

**BIOLOGY AND IMMATURE STAGES OF THE CRANE FLY  
*PTILOGYNA (PLUSIOMYIA) HERRONI* (ALEXANDER)  
(DIPTERA: TIPULIDAE) FROM NEW CALEDONIA,  
WITH DISCUSSION OF ITS PHYLOGENETIC PLACEMENT**

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*Abstract.*—The last instar larva and pupa of the crane fly *Ptilogyne (Plusiomyia) heroni* (Alexander) (Diptera: Tipulidae: Tipulinae) are described and illustrated from specimens collected in New Caledonia. The microhabitat of the last larval instar and pupa is discussed. Comparisons are made with larvae and pupae of other Tipulinae. This represents the first detailed description with illustrations for the larva and pupa of *Ptilogyne* Westwood. Pupal characters indicate a basal phylogenetic placement for this genus within the Tipulinae.

*Key Words:* Diptera, Tipulidae, crane fly, *Ptilogyne*, larva, pupa, New Caledonia

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The crane fly genus *Ptilogyne* Westwood (Tipulidae: Tipulinae) comprises 30 species and subspecies placed in three subgenera. Both *Ctenogyne* Macquart and *Ptilogyne* Westwood are subgenera endemic to the Australasian and Oceanian regions (Oosterbroek and Jonas 1986). The third subgenus, *Plusiomyia* Skuse, apparently has a trans-Antarctic or trans-Pacific distribution with 18 species in Australia, 4 in New Caledonia (Oosterbroek 1989), and 1 in Brazil (Alexander and Alexander 1970). Of the four *Ptilogyne* species recorded from New Caledonia, the adult of *P. heroni* (Alexander) has the least wing coloration, and the male has the longest antennal flagellar branches (Alexander 1948: Fig. 7).

Features of the immature stages are important for interpreting phylogenetic relationships within Tipuloidea (Oosterbroek and Theowald 1991). Knowledge of the immature stages of tipulid genera is very incomplete and this is especially true for gen-

era in the Southern Hemisphere. Lack of information on immatures for genera in the Southern Hemisphere has hindered their placement in phylogenetic classifications. Of 30 genera and subgenera of Tipulinae recorded from the Australasian and Oceanian Regions (Oosterbroek 1989), we know larvae for only ten (33%), and even those primarily are known from species occurring in the Nearctic Region (Alexander 1920, Rogers 1949, Byers 1961, Gelhaus 1986). The greatest number of genera and subgenera with unknown larval and pupal stages occur in the Australasian and Neotropical Regions. Recent detailed descriptions of immature stages of *Brachyprema* Osten Sacken (Gelhaus and Young 1991), *Leptotarsus* Guérin-Méneville (subgenera *Limoniodes* Alexander, *Pehlkea* Enderlein, and *Longurio* Loew) (Gelhaus and Young 1995), and *Tipula* Linnaeus (subgenus *Tipulodina* Enderlein) (Young 1999) has contributed information of phylogenetic signif-



icance. The successful rearing of several last instar larvae to adults by C. Dennis Hynes while conducting research on the crane fly fauna of New Caledonia (Hynes 1993) allows the first complete, illustrated description of both last instar larva and pupa for the genus *Ptilogyna*. Morphological characters of the pupa observed suggest a possible basal phylogenetic position for the genus within the Tipulinae.

Terminology of larval and pupal characters follows that of Byers (1961) and Gelhaus (1986). The term Tipulidae used here follows Alexander and Byers (1981) with three subfamilies (Tipulinae, Cylindrotominae, and Limoniinae). Catalogue of Palearctic Diptera recognizes three families: Tipulidae (Oosterbroek and Theowald 1992), Cylindrotomidae (Soós and Oosterbroek 1992), and Limoniidae (Savchenko, Oosterbroek and Starý 1992) that correspond to the subfamilies just mentioned (Byers 1992). Starý (1992) proposed the fourth family Pediciidae, formerly a subfamily within the Limoniidae. Accordingly, the term Tipulinae used here refers to all Tipulidae sensu stricto.

*Ptilogyna (Plusiomyia) herroni*  
(Alexander)  
(Figs. 1–13)

**Larval description.**—Mature larva: Body 35–38 mm long and 5–6 mm wide, tapering gradually toward both ends. Body sordid yellow, darker laterally.

**Head:** Broad, massive, well sclerotized, oval-shaped and slightly depressed, typical tipuline head capsule (Byers 1961, Young 1981, Gelhaus and Young 1991); antenna with cylindrical basal segment and apical sensory peg, about three times as long as its basal width, slightly tapering apically; mandible bifurcate with distinct, large ventral tooth and smaller dorsal tooth, two smaller teeth subapically along inner margin of ventral tooth, an additional tooth and hair tuft near base of mandible (Fig. 1); maxilla with hairy galea and lacinia; hypopharynx with five teeth, median tooth

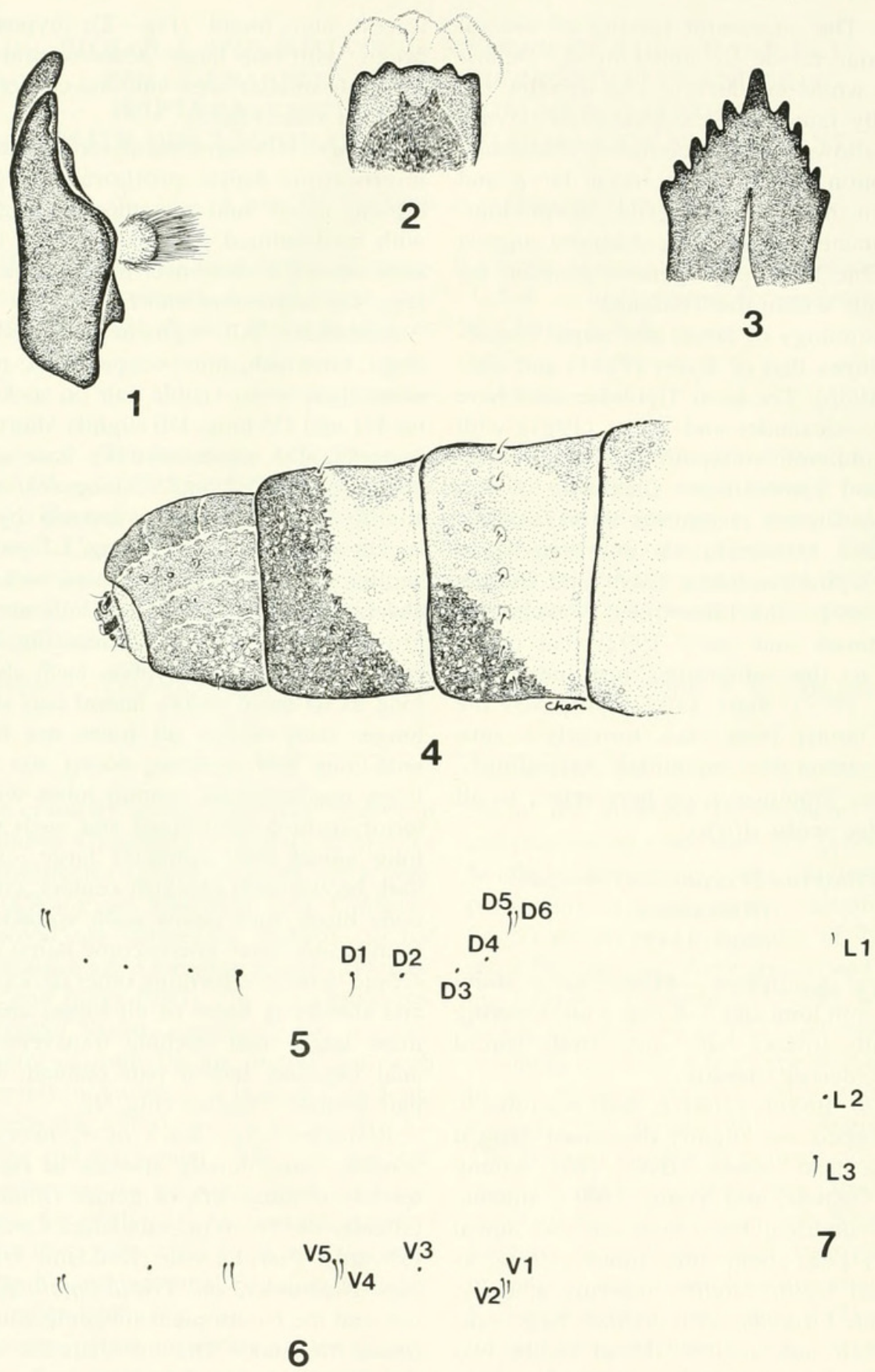
lowest and broad (Fig. 2); hypostomal bridge with one large, acute central tooth and four smaller ones and one corner tooth on each side (Fig. 3).

**Thorax:** All segments covered with short microscopic hairs; prothoracic segment brown; meso- and metathoracic segments with well-defined patches of short, brown with silvery iridescence, microscopic hairs (Fig. 4); macrosetae short.

**Abdomen:** All segments covered with short, brownish, microscopic hairs; macrosetae short to no visible hair on socket; setae D1 and D5 long, D6 slightly shorter and finer, D2–D4 represented by bare sockets (Fig. 5); setae V2 and V5 long, V1 and V4 slightly shorter, V3 represented by bare socket (Fig. 6); seta L3 long, L1 pale and shorter, L2 represented by bare socket, L4 absent (Fig. 7); abdominal cuticular outgrowths absent. Spiracular disc (Fig. 8) surrounded by six fleshy lobes, each about as long as its basal width; lateral pair slightly longer than others; all lobes not fringed with long hair or setae; dorsal and lateral lobes unsclerotized; ventral lobes with anterior surface sclerotized and each with a long apical seta; spiracles large, circular, dark brown with blackish centers; conspicuous black spot below each spiracle, surrounded by short microscopic hairs; microscopic hairs also forming other dark patches and streaks at bases of all lobes; anal segment large, anal opening transverse; four anal papillae, lateral pair conical, ventral pair broadly rounded (Fig. 9).

**Remarks.**—The larva of *P. herroni* resembles superficially species in the most terrestrial subgenera of genus *Tipula*, specifically the Nearctic subgenera *Lunatipula* Edwards, *Pterelachisus* Rondani, *Trichotipula* Alexander, and *Triplicitipula* Alexander, and the Neotropical subgenus *Eumicrotipula* Alexander. They all share the following morphological characters: body heavily covered with short microscopic hairs; spiracular lobes fleshy or partially sclerotized without border of setae; four or fewer distinct papillae (Gelhaus 1986). Notable dif-





Figs. 1-7. *Ptilogyna herroni* larva. 1, Mandible, dorsal. 2, Hypopharynx, dorsal. 3, Hypostomal bridge, ventral. 4, Thorax, lateral. 5-7, Abdominal macrosetal arrangements. 5, Dorsal setae. 6, Ventral setae. 7, Lateral setae.



ferences of *P. herroni* from the above subgenera are the brown with silvery iridescence band around the anterior portion of the mesothoracic segment, the brown with silvery iridescence patches on the latero-ventral part of the meso- and metathoracic segments, the unsclerotized dorsal and lateral spiracular lobes, and abdominal macrosetae D2, D3, D4, V3, and L2 represented only by bare sockets.

**Pupal description.**—Male: Length 26 mm, width 4.5 mm. Female: Length 25 mm, width 4.5 mm. Body brown, slightly darker on head and thorax.

**Head:** Antenna greatly expanded at base and antennal branches readily visible in male (Figs. 10–11); apex of antenna reaching about two-thirds length of mesothoracic tibia in male, reaching slightly beyond prothoracic tibia in female; paired short, wrinkled ridges between bases of antennae; maxillary palpus short, slightly curved at base, then curved upward toward apex; apex of maxillary palpus not recurved, reaching prothoracic tibia (Fig. 10).

**Thorax:** Length of respiratory horn 2 mm, minute annulations along its entire length; apex of wing nearly reaching end of abdominal segment II; apices of fore, middle, and hind tarsi in oblique alignment, with fore tarsus shortest and adjacent to each other at ventral midline; in female apex of fore tarsus reaching anterior edge of segment IV, apices of middle and hind tarsi reaching middle of segment IV; in male, apex of fore tarsus reaching middle of segment IV, apices of middle and hind tarsi reaching posterior end of segment IV; middle tarsus slightly longer than hind tarsus in both sexes.

**Abdomen:** Segments III–VII with well-defined anterior and posterior annuli; small hooked spines present laterally and along posterior margins of all segments; three spines laterally on segment III–VII; 10–12 dorsal spines along posterior margin of segments II–VII (Fig. 11); two ventral spines on segments III–IV and six ventral spines on segments V–VII; terminal segments

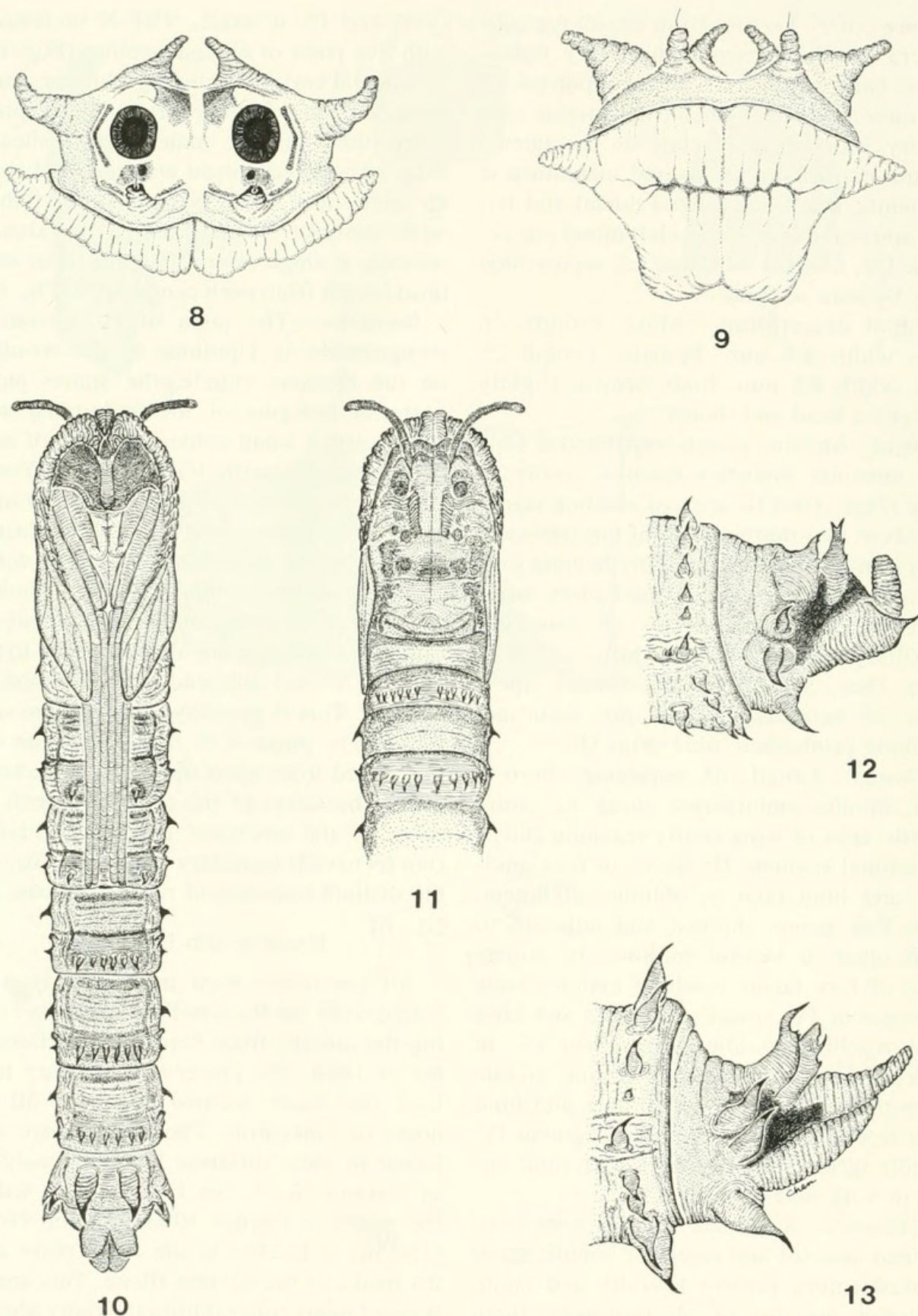
(VIII and IX in male, VIII–X in female) with five pairs of elongate spines (Figs 12–13); dorsal two pairs slightly blunt or acutely tipped, each with several smaller spines along their length; male genital sheaths (Fig. 12) curved dorsad with a lateral spine on each near bend beyond base; female with distinct cercal and hypovalvular sheaths, a single spine laterally near one-third length from each cercal apex (Fig. 13).

**Remarks.**—The pupa of *P. herroni* is recognizable as Tipulinae by the wrinkles on the thoracic cuticle, the spines along posterior margins of the abdominal segments, and a small spine near base of each male genital sheath (Gelhaus and Young 1995). The external structures of both male and female genital sheaths with lateral spine on the sheaths resemble those of *Leptotarsus* (*Limoniodes*) *sulphurellus* (Alexander). The distinct branches of the antennal sheath found in *Ptilogyna* are also observed in pupae of several subgenera of *Ctenophora* Meigen. This is possibly a convergent condition. The pupa of *P. herroni* can be distinguished from other tipulines by the combined characters of the ridges between the bases of the antennae, the nearly straight (not recurved) maxillary palpal sheaths, and the distinct branches of male antennae.

#### HABITAT AND BIOLOGY

All specimens used in this study were collected in the Rivière Bleue Preserve during the months from September to December of 1988. The preserve is primary lowland rain forest located about 20–30 km north of Ouénarou. The larvae were collected in three different localities assigned as Stations No. 5, No. 6, and No. 7 within the preserve (Hynes 1993). Station No. 5 (150 m) is located in the flood plain near the banks of the Rivière Bleue. This area is flooded many times during the rainy season, and water remains standing for long periods of time after such flooding. Station No. 6 (160 m), located near the edges of the river, is essentially the same vegetational type as Station No. 5, but the river does not peri-





Figs. 8-13. 8-9, *Ptilogyna herroni* larva. 8, Spiracular area. 9, Anal papillae, ventral posterior view. 10-13, *P. herroni* pupa. 10, Habitus, male ventral aspect. 11, Habitus, male anterodorsal aspect. 12, Male terminal abdominal segments, lateral. 13, Female terminal abdominal segments, lateral.



odically flood it during the rainy season. Station No. 7 (170 m) is on a steep hillside and differs greatly in vegetation and aridity from Stations No. 5 and No. 6.

The soil in the general collecting sites is typical of southern New Caledonia, the product of degradation of ultramafic rock. The soil consists of relatively small, nearly spherical particles, reddish in color and unable to hold enough organic material or moisture for the development of the immature stages of most Tipulidae. Fallen trees in various stages of decay, along with numerous small branches entrapping leaves from various trees, form a mat of decaying organic material accumulated on the forest floor. These accumulations attain lengths of 2–3 m and widths of 1–2 m. Many remain wet or damp for long periods of time. Larvae of *Ptilogyna* were collected mainly from fallen tree trunks, especially the interior sections with large amounts of dark brown, decomposed material. This material remains damp throughout extended dry periods. Occasionally the larvae were collected within other decaying organic material, especially between layers of leaves on the forest floor.

Larvae of *Ptilogyna* are considered as terrestrial species based on microhabitats in rotting logs away from aquatic situations, or in leaf debris on the forest floor. Larvae for rearing were kept within organic debris from rotten logs. Larvae pupated soon after capture, and adults started emerging in about eight days. Larvae, intact pupae of each sex, and exuviae of larvae and pupae were preserved in ethanol.

#### DISCUSSION

Hypotheses of phylogenetic relationships of genera within the Tipulidae have traditionally relied exclusively on morphological characters of adults. Oosterbroek and Theowald (1991) proposed a phylogenetic scheme for the Tipuloidea (families Limoniidae, Cylindrotomidae, and Tipulidae) based on larval and pupal characters. They provided informative characters in support

of phylogenetic relationships within the then proposed subfamilies of Limoniidae (Eriopterinae, Hexatominiae, Pediciinae, and Limoniinae), and also presented strong support for a sister group relationship between the Cylindrotomidae and Tipulidae s.s. However, the analysis of the family Tipulidae s.s. was excluded from their study due to the likely paraphyly of the currently recognized subfamilies (Dolichopezinae, Ctenophorinae, and Tipulinae). Starý (1992) has since elevated Pediciinae to family Pediciidae, and replaced Eriopterinae with Chioneinae, and Hexatominiae with Limnophilinae due to the rules concerning priority. Meager knowledge of the immature stages of Tipulidae has also placed limitations on the larval key of Alexander and Byers (1981) for the Nearctic fauna. The genera in this key do not appear in a phylogenetic sequence. The most recent larval key for Tipulinae is that of Gelhaus (1986), who presents a detailed taxonomic study of the genus *Tipula* in North America. No existing generic key is available for immature stages of Tipulinae.

The larva of *P. herroni* cannot be confused with other tipuline genera based on its distinct brown with silvery iridescence band and patches on the meso- and meta-thoracic segments. However, the arrangement of characteristic features around the spiracular disc with 1) unsclerotized dorsal and lateral spiracular lobes, 2) all lobes not fringed with long hairs, and 3) four reduced anal papillae, does bear a superficial resemblance to similar structures in several species of the most terrestrial subgenera of *Tipula*; thus the larva of *P. herroni* cannot be easily distinguished from larvae of those subgenera, as indicated above in remarks following the larval description.

Oosterbroek (personal communication) indicated that 11 teeth (nine teeth and two corners) on the hypostomal bridge of *P. herroni* is interesting because it is the highest number (5–11) found in Tipulidae s.s. In Cylindrotomidae, the supposed sister group of the Tipulidae s.s., there are about



17 teeth. Many teeth may be considered plesiomorphic for the Tipulidae s.s. However, larvae of *Ctenophora* and *Dendrotipula* apparently have retained this plesiomorphic number though they are not considered primitive, but the larvae live in dead or decaying wood, as do those of *P. herroni*.

Alexander (1927) proposed some presumed primitive generic lineages, including *Ptilogyna*, within Tipulinae based on the radial field of the wing. Other workers have attempted to place various lineages within Tipulinae based on pupal characters such as the shape of the maxillary palpal sheath, the length of the distal section of the antennal sheath, and the position of the antennal sheath. A straight or curved maxillary palpal sheath, short distal section of antennal sheath, and apices of antennal and palpal sheaths closely approximated (for example, *Megistocera* Wiedemann, *Brachypremna* Osten Sacken, and *Leptotarsus* Guérin-Méneville) are considered plesiomorphic within the Tipulinae (Oosterbroek and Theowald 1991, Gelhaus and Young 1995). A strongly recurved apex of the maxillary palpal sheath, an extended distal section of the antennal sheath, and apices of antennal and palpal sheaths widely separated (for example, *Dolichopeza* Curtis, *Nobilotipula* Alexander, *Platytipula* Matsumura, *Tipulodina* Enderlein, and most other Tipulinae) are considered apomorphic (Gelhaus and Young 1995).

In *Ptilogyna*, the shape of the maxillary palpal sheath is slightly curved without a strongly recurved apex (plesiomorphic), the distal section of the antennal sheath is elongated (apomorphic), and the apices of antennal and palpal sheaths are widely separated (apomorphic). Based on this limited information we postulate that the genus *Ptilogyna* is a member closes to the basal assemblage (*Brachypremna*, *Leptotarsus*, *Megistocera*, *Ozodicera* Macquart, *Clytocosmus* Skuse) of the subfamily Tipulinae and suggest a possible phylogenetic place-

ment of it between the primitive and the advanced genera within Tipulinae.

The discovery of the immature stages of *P. herroni* provides much-needed information in order to narrow the gap in our knowledge of the immature stages of Southern Hemisphere crane fly taxa. Our findings concur with several previous studies by various authors that many of the larval characters (including spiracular disc, spiracular lobes, anal papillae, hypostomal teeth), and the size and form of the respiratory horns of the pupa provide taxonomically important information for identification and probably have a close correlation of structure to habitats. These larval characters probably have evolved in their specific habitat to such a degree that they show a greater divergence than do some of the more conservative pupal characters such as maxillary palpal sheath, antennal sheath, and spines on genitalial sheaths. It is likely that the similarities of larval characters have evolved convergently because of habitat requirements, while the similarities of pupal characters have evolved by reason of common ancestry. This must be considered when using these characters in the placement of the genus within the subfamily Tipulinae. Chaetotaxy and additional pupal characters as mentioned in Gelhaus and Young (1995) may have applicability for establishing relationships but are not yet evaluated phylogenetically against a broad range of tipuline taxa. Further work is needed on the morphology of the immature forms of Tipulinae before such information can contribute to the understanding of the postulated relationships among these lineages.

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