, and abandoned gold mine.—Snowmelt streams and seeps from Mt. Juneau along the Mt. Juneau Trail and Perseverance Trail were investigated. Seeps in an abandoned mine in the basin also were searched.

Mt. Roberts Trail and Peak.—Streams and seeps were investigated along the Mt. Roberts trail, from the base of Mt. Roberts to its peak at 1.2 km.

Circumstantial association of the immature stages with adults of this species was established by the simultaneous capture of adults and immatures of this

unusual genus at the same localities, far away (nearly 2000 km) from the closest known populations of congeners. The phylogenetic relationships were inferred by observation of a nested hierarchy of uniquely shared morphological homologues (synapomorphies) (e.g., Schuh 2000). Wiggins (1973) considered *Manophylax* to be most similar to the genus *Allomyia* (which he called *Imania*). Therefore, we used

that genus as the outgroup for the phylogenetic analysis. Character state transformations are provided in Table 3 and a taxon-by-character matrix of those data is given in Table 4.

Type specimens are deposited in the following institutions: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH); Clemson University Arthropod Collection,

TABLE 1. Summary of habitat and life history information for the known species of *Manophylax*.

Species (Subgenus, Species Group)	Known locations	Larval habitat	Life-history notes	Reference(s)
<i>M. annulatus</i> (Subgenus <i>Manophylax</i> , <i>M. annulatus</i> Species Group)	Idaho, USA	Larval and pupal specimens taken from the surfaces of cascade boulders of a small stream (<0.5 m wide) in a thin film of flowing water. Empty pupal cases found on damp rocks at stream edge.	No information reported	Wiggins 1973
<i>M. alascensis</i> (Subgenus <i>Manophylax</i> , <i>M. annulatus</i> Species Group)	Alaska, USA	Larval and pupal specimens found on the wetted vertical surfaces of the large boulders near the bottom of the falls where glacial meltwater spilled into a lake at 28 m elevation, occasionally wandering onto dry rock surfaces, but soon returning to moist or hygropetric habitat. The rock surface was smooth, but not slippery. Unidentified algal or diatomaceous growth could be seen and felt in the thin water film of these rock faces.	Larvae, pupae, and adults co-occurred throughout July and August, suggesting overlapping generations and development times >1 y. Larvae feed on the periphyton community attached to the wet surface of the waterfall wall. Stomach contents of 4 th and 5 th instar larvae included algae, fungal hyphae and sporangia, and particulate organic matter embedded with fine sand grains.	This paper
<i>M. altus</i> (Subgenus <i>Madeophylax</i> , <i>M. altus</i> Species Group)	North Carolina, USA	Larvae found in cracks and crevices along a vertical, hygropetric, granitic rock surface or under large ice sheets. Subsequent observations describe this species' habitat as >1500 m in elevation, with dense tree cover, on large exposed rock faces of preCambrian silty metamorphosed sandstones and shale with some granitic intrusions. Habitat is wet or moist most of the year because of humidity and elevation.	Based on larval and pupal sizes, this species was assumed to be univoltine. However, subsequent studies suggested that this species' life history was similar to that of <i>M. butleri</i> . Pupae overwinter.	Huryn and Wallace 1984, Schuster 1997

TABLE 1. Continued.

Species (Subgenus, Species Group)	Known locations	Larval habitat	Life-history notes	Reference(s)
<i>M. butleri</i> (Subgenus <i>Madeophylax</i> , <i>M. altus</i> Species Group)	Kentucky and West Virginia, USA	Larval populations found in 3 distinct habitats at elevations <1500 m: 1) rock walls directly adjacent to stream channels; 2) rock walls that have been eroded to form cave-like depressions, which typically have waterfalls associated with them; and 3) rock walls that are in dense vegetation, but not closely associated with surface water. Gut analysis found diatoms and blue-green algae as the primary food source.	Adults emerge mid-March to early April, when the sandstone walls are moist from seasonal rains and snow melt. The adults are poor fliers and remain almost exclusively on the walls from which they emerged. Mating takes place on the walls, and females deposit their eggs in clear masses in wetter areas, often within small depressions. Eggs hatch in 3–4 wk. As the walls begin to dry, larvae go into periods of quiescence. Larvae remain inactive until the walls become wet again and remain wet for a period of time. Larvae go in and out of quiescence depending on environmental conditions. Larvae grow slowly and take 2–3 y to complete their life cycle. Pupae overwinter.	Schuster 1997
<i>M. futabae</i> (Subgenus <i>Madeophylax</i> , <i>M. futabae</i> Species Group)	Tadachi-no-taki waterfall, Nagano, Japan	Larvae found on the vertical sides of large rocks (10–30 m from mountain streams) or on a vertical rocky outcrop. These sites were not connected to stream flows and were assumed to be moistened only by precipitation and often were covered with mosses and lichens.	Based on slow larval growth rates, this species appears to require >3 y to complete its life cycle. During winter or dry months, these larvae seal the front opening with a silken membrane.	Nishimoto 1997
<i>M. omogoensis</i> (Subgenus <i>Madeophylax</i> , <i>M. futabae</i> Species Group)	Omogo-mura, Ehime Prefecture, Japan	Larvae were found on nearly dry, vertical rocky outcrops in woodland areas.	No information reported	Nishimoto 1997
<i>M. kyushuensis</i> (Subgenus <i>Madeophylax</i> , <i>M. futabae</i> Species Group)	Mt. Hikosan, Japan	Larvae found on the vertical sides of large rocks in a wooded area of Mt. Hikosan. In May, inactive larvae were found on dry rock and were withdrawn into their cases; however, active, early instar larvae were observed in a nearby seepage area.	Pupal cases containing pupae and prepupae were collected from the dry rock face. Adults emerged from the pupae within a month. These observations might indicate that this species requires >1 y to complete the life cycle, and pupation occurs a few weeks before adult emergence.	Nishimoto 2002

TABLE 2. Physical and chemical properties of water in Nugget Creek Waterfall, above Mendenhall Lake, Juneau, Alaska. DO = dissolved O₂. – = no data.

Variable	28 June 2004	26 July 2004
Temp (°C)	11.5	–
DO (mg/L)	9.31	–
Conductivity (µmhos/cm)	35.6	–
Total organic C (mg/L)	1.80	2.07
Soluble reactive P (µg/L)	3.30	4.60
Total N (mg/L)	0.100	0.955
Fl (µg/L)	–	81.4
Cl (µg/L)	806	271
NO ₃ (µg/L)	776	964

Clemson University, Clemson, South Carolina, USA (CUAC); and University of Alaska Museum of the North, University of Alaska, Fairbanks, Alaska, USA (UAMN).

Manophylax alascensis Chuluunbat and Morse, n. sp.

(Figs 1–15)

Diagnosis.—Based on a comparison with Wiggins' (1973; figs 13a–e) description and illustrations, the male of *M. alascensis* is most similar to that of *M. annulatus*, but can be distinguished by characters of the wing venation and genitalia as follows:

1. Forewing Cu2 is fused apically with Cu1 from near the wing base in *M. alascensis* (Fig. 3A), but Cu2 is fused apically with A1+A2+A3 from near the middle of the wing in *M. annulatus*.
2. The forewing has a very long posterior spurious vein (SV) separated from A1+A2+A3 by a unique, dorsally recurved fold (dashed line) in *M. alascensis* (Fig. 3A), but this spurious vein and fold are absent in *M. annulatus*.
3. Segment IX is short dorsally (Fig. 1C) and longer laterally, with its posterolateral margin straight below the subdorsal angle (Fig. 1A) in *M. alascensis*, but it is longer dorsally and shorter laterally, with its posterolateral margin concave below the subdorsal angle in *M. annulatus*.
4. The phallobase is short and only slightly curved and a midventral membranous endothelial lobe is present in *M. alascensis* (Fig. 1E), but the phallobase is long and curved nearly 90° and without an endothelial lobe in *M. annulatus*.

The female is most similar to that of *M. annulatus* (Wiggins 1973; figs 14a, b), but can be distinguished by characters of the genitalia:

1. The anterolateral portion of tergite VIII projects ventrolaterad in *M. alascensis* (Fig. 2A), but is smoothly rounded in *M. annulatus*.

2. Sternum VIII is more deeply emarginated posteriorly in *M. alascensis* (Fig. 2C) than in *M. annulatus*.
3. The ventromesal sclerite of segment IX forms an anterior lobe that is irregularly rounded anteriorly and much broader than long in *M. alascensis* (Fig. 2C), but forms a triangular lobe anteriorly that is as long as its basal width in *M. annulatus*.
4. The supragenital plate is convex apicomeresally in *M. alascensis* (Fig. 2C), but it is concave apicomeresally in *M. annulatus*.

The larva of *M. alascensis* most closely resembles that of *M. annulatus* (Wiggins 1973; figs 16a–e, 17, 18, 19a, b). Larvae of *M. alascensis* and *M. annulatus* can be separated by the following characters:

1. The gills are shorter, a pair of posterior subdorsal gills occurs on each of abdominal segments I and II, sublateral gills are absent, and a pair of posterior subventral gills occurs on each of abdominal segments II and III in *M. alascensis* (Fig. 4A); but gills are longer, a pair of posterior subdorsal gills occurs on each of abdominal segments I–III, a pair of anterior sublateral gills occurs on each of abdominal segments II and III, and a pair of posterior subventral gills occurs on each of abdominal segments II–VI in *M. annulatus*.
2. The basal part of the mandible is twice as long as the apical part in *M. alascensis* (Fig. 9), but 4 times as long in *M. annulatus*.
3. The prosternal horn of *M. alascensis* is shorter (Fig. 4A) than that of *M. annulatus*.
4. The ringlike sclerite on abdominal sternum I is oval and variously biforous (appearing to have 2 openings), confluent (with the membranous opening in the middle doubled; Fig. 12), or oval in *M. alascensis*, but it is oval with an oval membranous opening in *M. annulatus* according to Wiggins' description and drawing (fig. 16c) and no other variants are mentioned.

Adult.—Length (from front of head to tips of folded wings) of male 7.8 mm ($n = 7$), female 7.2 mm ($n = 1$). Head and appendages dark brown with dark brown setae; antennae thick, about as long as body, with dark brown basal annulations; maxillary palps each 3-segmented in males, 5-segmented in females. Thorax chestnut brown; pronotum light brown with 2 pairs of setal warts, and with long dark brown setae; mesonotum and metanotum dark brown; legs pale brown; tibial spurs short, light brown, 1-2-3 on each fore-, mid-, and hind tibia, respectively. Abdomen medium brown. Male forewings each about 6.5 mm long, narrow, brownish, without markings; forks 1, 2,

TABLE 3. Synapomorphies of monophyletic taxa/clades of species in the genus *Manophylax*. Character numbers correspond with those in the text, Fig. 16, and Table 4.

Character no.	Taxon/Clade	Outgroup	Synapomorphy	Illustration(s) of synapomorphy	Plesiomorphy	Illustration(s) of plesiomorphy
1	<i>Manophylax</i>	<i>Allomyia</i>	Hind wing Fork 1 absent	Fig. 3B, "R2+3"	Hind wing Fork 1 present	Nishimoto and Kuhara 2001, fig. 1C, "R2 and R3"
2	<i>Manophylax</i>	<i>Allomyia</i>	Female supragenital plate width 2× length	Fig. 2C, "spg.pl"	Female supragenital plate width 1× length	Nishimoto and Kuhara 2001, fig. 2F, "spg.pl"
3	<i>M. annulatus</i> Species Group	<i>M. futabae</i> Species Group	Internal branches of male segment X upturned	Fig. 1A, "tergum X"	Internal branches of male segment X straight	Nishimoto 1997, figs 3C, 13A and C, "int.br"
4	<i>M. annulatus</i> Species Group	<i>M. futabae</i> Species Group	Inferior branches of male segment X weakly sclerotized	Fig. 1C, "inf.br., seg.X"	Inferior branches of male segment X heavily sclerotized	Nishimoto 1997, fig. 3A, "inf.br"
5	<i>M. altus</i> and <i>M. futabae</i> Species Groups	<i>M. annulatus</i> Species Group	Male harpagones each bifid	Schuster 1997, fig. 3a, b; Nishimoto 1997, figs 3A, B, 13A, B, "te.inf"	Male harpagones each undivided	Fig. 1B, "terminal seg."
6	<i>M. altus</i> Species Group	<i>M. futabae</i> Species Group	Internal branches of male segment X widely separated	Schuster 1997, figs 3a, 4a	Internal branches of male segment X narrowly separated	Fig. 1A, C
7	<i>M. altus</i> Species Group	<i>M. futabae</i> Species Group	Male phallobase processes divergent	Schuster 1997, figs 6, 7	Male phallobase processes parallel	Fig. 1D, "apicodorsal arm"
8	<i>M. futabae</i> Species Group	<i>M. altus</i> and <i>M. annulatus</i> Species Groups	Male preanal appendages inconspicuous	Nishimoto 1997, figs 3A, 13A, "pr.app"	Male preanal appendages conspicuous	Fig. 1A, C, "pr.app"
9	<i>M. futabae</i> Species Group	<i>M. altus</i> and <i>M. annulatus</i> Species Groups	Inferior branches of male segment X forked	Nishimoto 1997, figs 3A, 13A, "inf.br"	Inferior branches of male segment X undivided	Fig. 1A, C, "inf.br., seg.X"
10	<i>M. kyushuensis</i> and <i>M. omogoensis</i>	<i>M. futabae</i>	Male forewing vein A1+A2+A3 swollen	Nishimoto 1997, fig. 12A; Nishimoto 2002, fig. 2A	Male forewing vein A1+A2+A3 not swollen	Nishimoto 1997, fig. 2A
11	<i>M. kyushuensis</i> and <i>M. omogoensis</i>	<i>M. futabae</i>	Male and female hind wing vein Cu with stout hairs	Nishimoto 1997, fig. 12B; Nishimoto 2002, fig. 3	Male and female hind wing vein Cu without stout hairs	Nishimoto 1997, fig. 2B

TABLE 4. Taxon-by-character matrix of *Manophylax* species. Character numbers correspond with those in the text, Fig. 16, and Table 3. 1 = apomorphic character, 0 = plesiomorphic character.

Taxa	Characters										
	1	2	3	4	5	6	7	8	9	10	11
<i>Allomyia</i> spp.	0	0	0	0	0	0	0	0	0	0	0
<i>M. alascensis</i>	1	1	1	1	0	0	0	0	0	0	0
<i>M. annulatus</i>	1	1	1	1	0	0	0	0	0	0	0
<i>M. altus</i>	1	1	0	0	1	1	1	0	0	0	0
<i>M. butleri</i>	1	1	0	0	1	1	1	0	0	0	0
<i>M. futabae</i>	1	1	0	0	1	0	0	1	1	0	0
<i>M. kyushuensis</i>	1	1	0	0	1	0	0	1	1	1	1
<i>M. omogoensis</i>	1	1	0	0	1	0	0	1	1	1	1

3, and 5 present; Cu2 fused with Cu1 at 1/6th length; A1 and A2 connected by long crossvein and looped and fused at 1/6th length; A3 independent of A1+A2 from base to arculus (Fig. 3A), separated from each other by longitudinal fold, with posterior edge of wing and A3 recurved dorsally over A1+A2; several short thick setae in fold near basal end. Hind wings light brown, each with 4 frenular hairs at base; forks 2, 3, and 5 present (Fig. 3B), although fork 5 sometimes absent. Male with row of stout hairs between bases of Cu1 and Cu2 and with scalelike setae between A2 and A3, as illustrated by Nishimoto (2002; figs 3, 4) for *M. kyushuensis*.

Male genitalia (Fig. 1).—Segment IX annular, dorsally short and forming narrow transverse strip; anterolateral margins sinuous; posterolateral margins with prominent subdorsal angle on each side and straight margin below it. Inferior appendages each 2-segmented, each concave mesally and convex laterally in ventral view; basal segment (coxopodite) about 1.65 times longer than tergum X and extending slightly beyond it in lateral view, gradually thickening from base to ~2/3rds length, then tapering slightly to upturned apex; distal segment (harpago) setose, 1/3 as long as basal segment, cupped mesad, with spinelike setae in cup and with stout spine apically. Tergum X membranous mesally, bounded laterally by pair of long sclerotized plates (internal branches of segment X; Nishimoto 1997, 2002), each bearing 4 lateral tufts of setae and ending in upturned hook; pair of weakly sclerotized inferior branches of tergum X clavate. Preanal appendages short, earlike. Phallus with short, slightly bent, tubular phallobase bearing pair of long apicodorsal arms (“parameres?,” Wiggins 1973; “parameres,” Nishimoto 2002) sinuous in dorsal view; endothelial membrane with midventral extension; phallicata with depressed distal 2/3rds broader than compressed basal 1/3 and more or less parallel-sided with apex truncate in dorsal view, proximal 1/3rd taller than distal 2/3rds and upturned to blunt apex in lateral view.

Female genitalia (Fig. 2).—Anterolateral portion of tergite VIII projected ventrolaterad (Fig. 2A); sternum VIII deeply emarginated posteromesally and separated from venter IX by membrane (Fig. 2C). Venter IX well developed and with many setae, separated from dorsum IX by membranous areas and meeting ventromesal sclerite ventrally along darkened lines of fusion (Figs 2A, C); this ventromesal sclerite irregularly rounded anteriorly and forming lobe much broader than long, posteriorly with tongue-like lobe striated and strongly curled dorsad and with its posterolateral angles each extended into bluntly rounded lobes. Supragenital plate twice as wide as long, posterior margin convex in ventral view (Fig. 2C). Segment X fused with dorsum IX (Fig. 2A) and extended posterad into 2 elongate flaps separated by V-shaped median notch about half as deep as fused segments (Fig. 2B, C).

Larva (Figs 4–13).—Length 3.5–7.8 mm ($n = 42$). Sclerites of head and thorax brown to dark brown. Head nearly globular; setae 14 and 15 on larval head close to each other (Fig. 6A), as in *M. annulatus*. Labrum with anterior margin membranous, 2 pairs of clear setae anteromesally (Fig. 8), as in *M. annulatus*. Mandibles without teeth, each with lower mesal margin broader than upper mesal margin, with row of long hairs on basal part; basal part separated from apical part by small notch; upper mesal margin of apical part only slightly shorter than basal part; lateral margin of apical part 1/2 as long as basal part (Fig. 9). Labium without mesal submental sclerites or median sclerite (Fig. 7). Ventral apotome subtriangular, longer than broad (Figs 6B, 7). Prosternal horn shorter than that of *M. annulatus*. Pronotum with dense row of short, fine setae on anterior margin, longer and thicker submarginal setae anteriorly, laterally, and posteriorly (Fig. 10). Mesonotal plates well developed (Fig. 10). Metanotal *sa1*, *sa2*, and *sa3* sclerites well developed, *sa1* sclerites each bearing 3–5 setae (Fig. 10). Legs with basal seta

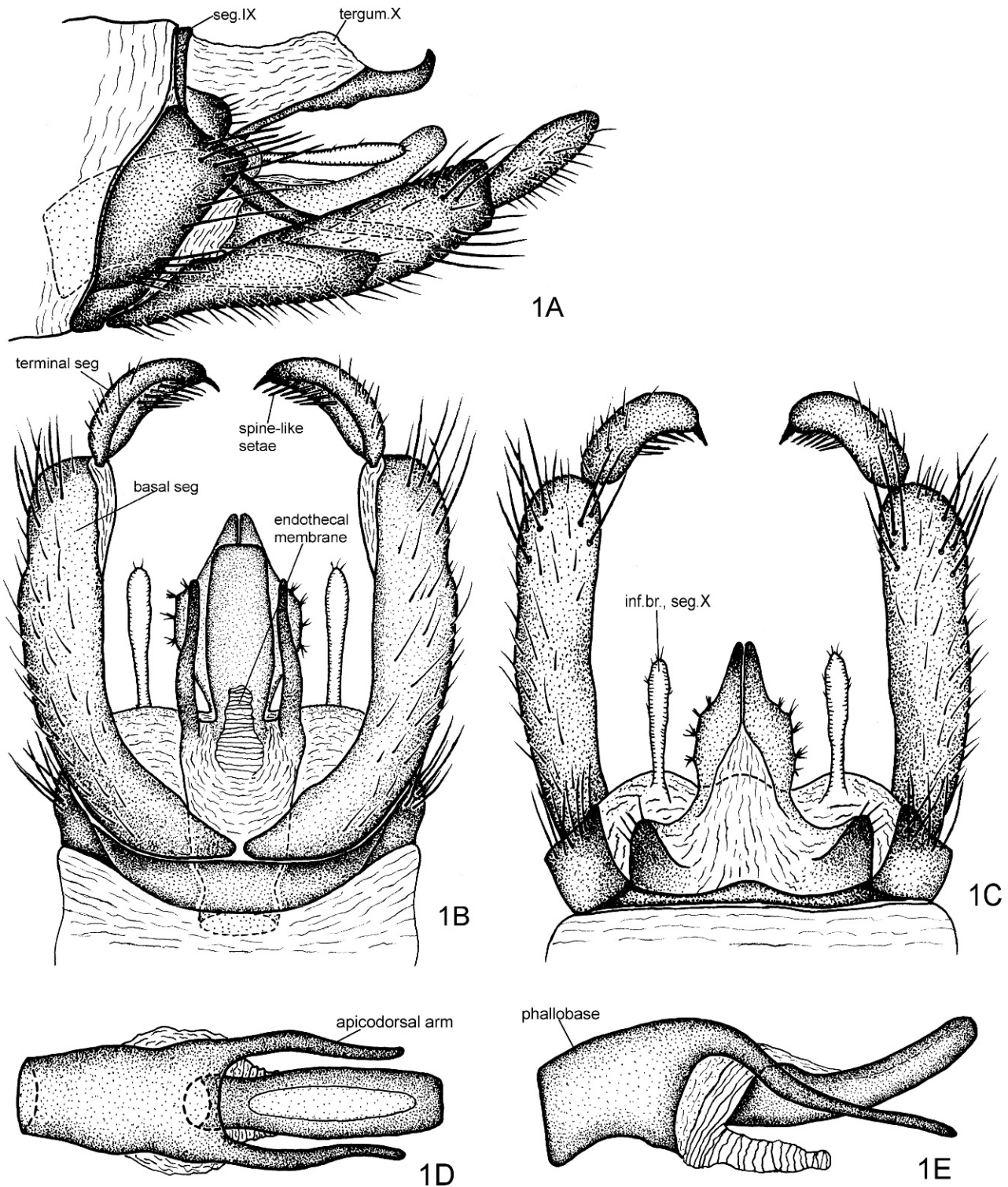


FIG. 1. Male genitalia of *Manophylax alascensis* n. sp. A.—Left lateral. B.—Ventral. C.—Dorsal. D.—Phallus, dorsal. E.—Phallus, left lateral. basal seg = basal segment of left inferior appendage; inf.br.,seg.X = right inferior branch of segment X; pr.app = left preanal appendage; seg.IX = abdominal segment IX; terminal seg = harpago or terminal segment of left inferior appendage.

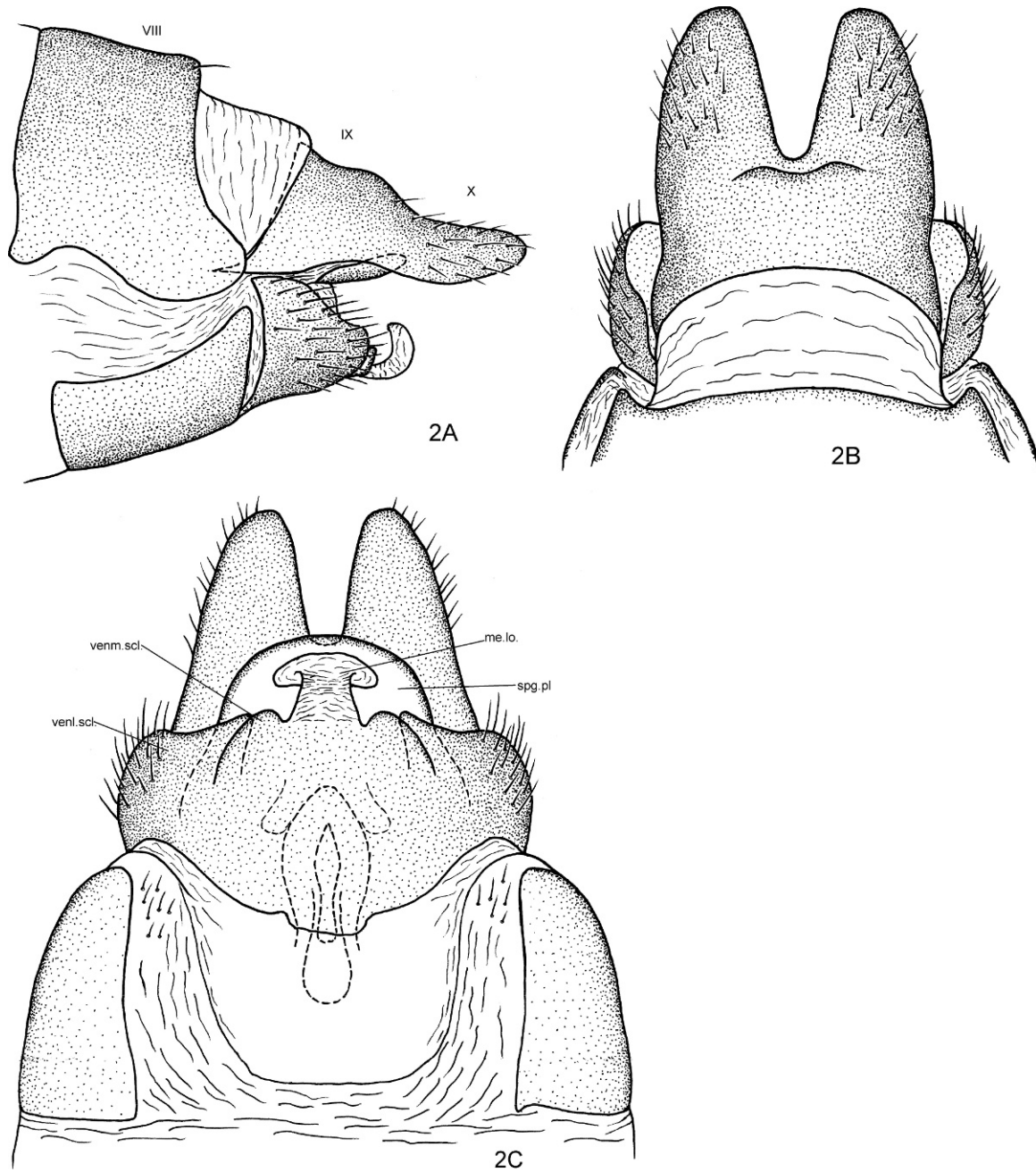


FIG. 2. Female genitalia of *Manophylax alascensis* n. sp. A.—Left lateral. B.—Dorsal. C.—Ventral. IX = abdominal segment IX, me.lo. = median lobe, spg.pl. = supragenital plate, venl.scl. = ventrolateral sclerite, venm.scl. = ventromesal sclerite, VIII = abdominal segment VIII, X = abdominal segment X.

of each claw nearly as long as claw (Fig. 4B). Forelegs shorter than middle and hind legs, fore-femur shorter but about as broad as middle and hind femora (Fig. 11). Abdomen with short single gills: pair of posterior subdorsal gills on each of abdominal segments I and II and pair of posterior subventral gills on each of abdominal segments II and III; lateral fringe on each side of abdominal

segments IV through VIII (Fig. 4A). Abdominal sternum I with anteromedian oval sclerite with central unsclerotized area biforous, confluent (Fig. 12), or oval. Chloride epithelia present ventrally on abdominal segments III–VII. Dorsal sclerite of abdominal segment IX about 2.5 times as wide as long, with 10–12 setae (Fig. 13). Anal claws each with well-developed accessory tooth.

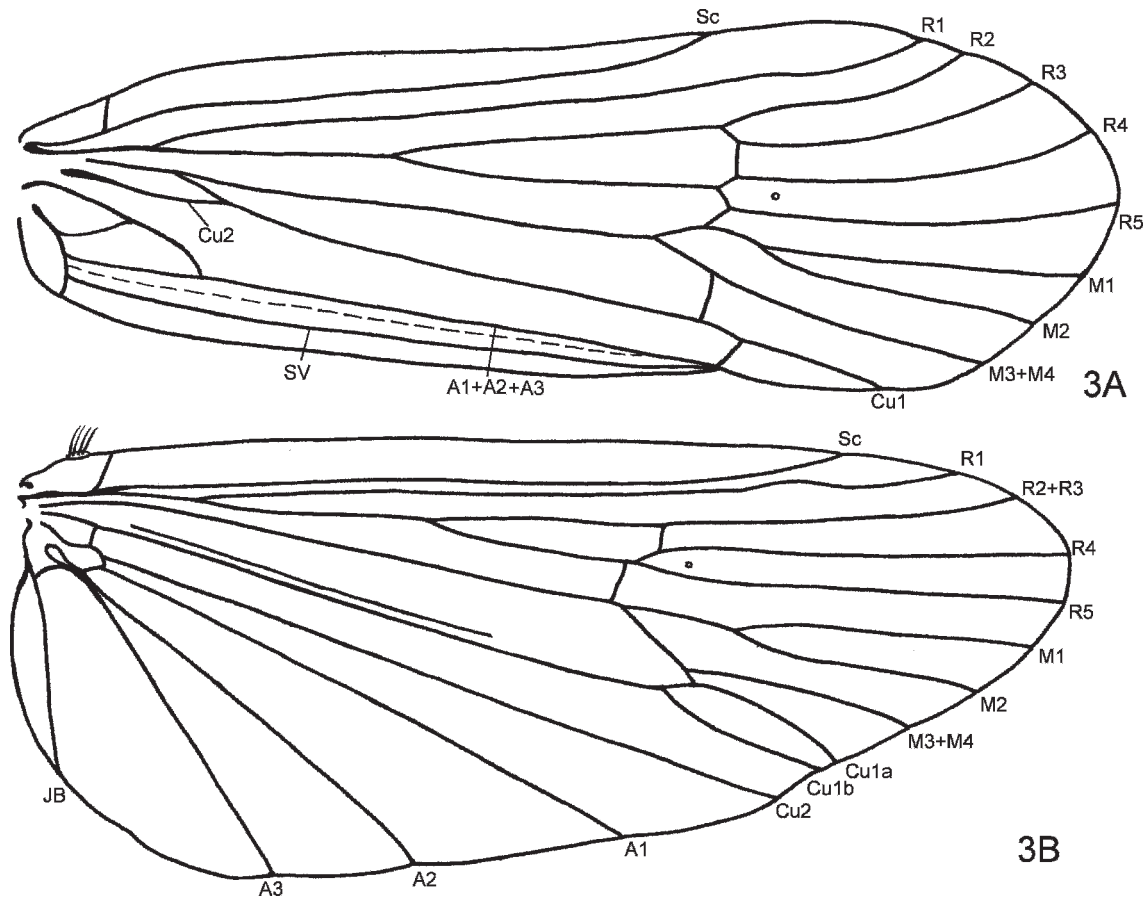


FIG. 3. Male right forewing and hind wing of *Manophylax alascensis* n. sp., dorsal. A.—Forewing. B.—Hind wing. A1, A2, A3, A1+A2+A3 = anal veins 1, 2, and 3, and these veins combined, respectively; Cu1a, Cu1b, Cu2 = cubital veins 1 anterior, 1 posterior, and 2, respectively; JB = jugal bar; M1, M2, M3+M4 = median veins 1, 2, and 3 and 4 combined, respectively; R1, R2, R3, R4, R5, R2+R3 = radial veins 1, 2, 3, 4, and 5, and radial veins 2 and 3 combined, respectively; Sc = subcostal vein; SV = spurious vein.

Larval case (Fig. 5).—Length 4.0–9.8 mm ($n = 38$). Similar to that of *M. annulatus*, constructed of fine rock fragments, tapered posteriorly and slightly convex ventrally, with attached moss and algal fragments dorsolaterally.

Pupa (Figs 14, 15).—Length 6.75 mm ($n = 2$). Similar to that of *M. annulatus*, distinguished by fewer gills and more setae on base of labrum. Heavily sclerotized mandibles pointed apically and each with mesal cutting edge having regularly arranged serrations (Fig. 14); labrum with 5 pairs of stout setae all apically hooked, 3 pairs of setae posteriorly near base of labrum (2 pairs in *M. annulatus*) and 2 pairs arising more apically (Fig. 14); abdomen dorsally with 7 pairs of sclerotized hook-bearing plates anteriorly on segments III–VII and posteriorly on segments I and V (Figs 15A, B); short pair of gills present dorsolaterally near posterior margin of segment II (Fig. 15A, on

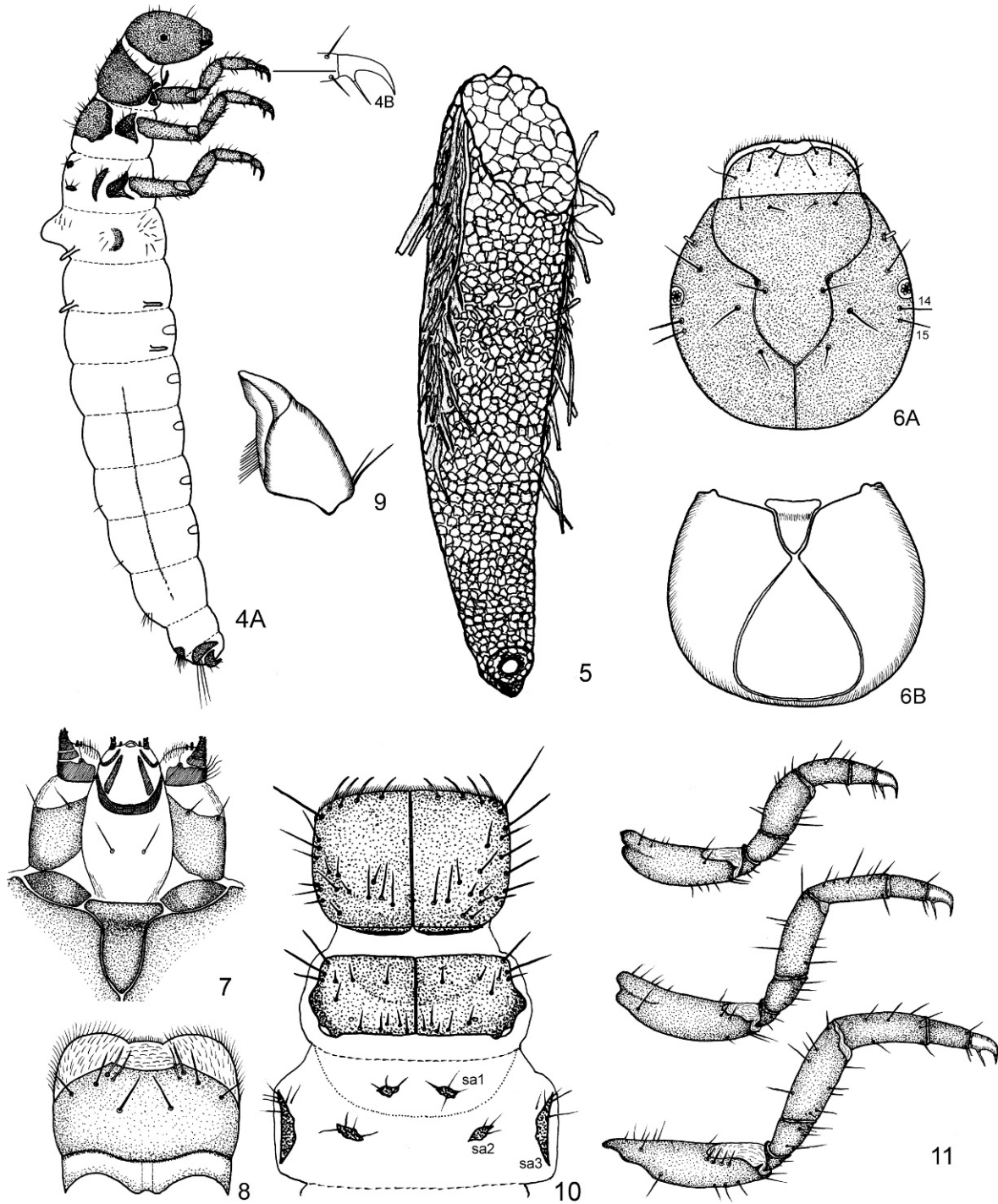
segments II and III in *M. annulatus*); lateral fringe present on segments V–VIII (Fig. 15A); anal processes long, stout, somewhat sclerotized, with strong apical hook having 3 long setae arising from mesal margin (Fig. 15C).

Pupal case.—Length 10.5 mm ($n = 8$). Resembling larval case, both ends closed with silk.

Holotype.—Male; USA: Alaska, Juneau, Nugget Creek Waterfall, above Mendenhall Lake, 22 July 2002, M. Wesener, J. Lessard, and E. Benbow (NMNH).

Paratypes.—2 males, same data as holotype (UAMN); 4 males, 1 female, same locality as holotype 22 Aug 2008, J. Hudson (2 males, 1 female NMNH; 2 males CUAC).

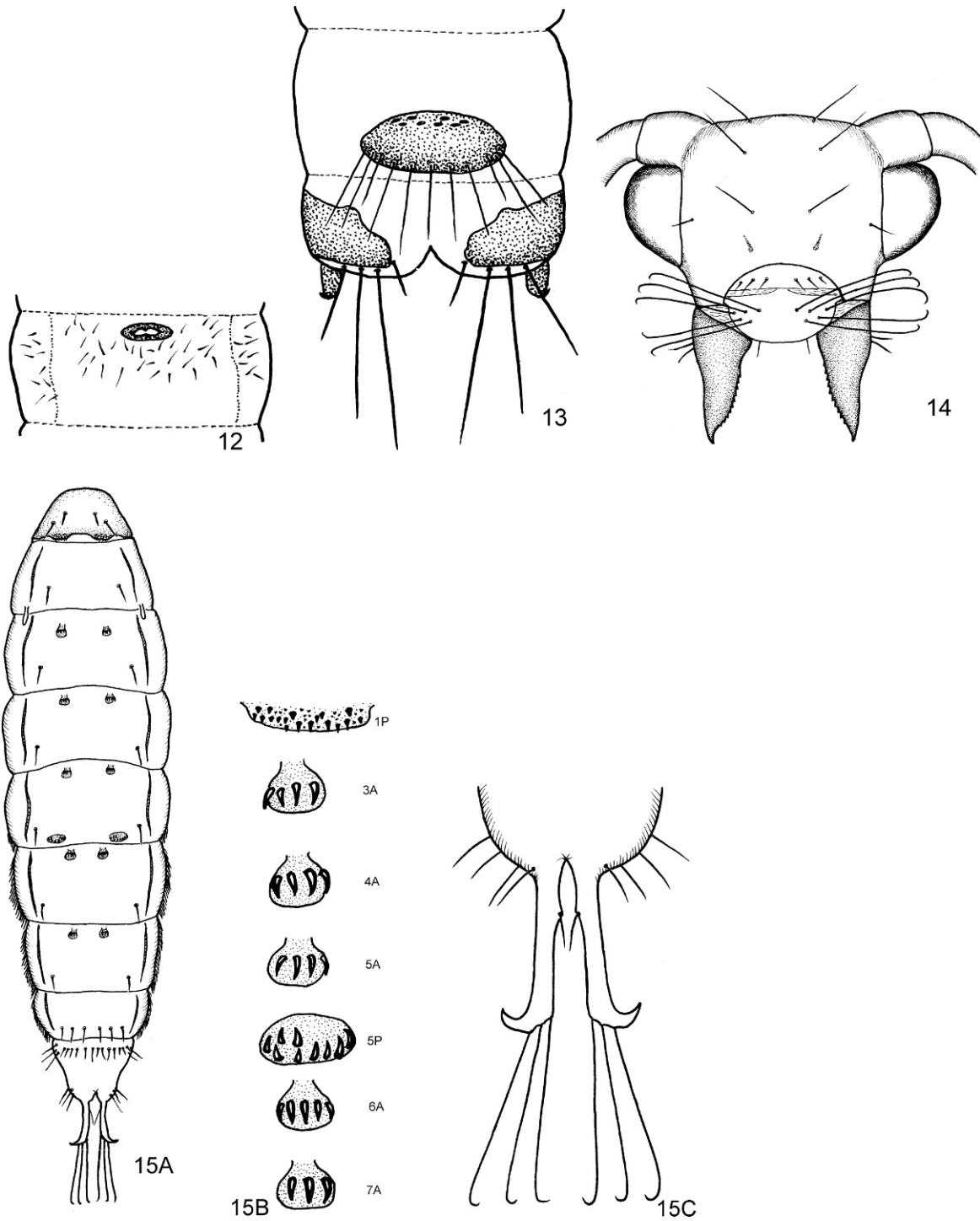
Larval and pupal material.—Same locality as type series, 3 larvae, 1 pupa, 11 July 2004 (NMNH); 4 larvae, 22 July 2002 (UAMN); 4 larvae, 26 July 2004



FIGS 4-11. Larva of *Manophylax alascensis* n. sp. 4A.—Larva, right lateral. 4B.—Enlarged right foretarsal claw, lateral/posterior; 5.—Larval case, ventrolateral. 6A.—Larval head, dorsal. 6B.—Head capsule and ventral apotome. 7.—Maxillae and labium of larva, ventral. 8.—Labrum, dorsal. 9.—Right mandible, dorsal. 10.—Thorax, dorsal. 11.—Right thoracic legs, lateral/posterior. 14, 15 = right head setae numbers 14 and 15, respectively; sa1, sa2, and sa3 = right setal areas 1, 2, and 3, respectively.

(CUAC); 4 larvae, 9 August 2004 (CUAC); 11 larvae, 22 August 2008 (NMNH); 9 larvae, 26 August 2004 (NMNH); 7 larvae, 1 pupa, 27 August 2008 (CUAC).

Etymology.—The name given to this species refers to the type locality.
Biology.—The species is currently known from only one area (hygropetric habitats adjacent to Mendenhall



FIGS 12-15. Larva and pupa of *Manophylax alascensis* n. sp. 12.—Larval first abdominal segment, ventral. 13.—Larval abdominal segments IX, X, and anal prolegs, dorsal. 14.—Pupal head, facial view. 15A.—Pupal abdomen, dorsal view. 15B.—Pupal hook plates enlarged, dorsal view. 15C.—Pupal anal processes, dorsal view. 3A, 4A, 5A, 6A, and 7A = right anterior hookplates on abdominal terga III, IV, V, VI, and VII, respectively; 1P and 5P = right posterior hook plates on abdominal terga I and V, respectively.

Glacier and similar habitats in a smaller nearby stream), near sea level, with relatively consistent discharge and humidity (i.e., no or very short periods of drying). Larvae and pupae of *M. alascensis* were

usually found in these hygropetric situations, with a thin film of water moving over most of them, or in moist cracks in the rock, with larvae occasionally wandering onto dry rock surfaces, but soon returning

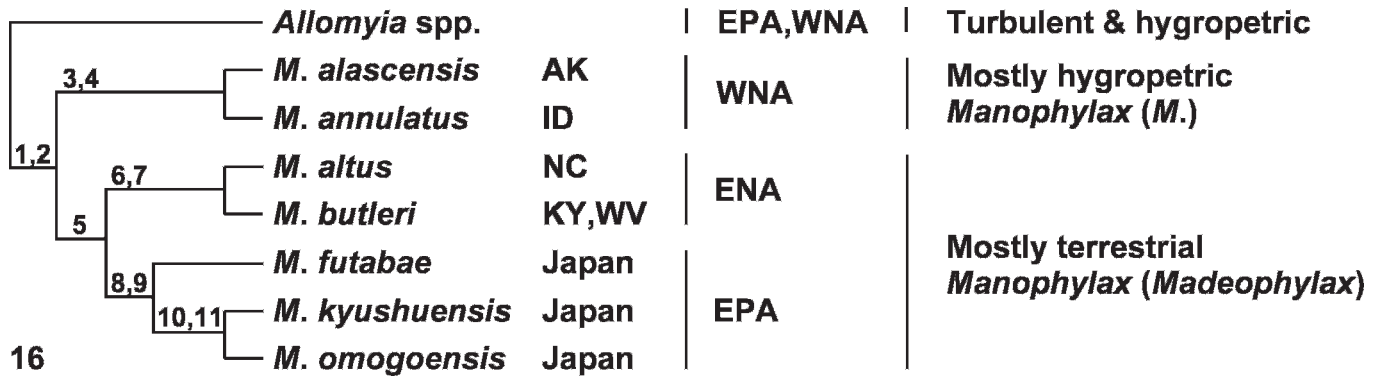


FIG. 16. Phylogeny of world *Manophylax* species, their political and biogeographic region distributions, and habitats and *Manophylax* subgenera. Numbers above the nodes in the phylogeny refer to synapomorphies discussed in the text and in Tables 3 and 4. AK = Alaska, ENA = eastern Nearctic Region, EPA = eastern Palearctic Region, ID = Idaho, KY = Kentucky, M. = *Manophylax*, NC = North Carolina, WNA = western Nearctic Region, WV = West Virginia.

to moist or hygropetric habitat. Some larvae in closed cases were on the fringe within ~10 cm of the wetted habitat, often in small crevices. Adults were captured from the drier portions of rock where they were fairly motionless; most of them were infested with red mites.

Larvae of this species feed on the periphyton community attached to the wet surface of the waterfall wall. Stomach contents of 4th- and 5th- instar larvae included algae, fungal hyphae and sporangia, and particulate organic matter embedded with fine sand grains (P. L. Hudson, US Geological Survey Great Lakes Science Center, Ann Arbor, Michigan, personal communication).

Mature larvae and pupae were observed from 11 July through 27 August, and adults were observed from 22 July through 22 August, suggesting overlapping generations and the probability that >1 y is required to complete development.

Phylogeny (Fig. 16).—Monophyly of species in the genus *Manophylax* is inferred from the following 2 synapomorphies (Tables 3, 4): 1) Hind wing fork I usually absent (Nishimoto 2002 reported an exceptional specimen of *M. kyushuensis*) and 2) female subgenital plate about twice as wide as long (Wiggins 1973). Within the genus, *M. annulatus* and *M. alascensis* are probably sister species, constituting the *M. annulatus* Species Group, as indicated by their 3) apically upturned internal branches of segment X and 4) weakly sclerotized inferior branches of segment X in the male genitalia. Monophyly of the other 5 species is supported by 5) the bifid apex of each harpago in the male genitalia. Two synapomorphies support a sister-group relationship for *M. altus* and *M. butleri*, comprising the *M. altus* Species Group: 6) the widely separated internal branches of segment X and

7) the divergent processes of the phallobase (“parameres,” Nishimoto 1997, 2002) of the males. Monophyly of *M. futabae*, *M. kyushuensis*, and *M. omogoensis*, which constitute the *M. futabae* Species Group, is supported by 8) the inconspicuous preanal appendages and 9) the forked inferior branches of segment X of the males. Within this Species Group, a sister-group relationship of *M. kyushuensis* and *M. omogoensis* is indicated by 10) the swelling on each male forewing A1+A2+A3 vein and 11) presence of stout hairs on the Cu vein of each hind wing in both sexes (Nishimoto 2002).

Historical biogeography.—The known species of *Manophylax* inhabit the Nearctic and eastern Palearctic Biogeographic Regions, with the species of the *M. annulatus* Species Group in northwestern North America (WNA; Alaska and Idaho), those of the *M. altus* Species Group in eastern North America (ENA; Kentucky, North Carolina, West Virginia), and species of the *M. futabae* Species Group in the eastern Palearctic (EPA; Japan). An area cladogram based on the phylogeny for these groups (Fig. 16), suggests a biological relationship between the eastern Nearctic and eastern Palearctic Biogeographic Regions that is more recent than a relationship with the western Nearctic Biogeographic Region, showing a pattern of (WNA[ENA+EPA]). This well-known pattern was most famously documented in detail for plants by Gray (1856, p. 216):

“Thus it appears . . . that, of our 19 extra-European orders not peculiarly American, only 3 or 4 are represented on the western or Pacific side of the United States, while all but one are represented in the corresponding parts of Eastern Asia;—indicating a curious analogy in the vegetation of the eastern sides of the two great continents in the northern

hemisphere, which is also borne out, though not so strikingly, in a comparison of the genera.”

This so-called “Asa Gray disjunction” (Krutzsch 1989) is currently recognized not only for many plant genera peculiar to the 2 widely separated areas, but also, for example, for fungi (Hongo and Yokoyama 1978, Wu and Mueller 1997), arachnids (Suzuki et al. 1977), millipedes (Enghoff 1993), ibaliid wasps (Nordlander et al. 1996), and freshwater fishes (Patterson 1981).

In a recent review of the plant data, Wen (1999, Abstract) concluded:

“Phylogenetic, molecular, geologic, and fossil data all support the hypothesis that the eastern Asian and eastern North American disjunct distributions are relicts of the maximum development of temperate forests in the northern hemisphere during the Tertiary. Fossil and geologic evidence supports multiple origins of this pattern in the Tertiary, with both North Atlantic and the Bering land bridges involved.”

This (WNA[ENA+EPA]) pattern was found by Hamilton and Morse (1990) in several other caddisfly taxa, including analyzed species groups in the genera *Ceraclea* and *Mystacides* (Leptoceridae), *Dolophilodes* and *Wormaldia* (Philopotamidae), *Glossosoma* (Glossosomatidae), and *Rhyacophila* (Rhyacophilidae), and by Ross (1956) in the genera *Wormaldia* and *Chimarra* (Philopotamidae). Examples of a contradictory pattern (ENA[WNA+EPA]) have been observed by Wiggins (2002) in the caddisfly subfamily Dicosmoecinae (Limnephilidae) and by Ross (1956) in caddisfly genera *Dolophilodes* and *Wormaldia* (Philopotamidae), *Glossosoma* (Glossosomatidae), and *Himalopsyche* and *Rhyacophila* (Rhyacophilidae). Ross (1956, 1967) discussed the timing and possible causes of dispersals across Beringia. His discussion suggested that many cold-adapted caddisflies associated with the Holarctic temperate deciduous forest, which would include *Manophylax* species, dispersed over the Beringian land bridge during the cooler Oligocene–Miocene Epochs (38–12 million y before present [ybp]) and their ranges probably fragmented during the even-colder Pliocene–Pleistocene Epochs (12 million–10,000 ybp) in response to climate changes and their geological consequences, including glaciations and opening of the Bering Strait ~3 million ybp. Wiggins and Parker (1997) discussed an ice-free corridor in the Pleistocene between the eastern Laurentide Glacier and the western Cordilleran Glacier during periods of interglacial recession that might have afforded suitable habitat for dispersals from northern Alaska to eastern

North America. Additional discussion about possible causes for these biogeographic patterns, including the effects of climate changes and orogenetic activity in the affected regions, can be found in the work by Manchester (1999).

Evolution of terrestrial habitat.—Larvae and pupae of the different species of *Manophylax* exhibit either mostly hygropetric or mostly terrestrial habits on vertical rock faces (Table 2). Current evidence indicates that the gill-possessing larvae and pupae of species of the *M. annulatus* Species Group almost always live in a thin film of water, whereas those of the *M. altus* and *M. futabae* Species Groups, without gills, persist only in habitats that are usually dry or only moist or occasionally wet and become quiescent or pupate during dry periods. The habitat requirements of the different species otherwise vary with regard to elevation, type of rock, forest cover, etc. Other habitat requirements are poorly known for these species and for most hygropetric biota in general. The phylogeny of these groups (Fig. 16) indicates that the more nearly terrestrial habitat in this genus evolved once with the ancestor of the sister *M. altus* and *M. futabae* Species Groups. Water in the hygropetric habitats inhabited by species of the *M. annulatus* Species Group flows reliably throughout the warmer months of the year from springs and melting glaciers, whereas water inhabited by most species of the *M. altus* and *M. futabae* Species Groups is ephemeral, flowing only after rains or snowmelt. When moisture is insufficient, larvae seal their cases and become quiescent pending the return of moist conditions. The tendency for species of *Manophylax* to be slow-growing and semivoltine, requiring 2 to 3 y to complete development, might be an advantageous preadaptation that readily accommodated these periods of interrupted growth. Species of the apparently closely related genus *Allomyia* live in small, cold, turbulent, mountainous streams and in hygropetric habitats (Wiggins 1996). Thus, the evolutionary pathway toward terrestrial habitats in the genus *Manophylax* apparently proceeded from streams (some *Allomyia* species) through mostly hygropetric habitats (some *Allomyia* species and species of the *M. annulatus* Species Group) to generally terrestrial habitats (species of the *M. altus* and *M. futabae* Species Groups).

Taxonomic conclusions.—The 3 monophyletic groups of *Manophylax* species (Fig. 16) are biologically, geographically, and morphologically distinct. For these reasons, the resurrection of the synonymized genus-group name *Madeophylax* seems particularly justified, at least as a subgenus of *Manophylax*. Therefore, *Madeophylax* Huryn and Wallace, New Status, is redefined as a subgenus that includes the

species of the *Manophylax altus* and *M. futabae* Species Groups, with *M. altus* as its type species.

Keys to the North American species of *Manophylax*

Males

- 1. Terminal segment (harpago) of each inferior appendage conical to quadrate, with 2 spinelike processes (Schuster 1997, figs 3a, b, 4a, b) Subgenus *Madeophylax*, 2
- Terminal segment of each inferior appendage elliptical, with single apical spine (Fig. 1B, C) Subgenus *Manophylax*, 3
- 2. Terminal segment (harpago) of each inferior appendage almost quadrate, with 2 long, stout, heavily sclerotized spines projecting mesad from mesal margin (Huryn and Wallace 1984, figs 2, 3) *M. altus*
- Terminal segment of each inferior appendage conical, with 2 short, sclerotized spines projecting apicad from apex (Schuster 1997, figs 2, 3a, 4a, b) *M. butleri*
- 3. Segment IX composed of dorsal, lateral, and ventral parts, defined by internal carinae (Fig. 1A); phallotheca with ventral tonguelike membranous process (Fig. 1B, D) ... *M. alascensis*
- Segment IX an undifferentiated ring, with dorsal, lateral, and ventral parts not defined by internal carinae (Wiggins 1973, fig. 13a); phallotheca lacking tonguelike membranous process (Wiggins 1973, figs 13d, e) *M. annulatus*

Females

- 1. Tergite X lobes apically pointed, triangular in dorsal or ventral view, with lateral margins sinuous; supragenital plate triangular (Huryn and Wallace 1984, fig. 7; Schuster 1997, fig. 9a) Subgenus *Madeophylax*, 2
- Tergite X lobes apically rounded, subtriangular in dorsal or ventral views, with lateral margins straight to slightly convex (Fig. 2B, C); supragenital plate more or less trapezoidal, apically convex (Fig. 2C) Subgenus *Manophylax*, 3
- 2. Posterior margin of sternum IX forming pair of triangles with deep notch between right and left sides of each (Huryn and Wallace 1984, fig. 7; Schuster 1997, fig. 9b) *M. altus*
- Venter IX forming pair of rounded lobes with shallow notch between right and left sides of each (Schuster 1997, fig. 9a) *M. butleri*
- 3. Supragenital plate margin concave apically; ventromesal sternite IX triangular and deeply extended anterad (Wiggins 1973, fig. 14b) *M. annulatus*

- Supragenital plate margin convex midapically; ventromesal sternite IX irregularly rounded and slightly expanded anteriorly (Fig. 2C) *M. alascensis*

Larvae

- 1. Abdominal gills present, single (Fig. 4A) Subgenus *Manophylax*, 2
- Abdominal gills absent (Schuster 1997, fig. 10) Subgenus *Madeophylax*, 3
- 2. Abdominal segments I-III with short gills (Fig. 4A); lateral base of each mandible twice as long as apical part (Fig. 9); labium without submental sclerite (Fig. 7) *M. alascensis*
- Abdominal segments I-VI with long gills (Wiggins 1996, fig. 12.3A); lateral base of each mandible 4 times as long as apical part (Wiggins 1996, fig. 12.3D); labium with submental sclerite (Wiggins 1973, fig. 24a) *M. annulatus*
- 3. Pebbling on frontoclypeus generally covering entire sclerite (Schuster 1997, fig. 13a); abdominal sternum I with transverse sclerite linear (Schuster 1997, fig. 15a) *M. butleri*
- Pebbling on frontoclypeus restricted to posterior and anterolateral angles of sclerite (Schuster 1997, fig. 13b); abdominal sternum I with transverse sclerite oval (Schuster 1997, fig. 15b) *M. altus*

Pupae

- 1. Abdominal gills present, single (Fig. 15A) Subgenus *Manophylax*, 2
- Abdominal gills absent Subgenus *Madeophylax*, 3
- 2. Abdominal gills present only dorsolaterally on segment II (Fig. 15A); clypeus with 3 setae on each side (Fig. 14) *M. alascensis*
- Abdominal single gills present dorsolaterally on segments II-III and ventrolaterally on segments III-V (Wiggins 1973, fig. 22a); clypeus with 2 setae on each side (Wiggins 1973, fig. 21) *M. annulatus*
- 3. Mandibles each with mesal cutting edge straight and without teeth or evident serrations (Schuster 1997, fig. 20a) *M. butleri*
- Mandibles each with mesal cutting edge convex and finely serrate (Schuster 1997, fig. 20b) *M. altus*

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