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Austroconops Wirth and Lee, a Lower Cretaceous Genus of Biting Midges Yet Living in Western Australia: a New Species, First Description of the Immatures and Discussion of Their Biology and Phylogeny (Diptera: Ceratopogonidae)

ART BORKENT¹ AND DOUGLAS A. CRAIG²

ABSTRACT

The eggs and all four larval instars of *Austroconops mcmillani* Wirth and Lee and *A. annettae* Borkent, new species, are described. The pupa of *A. mcmillani* is also described. Life cycles and details of behavior of each life stage are reported, including feeding by the aquatic larvae on microscopic organisms in very wet soil/detritus, larval locomotion, female adult biting habits on humans and kangaroos, and male adult swarming. *Austroconops annettae* Borkent, new species, is attributed to the first author.

Cladistic analysis shows that the two extant *Austroconops* Wirth and Lee species are sister species. Increasingly older fossil species of *Austroconops* represent increasingly earlier lineages. Among extant lineages, *Austroconops* is the sister group of *Leptoconops* Skuse, and together they form the sister group of all other Ceratopogonidae. *Dasyhelea* Kieffer is the sister group of *Forcipomyia* Meigen + *Atrichopogon* Kieffer, and together they form the sister group of the Ceratopogoninae. *Forcipomyia* has no synapomorphies and may be paraphyletic in relation to *Atrichopogon*. *Austroconops* is morphologically conservative (possesses many plesiomorphic features) in each life stage and this allows for interpretation of a number of features within Ceratopogonidae and other Culicomorpha. A new interpretation of Cretaceous fossil lineages shows that *Austroconops*, *Leptoconops*, *Minyohelea* Borkent, *Jordanoconops*

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Szadziewksi, *Archiaustroconops* Szadziewksi, and *Fossileptoconops* Szadziewksi form a monophyletic group. Within this assemblage *Leptoconops* and *Minyohelea* are sister groups and *Austroconops* and *Jordanoconops* are monophyletic (*Austroconops* is possibly paraphyletic in relation to *Jordanoconops*). All are considered to be members of Leptoconopinae Noë and the subfamily Austroconopinae Borkent, Wirth and Dyce is a **new synonym** of Leptoconopinae.

Extant and fossil distributional records suggest that *Austroconops* was displaced from its previously broad distribution by the emergence of *Culicoides* Latreille. Larval feeding on microorganisms is plesiotypic within the Ceratopogonidae and Chironomoidea, and living in small aquatic habitats is plesiotypic within each family of the Culicomorpha. Outgroup comparisons further suggest that diurnal feeding by adult females is plesiotypic within the Ceratopogonidae and Chironomoidea.

INTRODUCTION

Perhaps only fellow entomologists could appreciate the thrill of the following sado-masochistic scenario: the first author and his wife standing still on the edge of a golf course in Yanchep National Park, just north of Perth in Western Australia, being badly bitten on the face by hundreds of biting midges, with exclamations of joy and wonder. We realized that we were being attacked by a species considered to be an extremely rare “living fossil”, a member of a genus which was surviving only in this small corner of the globe but which was once a widespread and diverse lineage during the Early Cretaceous, 121 million years ago. Previously known from only a limited series of adult specimens of a single species and a moderate number of fossils, our study of this genus uncovered a wealth of new information: the discovery of the previously unknown eggs, larvae, and pupa; the presence of a second extant species (including its immatures); and observations of female biting behavior, male swarming, and more.

There are good reasons why we were excited to pursue these small beasts, and we committed ourselves to an extensive expedition to Western Australia to seek them out. In recent years cladistic analyses and an abundance of fossil material in amber of different ages have resulted in an increasingly detailed understanding of the phylogenetic relationships of the biting midges. The genus *Austroconops* Wirth and Lee plays a pivotal role in this analysis. Together with *Leptoconops* Skuse, these two ancient genera represent the earliest extant lineage in the family. However, unlike the rather modified mem-

bers of *Leptoconops*, species of *Austroconops* have a number of plesiomorphic features, allowing for an enhanced interpretation of character states within the family. Simply put, *Austroconops* is a group of primitive “living fossils”. Further to this, knowing that the Early Cretaceous species of *Austroconops* were morphologically similar to the extant species suggested that study of the biology of the living species would provide special insight into the adaptations of Ceratopogonidae existing 121 million years ago. Of particular interest and importance was the discovery of the eggs and larvae of the two extant species, as well as the pupa of one of these. One of the reasons that nematocerous Diptera are such excellent candidates for phylogenetic studies is that the different life stages show a remarkable degree of morphological divergence and therefore provide independent sources of character states to test phylogenetic hypotheses.

When *Austroconops* and its single species *A. mcmillani* was first described by Wirth and Lee (1958) only 39 females were known from four localities in the vicinity of Perth, Western Australia. These authors noted that the species seemed closest to *Culicoides* Latreille, well within the Ceratopogonidae, but mentioned that it shared some features with the early lineage *Leptoconops*. They were uncertain as to which subfamily the genus belonged. The only information on the species' biology was that females were recorded as biting humans, particularly on the eyelids. Then, in 1985, W.W. Wirth and A.L. Dyce collected the first males of the species, and study of these three specimens (plus an additional 10 females) led to a cladistic analysis of the early lineages of the family, demon-

strating that *Austroconops* belonged near the very base of the phylogeny of the Ceratopogonidae (Borkent et al., 1987). Since then, six fossil species have been described from Early to Late Cretaceous amber (from Lebanon, France, and Siberia), providing, within a cladistic analysis, further support that the genus indeed represents an early lineage of biting midge (Borkent, 2000a). Within the Ceratopogonidae, there is a striking correlation between cladistic patterns and the distribution of fossils in different ages of amber, with increasingly older fossils representing increasingly earlier lineages (Borkent, 2000a). Our study here further refines the phylogenetic position of *Austroconops*, interprets characters states of the newly discovered immatures, analyzes the implications for our interpretation of features of other Ceratopogonidae, and provides an interpretation of historical zoogeographical and bionomic features of early lineages of Ceratopogonidae and other Culicomorpha.

MATERIALS AND METHODS

The collecting trip to Western Australia was undertaken by the first author and his wife with the purpose of discovering further material of *Austroconops*. Sampling was primarily with a sweep net in a wide array of wet or aquatic habitats from October 12 to November 23, 2001, covering the area from Yanchep N.P., about 47 km north of Perth, south to Augusta, east to Albany, returning through Darkan to Augusta and then heading north to Yanchep N.P. once again. Mud samples were taken from wet habitats near the sites of where adult *Austroconops* were collected and immatures searched for (unsuccessfully) either manually or by floating debris and substrate using a saturated sugar solution. Female adult *A. mcmillani* were collected with a net and aspirator by Len Zamudio during December, 2001–January, 2002 and October, 2002–February, 2003 while the midges were attacking humans in Yanchep National Park.

To obtain eggs of *A. annettae*, an adult female was captured by sweeping and placed directly into a vial with mud/detritus (about 1 cm deep) taken from the spot where the adults of this species had been collected.

Subsequent care was as described below for *A. mcmillani*. Females of *A. mcmillani* were allowed to attack the face at site A (see fig. 22C), complete their feeding, and then were captured either by placing a small vial over the female until she finished feeding or by sticking one's head in an insect net and gently aspirating the fully fed females after they left the skin surface and flew into the net. These captured females of *A. mcmillani* were then cooled briefly in a refrigerator and when torpid, quickly placed in six groups of 7–12 females each and put into separate 2- or 3-dram vials containing about 1 cm of wet mud/detritus taken from the partially inundated margin at the south end of Loch McNess (fig. 22C; site B). Females of both species received a small smear of honey on the inside surface of the vial at about mid-height (none were seen to feed) and each vial was stoppered with a cotton ball. A drop of water was added periodically to the mud when it began to dry (so the mud remained quite wet). The vials were kept at more-or-less ambient temperature in a small cooler that was always kept in the shade. Females of *A. mcmillani* were transported from Australia to Canada with the addition of a large bottle of very warm water to the cooler to keep adults from becoming torpid and sticking to the mud surface. The eggs of *A. annettae*, which had been laid while in Australia, plus first instar larvae were transported to Canada in the same cooler. In Canada the eggs and larvae of *A. annettae* and the female adults, eggs and larvae of *A. mcmillani* were kept at about 23–28°C during the day and about 18°C at night. Most of the females of *A. mcmillani* that were transported died en route, probably because of excessive shaking of the vials during air travel; of 58 original females, only 12 survived the trip to Canada. Of these, at least one of three females laid eggs.

Eggs were allowed to develop in the vials, and after all had hatched, the mud contents with the larvae of each species was transferred to small (50 × 7 mm) plastic petri dishes with lids. The larvae could be easily observed moving or lying against the bottom of the dish by inverting the clear dish under the dissecting microscope. Vials and dishes were examined at least twice a day for the

great majority of larval and pupal development.

The mud/detritus substrate initially contained some small, unidentified microorganisms, but nearly all died shortly after obtaining the samples. When it became clear that the first-instar larvae were not feeding, between hatching and December 8, 2001, the following items were added as potential food at different times to the Petri dish with larvae of *A. mcmillani*—*Euglena* sp., yeast, a freshly killed ostracod and *Chaoborus* Lichtenstein larva, several species of unidentified green algae and cyanobacteria (from local fish tanks and ponds), dried blue-green algae (*Spirulina*) soaked in water, and the following cultured cyanobacteria and green algae: *Anabaena flosaquae*, *Oscillatoria* sp., and *Selenastrum capricornutum*. An unidentified species of rotifer was added between December 31, 2001 and January 31, 2002. A small amount of water was added to agar plates with a culture of the nematode *Caenorhabditis elegans* and the bacterium *Escherichia coli*, swirled around, and 2–5 drops of the water with *C. elegans* were added every 2–3 days to the mud/detritus in the Petri dishes with *A. mcmillani* and *A. annettiae* starting on December 31. These nematodes died within 12–24 hours. Beginning on December 17, 2–4 drops of an infusion made from fresh goat feces and water (first made on December 15) were added every 2–3 days to both dishes; these drops regularly included a small clot of feces. Water was added to the infusion to replace loss through evaporation (the infusion was not sealed), and a fresh infusion was made on August 9, 2002.

Five first-instar larvae of *A. mcmillani* were added to an agar plate with a culture of *C. elegans* and *E. coli* on December 14 and were seen feeding on clumps of *E. coli*, but all died within a few days. At least two of these larvae had their guts partially filled with white material, almost certainly *E. coli*. On June 28, 2002, three third-instar *A. mcmillani* were placed in a separate dish with some of the original mud/detritus, put into a dark cold room for four days at 13°C, and then placed in a refrigerator at 5–8°C. By August 1 all larvae had died and were preserved in 70% ethanol.

Some living larvae of different instars

were examined under both dissecting and compound microscopes by placing them in a well slide in which they were studied while warm and after they were cooled by ice. Cold larvae were examined for mouthpart and proleg movement.

Adult behavior of *A. mcmillani* was observed at the south end of Loch McNess (fig. 22C; site B) and on fairway 2 of the golf course (fig. 22C; site A) at Yanchep National Park. Biting times by female *A. mcmillani* were determined by observing a female land, waiting for initiation of feeding, and then carefully inverting a vial over the female until it ceased feeding, when it invariably flew up into the vial.

Specimens were examined, measured, and drawn using a Wild M3 dissecting microscope and a Zeiss Jenaval compound microscope. Larval head capsule length was measured from the posterolateral margin to the anterolateral margin of the head capsule (near the base of the mandible). A male and female of both species were cleared and compared in temporary glycerine slide mounts. These and other adults, as well as most eggs and larvae were mounted on microscope slides using the technique described by Borkent and Bissett (1990). Larvae to be studied with the scanning electron microscope were killed with hot water. Some eggs and larvae were critical point dried, sputter-coated at 30 angstroms with chrome, and studied with a Jeol JSM 6301 FXV scanning electron microscope.

Terms for structures follows those used in the *Manual of Nearctic Diptera* (McAlpine, 1981). More specific larval and pupal terms follow Lawson (1951). The kangaroos referred to in the text are all western grey kangaroos (*Macropus fuliginosus*). The name *Austroconops annettiae* is attributed solely to the first author.

Additional material was borrowed from the following museums:

- | | |
|------|----------------------------------------------------------------------------------------------------------------------------|
| ANIC | Australian National Insect Collection, Division of Entomology, CSIRO, P.O. Box 1700, Canberra City, A.C.T. 2601, Australia |
| BMNH | Nigel Wyatt, Department of Entomology, Natural History Museum, London, SW7 5BD, United Kingdom |

- BPBM Department of Entomology, Bernice P. Bishop Museum, 1525 Bernice Street, P.O. Box 19000A, Honolulu, HI, 96817 0916
- CNCI Canadian National Collection of Insects, Eastern Cereal and Oilseed Research Centre, Agriculture Canada, K.W. Neatby Building, Ottawa, Ontario, K1A 0C6, Canada
- USNM United States National Entomological Collection, Department of Entomology, U.S. National Museum of Natural History, Washington, DC 20560
- WAMP Department of Entomology, Western Australian Museum, Francis Street, Perth, WA, 6000, Australia

RESULTS

Austroconops Wirth and Lee

Austroconops Wirth and Lee, 1958: 337. Type species: *Austroconops mcmillani* Wirth and Lee, by original designation.

DIAGNOSIS: Male. The only extant or fossil Ceratopogonidae with flagellomere 13 (fig. 1A, B) with a subbasal constriction, with two well-developed radial cells, and r-m parallel to R_1 (fig. 1K). **Female.** The only extant or fossil Ceratopogonidae with two well-developed, clearly open, radial cells and r-m parallel to R_1 (fig. 1L). **Egg.** Only Ceratopogonidae with egg (fig. 2A) markedly elongate and remaining pale throughout larval development. **Larva (all instars).** The only Ceratopogonidae with markedly elongate antenna bearing an elongate blade and a prognathous head (figs. 2H, 3C, 12A, B). **Pupa.** The only Ceratopogonidae with the hindleg sheath not exposed from under lateral margin of wing sheath and with abdominal segments 2–8 with bifurcate setae (fig. 4A).

DESCRIPTION: Live adults of both sexes. With subcutaneous blue-green tissue (likely fat body) externally evident in all areas (head, thorax, abdomen) with membrane or thin cuticle (including tip of halter). Wings completely overlapping at rest. Male with permanently erect antennal setae. **Male adult. Head:** Ommatidia narrowly separated dorsomedially, with single vertex seta. Antenna (fig. 1A, B) with well-developed plume of permanently erect setae, 13 separate flagellomeres, flagellomeres 12–13 more elongate than preceding flagellomeres, flagello-

mere 12 with or without subbasal constriction, flagellomere 13 with subbasal constriction, flagellomere 1 with two patches of short sensilla trichodea, without sensilla coeloconica. Mouthparts moderately short to moderately long. Mandible elongate (ending near apex of labrum), with several slender terminal spicules. Lacinia elongate, simple. Palpus (fig. 1C, D) with 4–5 segments, segment 3 ovoid to elongate, slender, with capitate sensilla scattered on mesal surface or perhaps in pit, at least extant species with membranous area between segment 3 and 4 + 5. **Thorax:** With three anterior pronotal apodemes. Scutum with scattered elongate setae. Scutellum rounded or angular in dorsal view. Anapleural suture elongate. **Wing** (fig. 1K): Without macrotrichia, fine microtrichia present on all membrane. Alula with fringe of macrotrichia. Costa extending to or beyond apex of R_3 . Both radial cells present. r-m parallel to R_1 . M bifurcating distal to r-m. **Legs:** Femora, tibiae slender. Legs lacking armature, except in some species with stout setae on some or all of first tarsomeres, some with pair of thick setae on apex of tarsomeres 1–4. Tarsal ratio (Ta_1/Ta_2) of foreleg/hindleg = 1.4–1.9. Fore- and midleg trochanter without pair of thick setae. Midleg tibia with or without apical spur. Hindtibia apex with two rows of spines. Hindleg first tarsomere with or without thick basal spine, with scattered setae (fig. 1M, N). Claws on fore-, mid-, hindleg equal in size, both equal on each leg, each claw simple or toothed, apically bifid (possibly simple in Lebanese amber fossils). Slender empodium. **Genitalia:** Apicolateral process absent to well developed. Gonocoxite short to moderately elongate. Gonostylus variable, apical spine present or absent. Parameres fused medially (known only in extant species). Aedeagus short, setose lobe with ventral plate (known only in extant species).

Female adult. Head: Ommatidia narrowly separated dorsomedially, with single vertex seta. Antenna with 13 separate flagellomeres, flagellomeres gradually increasing in length from flagellomeres 2–13 or with flagellomeres 9–13 more elongate than preceding flagellomeres, flagellomere 1 with two groups of short sensilla trichodea, without sensilla coeloconica. Mouthparts moderately elongate, further details not visible in fossils.

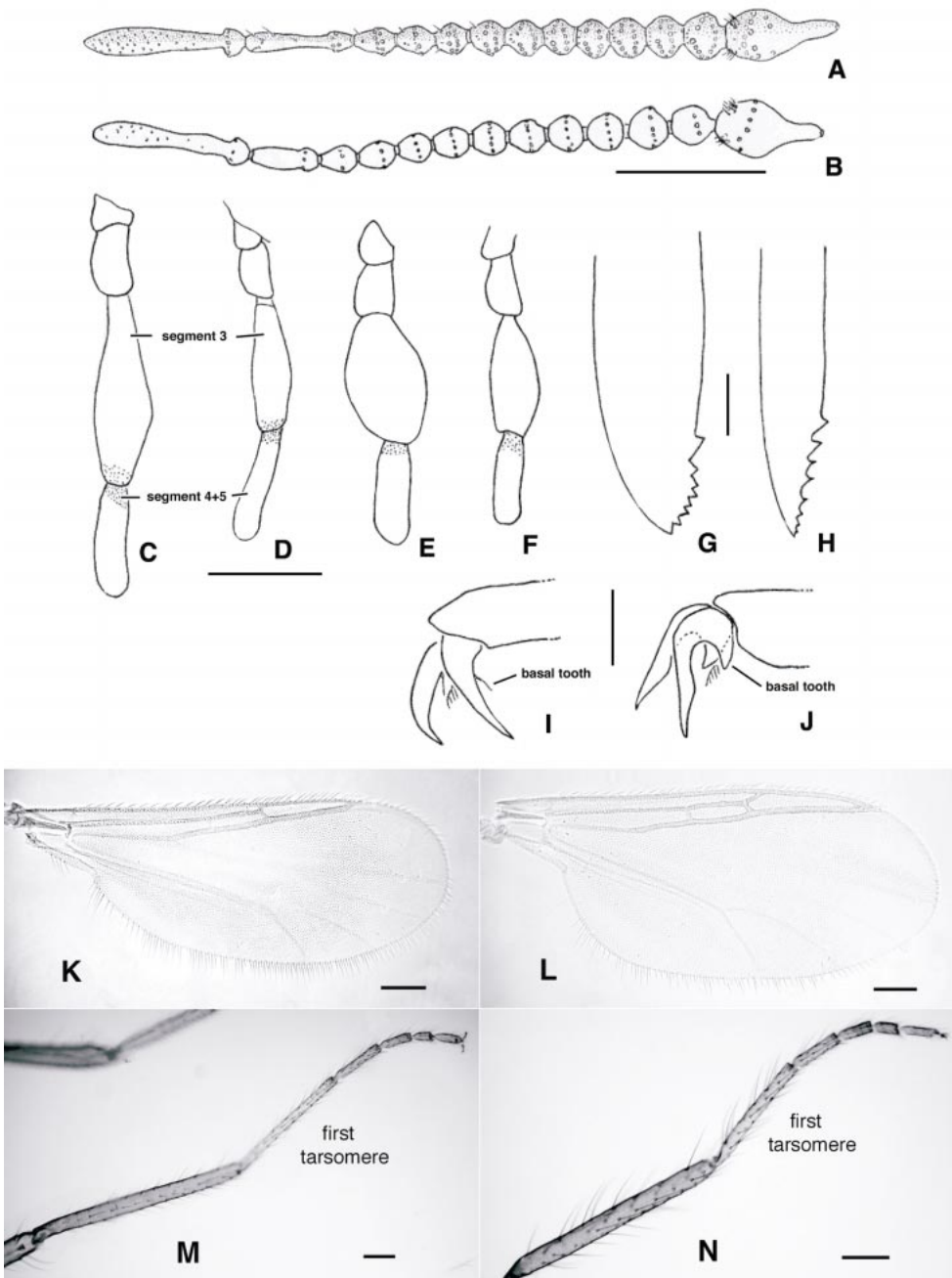


Fig. 1. Structures of adult *Austroconops*. **A.** Male antenna of *A. mcmillani*. **B.** Male antenna of *A. annettae*. **C.** Right palpus of male *A. mcmillani*. **D.** Right palpus of male *A. annettae*. **E.** Right palpus of female *A. mcmillani*. **F.** Right palpus of female *A. mcmillani*. **G.** Right mandible of *A. mcmillani* in anterior view. **H.** Right mandible of *A. annettae* in anterior view. **I.** Hindleg claws of *A. mcmillani*. **J.** Hindleg claws of *A. annettae*. **K.** Right wing of male *A. annettae*. **L.** Right wing of female *A. annettae*. **M.** Midleg of male *A. mcmillani*. **N.** Midleg of male *A. annettae*. Scale bars: A, B = 0.1 mm; C–F = 0.05 mm; G–J = 0.01 mm; K, L = 0.1 mm; M, N = 0.05 mm.

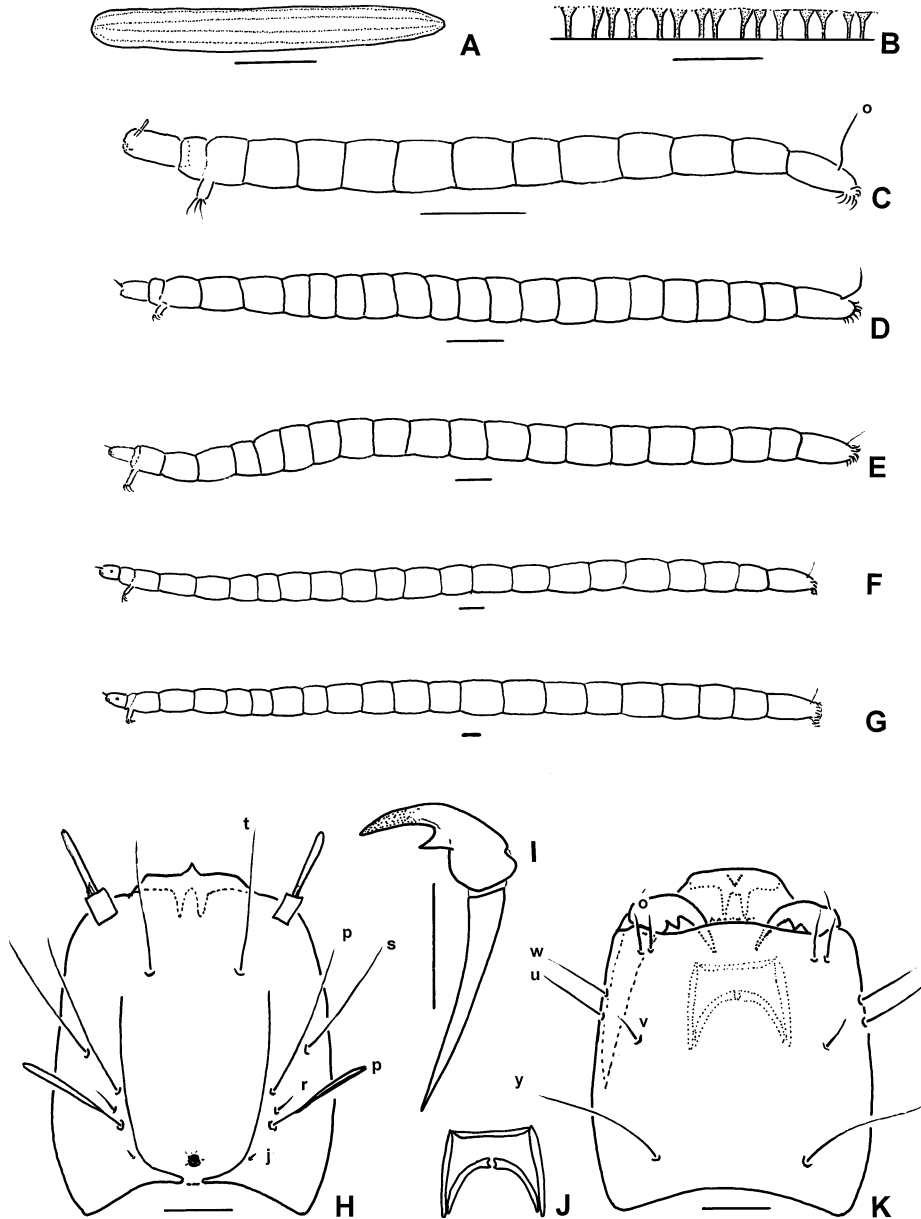


Fig. 2. Structures of immature *Austroconops*. **A**. Egg of *A. mcmillani*. **B**. Detail of tubercles on surface of egg of *A. mcmillani* in lateral view. **C**. First-instar larva of *A. annettae* in lateral view. **D**. First-instar larva of *A. mcmillani* in lateral view. **E**. Second-instar larva of *A. mcmillani* in lateral view. **F**. Third-instar larva of *A. mcmillani* in lateral view. **G**. Fourth-instar larva of *A. mcmillani* in lateral view. **H**. First-instar larval head capsule of *A. mcmillani* in dorsal view. **I**. First-instar larval right mandible and apodeme of *A. mcmillani* in dorsal view. **J**. First-instar larval pharyngeal complex of *A. mcmillani* from figure K. **K**. First-instar larval head capsule of *A. mcmillani* in ventral view. Scale bars: A, C-G = 0.1 mm; B, H-K = 0.01 mm.

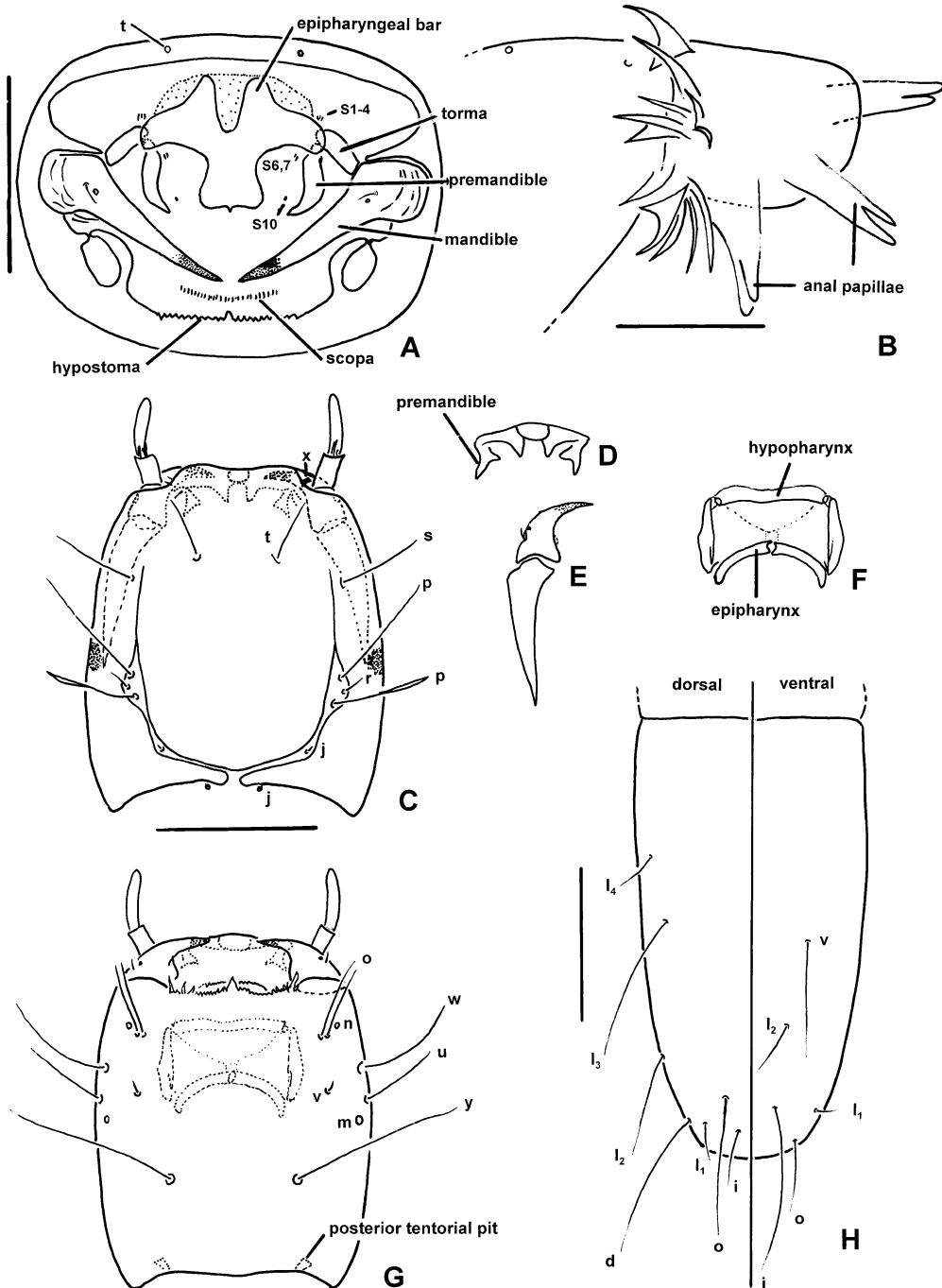


Fig. 3. Structures of larvae of *Austroconops*. **A.** Fourth-instar larval head capsule of *A. mcmillani* in anterior view; antennae and maxillae not shown. **B.** Third-instar larval posterior portion of segment 9 of *A. mcmillani* in lateral view. **C.** Fourth-instar larval head capsule of *A. annettae* in dorsal view. **D.** Fourth-instar larval epipharyngeal bar and premandibles of *A. annettae* in dorsal view. **E.** Fourth-instar larval left mandible and apodeme of *A. annettae* in dorsal view. **F.** Fourth-instar larval pharyngeal complex of *A. annettae*. **G.** Fourth-instar larval head capsule of *A. annettae* in ventral view. **H.** Fourth-instar larval segment 9 of *A. mcmillani* in dorsal and ventral view. Scale bars: A–G = 0.05 mm; H = 0.1 mm; D–F are from figures C and G.

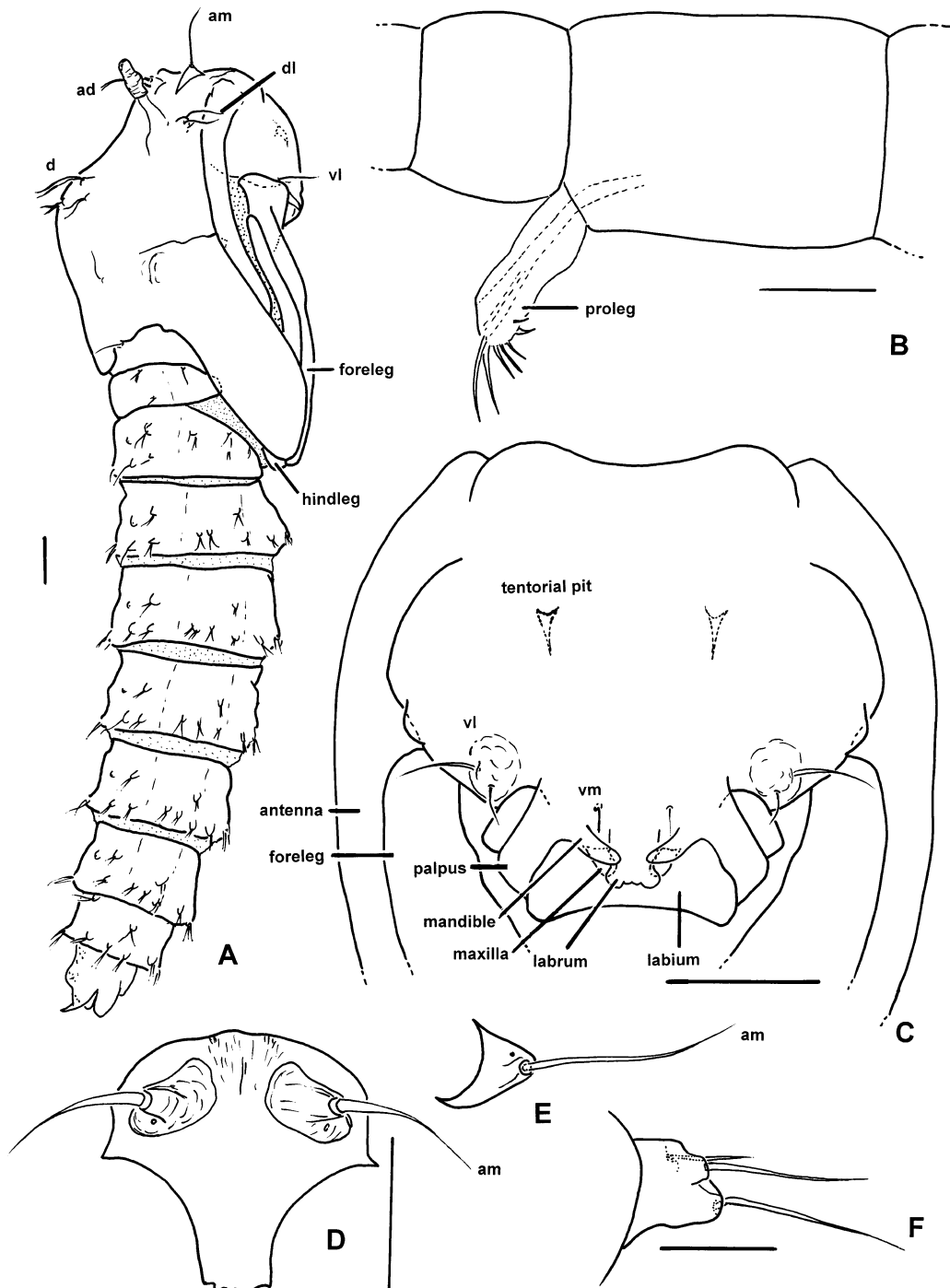


Fig. 4. Structures of immatures of *Austroconops mcmillani*. **A.** Habitus of pupa in lateral view; am = anteromedial, dl = dorsolaterals, ad = anterodorsal, vl = ventrolaterals, d = dorsals. **B.** Third-instar larval prothoracic segment in lateral view. **C.** Pupal head in ventral view; vm = ventromedial, vl = ventrolaterals. **D.** Pupal operculum. **E.** Pupal right anteromedial seta in anteroventral view. **F.** Pupal dorsolateral setae in dorsal view. Scale bars: A, C–E = 0.1 mm; B, F = 0.05 mm.

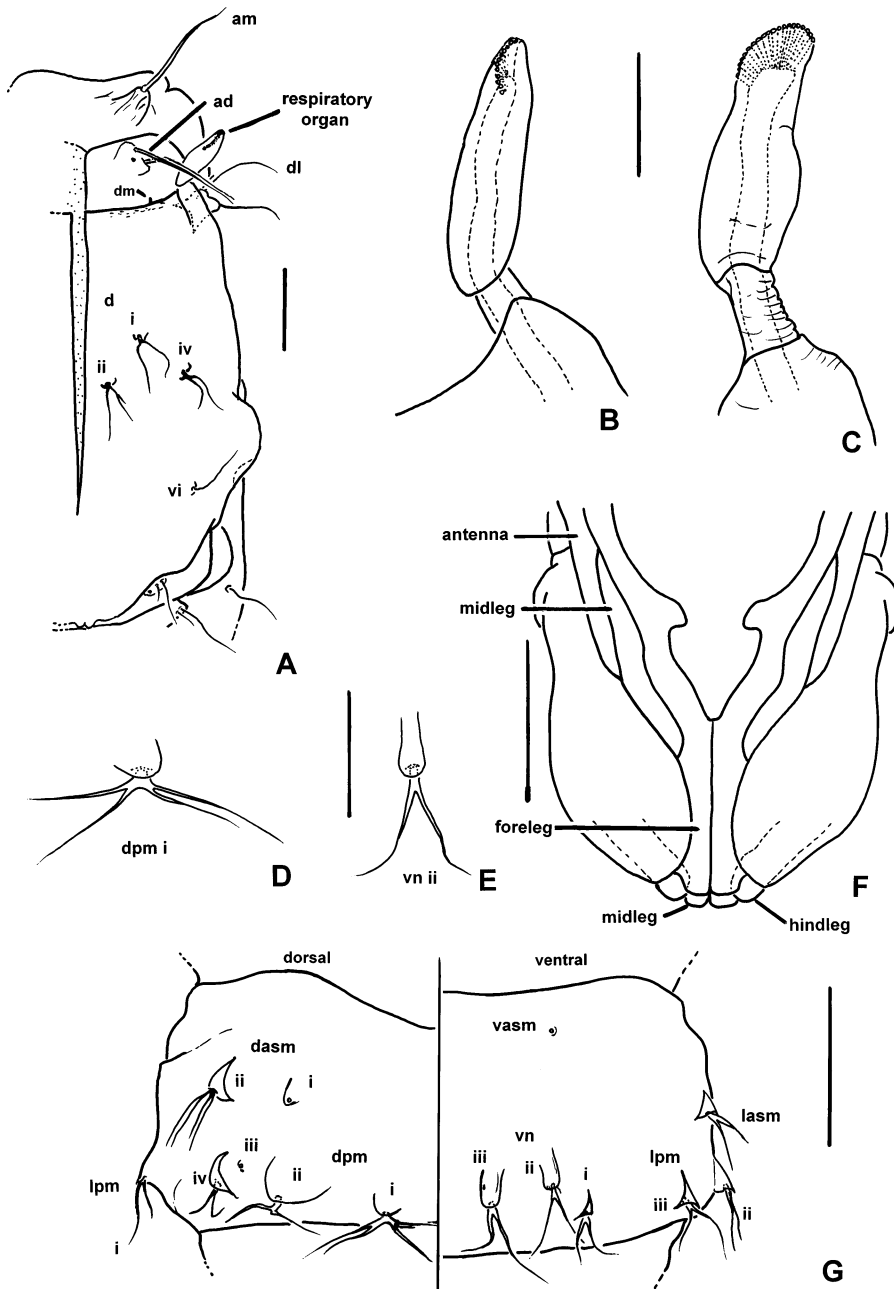


Fig. 5. Structures of the pupa of *Austroconops mcmillani*. **A.** Right portion of cephalothorax in dorsal view; am = anteromedial, dm = dorsomedial, dl = dorsolaterals, ad = anterodorsals, d = dorsals. **B.** Right respiratory organ in dorsal view. **C.** Right respiratory organ in lateral view. **D.** Seta dpm i in dorsal view. **E.** Seta vn ii in ventral view. **F.** Leg and wing sheaths in ventral view. **G.** Abdominal segment 4 in dorsal and ventral view. Scale bars: A, F, G = 0.1 mm; B–E = 0.05 mm.

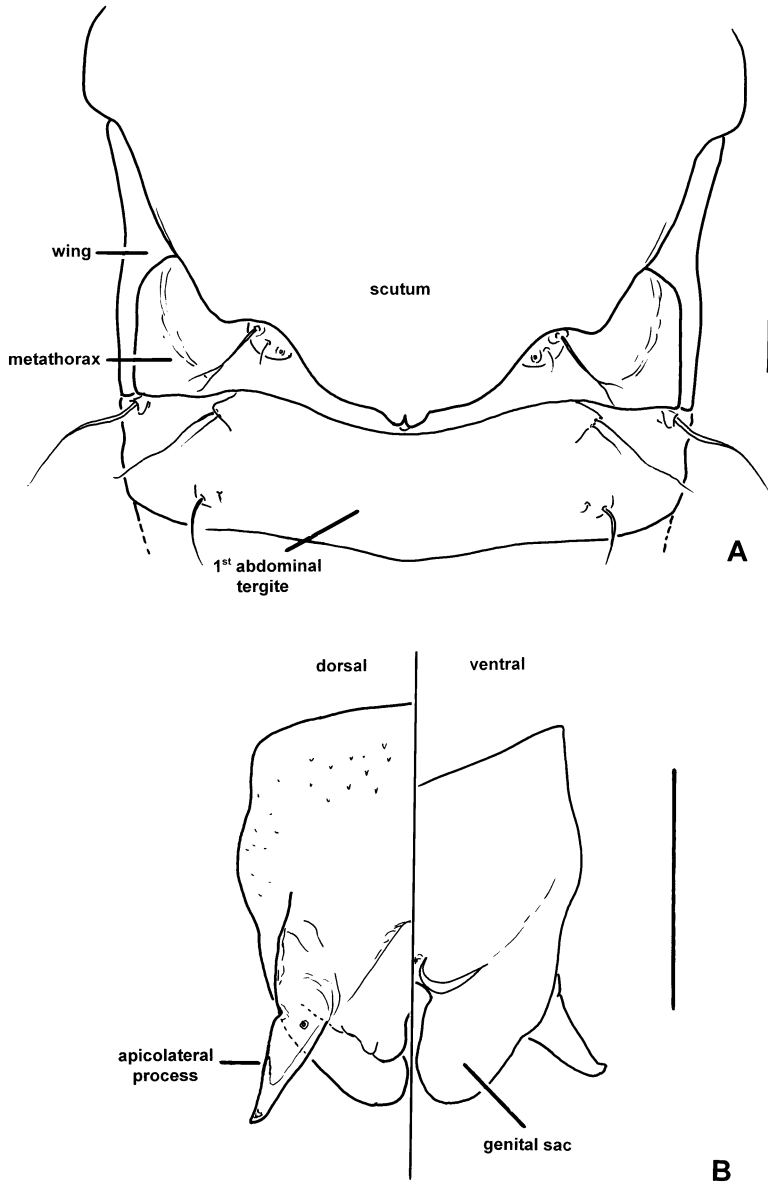


Fig. 6. Structures of the pupa of *Austroconops mcmillani*. **A.** Posterior portion of scutum, metathorax, and first abdominal tergite in dorsal view. **B.** Segment 9 in dorsal and ventral view. Scale bars = 0.1 mm.

Mandible (fig. 1G, H) and laciniae with fine teeth in extant species. Palpus (fig. 1E, F, 23D) with 4–5 segments, segment 3 ovoid to elongate, with capitate sensilla scattered on mesal surface, at least extant species with membranous area between segments 3 and 4 + 5. *Thorax*: With three anterior pronotal apodemes (known only in extant species).

Scutum with scattered elongate setae. Scutellum angular in dorsal view. Anapleural suture elongate. *Wing* (fig. 1L): Without macrotrichia, fine microtrichia present on all membrane. Alula with or without fringe of macrotrichia. Costa extending to or beyond apex of R_3 . Both radial cells present. M bifurcating distal to r-m. r-m parallel to R_1 .

Legs: Femora, tibiae slender. Legs lacking armature except in some with pair of stout setae on apex of tarsomeres 1–4 of all legs. TR of foreleg/hindleg = 1.7–2.2. Fore- and midleg trochanter without pair of thick setae. Midleg tibia with or without apical spur. Hindtibia apex with two rows of spines. Hindleg first tarsomere with or without thick basal spine, with scattered slender or stout setae. Claws on fore-, mid-, hindleg equal in size, both equal on each leg, each claw simple or toothed (fig. 1I, J). Empodium slender. *Genitalia:* Two large, one markedly smaller spermathecae. Sternite 9 continuous medially. Segment 10 with pair of setae. Cerci short to moderately elongate.

Egg (fig. 2A): Very light yellowish brown, appearing nearly white during development of larva. Elongate and slender. With 9–10 longitudinal rows of short, minute tubercles, each tubercle slender at base, expanded distally (fig. 2B). Anterior end more rounded than posterior end. Eggshell opening a single dorsal slit along most of length.

All larval instars: *Head capsule* (figs. 2H, K, 3A, C, G, 7A, B, 8A, B, 12A, B, 13A, B): Nearly square in dorsoventrally viewed outline; light brown, with only pigmentation present: dark epipharyngeal bar, premandible, apex of mandible; eye in later instars (some seconds, all thirds, fourths) a single, roughly circular to oval spot. Ecdysial suture extended anteriorly slightly beyond level of sensillum s, possibly longer but difficult to discern; area of thinner cuticle broad in area of sensilla j (anterior one), p, r. Ventral suture not present. Setae all simple (not bifurcate), arrangement as in figures 2H, K, 3C, G, 7A, B, 8A, 12A, B, 13A, B; following sensilla present: x (both setae present), t (or possibly an anteriorly placed q), s, p (two long setae, posterior one expanded distally), r (a short peg), j (anterior one a short peg on head capsule; other a more elongate seta on anterior margin of cervix), o (both an equally long seta), w, u, m, v, and y. Antenna (figs. 9A, B, 14A, B) elongate, with three segments; with well developed, short, basal segment, segments 2–3 short, slender, segment 3 tapering to slender, elongate apex; first segment otherwise bearing greatly elongate, multiporous blade and five other sensilla: accessory blade, sensilla 1–4; sensillum 1 long,

slender, with apical pit with small peg; sensillum 2 moderately elongate; sensillum 3 short, bilobed; sensillum 4 moderately elongate, with pores. Labrum (figs. 3A, 15A, B, 17C, 19) wide, with well developed torma, with well developed, dark, articulating, apically bent premandible; torma abutting lateral margin of stout, black, transverse epipharyngeal bar; epipharyngeal bar forming large, ventrally directed, internal, median lobe, posterodorsally directed bilobed apodeme and lateral apodeme abutting torma; labrum with 10 sensilla: sensilla 1–4 an anterodorsal group, with sensillum 1 a peg in pit, sensillum 2 a styloconicum on cuticular projection, sensilla 3, 4 lobe-shaped with 4 longer than 3, sensillum 5 an elongate seta, sensilla 6, 7 basally stout basiconica, sensilla 8, 9 laterally placed, sensillum 8 short seta, sensillum 9 a short peg, sensillum 10 a stout seta; ventral margin with well developed scopae, 18–21 more-or-less uniform teeth (three lateral teeth more stout) in undivided row. Mandible (figs. 2I, 3E, 10A) curved, apical half tapering to sharp, darkly pigmented, point, with dorsal and ventral grooves; with large to very small lobe (not visible in some specimens) on inner surface; with subbasal seta and minute peg in pit on outer margin; with well developed apodeme attached to dorsal margin of mandible, extending into posterior half of head capsule. Maxilla (figs. 10B, 16B, 17D) well developed, wide; palpus elongate; large lobelike, apically tapering plate dorsal to base of palpus; with postero-medial elongate seta; palpus with 4 apical or subapical sensilla, two lateral sensilla each with elongate slender nib; group of 7 thick sensilla lateral to palpus: sensillum 1 extending to about half length of palpus; sensillum 2 with rounded apex; sensillum 3 short, arising near base of sensillum 4; sensillum 4 with elongate apical nib; sensillum 5 on elongate cuticular extension; sensillum 6 with rounded apex, ribbed; sensillum 7 with rounded apex; lateral seta elongate. Pharyngeal complex (figs. 2J, 3F) well developed, epipharynx with two lateral arms, apparently lacking combs (present but difficult to discern in some other Ceratopogonidae). Hypopharynx with lateral arms articulating with lateral apices of lateral arms of epipharynx. *Thorax, abdomen:* Cuticle unpigmented,

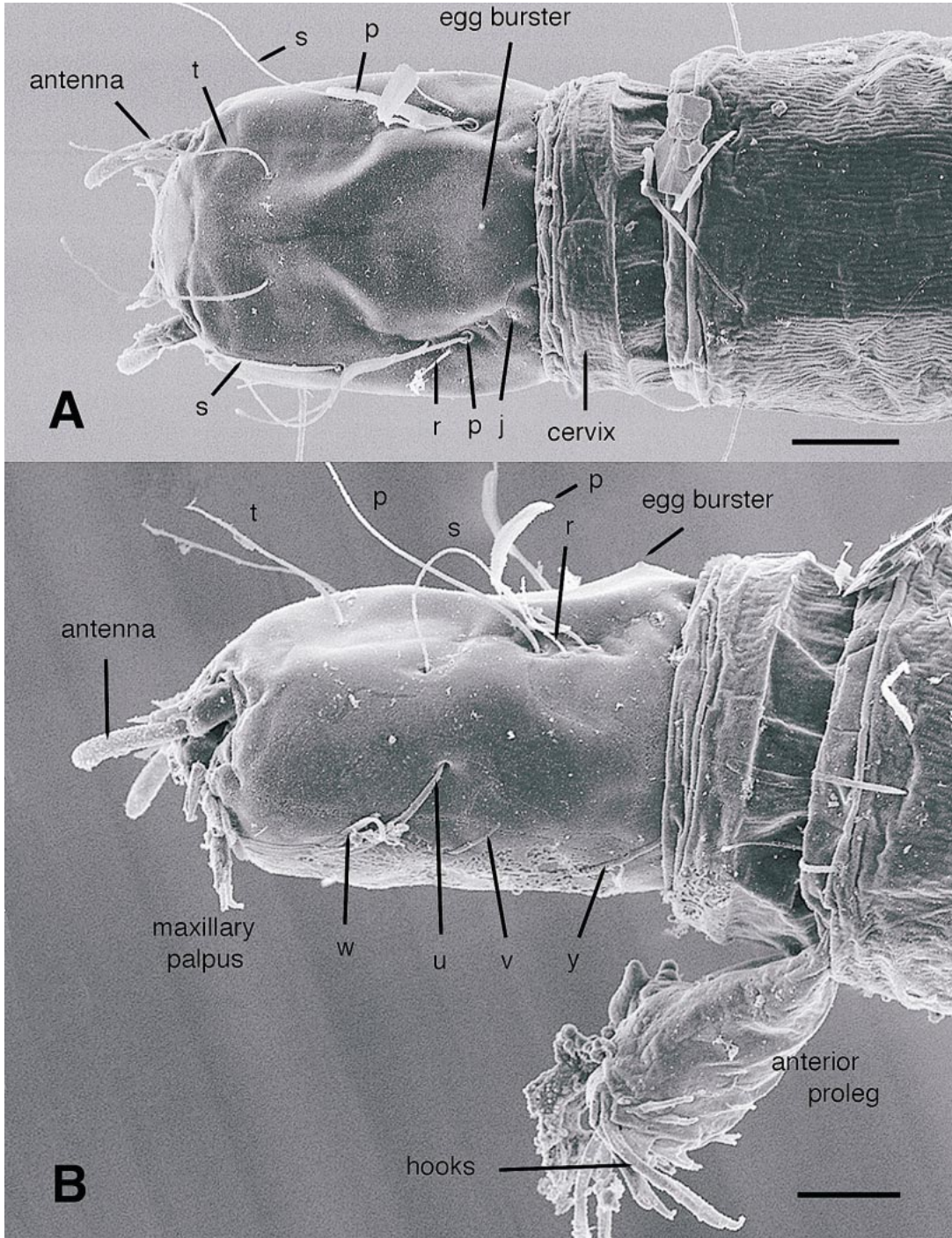


Fig. 7. Structures of the first-instar larva of *Austroconops mcmillani*. **A.** Head capsule in dorsal view. **B.** Head capsule and anterior proleg in lateral view. Scale bars = 10 μ m.

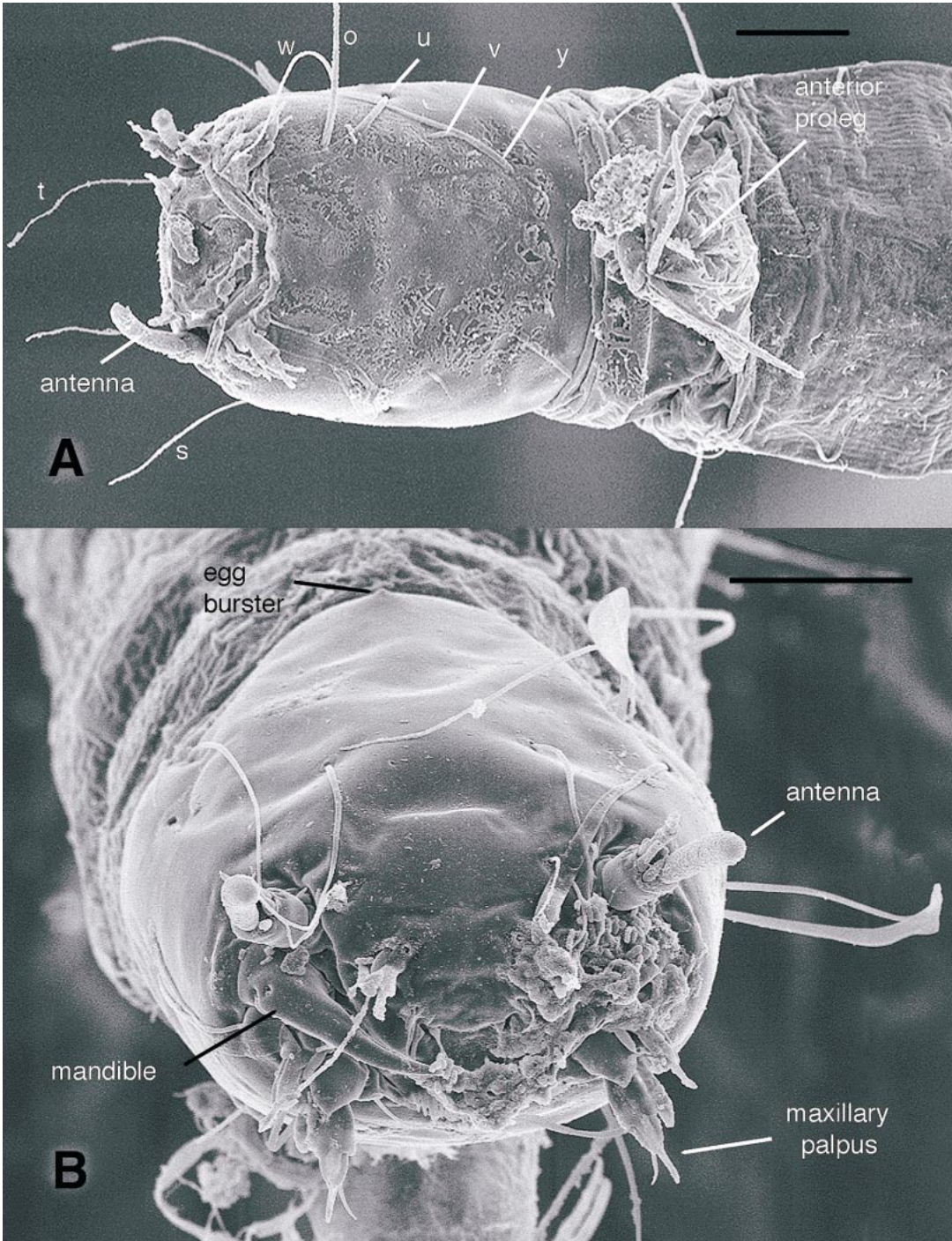


Fig. 8. Structures of the first-instar larva of *Austroconops mcmillani*. **A.** Head capsule and anterior proleg in ventral view. **B.** Head capsule in anterodorsal view. Scale bars = 10 μm .

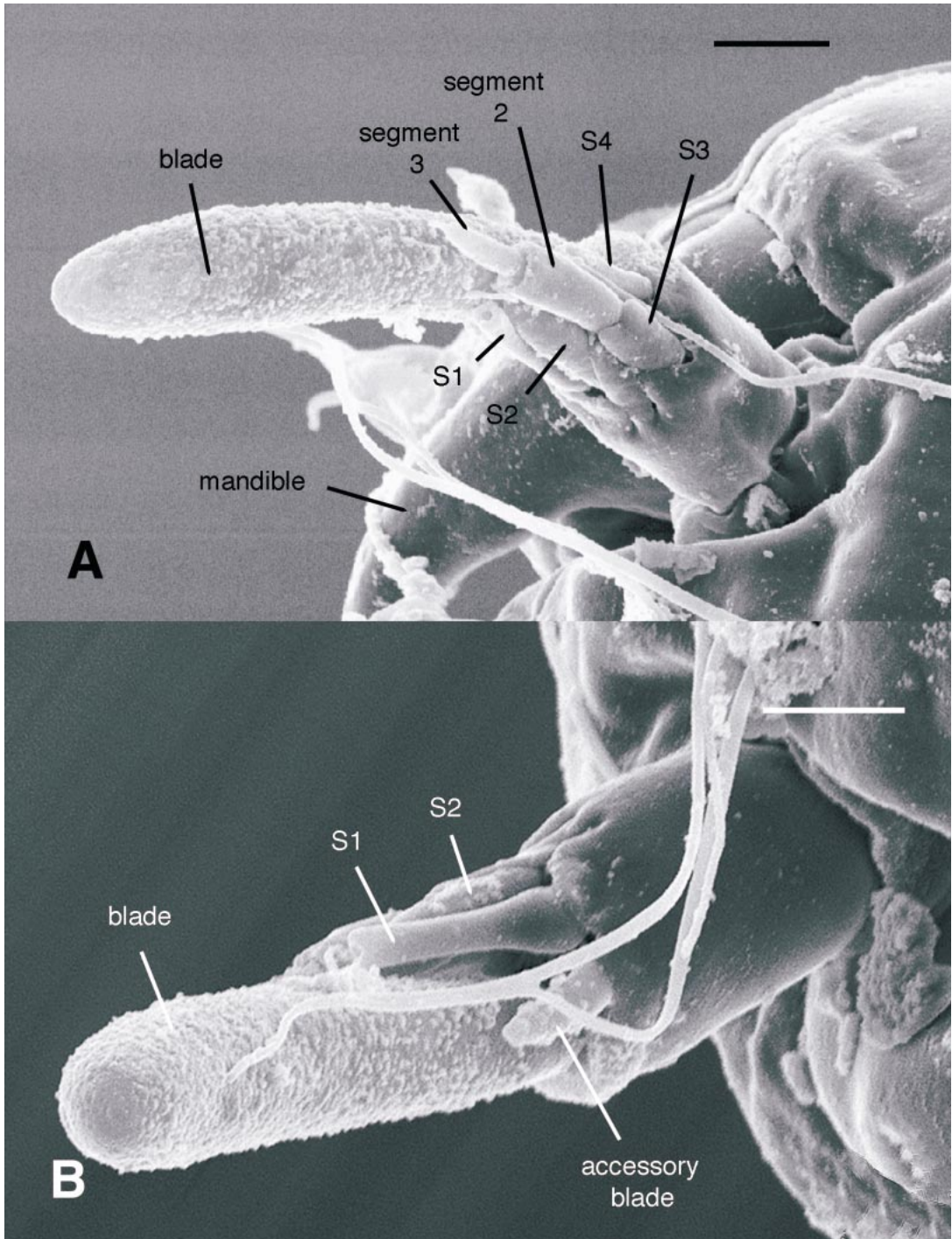


Fig. 9. Right antenna of the first-instar larva of *Austroconops mcmillani*; s = sensillum. **A.** In dorsal view. **B.** In mesal view. Scale bars: A = 2 μm , B = 1 μm .

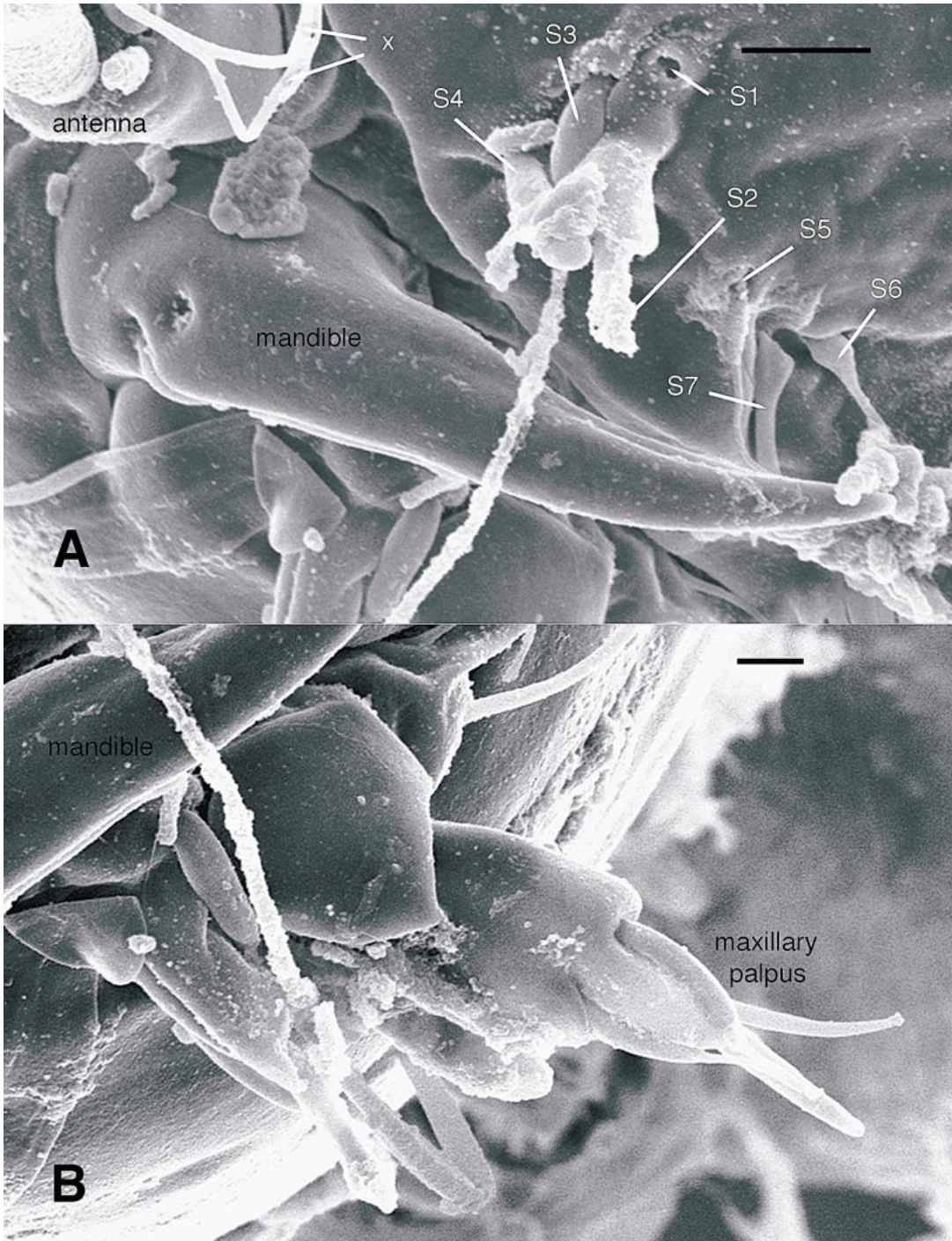


Fig. 10. Structures of the first-instar larva of *Austroconops mcmillani*; s = sensillum. **A.** Right mandible and right portion of labrum in anterodorsal view. **B.** Right maxilla in anterodorsal view. Scale bars = 2 μ m.

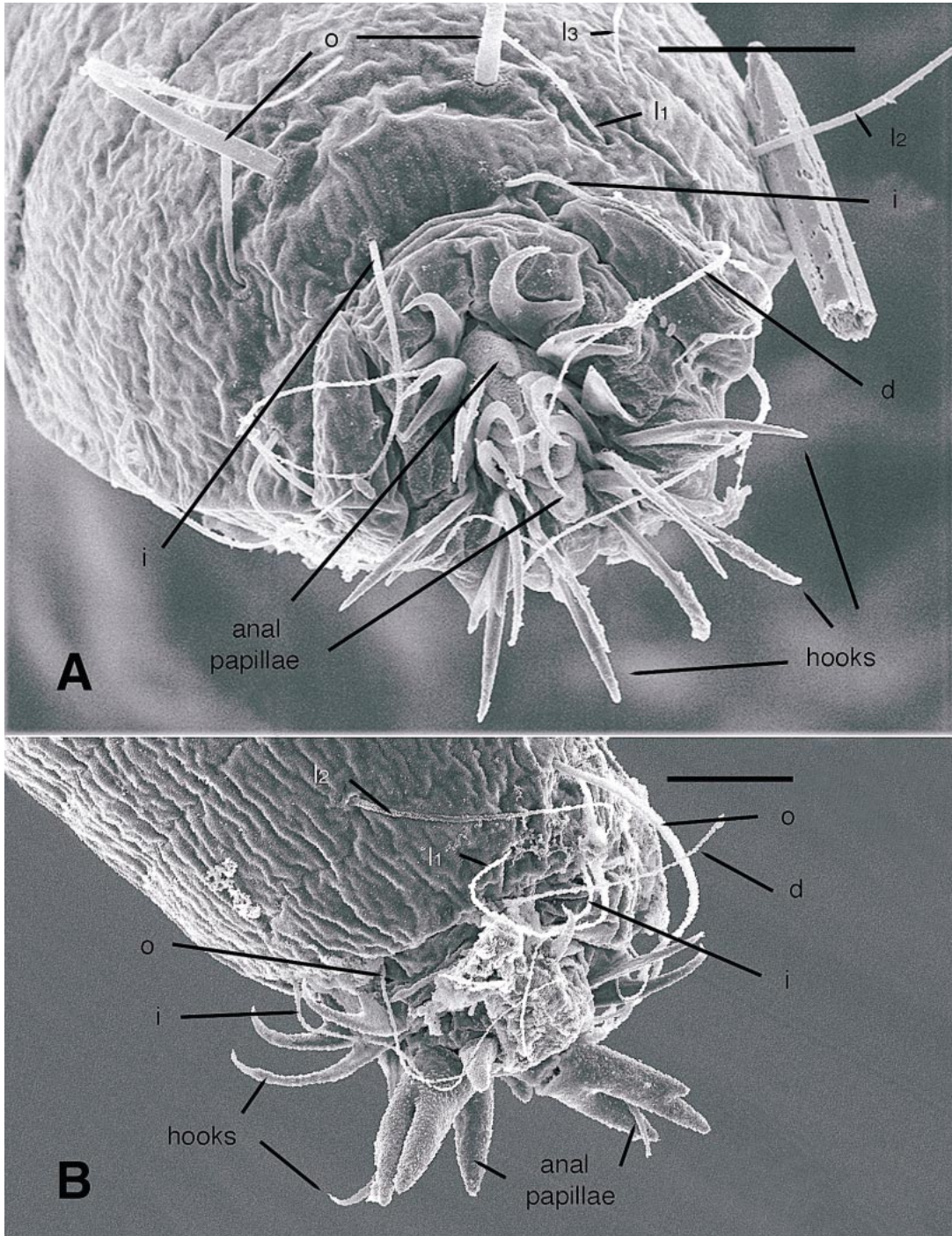


Fig. 11. Abdominal segment 9 of the first-instar larva of *Austroconops mcmillani*. **A.** With partially extruded proleg and anal papillae, in posterodorsal view. **B.** In lateral view. Scale bars = 10 μ m.

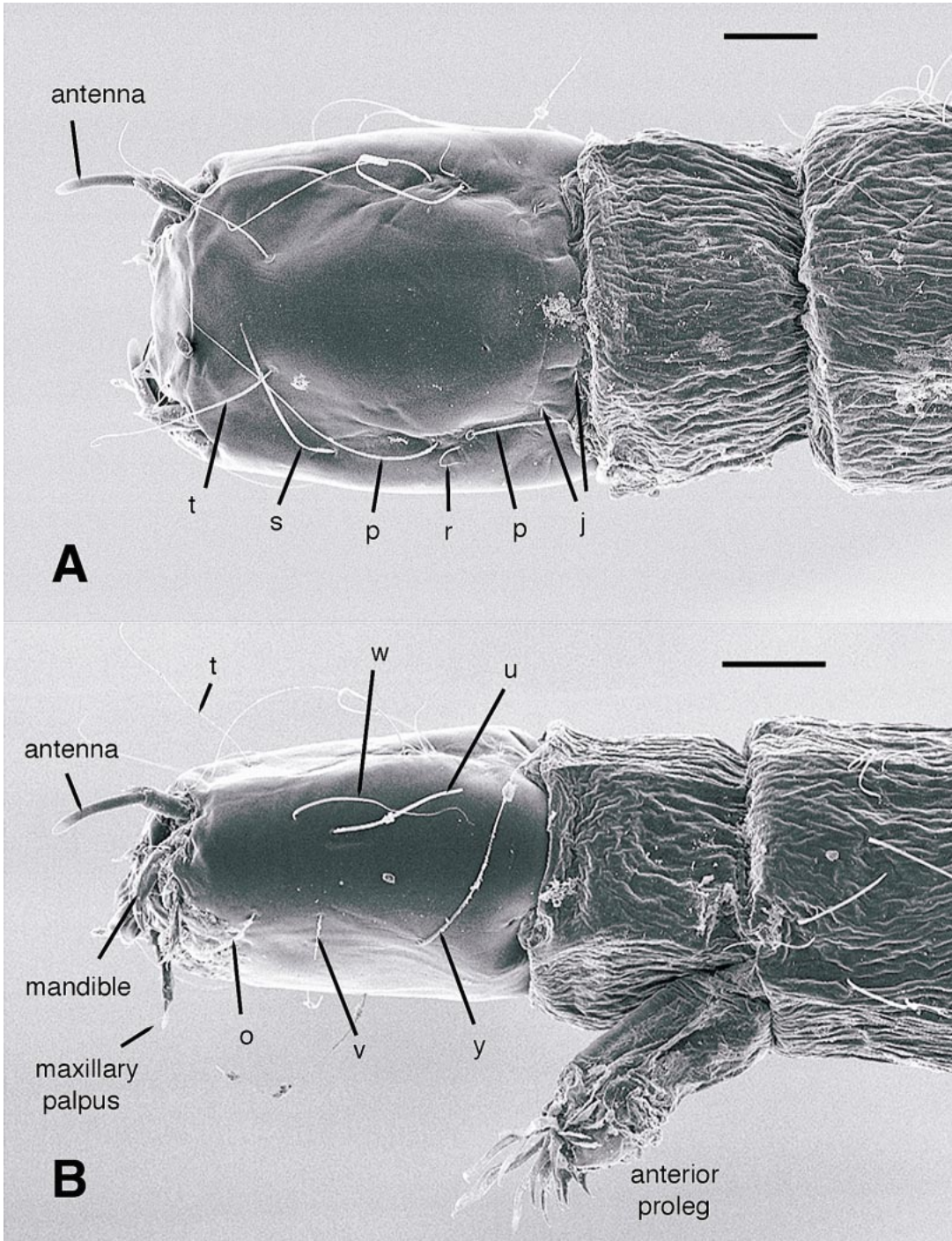


Fig. 12. Structures of the fourth-instar larva of *Austroconops mcmillani*. **A.** Head capsule in dorsal view. **B.** Head capsule and anterior proleg in lateral view. Scale bars = 20 μm .

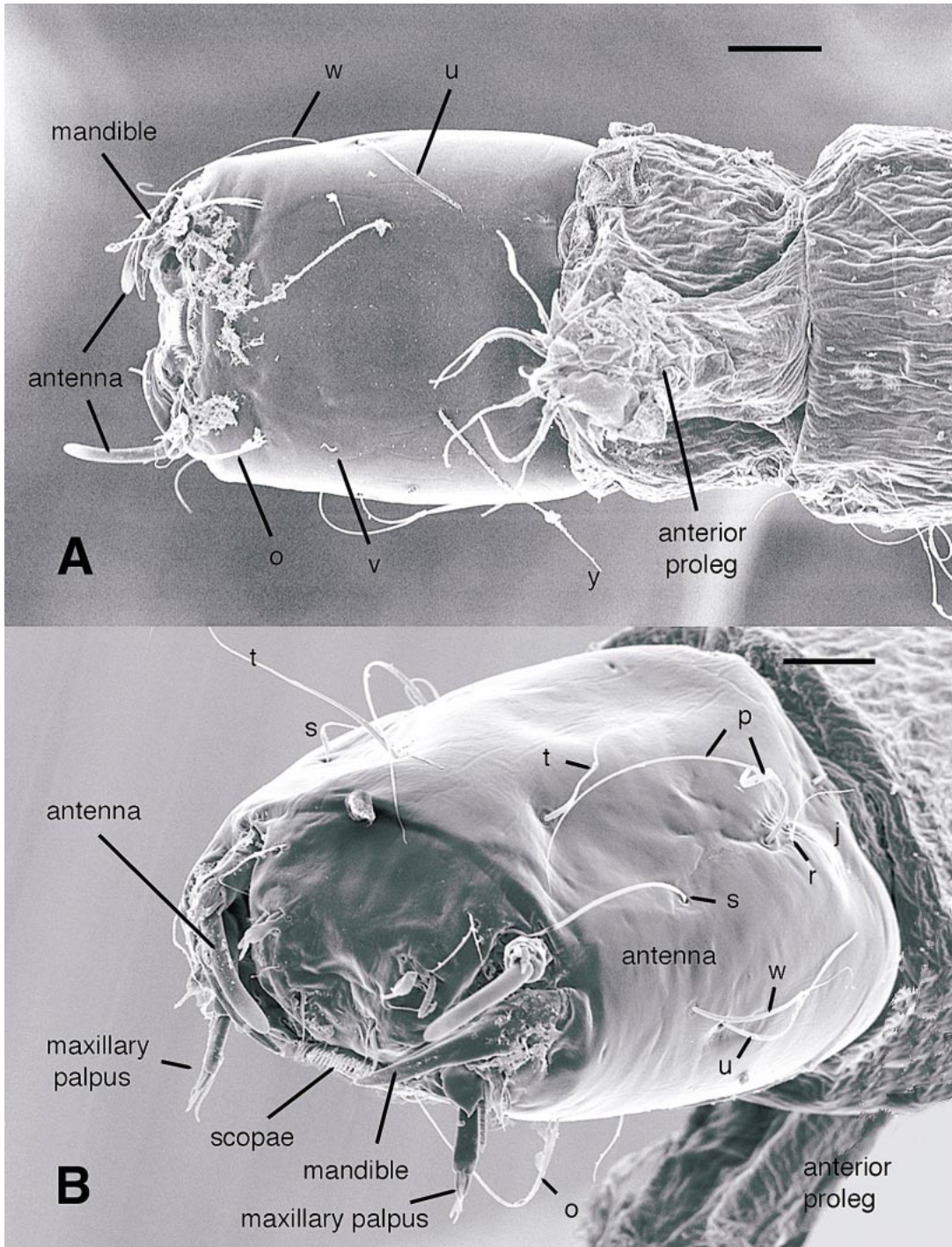


Fig. 13. Structures of the fourth-instar larva of *Austroconops mcmillani*. **A.** Head capsule and anterior proleg in ventral view. **B.** Head capsule in anterolateral view. Scale bars = 20 μm .

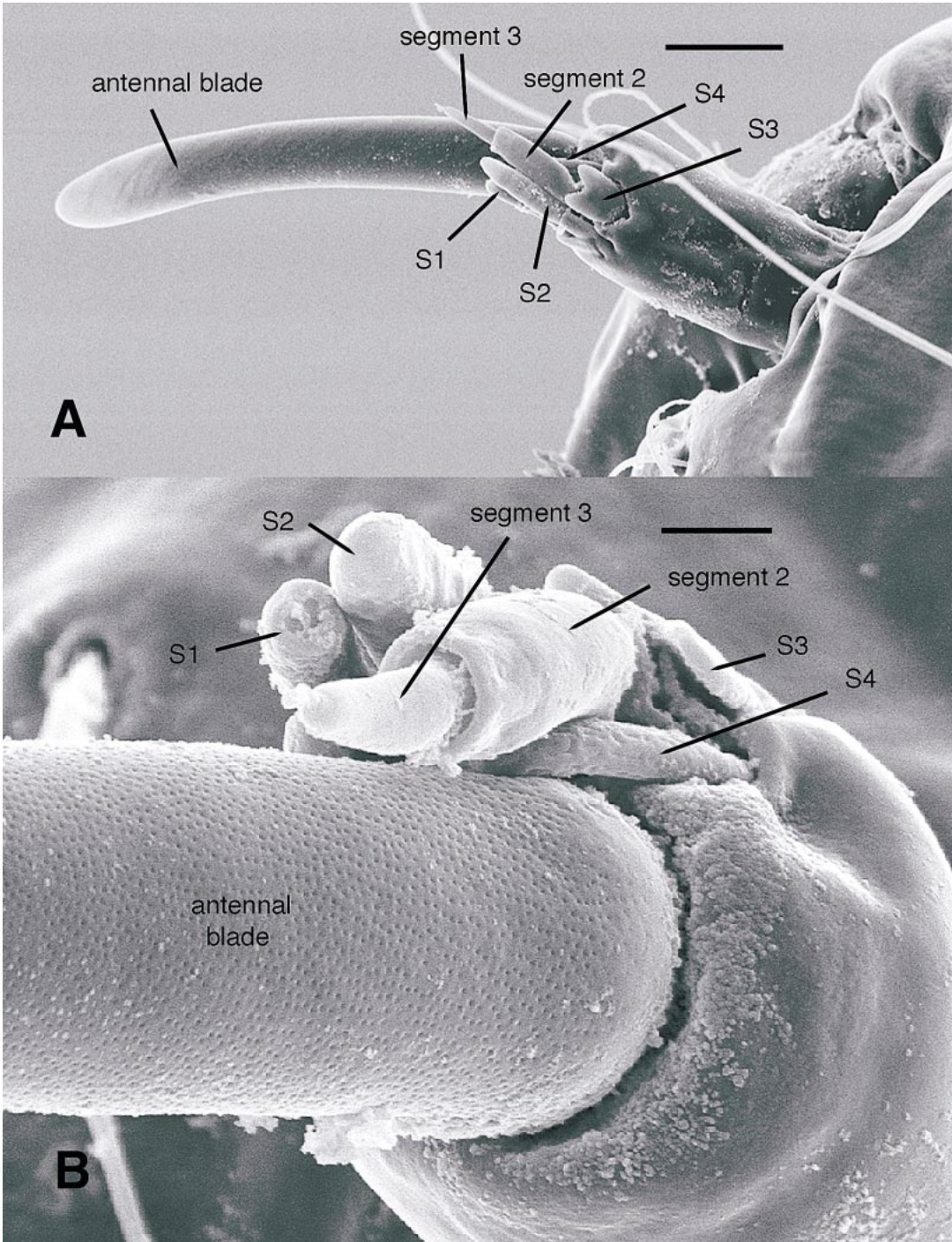


Fig. 14. Antennae of the fourth-instar larva of *Austroconops mcmillani*; s = sensillum. **A.** Right antenna in dorsal view (see fig. 12A for less magnified view). **B.** Left antenna in distal view. Scale bars: A = 5 μ m, B = 1 μ m.

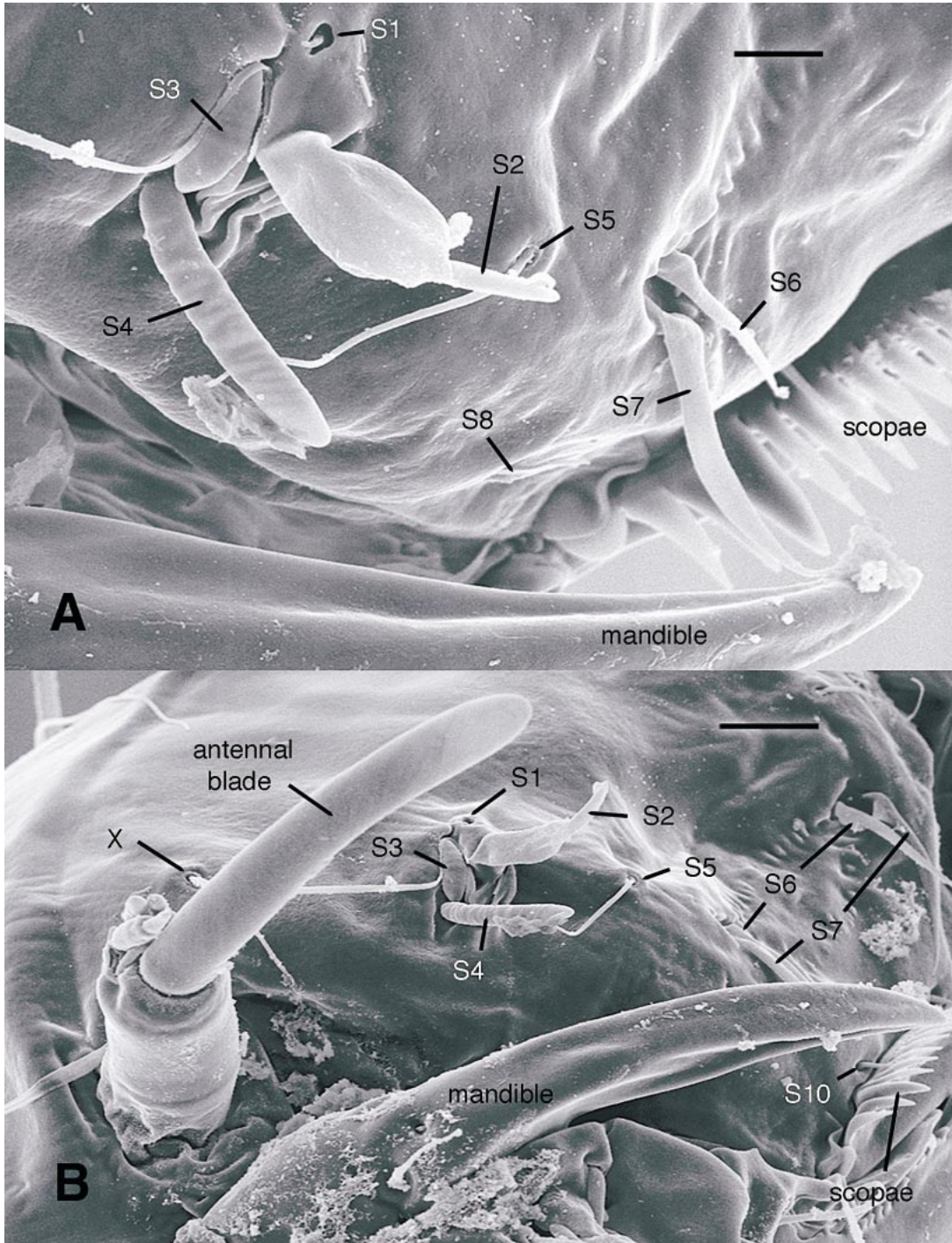


Fig. 15. Structures of the fourth-instar larva of *Austroconops mcmillani*; s = sensillum. **A.** Right portion of labrum in dorsoanterolateral view. **B.** Labrum, right antenna, and right mandible in anterolateral view. Scale bars: A = 2 μ m, B = 5 μ m.

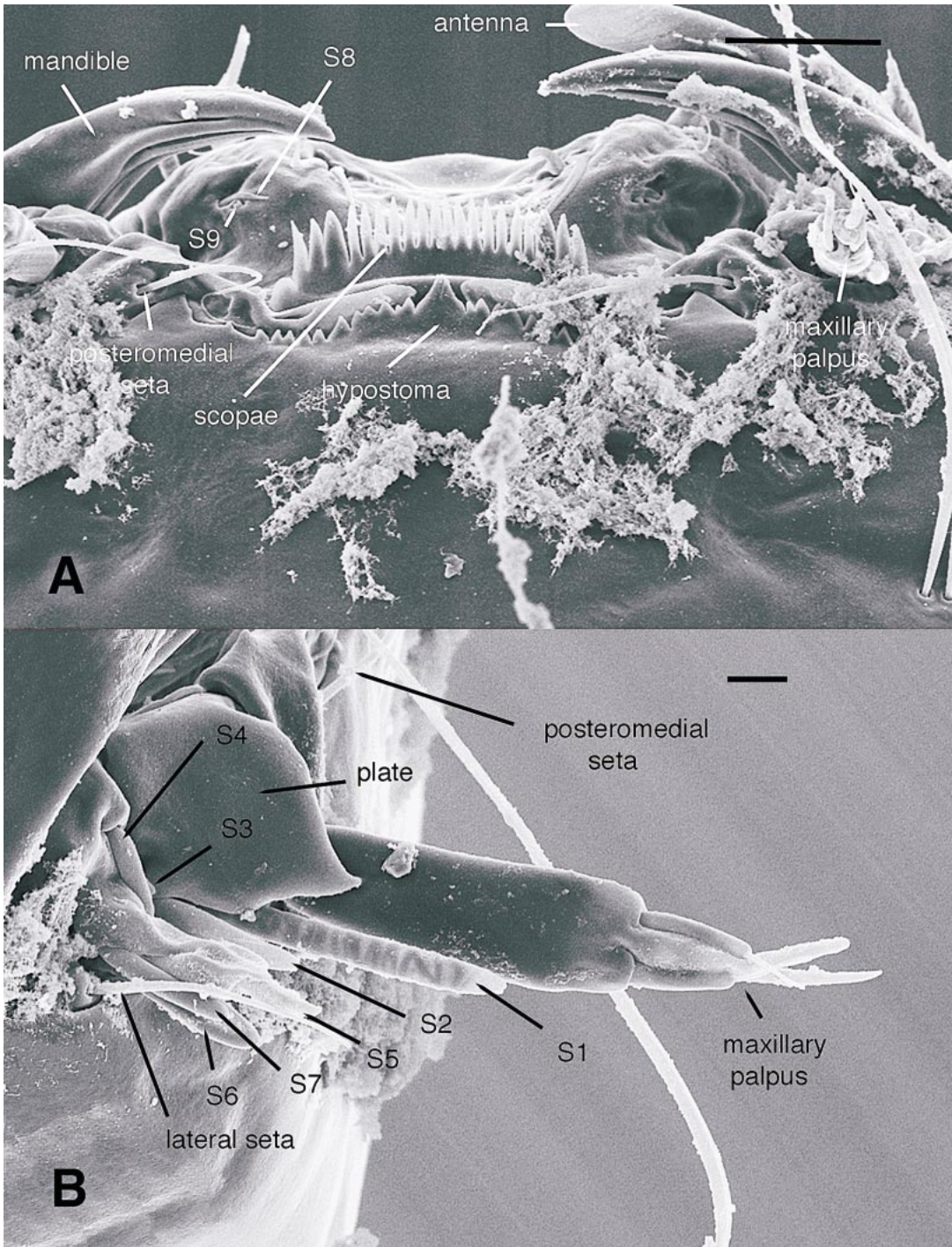


Fig. 16. Structures of the fourth-instar larva of *Austroconops mcmillani*; s = sensillum. **A.** Anterior portion of head capsule in ventral view. **B.** Right maxilla in anterolateral view (see Fig. 15B for less magnified view of base of maxilla). Scale bars: A = 10 μ m, B = 2 μ m.

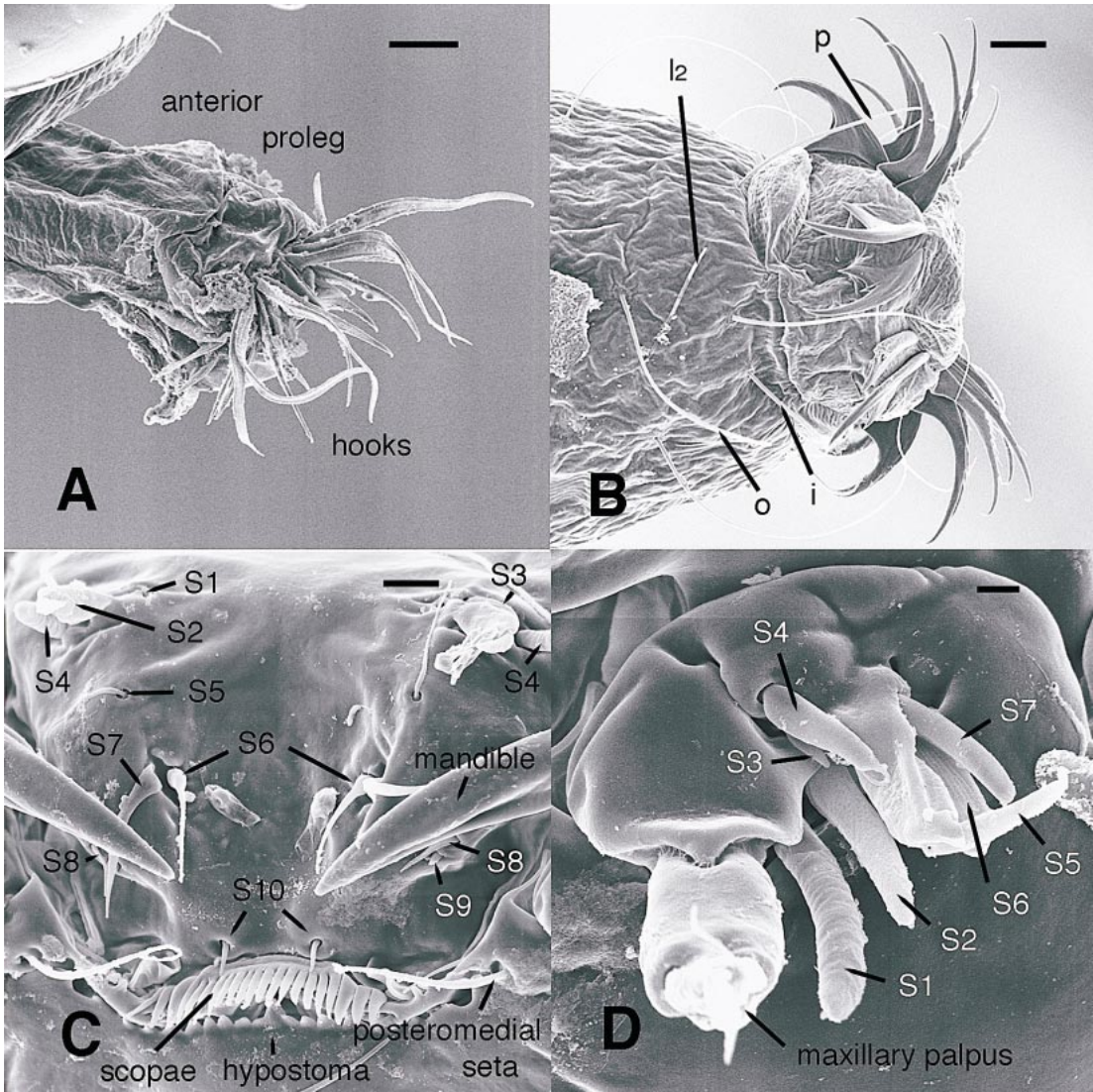


Fig. 17. Structures of larvae of *Austroconops mcmillani*; s = sensillum. **A.** Fourth-instar larval anterior proleg in anterolateral view. **B.** Fourth-instar larval posterior portion of abdominal segment 9 in dorsolateral view. **C.** Third-instar larval labrum in anterior view. **D.** Third-instar larval left maxilla in anterior view. Scale bars: A, B = 10 μm , C = 2 μm , D = 1 μm .

transparent, thin. Prothorax secondarily divided, with well developed cervix; with elongate proleg (figs. 2C–G, 4B, 7B, 12B, 17A, 18), with apical hooks, 5–6 (per half) anterior terminal hooks elongate, posterior hooks short; proleg capable in life of being withdrawn into prothorax (posterior to cervix). Segment nine (figs. 3B, H, 11A, B) with well-separated (with bases not closely ap-

proximated) setae: dorsal setae o, i, l_1 , d, l_2 , l_3 , l_4 , ventral setae i, o, l_1 , l_2 , v; posterior proleg (figs. 2C–G, 3B, 11A, B, 17B) a single posterior structure with about 15–20 well developed hooks, dorsal hooks with broader bases than ventral, more slender hooks; ventral hooks with spicules; proleg capable of being extruded or withdrawn into body cavity. Four anal papillae, each apically bifur-

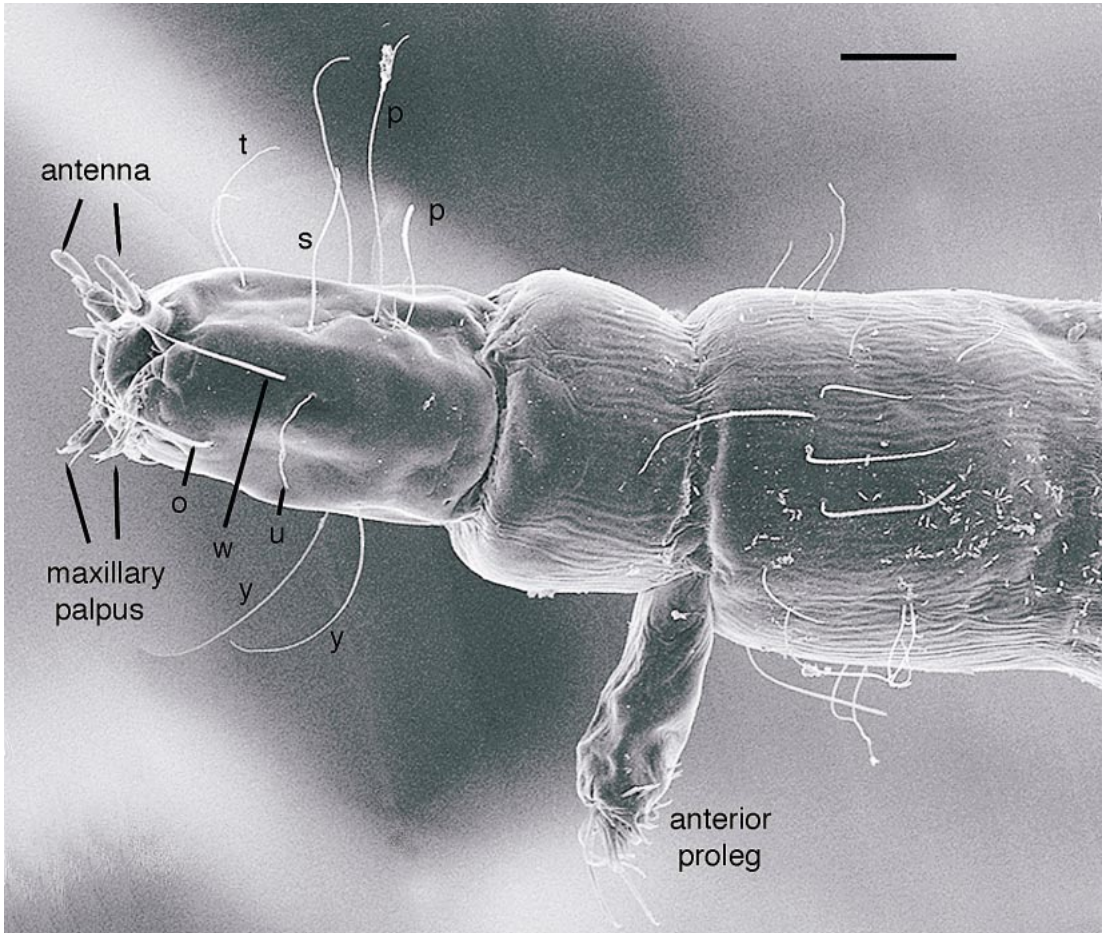


Fig. 18. Head capsule and anterior proleg of the third-instar larva of *Austroconops annettae* in lateral view. Scale bars = 20 μm .

cate. Midgut white, with annulations (obscured by fat body in some third- and fourth-instar larvae); anterior margin situated at midlength of fourth true abdominal segment (at anterior margin of apparent segment 8 in larvae with secondarily divided segments). With two Malpighian tubules.

First-instar larva: *Head capsule* (figs. 7A, B, 8A): With dorsal, darkly pigmented egg burster (figs. 2H, 7A, B, 8B). Without eyespot. Mandible (fig. 2I) with large triangular tooth on inner margin (not evident in some specimens). Hypostoma lacking teeth (figs. 2K, 8A) *Abdomen:* With or without segments 1–8 secondarily divided (so abdomen appears to have either 9 or 17 segments) (fig. 2C, D). Abdominal segment 9 (fig. 11A,

B) with at least dorsal setae o, i, d, 1_1 , 1_2 , 1_3 , ventral setae o, i present; others not visible but may be present; dorsal seta o notably thicker, longer than other setae on segment. Hemolymph unpigmented.

Second-instar larva: *Head capsule:* With or without eyespot. Mandible likely (not clearly visible) with moderately sized triangular tooth on inner margin. Hypostoma with well developed row of teeth. *Abdomen:* With segments 1–8 secondarily divided (so abdomen appears to have 17 segments) (fig. 2E). Abdominal segment 9 with uncertain number of setae; dorsal seta o at least slightly thicker than other setae on segment. Hemolymph unpigmented or very pale pink.

Third-instar larva: *Head capsule:* With

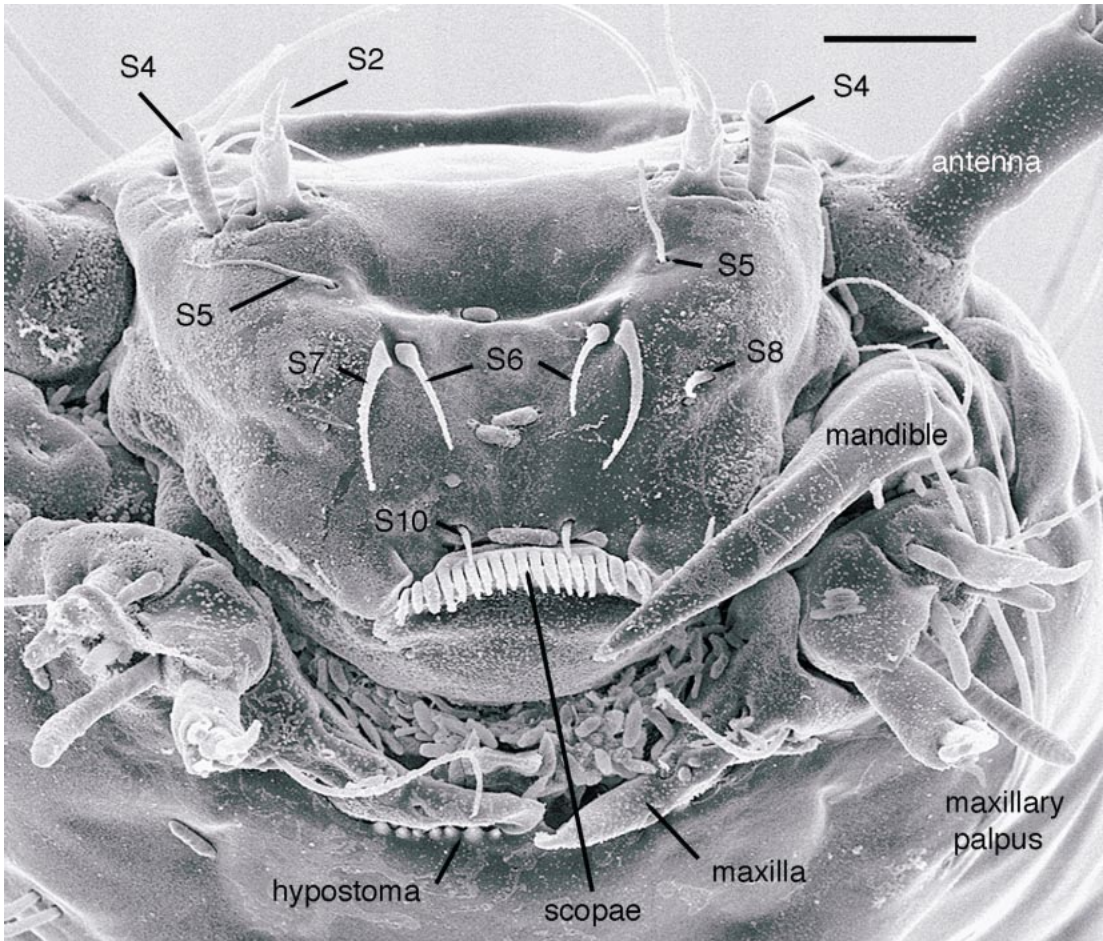


Fig. 19. Head capsule of the third-instar larva of *Austroconops annettae* in anterior view; s = sensillum. Scale bar = 5 μ m.

eyespot. Mandible with small bump on inner margin. Hypostoma (fig. 19) with well developed row of teeth, central tooth largest. *Abdomen*: With segments 1–8 secondarily divided (so abdomen appears to have 17 segments) (fig. 2F). Abdominal segment 9 with 7 dorsal, 5 ventral setae distributed as in figures 3H, 17B; dorsal seta o equal in diameter to other long setae on segment. Hemolymph unpigmented or pink. Some fat body visible in more mature larvae.

Fourth-instar larva: *Head capsule*: With eyespot. Mandible (fig. 3E) with small bump on inner margin. Hypostoma (figs. 3G, 16A) with well developed row of teeth, central tooth largest. *Abdomen*: With segments 1–8 secondarily divided (so abdomen appears to

have 17 segments) (fig. 2G). Abdominal segment 9 with 7 dorsal, 5 ventral setae distributed as in figures 3H, 17B; dorsal seta o equal in diameter to other long setae on segment. Hemolymph pink or reddish. Fat body present.

Pupa: Only pupa known is of *A. mcmilani*, described below.

DISTRIBUTION AND BIONOMICS

The only two extant species are restricted to southwestern Australia (fig. 22B), but Cretaceous fossils are known from France, Spain, Siberia, Lebanon, and Myanmar (Borkent, 2000a; Szadziewski, in press; Szadziewski and Arillo, 2001), proving that the

genus was once much more broadly distributed.

The only species in which females have been observed to bite are those of *A. mcmillani*, which feed on kangaroos and humans. However, the finely serrate mandible and retrorse lacinial teeth of the adult females of *A. annettae* strongly indicate that these too feed on vertebrates (Borkent, 1995: 129–132). The morphology of the claws of the female of *A. annettae* additionally may indicate that these feed on birds (see discussion below under that species). The mouthparts of fossil *Austroconops* are not visible (Borkent, 2000a), and therefore it is uncertain what they fed upon. The presence, however, of vertebrate blood-feeding in *A. mcmillani* and the phylogenetic position of the genus as an early lineage within the family where vertebrate blood-feeding is plesiotypic strongly suggest that all extinct species fed on vertebrates (Borkent, 1995, 2000a). Details of male swarming in *A. mcmillani* are given below.

First-instar larvae of *A. annettae* and *A. mcmillani* were both successfully reared to fourth-instar larvae (and *A. mcmillani* to the pupal stage) in very wet soil, with regular (generally every second day) additions of nematodes and a fecal infusion. All instars of the aquatic larvae were clearly attracted to fresh drops of fecal infusion as shown by the concentrations of larvae directly under these drops and they were rarely seen to feed on nematodes. This phenomenon, and the presence of well developed, finely toothed scopa (figs. 3A, 19) suggest that they are likely associated with feces or concentrated decomposing vegetation in nature (producing an abundance of microorganisms). Some second, nearly all third, and all fourth-instar larvae had pink or red hemolymph, indicating the presence of hemoglobin, which additionally suggests that they may be associated with an oxygen deficient wet habitat. Larvae cannot swim but use a combination of their anterior and posterior prolegs and, especially in later instars, a relatively slow serpentine body motion to move through wet substrate. Further details of behavior and habitat are provided below for each species.

Borkent et al. (1987) suggested that the blue-green pigmentation of live adult *A.*

mcmillani may have indicated that the then unknown larvae were feeding on algae because this coloration has been observed in some Ceratopogonidae such as some *Culicoides* species of the *schulzei* species group and some *Dasyhelea* Kieffer species which feed on algae as larvae. Our observations here show that the relationship between algal feeding and adult color is not substantiated for at least *A. mcmillani* as larvae matured to adulthood without feeding on algae. *Austroconops annettae* was also successfully reared to the fourth-instar without algae.

TAXONOMIC DISCUSSION

We consider the elongate, pale egg of *Austroconops* species unique within the family. Eggs laid by other Ceratopogonidae are initially pale but soon turn dark. However, of 103 extant genera, eggs have been described for only 18 genera and of those, 4 genera are known only as eggs described from within the female abdomen (so their final color cannot be determined).

We identified the four larval instars of both species based on the following evidence. First-instar larvae are easily identified by their darkly pigmented egg burster (figs. 2H, 7A, B, 8B). Because of the small number of measured second and fourth-instars of reared *Austroconops* larvae it was initially difficult to identify the instars 2–4. The fourth-instar of *A. mcmillani* was confidently identified because one of these molted to the pupal stage. Although the head capsule of this individual was not retrieved from the mud and therefore not measured, observations before it pupated showed that it was clearly close to, or within, the range of measurements reported here. Head capsule length increments of all instars followed Dyar's Law, increasing by a factor of 1.32, 1.31, and 1.34 for *A. mcmillani* and 1.33, 1.32, and 1.25 for *A. annettae*. The latter value, the factor of change for third to fourth-instar, may be due to the small sample size of fourth-instar *A. annettae* or perhaps to less than optimal feeding conditions (and hence smaller individuals). These values are similar to those reported for species of *Culicoides*, which are about 1.4 (Kettle and Lawson, 1952; Kettle and Elson, 1975).

There are significant statistical differences in egg characteristics (table 3) and larval head capsule lengths (table 4) of the different instars between *A. mcmillani* and *A. annettae*. Considering, however, that these immatures were obtained from eggs laid by a very few females, and that the larvae were reared under laboratory conditions, the size differences noted here may be artifacts. Otherwise, eggs and larvae of the two species could not be distinguished from one another.

Larvae of *Austroconops*, when compared to other Ceratopogonidae, are missing head capsule sensilla z, k (sensory pit), and q. Also, there are two additional dorsolateral setae on larval abdominal segment 9 (fig. 3H), here labeled as l_3 and l_4 , which have not been reported in other Ceratopogonidae.

The larval antennal sensilla of Ceratopogonidae have never been described in sufficient detail to determine most homologies within and outside the family. Larvae of *Austroconops* species have a well-defined basal segment bearing 6 apical sensilla and a further second and third segment (figs. 9A, B, 14A, B, 20A). Based on position, relatively large size, and a uniformly porous surface, the most elongate, porous sensillum is homologous to the "large lobe" present in *Culicoides* (Murphree and Mullen, 1991) and most other Ceratopogoninae (Borkent and Bissett, 1990; Borkent and Craig, 1999). Based on position and some details of structure, the following sensilla are likely homologous to sensilla in Chironomidae: most elongate, porous sensillum = blade; mesal short sensillum = accessory blade; short bilobed sensillum labeled sensillum 3 here = fused style and peg sensillum. The remaining three short sensilla do not have readily apparent homologies with Chironomidae; they are labeled here as sensilla 1, 2, and 4. Sensillum 1 has an open apex bearing a tiny peg. Sensillum 4 has a porous surface.

The labrum of *Austroconops* shows a number of similarities to other Ceratopogonidae. Sensilla 1–4 are clearly present as a group on the labra of most other Ceratopogonidae (Hribar and Mullen, 1991, labeled as "sensillum styloconicum"). In many Chironomidae the two sensilla SIVA and SIVB on the anterior portion of the labrum are morphologically very similar to S2 and S4, and

these are likely homologous. Chironomidae S1, just dorsal to the labral lamellae, probably is homologous to our S10, and the scopae present in *Austroconops* and Ceratopogoninae are probably homologous to the labral lamellae (Wiederholm, 1983). Further detailed comparisons require further study of these structures in numerous taxa (both SEM and study of nerves).

Borkent et al. (1987) reported an "M-shaped apodeme" in the female genitalia of *A. mcmillani*. In further study we are puzzled as to the nature of this structure, which varies in both *A. mcmillani* and *A. annettae* from a faint M-shaped sclerotization to the presence of a pair of laterally positioned, pigmented sclerites. Some other Ceratopogonidae also have sclerotized structures anterior to the fused or separated sternite 9 (e.g., some *Leptoconops*, some *Culicoides*, *Alluaudomyia* Kieffer, and others). Careful histological study is needed to better interpret this feature.

Cladistic analysis below indicates that, among extant taxa, *Austroconops* is the sister group of *Leptoconops* and that together they form the sister group to all remaining extant Ceratopogonidae. Eight species of *Austroconops* are now known: two of these are extant and six are Cretaceous fossils:

- A. annettae*, n.sp. Borkent, this publication. Australia (Western Australia)
- A. borkenti* Szadziewski and Schlüter, 1992: 78. France. Upper Cretaceous
- A. fossilis* Szadziewski, 1996: 38. Lebanon. Lower Cretaceous
- A. gladius* Borkent, 2000a: 378. Lebanon. Lower Cretaceous.
- A. gondwanicus* Szadziewski, 1996: 38. Lebanon. Lower Cretaceous
- A. mcmillani* Wirth and Lee, 1958: 337. Australia (Western Australia)
- A. megaspinus* Borkent, 2000a: 381. Lebanon. Lower Cretaceous.
- A. sibericus* Szadziewski, 1996: 40. Russia. Upper Cretaceous

The genus *Jordanoconops* Szadziewski was proposed as a monotypic genus to include a Lower Cretaceous Jordanian amber fossil, *Jordanoconops weitschati* Szadziewski (Szadziewski, 2000). It may actually be a member of *Austroconops* (see below under

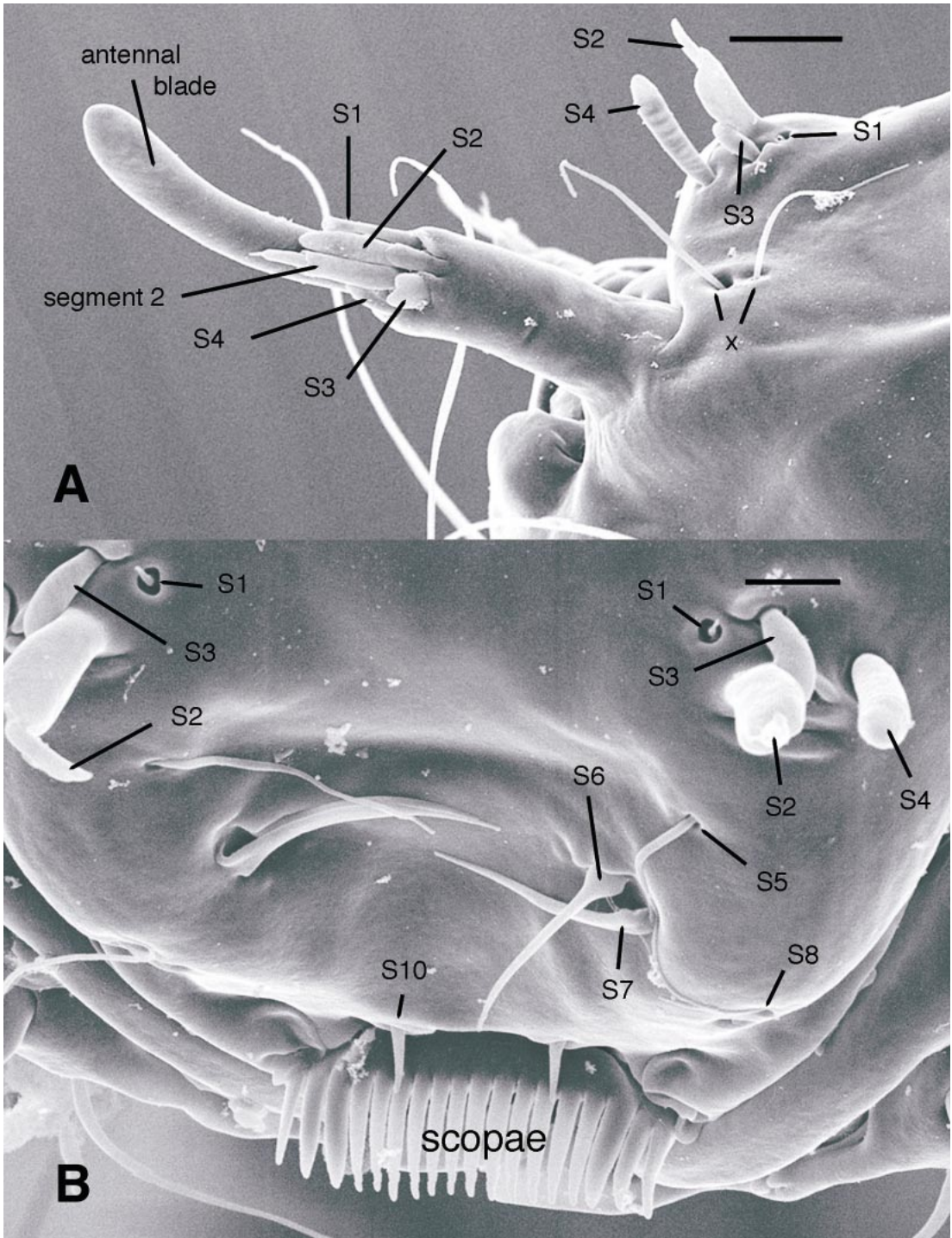


Fig. 20. Structures of third-instar larva of *Austroconops annettae*; s = sensillum. **A.** Left antenna and dorsal portion of labrum in dorsal view. **B.** Labrum in anterodorsal view. Scale bars: A = 5 μm , B = 2 μm .

Relationships Between Species of *Austroconops*.

KEY TO EXTANT SPECIES OF *AUSTROCONOPS*

Borkent (2000a) provided a key to extant and extinct males and females of *Austroconops*. The new species *A. annettae* may be distinguished as follows.

1. Ratio of male flagellomeres 12/13 = 0.62–0.77 (fig. 1A); female palpal segment 3 swollen in lateral view (fig. 1E); ratio of palpal segment 3/4 + 5 = 1.36–1.91 for the male, 1.43–1.75 for the female; female with only a very slender, setalike tooth on each claw (fig. 1I) *A. mcmillani*
- Ratio of male flagellomere 12/13 = 0.43 (fig. 1B); female palpal segment 3 relatively slender in lateral view (fig. 1F); ratio of palpal segment 3/4 + 5 = 1.04 for the male, 1.05–1.32 for the female; female with large tooth at the base of each claw (fig. 1J) *A. annettae*

Austroconops mcmillani Wirth and Lee

Austroconops mcmillani Wirth and Lee, 1958: 337. Holotype female, National Park, Perth, Western Australia, Australia, 12-XII-1954 (ANIC).

Austroconops mcmillani: Borkent, Wirth and Dyce, 1987. Male adult. Female adult (in part).

DIAGNOSIS: Male. The only extant *Austroconops* with flagellomere 12 elongate, 0.6–0.8 the length of flagellomere 13 (fig. 1A). **Female.** The only extant *Austroconops* with simple claws (each with only a very fine basal tooth) (fig. 1I). **Egg and larva (all instars).** Not distinguishable from those of *A. annettae* (see generic diagnosis above). **Pupa.** The only known pupa in the genus (see generic diagnosis above).

DESCRIPTION: Male adult: Descriptive statistics in table 1. **Head:** Antenna (fig. 1A) with well developed plume. Flagellomere 12 elongate, with subbasal constriction, 0.62–0.77 length of flagellomere 13 (fig. 1A). Mouthparts moderately long. Palpus (fig. 1C) with 4 segments, segment 3 ovoid in lateral view, with capitate sensilla scattered on surface or in shallow pits. **Thorax:** Scutellum angular in dorsal view. **Wing:** Costa extending to or just beyond apex of R₃. **Legs:** Legs lacking armature. Bristles on midleg tibia, first tarsomere of moderate length (fig. 1M).

Midleg tibia without apical spur. Hindleg first tarsomere without thick basal spine or stout setae. Claws simple, each claw apically bifid. **Genitalia:** In life, rotated about 90°. Apicolateral process absent. Gonocoxite short. Gonostylus mostly straight, tapering to curved apex, apical spine absent. Parameres fused medially. Aedeagus short, setose lobe with ventral plate. **Female adult:** Descriptive statistics in table 2. **Head:** Ommatidia narrowly separated dorsomedially. Flagellomeres gradually increasing in length from flagellomere 2 to 13. Mouthparts moderately elongate, mandible (fig. 1G) broad, with fine teeth, most directed laterally or ventrolaterally, laciniae with well developed, fine retrorse teeth. Palpus (fig. 1E) with 4 segments, segment 3 well developed, swollen in lateral view, with capitate sensilla scattered on surface or in shallow pits. **Thorax:** Scutellum angular in dorsal view. **Wing:** Costa extending to or just beyond apex of R₃. **Legs:** Femora, tibiae slender. Legs lacking armature. Midleg tibia without apical spur. Hindleg first tarsomere without thick basal spine or stout setae. Foreleg, midleg, hindleg claws (fig. 1I) slender, evenly curved, each with fine inner setalike tooth. **Genitalia:** Cercus short. **Egg:** Descriptive statistics in table 3. **First-instar larva:** Head capsule length statistics in table 4. Total body length 0.76–1.26 mm (n = 6). **Second-instar larva:** Head capsule length statistics in table 4. Total body length 1.44–2.13 mm (n = 2). **Third-instar larva:** Head capsule length statistics in table 4. Total body length 2.60–3.72 mm (n = 9). **Fourth-instar larva:** Head capsule length statistics in table 4. Total body length 3.78–4.84 mm (n = 3). **Pupa:** Total length 2.0 mm. General coloration of exuviae, including respiratory organs, light brown. Integument smooth with some fine rounded spicules on dorsal surface of anal segment. Initially, live individuals with reddish hemolymph, after 24 hours with reddish core of tissue, with subcutaneous bluish-green patches in thorax, abdomen (further developmental details given below). Length of cephalothorax/length of abdomen posterior to cephalothorax = 0.70. Dorsal margin of thorax angular in lateral view (fig. 4A). Operculum (fig. 4D) broad dorsally, narrow ventrally, with elongate anteromedial seta (fig. 4E) directed anteriorly,

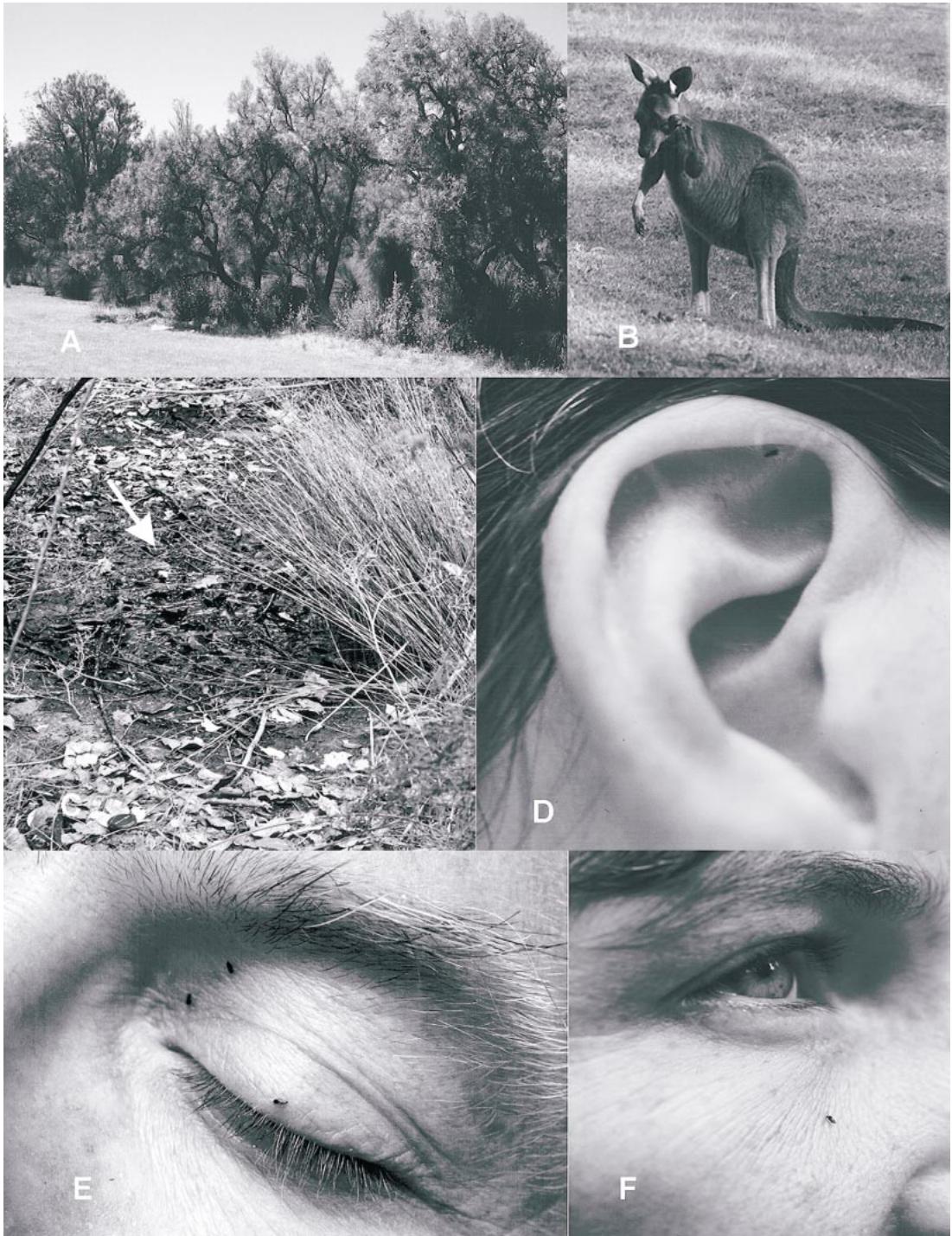


Fig. 21. **A.** Southwestern margin of fairway 2 at Yanchep National Park where adult *Austroconops mcmillani* were abundant. **B.** Western Grey Kangaroo (*Macropus fuliginosus*) rubbing eye in response to biting females of *A. mcmillani* at Yanchep National Park. **C.** Wet area from which adult *A. annettae* were collected at 5 km SSW of Forest Grove. Arrow points to wet patch; adults swept from tuft of

on well developed tubercle; with single pore; tubercle situated dorsally on operculum. Labral, mandibular, maxillary, labial sheaths (fig. 4C) well developed, palpal sheath short, not extending beyond apex of labial sheath. Anterodorsal setae (figs. 4A, 5A), two, both elongate, well developed, lying against dorsomedial surface of respiratory organ at about its midlength, with pore on dorsal surface of tubercle. Dorsolateral setae (fig. 4F), three; two elongate, with posterior one slightly thicker, on well developed tubercle; third seta short, arising from near base of tubercle. Single, small ventromedial seta (fig. 4C). Two ventrolateral setae (fig. 4C), lateral one longer, thicker. Metathorax (fig. 6A) with two setae, one pore, lateral seta bifurcate, elongate, medial seta simple, short. Antennal sheath (fig. 5F) apex anterior to apex of portion of midleg lying medial to it. Apex of all legs (fig. 5F) terminating near apex of wing sheath. Wing sheath (fig. 5F) rounded apically, without marginal tubercle. Only apex of hindleg (fig. 4A) visible under lateral margin of wing sheath. Respiratory organ (fig. 5B, C), on well developed pedicel, length = 99 μm , laterally compressed, with anterior and slight posterior bulge in lateral view, with 18 pores abutting, arranged in single, more-or-less longitudinal (somewhat anterolaterally to posteromedially) row at apex. Dorsomedial (fig. 5A) a minute seta on anterior margin of scutum. Four dorsal setae (fig. 5A); setae i, ii, iv well developed, bifurcate; sensillum vi well developed, simple seta. Metathorax (fig. 6A) nearly completely divided medially, with bilobed medial protuberance from scutum protruding nearly to posterior margin of metathorax. Abdominal segments 2–8 (fig. 4A) with all setae bifurcate, with a few divided further (fig. 5D, E); sensilla separate from one another (none on common tubercle). Following sensilla present on segment 4 (fig. 5G), all setae on short, well developed tubercles: 2 dasm, i a pore, ii a seta; 4 dpm, i, ii, iv setae, iii a pore; lasm, 3 lpm, 3 vn all setae; vasm a pore. Segment 9 (fig. 6B) with well developed,

posterolaterally directed apicolateral process with very apex slightly bent dorsally, bearing single pore near base; genital sac moderately elongate, slightly wider than rest of segment, situated ventrally.

DISTRIBUTION AND HABITAT

Austroconops mcmillani is known from three sites in southwestern Western Australia (fig. 22B). A fourth locality from “National Park, Perth” cannot be specifically located (see Taxonomic Discussion below).

Adult *A. mcmillani* were collected at five sites in Yanchep National Park during 2001–2002 (fig. 22C: sites A–E). On November 20–21, 2001 adults were extremely abundant at fairway 2 in the golf course (fig. 22C; site A). Biting females were very common along the southern margin of the fairway (fig. 21A) and at times were attacking humans at the rate of more than 50 per minute! Further observations on biting are given below. Swarming males were collected directly southeast of the tee-off area at the southwestern end of the fairway, which was the driest area on the fairway. The southeastern margin of the fairway had some very wet soil about halfway down its length, and the northeastern end included a ditch with open water. The vegetation included the following trees at the western drier end: *Agonis flexuosa* (Weeping Peppermint; native to Southwest of W.A., but introduced into the Park), *Allocasuarina fraseriana* (Common Sheoak), *Banksia attenuata* (Yellow Candle Banksia), *Banksia grandis* (Bull Banksia), and *Banksia menziesii* (Firewood Banksia). The shrubs and sedges were the same as listed for the eastern (wet) end as given below, but were sparse. Trees at the wet eastern end of the fairway were *Banksia littoralis* (Swamp Banksia); shrubs were *Acacia saligna* (Orange Wattle), *Spyridium globulosum* (Basket Bush), *Templetonia retusa* (Cockies Tongues), *Xanthorrhoea preissii* (Balga or Grass Tree) and sedges were *Lepidosperma longitudinale* (Pithy Sword-sedge), *Lepidosperma striatum*

←

grass. **D.** *A. mcmillani* attacking human ear at Yanchep National Park. **E.** *A. mcmillani* attacking human eyelid at Yanchep National Park. **F.** *A. mcmillani* attacking human cheek at Yanchep National Park.

TABLE 1
Measurements and Ratios of Male *Austroconops*
 Wing measurements in mm.

Character	<i>A. mcmillani</i>		<i>A. annettae</i>	
	<i>N</i>	Range (mean, 1.5 SD)	<i>N</i>	Measurement
Wing length	13	0.97–1.08 (1.04, 0.053)	1	0.84
Costa/wing length	13	0.75–0.79 (0.78, 0.014)	1	0.78
Flagellomeres 11–13/1–10	12	0.62–0.72 (0.66, 0.052)	1	0.59
Flagellomeres 12/13	12	0.62–0.77 (0.70, 0.072)	1	0.43
Palpal segment 3/4+5	11	1.36–1.91 (1.56, 0.271)	1	1.04
Foreleg Ta1/Ta2	12	2.37–2.61 (2.46, 0.138)	1	2.36
Foreleg TR/Hindleg TR	12	1.74–2.00 (1.88, 0.125)	1	1.86

(no specific common name; a sword-sedge), and a herb, *Centella asiatica* (Indian Pennywort). Samples of mud and detritus from the ditch at the east end of fairway and a few wet soil samples from about three-fourths down the fairway failed to produce immatures.

Austroconops mcmillani adults were also observed at the southern margin of Loch McNess (fig. 22C; site B), about 30 meters west of where a small stream enters the lake. The adult population was significantly smaller than at site A, and on November 18–20 females attacked, at best, at the rate of about 1–2/minute. One male was swept from the surrounding vegetation. This wooded area had a narrow inundation zone with very wet soil and mud and some small pools that partially filled after a short rain. The predominant tree at this specific site was *Melaleuca raphiophylla* (Swamp Paperbark) with shrubs of *Acacia saligna* (Orange Wattle), sedges *Carex fascicularis* (Tassel Sedge), *Lepidosperma effusum* (Spreading Sword-

sedge), *Schoenoplectus validus* (Lake Club-rush), and some *Typha orientalis* and a thick mat of an introduced herbaceous weed *Penisetum clandestinum* (Kikuyu Grass). Mud and wet fallen leaves sampled from this site produced no immatures after floating debris and substrate with sugar or sorting by hand.

Two females of *A. mcmillani* were collected on November 20 at the northeast corner of Loch McNess (fig. 22C; site C). This area was a very wet, but more open, inundation zone.

On November 20 from about 10:50 AM to 1:15 PM the first author and his wife walked completely around Loch McNess (fig. 22C), stopping 14 times at more-or-less even intervals around the lake for 3 minutes at a time, breathed deeply (to produce maximum CO₂), and waited for attacking females. The only spots where females were found were at sites B and C (fig. 22C), suggesting that the species is indeed restricted to some specific localities in the park. Females attacked within 5 minutes at site B when arriving at 2:55 PM

TABLE 2
Measurements and Ratios of Female *Austroconops*
 Wing values in mm, spermatheca (largest) in μm .

Character	<i>A. mcmillani</i>		<i>A. annettae</i>	
	<i>N</i>	Range (mean, 1.5 SD)	<i>N</i>	Range (mean)
Wing length	23	0.71–0.93 (0.86, 0.086)	3	0.84–0.93 (0.87)
Costa/ wing length	23	0.85–0.89 (0.87, 0.019)	3	0.84–0.84 (0.84)
Flagellomeres 9–13/1–8	11	0.71–0.92 (0.77, 0.097)	4	0.73–0.81 (0.78)
Palpal segment 3/4+5	10	1.43–1.75 (1.57, 0.173)	4	1.05–1.32 (1.19)
Foreleg TR/Hindleg TR	9	1.83–2.10 (1.94, 0.127)	4	1.80–2.10 (1.91)
Spermatheca width	10	38–48 (43, 4.4)	3	36–38 (37)

TABLE 3
Measurements and Ratios of Eggs of *Austroconops*
 Values given in μm .

Character	<i>A. mcmillani</i>		<i>A. annettae</i>	
	<i>N</i>	Range (mean, 1.5 SD)	<i>N</i>	Range (mean)
Length	8	360–440 (381, 38.5)	5	280–300 (292)
L/W	4	6.13–8.46 (7.26)	3	5.38–6.25 (5.93)

(November 19, 2001) and within seconds upon arrival at site A at 10 AM (November 20, 2001), further indicating the presence of quite localized populations of *A. mcmillani*.

All sites shared the presence of very wet soils, which corresponds well with the behavior of the reared larvae which actively burrowed through wet mud/detritus.

Additional biting females were collected by Len Zamudio at fairway 3 on January 3 and 9, 2002 by a small creek which traverses the fairway about halfway down its length (fig. 22C; site D) and at fairway 8 on January 9 and 31, 2002 (fig. 22C; site E).

The paratype specimens of *A. mcmillani* collected at Yanchep N.P. were collected on December 23, 1954 by B. McMillan “at the opening of a small cave to the right of the track leading north from the golf course” (A. L. Dyce, personal commun.) and this would represent another place in the park where *A. mcmillani* are known. However, the total park area has been progressively drying over the past number of years and it is unknown what impact this might have on the distribution of *A. mcmillani* in the park since 1954.

EGG LAYING, LARVAL AND PUPAL BEHAVIOR AND DEVELOPMENT

Eggs were laid by female *A. mcmillani* in a scattered pattern on the surface of wet mud in a vial or on the sides of the vial just above the mud where moisture had condensed on the vial wall. Three eggs of *A. mcmillani* that were laid on the sides of the vial were at least somewhat dried after they were laid and had partially collapsed but when immersed in water and rehydrated, they subsequently hatched. The sequence of egg laying, hatching, and larval development is given in table 5.

First-instar larvae burrowed very actively through moderately packed, quite wet mud/detritus with a serpentine motion. They used different means of propulsion depending on the nature of the substrate and whether they had located food. When larvae were in water, but with substrate to crawl upon, they used their anterior proleg in an anteroposterior motion, dragging the rest of the body along to produce a slightly jerky anterior movement. Larvae that were in very loose detritus and that wanted to move through the water from one clump of detritus to another used their posterior proleg as an anchor, extending

TABLE 4
Head Capsule Lengths of Larvae of *Austroconops*
 Values given in μm .

Instar	<i>A. mcmillani</i>		<i>A. annettae</i>	
	<i>N</i>	Range (mean, 1.5 SD)	<i>N</i>	Range (mean, 1.5 SD)
1	11	44–53 (49.1, 3.35)	8	42–45 (43.8, 1.57)
2	2	62–67 (64.8)	4	57–61 (58.2)
3	10	80–91 (84.8, 4.63)	9	70–83 (77.1, 5.36)
4	3	111–115 (114.0)	2	93–99 (96.1)

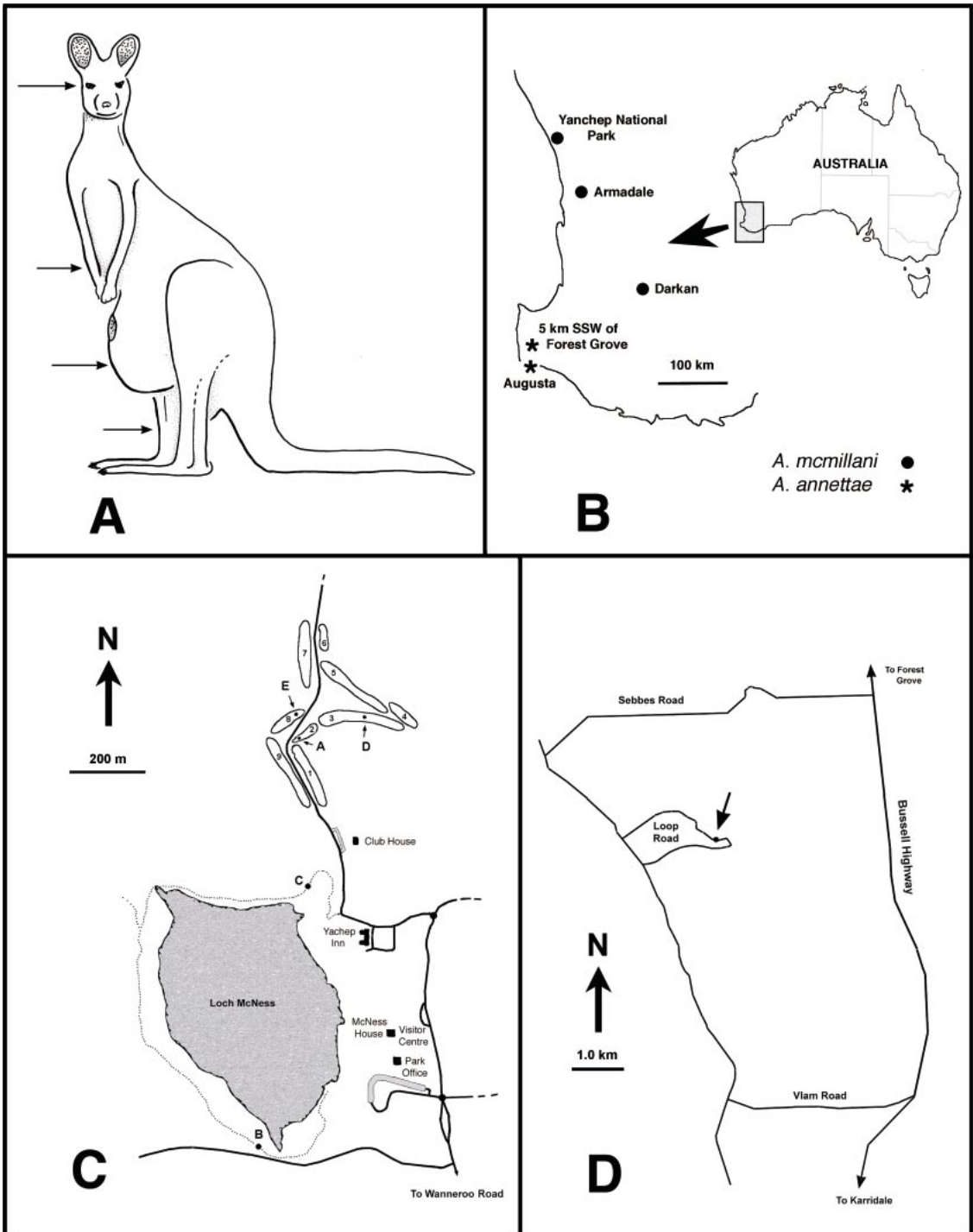


Fig. 22. **A.** Sketch of a kangaroo indicating the main areas of scratching (eyes, forelegs, backlegs, taut belly of female carrying joey). **B.** Map of Western Australia showing the distribution of extant species of *Austroconops*. **C.** Map of a portion of Yanchep National Park showing the distribution of *Austroconops mcmillani* within the park. Letters A–E indicate specific collection sites referred to in the

the head and length of the body through water to connect with another piece of detritus. In thicker substrate, at least some movement was facilitated by serpentine movements of the anterior half of the body with the abdomen being dragged behind and with the posterior proleg hooks withdrawn into the anus. In dense substrate (such as thick mud/detritus or agar), the head capsule would additionally be extended anteriorly, bent somewhat down to take hold of the substrate and then bent farther anteroventrally, helping to bring the body forward; these larvae also withdrew their anterior proleg into the body in the crease between the cervix and remaining prothorax. The proleg was withdrawn much like the inverting of a shirt sleeve, with the terminal hooks inverting first into the interior of the extended leg and being withdrawn toward the body and the rest of the proleg following suit. This inversion is almost certainly the result of muscles that insert at the apex of the proleg (fig. 4B). Extension of the proleg was the reverse of this sequence. Larvae removed from substrate and placed in a drop of water on a slide never withdrew the anterior proleg as they actively sought a substrate to latch on to, and it is clear that this structure is important to their locomotion.

As larvae were moving through substrate, their head capsules would move rapidly in a flicking motion left and right and dorsoventrally, apparently testing for potential food. The larvae would also periodically stop, at times anchoring themselves with their posterior proleg and poke their heads rapidly here and there among the detritus, again in an apparent search pattern. The larvae rested regularly and most often used their extended posterior proleg hooks as an anchor on the substrate. Such resting larvae were generally in a more-or-less elongate position (with some curves or bends in the body), but occasionally they would assume a tight U-shaped position, with the posterior proleg hooked into detritus.

When first-instar larvae were removed from very wet mud/detritus to water, they

immediately became very active, writhing and attempting to find a substrate upon which to take hold. Upon doing so, they immediately burrowed into the substrate and clearly preferred more solid clumps of detritus than fine, looser particles to burrow into. Larvae in detritus that were harassed by a probe quickly escaped with rapid use of the anterior prolegs and, in thick substrate, some undulations of their bodies.

Five first-instar larvae of *A. mcmillani* were observed feeding on *E. coli*, and when doing so they had their posterior proleg firmly hooked into the substrate and worked over acceptable substrates with their mouthparts. The head capsule moved back and forth, appressed to the agar, and the mouthparts moved rapidly, with the labrum contracting and apparently moving food into the mouth cavity. The pharyngeal complex periodically moved food into the gut. The gut contents appeared white in these individuals (same color as the *E. coli*). When feeding, the antennae actively moved independently of one another. After feeding on *E. coli* for 3 days, all five larvae died.

When drops of the fecal infusion, nematodes, and rotifers were introduced to the larvae in the mud/detritus substrate, further observations were made of feeding. Larvae were obviously attracted by the drops of fecal infusion and were often very concentrated directly underneath these small pools of feces. Occasionally, larvae would be seen lashing at a passing *Paramecium* or a slower rotifer. A few second-instars were seen to successfully attack and eat passing rotifers but missed most that were nearby. The strong impression of all larval instars was that they could at best only attack slow prey.

Second-instar larvae became increasingly fat and slower and by the third-instar and especially by the fourth-instar, larvae moved more clumsily, with a slow, serpentine motion. Serpentine movements of the body were obviously the most important basis for movement as the larvae worked their way through the mud/detritus substrate. To re-

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text. Numbers refer to the fairways at the golf course. **D.** Map of the type locality of *Austroconops annettae* at 5 km SSW of Forest Grove, Western Australia.

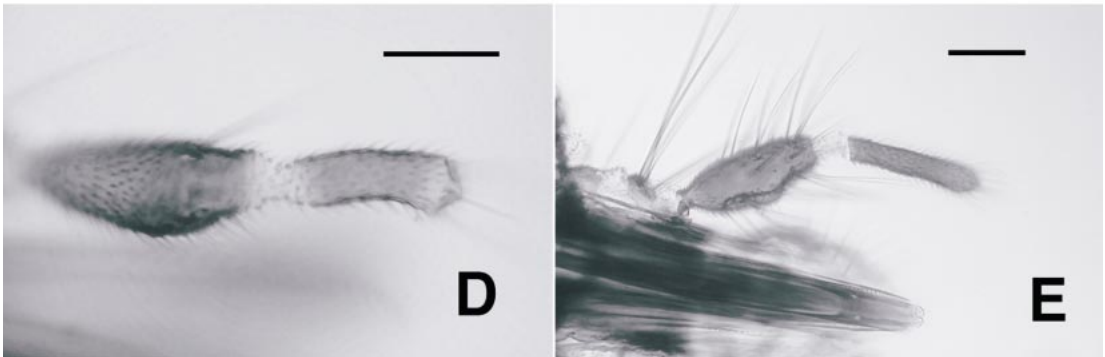
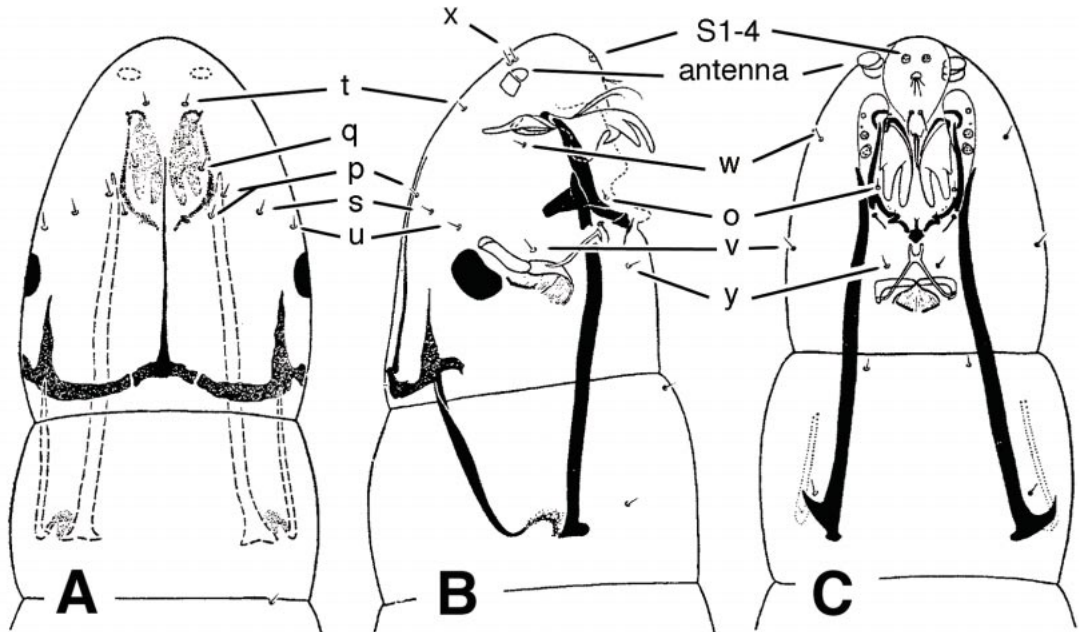


Fig. 23. Head capsule of *Leptoconops gallicus* identifying setae (after Clastrier, 1972) (A–C). Female adult left palpus (D–E). **A.** In dorsal view. **B.** In lateral view. **C.** In ventral view. **D.** *Austroconops annettae*. **E.** *Leptoconops freeborni*. Scale bars: D = 25 μm , E = 50 μm .

verse direction, a larva either simply reversed its serpentine movement or, by turning its head capsule and anterior portion of the thorax in a posterior direction, doubled back along the length of its body. The anal hooks were withdrawn into the anus when a larva moved and were often (but not always) exerted when the larva rested; in some instances the hooks were attached to substrate, but in more sparsely distributed substrate were simply exerted into the water without being anchored to anything. The anterior proleg also appeared to be rarely used by

third- and fourth-instar larvae and apparently was exerted only when the larva had difficulty finding any substrate ahead. Second-, third- and fourth-instar larvae always extended their anterior proleg in a groping motion when placed in a drop of water on a microscope slide and writhed helplessly, very similar to the more ponderous movements of *Dasyhelea* larvae. Larvae which were harassed with a probe quickly escaped with rapid serpentine undulations of their bodies through the surrounding substrate. When the substrate was shaken and larvae severely dis-

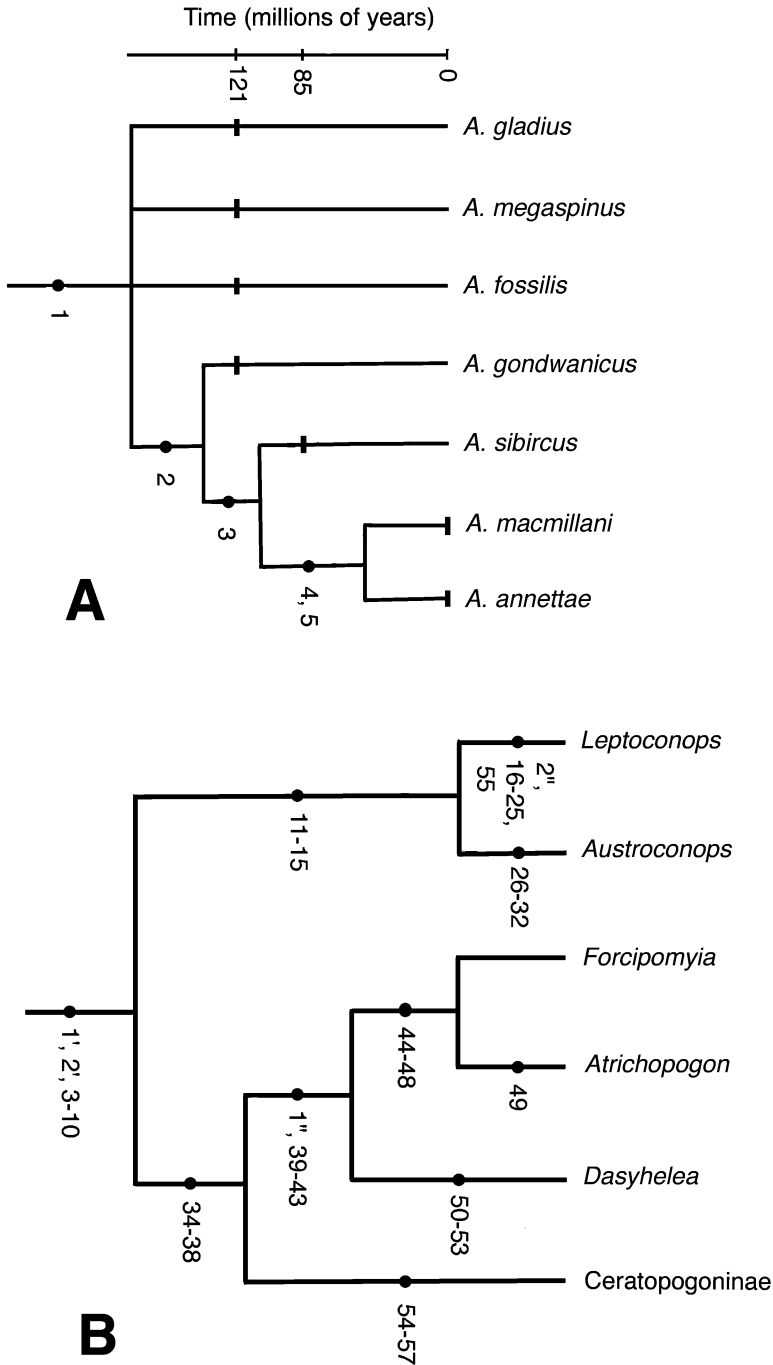


Fig. 24. **A.** Cladogram showing the relationships between fossil and extant species of *Austroconops*. The Cretaceous fossils *Jordanoconops weitschati* and *A. borkenti* share synapomorphy 1 but are not included here (see text for explanation). Bars on the cladogram indicate the age of the species. **B.** Cladogram showing relationships between extant lineages of Ceratopogonidae. Numbers refer to synapomorphies discussed in the text.

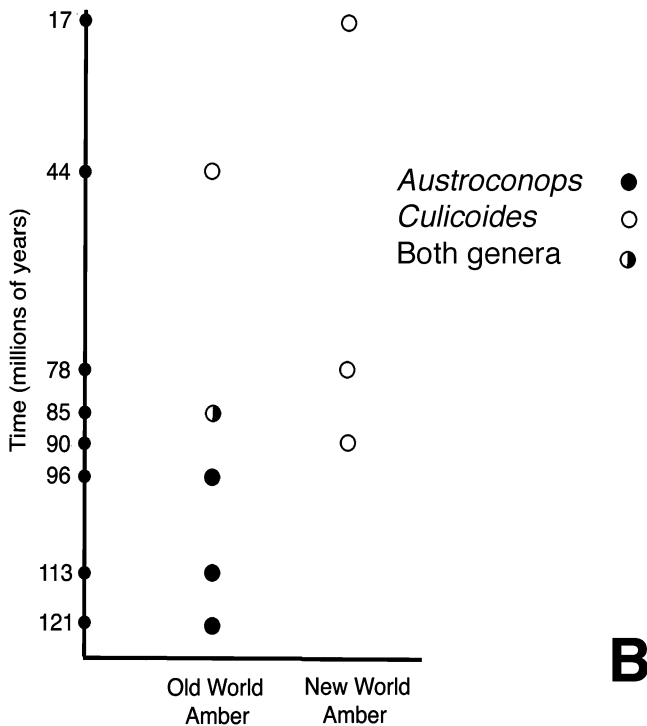
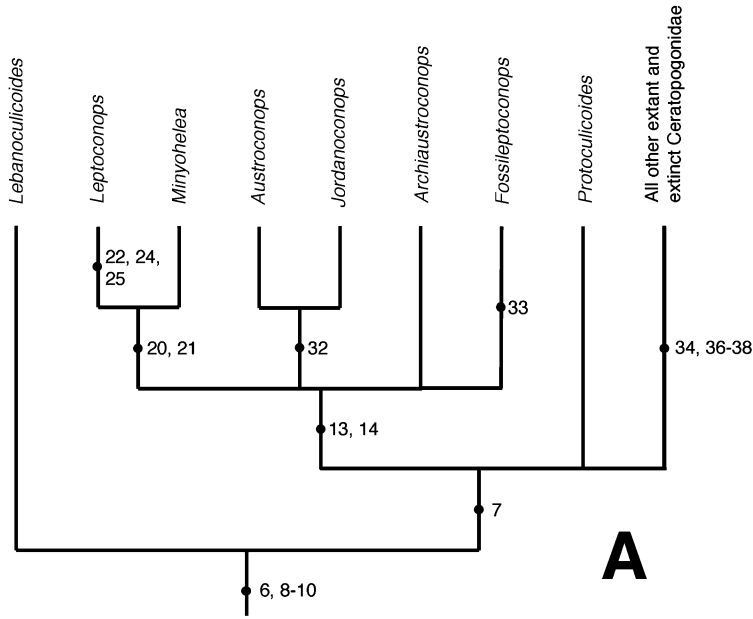
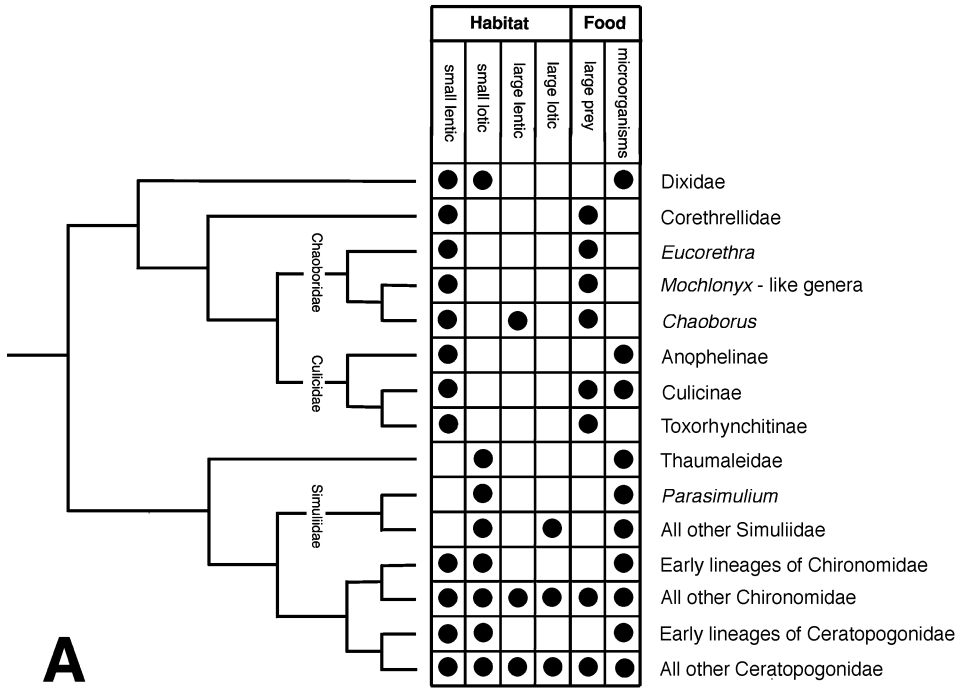
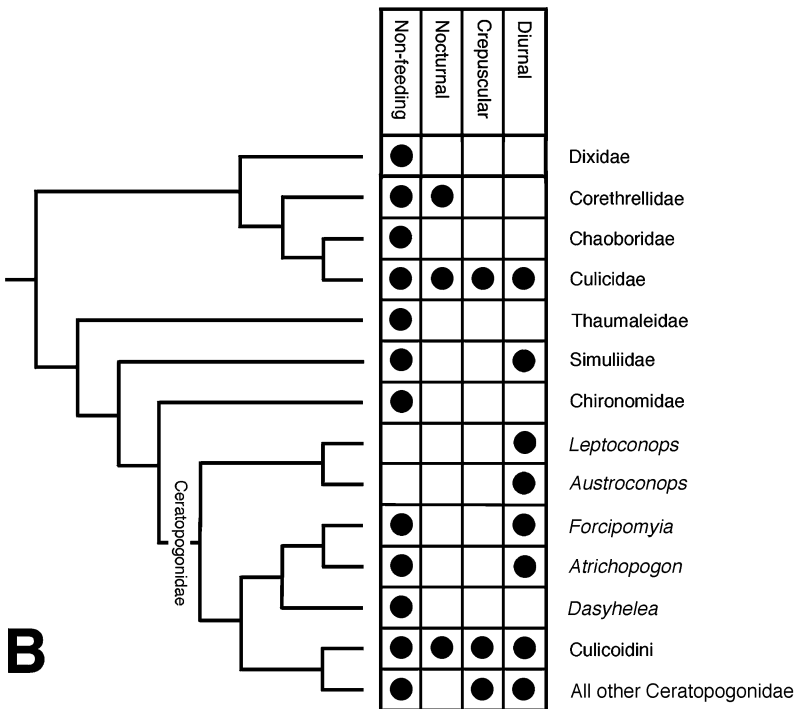


Fig. 25. **A.** Cladogram showing the relationships between early fossil and extant genera of Ceratopogonidae. Numbers refer to synapomorphies discussed in the text. **B.** Distribution of *Austroconops* and *Culicoides* in the fossil record.



A



B

Fig. 26. **A.** Larval food and habitats of Culicomorpha. **B.** Biting periods of adult female Culicomorpha.

TABLE 5

**Data on Rearing of *Austroconops mcmillani*
(2001–2002)**

Nov. 20	Females blood fed, captured and placed in vials
Nov. 24	At least 37 eggs laid (about 106 hours after blood meal taken)
Dec. 1	Six first-instar larvae seen
Dec. 17	Goat fecal infusion added
Dec. 31	Some second-instar larvae seen
Jan. 9	One third-instar larva seen
March 15	One fourth-instar larva seen
Aug. 31	Two fourth-instar larvae alive
Sept. 9	Pupa
Sept. 14	Adult male

turbed, fourth-instars often assumed a curled-up position (this was not attempted with earlier instars). The darting, probing search pattern of the head capsule continued in these stages. Larvae sometimes moved their antennae and, when ingesting food, moved their mandibles synchronously. Some second-instar and most third-instar larvae took on a pinkish hue. A few third-instar larvae remained unpigmented and translucent. All fourth-instar larvae were pink or reddish.

The day before the single fourth-instar larva pupated, its thorax was strikingly broad, the respiratory organs of the pharate pupa could be clearly seen, and the eyespots had moved posteriorly in the larval head capsule. The pupa, which completely shed the larval exuviae, was initially very pale, with red hemolymph, and, at 22–25°C, was very sluggish, although capable of very slow circular movements of the abdomen. It was buried in the wet substrate at about a 50–60° angle from the surface, with the tip of one respiratory organ just sticking out of the water; later, the tips of both respiratory organs were exposed. Throughout its development the pupa had the apex of either or both respiratory organs exposed to air. After 24 hours, the pupal cuticle appeared nearly transparent (except for the brown respiratory organs), with an inner core of reddish tissue surrounded by completely clear fluid and a few subcutaneous bluish-green patches in the thorax and abdomen. It was virtually motionless,

and flooding for 16 minutes (so that the respiratory organs were submerged) did not result in any pupal movement, nor did any very slight jarring of the surrounding substrate. At one point, upon turning on a bright microscope light, the pupa briefly moved its abdomen in small circular motions. After 48 hours, the pupa did not look much different from 24 hours earlier. After 72 hours, the interior of the pupa became somewhat darker. The blue-green patches were also present in the head (this may have been true earlier but the head could not be seen clearly then). The pupa was very lethargic and moved only slightly when bright light was suddenly shone on it. At 84 hours the developing adult eyes became visible. At 96 hours, the developing adult had darkened further, with the blue-green patches more extensively developed. At 108 hours, the dark adult appeared to be more-or-less completely developed and its black head and thoracic cuticle could be clearly seen. Shortly before the adult male emerged, at 120 hours after pupation, the pupa slowly wriggled its way out of its circular burrow and lay on the wet mud surface. The adult emerged during daylight hours (early afternoon) but failed to completely expand its wings (they were entrapped by the wet mud surface); in all respects it appeared normally developed and a hindleg first tarsomere length of 176 µm (males in nature = 178–214 µm, $N = 13$) indicated that the rearing conditions and food provided to the larva was of sufficient quality to produce a typical adult.

BITING ACTIVITY AND BEHAVIOR

Of those female adults of *A. mcmillani* biting humans at Yanchep National Park, most bit on the face (fig. 21D, F); less than 15% of individuals fed elsewhere on the body (mostly shoulders, arms, legs). Females on the face clearly favored areas without hair and, of those attacking the face, were primarily close to the eyes and directly on the ears, with fewer on the cheeks and forehead. A few fed among hairs right at the hairline, including the scalp, eyebrows, eyelashes, and the first author's beard. We are unable to suggest the cues used by females to preferentially attack the face. When bare arms were

held up and appressed against the face, the face was still preferred; however, in such a position a few females attacked the armpit (no deodorants used), suggesting that secretions of the skin may be involved as an attractant. Slightly elevated heat from these areas cannot be excluded but this seems unlikely, since females were not attracted to handheld cups of warm or hot water, as are females of some species of *Culicoides* and Culicidae. It is probable that female *A. mcmillani* were attracted by CO₂. At the south end of Loch McNess (fig. 22C; site B) when the frequency of biting decreased, the number of incoming females could be increased within 3–5 minutes by doing on-the-spot exercises or by intentionally breathing deeply and rapidly.

Females flew about the head for a period before landing. Those landing on the hair nearly always quickly flew off the surface to resume hovering. After landing on skin, nearly all females began feeding immediately (very little walking about on the skin surface).

Kangaroos were closely observed during the first sampling period of October 16–20, 2001, before the emergence period of *A. mcmillani*. They very rarely scratched or rubbed themselves. When the first author and his wife were experiencing very intense biting on the golf course in Yanchep N.P. on November 20–21, it was clear that the kangaroos were also being severely bothered by midges (figs. 21B). Many rubbed their eyes and scratched at their forelegs and the shins of the hindlegs with their foreleg feet (fig. 22A). Female kangaroos carrying well developed joeys (baby kangaroos) also often scratched at the front of their extended pouches. The midges attacked the eyes and areas with a minimum of hair. The first author chased kangaroos with an aerial net during these observations and collected numbers of *A. mcmillani* females, but it was uncertain if these specimens were attacking the kangaroos, were attracted to the first author, or were merely free flying in the area.

Females assumed a biting posture similar to those of *Leptoconops* and *Culicoides* that the first author has examined, with the body virtually parallel to the skin surface but very slightly elevated posteriorly (fig. 21D, F). Of

27 females studied, total time to complete blood feeding ranged from 1:05 to 4:40 minutes:seconds (mean = 2:42), when ambient air temperatures ranged from 22 to 29°C (taken in shade). There was no significant correlation between temperature and biting time, although all the feeding times longer than 3 minutes ($N = 8$) were at temperatures at or below 25°C. We found the bite of female *A. mcmillani* to be more painful than those of other ceratopogonids that we have experienced (*Leptoconops*, *Culicoides*), perhaps because they concentrated on the more tender facial area.

Females fed only during the day when temperatures were above at least 21°C. On November 21 females began feeding at fairway 2 (fig. 22C; site A) at 7:50 AM, when the ambient temperature was 22°C. On November 18, at the south end of Loch McNess (fig. 22C; site B), they ceased attacking by 5:45 PM as the light was fading and the temperature was 24°C. Females in vials became lethargic at about 18–19°C and at about 16–17°C were nearly torpid. It appeared that stronger winds dampened activity, although females continued to bite in sheltered areas, such as the leeward sides of trees, a behavior typical of many biting ceratopogonids. High temperatures (generally above 24°C) and increased humidity appear to greatly increase biting rates (L. Zamudio, personal commun.). Cloudy weather and even a light rain did not stop females from attacking, although a steady drizzle did stop biting activity on the afternoon of November 18, 2001.

ADULT SEASONALITY

Intense collecting of Ceratopogonidae in Yanchep National Park showed that no *A. mcmillani* adults were present October 16–20, 2001. November 5 produced moderate numbers of females, which slowly increased with large numbers biting on November 18. Biting activity varied, depending on environmental conditions, until at least January 31, 2002, indicating a nearly 3-month period of female adult biting activity. Populations in the 2002–2003 season were substantially less at Yanchep N.P. (possibly due to a very dry season; L. Zamudio, personal commun.) and biting female adult *A. mcmillani* were col-

lected from November 14, 2002 until January 1, 2003. Two female *A. mcmillani* were sampled from kangaroo feces on January 21, 2003 (L. Zamudio, personal commun.), indicating that the emergence period was still about 3 months long in the 2002–2003 season.

Records from three years show males have been collected Oct. 22–23 and Nov. 1, 1985; Nov. 19–21, 2001; Nov. 20, Nov. 22, Dec. 6, and Dec. 12, 2002.

MALE SWARMING

Male swarms were observed on November 21, 2001 on fairway 2 of the golf course at Yanchep National Park (fig. 22C; site A) from 6:45 to 9:15 AM. At 6:45 the temperature was only 15°C (in shade, warmer in sun) and calm. At 7:50 AM and 22°C a single, small (about 30 cm in diameter), more-or-less spherical swarm was seen about 1 meter above the grass and about 6 meters from the margin of short trees at the edge of the fairway. A light wind began blowing. Several similarly situated swarms were seen during the next 40 minutes. The swarms started to increase in size, became more elongate vertically, and moved to within 3 meters of the leeward side of the trees, just south of the tee-off area. No obvious swarm markers were evident, other than being on the leeward side of the trees. By 8:05 AM the bottom of the swarms were 2–3 meters above the ground and larger (about 50 × 100 cm) and withstood some wind, albeit being periodically blown about and then regrouping. Swarming activity ceased in this immediate area at about 8:30 AM but continued a short distance farther east along fairway 2 (where it was a bit cooler) and then began in the first area again at 8:37 AM for at least 30 minutes. One swarm collected at 9:00 AM with a rapidly swept aerial net consisted of 160 males and 10 females (the latter may have been captured because females had begun biting by then). By 9:15 AM swarming had ceased and did not resume for the next 30 minutes, at which time observations were terminated.

A male and a female of *A. mcmillani* were collected in copula at 8:47 AM during these observations by sweeping from ground level to about 1 meter in height in the nearby vi-

cinity of the swarms; the pair separated after about 20 seconds while in the net. While still attached the pair stood on the net mesh facing in opposite directions, showing that the male can at least opportunistically rotate his genitalia 180° (they are otherwise generally held at about 90°). Small white sheets (about 1 × 1 m) were placed on the ground under the swarms of males but no mating pairs settled on these. The fact that females captured immediately after they had completed feeding were able to lay fertile eggs proves that mating occurs before feeding.

OTHER OBSERVATIONS

On November 21, 2002 females did not attack the first author on fairway 2 in Yanchep N.P. before 7:50 AM. From 6:15 until 6:45 AM females were sampled by dropping a net over one or more fresh (wet) kangaroo feces and then disturbing the feces with a stick slipped under the margin of the net that was appressed against the grass. Some females were sampled by kicking at the feces and then immediately sweeping briskly over the area. In virtually every patch, some females were collected, with numbers varying from 0 to 8 individuals (58 collected in 30 minutes). Three attempts at collecting females from dry kangaroo feces failed to produce any specimens. This suggests that the females were imbibing nutrients from the wet feces but further observations are required. That reared larvae obtained nutrients from a fecal infusion in the laboratory might suggest the possibility that the females were laying eggs on or near the kangaroo feces, but most of the feces were in an area with normal soils, and the clearly aquatic larvae of *A. mcmillani* could almost certainly not survive there.

Of 280 preserved male *A. mcmillani* collected from swarms in Yanchep National Park on November 21, 2001, one specimen had a phoretic female mite intertwined between its legs. The mite belongs to an undescribed species of *Blattisocius* Keegan (Ascidae) (E. Lindquist, personal commun.). This mite genus is virtually cosmopolitan, and 11 of the 12 known species are, or are likely to be, predators (the twelfth is an ectoparasite in noctuid moth ears). No obvious

internal parasites (e.g., no nematode infestation) were seen among the specimens examined.

Female adults clean their antennae with the foretibial spurs. The wings were cleaned by opening the wings very slightly and hooking one hindleg over the anterior margin of the wing and pushing it alongside and under the abdomen where both hindlegs rubbed their tarsi against each corresponding wing surface (so that the left leg rubbed the dorsal surface of the left wing and the right leg rubbed its underside). After wing cleaning, the wings were sometimes left at an angle but shortly after “clicked” back to the typical overlapping position over the abdomen. The hindleg tarsi were cleaned by rubbing them against each other under the body.

TAXONOMIC DISCUSSION

The adult male and female of *A. mcmillani* were described in some detail by Borkent et al. (1987). There is some confusion about the exact location of the type locality, recorded on the labels of the type series as “National Park, Perth, W.A., 21-XII-1954”. There is not, and has never been, a national park in Perth, although the renowned 4-km² Kings Park may have been a candidate in the mind of the collector. More likely, the labels may refer to John Forrest National Park, the first national park in Western Australia, located about 22 km northeast of Perth city center. An old “Caltex” roadmap in the possession of the first author, probably from the 1950s or 1960s, indicates John Forrest N.P. merely as “National Park”, perhaps confirming that this is actually the type locality. The original collector, B. McMillan, is deceased (A.L. Dyce, personal commun.). The holotype is housed in the ANIC.

Wirth and Lee (1958) recorded the following original material, all females: holotype and 16 paratypes from “Perth National Park”, 9 paratypes from Yanchep National Park, 11 non-paratypes from 10 miles SE of Darkan and two nonparatypes from Armadale. We were unable to locate 5 paratypes from “Perth National Park”, 1 paratype from Yanchep National Park, and 10 of the specimens from 10 miles SE of Darkan, and these appear to be lost (A.L. Dyce, personal com-

mun.). The specimens we examined from Armadale and 10 miles SE of Darkan are labeled as paratypes, although they were excluded from the type series in the original publication. Furthermore, a specimen from “Perth National Park” (ANIC) was not labeled as a paratype although it almost certainly is one. The slide label is written in W.W. Wirth’s handwriting and the specimen is mounted in his typical fashion; we have added a paratype label to indicate this.

The female adults from Yanchep N.P. were larger than most of the specimens from farther south. The following are the ranges and means of wing lengths for the limited specimens available: Yanchep N.P., 0.82–0.93 mm, 0.89 ($N = 16$); “Perth N.P.”, 0.80–0.83 mm, 0.81 ($N = 4$); Armadale, 0.71–0.79 ($N = 2$); Darkan, 0.82 ($N = 1$). This may indicate the possibility of clinal variation, but further specimens and study are required to determine this.

The pupal dorsal setae are here labeled as i, ii, and iv. Based on their position on the thorax, setae i and iv are likely homologous to those named as such in other Ceratopogoninae. However, seta ii could equally be homologous to seta iii of the Ceratopogoninae.

SPECIMENS EXAMINED

Yanchep National Park, Nov. 18–21, 2001: 442 males, 201 females; Yanchep National Park from females captured Nov. 20, 2001: 10 eggshells, 2 eggs, 1 eggshell with first-instar stuck during emergence, 10 first-instar larvae, 2 second-instar larvae, 8 third-instar larvae, 3 fourth-instar larvae, 1 pupal exuvia and associated male (CNCI); Yanchep National Park, golf course, Dec. 11, 2001–Jan. 31, 2002: 32 females; Yanchep National Park, Oct. 22–Nov. 1, 1985: 3 males (ANIC, CNCI), 5 females (ANIC, CNCI, WAMP); Yanchep National Park, Dec. 23, 1954: 4 female paratypes (BMNH, BPBM, USNM, WAMP); Yanchep National Park, golf course, Nov. 14, 2002–Jan. 1, 2003: 55 males, 1833 females; Armadale, Jan. 4, 1936: 2 females (labeled as paratypes) (ANIC, USNM); Darkan, Jan. 29, 1953: 1 female (labeled as paratype) (USNM); Perth National Park, Dec. 21, 1954: 3 female para-

types, 1 female not labeled but likely a paratype (new paratype label added) (3, USNM; 1, ANIC).

In addition to the above material, more eggs, eggshells, and specimens of the different larval instars were studied but were either left to develop or were subsequently lost. Therefore, the numbers in tables 3 and 4 recording numbers of specimens does not match that listed above.

DERIVATION OF SPECIFIC EPITHET

The species was named by Wirth and Lee (1958) after the collector of the type series, B. McMillan.

Austroconops annettae Borkent, new species

Austroconops mcmillani: Borkent, Wirth, and Dyce, 1987. Female adult (in part).

DIAGNOSIS: Male. The only extant *Austroconops* with flagellomere 12 short, 0.4 the length of flagellomere 13 (fig. 1B). **Female.** The only extant *Austroconops* with each claw with a well developed basal tooth (fig. 1J). **Egg and larva (all instars).** Not distinguishable from those of *A. mcmillani* (see generic diagnosis above). **Pupa.** Unknown.

DESCRIPTION: Male adult: Descriptive statistics in table 1. **Head:** Antenna with well developed plume. Flagellomere 12 elongate, with subbasal constriction, 0.43 length of flagellomere 13 (fig. 1B). Mouthparts moderately long. Palpus (fig. 1D) with 4 segments, segment 3 slightly ovoid in lateral view (more slender than in *A. mcmillani*), with capitate sensilla scattered on surface or in shallow pits. **Thorax:** Scutellum angular in dorsal view. **Wing** (fig. 1K): Costa extending just beyond apex of R_3 . **Legs:** Legs lacking armature. Bristles on midleg tibia, first tarsomere elongate (fig. 1N). Midleg tibia without apical spur. Hindleg first tarsomere without thick basal spine or stout setae. Claws simple, each claw apically bifid. **Genitalia:** In life, rotated about 50° . Not distinguishable from that of *A. mcmillani*. **Female adult:** Descriptive statistics in table 2. **Head:** Ommatidia narrowly separated dorsomedially. Antenna as for *A. mcmillani*. Flagellomeres gradually increasing in length from flagellomere 2 to 13. Mouthparts moderately elon-

gate, mandible (fig. 1H) narrow, with fine teeth, most directed dorsolaterally, laciniae with well developed, fine retrorse teeth. Palpus (fig. 1F) with 4 segments, segment 3 ovoid, slightly swollen in lateral view, with capitate sensilla scattered on surface or in shallow pits. **Thorax:** Scutellum angular in dorsal view. **Wing** (fig. 1L): Costa extending to or just beyond apex of R_3 . **Legs:** Femora, tibiae slender. Legs lacking armature. Midleg tibia without apical spur. Hindleg first tarsomere without thick basal spine or stout setae. Foreleg, midleg, hindleg claws (fig. 1J) nearly straight for apical three-fourths, with stout basal tooth. **Genitalia:** Indistinguishable from that of *A. mcmillani*. **Egg:** Descriptive statistics as in table 3. **First-instar larva:** Head capsule length statistics in table 4. Total body length 0.67–0.77 mm ($N = 7$). **Second-instar larva:** Head capsule length statistics in table 4. Total body length 1.43–1.82 mm ($N = 4$). **Third-instar larva:** Head capsule length statistics in table 4. Total body length 2.05–2.61 mm ($N = 8$). **Fourth-instar larva:** Head capsule length statistics in table 4. Total body length uncertain. **Pupa:** unknown.

DISTRIBUTION AND BIONOMICS

Austroconops annettae is known from two sites in southwestern Australia (fig. 22B). The type locality (fig. 22D) is on Loop Road, 5 km SSW of Forest Grove, WA. One male and four females (one lost after being collected) were swept from a very small patch of low vegetation immediately beside a very shallow (less than 3 cm deep) small pool less than a meter in diameter (fig. 21C). The pool was immediately beside and south of the narrow track of Loop Road and was located in a dry, shallow streambed (likely with running water during the winter). Surrounding vegetation was composed of an open Jarrah-Marri forest with thick stands of shrubs (*Leucopogon parviflorus* was common).

The single female from Augusta (fig. 22B) was collected with a sweepnet and was either collected 1.6 km south of Augusta (most likely) or about 1.6 km east of Jewel Cave (about 7.5 km NW of Augusta) (D. Colless, personal commun.).

Two females found on November 2, 2001

at the type locality were collected between 3:00 and 4:00 PM when the ambient temperature was 20°C (but substantially warmer in the sun). When the single female retained live in a vial was at 17°C, she became very lethargic (nearly torpid), but when the vial was warmed up, she again became very active. A third female collected on November 4 was lost but was collected at 12:50 PM and at 22°C. One male was collected on November 13 at 1:15 PM at 33°C, and one female was found on the same date and temperature at 3:30 PM. Fervent and repeated sweeping all around this immediate site on each of the above dates failed to produce any further specimens, which suggests that the few adults were indeed concentrated at the small pool that appeared to be the only open water (although very small) in a large area. Samples of mud from the edge and bottom of this small pool failed to produce any immatures.

The distinctive claw of female *A. annettae* (fig. 1J), with a pronounced inner basal tooth more-or-less situated in the same plane as the rest of the claw, may indicate the type of host upon which the female feeds. Within the Simuliidae, females of species with a similarly shaped claw are restricted to those which feed on birds (Crosskey, 1990). Within the Ceratopogonidae, the only species of vertebrate feeders with variation regarding the presence or absence of an inner basal tooth are those in the genus *Leptoconops* (*Forcipomyia* Meigen (*Lasiohelea* Kieffer) and *Culicoides* all have simple claws with at most, a small, very slender spicule). Nearly all *Leptoconops* which bite mammals have a simple claw or a claw with a small basal spicule. Species with a claw with a pronounced inner basal tooth feed either on humans (e.g., *L. spinosifrons* (Carter) and *L. siamensis* Carter; Chanthawanich and Delfinado, 1967) or on birds (*L. werner* Wirth and Atchley; Wirth and Atchley, 1973), indicating that the shape of the claw may not strictly indicate host type in *Leptoconops*. Other species which have a claw shape virtually identical to *A. annettae* are *L. freeborni* Wirth, *L. melanderi* Wirth and Atchley and *L. patagoniensis* Ronderos, but their hosts are unknown. Further research is warranted because we do not have host records for many species of *Leptoconops*. Lane

TABLE 6
Data on Rearing of *Austroconops annettae*
(2001–2002)

Nov. 13	Female captured and placed in vial
Nov. 18	Eggs first seen but may have been laid earlier
Nov. 23	Some first-instar larvae seen
Dec. 17	Goat fecal infusion added
Dec. 26	Some second-instar larvae seen
Jan. 7	One third-instar larva seen
Feb. 14	One fourth-instar larva seen
Feb. 18	Last fourth-instar larva seen, died shortly after this date

(1977) has shown that the claw shape of females of species of *Forcipomyia* (*Trichohelea* Goetghebuer) are adaptations to cling to the scales of butterfly wings as females feed on butterfly blood (they pierce the wing veins to obtain this). If further study shows a relationship between the claw shape of females of *Austroconops* and *Leptoconops* and vertebrate host type, it will provide the basis for interpreting such variation in the fossil record: Lebanese amber species *Austroconops gladius* and *A. gondwanicus*, 121 million years old, both have large basal teeth on their claws similar to those of *A. annettae* (Borkent, 2000a).

The female allotype collected on November 13 laid eggs scattered separately on the surface of wet mud in a vial or on the sides of the vial just above the mud. The sequence of egg laying, hatching, and larval development is given in table 6. Larval behavior was indistinguishable from that of *A. mcmillani* (see above). In addition to the feeding observations associated with the fecal infusion described under *A. mcmillani*, one first-instar larva *A. annettae* was observed to eat a small live nematode whole (in less than 2 seconds). A second larva, upon encountering a somewhat moribund large nematode, pierced it at midlength. This was followed by rapid movement of the pharyngeal complex and ingestion of part of the nematode; it did not complete feeding on the nematode. In spite of these observations, the first- to fourth-instar larvae mostly ignored the large number of nematodes added to the Petri dishes every 2–3 days and, similar to larvae of *A. mcmil-*

lani, congregated near fresh drops of the fecal infusion, suggesting that they too primarily feed on microorganisms.

TAXONOMIC DISCUSSION

Austroconops annettae is very similar to *A. mcmillani* in all its stages (pupa not known) and we were unable to distinguish differences in male or female genitalia, eggs, or the different larval instars (except for some size differences in the immatures, which may have been due to restricted sample size or laboratory rearing conditions; tables 3, 4).

The first-instar larvae are described as having nine undivided segments (fig. 2C). However, in *A. mcmillani*, early first-instar larvae also appear to have undivided segments, whereas older first-instar larvae have divided segments. The same is likely true for *A. annettae*.

The female from Augusta was included as a specimen of *A. mcmillani* in the analysis by Borkent et al. (1987).

TYPE MATERIAL

Holotype, male adult on microscope slide, labeled "HOLOTYPE *Austroconops annettae* Borkent, 5 km SSW of Forest Grove, Loop Road, WA, Australia, 13-XI-2001, A. Borkent, CD1998" (WAMP); allotype, female adult on microscope slide, labeled as for holotype and "Female which laid eggs, resulting in 1–4 instar larvae" (WAMP); paratypes 3 females, 7 eggshells, 8 first-instar larvae, 6 second-instar larvae, 9 third-instar larvae, 1 fourth-instar larva, 1 terminal portion of abdomen of second- or third-instar larva, all reared from eggs laid by female allotype; 2 females from type locality but collected 2-XI-2001 (CNCI); 1 female from Augusta, WA, 3-X-1970 (ANIC); immatures (CNCI).

In addition to the above material, more eggs, eggshells, and specimens of the different larval instars were studied but were either left to develop further or were subsequently lost. Therefore, the numbers in tables 3 and 4 that record specimens do not match that listed above.

DERIVATION OF SPECIFIC EPITHET

This species is named after the first author's wife, Annette Borkent. She shared in virtually every aspect of the six-week expedition to study *Austroconops*, and the results of this paper would not have been possible without her continuous support.

PHYLOGENETIC CONCLUSIONS

Due to its phylogenetic position in the family, the genus *Austroconops* plays a pivotal role in the interpretation of character states (both morphological and bionomic) within the Ceratopogonidae. Because it has remained morphologically conservative (unlike its divergent sister genus *Leptoconops*), the character states in this group allow for a far better understanding of the diversification of features of other ceratopogonids. Furthermore, considering how similar the extant species are to Lower Cretaceous fossils of *Austroconops* 121 mya, it seems very likely that the biology of the extant species are also similar to those species from so long ago. In short, information on this genus is a window on how at least some Ceratopogonidae were living at a very early stage of their evolution. There are not many families of extant metazoans which include such long-lived genera.

In this section we interpret the phylogenetic relationships between early lineages of ceratopogonids, followed by an analysis of their zoogeography and bionomic divergence. As further characteristics of Ceratopogonidae and other Culicomorpha become better known, *Austroconops* will remain a critically important group to interpret such features.

CLADISTIC ANALYSIS

In this section we discuss our hypotheses of the relationship of species of *Austroconops* to each other and the relationship between *Austroconops* and extant and extinct genera of Ceratopogonidae. Borkent et al. (1987) provided the first cladistic analysis of the relationships between the early lineages of Ceratopogonidae. They concluded that, of extant lineages, *Leptoconops* was the sister group to all other Ceratopogonidae and that *Austroconops* was the sister group of all Cer-

atopogonidae other than *Leptoconops*. These authors, recognizing some conflicting evidence, provided an alternative hypothesis, suggesting that *Leptoconops* and *Austroconops* were sister groups and that, together, they formed the sister group of all remaining Ceratopogonidae. As shown below, this alternative hypothesis is now strongly supported.

Since Borkent et al. (1987) provided a cladogram of early lineages, a wealth of fossil ceratopogonid material has been described from virtually every insect-bearing amber deposit in the world (see summary in Borkent, 2000a). Some of those fossils, particularly those from the Cretaceous, represent other early lineages in the family and their cladistic relationships to each other and to extant *Austroconops* and *Leptoconops* have been analyzed by Borkent (2000a). Members of species of both *Austroconops* and *Leptoconops* are present in the oldest amber, from 121 million years ago (Borkent, 2000a, 2001).

The discovery of a second extant species of *Austroconops* and, in particular, the immatures of the extant species provides the means to further test and improve our understanding of these relationships as presented below.

RELATIONSHIPS BETWEEN SPECIES OF *AUSTROCONOPS*

In this section we consider the relationships between the two extant and six extinct species of *Austroconops* (fig. 24A). As is the nature of fossils, some character states are missing for some species, and this makes our conclusions rather tentative. Nevertheless, our hypothesis provides a framework for further analysis. The Cretaceous fossils *Jordanconops weitschati* and *A. borkenti* are each known as a single female and both have the derived state of character 1 below. However, further features are either not known or are not informative and the two species are not considered further in the analysis (but see comment section below). The following character states were considered.

1. Wing with r-m transverse or oblique (plesiomorphic); r-m more-or-less parallel to R₁ and R₃ (apomorphic). This feature ap-

pears to be unique within the Culicomorpha and is restricted to members of the genus *Austroconops* (fig. 1K, L). The condition in *Leptoconops* is impossible to score because all members of this genus lack r-m. Therefore, this derived condition may, in fact, have evolved in the ancestor of the extant *Austroconops* + *Leptoconops* with subsequent loss in *Leptoconops*. However, we consider the fossil genus *Minyohelea* Borkent, with an oblique r-m, to be the sister group of *Leptoconops* (fig. 25A), and this would indicate that the derived condition was not present in the ancestor of *Leptoconops*.

2. Male tergite 9 with well developed apicolateral processes (plesiomorphic); tergite 9 with very short or without apicolateral processes (apomorphic). Apicolateral processes have been repeatedly lost within the Ceratopogonidae. Nevertheless, they are present in at least some members of all early lineages for which males are known. They are present in the earliest lineage of Ceratopogonidae, the 121 million-year-old *Lebanoculicoides* (Borkent, 2000a). In *Leptoconops* apicolateral processes are present in most species but are absent or very reduced (leaving only one seta arising from the posterior margin of tergite 9) in the two subgenera *Styloconops* Kieffer and *Megaconops* Wirth and Atchley. Apicolateral processes are also present in the fossil genera *Archiaustroconops* Szadziewski and *Protoculicoides* Boesel and are present or absent in *Minyohelea* (Borkent, 2000a; Szadziewski, 1996). Within extant genera, they are present in *Dasyhelea*, absent or reduced to a single seta in *Forcipomyia* and *Atrichopogon* Kieffer (a very few species with a secondarily derived pair of small projections), present in the Culicoidini, and present or absent in the remaining Ceratopogoninae.

Further outgroup comparisons were provided by Borkent (1995: char. 3). The presence of apicolateral processes is likely a synapomorphy of the Ceratopogonidae (see character 9 below in the analysis of generic relationships). Their absence (or reduction to a group of strong setae) in some species of *Austroconops* is therefore considered to be derived, although there is homoplasy in various lineages.

3. Wing with costa extending well be-

yond apex of vein R_3 (plesiomorphic); costa not extending or only slightly extending beyond apex of vein R_3 (apomorphic). In Thaumaleidae, Simuliidae, and early lineages of Chironomidae (e.g., all Podonominae, many Tanypodinae, some Telmatogetoninae; Brundin, 1966; Wiederholm, 1989) the costa extends to and, in early lineages in these families, past the apex of R_{4+5} . In Culicoidea, the costa appears to continue along the posterior margin of the wing. Within the Ceratopogonidae, *Lebanoculicoides* Szadziewski has a short extension past the apex of R_{4+5} ; there is an extension in the earliest lineage of *Leptoconops* (subgenus *Palaeoconops* Borkent), but there is none in extant species of this genus, it is present in the fossil genus *Protoculicoides*; it is short to long in the fossil genus *Archiaustroconops*; it is absent to long in the fossil genus *Minyohelea*; it is absent in the monotypic fossil genera *Fossileptoconops* Szadziewski and *Alautunmyia* Borkent; and it is absent in virtually all extant Ceratopogonidae (Borkent, 1995: char. 46; Borkent, 1998).

It appears, therefore, that a costal extension is present in at least early lineages of other families of Chironomoidea and is present in at least some members of early lineages of Ceratopogonidae. We therefore consider the absence of the costal extension in some *Austroconops* as derived.

4. Midleg tibia with apical spur (plesiomorphic); midleg tibia without apical spur (apomorphic). Borkent (2000a) used this feature (as character 13) as evidence for the monophyly of Ceratopogonidae other than *Leptoconops* and *Austroconops*. It was recognized that the feature was homoplastic in all early fossil lineages (other than the monotypic *Fossileptoconops* and *Alautunmyia*, which either lack the spur or have a very small one). This suggests that the presence of the apical spur is likely plesiomorphic within the family, with repeated reductions or losses. All Lebanese amber species of *Austroconops* have the spur, and the state is unknown in *A. sibiricus* and *A. borkenti*. It is definitely absent in both extant species of *Austroconops*. The loss of a midleg tibial spur is therefore considered a synapomorphy of these two species, although it may actually include both *A. sibiricus* and *A. borkenti*.

5. Gonostylus with apical spine (plesiomorphic); gonostylus without apical spine (apomorphic). This feature is difficult to interpret, mostly because of the difficulty of observing the feature in fossil material (Borkent, 2000a: char. 8). The feature is present in at least some species of all early lineages, other than *Lebanoculicoides* where the condition is uncertain. Within *Austroconops*, the condition is known only in *A. fossilis* and *A. sibiricus* where the spine is present. The absence of the spine is therefore considered derived for the two extant species *A. mcmillani* and *A. annettae*.

DISCUSSION

This tentative analysis (fig. 24A) indicates that there is a close correspondence between the age of species of *Austroconops* and the pattern of cladogenesis within the genus. The oldest species in Lebanese amber are also the earliest lineages within the genus. The two extant species are sister species; they are also morphologically very similar, with the male and female genitalia and many other features (including all larval features) being presently indistinguishable. The congruence between fossil lineages and patterns of cladogenesis is similar to that present within the entire family (Borkent, 2000a).

The Jordanian Cretaceous amber fossil *Jordanoconops weitschati* (Szadziewski, 2000) may actually be a member of *Austroconops*, as it shares with *Austroconops* the distinctive wing modification described in character 1 above. The sole feature distinguishing it from *Austroconops* is the loss of one of the radial cells, and as an autapomorphy, this loss may have occurred as a sister group of *Austroconops*, but equally well may have occurred within the genus. *Jordanoconops weitschati* belongs between synapomorphy 1 and 3 on the cladogram (characters 2, 4, and 5 are unknown for this fossil). Recognizing *Jordanoconops* as a valid genus leaves *Austroconops* without any defining synapomorphy grouping all extant and extinct species. For the time being, we are considering it as the sister group of *Austroconops* although there is no logical reason to do so.

RELATIONSHIPS BETWEEN THE EARLY
LINEAGES OF CERATOPOGONIDAE

Borkent (2000a) provided the latest cladistic analysis of the relationship between *Austroconops* and other early lineages of Ceratopogonidae, including those known only as fossils. Our results differ primarily in our conclusion that among extant taxa, *Leptoconops* and *Austroconops* are sister groups (fig. 24B) and that among genera known as fossils, *Leptoconops*, *Minyohelea*, *Austroconops*, *Jordanoconops*, and *Archiaustroconops* form a monophyletic group (fig. 25A).

The relationships between early lineages of extant Ceratopogonidae are illustrated in figure 24B. As is always the case, fossils permit study of only a subset of potential character states important to the interpretation of their relationships to each other and to the extant fauna. We therefore provide a separate cladogram (fig. 25A) indicating the relationships between all early lineages, including both extant *Austroconops* and *Leptoconops* and some fossil genera of Ceratopogonidae, using those characters from below which can be utilized in their interpretation.

As in the previous analysis by Borkent (2000a), the monotypic fossil genus *Alautunmyia* is not included here. It is known from two females in New Jersey Cretaceous amber, but some critical character states are obscure (Borkent, 1996, 2000b). Its phylogenetic placement must await further specimens, including males.

The following character states were considered in our analysis. For a given node, characters are arranged sequentially according to eggs, larvae, pupae, males, and females and dorsal to ventral and anterior to posterior.

1. Egg short, oval to somewhat elongate (plesiomorphic); egg very elongate (apomorphic'); egg short (apomorphic'). Most Ceratopogonidae have very elongate eggs, with a length/width ratio of more than 5.0 (fig. 2A). Other Culicomorpha have short to somewhat elongate eggs, with some Chironomidae having a maximum L/W ratio of 4.6 (Nolte, 1993). There are two exceptions within the Ceratopogonidae. Smith and Lowe (1948) reported that the egg of *L. arnaudi*

Clastrier and Wirth (as *Holoconops kerteszi* Kieffer) had a L/W ratio of only 3.4, and they drew the egg as short and more-or-less oval but reported its shape as "banana-shaped". They indicated that *L. carteri* Hoffman (as *L. torrens* (Townsend)) had a similar egg. However, papers on seven other species of *Leptoconops* reported that these have the similar elongate egg as shown here for *Austroconops*. We suspect that Smith and Lowe (1948) misidentified the eggs as *Leptoconops*.

Forcipomyiinae and *Dasyhelea* have short eggs and we consider this a secondarily derived condition within the Ceratopogonidae (apomorphic").

2. Larval head capsule setae o distant from one another (plesiomorphic); setae o closely associated, with bases nearly abutting (apomorphic'); setae o represented by a single seta (apomorphic'). All Ceratopogonidae larvae other than *Leptoconops* have a pair of setae called "o" on the anteroventral area of the head capsule, and in those taxa with two setae, they are close to one another (figs. 2K, 3G). Larvae of *Leptoconops* appear to have only one o seta (fig. 23C). Some Forcipomyiinae may also have only one o seta but others are reported as having two; further study is needed.

The interpretation of this character is somewhat difficult. We have been unable to accurately homologize the setae on the head capsule of Ceratopogonidae with those of other Culicomorpha; nevertheless we are confident that this is possible, especially through the study of first-instar larvae and innervation patterns. However, other Culicomorpha do not appear to have a closely associated pair of setae on the anteroventral area of the head capsule, although the head capsule setae S9 and S10 of Chironomidae (Saether, 1980) may be homologous to the o setae illustrated here. In some chironomids the two setae S9 and S10 are close to one another. We therefore consider the paired setae o of all Ceratopogonidae, other than those of *Leptoconops*, a synapomorphy for the family.

The chaetotaxy of the head capsule of *Leptoconops* has never been homologized with those of other Ceratopogonidae, likely because of the rather modified nature of their

head capsules. Based on the illustration of *L. gallicus* Clastrier by Clastrier (1972; identified as *L. kerteszi*) we provide a tentative identification of the setae (fig. 23A–C). Even if we have not correctly identified seta *o* in *Leptoconops*, it appears that there are no setal pairs on the head capsule of any *Leptoconops* and this is likely derived. The larvae of *Leptoconops* require further study with scanning electron microscopy.

3. Larval pharyngeal complex present and acting as a sieve or absent; not acting as a crushing structure (plesiomorphic); pharyngeal complex a grinding and sifting structure (apomorphic). Borkent et al. (1987: char. 2) discussed this character and predicted that the then unknown larva of *Austroconops* would also have a pharyngeal complex (as described here: figs. 2J, 3F). However, the pharyngeal complex of *Austroconops* apparently lacks brushes or teeth as do some, but not all *Leptoconops* (Clastrier, 1971; Hribar and Mullen, 1991; Smith and Lowe, 1948). Brushes or teeth are present in larvae of other ceratopogonid genera but can be difficult to detect.

4. Larval anal papillae simple (plesiomorphic); anal papillae bifid (apomorphic). Within Ceratopogonidae, the anal papillae are bifid in *Austroconops* (figs. 3B, 11B), nearly all *Forcipomyia* and *Atrichopogon*, all *Dasyhelea*, and in all Ceratopogoninae (poorly known). *Leptoconops* have simple papillae (Aussel, 1991; Ishigami, 1959; Smith and Lowe, 1948); we consider this as a reversal to the plesiomorphic condition. Most other Culicomorpha appear to have simple anal papillae. Simuliidae have anal papillae that are apically simple although many species of Simuliini have anal papillae which bear a few to many small basal lobules, clearly a secondarily derived state. Chironomidae, Thaumaleidae, and Culicoidea larvae have simple anal papillae. These outgroup comparisons support the presence of bifid anal papillae as a derived condition.

5. Pupal respiratory organ with apical porous plate (plesiomorphic); respiratory organ with open pores arranged in a row (apomorphic). The apomorphic condition is nearly unique within the Culicomorpha and is therefore likely derived. Chironomoidea other than Ceratopogonidae have a plastron

and Culicoidea have an apical sieve plate (with larger holes). Simuliidae and some Chironomidae have respiratory organs which function as a physical gill and obtain their oxygen directly from aerated water (not from the surface). One group of *Corethrella* Coquillett species in the New World has remarkably flattened respiratory organs, each of which has a row of pores along the outer edge. The pores are broadly spaced and each has a trachea which gradually merge together near the base of the organ. This condition is likely independently derived in *Corethrella*.

6. Setae on vertex of adult head capsule scattered or in dorsolateral arrangement (plesiomorphic); in addition to other setae on vertex, a single seta located medially, just dorsal to where the eyes meet or, in groups where the eyes are separated dorsomedially, between these (apomorphic). This character was discussed by Borkent (2000a: char. 9) as evidence that *Leptoconops* was the sister group of all other Ceratopogonidae, including *Austroconops* (i.e., the derived condition is absent in *Leptoconops*). This feature requires further analysis and study since the discovery that *Austroconops* and *Leptoconops* are sister groups.

Within the Ceratopogonidae, the condition is not known in the fossil genus *Lebanoculicoides*. Nearly all Ceratopogonidae other than *Leptoconops* and *Fossileptoconops* have the apomorphic condition (a few derived species groups have secondarily lost the medial seta; Borkent, 2000a). We are reluctant to interpret the significance of the absence of the medial seta in the single known amber specimen of *Fossileptoconops*; if true and if the median seta is present in *Lebanoculicoides*, the absence in *Fossileptoconops* may be a synapomorphy shared with *Leptoconops*. If so, it would draw into question the synapomorphies proposed here for *Leptoconops* + *Minyohelea* (characters 20 and 21).

We have surveyed further extant species of *Leptoconops* for this character. It is indeed true that all are lacking the median seta, which is here considered a secondary loss, perhaps related to the adult female habit of burying itself in sand to rest and lay eggs.

As hypothesized here, the presence of the median vertex seta is a synapomorphy of all Ceratopogonidae and has been secondarily

lost in *Leptoconops* (and possibly *Fossileptoconops*). For fossil taxa, we have placed this feature on the same node as synapomorphies 8–10, even though it is unknown for *Lebanoculicoides* (fig. 25A).

7. Wing with well developed R_{4+5} (plesiomorphic); R_{4+5} thin and faint, very poorly defined or absent (apomorphic). This was discussed by Borkent (2000a: char. 4), with further modification by Borkent (2001: 8). There are some puzzling patterns here. It is clear that there is a strongly and well developed R_{4+5} in the Lebanese amber fossil genus *Lebanoculicoides*, and this provides good evidence that this genus forms the sister group of all other Ceratopogonidae, fossil and extant. However, the lesser but still clearly evident R_{4+5} in the Lebanese amber subgenus *Leptoconops* (*Palaeoconops*) is more difficult to interpret. As placed here, the reduction of R_{4+5} occurred in the ancestor of all other *Leptoconops*, and its complete loss occurred independently in at least three other lineages (fig. 25A) and possibly more, depending on the relationships of unresolved lineages.

8. Hindtibia with single transverse row of apical spines (= tibial comb of some authors) present or absent (plesiomorphic); hindtibia with two transverse rows of spines (apomorphic). This feature was discussed by Borkent (2000a: char. 1).

9. Male adult tergite 9 without apicolateral process or, if present, lacking setae (plesiomorphic); pair of apicolateral processes present and each bearing at least one seta (apomorphic). This character is discussed above as character 2 in the analysis of the relationships between species of *Austroconops*.

10. Genital fork (sternite 9) of female genitalia well developed, with vaginal apodeme extending along dorsal wall of common oviduct (plesiomorphic); vaginal apodeme very reduced or absent (apomorphic). This character was discussed by Borkent et al. (1987: char. 1). The feature was not clearly visible in any Lebanese amber fossils. It will be particularly important to discover if it is present in the Cretaceous lineage *Lebanoculicoides* (as the earliest lineage of Ceratopogonidae, fig. 25A).

11. Larval instars 1–4 with abdominal

segments 1–8 undivided (plesiomorphic); abdominal segments 1–8 secondarily divided (apomorphic). The larvae of all instars of *Austroconops* and *Leptoconops* have secondarily divided abdominal segments 1–8 (fig. 2D, G). First-instar larvae of *Austroconops* do not appear to have the condition when they first emerge from the egg (fig. 2C) but display the condition upon lengthening. No other Culicomorpha larvae have divided segments. Several lineages within the Psychodomorpha have independently acquired the derived condition but these differ in structural details, further indicating their independent acquisition of this feature. The larvae of Anisopodidae have secondarily divided abdominal segments but with the anterior portion shorter than the posterior portion for each of these. Larvae of Trichoceridae have secondarily divided first and terminally divided segments with abdominal segments 2–6 divided into three divisions. Some Psychodinae also have secondarily divided abdominal segments with associated sclerotized plates to indicate their position.

Although some *Leptoconops* larvae have only abdominal segments 1–8 subdivided (Aussel, 1991; Laurence and Mathias, 1972; Smith and Lowe, 1948), other species appear to have further divisions of thoracic and/or abdominal segments (Clastrier; 1971, 1972). All *Leptoconops* larvae have a well developed cervix as a subdivision of the prothorax, as do most (all?) Ceratopogoninae.

12. Fourth-instar larvae without hemoglobin in hemolymph (plesiomorphic); with hemoglobin (apomorphic). Fourth-instar larvae of *Austroconops* have a red hemolymph which is assumed here to be due to the presence of hemoglobin. This feature appears to be unique with the Ceratopogonidae. However, at least some larvae of *Leptoconops* have orange hemolymph, which is here considered to be homologous to that of *Austroconops*: *L. americanus* Carter (as *L. kerteszi*, Rees et al., 1971), *L. bequaerti* (Kieffer) (as *Leptoconops* sp., Painter, 1927), *L. arnaudi* (as *Holoconops kerteszi* in Smith and Lowe, 1948), and *L. gallicus* (as *L. kerteszi*, Clastrier, 1972). *Leptoconops borealis* Gutsevich larvae are pale yellow (Krivoshina, 1962). Other *Leptoconops* larvae have been described as being entirely white: *L. al-*

biventris de Meijere (Aussel, 1991), *L. bezzii* (Noè) (Dzhafarov, 1962), *L. carteri* (as *L. torrens*, Smith and Lowe, 1948), *L. irritans* (Noè) (Clastrier, 1971), and *L. spinosifrons* (Laurence and Mathias, 1972). It is possible that at least some of these reports of white larvae were due to examination of preserved material (hemoglobin being no longer red when preserved), but at least some of these reports must be accurate (e.g., authors who examined live larvae). We interpret these pale larvae as having secondarily lost the pigmentation. The reddish hemolymph of fourth-instar larvae *Austroconops* and those of *Leptoconops* with orange hemolymph generally appear during the third-instar, although a few second-instar larvae of *A. mcmillani* were pale pink.

Culicomorpha larvae with red or orange hemolymph are otherwise known only in some Chironomidae (some Tanypodinae, many Chironominae), where this feature is almost certainly independently derived.

13. Male antennal flagellomere 13 without subbasal constriction (plesiomorphic); flagellomere 13 with subbasal constriction (so flagellomere has a basal bulb) (fig. 1A, B) (apomorphic). Borkent et al. (1987: 597) discussed this feature and stated that it was unique within the Chironomoidea. However, within the Culicoidea, a similar condition appears in the Chaoboridae and some Culicidae.

Among fossil taxa, this feature is present in males of species of *Archiaustroconops*. Males of *Jordanoconops* and *Fossileptoconops* are unknown. *Minyohelea* is considered the sister group of *Leptoconops* on the basis of other character states (see characters 20 and 21 below) and is therefore considered to have lost the derived condition in the scenario presented here.

14. Male and female adult with five palpal segments (plesiomorphic); with four palpal segments (apomorphic). Extant adult *Austroconops* and *Leptoconops* have only four palpal segments (figs. 1C–F, 23D, E), with segments 4 and 5 being fused (as evidenced by the landmark capitata sensilla on segment 3). Culicomorpha other than Ceratopogonidae have 5 palpal segments with only a few representatives of Chironomidae, and many Culicidae having a reduced num-

ber. Nearly all other Ceratopogonidae have five segments but there have been a number of reductions in unrelated taxa (listed by Borkent et al., 1987: 598); also in *Diaphanobezzia* Ingram and Macfie, in some *Forcipomyia*, and in some *Atrichopogon*.

Within fossil lineages there are reversals to the plesiomorphic condition in one of the six fossil species of *Austroconops* (*A. gondwanicus*) and in four out of the six known species of *Archiaustroconops* (*A. szadziewskii* Borkent, *A. hamus* Borkent, *A. bocaparyus* Borkent, *A. alavensis* Szadziewski and Arillo).

15. Male and female adult with palpal segments entire (plesiomorphic); apex of palpal segment 3 and base of segments 4 + 5 membranous (apomorphic). The adults of both species of *Austroconops* and nearly all species of *Leptoconops* have a membranous connection at the apex of segment 4 and base of segment 4 + 5 (fig. 23D, E). This condition is not known elsewhere in the Culicomorpha and is therefore a synapomorphy of these two genera. The derived condition, although present in nearly all species of *Leptoconops*, appears to be absent in a few species (e.g., *L. asilomar* Clastrier and Wirth, *L. stygius* Skuse), which we consider to be reversals.

The feature unfortunately is not clear in the fossil material the first author has examined and therefore cannot be presently interpreted for those taxa.

16. Larval mandible positioned laterally on head capsule (plesiomorphic); mandible positioned more medially (apomorphic). The mandibles of *Leptoconops* are unique in the family in lying side by side (fig. 23C). All others are more separated medially. Other Culicomorpha larvae have moderately to widely separated mandibles with most operating in opposition or at an oblique angle.

17. Larval mandible with short to moderately elongate apodeme, simply attached to base of mandible (plesiomorphic); mandibular apodeme very elongate, anteriorly broken into separate parts (apomorphic). Larvae of *Leptoconops* have an unusual and elongate apodeme extending from near the base of the mandible posteriorly to inside the prothorax, and this feature is unique in the

Culicomorpha. The apodeme has been referred to as a ventrolateral rod by previous authors. The anterior portion of the mandibular apodeme of *Leptoconops* appears to be separated into two or more different portions intimately associated with the base of the mandible, identified by Smith and Lowe (1948) as the mandibular lever, by Clastrier (1971, 1972) as “plaques de l’arc génien” (sclerites of the genial arch), and as the subgenal sclerite by Laurence and Mathias (1972). These small apodemes may actually be part(s) of the mandible itself. This complex of apodemes at the base of the mandible is also unique within the Culicomorpha. The homology of the “ventrolateral rod” with the mandibular apodeme of other Culicomorpha is confirmed by its intimate connection with the base of the mandible (via the small anterior separate portions) and by the presence of large adductor muscles attached to the “ventrolateral rod” which serve to adduct the mandible (Laurence and Mathias, 1972).

The larva of *Austroconops* also has a relatively long mandibular apodeme (figs. 2I, 3E). Larvae of other Ceratopogonidae have either a very short apodeme or lack them altogether. Chironomidae are variable, but the Podonominae we examined had short apodemes. We have not yet made further outgroup comparisons but these may show a more elongate apodeme to be a synapomorphy of *Leptoconops* and *Austroconops*, with the apodeme becoming longer and more modified in *Leptoconops* larvae.

18. Larvae with four anal papillae (plesiomorphic); with two anal papillae (apomorphic). *Leptoconops* larvae are unique within the Culicomorpha in having only two anal papillae (Aussel, 1991; Ishigami, 1959). Larvae of all other Ceratopogonidae and nearly all other Culicomorpha have four of these structures. The larvae of Simuliidae have three and those of Chironomidae have either two, four, or six, but nearly all have four (almost certainly the plesiomorphic condition in that family). Thaumaleidae and all Culicoidea have four anal papillae.

19. Pupal apicolateral processes pointed (plesiomorphic); apicolateral processes rounded (apomorphic). *Leptoconops* is the only ceratopogonid genus whose pupae have rounded apicolateral processes. Because

those of *Austroconops* (the sister group of *Leptoconops*) are pointed (fig. 6B), as are those of all other Ceratopogonidae, we consider the condition in *Leptoconops* as derived. Outgroup comparisons support this interpretation. Chironomidae have a wide array of apicolateral processes from pointed to membranous; the pointed condition, however, is present in many, including early lineages (Brundin, 1966; Wiederholm, 1986). Simuliidae, Dixidae, Corethrellidae, and most but not all Thaumaleidae pupae have pointed apicolateral processes (called terminal spines in Simuliidae). Chaoboridae and Culicidae have articulated, membranous pupal paddles in place of the apicolateral processes. The rounded, lobelike apicolateral processes of *Leptoconops* appear to be unique in the Culicomorpha.

20. Wing with long radial cells (plesiomorphic); radial cells very short (apomorphic). This character was discussed by Borkent (2000a: char. 12) but was presented as a derived condition independently evolved in *Leptoconops* and *Minyohelea*. We here consider it to be a synapomorphy of these two genera. This character may merely be another expression of synapomorphy 21. However, there are other Ceratopogonidae (derived lineages) in which reduction of the radial cells does not produce a stigma (e.g., *Baeohelea* Wirth and Blanton, *Baeodasymyia* Clastrier and Raccurt, and *Nannohelea* Grogan and Wirth).

21. Female wing with R₁ and R₃ joining costa without thickening (plesiomorphic); female wing with R₁ and R₃ joining costa as a strong, thickened stigma (apomorphic). Borkent (2000a: char. 6) considered this feature to have evolved independently in *Leptoconops* and *Minyohelea*. Because of the discovery that *Austroconops* is the extant sister group of *Leptoconops*, we considered them to be homologous here. The condition is better developed in some *Minyohelea* species than in others (Borkent, 2000a: figs. 19f, 20a).

22. Wing with r-m (plesiomorphic); wing lacking r-m (apomorphic). The wing of *Leptoconops*, in lacking a r-m, appears to be unique within at least the Culicomorpha.

23. Female antenna with 13 flagellomeres (plesiomorphic); female antenna

with 10–12 flagellomeres (apomorphic). This character was discussed by Borkent (2001). The feature may be used only as evidence for the monophyly of extant *Leptoconops* subgenera. Within this genus, the extinct Lower Cretaceous subgenus *Palaeoconops* has 13 flagellomeres.

24. Posteromedial margin of female sternite 8 with or without semicircular concavity, without semicircular row of stout setae (plesiomorphic); with semicircular concavity bearing four or more stout setae on its margin (apomorphic). The apomorphic condition is unique within at least the Culicomorpha. All female *Leptoconops* examined have the feature (Clastrier and Boorman, 1987; Herzi and Sabatini, 1983; Wirth and Atchley, 1973).

25. Female cercus short, rounded in lateral view (plesiomorphic); cercus elongate, laterally compressed (apomorphic). This feature was discussed by Borkent (1995: char. 6) but as a synapomorphy for only some *Leptoconops*. Subsequent discoveries of Lebanese amber *Leptoconops* (Borkent, 2001), which are the sister group of all extant *Leptoconops*, showed that elongate cerci are basal to the genus and that the short cerci of the females in the subgenera *Styloconops* and *Brachyconops* Wirth and Atchley are reversals to the plesiomorphic condition.

The condition is unique within the Ceratopogonidae, and within the Culicomorpha occurs only in members of the Telmatogoninae (Saether, 1977), which are clearly specialized (marine) Chironomidae. The elongate cerci of some *Leptoconops* species are likely used to oviposit in sand. Females of at least some *Leptoconops* in the subgenus *Styloconops*, which have short cerci, lay their eggs directly on the sand surface (Aussel, 1993).

26. Larval antenna short, with short blade (plesiomorphic); antenna long, with elongate blade (apomorphic). Within the Ceratopogonidae, larvae of nearly all species have short antenna and a short, squat, somewhat bulbous blade. Larvae of *Austroconops* have an elongate antenna and a strikingly elongate antennal blade (figs. 2H, 3C, G, 9A, B, 14A). The larvae of most species of *Forcipomyia* and all *Atrichopogon* have very elongate antennae, but we considered these

to have evolved independently; their antennae are each situated on a cuticular tubercle and either do not appear to have any sensilla or have very short sensilla restricted to the very apex of the antenna (Jeu and Rong, 1980). Within *Forcipomyia* only the distinctive larvae of the subgenus *Phytohelea* Remm have short antennae, which seems almost certainly to be a secondary reduction. Saunders (1957; as *F. (Trichohelea)*) stated that the antennae are reduced to "windows" which bear minute sensilla. Larvae of species of *Brachypogon* Kieffer have somewhat elongated blades (not nearly as long as those of *Austroconops*), but this likely represents convergence.

Outgroup comparisons indicate that other Culicomorpha have elongate antennae and many Chironomidae have an elongate blade, perhaps indicating that the condition in *Austroconops* is plesiomorphic and that the short antenna and blade in *Leptoconops* is independently derived from those of *Dasyhelea* and Ceratopogoninae.

27. Larval head capsule with seta q (plesiomorphic); without seta q (apomorphic). As discussed above, the lack of seta q in *Austroconops* (figs. 2H, 3C) may be a misinterpretation. It may be that seta t is missing and that q is actually more anteriorly placed in *Austroconops*. Regardless, either seta q or t is absent in *Austroconops* and, because both of these setae are present in other Ceratopogonidae, this is likely a synapomorphy. The homology of these setae with those in other Culicomorpha is not yet understood.

28. Larval head capsule with posterior seta of setae p simple, tapering (plesiomorphic); with posterior seta of setae p subapically expanded (figs. 7A, B, 12A, 18) (apomorphic). Within the Ceratopogonidae the apomorphic condition is otherwise known only in some *Forcipomyia* species where it almost certainly secondarily derived; the shape of the single seta p (see character 45 below) is very diverse in different species of *Forcipomyia*. Chironomidae, Simuliidae, and Culicoidea do not have apically expanded dorsal head setae and only some Thaumaleidae have plumose setae.

29. Apex of pupal palpus extending to level of or posterior to apex of labium (plesiomorphic); apex of palpus anterior to

apex of labium (apomorphic). This feature is nearly unique within the Culicomorpha (fig. 4C). In Chironomidae the palpus is directed laterally and therefore cannot be scored here, although they are long enough that if they were directed posteriorly, they too would extend beyond the apex of labium.

30. Pupa with simple setae (plesiomorphic); dorsal setae 1, 2, 4 and all setae on abdominal segments 2–8 bifurcate (some divided into 4) (apomorphic). The derived condition is nearly unique within the Ceratopogonidae (figs. 4A, 5A, G). Only two species of *Stilobezzia* Kieffer (Borkent and Craig, 2001) and *Pellucidomyia leei* Wirth have bifurcate setae and these are almost certainly secondarily derived. The bifurcate setae of the pupa of *Austroconops mcmillani* are bifurcate at their bases while in these other taxa, the setae are bifurcate at midlength or beyond. The pupa of *A. annettae* is unknown and so this synapomorphy may actually be an autapomorphy of *A. mcmillani*.

Within the Culicomorpha, only Corethrellidae, Chaoboridae, and Culicidae have some plumose seta. A few genera of Chironomidae have pupae with some plumose setae but most have simple setae. Simuliidae and Thaumaleidae all have simple setae.

31. Pupa with anterodorsal setae short, or if more elongate, not abutting against respiratory organ (plesiomorphic); anterodorsal setae elongate and abutting against respiratory organ (apomorphic). The apomorphic condition appears to be unique in *A. mcmillani* (figs. 4A, 5A). The position of the two strong anterodorsal setae abutting against the respiratory organs clearly functions to support the respiratory organs and keep them from bending either medially or posteriorly. Why this might be necessary in nature is not known.

32. Wing veins with r-m transverse or oblique (plesiomorphic); r-m more-or-less parallel to R₁ and R₃ (apomorphic). The feature appears to be unique within the Culicomorpha and is restricted to members of the genus *Austroconops* and the extinct Cretaceous genus *Jordanoconops*. See character 1 and the comment section of the analysis between species of *Austroconops* for further discussion.

33. Female cercus with short to moder-

ately long setae (plesiomorphic); with very elongate setae (apomorphic). The derived condition, present only in *Fossileptoconops*, appears to be unique within the Culicomorpha.

34. Male adult antennal pedicel with large basal foramen (plesiomorphic); pedicel with moderately sized or narrow basal foramen (apomorphic). This feature, discussed by Borkent (1995: char. 17), could be seen clearly in only one specimen of the fossil genus *Protoculicoides* (Borkent, 2000a) and it had the plesiomorphic condition. Unfortunately, this character is impossible to observe in most fossils.

35. Pupa with hindleg sheath not visible or barely visible along lateral margin of wing sheath (plesiomorphic); hindleg sheath clearly visible (apomorphic). Within the Ceratopogonidae, all pupae other than those of *Austroconops* (fig. 4A) and *Leptoconops* have the hindleg sheath clearly visible along the lateral margin of the wing sheath. Blanton and Wirth (1979: fig. 35B, C) provided a good illustration of a *Culicoides* pupa showing this feature as the sclerite between the “wing pad” and “abdomen 2”. In *Austroconops* and *Leptoconops* (Clastrier, 1972: fig. 4B; Ishigami, 1959: fig. 8; Laurence and Mathias, 1972: fig. 9) there is only membrane present between the wing sheath and second abdominal segment, and the hindleg is completely under the wing sheath (except for its apex medially).

Other Culicomorpha exhibit some variation. Within the Chironomidae, virtually all have the wing sheath not visible. However, in the Podonominae genus *Boreochlus* Edwards the hindleg sheath is apparently present (Brundin, 1966: 307); other Podonominae have the sheath hidden. In other Culicomorpha, the sheath is either not visible or is present (e.g., Simuliidae). We consider the situation in *Boreochlus* and Simuliidae to be convergent with that present in the Forcipomyiinae + Dasyheleinae + Ceratopogoninae.

36. Adult thoracic anapleural suture well developed, extending to anterior margin of anepisternal cleft (plesiomorphic); anapleural suture short, extending to posterior margin of anepisternal cleft (apomorphic). This character was discussed by Borkent (2000a: char. 14). The feature is

probably an excellent indicator of relationship; no instances of homoplasy are known. All Lower Cretaceous ceratopogonids have the plesiomorphic condition.

37. Trochanter of fore- and midleg with only slender, simple setae (plesiomorphic); trochanter of fore- and midleg each with pair of thick, contiguous setae (apomorphic). This character was discussed by Borkent (2000a: char. 15).

38. Adult midleg tibia with spur (plesiomorphic); midleg tibia lacking spur (apomorphic). This feature was discussed by Borkent (2000a: char. 13). No member of this lineage has a midleg tibial spur. The derived condition is susceptible to homoplasy in the outgroup, with numbers of losses (see character 4 in the analysis between *Austroconops* species above).

39. Larval head capsule prognathous (plesiomorphic); head capsule at least partially hypognathous (apomorphic). The larvae of *Dasyhelea* are partially hypognathous and those of nearly all Forcipomyiinae are completely hypognathous. Only members of the subgenus *F.* (*Phytohelea*) are prognathous and those of *Forcipomyia* (*Warmkea* Saunders) are only partially hypognathous; because other *Forcipomyia* and all *Atrichopogon* are hypognathous, these are probably reversals. It seems likely that the completely hypognathous condition is actually a synapomorphy of the Forcipomyiinae, but a cladistic analysis of the Forcipomyiinae is required to confirm this. Outgroup comparisons indicate that all other Culicomorpha are prognathous, except for the larvae of Thaumaleidae, which are also hypognathous, and this must certainly be due to homoplasy.

40. Larval mandibles articulating with head capsule (plesiomorphic); mandibular articulation reduced (apomorphic). Lieven (1998) showed that the mandibles of larvae of Forcipomyiinae and *Dasyhelea* are uniquely disarticulated.

41. Larval head capsule with pharyngeal complex moderately developed (plesiomorphic); pharyngeal complex massive (apomorphic). This feature (Lieven, 1998) is nearly unique within the Ceratopogonidae. Larvae of species of *Culicoides* (*Monoculicoides* Khalaf) also have large pharyngeal complexes (Murphree and Mullen, 1991),

but this is certainly due to homoplasy. Other Culicomorpha do not have a large pharyngeal complex in the center of their head capsules.

42. Larval salivary duct opening near margin of hypostoma (plesiomorphic); salivary duct opening near center of head capsule (apomorphic). Lieven (1998) showed that, within the Chironomoidea, this feature is restricted to Forcipomyiinae and *Dasyhelea*. It would be valuable to study additional taxa within and outside of the family to confirm this. Furthermore, this character may be another expression of character 41, in which the pharyngeal complex is situated in the middle of the head capsule.

43. Male antenna with setae on flagellomere 1 of similar length to those on subsequent flagellomeres (other than those few terminal flagellomeres which have shorter setae) (plesiomorphic); setae on flagellomere 1 much shorter than those on more distal flagellomeres (apomorphic). This feature was discussed by Borkent (2000a: 403). Although there is some homoplasy in higher lineages within the Ceratopogoninae, this feature appears to be a good indicator of relationship.

44. Larvae with short, slender setae (plesiomorphic); with prominent, strong setae (apomorphic). Forcipomyiinae larvae are unique within the family in having prominent, strong setae on the head, thorax, and abdomen. Many taxa have these setae on raised tubercles. Within the Culicomorpha, strong setae are also present in Thaumaleidae, which is likely an independently derived feature.

This character was discussed by Borkent et al. (1987: char. 9) as “setae arising from cuticular projections”. Some *Forcipomyia* do not have cuticular projections, although these are almost certainly reversals.

45. Larval head capsule with two setae p (plesiomorphic); with one seta p (apomorphic). Larvae of all Ceratopogonidae, other than those of *Atrichopogon* and nearly all *Forcipomyia*, have two setae p. Only two species in the highly modified subgenus *F.* (*Phytohelea*) have two setae p and this must be considered a reversal (Chan and LeRoux, 1971; *F. nicopina* Chan and LeRoux, *F. grandis* Chan and LeRoux). Further outgroup

comparisons to other Culicomorpha are not yet possible because we are uncertain of homologies.

46. Larval antenna close to anterior margin of head capsule (plesiomorphic); antenna on basal half of head capsule (apomorphic). Forcipomyiinae are nearly unique in the Culicomorpha in having posteriorly displaced antennae. Within the genus only members of the modified *F. (Phytohelea)* have anteriorly placed antennae, almost certainly a case of reversal. Within the Culicomorpha, only Thaumaleidae, which superficially resemble Forcipomyiinae, have posteriorly positioned antennae.

This character may be an expression of the head capsule having become hypognathous (see character 39 above) and perhaps is not an independent indicator of relationship.

47. Adult terminal flagellomere tapering or rounded apically (plesiomorphic); terminal flagellomere with basally constricted nipple at apex (apomorphic). This feature is unique within the Culicomorpha. However, some species of *Atrichopogon* do not have the derived condition, which we interpret as a reversal to the plesiomorphic state.

48. Male adult tergite 9 with pair of apicolateral processes present and each bearing at least one seta (plesiomorphic); without apicolateral processes or each represented merely by a single seta (apomorphic). The plesiomorphic feature is considered a synapomorphy of the Ceratopogonidae (character 9 above). Many *Forcipomyia* have a pair of setae on the posterior margin of tergite 9 but others lack even these. *Forcipomyia* generally do have posterior projections, sometimes drawn as arising from the posterior margin of tergite 9, but in fact these are the cerci.

49. Adult thoracic paratergite without setae (plesiomorphic); paratergite with 1–6 setae (apomorphic). This character was discussed by Borkent (1995: char. 22). Instances of homoplasy within the family (Kaczorowska, 2000: 104) are certainly independently derived (restricted to Palpomyiini and Stenoxenini).

50. Egg ovoid to elongate (plesiomorphic); egg c-shaped (apomorphic). This char-

acter was discussed by Borkent (1995: char. 25).

51. Male and female adult scape lacking ventral apodeme (plesiomorphic); scape with ventral apodeme (apomorphic). This character was discussed by Borkent et al. (1987: char. 11).

52. Male adult flagellomeres lacking longitudinal striations (plesiomorphic); flagellomeres with longitudinal striations (apomorphic). This character was discussed by Borkent et al. (1987: char. 10).

53. Male and female with foretibial spur (plesiomorphic); without foretibial spur (apomorphic). This character was discussed by Borkent and Craig (1999, as character 3).

54. Larvae swim with a slow thrashing motion (plesiomorphic); larvae swim with very rapid serpentine motion (apomorphic). Mullen and Hribar (1988) pointed out that the rapid swimming motion of most Ceratopogoninae is unique among Diptera. Some lineages within the subfamily have secondarily lost this motion. However, it is worth noting that some larger larvae have a lower swimming beat rate than do their earlier instars (Linley, 1986), and comparing earlier and later instars may indicate that only later instars have lost the serpentine swimming ability. Regardless, it is clear that this behavior has been lost by some lineages (e.g., *Culicoides (Avaritia)* Fox)).

Other Ceratopogonidae move on substrates either by crawling (Forcipomyiinae, some *Dasyhelea*) or with a serpentine movement (*Leptoconops*, *Austroconops*, some *Dasyhelea*).

55. Larva with posterior proleg (plesiomorphic); without posterior proleg (apomorphic). Larvae of *Leptoconops* and Ceratopogoninae are the only members of the family without a posterior proleg, and we consider these as independent losses. Posterior prolegs with hooks are present in all other Chironomoidea. In Corethrellidae and Chaoboridae they are reduced so that only apical hooks are present (Cook, 1956).

56. Pupae with at most one seta and one pore on anterior portion of abdominal tergite 4 (plesiomorphic); with two setae (apomorphic). Nearly all Ceratopogoninae pupae have two anterior setae on abdominal tergite 4 (called dasm for Ceratopogonidae).

The only exception are species of *Parabezzia* Malloch, where only one seta is present; pupae of this genus are otherwise quite modified. Other Ceratopogonidae have either one seta, one pore, or one seta and one pore (fig. 5G). Other Culicomorpha generally have only one or no seta. Only within Chironomidae are there some taxa with more setae scattered on the tergite (Wiederholm, 1986), but at least within the Podonominae, there appears to be only one anterior seta (Brun-
din, 1966; personal obs.).

57. Sternite 9 of female terminalia forming a continuous band ventrally (plesiomorphic); sternite 9 discontinuous medially, forming two halves (apomorphic). This feature was discussed by Borkent (1995: char. 26).

DISCUSSION

When Wirth and Lee (1958) first described *Austroconops* and puzzled over its classification, they stated that "Final disposition of the genus *Austroconops* would best await the discovery of the male or, perhaps better still, the immature stages." Our discovery and interpretation of the eggs, larvae, and pupae amply confirm their prediction! Among extant taxa, we demonstrate here that *Austroconops* and *Leptoconops* are sister groups. Of these two genera, *Leptoconops* is overall a highly derived group, while *Austroconops* is generally plesiomorphic.

In the first cladistic analysis of the Ceratopogonidae, there were two character states proposed by Borkent et al. (1987) to unite *Austroconops* with all Ceratopogonidae other than *Leptoconops*. We now consider the first character state, the presence of a medial adult head capsule seta in *Austroconops* and all Ceratopogonidae other than *Leptoconops*, to have been secondarily lost in *Leptoconops* (see character 6 above). The second character state is problematic. Borkent et al. (1987) pointed out that the postoccipital ridge was relatively poorly sclerotized and that the posterior portion of the tentorium was directed in a more posterodorsal angle in adult *Leptoconops* and that this was also the condition present in Chironomidae (hence plesiomorphic). *Austroconops* and remaining Ceratopogonidae have a more sclerotized postoc-

cipital ridge and a horizontal tentorium and this was interpreted as evidence of the sister group relationship between these two lineages. This character state is in conflict with the conclusions here and requires further study, especially of the state in further Chironomidae and other Culicomorpha.

Our new analysis also results in significant changes in the interpretation of fossil genera, recognizing for the first time the following as a monophyletic group: the extant *Austroconops* and *Leptoconops* and the fossil genera *Minyohelea*, *Jordanoconops*, *Archiaustroconops*, and *Fossileptoconops* (fig. 25A). Of these, *Leptoconops* and *Minyohelea* are now considered as sister groups. There is one previously published character state which suggested different phylogenetic relationships. Borkent (2000a) and Szadziewski (1996) considered a hindleg tarsal ratio/foreleg tarsal ratio of ≥ 1.40 as derived and evidence for the monophyly of the Austroconopininae, at that time including *Austroconops*, *Archiaustroconops*, and *Minyohelea*. Considered to be a nearly unique feature within the family, Borkent (2000a) noted there was some homoplasy within *Forcipomyia*. Since then, further instances of homoplasy with values as high as 1.8 have become evident within some extant and some fossil *Leptoconops* (Szadziewski, in press). We now therefore no longer recognize any synapomorphies for Austroconopininae.

Other relationships shown in figure 24B are those that have been hypothesized earlier (Borkent, 1995), but we have added substantial support through the addition of further characters, especially from the immatures. In particular, the monophyly of Forcipomyiinae and *Dasyhelea* is confirmed. This is especially important because two characters given by Borkent (1995) have since been shown to be suspect (Borkent, 2000a: 403). In addition, the Ceratopogoninae have further support as a monophyletic group. A recent molecular study of the mitochondrial cytochrome oxidase subunit 2 of a variety of Ceratopogonidae by Beckenbach and Borkent (2003) supported all the relationships shown in figure 24B.

In our analysis here we have excluded the monotypic genus *Washingtonhelea* Wirth and Grogan, which may form the sister group

either of the Forcipomyiinae + Dasyhelea, of the Ceratopogoninae, of Forcipomyiinae + Dasyhelea + Ceratopogoninae, or potentially of a subgroup of the Ceratopogoninae (Borkent, 1995). Female *Washingtonhelea frommeri* Wirth and Grogan have broadly serrate mandibles, a character state restricted to a subgroup within the Ceratopogoninae, suggesting that the genus may be a member of the Ceratopogoninae. It will be fascinating to examine the features of the immatures of this genus once they are discovered.

It is striking that we have been unable to identify a synapomorphy for *Forcipomyia*. We suspect that the genus will be found to be paraphyletic in relation to *Atrichopogon*. There is a wealth of character states in both of these genera, and a cladistic analysis is long overdue. Such an analysis would further test or refine some character states used in our analysis here (characters 2, 26, 39, 45–48).

Because of their phylogenetic conclusions, Borkent et al. (1987) proposed that *Austroconops* be placed in the new subfamily Austroconopininae. The discovery here that the extant *Leptoconops* and *Austroconops* and the extinct *Minyohelea*, *Jordanoconops*, *Archiaustroconops*, and *Fossileptoconops* form a monophyletic group negates the necessity of recognizing a separate subfamily Austroconopininae, and we here place all these genera in the subfamily Leptoconopininae (**new synonym**).

There are several features of ceratopogonids discussed in earlier publications which require some comment. Borkent (1995, 2000a) argued that the presence of an anterior larval proleg must be plesiomorphic within the Ceratopogonidae because it is present in all other Chironomoidea and first-instar Corethrellidae (Borkent and McKeever, 1990). As predicted by Borkent (1995: 103–104), *Austroconops* larvae have an anterior proleg. Therefore, within the Ceratopogonidae the anterior proleg has been independently lost by *Leptoconops*, by *Dasyhelea* and by the Ceratopogoninae (first-instar larvae of *Culicoides* species have the feature but it is lost in the second-instar; Jobling, 1953).

Borkent (2000a: char. 17) indicated that the row of palisade setae on the first tarso-

mere of the hindleg was a synapomorphy of all Ceratopogonidae other than those known as Lower Cretaceous fossils. That was in error and the feature, as discussed here, is restricted to those Ceratopogoninae which form the sister group of the Culicoidini.

The male adults of *A. mcmillani* and *A. annettae* have permanently erect antennal plumes. All other male Ceratopogonidae have erect plumes only when they are in a sexually aroused state during swarming periods. Indeed, this is the basis for the name of the family: *Ceratopogon* Meigen means “bearded horn”, referring to the decumbent male antennal plume. In other Culicomorpha, most families with males possessing a plumose antenna (Chironomidae, Corethrellidae, Chaoboridae) have the plumes permanently erect. Male *Anopheles* Meigen also have decumbent plumes but other mosquitoes have permanently erect plumes. These outgroup comparisons suggest that the decumbent state has either evolved twice in Ceratopogonidae (in *Leptoconops* and most Ceratopogonidae) or the plesiomorphic condition has been re-acquired by *Austroconops*. Nijhout and Sheffield (1979) described the mechanism by which male *Anopheles* erect their plume, and it would be a test of homology to see if the same is present in Ceratopogonidae.

In our analysis we reported only 12 synapomorphies for the genus *Leptoconops*. In reality, it would be possible to report many more by interpreting each detail of the larval and pupal chaetotaxy and more details of the larval mouthparts (maxillae, buccal cavity, etc.) and other modifications. It is clear that *Leptoconops* is highly derived in many of its features.

Our proposal that *Leptoconops* and *Minyohelea* form a monophyletic group suggests that the extinct *Minyohelea* had elongate eggs (character 1), larvae with secondarily divided abdominal segments (character 11), and hemolymph with hemoglobin (character 12), as well as those features shared by all Ceratopogonidae (characters 2–4).

ZOOGEOGRAPHY

Although the two extant species of *Austroconops* are presently restricted to the southwestern corner of Western Australia,

the genus was much more broadly distributed in the past, with fossils recorded from Lebanese, Spanish, French, Siberian, and Burmese ambers. There are two interesting distributional features of these fossils. First, *Austroconops* fossils are known only from Old World ambers. Second, all *Austroconops* fossils are known only from the Cretaceous, dating from 85–121 mya (fig. 25B). By 44 mya, *Austroconops* had been eliminated from at least northern Europe, as suggested by its absence in Baltic amber (with 1103 specimens and 101 ceratopogonid species recorded; Szadziowski, 1988, 1998). Ceratopogonidae from other Old World Tertiary deposits either remain unidentified or include too few specimens to be interpreted here. *Austroconops*, therefore, was diverse in Old World Cretaceous ambers and sometime since its last record 85 mya it became restricted to Western Australia.

What might be the reasons for the present day relict distribution of *Austroconops*? We suggest that the answer lies in an understanding of the nature of the adaptations of the early lineages of Ceratopogonidae. It is striking that the genus *Leptoconops*, as the sister group of *Austroconops*, is known from every significant amber deposit (Old World and New), except for the relatively recent deposits on the Dominican Republic (which otherwise have a reduced ceratopogonid fauna; Borkent, 2000a), and is found today worldwide. *Leptoconops* is an example of an ancient lineage that has survived and thrived by developing a peculiar life cycle with an accompanying wide array of autapomorphies. Species are restricted to areas of beach (or alkaline soils) where the larvae burrow through the sand, and forage on microorganisms; in many places they are the dominant macroorganism in this specialized habitat. Adult females of most (perhaps all) species rest by burrowing into sand, either at night for unfed females or both day and night after blood-feeding. The larval, pupal, and adult stages all have unusual features and have diverged so much that it is difficult to homologize many of the larval and pupal features with those of other ceratopogonids or Culicomorpha. On the other hand, *Austroconops* is in many ways the quintessential “living fossil”, preserving many plesiomorphic fea-

tures in each life stage. Indeed, this was a primary motivation to discover the immatures; the adults were earlier recognized as conservative, and it was expected that the immatures would be the same. True to expectations, the features of the immatures were easily homologized with those of other Ceratopogonidae, especially those of *Dasyhelea* and Ceratopogoninae (Forcipomyiinae larvae and pupae are rather divergent). We suggest that this is why *Austroconops* now has such a restricted distribution—the Ceratopogoninae, and especially species of *Culicoides*, have retained many of the basic features of *Austroconops* and have replaced *Austroconops* throughout most of its historic range. There are two pieces of evidence supporting this assertion. First, there is a general pattern of mutual exclusion in the fossil record (fig. 25B). *Austroconops*, as noted above, is restricted to amber 85–121 million years old. The earliest records of the Ceratopogoninae, including the genus *Culicoides*, are in New Jersey amber (88–93.5 mya), which does not contain *Austroconops*. Siberian amber from Yantardakh (83–88 mya) includes the last fossil record of *Austroconops* and the first Old World record of *Culicoides*, and we suggest that this provides a snapshot of the transition from the one genus to the other. As noted earlier, Baltic amber at 44 mya includes an abundant and diverse group of Ceratopogoninae and no *Austroconops*.

Second, mutual exclusion between *Austroconops* and *Culicoides* is also suggested in the present day local distribution of *Austroconops*. Although *Culicoides* is otherwise diverse in Western Australia, we did not encounter any biting *Culicoides* at Yanchep National Park during the entire adult season of *A. mcmillani* (sampled for 2 years). Neither did we encounter biting *Culicoides* at the type locality of *A. annettae*, and this further suggests that, to this day, the two lineages exclude one another.

Considering that the oldest New World amber is from New Jersey (88–93.5 mya) (fig. 25B), it is quite possible that *Austroconops* was present in the New World before they were, as hypothesized here, eliminated through competition by the evolution of the Ceratopogoninae (particularly *Culicoides*). If ceratopogonid-bearing amber older than 95

mya is discovered in North America, we suggest that it will include *Austroconops*. In examining maps of land distributions from the Cretaceous (Barron, 1987), it is clear that the Cretaceous islands of Europe that preserved amber were close to coastal New Jersey (with its 88–93.5 mya amber) and there were also connections between eastern Russia and western North America at that time. All amber is preserved in coastal environments and it would be hard to suggest what factor could keep early to mid-Cretaceous Old World *Austroconops* out of the New World. Finally, it will be particularly fascinating to see if *Austroconops* shows up in the 53 million-year-old Eocene amber of Le Quesnoy, France (Nel et al., 1999) or the 57–65 million-year-old Sahkalin, Russia amber (Szadziewski, 1990). Our hypothesis here suggests that *Austroconops* should not be present in any Tertiary amber deposits in the Holarctic region because *Culicoides* was well established throughout the region by that time.

If the above pattern is correctly interpreted, we suggest that there may be a good basis for the mutual exclusion between *Austroconops* and *Culicoides*. It was striking to us that larvae of *Austroconops* moved relatively slowly, both in seeking out food and in response to disturbance, when compared to those of most species of *Culicoides*. In addition, larvae of *Austroconops* could not swim, again in contrast to the distinctive, remarkably fast swimming motion of *Culicoides* (and most Ceratopogoninae). Such swimming abilities allow *Culicoides* larvae a rapid escape response, as well as dispersal to other nearby habitat. We speculate that *Culicoides* larvae may have a distinct selective advantage to those of *Austroconops* but, of course, this needs to be tested.

BIONOMIC DIVERGENCE

The larval feeding habits of Ceratopogonidae are quite diverse, ranging from grazing on microorganisms to being obligate predators, eating either whole prey or attacking and invading the larval bodies of much larger Chironomidae (Hribar and Mullen, 1991; Mullen and Hribar, 1988). The discovery that *Austroconops* larvae could be reared on microorganisms present in a fecal infusion fits

the general pattern within the family (fig. 26A). The larvae of *Leptoconops*, Forcipomyiinae, *Dasyhelea*, and many early lineages within the Ceratopogoninae (most *Culicoides*, many Ceratopogonini) feed on microorganisms, fungi, and algae. Some *Dasyhelea* also feed on dying or decayed invertebrates and one species is a leaf-miner (personal obs.). Many members of the Culicoidini and Ceratopogonini appear to include both microorganisms and small prey organisms in their larval diet. Ceratopogonid species that are completely predaceous as larvae appear to be restricted to the lineage composed of the Heteromyiini + Sphaeromyiini + Palpomyiini + Stenoxenini. It is clear therefore that feeding on microorganisms is plesiotypic within the family. Within the Chironomidae all early lineages feed on microorganisms and predation is restricted to all Tanypodinae, some Chironominae, and a few Orthocladinae. The larvae of all Thaumaleidae, Simuliidae, and Dixidae are also browsers on microscopic organisms and small organic particles. Within the Culicoidea it appears that predation evolved at least four times: in Corethrellidae, Chaoboridae, and, within the Culicidae, at least some Culicinae (e.g., some *Psorophora* Robineau-Desvoidy) and all Toxorhynchitinae. It thus seems likely that feeding on microorganisms is plesiotypic for the entire Culicomorpha.

Although we were unable to discover the larval habitat of *Austroconops* species in nature, it was clear from laboratory rearings that the larvae require wet, loose detritus/mud in which to move about and feed. If the mud compacted at all, the larvae experienced difficulty in moving about. When placed in free-standing water the larvae became frantic, looking for attachment on any piece of detritus; upon contact with a substrate they immediately began burrowing. This strongly suggests that the larval habitat in nature must be a permanently wet substrate that would not be disturbed by either current or wave action. Such a restricted aquatic habitat would be congruent with the pattern otherwise present within the family. Ceratopogonid larvae occur in a wide variety of semi-aquatic and aquatic habitats, ranging from decaying vegetation and wet mosses to rivers and lake bottoms. However, nearly all mem-

bers of the early lineages (fig. 26A) are present in small or restricted habitats, such as rock pools, epiphytes, and wet soils at the margins of lotic and lentic habitats. The immatures of *Leptoconops* are generally found in wet or damp sand or sandy soil near freshwater or marine beaches, although a few species are known from seepage areas in desert oases, the wet margins of salt flats, the margin of vernal ponds in desert areas, in halomorphic, calcareous soil, or in cracked clay soils. Forcipomyiinae and *Dasyhelea* are either in small aquatic habitats or live in or on wet vegetation (many feeding on algae). All of the early lineages within the Ceratopogoniinae are either in small aquatic or very wet habitats (e.g., wet soil and pools) or on the margins of rivers and lakes. Only some species of the lineage Heteromyiini + Sphaeromyiini + Palpomyiini + Stenoxenini truly occur in rivers and lakes. Small aquatic habitats and/or wet areas appear to be the plesiotypic habitat for the Ceratopogonidae. Outgroup comparisons suggest that this feature is actually plesiotypic for the entire Culicomorpha. The pattern within the Chironomidae is somewhat uncertain for two reasons. First, the most recent phylogenetic interpretations of the family (Saether, 2000) included character states that have not been polarized using outgroup comparisons. Second, the Chironomidae are markedly diverse in their larval habitats. We agree with Cranston et al. (1987) that the earliest Chironomidae were present in small lotic and lentic habitats and that presence of spiracles in these taxa is plesiomorphic. Further outgroup comparisons are more clear. The earliest lineage of Simuliidae, the genus *Parasimulium* Malloch, is restricted to small seeps, and Thaumaleidae are restricted to wet rock faces. Within the Culicomorpha, nearly all are restricted to small aquatic habitats. Only some species in the derived Chaoboridae genus *Chaoborus* are found in lakes; presence in lakes is likely a plesiotypic feature of *Chaoborus* because a number of the larval features are clearly related to predation pressures by fish. Other genera of Chaoboridae, representing earlier lineages in that family, are restricted to small pools and ponds. This pattern shows that presence in small aquatic habitats is a plesiotypic feature of the entire Culicomorpha.

Borkent (2000a) pointed out that both *Leptoconops* and *Austroconops* species are xerically adapted (only a very few species of *Leptoconops* occur in more mesic areas). Considering that the two genera are now known to be sister groups, it is likely that this adaptation was present in their common ancestor as well as in the extinct genus *Minyohelea* (fig. 25A).

There is a pattern of dispersal capabilities among the early lineages of Ceratopogonidae. Borkent (1991) showed that the ceratopogonid fauna of volcanic oceanic islands worldwide is virtually always restricted to species of four genera: *Forcipomyia*, *Atrichopogon*, *Dasyhelea* and *Culicoides*. These genera include many species which live in ephemeral habitats, such as small bodies of water and wet, decaying vegetation, and it was concluded that these temporary habitats selected for taxa which were good dispersers. All four genera are distributed worldwide. They also are early lineages within the Ceratopogonidae (fig. 24B), suggesting that frequent dispersal was an early characteristic of the ancestor of the Forcipomyiinae + *Dasyheleinae* + Ceratopogoninae (*Culicoides* is an early lineage within the Ceratopogoniinae). The lineage *Leptoconops* + *Austroconops* shows a different pattern. The absence of *Leptoconops* species on nearly all islands reflects the permanency of its primary habitat on marine and freshwater beaches, even though it has an extensive fossil record extending to 121 mya. The restriction of *Austroconops* to Western Australia likewise suggests that it is a weak disperser and that its larval habitat, once found in nature, will be a predictable, stable environment. The ancestor of *Leptoconops* and *Austroconops* therefore was likely in a stable habitat as well and was a poor disperser.

One of the striking features of female adult *Austroconops* is that they are diurnal biters. To interpret this feature phylogenetically, figure 26B shows the distribution of the times when female adult Culicomorpha bite. Virtually every lineage includes species which do not feed at all. Within the Ceratopogonidae, female adult *Leptoconops*, *Austroconops*, and *Forcipomyia* (*Lasiohelea*) (the only *Forcipomyia* that feeds on vertebrates) all feed during the day. Other *Forcipomyia* and

Atrichopogon feed on larger insects, and limited records indicate that they too attack their hosts during the day. Female *Dasyhelea* do not suck blood, and *Culicoides* females may attack at any time (species' behaviors vary within the genus). Other biting Ceratopogoninae feed on insects of approximately the same size (up to two to three times their own length), with most entering male swarms of other Nematocera, males of their own species, or, for a few species, attacking Ephemeroptera. They may be diurnal or crepuscular. This pattern within the family strongly suggests that diurnal feeding is probably plesiotypic within the family and that the crepuscular and nocturnal feeding periods of some *Culicoides* and other Ceratopogoninae are a derived behavior.

Outgroup comparisons suggest that diurnal feeding is plesiotypic to at least the Chironomoidea. The feeding period of the only biting Chironomidae (*Archaeochlus* Brundin, *Austrochilus* Cranston) are unknown, but Simuliidae bite only during the day. The Culicoidea are either nocturnal feeders (Corethrellidae bite calling frogs), feed at variable times (Culicidae), or do not feed at all (Dixidae, Chaoboridae).

What might be the significance of diurnal feeding in Simuliidae and early lineages of Ceratopogonidae? The oldest fossil Culicomorpha are members of the Chironomidae and are recorded from the Upper Triassic (Krzeminski and Jarzembowski, 1999). As the Chironomidae are the sister-group of the Ceratopogonidae, the latter must be considered equally as old, and the earlier divergence of the Simuliidae shows that the blackflies must have been present in the Upper Triassic as well. This pattern suggests that the diurnal biting habit shared by early lineages of Ceratopogonidae and Simuliidae originated during or, more likely, earlier than the Upper Triassic. The Middle and Upper Triassic was the time during which the dinosaurs and mammals, respectively, first arose. The diurnal feeding habit may, therefore, reflect an early stage of bloodfeeding, in which Ceratopogonidae and Simuliidae depended primarily on visual cues and detection of heightened CO₂ production by their daytime hosts. Apparently extant Simuliidae do not use heat to detect their endo-

thermic hosts (Crosskey, 1990). Perhaps the original hosts of biting Culicomorpha were ectotherms and detection of their hosts was only possible when hosts were active during the day (producing more CO₂ and visually apparent). Similar to Culicidae (Bock and Cardew, 1996), female adult *Culicoides*, including those that feed nocturnally, use a combination of olfactory, visual, and thermal cues to detect their hosts (Kline and Lemire, 1995). It would be interesting to know what else attracts *Leptoconops* and *Austroconops* females to their hosts, other than their known attraction to CO₂ (Brenner et al., 1984) and especially if they are attracted by heat. Our interpretation here would predict that they are not attracted by thermal cues.

Both species of *Austroconops* almost certainly overwinter in the larval stage (tables 5, 6) and this is by far the most prevalent mode of Ceratopogonidae in temperate areas. Only a few species of *Culicoides* appear to overwinter in the egg stage (Jobling, 1953; Parker, 1950). Overwintering in the larval stage is therefore plesiotypic within the Ceratopogonidae.

SUGGESTIONS FOR FUTURE RESEARCH

As always in science, more information means more questions. This study indicates several areas where further investigation would be fruitful.

- Locate the larvae and pupae of *Austroconops* species in their natural habitat. This would give a better understanding of the adaptations of these species and enhance the likelihood of conserving these "living fossils".
- Describe the pupa of *A. annettae* to test the purported pupal synapomorphies detailed here.
- Investigate the presence of female adults of *A. mcmillani* on wet kangaroo feces and determine the significance of that behavior.
- Determine whether *Austroconops* transmits any diseases between its hosts. The host of *A. annettae* is unknown.
- Determine further homologies with other Culicomorpha. Comparison of the first-instar larvae of Culicomorpha would be particularly valuable because these seem to generally be more conservative. Within the Ceratopogonidae, an SEM study of the larva and pupa of a species of *Leptoconops* would allow ho-

mologies of this divergent group to be better understood.

- Study of Forcipomyiinae cladistically.
- A comparative morphological study of the larvae and pupae of Ceratopogonidae is basic to good keys to the genera and would provide further phylogenetically important characters (Borkent, in prep.).

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