

**LIFE HISTORY AND DESCRIPTION OF ADULTS AND IMMATURE STAGES
OF *PROCECIDOCHARES BLANCI*, N. SP. (DIPTERA: TEPHRITIDAE) ON
ISOCOMA ACRADENIA (E. GREENE) E. GREENE (ASTERACEAE) IN
SOUTHERN CALIFORNIA**

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Abstract.—*Procecidochares blanci*, n. sp. is described as eggs, first-, second- and third-instar larvae, puparia, and adults. Adults are readily distinguished from all North American congeners, for which a preliminary key is provided, by the absence of dark pigmentation on the anterior abdominal segments or portions thereof. The first instar has a dorsally grooved, anterior mouthhook; the mouthhook of the second instar has four teeth, the most reported to date among nonfrugivorous tephritids. The anterior spiracles of the second and third instars are flattered and recessed. The oral ridges increase from none in the first instar, to one in the second instar, to two in the third instar. *Procecidochares blanci* is a true monophage on *Isocoma acradenia* (E. Greene) E. Greene, on which it produces two annual generations, one florivorous, which alternates with a longer generation that spends most of the winter, spring, and summer as a first instar inside a slowly developing, axillary bud/branch gall. The florivorous generation feeds within chambers excavated from adjacent, hypertrophied ovules. *Mesopolobus* sp. (Hymenoptera: Pteromalidae), *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae), and *E. sp. nr. tumoris* are reported as primary, solitary, larval-pupal endoparasitoids of *P. blanci*.

Key Words: Insecta, *Procecidochares*, Asteraceae, *Isocoma*, *Haplopappus*, nonfrugivorous Tephritidae, new species, adult taxonomy, key, biology, taxonomy of immature stages, flower-head feeding, galls, aggregative life cycle, seed predation, parasitoids

Until recent taxonomic revision of the California flora (Hickman 1993), the genus *Haplopappus* (Asteraceae) represented one of our most prominent and widespread native plant genera, yet one on which after a decade and a half of careful examination by RDG and his coworkers, they had failed to detect any galls formed by fruit flies (Diptera: Tephritidae). Finally, in 1995, Jeff

Teerink and RDG found the galls of the new species described herein, but by that time, the genus of this host plant and all of its former congeners had been changed (Hickman 1993)! This paper is dedicated to the late F. L. (Louie) Blanc who passed away in 1999 and who first introduced RDG to the fruit flies of California and encouraged his studies of the previously ne-

glected, native, nonfrugivorous species among them.

MATERIALS AND METHODS

The present study was based in large part on dissections of samples of flower heads and galls on *Isocoma acradenia* (E. Greene) E. Greene (formerly *Haplopappus acradenius*, Hickman 1993) (Asteraceae) mainly collected along the westernmost portion of the secondary road connecting Interstate Highway 10 at the Whitewater exit with State Highway 111 near West Palm Springs (hereafter called the Whitewater site) at the eastern end of the San Gorgonio Pass at 390-m elevation, Riverside Co., from 1995 to 1999. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia, as well as basal portions of branches sampled monthly from non-flowering, gall-bearing plants during 1998 and 1999 were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Three eggs, six first-, 14 second-, and 15 third-instar larvae and seven puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged

in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$ and 14/10 (L/D) photoperiod. Twenty-two pairs of virgin flies, each consisting of one or two males and a female obtained from emergence cages, also were held in clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Format used to describe the adults follows Blanc and Foote (1961) and Goeden and Teerink (1997a). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b, c, d, 2001), Goeden and Headrick (1999), Goeden and Teerink (1997a, b, 1999a, b), Teerink and Goeden (1999), and earlier works cited therein. Means \pm SE are used throughout. The holotype, allotype, and 23 reared paratypes of each sex of this new species are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). The holotype, allotype, and 22 paratypes used for measurements to describe *P. blanci* originated from one collection on 23.X.1996 at the Whitewater site. All remaining paratypes and voucher specimens not designated as paratypes and all reared parasitoids reside in RDG's research collections.

RESULTS AND DISCUSSION

TAXONOMY

The following key written by ALN incorporates several species described since

the publication of the most recent key to *Procecidochares* north of Mexico (Foote et al. 1993), as well as some additional characters. It is provided as a provisional key until this genus can be revised comprehensively. Users should be aware that several additional, undescribed species are already known.

PRELIMINARY KEY TO THE SPECIES OF
PROCECIDOCHARES OF THE UNITED STATES
AND CANADA

1. Wing with crossvein between costa and vein R_{2+3} about midway between apices of R_1 and R_{2+3} (Foote et al. 1993, fig. 172). Anterior notopleural and postsutural supra-alar setae usually absent. Anepisternum with small anterodorsal nonmicrotrichose shiny area. A cluster of 2–4 setae in normal position of anterior orbital seta (Foote et al. 1993, fig. 33). Facial ridge and parafacial with numerous white, lanceolate setulae. Scutum with row of postsutural intra-alar setulae. Scutellum with white setulae near basal seta. Hosts *Ambrosia* spp. Canada (Nova Scotia) & eastern USA west to Iowa & Texas *P. gibba* (Loew)

– Wing without crossvein to costa between apices of R_1 and R_{2+3} , rarely a stump present on vein R_{2+3} . Anterior notopleural and postsutural supra-alar setae present. Anepisternum either entirely microtrichose or with large nonmicrotrichose shiny area covering at least anterodorsal and anteroventral sections. Usually only a single anterior orbital seta. Facial ridge setulae often yellow or white, but rarely lanceolate. Parafacial usually nonsetose; setulae, if present, acuminate. Row of intra-alar setulae and scutellar setulae present or absent 2

2. Anepisternum and notopleuron entirely microtrichose (Fig. 1D). Katepisternum entirely microtrichose except in *P. pleuralis*. Scutum with 1 or a cluster of several white, lanceolate setulae immediately anterior to postsutural supra-alar seta. Scutellum without white setulae basally. Cell r_{2+3} with marginal hyaline area variable in shape, but often broadest near midpoint or subapically, absent or narrow bordering apex of vein R_{4+5} (Foote et al. 1993, figs. 342, 344) 3

– Anepisternum with large nonmicrotrichose shiny area, at least anterodorsally and anteroventrally (Fig. 1C). Anterior half of notopleuron mostly or entirely nonmicrotrichose and shiny. Katepisternum with large nonmicrotrichose shiny area. Scutum usually with-
- out white lanceolate setulae immediately anterior to postsutural supra-alar seta. Scutellum often with 1 to several white setulae near basal scutellar seta (Fig. 1A). Cell r_{2+3} with marginal hyaline area absent or narrowest near middle, broader bordering apex of vein R_{4+5} (Foote et al. 1993, figs. 346–350), sometimes not quite touching vein apex in *P. australis* Aldrich (Foote et al. 1993, fig. 351) 5

3. Katepisternum and postpronotal lobe entirely microtrichose (Fig. 1D). Cell r_{2+3} with marginal hyaline area broadest near midpoint or subapically, absent or narrow bordering apex of vein R_{4+5} (Foote et al. 1993, figs. 342, 344). Scutum with cluster or row of setulae extending to or towards presutural supra-alar seta anteromesal to it (Fig. 1B) (*P. utilis* group) 4

– Katepisternum with large nonmicrotrichose shiny area. Postpronotal lobe with dorsomesal nonmicrotrichose shiny area. Cell r_{2+3} with marginal hyaline area absent or narrowest near middle, broader bordering apex of vein R_{4+5} (Foote et al. 1993, fig. 345). Scutum without setulae anteromesal of presutural supra-alar seta. Host “sunflower”. USA (Arizona), Mexico (Durango). *P. pleuralis* Aldrich

4. Posterior orbital seta very small, but present (Foote et al. 1993, fig. 42). Femora often largely brown. Wing bands generally brown (Foote et al. 1993, fig. 342). Apical and subapical bands not connected. Hosts *Brickellia* spp. USA (California, New Mexico), Mexico (Baja California) *P. flavipes* Aldrich

– Posterior orbital seta absent. Legs entirely yellow. Wing bands generally yellow or pale brown (Foote et al. 1993, fig. 344). Apical and subapical bands sometimes connected along vein R_{4+5} . Hosts unknown. USA (Montana, Colorado) *P. montana* (Snow)

5. Basal and discal bands connected at least in cells r_1 and br or br and bm (Fig. 2; Foote et al. 1993, fig. 346; this character should be observed carefully with transmitted light). Scutum with one postsutural dorsocentral seta; usually with row of setulae from transverse suture to or towards intra-alar seta along intra-alar line (Fig. 1A) (absent in *P. kristinae* Goeden, variable in *P. stonei* Blanc & Foote). Scutellum usually with 1 to several white setulae near basal scutellar seta (Fig. 1A) (often absent in *P. stonei*) 6

– Basal and discal bands separate or narrowly connected only in cell br (rarely only in cell bcu). Scutum with 1–2 dorsocentral setae, the second presutural if present; with or without row of intra-alar setulae. Scutellum with or

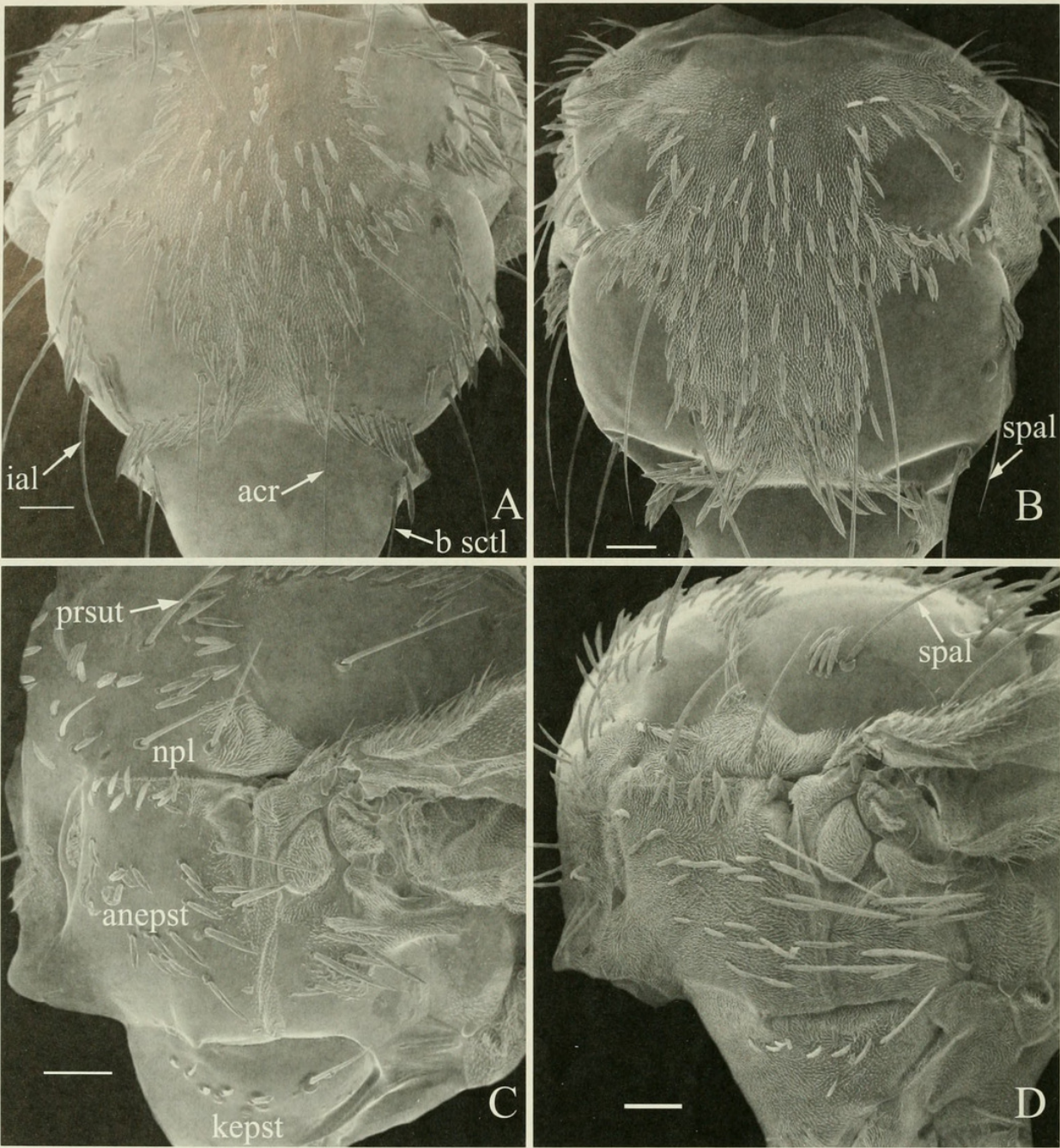


Fig. 1. Thoraces of *Procecidochares blanci*: (A) dorsal view; (C) lateral view; and *P. flavipes*: (B) dorsal view; (D) lateral view. anepst - anepisternum, b sctl - basal scutellar seta, ial - intra-alar seta, kepst - katepisternum, npl - notopleuron, prsut - presutural supra-alar seta, spal - postsutural supra-alar seta.

- without white setulae near basal scutellar seta
.....

6. Abdomen partially yellow, at least basolaterally. Gena without brown spot. Scutum with medial areas of white setulae and microtrichia relatively narrow, neither entirely enclosing acrostichal seta (Fig. 1A). Pterostigma entirely brown (Fig. 2). Apical band usually connected to subapical band in cell r_{2+3} and sometimes cell r_1 . In lateral view (Fig. 1C), lateralmost setulae in ring of presutural lateral scutal setulae closer to anterior notopleural
- 9
- seta than to presutural supra-alar seta or mid-way between them. Host *Isocoma acradenia*. USA (California)
..... *P. blanci* Goeden and Norrbom, n. sp.

- Abdomen entirely brown. Gena often with large brown spot bordering eye. Scutum with area of medial white setulae and medial microtrichose area relatively broad, acrostichal seta within area of white setulae and at lateral border of or within microtrichose area. Pterostigma often with yellow or paler brown area basally. Apical band connected to or separate

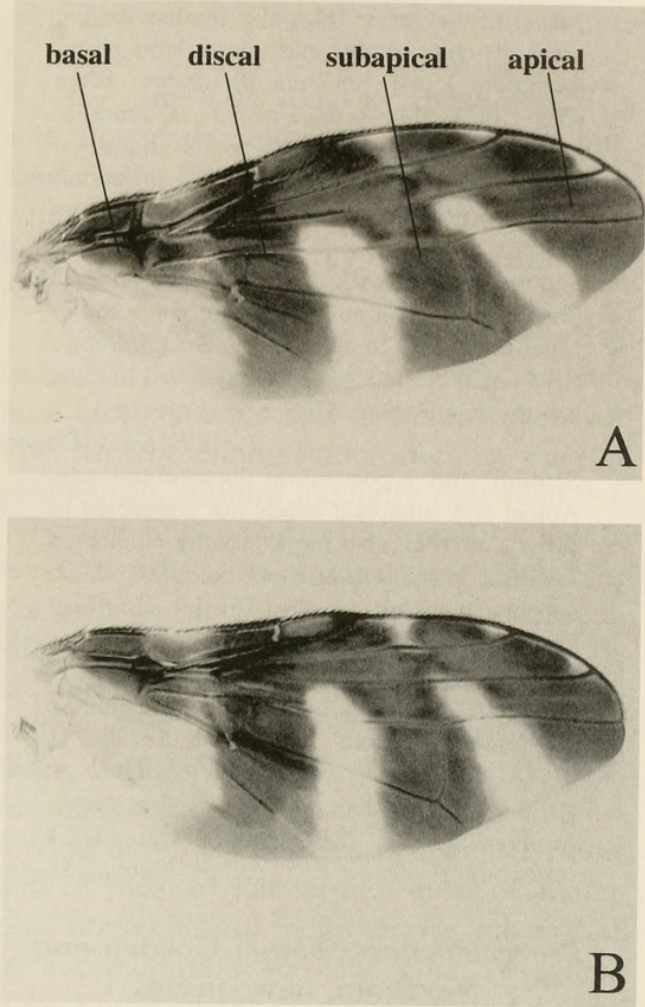


Fig. 2. Right wings of *Procecidochares blanci*: (A) female with bands labelled; (B) male.

from subapical band. In lateral view, lateral-most setulae in ring of presutural lateral scutal setulae often closer to presutural supra-alar setae than to anterior notopleural seta or surrounding it 7

7. Gena without large brown spot. Scutum without row of setulae from transverse suture to or towards intra-alar seta along intra-alar line; with 1 or a cluster of several white lanceolate setulae immediately anterior to postsutural supra-alar seta. Scutellum with 1 to several white setulae near basal scutellar seta. Pterostigma usually with yellow or paler brown area basally (Goeden and Teerink 1997, fig. 1). Apical band usually connected to subapical band in cell r_{2+3} and sometimes cell r_1 . Host *Ambrosia dumosa* (Gray) Payne. USA (California, Nevada, Arizona)
. *P. kristineae* Goeden (in part)

– Gena usually with large brown spot bordering eye. Scutum with or without intra-alar and supra-alar setulae (*P. lisae* Goeden with intra-alar, without supra-alar; both variable in *P. stonei*). Scutellum with or without 1 to several

white setulae near basal scutellar seta. Pterostigma with or without yellow or paler brown area basally. Apical band usually separate from subapical band 8

8. Discal band reduced, in male not extended beyond vein A_1+Cu_2 , in female at most narrowly reaching posterior wing margin, but if so, part posterior to A_1+Cu_2 much paler than rest of band (Goeden & Teerink 1997, fig. 2). Cell c entirely brown or at most yellow medially. Pterostigma usually with yellow or paler brown area basally. Scutellum with 1 to several white setulae near basal scutellar seta. Host *Ambrosia eriocentra* (Gray) Payne. USA (California) *P. lisae* Goeden

– Discal band not reduced, broadly and distinctly reaching posterior wing margin in both sexes (Foote et al. 1993, fig. 346). Cell c with large medial hyaline area. Pterostigma evenly brown. Scutellum with or without white setulae near basal scutellar seta. Hosts *Viguiera* spp. USA (California)
. *P. stonei* Blanc and Foote

9. Legs entirely yellow. Scutum with 1 postsutural dorsocentral seta. Scutellum with 1 to several white setulae near basal scutellar seta. Apical and subapical bands not connected (Foote et al. 1993, fig. 343). Hosts *Solidago* spp. USA (Massachusetts south to Florida, Mississippi) *P. polita* (Loew)

– Femora usually mostly brown, if yellow, scutum with 2 dorsocentral setae (1 presutural) or scutellum without white setulae. Apical and subapical bands sometimes connected 10

10. Scutum with row of setulae from transverse suture to or towards intra-alar seta along intra-alar line; with 2 dorsocentral setae (1 presutural) 11

– Scutum rarely with partial row of intra-alar setulae, if present, with only 1 dorsocentral seta 12

11. Scutum with presutural microtrichia extended laterally no more than one fourth distance from dorsocentral line to presutural supra-alar seta. Acrostichal seta usually at margin of medial microtrichose area of scutum. Subapical and apical bands separate (Foote et al. 1993, fig. 350). Hosts *Grindellia* spp. USA (California, Colorado) *P. grindelliae* Aldrich

– Scutum with presutural microtrichia extended laterally more than half distance from dorsocentral line to presutural supra-alar seta, usually reaching it. Acrostichal seta usually within medial microtrichose area of scutum. Subapical and apical bands sometimes connected in cell r_{2+3} , Hosts *Heterotheca* spp. USA (Texas), Mexico *P. australis* Aldrich

12. Hyaline triangular area between discal and

- subapical bands distinctly broader along posterior wing margin than hyaline area between subapical and apical bands (Foote et al. 1993, fig. 347). Acrostichal seta usually at margin of or within medial microtrichose area of scutum. Scutellum without white setulae. Subapical and apical bands sometime connected in cell r_1 . Hosts *Solidago* spp. Southeastern Canada, northern and eastern USA
- *P. atra* (Loew)
- Hyaline triangular area between discal and subapical bands at most slightly broader than hyaline area between subapical and apical bands. Other characters variable 13
13. Scutum with 1 or a cluster of several white, lanceolate setulae immediately anterior to postsutural supra-alar seta; area of medial white setulae relative broad, including acrostichal seta; medial microtrichose area also broad but short, enclosing acrostichal seta laterally, but bare area sometime touching it posteriorly. Pterostigma usually with yellow or paler brown basal area (Goeden & Teerink 1997, fig. 1). Scutellum with 1 to several white setulae near basal scutellar seta. Host *Ambrosia dumosa*. USA (California, Nevada, Arizona) *P. kristinae* Goeden (in part)
- Scutum without white setulae immediately anterior to postsutural supra-alar seta; area of medial white setulae usually narrower, acrostichal seta usually lateral to or at its border; medial microtrichose area usually narrower and longer, usually at most partially enclosing acrostichal seta (the latter sometimes within indentation of bare area). Pterostigma without paler basal area. Scutellum usually without white setulae basally 14
14. Scutum with presutural microtrichia extended laterally at least half distance from dorsocentral line to level of presutural supra-alar seta, at least along anterior part of ring of white setulae 15
- Scutum with presutural microtrichia extended laterally no more than one fourth distance from dorsocentral line to presutural supra-alar seta 16
15. Scutum usually with 2 dorsocentral setae, 1 presutural; without intra-alar setulae; medial areas of white setulae and microtrichia sometimes including acrostichal seta. Scutellum without white setulae basally. Body usually redbrown; postpronotal lobe and propleuron usually partially yellow. Apical and subapical bands separate or connected along vein R_{4+5} . Hosts *Heterotheca* and *Conyza* spp. USA (Florida, South Carolina, Maryland?)
- sp. 1 near *P. australis*
- Scutum with 1 dorsocentral seta; often with partial row of white intra-alar setulae; medial areas of white setulae and microtrichia rarely including acrostichal seta. Scutellum often with 1 or 2 white setulae near basal scutellar seta. Apical and subapical bands connected along vein R_{4+5} . Body, including postpronotal lobe and propleuron dark brown. USA (Texas) sp. 2 near *P. australis*
16. Scutum usually with 2 dorsocentral setae, 1 presutural. Apical and subapical bands sometimes connected in cell r_1 only. Host *Solidago californica* Nuttall. USA (Oregon & Montana south to California, Arizona & Colorado) *P. anthracina* (Doane)
- Scutum with 1 postsutural dorsocentral seta. Apical and subapical bands not connected in cell r_1 , or if so, also more broadly connected in cell r_{2+3} . (*minuta-blantoni* complex, which appears to include at least several additional cryptic species) 17
17. Parafacial less than half as wide as first flagellomere. Hosts various. USA (Washington & Montana south to California & Texas) *P. minuta* (Snow)
- Parafacial about half as wide as first flagellomere. Hosts *Heterotheca* spp. USA (Oregon) *P. blantoni* Hering

Procecidochares blanci Goeden and Norrbom, new species
(Figs. 1A, C, 2–8)

Adult female.—*Head*: Generally pale colored except occiput and often ocellar tubercle and orbital plates brown, entirely microtrichose. In profile 0.6–0.7 times as long as high, face and frons meeting at about 120° angle; parafacial about 0.8 times as wide as first flagellomere; gena about 0.2 times as high as eye; eye 0.5–0.6 times as wide as high; frons ochereous brown to yellow, at vertex 1.2–1.4 times as wide as eye in lateral view, 1.2–1.4 times as wide as length from vertex to lunule; lunule about 0.7 times as high as wide; face and lunule white, paler than frons, face concave with moderate carina; antenna short, yellow, sometimes white or ochereous brown, microtrichose, arista ochereous brown to brown, extreme base yellow. Usually 2 brown frontal setae, occasionally 3 on one side, or rarely 3 on both sides, or 1 on one side. 1 brown orbital seta, posterior seta absent. Ocellar and medial vertical setae brown,

well developed. Lateral vertical seta yellow to white, slightly to distinctly lanceolate, 0.5–0.7 times as long as medial vertical seta. Postocular and postocellar setae white, lanceolate. Facial ridge setulae yellow or white, acuminate. Gena without distinct brown spot bordering eye, genal seta brown.

Thorax (Figs. 1A, C): Mostly dark brown to black, posterodorsal corner of anepisternum and posterior half of notopleuron yellow. Mostly shining, microtrichose only on propleuron, scutum medially (between dorsocentral lines anteriorly, slightly wider at level of transverse suture, then narrowing posteriorly; at level of acrostichal setae slightly narrower than distance between setae) and on extreme lateral margin (at or below level of postpronotal seta), on posterior half of notopleuron, posterodorsally on anepisternum, dorsally on anepimeron, medial or ventral margin of katepisternum, part or most of katatergite, most of anatergite, dorsal half of mediotergite, most or all of subscutellum, and underside of scutellum. Postpronotal, 2 notopleural, pre- and postsutural supra-alar, intra-alar, postalar, 1 postsutural dorsocentral (approx. midway between suture and level of supra-alar seta), acrostichal, 2 scutellar setae well developed, brown. Mesonotal setulae relatively large, stout, lanceolate, white, in pattern as follows: large medial area of continuous setulae between dorsocentral setae, with unpaired medial and paired dorsocentral rows extending anteriorly, the latter joining row along anterolateral margin, margin of notopleuron and anterior margin of transverse suture to form circular arrangement (in lateral view, lateralmost setulae midway between anterior notopleural and presutural supra-alar setae or slightly closer to one of those setae); rarely with 1 to several setulae anteromesal to presutural supra-alar seta; another row extending laterally along posterior margin of transverse suture, curving posteriorly and extending to intra-alar seta and sometimes laterally to postalar seta; main medial area of setulae narrowing pos-

teriorly, between acrostichal setae dividing into paired submedial rows that curve laterally and then extend to posterior margin; rarely 1 to several setulae immediately anterior to postsutural supra-alar seta. Postpronotal lobe with several additional lanceolate white setulae. Scutellum with 1 to several lanceolate white setulae near base of basal scutellar seta. Anepisternum with 1 brown seta and 1–2 large lanceolate white setulae posteriorly, and numerous smaller white lanceolate setulae. Anepimeron with only several large lanceolate white setulae. Katepisternum with a few lanceolate white dorsal setulae and 1 white or brown seta. Scutellum stout in vertical and horizontal planes, rounded. Legs mostly yellow to ocherous.

Wing (Fig. 2): With base and 3 broad bands brown. Basal band (usually isolated in other *Procecidochares* species) extended posteriorly to base of vein Cu, broadly connected to discal band in cells, sc, r_1 , and br, and almost always in bm, sometimes also in cell c or rarely in cell bcu, although area connecting bands often paler than bands. Discal, subapical, and apical bands extended to posterior wing margin. Discal and subapical bands connected anteriorly in pterostigma and cells r_1 and r_{2+3} . Subapical and apical bands usually broadly, sometimes narrowly connected in cell r_{2+3} and to lesser extent in cell r_1 , rarely narrowly separated in both cells. Apical band broad, with small marginal hyaline spots at apices of veins R_{2+3} and R_{4+5} and often a very narrow hyaline area connecting them. Pterostigma about 2–3 times as long as wide and evenly brown. Distance between crossveins R-M and DM-Cu about equal to length of R-M. Haltere shaft ocherous yellow, knob pale yellow.

Abdomen: Partially to entirely yellow, non-yellow areas dark brown. Syntergite 1+2 yellow laterally, often brown medially. Tergites 3–4 usually yellow laterally and often medially. Tergite 5 and especially tergite 6 usually brown at least medially. At least sternites 1, 2, and usually 3 yellow.

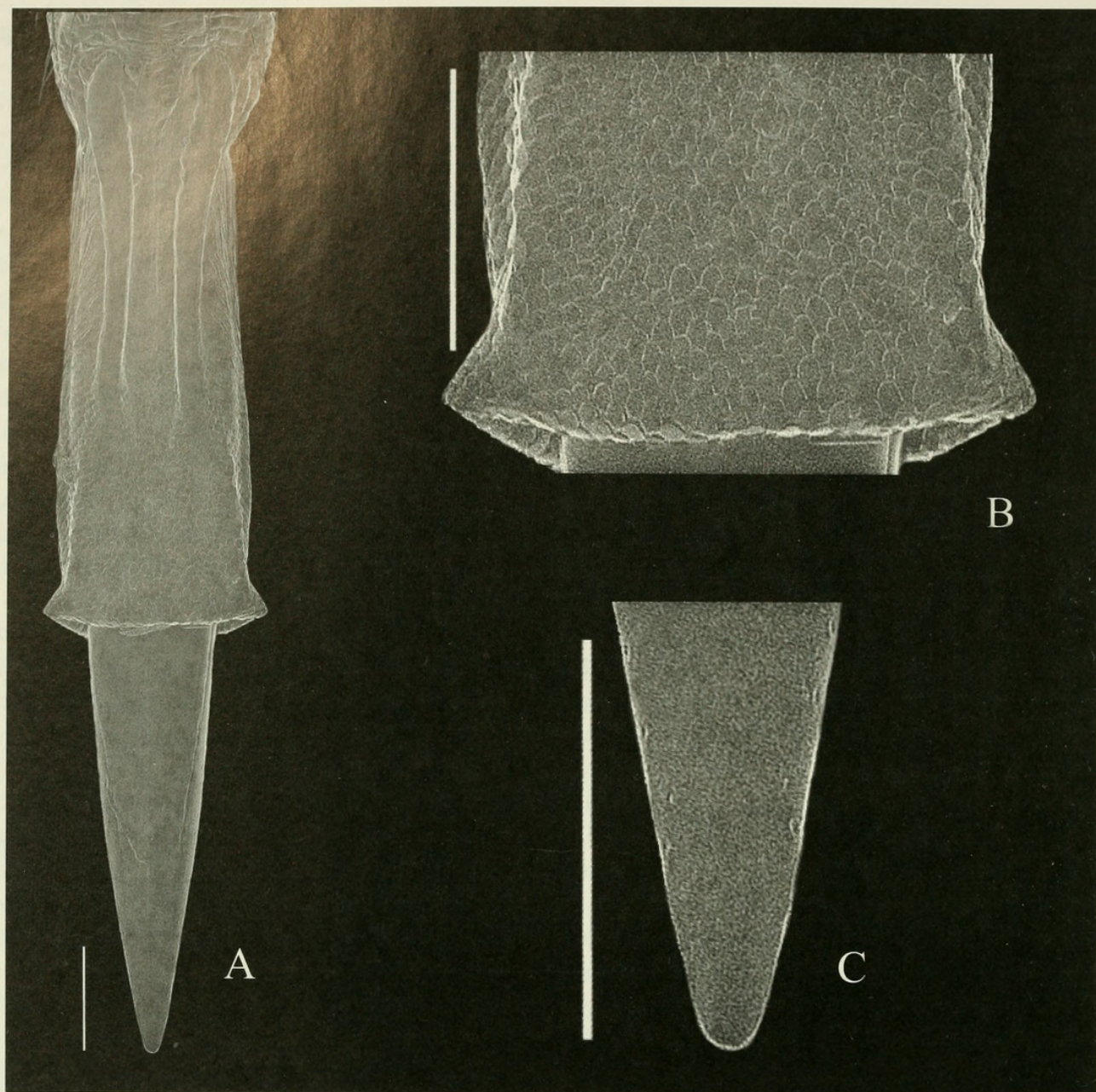


Fig. 3. Eversible membrane and aculeus of *Procecidochares blanci*, dorsal view. (A) partially everted; (B) middle of eversible membrane, enlarged; (C) aculeus tip.

Setulae more or less evenly covering tergites, mostly white and lanceolate, often more acuminate and/or yellow laterally. Syntergite 1+2 except posterior corner, tergite 3 except laterally, usually broad basomedial area of tergite 4, and often narrow basomedial area of tergite 5 microtrichose. Oviscape, in dorsal view, $2/3$ length of rest of abdomen; brown, nonmicrotrichose, shiny; setulae acuminate. Aculeus tip acute, simple (Fig. 3).

Male.—*Head*: Similar to female, but par-

afacial about 0.8 times as wide as first flagellomere; gena 0.13–0.20 times as high as eye; frons at vertex 1.0–1.3 times as wide as eye in lateral view, 1.1–1.3 times as wide as length from vertex to lunule; lunule 0.4–0.5 times as high as wide. *Thorax*: Similar to female. *Wing* (Fig. 2B): Similar to female. Basal band usually connected to discal band in cell c. *Abdomen*: Color and vestiture similar to female. Tergite 5 nonmicrotrichose. Epandrium and surstyli brown.

Variation.—Examination of reared *P.*

Table 1. Variation in number and color of frontal setae of *P. blanci*. b = black, w = white.

No. Setae/Side	Females		Males	
	No.	%	No.	%
2b:2b	98	81.7	84	74.3
1b1w:1b1w	1	0.8	2	1.8
2b:1b1w	2	1.7	5	4.4
2w:1b1w	0	0	1	0.9
1b:1b	1	0.8	1	0.9
1b:0	0	0	1	0.9
1b:3b	0	0	1	0.9
2b:1b	8	6.7	8	7.1
2b:3b	3	2.5	5	4.4
2b:2b1w	1	0.8	0	0
2b:4b	0	0	1	0.9
3b:3b	3	2.5	3	2.7
2b1w:2b1w	2	1.7	1	0.9
3b:2b1w	1	0.8	0	0

blanci specimens with intact setation indicated that the number of frontal setae varies from one to six, even greater than the variation from two to five noted for the genus by Foote et al. (1993). The variation in frontal seta color and number is summarized in Table 1.

Diagnosis.—Adults of *P. blanci* can be distinguished from those of most other species of *Procecidochares* known from north of Mexico by their partially yellow abdomen. This character otherwise appears to occur only in some specimens from Florida that have been regarded as *P. australis* (see Foote et al. 1993), but they are readily distinguished from *P. blanci* by the presence of presutural dorsocentral setae, which are always absent in *P. blanci*. In other characters *P. blanci* most closely resembles *P. kristineae*, *P. gibba*, *P. lisae*, and *P. stonei* which also have the basal and discal bands broadly connected (usually less broadly in *P. kristineae*). These species differ in having broader medial areas of white setulae and microtrichia on the scutum. Several other useful diagnostic characters include: the gena without a large brown spot; thoracic microtrichia generally reduced (e.g., postpronotal lobe, anterior half of notopleuron, most of anepisternum and katepister-

num bare); scutum with a row of white postsutural intra-alar setulae (absent in *P. kristineae*); scutellum with one to several small white setulae near basal scutellar seta; pterostigma without a yellow or paler brown basal area; and the apical band usually connected to the subapical band in cell r_{2+3} and sometimes cell r_1 . This is the only *Procecidochares* species known to infest *Isocoma acradenia*.

Types.—Holotype, ♀ (USNM); along Whitewater Rd. SW of Whitewater, S of I-10, N of Hwy 111, 1270 ft, Riverside Co., CA; 23.x.1996; R. D. Goeden, coll. (hereafter RDG)/J. A. Teerink, coll. (hereafter JAT); reared from flower head of *Isocoma* (= *Haplopappus*) *acradenia* on 6.xi.1996. Allotype, ♂; same data as holotype (USNM). Paratypes: CALIFORNIA: 65 ♂ and 60 ♀; same data as holotype (24 ♂ and 23 ♀ to USNM). 1 ♂ and 3 ♀; Coyote Wells, Imperial Co., 6.xi.1986; RDG. 2 ♂ (1 missing abdomen), E of Ocotillo, CA at Coyote Wells, SW Imperial Co., 140 ft elevation, 15.xi.1990, reared from flower head of *I. acradenia* (as *H. acradenius*). 8 ♂ and 4 ♀; Coyote Wells, 140 ft, Imperial Co., 17.xi.1994, RDG/JAT; reared 22.xi.1994. 14 ♂ and 31 ♀; same location as holotype, 26.x.1995; RDG/JAT. 2 ♂ and 1 ♀; Frontage road to In-Koh-Pah Tower, N of Interstate Hwy 8, 2880 ft, San Diego Co., 2.x.1997; RDG/JAT. 18 ♂ and 18 ♀; same location as holotype, 29.x.1997; RDG/JAT.

Etymology.—*Procecidochares blanci* is named in honor of the late F. L. (Louie) Blanc, noted California tephritologist, who first introduced RDG to the Tephritidae, previewed all of RDG's manuscripts on nonfrugivorous fruit flies prior to Louie's death, and served as a constant source of encouragement for RDG's studies of these flies.

Egg.—Sixty-two eggs dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.55 ± 0.004 (range, 0.48–0.64) mm long, 0.16 ± 0.002 (range, 0.12–0.20) mm wide,

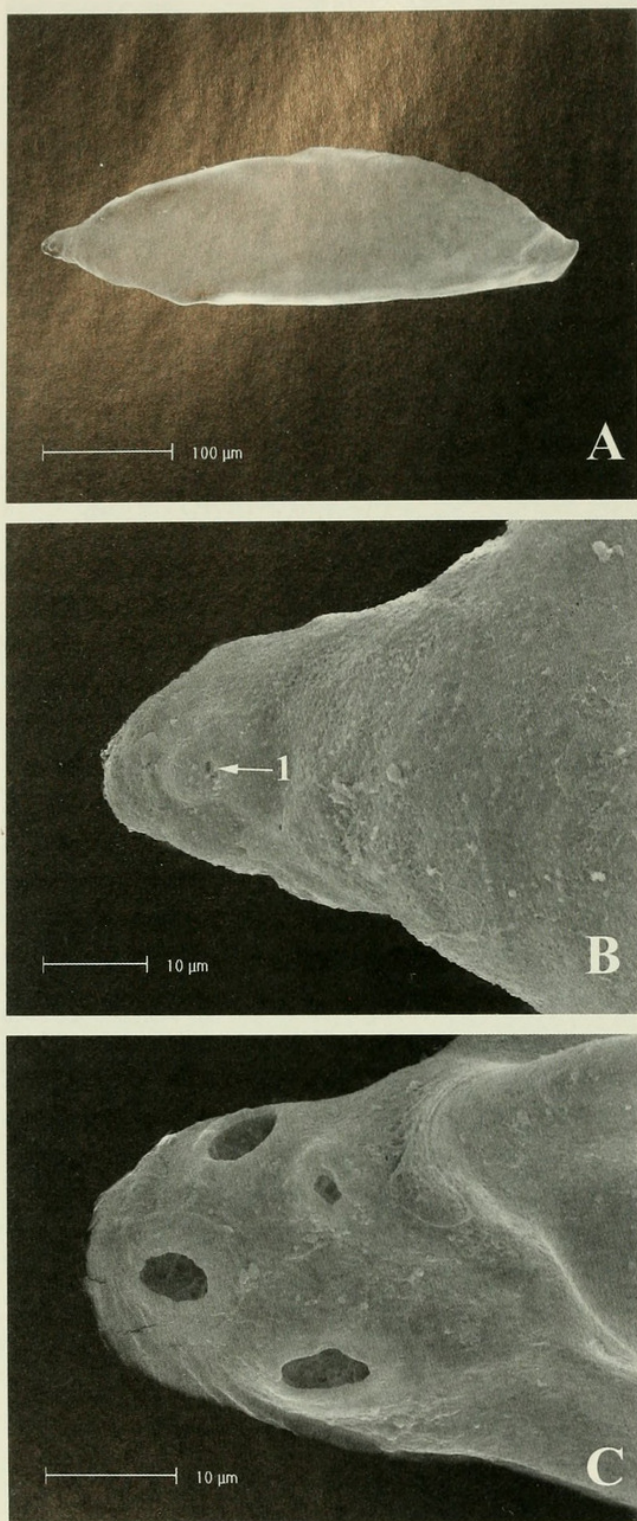


Fig. 4. Egg of *Procecidochares blanci*: (A) habitus, anterior end to left; (B) pedicel showing 1- small aeropyle; (C) pedicel of a different egg with aeropyles.

smoothly rounded at tapered basal end (Fig. 4A); pedicel nipple-like, 0.03 mm long, circumscribed by few, very small (Fig. 4B-1) to several larger, oval (Fig. 4C) aeropyles scattered around the pedicel (Fig. 4C).

The egg of *P. blanci* is similar in general shape to that of *P. stonei*, which also has few small aeropyles on a less pronounced pedicel (Green et al. 1993); however, the pedicel with the sole, tiny aeropyle shown in Fig. 4B probably was an aberration or the result of plugging during preparation for SEM, as suggested by the circular areas anterior to the arrow. The egg of *P. kristineae* was described as navicular by Silverman and Goeden (1994), which agrees with photos in Goeden and Teerink (1997a), with a prominent pedicel circumscribed \pm in a row by a few small subcircular aeropyles. In contrast, the prominent pedicel of the egg of *P. anthracina* has only a few, large aeropyles (Goeden and Teerink 1997b). The eggs of *P. flavipes* are slightly larger and wider on average (Goeden et al. 1994) than those of *P. blanci* (Fig. 4A), as are those of *P. lisae* (Goeden and Teerink 1997a), all three of which are longer and wider on average than those of *P. kristineae* (Silverman and Goeden 1980), *P. anthracina* (Goeden and Teerink 1997b), and *P. stonei* (Green et al. 1993).

First-instar larva.—White, cylindrical and bluntly rounded anteriorly and posteriorly when newly hatched, becoming subglobose (Fig. 5A); body segments well defined, finely wrinkled (probably as a result of preparation for SEM), free of minute acanthae; gnathocephalon finely wrinkled, flattened (Fig. 5B), dorsal sensory organ a well-defined, flat pad (Figs. 5B-1, C-1); anterior sensory lobe (Figs. 5B-3, C-2) bears terminal sensory organ (Figs. 5B-4, C-3); lateral sensory organ (Fig. 5C-4), supralateral sensory organ (Fig. 5C-5), and pit sensory organ (Fig. 5B-2); stomal sense organ poorly defined, reduced to two pore sensilla, ventrolaterad of terminal sensory organ (Fig. 5C-6); mouthhook bidentate (Fig. 5B-5), apical tooth grooved dorsally (Figs. 5B-6, C-7); median oral lobe laterally compressed, apically rounded (Figs. 5B-7, C-8); anterior spiracle absent; lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorso- and ventrolaterad

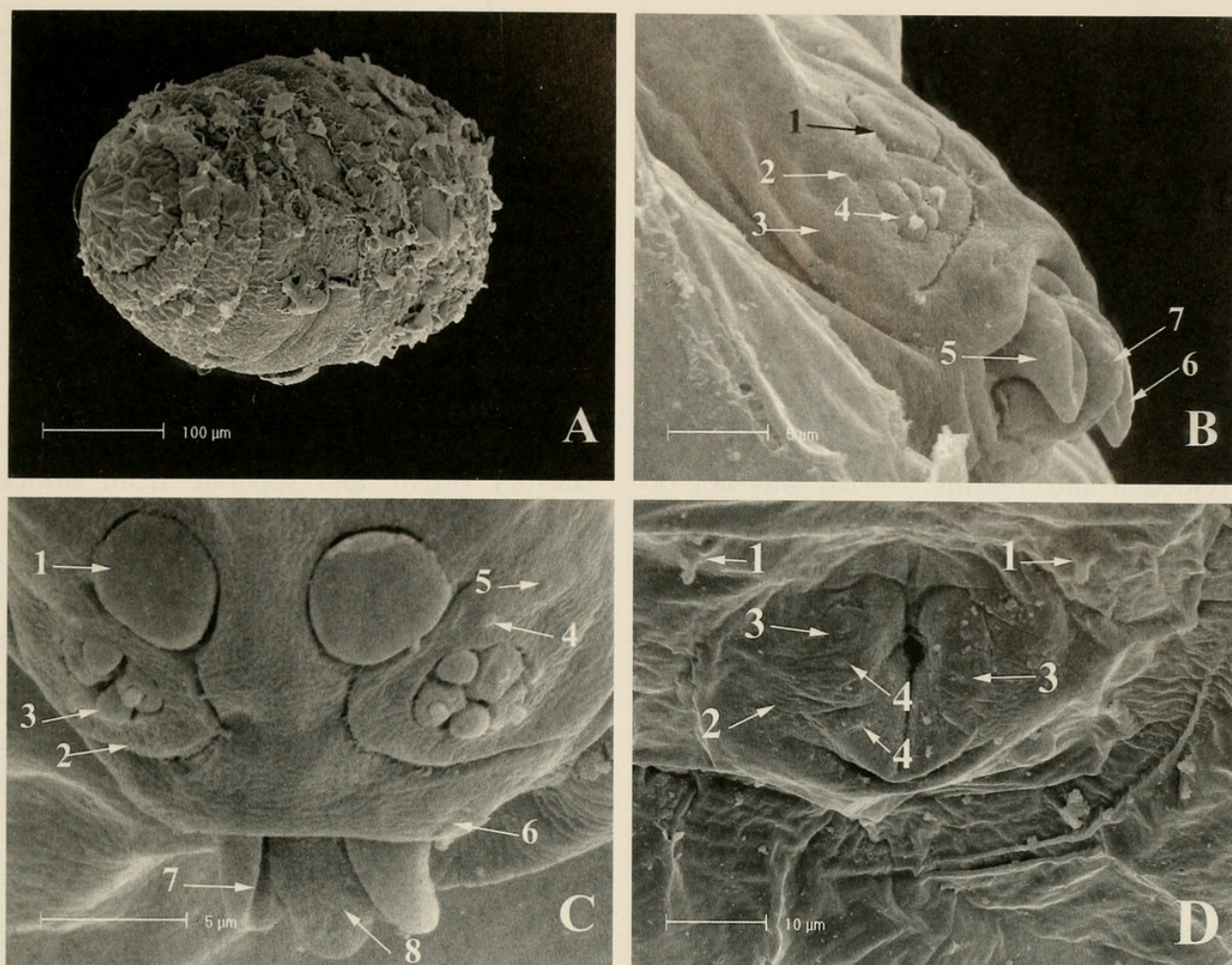


Fig. 5. First instar of *Procecidochares blanci*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1- dorsal sensory organ, 2- pit sensory organ, 3- anterior sensory lobe, 4- terminal sensory organ, 5- mouthhook, 6- dorsally grooved, apical tooth of mouthhook, 7- median oral lobe; (C) gnathocephalon, dorsal view, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- stomal sense organ, 7- dorsally grooved apical tooth of mouthhook, 8- median oral lobe; (D) caudal segment, 1- dorsolateral stelex sensillum, 2- posterior spiracular plate, 3- rima, 4- interspiracular process.

(Fig. 5D-1) of posterior spiracular plate (Fig. 5D-2); posterior spiracular plate bears two elliptical rimae, ca. 0.01 mm in length (Fig. 5D-3), and four, small, hemispherical, much reduced, unbranched, interspiracular processes (Fig. 5D-4); no intermediate sensory complex observed.

The first instar habitus shortly after eclosion has the cylindrical form ascribed to *P. anthracina* (Goeden and Teerink 1997b) and *P. lisae* (Goeden and Teerink 1997a), but later during this long stadium more closely assumes the barrel shape ascribed to *P. stonei* (Green et al. 1993) and *P. kristineae* (Goeden and Teerink 1997a) with this

change of shape with growth probably accounting for these reported, apparent differences. No minute acanthae circumscribe the intersegmental lines as reported for *P. kristineae*, *P. lisae* (Goeden and Teerink 1997a), and *P. anthracina* (Goeden and Teerink 1997b). The dorsal sensory organ of the first instar of *P. blanci* is well-defined (Figs. 5B-1, C-1), but flattened, not dome-shaped, as reported for *P. kristineae*, *P. lisae* (Goeden and Teerink 1997a) and *P. anthracina* (Goeden and Teerink 1997b), nor as pictured for *P. stonei* (Green et al. 1993). The apical tooth of the two-toothed mouthhook of *P. blanci* is dorsolaterally grooved

(Figs. 5B-6, C-7), and this tooth appears grooved dorsomedially in *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a). In these three species, this character provides a ready means of separating the first from the second instars, which lack dorsal grooves. However, photos of this anterior tooth in the first instar of *P. stonei* (Green et al. 1993) show no such groove, nor was such a groove reported in the description of the first instar of that species. The mouthhook of the first instar of *P. anthracina* (Goeden and Teerink 1997b) was not observed for comparison. Evaluation of the locations and presence or absence of this character among first instars of *Procecidochares*, a character not seen in other genera of Tephritidae that we have studied (i.e., *Aciurina*, *Neaspilota*, *Trupanea*), awaits descriptions of first instars of additional *Procecidochares*.

Two stelex sensilla dorso- and ventrolaterad of each posterior spiracular plate are reported in the first instar of *P. blanci* (Fig. 5D-1); however, in the first instar of *P. lisae* (Goeden and Teerink 1997a), these sensilla are verruciform and "compound" (i.e., paired verruciform), respectively. The caudal segment of *P. anthracina* (Goeden and Teerink 1997b) was reported to be circumscribed by stelex "sensilla", thus, presumably by at least two pairs. In the first instar of *P. kristineae*, only a ventrolateral pair of stelex sensilla was seen, photographed, and reported (Goeden and Teerink 1997a). The first instars of *Neaspilota wilsoni* (Goeden and Headrick 1999), *N. footei* (Goeden 2001), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c) also have four (two pairs of) stelex sensilla reported to ring the caudal segment; however, these stelex sensilla characteristically are ringed by different-shaped, minute acanthae, unlike *P. blanci*, which lacks a basal ring of minute acanthae.

Second instar larva.—White, elongate-ovoidal, rounded anteriorly, truncated posteriorly (Fig. 6A), body segments well-defined, prothorax circumscribed by many

round, oval or elliptical, flattened, rugose pads of different size (Fig. 6B-1), few rugose pads on gnathocephalon (Fig. 6B), rugose pads absent from remaining thoracic and abdominal segments; dorsal sensory organ well-defined, flattened (Figs. 6B-2, C-1); anterior sensory lobe (Fig. 6C-2) with terminal sensory organ (Fig. 6C-3), lateral sensory organ (Fig. 6C-4), supralateral sensory organ (Fig. 6C-5), and pit sensory organ (Fig. 6C-6); oral ridge (Figs. 6B-3, C-7) with entire margins, lateral to terminal sensory organ, and separate from stomal sense organ (Figs. 6B-4, C-8), which lies ventrolaterad of anterior sensory lobe; mouthhook (Figs. 6B-5, C-9) with four teeth (Fig. 6D); median oral lobe laterally compressed, apically rounded (Figs. 6B-6, C-10); anterior thoracic spiracle recessed in body fold, with three, indistinct, flattened "papillae" (Fig. 6E); lateral spiracular complexes not seen; each posterior spiracular plate bears three ovoid rimae (Fig. 6F-1), ca. 0.009 mm long, and four, unbranched spiniform interspiracular processes (Fig. 6F-2) 0.006 mm long; sensilla lateral to spiracular plate and intermediate sensory complex not seen.

The habitus of the second instar of *P. blanci* (Fig. 6A) probably actually differs little in shape from the "barrel-shaped" (doliform) second instars of *P. stonei* (Green et al. 1993) and *P. kristineae* (Goeden and Teerink 1997a) or the cylindrical shape ascribed to *P. anthracina* (Goeden and Teerink 1997b) and *P. lisae* (Goeden and Teerink 1997a). However, only *P. blanci* among them has the prothorax circumscribed by the numerous, different sized, rugose pads described above (Fig. 5B-1). The dorsal sensory organ is well-defined in the first and second instars of all six congeneric species (Figs. 6B-2, C-1; Green et al. 1993; Goeden et al. 1994; Goeden and Teerink 1997a, b), unlike certain *Neaspilota* spp. in which the definition of this character differs between these instars and can be used to separate them (Goeden 2001). The single oral ridge present in *P. blanci* (Figs.

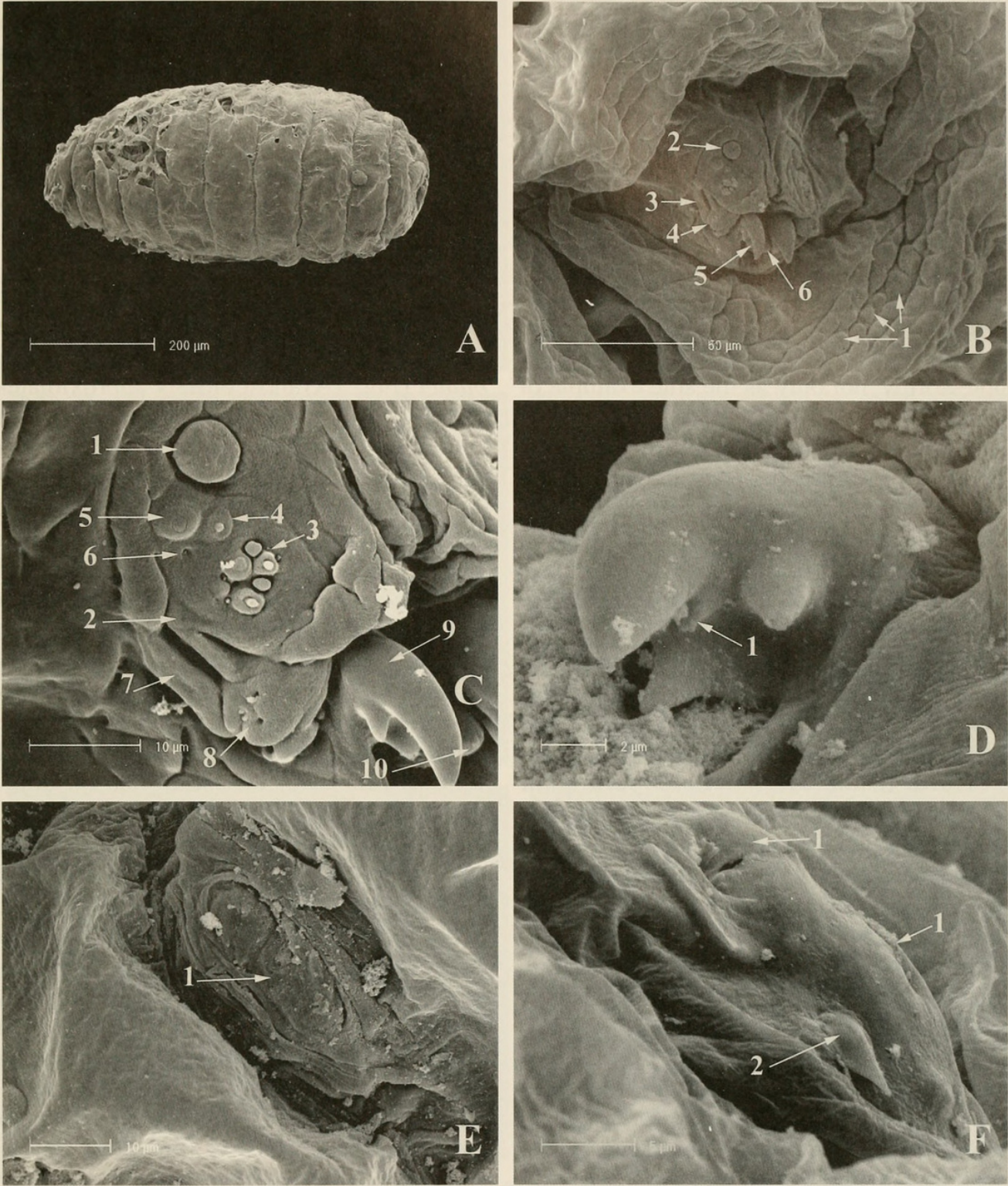


Fig. 6. Second instar of *Procecidochares blanci*: (A) habitus, anterior to left; (B) gnathocephalon, anteriolateral view, 1- rugose pads, 2- dorsal sensory organ, 3- oral ridge, 4- stomal sense organ, 5- mouthhook, 6- median oral lobe, (C) 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- pit sensory organ, 7- oral ridge, 8- stomal sense organ, 9- mouthhook, 10- median oral lobe; (D) ventral view of mouthhook with four teeth; 1- small inner tooth; (E) anterior thoracic spiracle; (F) posterior spiracular plate, 1- rima, 2- interspiracular process.

6B-3, C-7) went unmentioned and uncounted in second instars of *P. anthracina*, *P. kristineae*, *P. lisae* (Goeden and Teerink 1997a, b) and *P. stonei* (Green et al. 1993). Only in *P. anthracina* (Goeden and Teerink 1997b) could the distinct separation of the stomal sense organ from adjacent oral ridges in *P. blanci* (Figs. 6B-4, C-8) also be seen from published illustrations compared to those other congeners. The discovery of a mouthhook with four teeth in the second instar of *P. blanci* (Fig. 6D) is especially noteworthy, not only as the sole example of this many teeth in this instar, but also of any instar of other tephritids examined by RDG and coworkers to date. Because of the usually hidden, central, ventral location of this small fourth tooth, it posits the question of whether such a tooth or teeth may have been overlooked in other larvae. The view in Figure 6D is not usually obtained with specimens prepared for scanning electron microscopy, because much of the gnathocephalon all-too-often is withdrawn inside the prothorax.

Third instar larva.—Pale yellow or white, elongate-ellipsoidal, tapering anteriorly, truncated posteriorly, distinctly segmented (Fig. 7A), rugose pads circumscribe anterior halves of pro-, meso- and metathorax (Fig. 7B-1), but not abdominal segments, which are finely, smoothly wrinkled; gnathocephalon conical, flattened dorsally and anteriorly (Fig. 7B-2); dorsal sensory organ well-defined, flattened (Fig. 7C-1); anterior sensory lobe (Fig. 7C-2) bears terminal sensory organ (Fig. 7C-3), lateral sensory organ (Fig. 7C-4), supralateral sensory organ (Fig. 7C-5), and pit sensory organ (Fig. 7C-6); two oral ridges (Fig. 7C-7) laterad and ventrolaterad of anterior sensory lobe, entire, and separated from stomal sense organ (Fig. 7C-8) ventrad of anterior sensory lobe; mouthhook (Fig. 7B-3) tridentate (Fig. 7D-1); median oral lobe, thickened basally, smoothly rounded apically (Fig. 7D-2); anterior thoracic spiracle recessed on posterior margin of prothorax with two, flattened “papillae” (Fig. 7E);

lateral spiracular complexes not seen; each posterior spiracular plate (Fig. 7F) bears three ovoid rimae, ca. 0.022 mm in length (Fig. 7F-1), and four, unbranched, single or paired spiniform interspiracular processes, each 0.007 mm long (Fig. 7F-2); stelex sensilla dorsolaterad and ventrolaterad of spiracular plate, a verruciform sensillum lateral of spiracular plate.

Although the general appearances of the third instars of *Procecidochares* spp. are similar, the habitus of the third instar of *P. blanci* (Fig. 7A) most closely approximates that of *P. flavipes* (Goeden et al. 1994) among the six species studied in California to date (Green et al. 1993, Goeden and Teerink 1997a, b). The gnathocephala of *P. blanci* and *P. flavipes* are flattened dorsally and anteriorly (Fig. 7B-2), whereas those of the others are more or less conical. Both species have rugose pads on the thoracic segments; however, these fully circumscribe the anterior half of these segments in *P. blanci* (Fig. 7B), but circumscribe the prothorax only and cover the lateral and ventral surfaces of the meso- and metathorax in *P. flavipes* Aldrich (Goeden et al. 1994). The dorsum and intersegmental membranes of the abdomen of *P. flavipes* bear clawlike minute acanthae, absent in *P. anthracina*, *P. blanci*, *P. kristineae*, *P. lisae* (Goeden and Teerink 1997a, b) and *P. stonei* (Green et al. 1993). *Procecidochares anthracina* (Goeden and Teerink 1997b) has rugose pads anteriorly circumscribing its prothorax only.

The dorsal sensory organ is prominent in the third instar of all six species of *Procecidochares* that we have studied; however in *P. flavipes*, this organ is verruciform (Goeden et al. 1994), protruding and dome-shaped in *P. stonei* (Green et al. 1993), *P. anthracina* (Goeden and Teerink 1997b), *P. lisae*, and *P. kristineae* (Goeden and Teerink 1997a), but is flattened in *P. blanci* (Fig. 7C-1). Two oral ridges (rugose pads) are present in the third instar of *P. blanci* (Fig. 7C-7), one more than in the second instar (Figs. 7B-3, C-7). However, as no

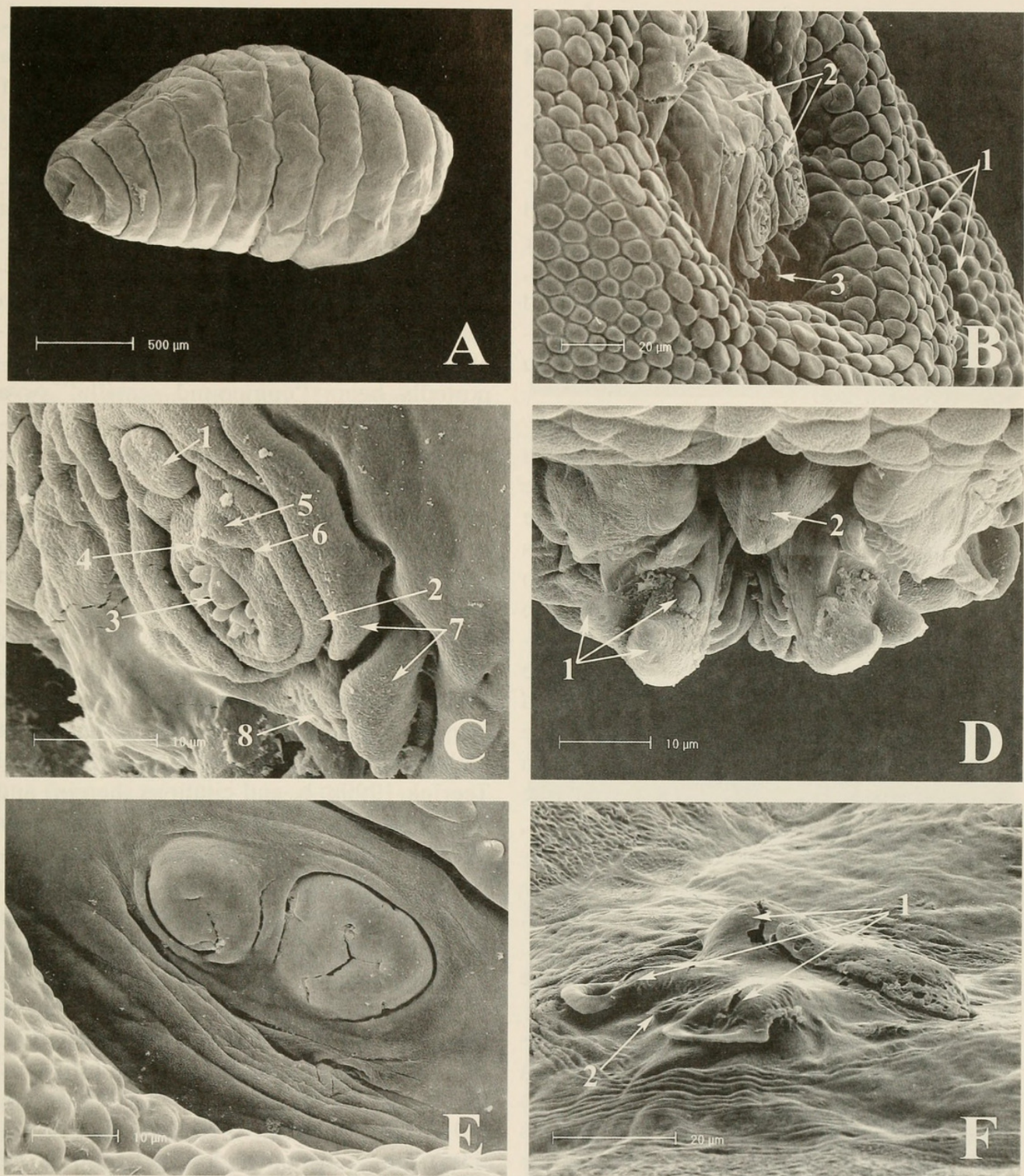


Fig. 7. Third instar of *Procecidochares blanci*: (A) habitus, anterior to left; (B) gnathocephalon, anteriolateral view, 1- rugose pads, 2- gnathocephalon, 3- mouth hook; (C) gnathocephalon, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- pit sensory organ, 7- oral ridges, 8- stomal sense organ; (D) oral cavity, ventral view, 1- three teeth of mouthhook, 2- median oral lobe; (E) anterior thoracic spiracle; (F) posterior spiracular plate; 1- three rimae, 2- interspiracular process.

oral ridges were reported as present in third instars of *P. stonei* (Green et al. 1993), *P. flavipes* (Goeden et al. 1994), *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a),

the following comparisons are now made. The third instar gnathocephalon of *P. flavipes* pictured in Goeden et al. (1994) shows at least six oral ridges laterad of the

anterior sensory lobe, one such oral ridge in *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a), at least two are seen in *P. anthracina* (Goeden and Teerink 1997b), but none are discernable in *P. stonei* (Green et al. 1993). The lateral margins of the rugose pads of *P. anthracina* (Goeden and Teerink 1997b) approach being serrate, or are at least, uniquely strigosely margined. The number, arrangement, and serrated margins of these oral ridges are prime taxonomic characters for larvae of *Neaspilota* spp. (Goeden 2001).

The progression of teeth on each mouthhook of *P. blanci* from two teeth in the first instar (Figs. 5B-5, C-7), to four teeth in the second instar (Fig. 6D), to three teeth in the third instar (Fig. 7D-1) is noteworthy, as usually this progression is from fewer to greater numbers of teeth among the larvae of Tephritinae that we have studied. Accordingly, and more conventionally, the number of oral ridges in *P. blanci* increased from none in the first instar, to one in the second instar (Figs. 6B-3, C-7), to two in the third instar (Fig. 7C-7). However, like the number of teeth on the mouthhook, starting with the usual lack of anterior spiracles in the first instar, the number of papillae is three in the second instar (Fig. 6E), but decreases to two in the third instar (Fig. 7E), the number of papillae also helps one to distinguish these instars in *P. blanci*.

The recessed location and flattened nature of the anterior spiracle of *P. blanci* in both the second (Fig. 6E) and third instars (Fig. 7E) apparently is unique so far to this species of *Procecidochares*; in other larvae of California Tephritinae this organ is not recessed and projects above the surrounding integument. However, this recessed condition also could be an artifact of specimen preparation for SEM.

The spiniform interspiracular processes on the posterior spiracular plate of the third instar of *P. blanci* (Fig. 7F-2) match those reported for this instar of *P. stonei* (Green et al. 1993), *P. kristineae* and *P. lisae* (Goeden and Teerink 1997a), *P. anthracina*

(Goeden and Teerink 1997b), and *P. flavipes* (Goeden et al. 1994). The stelex sensilla reported dorsolaterad and ventrolaterad of the posterior spiracular plate of *P. blanci* apparently are unique for this species compared to other congeners examined to date. Stelex sensilla surround the caudal segment of *P. flavipes* (Goeden et al. 1994) in a four-dorsal, six ventral arrangement (or two-dorsal, three-ventral arrangement relative to each posterior spiracular plate). Additionally, the caudal segment of *P. flavipes* reportedly bears "compound sensilla" or a pair of stelex sensilla ventrad of each posterior spiracular plate (Goeden et al. 1994); however, the "compound sensilla" in this position on the third instars of *P. kristineae* and *P. anthracina* consist of a verruciform sensillum and a stelex sensillum (Goeden and Teerink 1997a, b), but in *P. lisae*, two verruciform sensilla (Goeden and Teerink 1997a). These so-called compound sensilla may be homologous with the intermediate sensory complexes reported in larvae of California *Trupanea* spp. (Goeden and Teerink 1999a, b, and citations therein) and *Neaspilota* spp. (Goeden 2001 and citations therein). No additional sensilla were reported lateral or dorsal of the spiracular plates of *P. stonei*, *P. kristineae*, or *P. lisae* (Green et al. 1993, Goeden and Teerink 1997a).

Puparium.—Ellipsoidal, mostly translucent white, with elliptical or ovoidal (Fig. 8A), irregularly margined, dark brown to black spot ($n = 14$), 1.11 ± 0.07 (range, 1.0–1.25) mm long, $0.70 \pm$ (range, 0.55–0.95) mm wide on abdominal tergites A3 or A4 to A7 (Fig. 8D); anterior half to all of mesothorax also dark brown or black in about one in ten puparia; anterior end bears the small, somewhat protuberent, invagination scar (Fig. 8B-1), anterior thoracic spiracles not discernable; caudal segment bears posterior spiracular plates, each with three broadly elliptical, raised rimae (Fig. 8C-1), and four, single or paired, spiniform, interspiracular processes (Fig. 8C-2). Ninety-three puparia averaged 2.56 ± 0.03

(range, 1.78–3.42) mm in length; 1.34 ± 0.02 (range, 0.91–2.00) mm in width.

DISTRIBUTION AND HOSTS

Procecidochares blanci is a true monophage, with *Isocoma acradenia* as its only known host plant. The distribution of *P. blanci* may coincide wholly or in part with that of its host plant, which as a desert subshrub inhabits sandy or clay soils in alkaline or gypsum flats or slopes below 1,300 m in California, Arizona, and Nevada, and Baja California, Mexico (Hickman 1993). Dodson and George (1986) demonstrated convincingly that the gall-forming tephritids, *Aciurina bigeloviae* (Cockerell) and *A. trixa* Curran, are less widely distributed than their host plants within four southwestern States.

BIOLOGY

Procecidochares blanci is a bivoltine species in southern California in which a flower-head-infesting (F_1) generation alternates with a gall-forming generation (F_2) on the same host plant. Accordingly, the biology of each generation differs considerably and is treated separately as follows.

Florivorous (F_1) generation.—*Egg*: In each of 17, closed, preblossom, immature flower heads of *Isocoma acradenia* an average of 5.5 ± 1.0 (range, 1–15) eggs of *P. blanci* were inserted separately, or more commonly side-by-side, in groups of three or more, pedicel-last, between the phyllaries (Fig. 9A). All 93 eggs rested with their long axes parallel to the long axes of the flower heads (Fig. 4A). Only one egg (1%) penetrated an outer ovule adjacent to an inner phyllary; otherwise, no other ovules were damaged by oviposition. The receptacles of these preblossom heads that contained eggs averaged 0.79 ± 0.05 (range, 0.28–1.14) mm in diameter.

Larva: Upon eclosion, the 88 first instars found in 32, closed, preblossom flower heads moved to an ovule (Fig. 9B) or between two adjacent ovules on which they fed from an external position (Fig. 9B).

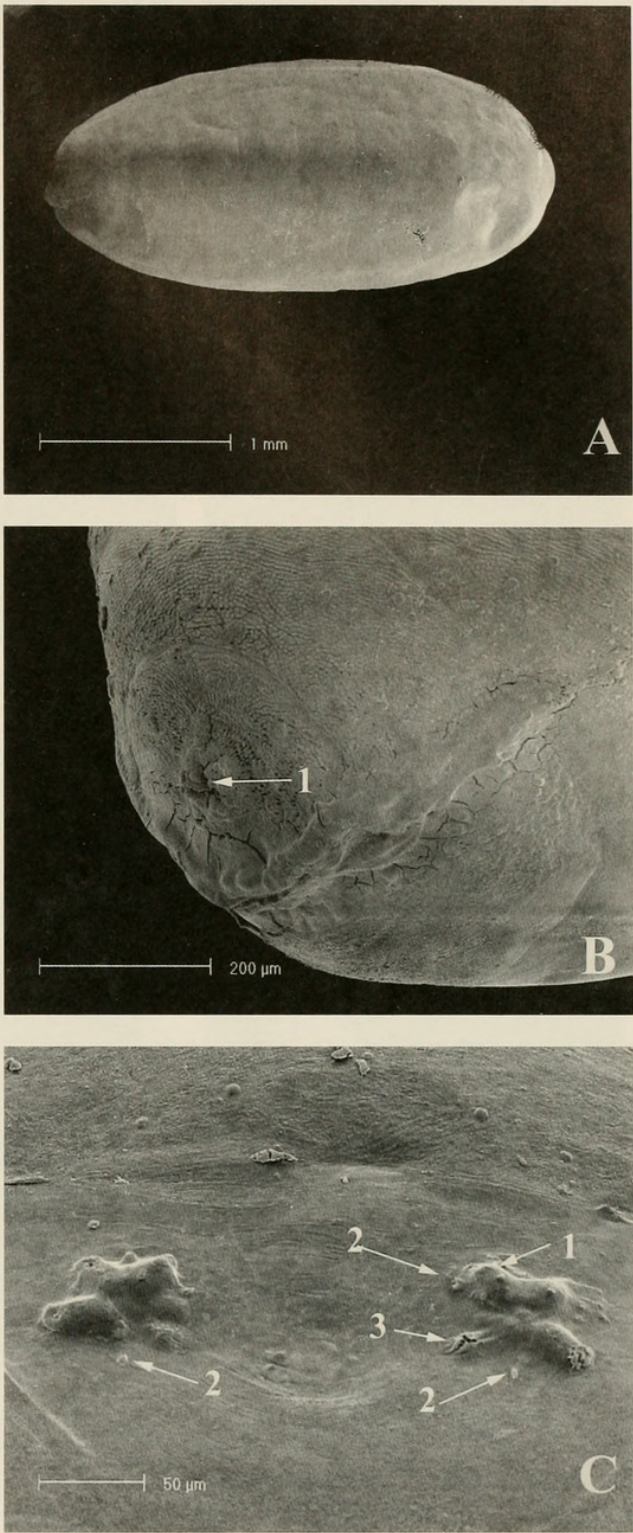


Fig. 8. Puparium of *Procecidochares blanci*: (A) habitus, anterior to left; (B) anterior end, 1- invagination scar; (C) caudal segment, 1- rima, 2- interspiracular process, 3- ecdysial scar.

Thus, an average of 2.75 ± 0.3 (range, 1–8) first instars were found in these 32 heads. Usually the attacked ovules were located on the periphery of a head (Fig. 9B), and each larva fed independently of the other larvae

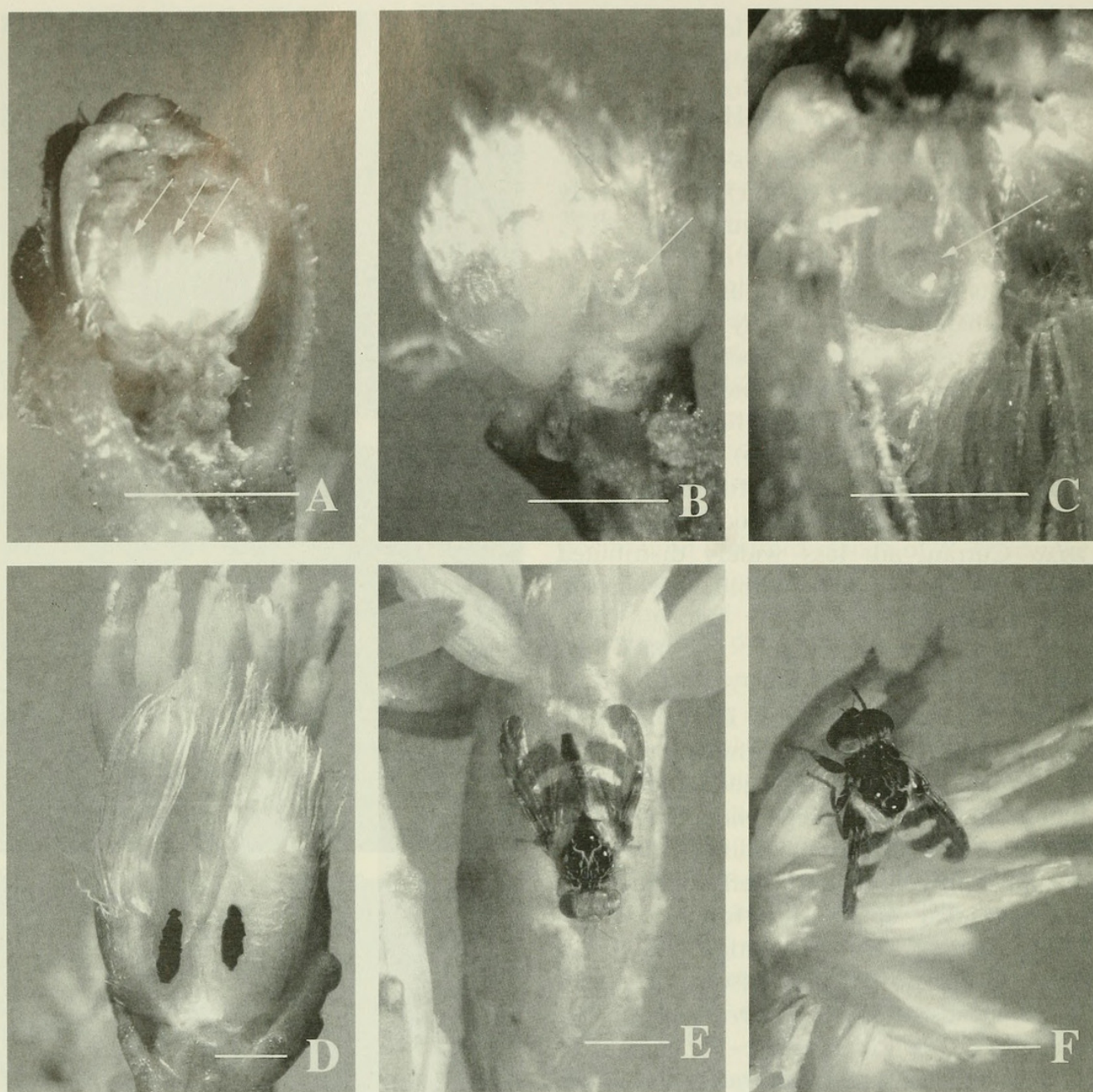


Fig. 9. Life stages of the F_1 florivorous generation of *Procecidochares blanci* in *Isocoma acradenia*: (A) three eggs (arrows) in closed, preblossom flower head; (B) first instar (arrow) feeding on ovule; (C) second instar (arrow) feeding in cell in expanded ovule; (D) two puparia (note black spots on dorsa) in cells formed from expanded achenes; (E) female fly on open flower head; (F) male fly on open flower head. Lines = 1 mm.

in a flower head, although the same ovule sometimes was attacked from opposite sides by different larvae. The receptacles averaged 1.02 ± 0.03 (range, 0.85–1.42) mm in diameter and an average of 3.2 ± 0.4 (range, 1–7) ovules were attacked in these 32 flower heads, or about 21% of an average total of 15 ± 0.3 (range, 7–21) ovules/achenes counted in 99 preblossom

and blossom flower heads. No receptacle was abraded or pitted by larval feeding.

Second instars (Fig. 9C) continued feeding on the ovules in preblossom flower heads which remained closed. They fed with their bodies \pm perpendicular to, but always well above the receptacles, scraping away with their mouthhooks from a position between adjacent sides of two, or

sometimes three ovules, which began to enlarge, the excavation forming a cell within which each larva developed separately (Fig. 9C). Receptacles of eight flower heads containing 12 second instars averaged 1.21 ± 0.04 (range, 1.14–1.42) mm in diameter. Thus, these flower heads each contained an average of 1.5 ± 0.5 (range, 1–5) larvae that had collectively damaged an average of 3 ± 1 (range, 2–10) ovules, or about 20% (range, 13–66%) of the average total of 15 ovules per flower head.

Third instars continued to feed mainly on the expanded ovules in preblossom and blossom flower heads. Twenty-five flower heads that averaged 1.5 ± 0.03 (range, 1.4–1.99) mm in diameter each contained an average of 1.8 ± 1.1 (range, 1–5) third instars. An average of 3.4 ± 4.2 (range, 1–8) of the soft achenes therein were expanded and damaged, or about 23% (range, 7–53%) of the average total of 15 ovules/soft achenes per flower head. Third instars in flower heads fed within their individual cells formed from two or three excavated, enlarged ovules (Fig. 9D). No receptacles were abraded or pitted. Upon completing their feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 9D).

Pupa: The receptacles of 45 overwintered flower heads that contained 95 puparia, or an average of 2.1 ± 0.2 (range, 1–6) puparia per head, each averaged 1.7 ± 0.05 (range, 1.28–2.85) mm in diameter (Fig. 9D). An average of 4.3 ± 0.4 (range, 2–12) soft achenes therein had expanded and were damaged, or about 29% (range, 13–80%) of the average total of 15 ovules/soft achenes per flower head.

Adult: Adults (Figs. 9E, F) are short-lived. Under insectary conditions, 31 unmated males lived an average of 6.6 ± 0.7 (range, 3–19) days, and 36 virgin females averaged 5.1 ± 0.4 (range, 3–15) days. The flies mate shortly after their emergence from flower heads (Fig. 7F) and soon thereafter begin oviposition; description of mat-

ing behavior is deferred until after the biology of the immature stages of the gall-forming (F_2) generation is described next.

Gallicolous (F_2) generation.—Egg: In each of 18 axillary buds on basal, woody, previous year's branches of *Isocoma acradenia* an average of 2.3 ± 0.3 (range, 1–6) eggs of *P. blanci* were inserted separately, or more commonly, side-by-side, in pairs or groups of three, pedicel-last, usually between the leaves at the base of the bud (Fig. 10A). Most eggs were found in axillary buds on basal branches an average of 10.5 ± 1.3 (range, 0–21) cm above the branch juncture with a stem. All 41 eggs rested with their long axes parallel to the long axes of the axillary bud (Fig. 10A). Three and one (10% of total) eggs were inserted into the centers of two separate buds, but none of the 41 eggs penetrated any plant tissue, thus no buds were damaged by oviposition. The diameters of these buds bearing eggs averaged 1.06 ± 0.08 (range, 0.56–1.54) mm.

Monthly samplings of branch segments at the Whitewater location showed that the embryos remained within the egg chorions for as long as 2 months, eclosion apparently occurring along with the onset of axillary bud growth triggered by winter rainfall. From one to four first instars were found in eight infested buds out of hundreds of buds sampled at random during the first three months following oviposition, as nothing distinguished axillary buds bearing eggs or newly eclosed larvae. The newly eclosed first instars moved to the base of the bud where they entered the central pith below the apical meristem and began to excavate a single open chamber in which they fed singly or gregariously (Fig. 10B). Furthermore, the larvae remained as first instars during subsequent months as the galls slowly developed and grew to full size (Fig. 10C). Each gall represented a foreshortened axillary branch circumscribed by up to 20 ranks of scale-like, lanceolate, entire-margined leaves demarking stunted internodes. Eventually, the gall-bearing branches elon-

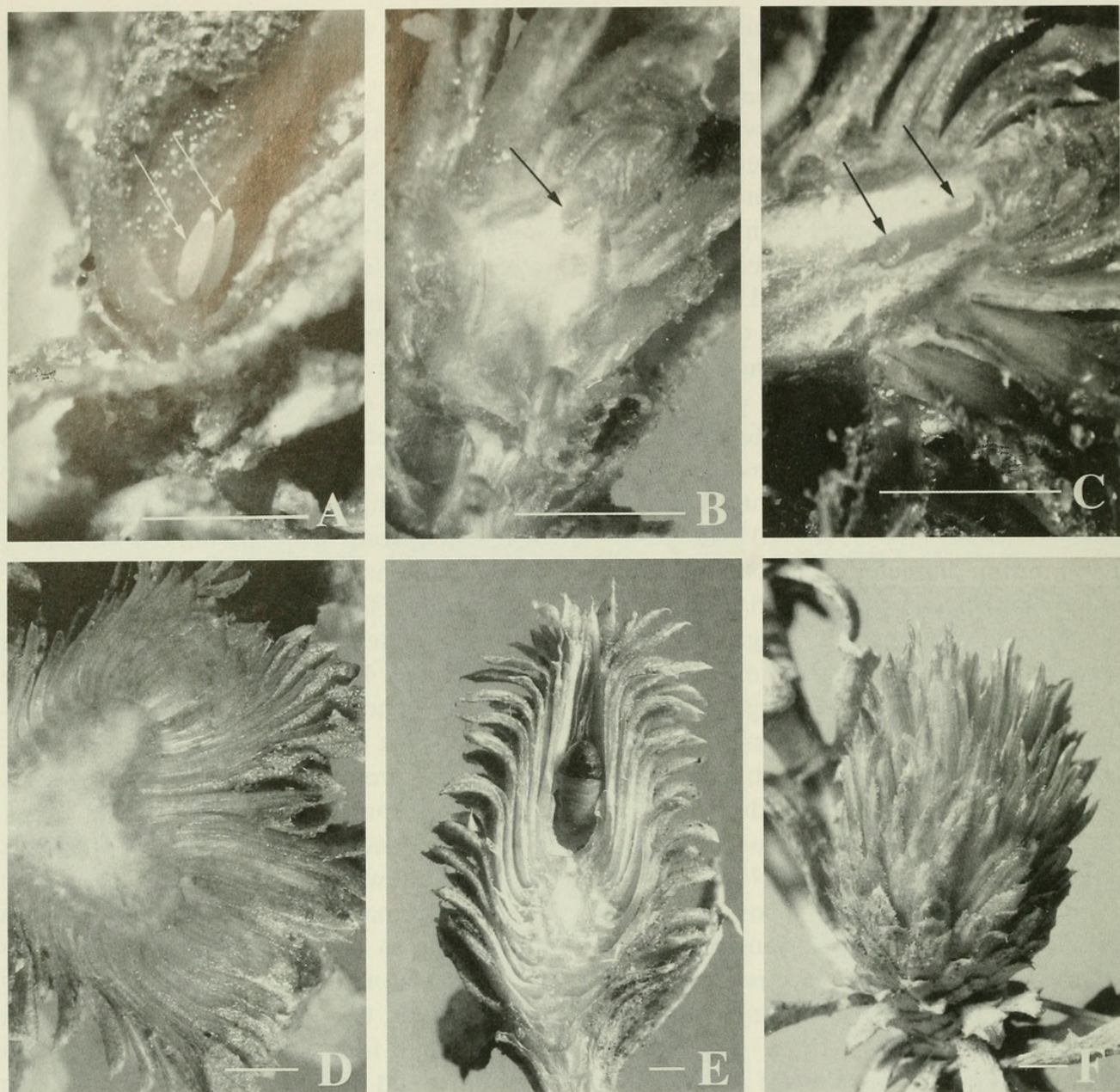


Fig. 10. Life stages of the F_2 gallicolous generation of *Procecidochares blanci* in *Isocoma acradenia*: (A) two eggs (arrows) in axillary bud; (B) first instar (arrow) feeding in cell in pith beneath apical meristem of expanding axillary bud in saggital section; (C) first instar (arrow) continuing to feed in cell in pith of stunted axillary branch comprising gall; (D) saggital section through gall showing two branches formed as two first instars in gall separated; (E) empty puparium in open, mature gall, (F) intact mature gall. Lines = 1 mm.

gated noticeably more slowly than unfested axillary branches and thus were detected and sampled much more readily. The first instars fed in open, linear cells in the center of the expanded pith of the galled branches (Figs. 10B, C). However, at some indeterminate point from 2 to 10 mm above the gall base, multiple larvae within single galls separated and split off from their common chamber and began individual branch

tunnels (Fig. 10D). These first instars continued to extend their separate tunnels, feeding just below the apical buds topping each gall branch (Fig. 10D). As the gall grew apically, the parenchyma lining the gall cavity grew together basally sealing the tunnel behind each apically feeding larva (Fig. 10E). The basal leaves died and desiccated while the upper leaves remained green, and as these dead leaves abscised,

and the galls added growth apically, each gall became seated on a stalk of varying length. Gall growth ceased when the larva, still in the first instar, consumed the gall meristem and nipped off the terminal leaf-bracts at their bases, forming a bundle that plugged the future exit tunnel of the gall. The larva then molted to the second instar and rapidly passed through the second and third stadia as it expanded the gall chamber to accommodate its larger size, leaving no frass, only the discarded cephalopharyngeal skeleton of the second instar at the bottom of this cell. The second and third stadia plus pupariation and the pupal period ending in adult emergence altogether lasted about 1 month. The adult emerged from the puparium by pushing outward the aforementioned plug of basally-excised terminal bracts and exiting through the exit tunnel so formed (Fig. 10E). Mature galls ranged in shape from ovoidal to cylindrical to flattened-obovoid (Fig. 10F). Galls from which adults emerged were denoted by browned apices, with the entire gall subsequently dying and turning from blue- to yellow-green to brown. Twenty-six mature galls contained an average of 1.5 ± 0.1 (range, 1–3) puparia. They were borne on pedicels that averaged 5.8 ± 0.9 (range, 3–18) mm in length, and measured 12.6 ± 0.4 (range, 8–15) mm long by 9.1 ± 0.4 (range, 6–13) mm wide. Thus, the stunted axillary branches comprising these galls, including pedicels, averaged 18 ± 0.6 (range, 15–22) mm in length.

Mating behavior.—The premating, mating, and postmating behaviors of *P. blanci* were not studied in the field, but were observed in petri dish arenas of the type found to be so useful with many other nonfrugivorous, tephritid species (Headrick and Goeden 1994). In these arenas, adults exhibited behavior typical of other circumnata, gallicolous species of *Procecidochares* studied in southern California, i.e., a lack of courtship behavior, the exhibition of enantion type of wing movements by both sexes, and male stalking of females prior to

mating (Green et al. 1993, Headrick and Goeden 1994). Moreover, both sexes displayed wing supination blending into rapid wing enantion during copulation if agitated, especially the females, just prior to post-copulatory separation.

Mating behavior of *P. blanci* was similar to that reported for *P. kristineae* by Silverman and Goeden (1980) and Goeden and Teerink (1997a). Males tracked females slowly from behind and mounted females by jumping onto their dorsa, either headfirst or from behind. Once mounted, males clasped the dorsolateral anterior margins of the dorsum of the females with their fore-tarsal claws; the middle tarsi grasped the base of the oviscap laterally, and the hind-tarsi were crossed under the oviscap (Fig. 11C). The wings of the female were parted at 80 to 90° (Figs. 11A–B), those of the male at 30 to 40° (Figs. 9A–B), with both pairs of wings more or less centered over the midlines of both flies. The mouthparts of the male were held above the scutellum of the female. The oviscap of the female was elevated about 30° above the horizontal, with the rest of her body more or less parallel to the substrate (Fig. 11C); the body of the males was angled upward 30° (Fig. 11C). The male generally maintained no contact with the substrate during copulation (Fig. 11C).

Eleven copulations (Figs. 11A–C) averaged 94 ± 13 (range, 19–158) minutes in duration and usually occurred after midday, when the flies were most active in bright sunlight. Males mounted females perfunctorily and aggressively initiated copulation, sometimes wrestling the females into submission on the substrate. This strong male sex drive was also demonstrated by one male persistently attempting coitus with a dead female and commonly by males wedging themselves between a copulating pair (Fig. 11D) or attempting to mate by climbing onto a male already in copula. This latter behavior often caused the male to extend the time the pair remained in copula and to remain atop the female after copulation and

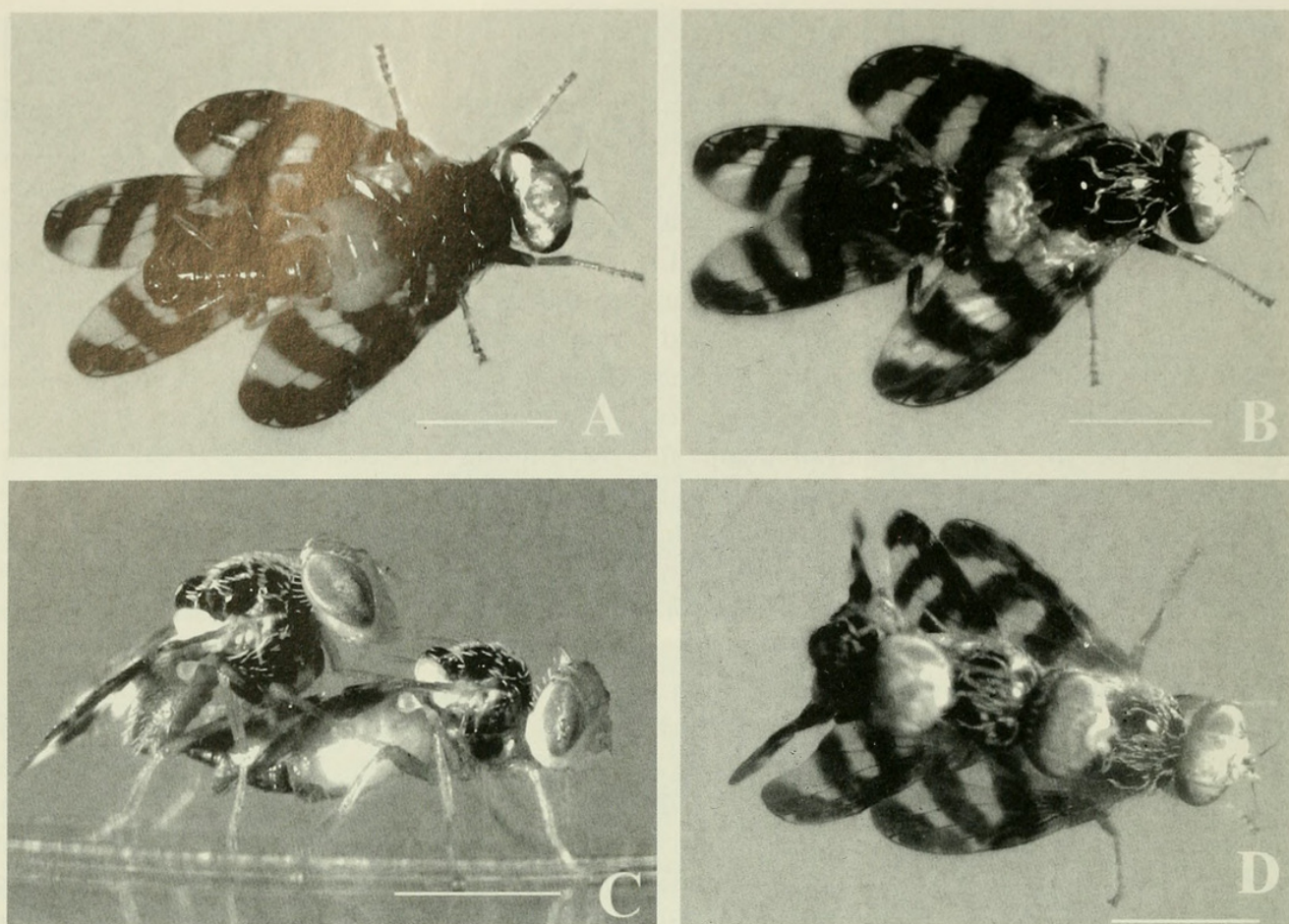


Fig. 11. Mating pairs of *Procecidochares blanci*: (A) ventral view; (B) dorsal view; (C) lateral view; (D) second male has inserted itself between mating pair (see text). Lines = 1 mm.

reattempt, and sometimes successfully resume, copulation. Four instances of post-copulatory separation were noted in which the male rapidly dismounted from the female posteriorly and continued walking as his phallus was pulled free; three such uncouplings lasted less than 10 seconds, and the fourth 12 seconds.

Seasonal history.—*Procecidochares blanci* is a bivoltine, circumnatal species (Headrick and Goeden 1994, 1998) on *Isocoma acradenia* in southern California. Reproduction by the florivorous F_1 generation parallels flower head development by its host plant. Eggs are laid in flower heads in late summer (September) and the larval and pupal stages are completed by early fall (November), when the F_1 adults emerge, mate and oviposit in axils of axillary buds on last year's branches. As noted above, these eggs remain unhatched with the slow-

ly developing embryos inside until January when larval eclosion and gall initiation coincide with axillary bud growth stimulated by the resumption of winter rainfall. The gallicolous, F_2 generation larvae remain as first instars throughout the remainder of the winter, the spring, and summer, as the galls slowly reach their full size about August. Then, within a month, the F_2 generation rapidly passes through the second and third stadia, pupariates, and the adults emerge from galls to repeat the reproductive cycle.

Natural enemies.—Many individual *Mesopolobus* sp. (Hymenoptera: Pteromalidae), *Eurytoma veronia* Bugbee (Hymenoptera: Eurytomidae), and *E. sp. nr. tumoris* were reared from puparia of *P. blanci* as solitary, larval-pupal endoparasitoids.

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