PROC. ENTOMOL. SOC. WASH.
107(4), 2005, pp. 835–845

NEW APHIDOIDEA (HEMIPTERA: STERNORRHYNCHA) IN BURMESE AMBER

GEORGE POINAR, JR. AND ALEX E. BROWN

(GP) Department of Zoology, Oregon State University, Corvallis, OR 97331, U.S.A. (e-mail: poinarg@science.oregonstate.edu); (AB) 629 Euclid Avenue, Berkeley, CA 94708, U.S.A. (e-mail: alex.brown3@comcast.net)

Abstract.—Three new aphid taxa (Hemiptera: Sternorrhyncha) are described from Lower Cretaceous amber from Myanmar (Burma). A **new family,** the **Verrucosidae Poinar and Brown,** is described for the **new genus and species *Verrucosa annulata* Poinar and Brown,** which is characterized by 3-segmented antennae, with the third segment composed of 20 annuli, forewing containing only 3 veins radiating from the main vein (Rs, M and distal C), and the forewing membrane covered with scalelike warts. Another **new family,** the **Burmitaphidae Poinar and Brown,** is described for the **new genus and species *Burmitaphis prolatum* Poinar and Brown,** and the **new genus and species *Caulinus burmitis* Poinar and Brown.** This family is characterized by greatly reduced (stublike) hind wings, 7- segmented antennae, and a greatly reduced rostrum and frons with a protruding median tubercle. In *B. prolata,* the forewing has only 3 veins radiating from the main vein and the aedaegus is long and highly sclerotized. In *C. burmitis,* the forewing has 4 veins departing from the main vein and an elongate cauda is present. These new taxa, together with previously described aphids from Mesozoic deposits, show a high degree of morphological diversity in Cretaceous aphids.

Key Words: Verrucosidae n. fam., *Verrucosa* n. gen., *Verrucosa annulata* n. sp., Burmitaphidae n. fam., *Burmitaphis* n. gen., *Burmitaphis prolatum* n. sp., *Caulinus* n. gen., *Caulinus burmitis* n. sp., Burmese amber, Cretaceous

During an investigation of insects in Burmese amber, several unique members of the Aphidoidea were discovered. Since they could not be placed in any extant or extinct genera, they are described below in two new families. Amber from Burma (Myanmar) occurs in lignitic seams in sandstone-limestone deposits in the Hukawng Valley. Palynomorphs obtained from the amber beds where the fossil piece originated have been assigned to the Upper Albian (~ 105–100 mya) (Cruickshank and Ko 2003). Nuclear magnetic resonance (NMR) spectra of amber samples taken from the same locality as the fossils indicated an araucarian (possibly *Agathis*) plant source (Lambert and Wu, personal communication).

MATERIALS AND METHODS

The amber pieces were repolished to better view the specimens. The amber piece containing the holotype of *Verrucosa annulata* (B-He-13A) is roughly rectangular, measures 14 mm long, 8 mm wide and 1 mm deep. The amber piece containing the paratype of *Verrucosa annulata* (B-He-13B) is almost cuboid in outline, measuring 3 mm long, 2 mm wide, and 2 mm deep. The amber piece containing the holotype and paratype of *Burmitaphis prolatum* (B-

He-14A, B) is 6 mm long, 4 mm wide and 2 mm deep. The amber piece containing another paratype of *Burmitaphis prolatum* (B-He-14C) is 7 mm long, 3 mm wide, and 1.5 mm deep. The amber piece containing the holotype of *Caulinus burmitis* (B-He-15) is 7 mm long, 4 mm wide, and 4 mm deep. Observations, drawings, and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot TM compound microscope (with magnifications up to 650×). All measurements are in microns unless otherwise noted.

Verrucosidae Poinar and Brown, new family

Description.—With 3-segmented, extremely thick antennae composed of deep ringlike structures; rostrum very long with extremely long apical segment; proximal branch of cubitus in fore wing greatly reduced (possibly absent); media with one branch; eyes without ocular tubercles (triommatidia); forewing membrane covered with scalelike warts; siphunculi well developed.

Etymology.—"*Verrucosus*" is Latin for "full of warts" in reference to the wing armature.

Diagnosis.—There is no aphid family, extinct or extant, with the above combination of forewing characters. While members of the Adelgidae and Phylloxeridae also have only 3 veins behind the pterostigma reaching or almost reaching the wing margin, these represent the M, distal Cu, and proximal Cu veins (Annand 1928). In the Verrucosidae, the three veins are the Rs, M, and distal Cu, with the proximal Cu vein absent or greatly reduced, possibly represented by a faint, indistinct zone at the base of the forewings.

Type genus.—*Verrucosa,* n. gen.

Verrucosa Poinar and Brown, new genus

This new genus is based on two alate females (B-He-13A; B-He-13B) in separate pieces of Burmese amber. One specimen (B-He-13B) is poorly positioned in cloudy amber and cannot be adequately described, other than to verify the structure of the rostrum, antennae and wing venation. The description is based on the holotype of the new species (B-He-13A), which is well preserved with only the tip of the abdomen somewhat distorted and the right hind leg and middle leg missing.

Description.—With characters listed under family description; antenna 3-segmented, with third segment composed of 20 annuli.

Etymology.—The generic name is taken from the Latin "verrucosus" for "full of warts" in reference to the wing armature. The gender is feminine.

Diagnosis.—There is no extinct or extant aphid genus with the above characters.

Type species.—*Verrucosa annulata,* n. sp.

Verrucosa annulata Poinar and Brown, new species

(Figs. 1–5)

Description.—Characters as listed under family and generic descriptions. Alate viviparous female; brown; dorsum densely covered with short setae; body length 737.

Head: Compound eyes ventrally orientated, composed of 13–15 ommatidia; ocelli not observed; rostrum 4-segmented (broken between second and third segments), narrow, length 887, all segments bearing setae, length stylet bundle 950; antenna 3 segmented, first and second segments subequal, second segment appears subdivided into two or three overlapping portions; third segment composed of 20 closely placed annuli; rhinaria not observed; length antennal segments; 1, 50; 2, 49; 3, 141.

Thorax: Forewing length 867; width 411; membrane transparent but covered with small crescent-shaped warts; warts denser in pterostigma portion of wing; pterostigma 277 long, 111 wide; radial sector departing from subapical part of pterostigma, media departing from proximal edge of pterostigma, with one fork, stem 418, an-

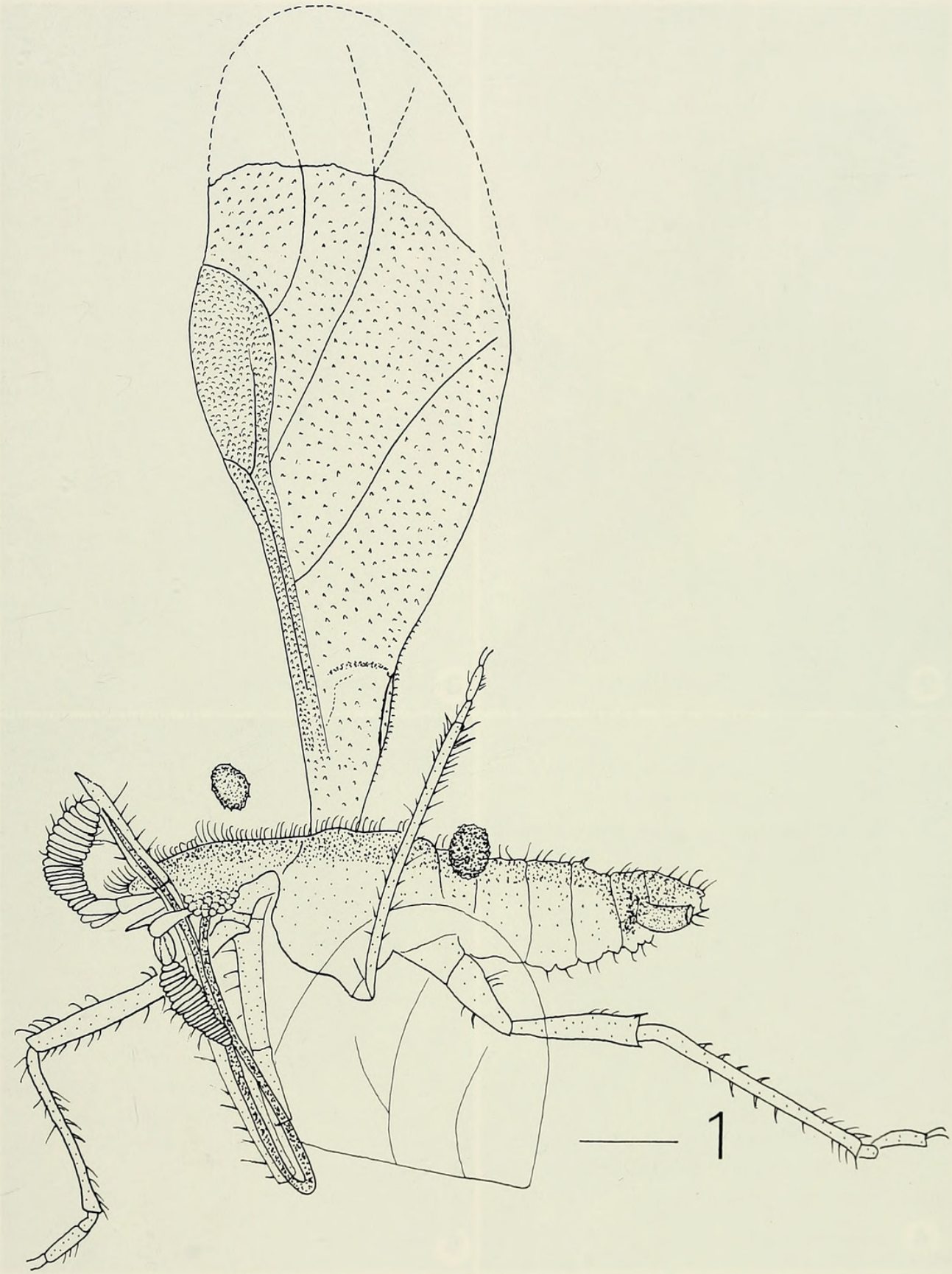
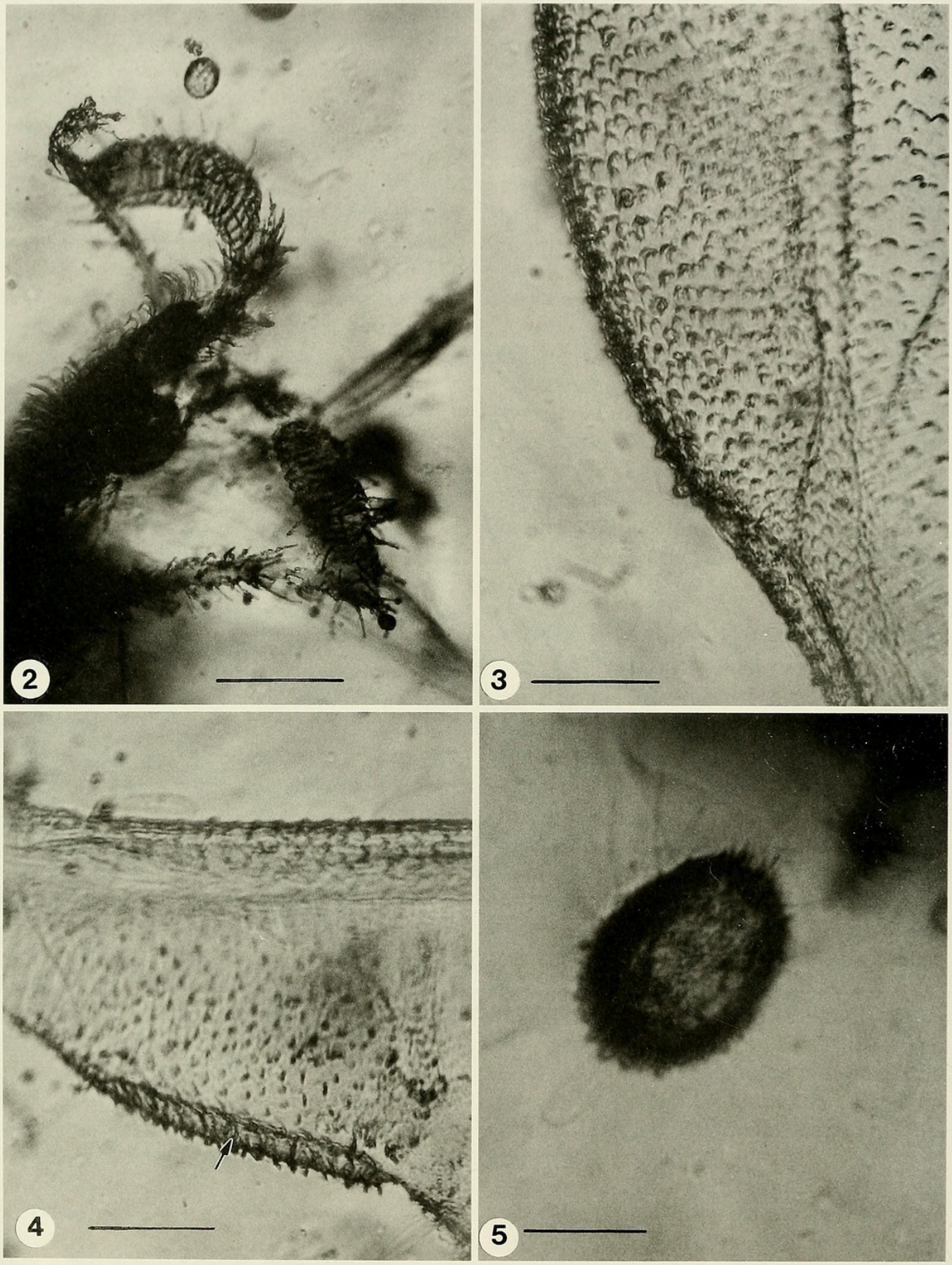


Fig. 1. Lateral view of alate female holotype of *Verrucosa annulata* in Burmese amber. Note dark oval objects. Tip of right forewing is reconstructed based on venation observed in left forewing and in paratype. Bar = 126 μm.



Figs. 2–5. Alate female holotype of *Verrucosa annulata* in Burmese amber. 2, Head region showing third antennal segment composed of 20 annuli. Bar = 85 μm. 3, Detail of pterostigma of forewing showing dense concentration of scalelike warts on wing surface. Bar = 46 μm. 4, Detail of basal portion of forewing showing claval fold (arrow). Bar = 40 μm. 5, Spherical object adjacent to aphid. Bar = 33 μm.

terior branch 191, posterior branch 111, distal cubitus slightly curved in middle, departing from main vein 161 from root of media; claval fold near wing base, length 101, width, 10; hind wings not observed; legs long, femora and tibia with setae; tarsi 2-jointed, basal segment short; setae on fore- and mid-tarsi; tarsal claws 2, equal, simple, slightly curved.

Abdomen: With at least 6 segments; one definite siphunculus observed on left side of body, other siphunculus partly obscured, no sculpturing evident, length 73, diameter of opening 24; oval objects (N = 2) adjacent to specimen, length 63–68; width 40–45; surface covered with raised granules.

Material examined.—Holotype female in Burmese amber from the Hukawng Valley, deposited in the Poinar amber collection maintained at Oregon State University (accession number B-He-13A). One paratype, same data and depository (number B-He-13B).

Etymology.—The specific epithet "annulata" pertains to the annulated condition of the third antennal segment.

Comment.—The oval objects adjacent to the fossil are similar in size, shape and armature and occur nowhere else in the amber. Could they represent eggs of *V. annulata*? The objects are smaller than most aphid eggs (Miyazaki, 1987), yet Essig (1917) described the egg of *Myzocallis arundicolens* (Clark) as 70 μm in length, which is in the size range of the oval objects (63–68 μm). However, aphid eggs are normally smooth and these objects have definite surface irregularities. They could also be pollen grains introduced by the aphid and may indicate the plant host. Vesiculate wingless pollen grains in this size range are produced by some conifers, as the North American *Tsuga canadensis* (L.) Carr. (Kapp et al. 2000).

Burmitaphidae Poinar and Brown, new family

Description.—Hind wing reduced to stubs; antenna 7-segmented, very short; frons with protruding median tubercle; media with one branch; rostrum absent; siphunculi absent.

Etymology.—Burmitaphididae is based on the country of origin of the fossils.

Diagnosis.—The greatly reduced, stub-like hind wings separate this family from all other extant and extinct aphid genera.

Type genus.—*Burmitaphis*, n. gen.

Burmitaphis Poinar and Brown, new genus

The description is based on two males (B-He-14A; B-He-14B) in a single piece of amber and one male (B-He-14C) in a second piece of amber. Two specimens (B-He-14B and B-He-14C) are poorly preserved-however,they have all the diagnostic characters of the family and genus. The generic and specific descriptions are based mainly on the holotype (B- He-14A).

Description.—With characters listed under family description. Mouthparts atrophied, rostrum absent; with extended copulatory organ; forewing with 3 veins departing from main vein.

Etymology.—"Burmit-" represents the country of origin of the specimen. The gender is neuter.

Type species.—*Burmitaphis prolatum*, n. sp.

Diagnosis.—There is no aphid family, extinct or extant with the above combination of characters. Especially significant are the reduced hind wings.

Burmitaphis prolatum Poinar and Brown, new species

(Figs. 6, 8–10)

Description.—Alate male, with characters as listed under family and generic descriptions; general coloration brown; body length 832.

Head: Width across eyes 189; longitudinal diameter of eye 76; ocelli not observed; antenna 7- segmented; length segments, 1, 35; 2, 16; 3, 70; 4, 23; 5, 23; 6, 23; 7, 43; rostrum not observed, greatly reduced or absent.

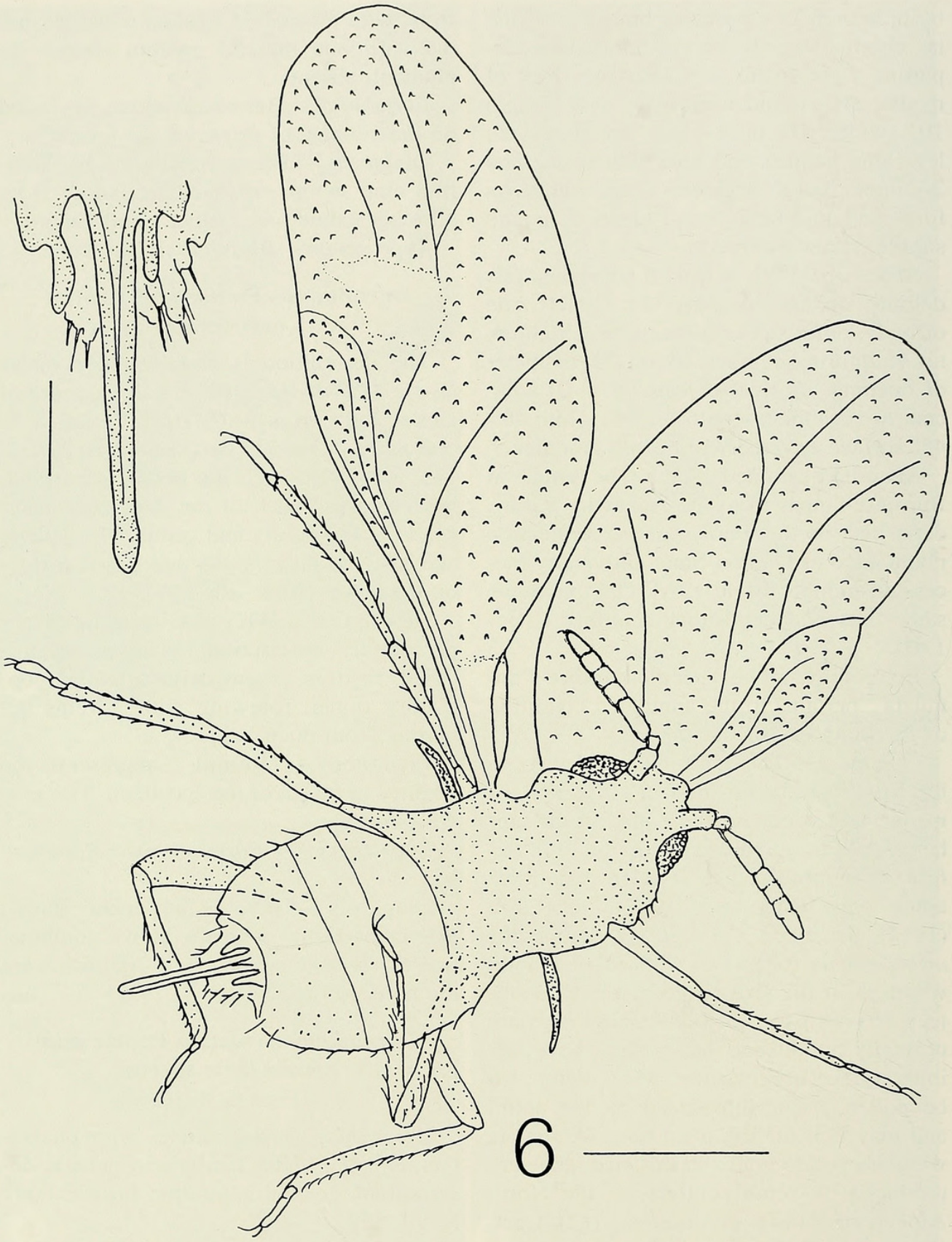


Fig. 6. Dorsal view of holotype male of *Burmitaphis prolatum* in Burmese amber. Bar = 252 μm. Upper left shows detail of copulatory organ. Bar = 45 μm.

Thorax: Width prothorax 246; length forewing 1090; greatest width forewing 409 (378); membrane transparent but covered with small crescent-shaped warts; warts denser in pterostigma portion of wing; with three well-developed veins; radial sector departing from subapical edge of pterostigma (root not visible), length 88; media departing from proximal edge of pterostigma (root not visible), stem 277 long, anterior branch 271 long, posterior branch 164 long; distal cubitus (root not visible) departing from main vein, 170 from base of media; claval fold (158 long by 19 wide) in basal part of wing; hind wing represented by narrow stub, 100 (138) long and 19 wide; legs short, with retrose hairs running length of all tibiae and on some portions of femora; tarsi 2 segmented; claws well developed, without basal thickening.

Abdomen: Short, nearly as wide as long, 334 long (without copulatory organ), 315 wide; siphunculi not visible; copulatory organ elongate, directed ventrally at about 45°; 193 long, flanked by a pair of shorter lobes (claspers, parameres?) 34 long; tip of copulatory organ slightly swollen.

Material examined.—Holotype male in Burmese amber from the Hukawng Valley, deposited in the Poinar amber collection maintained at Oregon State University (accession number B-He-14A). Two paratypes (B-He-14B, B-He-14C), same data and depository.

Etymology.—The specific epithet "prolatus" is from the Latin "*prolatus*" for extended, elongated in reference to the long copulatory organ.

Comment.—Males, even today, are considered rare and finding three of the same type in one amber deposit is interesting and may indicate that parthenogenetic reproduction had not yet occurred in this genetic line (Heie 1987), or that at this stage of their evolutionary development, sexual reproduction was very important as a means of obtaining a high degree of genetic diversity to cope with the changing landscape (evolution of Angiosperms).

Caulinus Poinar and Brown, new genus

The holotype of the type species (B-He-15) is essentially complete with only the left hind leg and tip of the cauda missing. While the right forewing is present, it is positioned in a fracture and could not be clearly portrayed.

Description.—Antenna 7-segmented, third segment longest; rostrum absent; forewing with 4 veins departing from main vein; media with one branch; small scalelike warts on pterostigma and along outer margin of forewing; hind wing reduced to stub; cauda elongate (tip missing); siphunculi absent.

Etymology.—"caulinus" is from the Latin "*caulis*" for stem or stalk referring to the reduced hind wings. The gender is masculine.

Type species.—*Caulinus bursitis*, n. sp.

Diagnosis.—The wing venation and antennae are similar to some members of the subfamily Pemphiginae. However, the reduced hind wings separate this genus from all extinct and extant aphids.

Caulinus burmitis Poinar and Brown, new species

(Figs. 7, 11)

Description.—Holotype alate female; with characters listed under generic description. Generally brown, body length 1900.

Head: With 3 ocelli; compound eyes prominent, longitudinal diameter of compound eye 98; width across compound eyes 357; rostrum absent; antenna 7-segmented, first and second and third and fourth segments closely appressed; length of segments 1, 35; 2, 42; 3, 266; 4, 98; 5, 91; 6, 84; 7, 119; all visible segments with multiple rings except first and second one each with only a few rings.

Thorax: With anteriolateral angles projecting outward; length forewing 2000; greatest width forewing 805; membrane transparent but outer margin covered with small scalelike warts; warts denser in pterostigma portion of wing; pterostigma 511

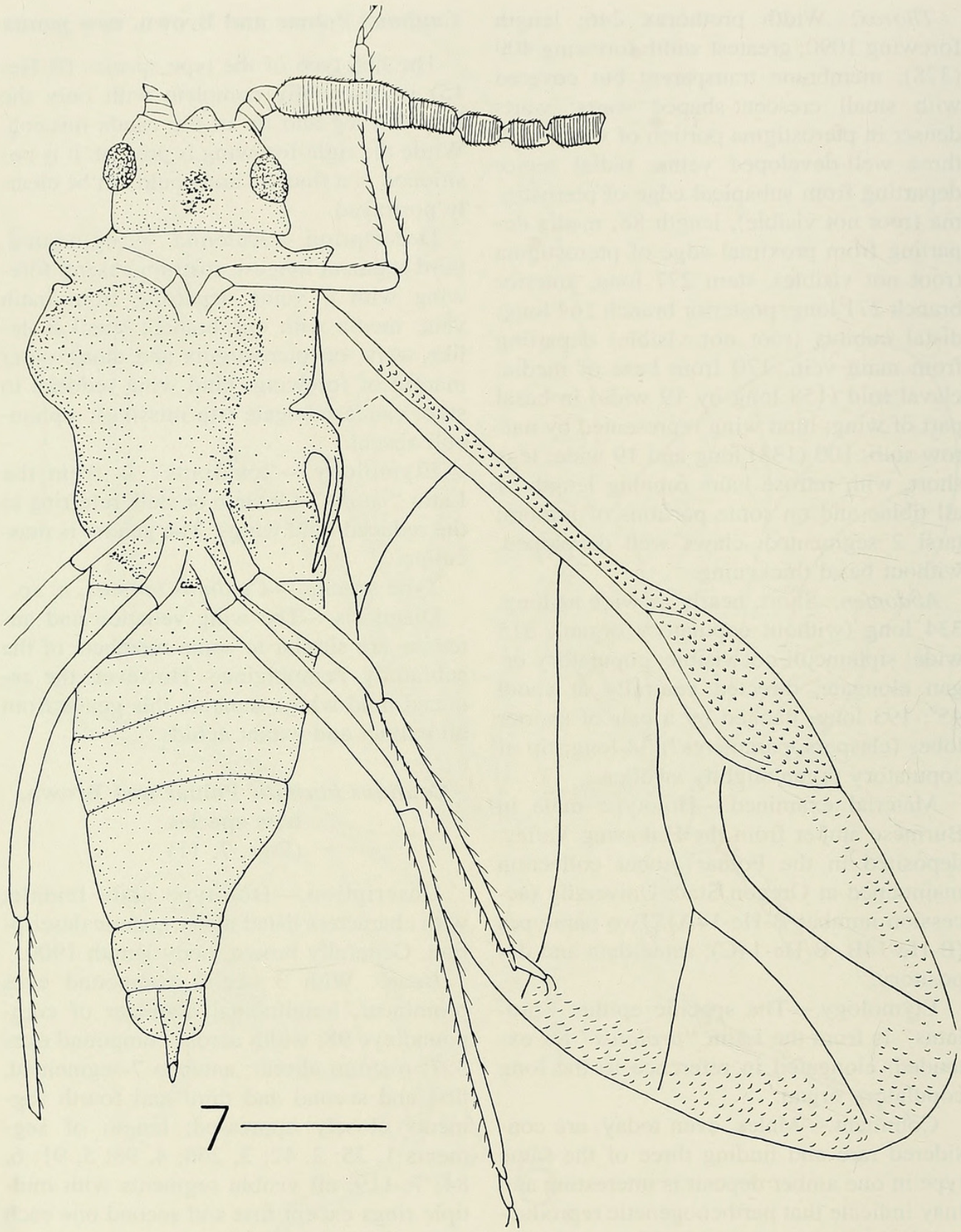
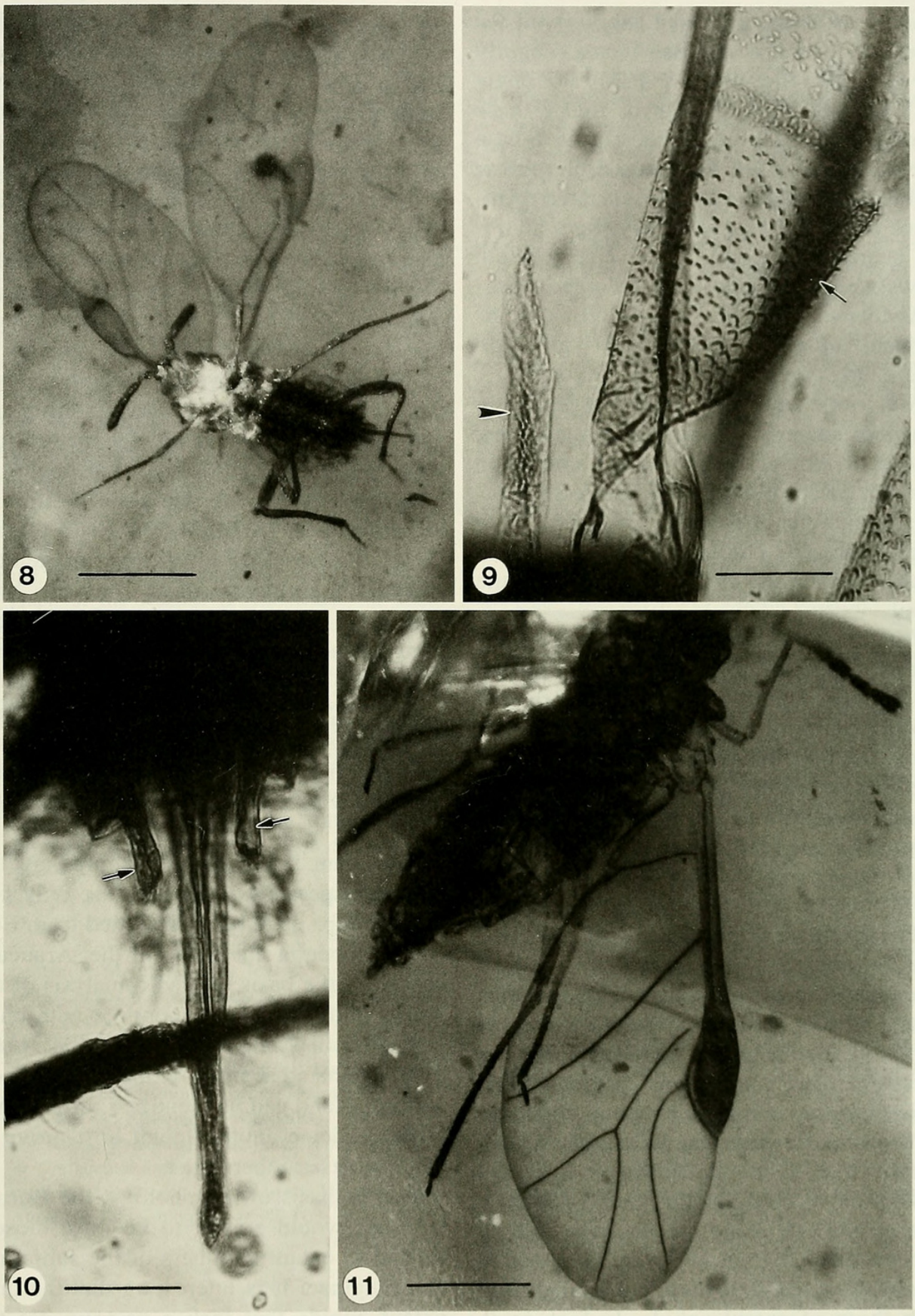


Fig. 7. Ventral view of holotype of *Caulinus burmitis* in Burmese amber. Bar = 280 μm.

long, 189 wide; radial sector (root not visible) departing from subapical part of pterostigma, 679 long; media (root not visible) departing from proximal edge of pterostigma with one fork, stem 448 long, anterior branch 531 long, posterior branch 357 long; distal cubitus curved at apex, departing from main vein 280 from root of proximal



Figs. 8–11. Aphidoidea in Burmese amber. 8. Ventral view of holotype male of *Burmitaphis prolatum*. Bar = 354 μm. 9, Detail of basal portion of wing of *B. prolatum* showing elongate claval fold (arrow) in forewing and narrow stublike hind wing (arrowhead). Bar = 45 μm. 10, Copulatory organ of *B. prolatum*. Arrows show basal lobes (parameres, claspers?). Bar = 43 μm. 11. Ventral view of holotype of *Caulinus burmitis*. Bar = 388 μm.

branch, 880 long; proximal cubitus well developed, as thick as other veins, slightly curved, 350 long, forming nearly 90º angle with main vein; faint vein or fold at base of main vein, 91 long; no claval fold at base of wing; hind wing represented by narrow pointed stub, 304 long, no associated membrane observed; legs relatively short, all tibiae bearing long setae; tarsi 2-segmented; claws well-developed, with enlarged base.

Abdomen: Length 1120, width 476; siphunculi absent; posterior end with elongate cauda (tip missing).

Material examined.—Holotype female in Burmese amber from the Hukawng Valley, deposited in the Poinar amber collection maintained at Oregon State University (accession number B-He-15).

Etymology.—The specific epithet "burmitis" is from the country of origin of the fossil.

Diagnosis.—This species has some characteristics of the subfamily Pemphiginae; i.e. wing venation, antennal structure (except for an extra segment) and the absence of both siphunculi and a rostrum. The scale-like warts along the margin of the forewing closely resemble those of the extant *Eriosoma lanigerum* (Hausmann) (Baker 1915).

Discussion

The antennae of the fossil forms reported here are unusual. The maximum number of antennal segments in extant aphids is 6 (Miyazaki 1987), which is one less than is found in members of the Burmitaphidae. Certainly, there is no extant or extinct aphid which has the annulated antennal condition of *V. annulata,* and this clade probably became extinct in the Cretaceous.

The claval fold, which actually appears as a closed cell along the posterior margin of the forewing, is posteriorly positioned in *V. annulata* and *B. prolatum* in comparison with those of extant aphids. In fact, in *B. prolatum,* it is positioned at the very base of the wing, possibly reflecting the reduced condition of the hind wings. On the anterior border of the shortened hind wings of *B. prolatum* are some roughened areas that could represent vestigial hamuli (Miyazaki 1987). The location and size of the claval fold differs in *B. prolatum* and *V. annulata,* suggesting that these features could be used as diagnostic characters in aphids.

The presence of reduced stublike hind wings in *B. prolatum* and *C. burmitis* is interesting, since this is the first record of this degree of hind wing reduction in aphids (Miyazaki 1987). At first, it was thought that the stubs represented the remains of damaged wings. However, on both species, the opposing appendages are similar in size and shape, and there is no evidence of torn wing membranes associated with them. As mentioned previously, the basal position of the claval fold in *B. prolatum* and the absence of a claval fold in *C. burmitis* tend to support the observations that the hind wings are greatly reduced. Such reduced wings could be considered hamulohalters, which are reduced metathoracic wings in male coccids. The Burmitaphidae would then represent an ancient group, apparently disappearing in the Cretaceous, in which the hind wings were reduced to hamulohalters.

The plant hosts of these aphids are unknown, especially since thus far, only two plant groups have been identified from Burmese amber, a member of the Araucariaceae, on the basis of NMR analysis of the amber and a grasslike monocot with characteristics of a bamboo (Poinar 2004). If the oval objects adjacent to *V. annuata* are pollen grains and can be identified further, they might indicate another plant host group in the Burmese amber forest.

On the basis of morphology, the Burmitaphidae would appear to be most closely related to extant members of the subfamily Pemphiginae. It is interesting that the only extant aphids that lack a rostrum are the sexuales of the Pemphiginae and the males of *Stomaphis* Walker (Lachnidae) (Miyazaki 1987). Some extant species of pemphigines, such as *Smynthurodes betae* West-

wood, include bamboos in their range of plant hosts (Blackman and Eastop 1994).

The present fossils, together with others from a variety of Mesozoic fossil sites (Heie 1996; Heie and Wegierek 1998; Heie and Pike 1992; Richards 1966; Essig 1938; Heie and Azar 2000; Kononova 1975, 1976, 1977; Wegierek 2000; Zhang 2000) show that aphids were quite diverse in the Cretaceous.

Acknowledgments

The authors thank Roberta Poinar for editorial comments on earlier drafts of this manuscript. We also thank two anonymous reviewers for their helpful comments.

Literature Cited

Annand, P. N. 1928. A contribution toward a monograph of the Adeline (Phylloxeridae) of North America. Stanford University Publications, University Series, Biological Sciences 6: 1–146.

Baker, A. C. 1915. Identity of *Eriosoma pyri.* Journal of Agricultural Research 5: 1115–1120.

Blackman, R. L. and V. F. Eastop. 1994. Aphids on the World's trees. CAB International, Wallingford, UK, 986 pp.

Cruickshank, R. D. and K. Ko. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21: 441–455.

Essig, E. O. 1917. Aphididae of California. University of California Technical Bulletin 1: 301–346.

———. 1938. Family Aphididae, pp. 17–21. *In* Carpenter, F. M. et al., eds. Insects and Arachnids from Canadian amber. Toronto, University of Toronto Series 40.

Heie, O. E. 1987. Palaeontology and Phylogeny, pp. 367–391. *In* Minks, A. K. and P. Harrewijn, eds. Aphids, Their Biology, Natural Enemies and Control, Vol. A. Elsevier, Amsterdam.

———. 1996. Palaeoaphididae and Tajmyraphididae in Cretaceous amber from Alberta, Canada (Hemiptera: Aphidinea). Annals of the Upper Silesian Museum, Entomology 6–7: 97–103.

Heie, O. E. and D. Azar. 2000. Two new species of aphids found in Lebanese amber and a revision of the family Tajmyraphididae Kononova, 1975 (Hemiptera: Sternorrhyncha). Annals of the Entomological Society of America 93: 1222–1225.

Heie, O. E. and T. Pike. 1992. New aphids in Cretaceous amber from Alberta, Canada (Insecta: Homoptera). The Canadian Entomologist 124: 1027–1053.

Heie, O. E. and P. Wegeirek. 1998. A list of fossil aphids (Homoptera: Aphidinea). Annals of the Upper Silesian Museum, Entomology 8–9: 159–192.

Kapp, R.O., O.K. Davis, and J. E. King. 2000. Pollen and spores. 2nd Edition. American Association of Stratigraphic Palynologists: College Station, Texas, 279 pp.

Kononova, E. L. 1975. A new family of aphids (Homoptera, Aphidinea) from the Upper Cretaceous of the Taymyr. Entomologicheskoe Obozrenie 54: 60–68 (English translation, Entomological Review 54: 60–68).

———. 1976. Extinct aphid families (Homoptera, Aphidinea) from the Late Cretaceous. Paleontological Zhurnal 3: 117–126 (in Russian).

———. 1977. New species of aphids (Homoptera, Aphidinea) from the Upper Cretaceous deposits of Taimyr. Entomologicheskoe Obozrenie 56: 72–80 (English translation, Entomological Review 56: 72–80).

Miyazaki, M. 1987. Morphology of aphids, pp.1–25. *In* Minks, A. K. and P. Harrewijn, eds. Aphids, Their Biology, Natural Enemies and Control, Vol. A. Elsevier, Amsterdam.

Poinar, Jr., G. O. 2004. *Programinis burmitis* gen. et sp. nov., and *P. laminatus* sp. nov., Early Cretaceous grass-like monocots in Burmese amber. Australian Systematic Botany 17: 497–504.

Richards, W. R. 1966. Systematics of fossil aphids from Canadian amber (Homoptera: Aphididae). The Canadian Entomologist 98: 746–760.

Wegierek, P. 2000. A new genus and species of aphid (Hemiptera: Aphidinea) from Cretaceous amber, pp 141–145. *In* Grimaldi, D., ed. Studies on Fossils in Amber with Particular Reference to the Cretaceous of New Jersey, Backhuys. Leiden.

Zhang, J.-F. 2000. On problems of classification and descriptions of genera and species of Chinese aphids from the Late Mesozoic. Acta Palaeontologica Sinica 39: 558–572.