

**IOWANA FRISONI HOTTES (HEMIPTERA: APHIDIDAE) REDESCRIBED,
WITH NOTES ON ITS BIOLOGY**

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Abstract.—*Iowana frisoni* Hottes was collected and studied for the first time since its original collection in 1925. It was found in remnant prairies where it fed on the basal stem of the endemic plants *Silphium laciniatum* L. and *S. terebinthinaceum* Jacquin (Asteraceae). Later in the season it fed on the stem or leaf stipules within the cavity created by the leaf axil. The aphid was always tended by ants, *Lasius flavus* (F.), *L. neoniger* Emery, and two *Crematogaster* species, which housed the aphids by building soil collars around the bases of plants and sealing leaf axils with soil and dead plant material. The ants also carried *I. frisoni* underground when the aphid colony was disturbed. We redescribe the apterous vivipara morph of *I. frisoni* and describe for the first time the fundatrix, alate vivipara, male, ovipara, and egg.

Key Words: *Silphium*, *Lasius*, endemic species, prairie remnant, symbiosis

In 1925, G. Hendrickson collected a few aphids in a leaf axil of *Silphium laciniatum* L. (compass plant, Asteraceae) in Ames, Iowa. Twenty-nine years later, F. C. Hottes described a new genus and species based on two specimens (Hottes 1954). As far as we can surmise, the aphid, *Iowana frisoni* Hottes (Hemiptera: Aphididae), had not been seen in the 75 years since its original collection.

In the summer of 2000, we discovered *I. frisoni* feeding on flowering stems of *S. laciniatum* and *S. terebinthinaceum* Jacquin (prairie dock) at Loda Cemetery Prairie Nature Preserve (~1.4 ha in area; Iroquois Co., IL, 40°31.62'N × 88°4.57'W), a prairie remnant (White 1988). Both *S. laciniatum* and *S. terebinthinaceum* are common perennials in prairies of central Illinois and produce as many as 12 flowering stems per plant that can reach heights of 2–4.5 m (Weaver 1954).

Here, we redescribe the *I. frisoni* apterous vivipara and describe for the first time the fundatrix, alata, male, ovipara, and egg. We also discuss the biology of the aphid with regard to host plants and attendant ants, *Lasius flavus* (F.), *L. neoniger* Emery, and two unidentified *Crematogaster* species.

MATERIALS AND METHODS

To evaluate the distribution of *I. frisoni* in east central Illinois, we surveyed three other prairie remnants and three prairie restorations where both species of *Silphium* were present, thoroughly canvassing these sites for aphids on plants of both species. Remnants were Prospect Cemetery Prairie Nature Preserve (~2 ha; 40°26.71'N × 88°5.87'W) and Paxton Railroad Prairie (~2 ha; 40°26.17'N × 88°06.36'W) in Ford County and Grant Creek Prairie Nature Pre-

serve (~31 ha; 41°22.10'N × 88°11.55'W) in Will County. The restorations were all in Champaign Co.: Red Bison Prairie Corridor (~1.7 ha; 40°4.81'N × 88°14.83'W), Trelease Prairie (~7.3 ha; 40°7.76'N × 88°8.59'W), and Meadowbrook Prairie (~24 ha; 40°4.72'N × 88°12.41'W). See Tooker et al. (2002) and Tooker and Hanks (in press), for more information on sites.

To estimate the abundance of *I. frisoni* and its attendant ant species at Loda Cemetery Prairie, we established five east-west transects across the long axis of the prairie (~200 m). We walked transects on 12, 19, and 26 July, 27 August, and 6 September 2002, examining plant stems within 1 m of transects for *I. frisoni* and ants ($n = 75$ *S. laciniatum* stems, 106 *S. terebinthinaceum* stems). We also assessed the prevalence of *I. frisoni* at Prospect Cemetery Prairie in August 2002 by walking a single transect (~50 m long) through a patch of *S. terebinthinaceum* and recording the presence of *I. frisoni* and ants. Because flowering stems of *S. laciniatum* were not abundant at that site, we examined all plants of that species.

We collected aphids ($n = 42$) and ants ($n > 30$) during the growing seasons in 2001 and 2002. On 6 October 2002, a colony was brought back to the lab and reared on a cut stem of *S. terebinthinaceum*. This colony produced males ($n = 6$), oviparae ($n = 8$), and eggs ($n = 11$), which were laid randomly along the stem under a leaf stipule. Collected aphids were cleared with a KOH and chloral phenol procedure and slide-mounted in Canada balsam. Species identity was confirmed with the holotype (the single paratype is a nymph) and associated ants were identified. Aphid and ant specimens are deposited at the Illinois Natural History Survey insect collection and exemplars of each aphid morph were sent to the National Museum of Natural History (aphid collection, Beltsville, MD). Fifty-seven aphids were measured with an ocular micrometer on a compound microscope. Specimen photos were taken using a Nikon Eclipse E600 microscope, Spot Insight dig-

ital camera model 3.2.0, and Spot Advanced software (Diagnostic Instruments, Inc., Sterling Heights, MI).

Because no obvious morphological differences distinguished three putative fundatrices, we performed canonical discriminant function analysis to confirm that they were indeed morphometrically distinct from the other apterous viviparae. Discriminant factor analysis of aphids has been used to discriminate between species (Brown and Blackman 1994) and populations of the same species (Footitt and Mackauer 1980). Hand (1986) used this method to discriminate holocyclic and anholocyclic alate aphids of the same species. To confirm that aphids collected as solitary adults early in the season were fundatrices and not other viviparae, discriminant function analysis was conducted (SYSTAT® 10 software, SPSS Inc. 2000) using 10 characters to confirm morphological distinctness (Albrecht 1980): lengths of the whole body, antennal segment II, antennal segment IV, the base of antennal segment V, the processus terminalis of antennal segment V, rostral segment III, siphunculus, metafemur, metatibia, and counts of rhinaria on antennal segment II. To maintain a large sample size, some typical measurements (ultimate rostral segment, for instance) were omitted if they were not available for all three putative fundatrices.

The groupings in the analysis were apterous viviparae, alate viviparae, oviparae, and males; we also added the three putative fundatrices and the holotype (apterous vivipara) to determine their association with the other groups. If putative fundatrices did not group with apterous viviparae, for example, we could conclude that they were indeed a distinct morph. To control for possible seasonal variation in aphid morphometrics (Debaraj and Singh 2000), we used apterous viviparae from throughout the growing season, including early-season collections made soon after the putative fundatrices had been collected. We tested for

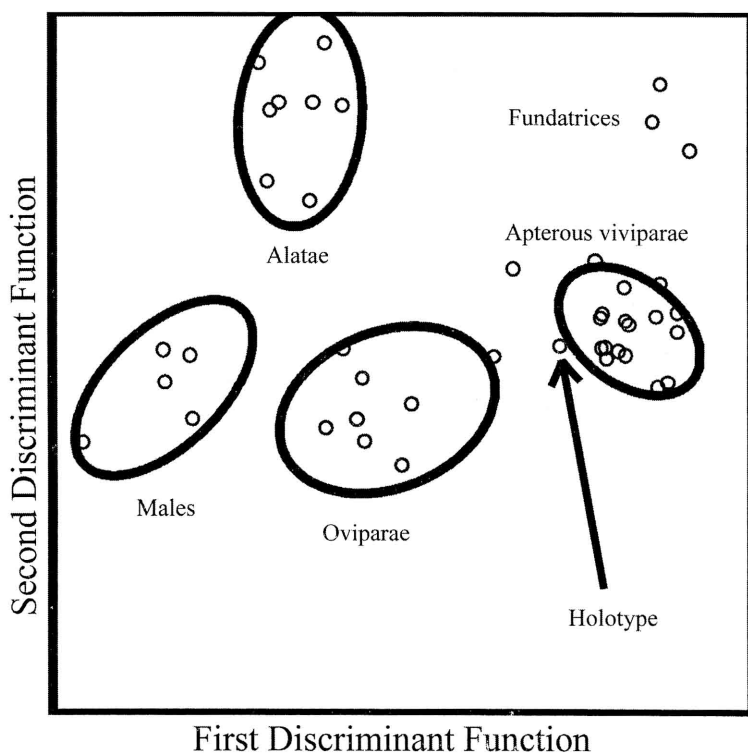


Fig. 1. Graph of first and second discriminant factors showing the fundatrices as distinctly different from the other apterous viviparae. Ovals are 95% confidence intervals.

distinctness using the first through fifth discriminant factors.

RESULTS AND DISCUSSION

Populations of *I. frisoni* were present in all four prairie remnants but were not observed in any of the three restorations, suggesting it may be a remnant dependent species (Panzer et al. 1995). We did not search for or collect the ant species in the restorations. The aphid fed on both *S. laciniatum* and *S. terebinthinaceum* at all four sites, but not on *Silphium integrifolium* Michaux, which was also present at all four sites. Neither have we seen *I. frisoni* on *Silphium perfoliatum* L. at Meadowbrook Prairie or several railroad rights-of-way in east central Illinois.

Because all colonies of *I. frisoni* observed were tended in summer by the ants *L. flavus*, *L. neoniger*, or one of two *Crematogaster* species, it seems likely that the

symbiosis is obligate, as is true for some other aphid species (Eastop 1953, Carter 1983). In October, ants were absent in the several declining aphid colonies, the ants having retreated below ground to overwinter. The ant species never co-occurred on the same plant, but occasionally tended aphids on adjacent plants. *Lasius flavus* is a common species that ranges across North America and Eurasia (Wilson 1955), may be completely subterranean, and tends a diversity of aphid species (Wilson 1955, Zwölfer 1958). This ant is known to carry aphid eggs into its nest for overwintering (Pontin 1960), but it also may be an aphid predator (Pontin 1958, 1978). *Lasius neoniger* is a dominant ant species in open, grassy habitats of eastern North America and commonly tends aphids, including the corn root aphid, *Aphis maidiradicis* Forbes (Wilson 1955, Traniello and Levings 1986), which also may be entirely dependent on

ants (Hottes and Frison 1931). The identity of the two *Crematogaster* species remains uncertain because their colonies appear rare and we have collected very few individuals, even after further searches during the summer of 2003. Nevertheless, the genus is cosmopolitan (Hölldobler and Wilson 1990) and tends hemipterans, including other aphid species (Dejean et al. 1991).

Ant species appeared to nest at the base of individual plants and built a collar of soil (~4–8 cm in height) encircling the bases of a few to several flowering stems of *S. laciniatum* and *S. terebinthinaceum* (we did not observe the aphid on leaf stems). *Iowana frisoni* fed within this ant-built refuge. Some soil collars had tunnels isolated from the stem through which ants could move around the base of the plant and down into the nest. When *I. frisoni* colonies were disturbed, the ants of all species carried the aphids underground, moving the entire colony within the course of a few minutes. Aphids also occurred in leaf axils feeding on either the stem or clasping leaf stipules, where they were also tended by ants (Fig. 2). *Lasius neoniger* usually sealed these leaf axils with soil and/or dead plant material, housing the aphids, but did not transport aphids from these feeding sites. Late in the season (September), a few plants of both species had ants and aphids present in every leaf axil and even in axils of branches and modified leaves in proximity to flowers (>2 m above the ground).

In our transects at Loda Cemetery Prairie, *I. frisoni* was present on only one of 75 *S. laciniatum* plants (1.3% of all plants) and this one aphid colony was tended by *L. neoniger*. *Iowana frisoni* was present on 34 of 106 (32%) *S. terebinthinaceum* plants and the majority of these were tended by *L. neoniger*. At Prospect Cemetery Prairie, *I. frisoni* was present on three of five *S. laciniatum* (40%) and 10 of 12 *S. terebinthinaceum* (83%), and *L. neoniger* was the dominant ant species tending these aphid colonies.

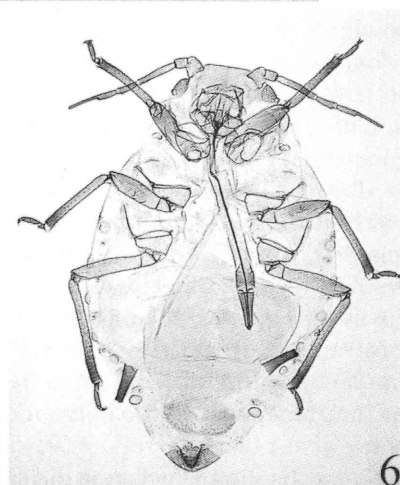
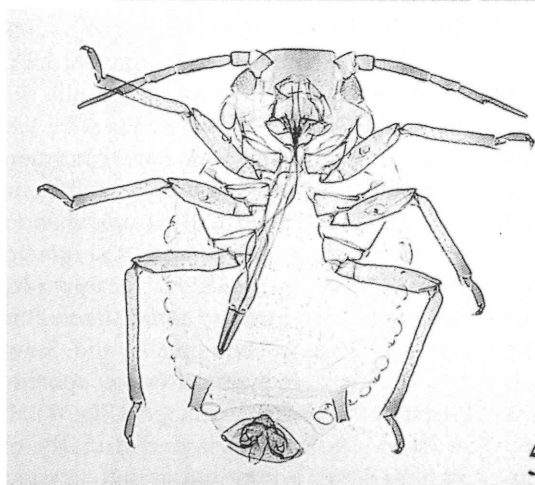
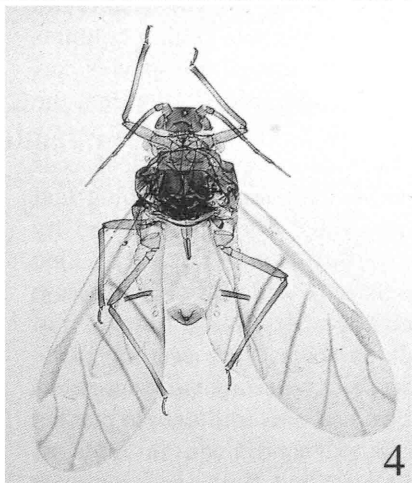
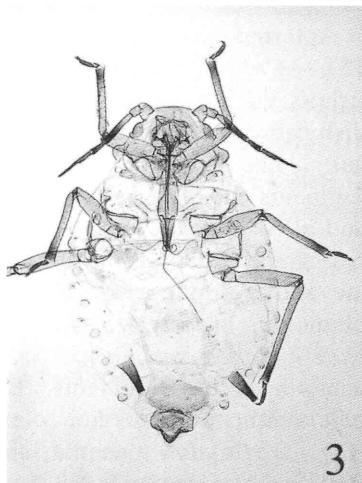
The first discriminant factor did not dis-

tinguish the fundatrices as separate from the other apterous viviparae. This was not unexpected because the first discriminant factor may be a function of size (Footitt 1992) and the greatest size variation was between alatae and apterae, and not between fundatrices and other apterae. The second discriminant factor did separate the putative fundatrices from the other apterous viviparae (Fig. 1), but the third, fourth and fifth factors did not discriminate any of them. Based on these results we believe that our three specimens were indeed fundatrices and we describe them as such below.

DESCRIPTION

Iowana frisoni Hottes 1954 (Figs. 2–19)

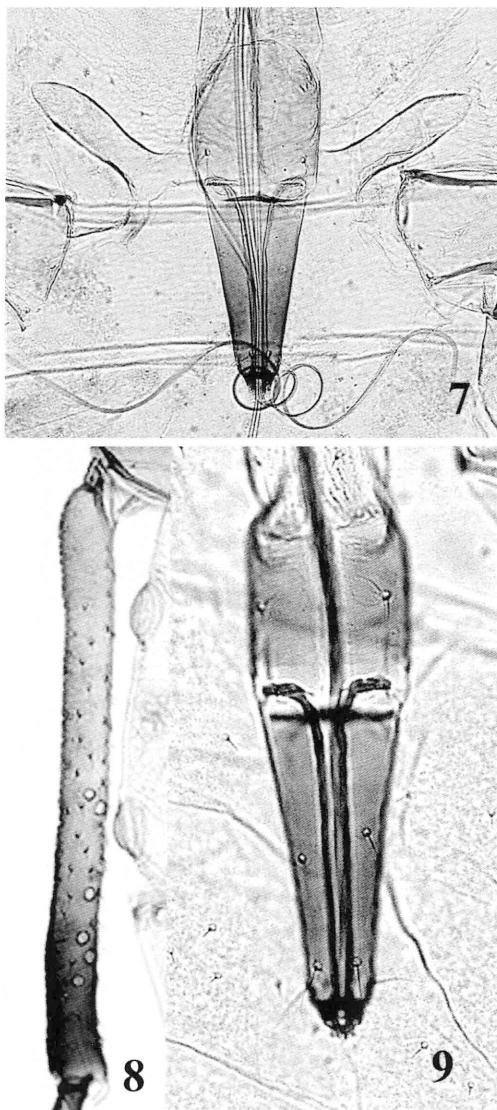
Apterous vivipara (Table 1, Figs. 3, 7, 10, 15).—*Color (alive)*: Body pale green. Adults with head and prothorax light reddish brown. Eyes dark brown to red. All of ant. I, ant. II, and proximal $\frac{1}{3}$ of ant. III segments pale green; distal $\frac{2}{3}$ of ant. III, and all of ant. IV and ant. V brown. Legs pale green except distal-most portion of tibiae and both tarsal segments brown. Siphunculus brown. *Morphology of cleared, slide-mounted specimens*: See Table 1 for anatomical measurements. Body entirely pale, neither sclerites nor scleroites present (Fig. 3). *Head*: Frons flat, smooth with a few scattered minute hairs. Rostrum reaches abdominal segment I. Rostral segments III to V dark, each darker than one before (Fig. 7). Rostral segment IV with 2 small accessory setae (Fig. 9), these may not be visible in some specimens. Antenna 5 segmented, dark and imbricated beyond base of ant. III (Fig. 10). Ant. III with 0–21 apical and subapical rhinaria. Ant. IV with a single apical primary rhinarium. *Thorax*: Large prothoracic tubercles, usually small lateral tubercles on thoracic segments 2 and 3 which may be hard to see on some specimens. Furculum broadly V-shaped (Fig. 7). Legs short. Metatibia darkened distally only, with darkening continuing into tarsus; no



Figs. 2-6. *Iowana frisoni*. 2, Feeding on the inside of a leaf stipule of *Silphium laciniatum*, tended by *Crematogaster* sp. 3, Apterous vivipara. 4, Alate vivipara. 5, Male. 6, Ovipara.

Table 1. Morphological measurements, mean and range, in mm, for five morphs of *Iowana frisoni* and the holotype.

Morph/Body Part	Holotype	Apterous vivipara (n = 28)	Apterous fundatrix (n = 3)	Alate vivipara (n = 11)	Apterous ovipara (n = 8)	Apterous male (n = 6)
Body (frons to cauda)	2.21	2.32 (1.75–3.06)	2.43 (2.10–2.72)	1.62 (1.38–1.95)	1.76 (1.50–2.02)	1.14 (1.07–1.23)
Frons (between antennal sockets)	0.230	0.241 (0.214–0.270)	0.233 (0.232–0.233)	0.204 (0.192–0.235)	0.211 (0.195–0.226)	0.170 (0.151–0.182)
Ant. III	0.289	0.327 (0.195–0.435)	0.374 (0.365–0.383)	0.342 (0.304–0.37)	0.215 (0.182–0.264)	0.161 (0.145–0.176)
Ant. IV	0.124	0.139 (0.082–0.193)	0.134 (0.128–0.138)	0.141 (0.115–0.154)	0.109 (0.101–0.119)	0.078 (0.075–0.088)
Ant. V base	0.098	0.113 (0.088–0.138)	0.106 (0.091–0.118)	0.107 (0.093–0.124)	0.101 (0.069–0.126)	0.091 (0.082–0.123)
Ant. V PT	0.154	0.172 (0.101–0.216)	0.175 (0.159–0.190)	0.184 (0.163–0.203)	0.142 (0.119–0.163)	0.108 (0.094–0.126)
Rostrum III	0.157	0.156 (0.132–0.177)	0.151 (0.144–0.164)	0.143 (0.122–0.157)	0.131 (0.113–0.151)	0.108 (0.101–0.119)
Rostrum IV	0.160	0.179 (0.152–0.207)	0.160 (0.160–0.160)	0.157 (0.146–0.172)	0.176 (0.163–0.189)	0.126 (0.119–0.132)
Metafemur	0.43	0.49 (0.33–0.69)	0.47 (0.45–0.50)	0.47 (0.40–0.52)	0.33 (0.30–0.38)	0.23 (0.21–0.25)
Metatibia	0.67	0.79 (0.56–1.07)	0.77 (0.73–0.81)	0.83 (0.70–0.90)	0.55 (0.50–0.65)	0.39 (0.36–0.41)
Metatarsus I, ventral	0.047	0.046 (0.038–0.053)	0.047 (0.045–0.049)	0.045 (0.039–0.049)	0.039 (0.031–0.044)	0.028 (0.025–0.031)
Metatarsus II	0.122	0.123 (0.063–0.145)	0.114 (0.104–0.124)	0.123 (0.112–0.133)	0.108 (0.101–0.119)	0.091 (0.088–0.094)
Siphunculus length	0.249	0.299 (0.176–0.428)	0.284 (0.265–0.301)	0.235 (0.188–0.263)	0.180 (0.157–0.220)	0.093 (0.082–0.107)
Siphunculus width at base	0.093	0.085 (0.057–0.118)	0.076 (0.056–0.094)	0.062 (0.046–0.085)	0.061 (0.050–0.069)	0.042 (0.038–0.047)
Cauda length	na	0.110 (0.094–0.130)	0.108 (0.093–0.123)	0.106 (0.082–0.120)	0.103 (0.094–0.107)	0.050 (0.044–0.063)
Cauda width at base	na	0.119 (0.088–0.145)	0.138 (0.125–0.150)	0.110 (0.093–0.128)	0.112 (0.107–0.138)	0.079 (0.069–0.094)
Prothoracic tubercle length	0.113	0.100 (0.069–0.138)	0.096 (0.079–0.114)	0.096 (0.077–0.108)	0.078 (0.069–0.088)	0.068 (0.063–0.075)
Prothoracic tubercle height	0.065	0.071 (0.038–0.107)	0.074 (0.059–0.089)	0.067 (0.055–0.089)	0.043 (0.031–0.050)	0.044 (0.044–0.044)



Figs. 7–9. *Iowana frisoni*. 7, Ultimate rostral segment and thoracic furculum of apterous vivipara. 8–9, Metatibia and ultimate rostral segment of ovipara.

darkening of the knees. *Abdomen*: Tergum smooth with a few scattered minute hairs, <0.01 mm long. Venter with scattered minute hairs and faint imbrications. Large lateral tubercles on abdominal segments I–V and VII. A small lateral tubercle on either, neither, or both sides of segment VI. Subgenital plate with short hairs profuse only on hind margin, sparse elsewhere. Cauda short, roughly as broad at base as it is long.

Three rudimentary gonapophyses. Siphunculus dark, imbricated, with rounded flange and slight constriction just below distal end (Fig. 15). *Collection dates*: 8 June, 8 August 2001, 27 August 2002.

Apterous fundatrix (Table 1, Figs. 11, 16).—As apterous vivipara except for following. *Head*: Ant. III with 6–11 rhinaria (Fig. 11). *Collection date*: 9 May 2002.

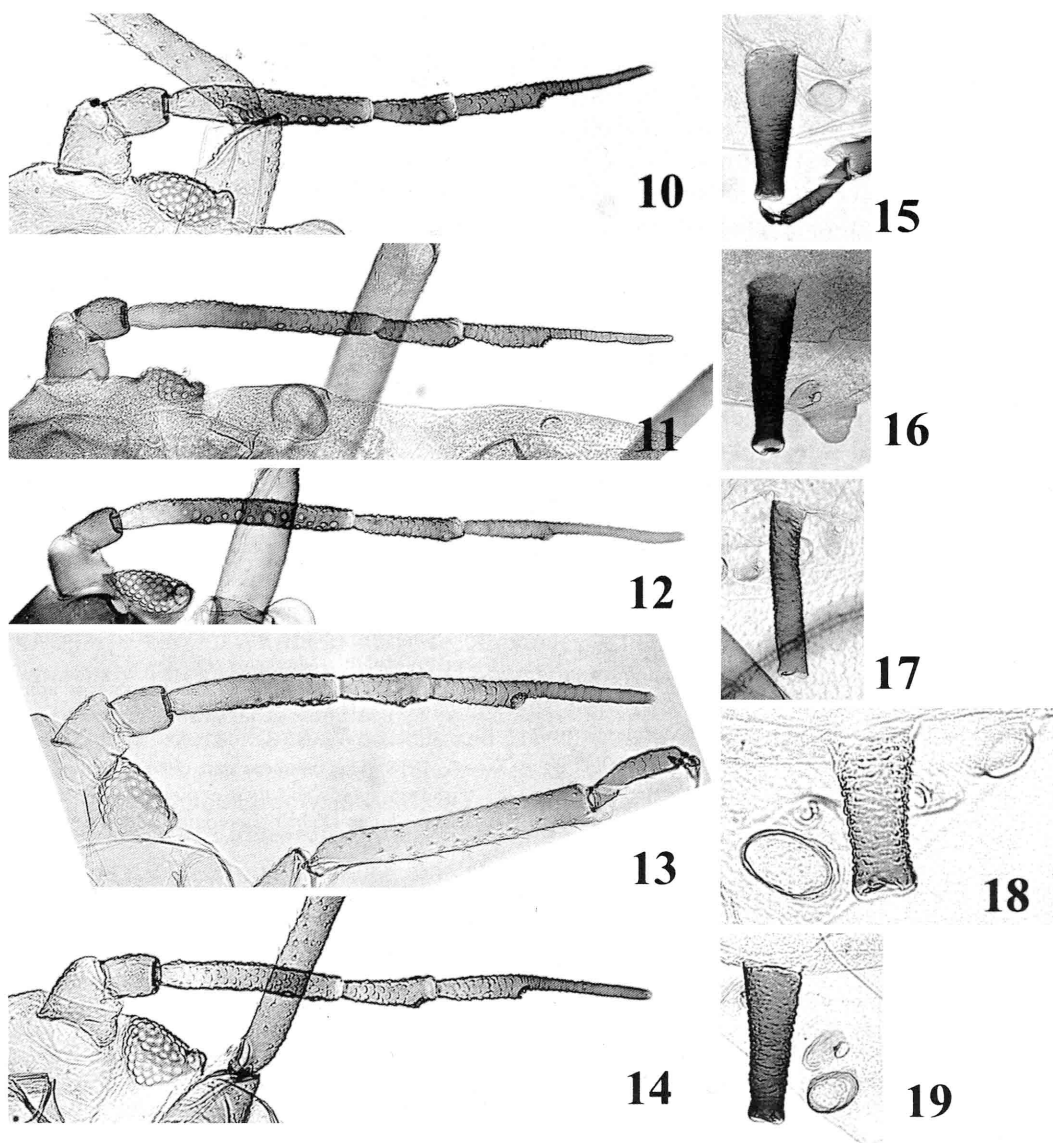
Alate vivipara (Table 1, Figs. 4, 12, 17).—As apterous vivipara except for following. *Head*: Ant. III with 12–22 rhinaria (Fig. 12). *Thorax*: Media once (Fig. 4) or twice forked, if twice, second branch arises right before apex of wing. *Abdomen*: Siphunculus parallel-sided and straight, with or without slight flange (Fig. 17). *Collection dates*: 22 May, 8 June, 8 August 2001.

Apterous male (Table 1, Figs. 5, 13, 18).—As apterous vivipara except for following. *Head*: Rostrum reaches abdominal segment V. Ant. III with 5–11 rhinaria. Ant. IV with 0–2 secondary rhinaria, 1 primary rhinarium (Fig. 13). *Abdomen*: Siphunculus only about twice as long as wide, lightly pigmented (Fig. 18). Male genitalia with 2 setose claspers anteriorly, aedeagus centrally, and 2 sclerotized apophyses posteriorly. *Collection date*: 6 October 2002.

Apterous ovipara (Table 1, Figs. 6, 14, 19).—As apterous vivipara except for following. *Head*: Rostrum reaches abdominal segment V. Ant. III with 1–9 rhinaria (Fig. 14). *Thorax*: Metatibia with 10–18 sensoria. *Collection date*: 6 October 2002.

Egg.—Oval, smooth, shiny and black, 0.34–0.36 mm wide by 0.78–0.93 mm long (means of 11 measurements are 0.351 and 0.853 mm, respectively). *Collection date*: 6 October 2002.

Diagnosis.—The viviparae (apterae and alatae) of *I. frisoni* are similar to *Aphis* species in having the same lateral tubercle placement (ventral to the line joining the first two abdominal spiracles), the siphunculus longer than the cauda, and the processus terminalis longer than the base of terminal antennal segment. *Iowana frisoni* is unique with its enlarged lateral protho-



Figs. 10–19. *Iowana frisoni*. 10–14, Antenna. 15–19, Siphunculus. 10, 15, Apterous vivipara. 11, 16, Fundatrix. 12, 17, Alate vivipara. 13, 18, Male. 14, 19, Ovipara.

racic and abdominal tubercles, five-segmented antenna, and sparse and minute setae. The alate morph is also unusual in having the medial vein either forked once, or the second fork arising only at the wing apex.

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