

# A KEY TO THE *EMPOASCA SOLANA* COMPLEX WITH DESCRIPTIONS OF NEW SPECIES<sup>1</sup>

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In the extremely useful synopsis of the complex by Young (1953a), 12 species were recognized and since that time Young (1953b) has added one more described species. Examination of large collections of *Empoasca* from chiefly the circum-Caribbean area in connection with *Empoasca fabae* studies has disclosed the existence of an additional 11 species, bringing to 24 the total number of known species in the complex. No species are known outside the western hemisphere. In this paper a key is given to these 24 species; newly discovered species are described and their relationships indicated. Unless otherwise indicated, types are deposited in the collection of the Illinois Natural History Survey with paratypes where available deposited in the D. M. DeLong collection and the U. S. National Museum.

We wish to take this opportunity to express our deep gratitude to Dr. G. C. Decker, our co-investigator in Project NC-29, for his untiring efforts in collecting and procuring study material in this group. Dr. J. E. Porter and Dr. Irving Fox, U. S. Public Health Service, and Captain R. M. Altman, U. S. Navy, have also been extremely generous of their time in sending us residues from light trap collections containing *Empoasca* specimens.

In attempting to determine the species limits in this complex, we encountered the usual difficulties as regards the status of several unique specimens and short series. In this we were aided greatly by the very large series of specimens available for *E. solana*, *manda*, *stevensi*, and four or five other species in the complex. In these species the discernible variation was of much smaller magnitude than that occurring between several of the unique specimens which were ultimately considered as valid species. It is somewhat peculiar that the species represented by small series are almost invariably much better differentiated morphologically than some of the commoner species which apparently occur in great numbers.

## GENERAL DESCRIPTION OF COMPLEX

All the species in this complex are remarkably similar in general characteristics and the following description applies to all the new and old species mentioned or described in this paper, except where noted: Length 3.5 mm; color in life pale green with inconspicuous translucent markings on the head and thorax; male abdomen with long apodemes 2S which may be either slightly truncate or rounded at apex and which extend almost three segments into the abdomen; apodemes 3T very small and represented by either a linear structure or a very slight elliptic widening. Hook of tenth segment moderately large but forming a rounded plate without points or spurs, only slightly sclerotized and inconspicuous (DeLong 1931, fig. 10). Aedeagus having a pair of spines situated on or below the shaft.

In most species the shaft has an internal clear area which in transmitted light is sharply defined; this area, here called the aedeagal sinus, usually ends dorsally in a tapered point and in many species has a diagnostic shape.

### *Key to Species - Males*

1. Apodemes 3T larger and as long as apodemes 2S, fig. 15. Widespread . . . . .  
*thela* Davidson and DeLong
- Apodemes 3T no longer than in fig. 14, apodemes 2S much larger, fig. 16 . . . . . 2

<sup>1</sup>A contribution from North Central Regional Project NC-29.

2. Aedeagal spines short and situated far out on shaft (Young 1953a, fig. 1B). Haiti. . . . .  
*canavalia* DeLong  
 Aedeagal spines arising at or below base of shaft . . . . . 3
3. Both shaft and aedeagal spines short and wide, fig. 3A. Panama. . . . . *canthella* n. sp.  
 Shaft and aedeagal spines much longer, figs. 5, 6 . . . . . 4
4. Shaft elongate and slender, as in figs. 1A, 13A . . . . . 5  
 Shaft more robust . . . . . 9
5. Aedeagal spines appressed to sides of shaft (Young 1953a, fig. 8B); brachones swollen.  
 Tropical . . . . . *wolcotti* Young  
 Aedeagal spines situated beneath shaft, fig. 13A; brachones not swollen . . . . . 6
6. Aedeagal spines fused for about three-fourths of their length, fig. 13D. Mexico. . . . .  
*caldwelli* Davidson and DeLong  
 Aedeagal spines separate . . . . . 7
7. Tip of aedeagus forming a narrow, sharp point (Young 1957, fig. 27C). Bolivia. . . . .  
*hyalina* (Osborn)  
 Tip of aedeagus as thick as in fig. 1A . . . . . 8
8. Posterior aspect of brachone with tip smoothly sinuate. Widespread. . . . .  
*plebeia* DeLong and Davidson  
 Posterior aspect of brachone with tip having a fairly abrupt, steplike notch, fig. 1C.  
 Southwestern U. S., Mexico . . . . . *ophiodera* n. sp.
9. Shaft with a well-marked ventral corner and aedeagal spines extending at most only a  
 trifle beyond this corner (Young 1953a, fig. 3B) . . . . . 10  
 Shaft without a well-marked ventral corner and aedeagal spines longer, figs. 4A, 12A . . . . . 12
10. Aedeagal spines running close to ventral edge of shaft; aedeagal sinus trianguloid  
 (Young 1953a, fig. 3B). Widespread . . . . . *solana* DeLong  
 Aedeagal spines arising below base of shaft, sometimes angling or curving to touch ventral  
 corner of shaft . . . . . 11
11. Brachone having a broad angulate shoulder just below tip (Young 1953c, fig. 4D);  
 aedeagal sinus fairly shallow and arcuate. U. S., West Indies. . . . .  
*manda* Davidson and DeLong  
 Brachone without subapical shoulder but sinuate as a whole; aedeagal sinus and ventral  
 corner of shaft produced postero-ventrally into an acute angulation (Young 1953a,  
 fig. 2B). Widespread. . . . . *stevensi* Young
12. One aedeagal spine large and thick, the other much shorter, either wide and sharp, figs.  
 6A, 7A, narrow, or obsolescent, figs. 8A, D . . . . . 13  
 Both aedeagal spines of about the same length . . . . . 15
13. Shorter aedeagal spine as long as in figs. 6A and 7A . . . . . 14  
 Shorter aedeagal spine shorter and rounded, figs. 8A, D, or represented only by an in-  
 distinct swelling. Florida, Central America . . . . . *deckeri* n. sp.
14. Shorter aedeagal spine slender and projecting outside orbit of larger spine (Young 1953b,  
 fig. 7B). Argentina . . . . . *tritabulata* Young  
 Shorter aedeagal spine stout and projecting within orbit of larger spine, figs. 6A, 7A.  
 Puerto Rico, Panama . . . . . *teneris* n. sp.
15. Aedeagal spines contiguous with edge of shaft, figs. 2A, 5A, 9A, 10A . . . . . 16  
 Aedeagal spines angling away from shaft then curving back to touch or overlap it, figs.  
 4A, 11A, 12A . . . . . 20
16. Aedeagal sinus fairly short and stout, not extending beyond tips of aedeagal spines,  
 fig. 2A. Central America . . . . . *cristella* n. sp.  
 Aedeagal sinus longer . . . . . 17
17. Apex of aedeagus curved back on its base very gently, fig. 5A. Puerto Rico . . . . . *foxi* n. sp.  
 Apex of aedeagus sharply angled back over its base, figs. 9A, 10A . . . . . 18
18. Aedeagal spines sinuate, aedeagal sinus pinched almost to a thread below apex (Young  
 1953a, fig. 7B). Widespread subtropical . . . . . *tamiama* Davidson and DeLong  
 Aedeagal spines curved, fig. 9A . . . . . 19

19. Shaft short, aedeagal sinus narrow and tapering at apex, fig. 9A. Panama . . . . .  
*alceda* n. sp.  
 Shaft long and stout, aedeagal sinus wide almost to tip, fig. 10A. Peru . . . *robacki* n. sp.
20. Shaft only slightly curved, aedeagal sinus short, narrow, and gently arcuate (Young 1953a,  
 fig. 5B). Southwestern U. S. . . . . *dilitara* DeLong and Davidson  
 Shaft abruptly angled back over its base, fig. 11A . . . . . 21
21. Shaft and aedeagal sinus long, slender, and sinuate, fig. 11A. Panama . . . *sinusina* n. sp.  
 Shaft and aedeagal sinus either short or not sinuate . . . . . 22
22. Aedeagal sinus having an enlarged, rounded apex, fig. 12A. Mexico . . . . *tecpatana* n. sp.  
 Aedeagal sinus ending in a tapering, pointed apex . . . . . 23
23. Shaft short and stocky, its tip wide, fig. 4A. Honduras . . . . . *laceiba* n. sp.  
 Shaft longer, its tip forming a narrow, bent portion, (Young 1957, fig. 29C). Brazil . . .  
*olivatula* Osborn

*Descriptions of New Species*

***Empoasca canthella* n. sp.**

*Male*.—Size, color, and general structure typical for the complex. Brachone (fig. 3B, C) with lateral aspect swollen toward base of apex, the apex itself narrow and nearly straight; with posterior aspect having a broad lateral shoulder at base of apical portion, the apical portion itself narrow and sinuate. Aedeagus (fig. 3A) with shaft small, somewhat irregular, with a short, sharp sinus clearly indicated; aedeagal spines short and blunt, arising at the base of shaft but projecting almost straight out.

*Holotype male*.—Balboa, C. Z., Panama, July 13, 1946, A. O. Meyer.

*Paratype*.—Farfan, C. Z., Sept. 15, 1955, R. M. Altman, light trap, 1 male.

The shape of the aedeagus of this species differs remarkably from any other described type in the complex, in both the low shaft and the very short spines. When the first specimen was encountered, we thought it might be a freak but the second specimen agrees so perfectly with the first that there seems to be a good chance that this is a distinctive species. The short and distinct sinus is reminiscent of *solana* and the swollen brachone is reminiscent of *manda*; on the basis of these two hints it is probable that this species represents an aberrant offshoot which arose from the *solana-manda* section of the complex.

***Empoasca laceiba* n. sp.**

*Male*.—Size, color, and general structure typical for the complex. Brachone (fig. 4B, C) with lateral aspect only slightly swollen before apex, the apex slightly curved ventrad; and with posterior aspect more slender, again only slightly swollen, the apex narrow and very slightly sinuate. Aedeagus (fig. 4A) with sinuate base and with a very broad shaft which is angled fairly sharply back over the base; aedeagal sinus narrow, long at the base and also bent sharply and ending in a narrow point; aedeagal spines long, arising below main body of shaft and curving to overlap ventral corner of shaft, one of the spines wider than the other.

*Holotype male*.—Laceiba, Honduras, May 28, 1949, E. C. Becker, at light.

This species is closest in general structure to *stevensi*, from which it differs in the longer aedeagal spines and the longer basal part of the aedeagal sinus. In these two characters *laceiba* is strikingly similar to *olivatula*, but from *olivatula* it differs in the pronounced ventral corner of the shaft and the short and extremely stubby apex of the shaft, both characters distinctive for *stevensi*. This unusual combination of characters distinctive to widely separated phyletic lines may indicate that *laceiba* is of hybrid origin.

***Empoasca cristella* n. sp.**

*Male*.—Size, color, and general structure as described above for the complex. Brachone (fig. 2B, C) with lateral aspect narrow and very slightly sinuate, the apical portion short and merging imperceptibly with the long slender base; with the posterior aspect also narrow, the apical portion curved and its mesal margin markedly concave. Aedeagus (fig. 2A) with the base fairly straight and the shaft broad, fairly short, and very slightly curved anteriorly; aedeagal sinus well marked, unusually broad, nearly touching the ventral margin and ending abruptly

in a short, sharp point; aedeagal spines appressed to ventral margin of shaft, extending above the level of the apex of the sinus, both spines fairly slender.

*Holotype male*.—Laceiba, Honduras, May 28, 1949, E. C. Becker, at light.

*Paratype*.—Farfan, C. Z., Panama, June 4, 1957, R. M. Altman, 1 male.

This species approaches only *dilitara* in the shape of the shaft but is readily distinguished from that species by the very wide aedeagal sinus and the longer aedeagal spines appressed to the shaft; in *dilitara* the aedeagal sinus is narrow and almost hornlike and the aedeagal spines curve well below the ventral margin of the shaft. There is also a marked resemblance between the aedeagus of *cristella* and that of *foxi* but in *foxi* the apex of the shaft is markedly curved anteriorly and the sinus, which is not well defined basally, extends well into the apex of the shaft. These comparisons indicate that *cristella* probably arose from the base of the *dilitara* line and is a primitive member of the complex.

#### *Empoasca foxi* n. sp.

*Male*.—Size, color, and general structure as described above for the complex. Brachone with lateral aspect narrow and even, the apical portion marked by a sinuate dark area, as in figure 8B; the posterior aspect also straight and narrow, the apex much like the lateral aspect. Aedeagus (fig. 5) with base slightly curved and with shaft fairly broad, its apex curved back anteriorly over the base; aedeagal sinus indistinct at base, its apex reaching well into the apical portion of the shaft and its posterior side near the posterior margin of the shaft; aedeagal spines slightly unequal, their tips curved anteriorly, both of the spines following fairly closely the margin of the shaft.

*Holotype male*.—Isla Verde, near San Juan, Puerto Rico, October-November, 1957, Irving Fox, at light.

*Paratypes*.—Same data as for holotype but July, 1 male; same but June, 1958, 2 males.

This species, undoubtedly a primitive one, is most similar to *cristella* but differs from it in the curved apex of the shaft and the much longer aedeagal sinus. This species was undoubtedly recorded from Puerto Rico by Caldwell and Martorell 1952 under the name *canavalia*, as evidenced by their remark that in some of their specimens the aedeagal spines are subequal. The holotype of *canavalia*, however, is unusual and quite different in its extremely reduced aedeagal spines, illustrated by Young (1953a, fig. 1B). The only additional specimen we have seen agreeing with the holotype of *canavalia* is a male collected by Capt. R. M. Altman, Dec. 11-18, 1956, at Ft. Kobbe, Canal Zone, Panama.

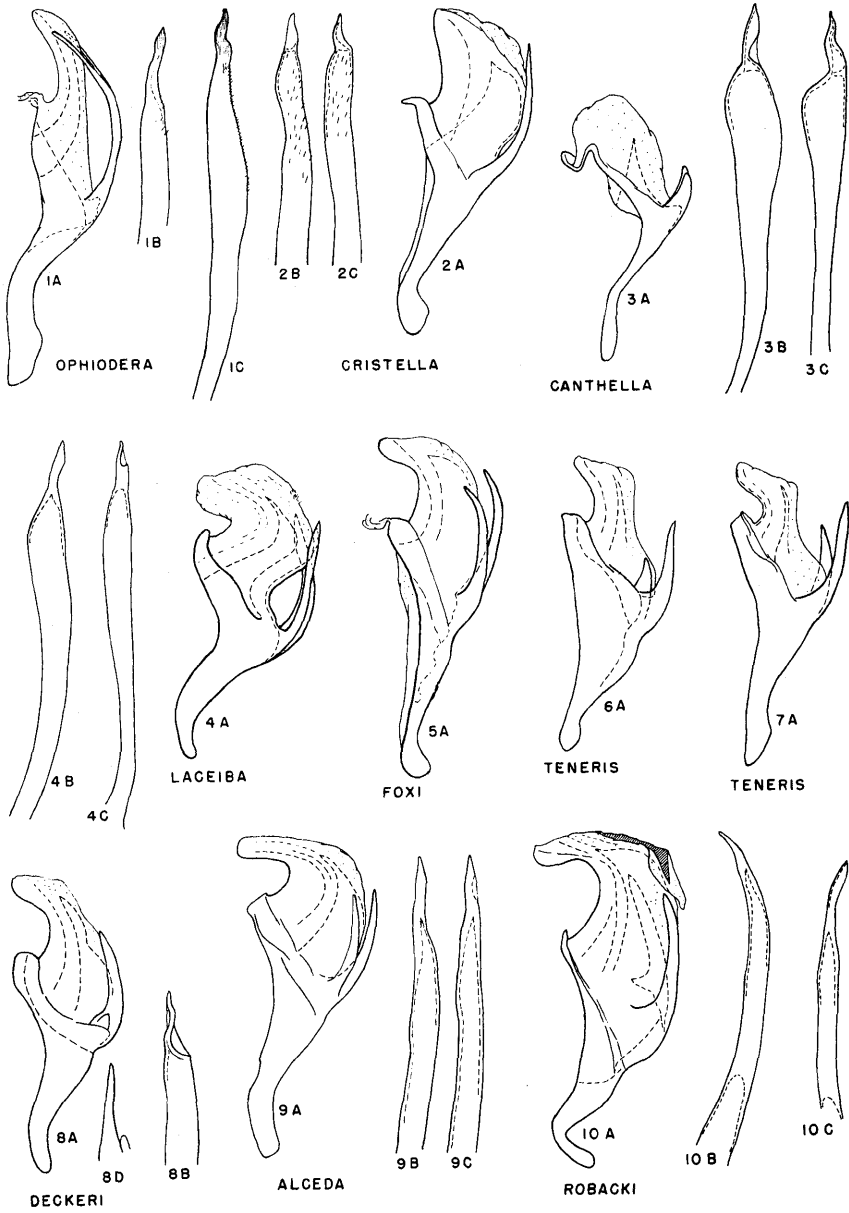
#### *Empoasca deckeri* n. sp.

*Male*.—Size, color, and general structure as described above for the complex. Brachone very long and slender (fig. 8B) the lateral aspect parallel-sided and ending in an apical portion which appears incised ventrally in steplike fashion; this steplike appearance, however, is due to a narrow sinuate darkening mesad of which there is an inconspicuous, poorly sclerotized area, so that the apex of the brachone is actually triangular. Aedeagus (fig. 8A) with base slightly sinuate; shaft broad at base, not very long but narrowed and slightly constricted below the apex, the whole curved markedly anteriorly over its base; aedeagal sinus poorly defined at the base and narrow and elongate apically; aedeagal spines extremely dissimilar, consisting of a long stout one appressed to margin of shaft, and a minute rounded stub contained within the silhouette of the base of the larger spine, this small one sometimes represented only by a darkened spot at the base of the larger spine. In some specimens the large spine is the right one and the small one the left one (fig. 8D) and in other specimens it is the reverse.

*Holotype male*.—Miami, Florida, Feb. 19, 1957, G. C. Decker, on purple morning glory.

*Paratypes*.—70 males from the following localities—Canal Zone, Panama: Farfan, Fort Cobbe, Curundu, Cocoli; Honduras: Laceiba, 12 k. west of Olanchito; Florida: Coral Gables, Key Largo, Miami, Key West, Homestead, Dade County; Nicaragua: Managua.

This species and the next are most closely related to *foxi*, from which *deckeri* may be separated by the extreme reduction of the smaller aedeagal spine and by the constricted apical portion of the shaft. From the following species, *teneris*, *deckeri* may be differentiated by the fact that the small aedeagal spine in lateral view is always contained within and obscured by the extreme base of the larger spine.



FIGURES 1-10. Male genitalia of species in the *Empoasca solana* complex. A—lateral aspect of aedeagus; B—lateral aspect of brachone; C—posterior aspect of brachone; D—posterior aspect of aedeagal spines.

**Empoasca teneris** n. sp.

*Male*.—Size, color, and general structure as described above for the complex. Male genitalia extremely similar to those of *deckeri*. Brachone long and parallel-sided, exactly like those of *deckeri* (see fig. 8B). Aedeagus (fig. 6 and 7) with nearly straight base; shaft broad at base and tapering to constricted central portion, beyond which it flares out again, the apex curved anteriorly back of its base; the posterior and ventral portion of the shaft is composed of rather delicate membranes which are frequently difficult to detect; aedeagal sinus with basal portion indistinct, its apical portion narrow and curving to a pointed apex. Aedeagal spines markedly asymmetrical, the longer one stout and angled dorsally away from the shaft; the shorter one, also stout and sharply pointed, projecting between the longer one and the base of the shaft as seen from lateral view. The length of the shorter spine varies considerably between the two extremes illustrated in figures 6 and 7. As in *deckeri*, both right and left-handed forms occur.

*Holotype male*.—Isla Verde near San Juan, Puerto Rico, July, 1957, Irving Fox, at light.

*Paratypes*.—Panama, Canal Zone: Fort Cobbe, January 3–7, 1957, R. M. Altman, at light, 1 male; and 140 males from various dates collected at the holotype locality.

This species is a close relative of *deckeri*, sharing with it the characteristically constricted shaft and the remarkable asymmetry of the aedeagal spines. From *deckeri*, *teneris* can be differentiated by the outwardly directed larger aedeagal spine and the longer and sharper, small and inner aedeagal spine.

This is the species described and illustrated from Puerto Rico by Caldwell and Martorell (1952, plate 53) under the name *canavalia* (see note concerning type of *canavalia* in description of *foxi* above).

**Empoasca alceda** n. sp.

*Male*.—Size, color, and general structure as described above for the complex. Brachone (fig. 9B, C) with lateral aspect elongate, parallel-sided, and slender, the apical portion represented by a more slender and pointed straight terminus; the posterior aspect also narrow and slender although slightly irregular, the apical portion narrow and pointed. Aedeagus (fig. 9A) with base sinuate; shaft with basal portion deep and apex angled anteriorly back over base to form an almost rectangular portion; aedeagal sinus wide at base, its posterior and ventral margin merging with the margin of the shaft, its apex produced into a moderately long, narrow, and sharp tip. Aedeagal spines moderately short and slender, appressed to the shaft for much of their length.

*Holotype male*.—Camp Pina, Canal Zone, Panama, July 5, 1955, R. M. Altman, at light.

*Paratypes*.—Canal Zone, Panama: Same data as for holotype, 1 male; Cocoli, September 16, 1955, R. M. Altman, at light, 1 male; Fort Gulick, February 8, 1957, R. M. Altman, at light, 1 male.

The strongly reflexed apex of the shaft indicates a relationship between this species and *olivatula* and its allies; from this group of species *alceda* differs in having shorter and thinner aedeagal spines. Other characters of the aedeagus indicate a similarity with *foxi*, from which *alceda* differs in the strongly reflexed shaft and the narrow, pointed apex of the aedeagal sinus. This combination of characters suggests strongly that *alceda* represents an offshoot from a primitive stock of the complex and that this offshoot was also the base of the more specialized species such as *olivatula* in which the reflexed shaft is prominent.

**Empoasca robacki** n. sp.

*Male*.—Size, color, and general structure as described above for the complex. Brachone (fig. 10B, C) with lateral aspect curved gently dorsad, the basal portion narrowing imperceptibly into an elongate, slightly sinuate, sharply pointed apex, with posterior aspect also narrow and parallel-sided, narrowing more abruptly into an apical portion which is parallel-sided and curved slightly mesad. Aedeagus (fig. 10A) with base small and curved; shaft large and massive, its apex reflexed sharply and its postero-dorsal portion having unusually developed folds of membrane; aedeagal sinus indistinct at base but the apical portion broad and extending to the top of the shaft. Aedeagal spines large and massive, contiguous with or overlapping the shaft.

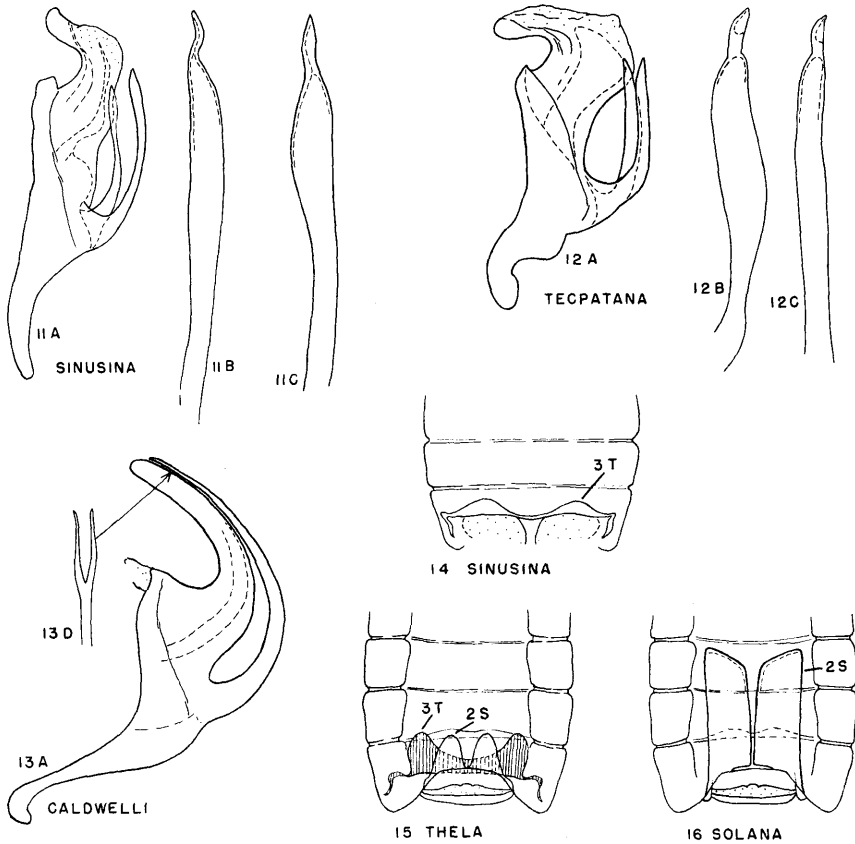
*Holotype male*.—Tinga Maria, Peru, October 6, 1955, S. Roback, at light.

This species is most closely related to *alceda* but differs from it in the unusually large and

massive shaft and the broader aedeagal spines. The more massive shaft is somewhat suggestive of the two following species but in these the aedeagal spines curve far below the body of the shaft.

***Empoasca sinusina* n. sp.**

*Male*.—Size, color, and general structure as described above for the complex. Apodemes 3T (fig. 14) produced into fairly wide crescentic arcs. Brachone (fig. 11B, C) with lateral aspect fairly narrow, tapering to a fairly long apical portion which is curved and narrow; and with the



FIGURES 11-13. Male genitalia of species in the *Empoasca solana* complex. A—lateral aspect of aedeagus; B—lateral aspect of brachone; C—posterior aspect of brachone; D—posterior aspect of apex of aedeagal spines.

FIGURES 14-16. Base of male abdomen of species in the *Empoasca solana* complex. 14—dorsal aspect of apodemes 3T; 15—ventral aspect of apodemes 2S and 3T; 16—ventral aspect of apodemes 2S.

posterior aspect somewhat swollen toward the apex, this swollen portion narrowing gradually to the base of the apical portion which is slightly constricted below middle and pointed at the tip. Aedeagus (fig. 11A) with nearly straight base; shaft narrowing abruptly just beyond base, fairly long, and with the apex reflexed markedly over the base; the posterior margin of the shaft is membranous and sinuate; aedeagal sinus extremely narrow, sinuate, and varying in thickness, ending

in a sharp, narrow point. Aedeagal spines elongate, one slightly shorter and more slender than the other, both curving away from the shaft and then curving back toward it.

*Holotype male*.—Navy Ordnance Headquarters, Canal Zone, Panama, June 1, 1955, R. M. Altman, at light.

This species is most closely related to *olivatula* but differs from it in the much narrowed shaft and aedeagal sinus. The species undoubtedly represents an offshoot of the *olivatula* line.

#### ***Empoasca tecpatana* n. sp.**

*Male*.—Size, color, and general structure as described above for the complex. Brachone (fig. 12B, C) with lateral aspect unusually wide, tapering to a much narrower and somewhat finger-like apical portion; posterior aspect narrow and parallel-sided, nearly straight, narrowing to the apical portion which is somewhat finger-like from this aspect also. Aedeagus (fig. 12A) with short curved base, the posterior margin having a produced rounded lobe just below the bases of the aedeagal spines; shaft moderately wide, its apex reflexed sharply over its base, its posterior margin concave; aedeagal sinus well marked for its entire length, its apical portion expanded and ending in a broadly rounded lobe. Aedeagal spines nearly equal in length and size, first angling away from and beneath body of shaft, then curving into straight portions which touch the posterior corner of the shaft.

*Holotype male*.—Tecpatan, Chiapas, Mexico, August 30, 1946, A. Dampf, at light.

This species is most closely related to *olivatula*, differing from it in the nearly equal aedeagal spines (in *olivatula* one is about the width of the other) and in the wide and rounded aedeagal sinus. In *tecpatana* the lateral aspect of the brachone is much wider than in *olivatula*. It seems highly likely that *tecpatana* represents a specialized offshoot of the *olivatula* line. It is of further interest that the species *tamiama* which has a peculiar conformation of the aedeagus (illustrated by Caldwell and Martorell, 1952, plate 53, as *everaformis*) is very likely a specialized offshoot of *tecpatana*. If one visualizes starting with an aedeagus such as that in *tecpatana*, squeezing the sinus together until it is divided in the middle, twisting the aedeagal spines so that they lie against the shaft, and enlarging the bulge on the base below the aedeagal spines, the result is essentially that of the structure found in *tamiama*.

#### ***Empoasca ophioidera* n. sp.**

*Male*.—Size, color, and general structure as described above for the complex. Brachone (fig. 1B, C) with lateral aspect long, slender, and parallel-sided, tapering to a more slender apex; posterior aspect with ventral portion slightly enlarged and with apex sinuate and having a somewhat steplike notch on the mesal margin. Aedeagus (fig. 1A) with base sinuate and narrow; shaft also narrow and elongate, slightly curved anteriorly and with a simple type of gonopore, without any indication of a sinus. Aedeagal spines long and slender, curving away from the shaft at base but recurring to overlap the tip of the shaft.

*Holotype male*.—Sabino Canyon, Tucson, Arizona, October 13, 1957, Bibby and Benny, on *Salix*.

*Paratypes*.—Arizona: Tortilla Flat, October 27, 1957, F. F. Bibby, on *Baccharis glutinosa*. Mexico: Cotaxtla, Veracruz, September 10, 1957, W. W. Gibson, on *Sesamum*.

This species is closely related to *plebeia* from which it differs in the shorter, thicker, and incised apex of the brachone; in *plebeia* the apex of the brachone is more slender, longer, and smoothly sinuate.

#### EVOLUTION OF THE COMPLEX

In surveying the various species described in the *solana* complex, it is apparent that all of the species form a closely knit complex sufficiently distinct from all other described species in the genus that the complex is monophyletic. Deducing the ancestral form from which the complex arose, however, is fraught with some difficulty. In the present attempt to arrange the species in a logical evolutionary sequence, the most satisfactory and plausible arrangement has been achieved by considering that forms such as *ophioidera* (fig. 1) or *foxi* (fig. 5) are the closest approach to the ancestor of the group. In these the aedeagal spines are long and



equal, the aedeagal sinus is poorly defined, and the shaft is not markedly angulate either in the form of a recurving apex or a postero-ventral shoulder. If the ancestor of *ophiodera* ever did have an aedeagal sinus, then this line probably arose early in the evolution of the complex and forms with *plebeia* a separate branch. If this is the case, the ancestral form of the complex also had aedeagal spines which bowed out below the shaft so that the hypothetical ancestor for the rest of the complex would probably have represented a combination of the shaft of *foxi* (fig. 5) and the aedeagal spines of *dilitara*, much like those in figure 4A. From such an ancestor two main lines probably arose, one characterized by a shortening of the aedeagal sinus and the development of a pronounced postero-ventral shoulder on the shaft; *cristella* (fig. 2) and *dilitara* may represent early stages in this lineage and *stevensi* a later stage. The development of the postero-ventral shoulder of the shaft was accompanied by the shortening of the aedeagal spines. To this entire branch we are assigning *cristella*, *dilitara*, *solana*, *canthella*, *manda*, *laceiba*, and *stevensi*. The species *canthella* (fig. 3) would appear to be an example of extreme reduction of the aedeagal parts. The species *laceiba* (fig. 4) is the only misfit and it will be discussed later. The other main branch of the genus contains a group of nine species in which the apex of the shaft bent back over its base and in extreme cases became almost angular in this relationship. The first step in this development is represented by *foxi* (fig. 5) *teneris* (figs. 6, 7) *deckeri* (fig. 8) and perhaps *tritabulata*, which have the apex of the shaft only gradually reflexed. The next step is probably best represented by *alceda* (fig. 9) and *robacki* (fig. 10) in which the apex of the shaft is much more angularly reflexed. This characteristic is present also in *olivatulula*, *sinusina* (fig. 11), *tecpatana* (fig. 12), and *tamiama*, indicating that these species arose from an *alceda*-like progenitor. This leaves unplaced the three species *hyalina*, *caldwelli* (fig. 13) and *thela*, in which the shaft is long, extremely slender, and also curved markedly anteriorly though not angled as in the *alceda* complex. It is probable that these three species form a monophyletic branch which could have arisen either from the *plebeia* line or even possibly from the base of the *alceda* line. The species *canavalia* is impossible to place with any degree of certainty because it is so dissimilar from other species.

The species *laceiba* introduces an interesting point of speculation. In the *solana* branch it would appear as if the development of the postero-ventral corner of the shaft had gradually become more and more pronounced and as if the sinus had been pulled down into the corner of the shaft. The shape of the aedeagus of *stevensi* is further suggestive that the entire shaft has been distorted postero-ventrally. If this is the case then the angulation produced on the anterior margin of the shaft is the result of this pull and presumably this same trend has brought about the shape of the shaft in *laceiba*. In *laceiba*, however, the aedeagal spines are elongate, more as in *tecpatana* or *olivatulula*. There is here a suggestion that *laceiba* may be the result of hybridization between a form somewhat like *stevensi* and one somewhat like *olivatulula*.

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