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HETEROGONY IN *BELONOCNEMA TREATAE* MAYR (HYMENOPTERA: CYNIPIDAE)

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Abstract.—Through experimental rearing we demonstrated that heterogony (the alternation of unisexual and bisexual generations) occurs in the cynipid species *Belonocnema treatae* Mayr 1881. Female *B. treatae* (bisexual generation) induce galls on the leaves of *Quercus fusiformis* Small (Fagaceae), from which unisexual females, previously described as *B. kinseyi* Weld 1921, emerge. Unisexual females induce galls on the roots of *Q. fusiformis.* The name *B. treatae* has priority, so *B. kinseyi* becomes a **new synonym.** The adults of each generation and the galls induced by females of each generation are described. Timing events in the life cycle of both generations are documented as well as hymenopterans associated with both gall types.

Key Words: Heterogony, cynipid gall wasps, *Quercus fusiformis,* parasitoids, synonymy

Phytophagous members of the family Cynipidae induce a spectacular diversity of plant galls that are often complex in structure. Worldwide, approximately 2,000 species of Cynipidae have been described, with 805 occurring in North America (Dreger-Jauffret and Shorthouse 1992). Typically, individual cynipid species induce galls on a single species of host plant or on a series of closely related plant species. In the case of phytophagous cynipids that induce galls on oaks, all host species are typically in the same subgenus. Knowledge of the biology, life cycle, and life history of known cynipid species is largely fragmentary, and there remain many undescribed species (Askew 1984, Meyer 1987, Dreger-Jauffret and Shorthouse 1992).

Cynipid wasps can exhibit an alternation of generations known as heterogony in which an all-female generation alternates with a bisexual generation (Lyon 1963, 1964, Felt 1965, Askew 1984, Rey 1992). The unisexual generation produces eggs parthenogenetically, and those eggs are usually inserted into a specific plant part. At the site of oviposition galls are induced within which a bisexual generation develops and later emerges. Emergent males and females mate, and females in turn initiate galls from which the unisexual generation emerges. Females of the two generations may be morphologically dissimilar and may induce galls that differ greatly morphologically whether oviposition occurs in the same or different plant organs (Felt 1965, Lyon 1969, 1970, Meyer 1987, Rey 1992). Differences in the morphology of both female wasps and galls between generations, coupled with incomplete knowledge of life cycles, has led to considerable taxonomic confusion within the Cynipidae. Alternating generations of numerous species have been described as separate species or even genera

(Dreger-Jauffret and Shorthouse 1992, Rohfritsch 1992).

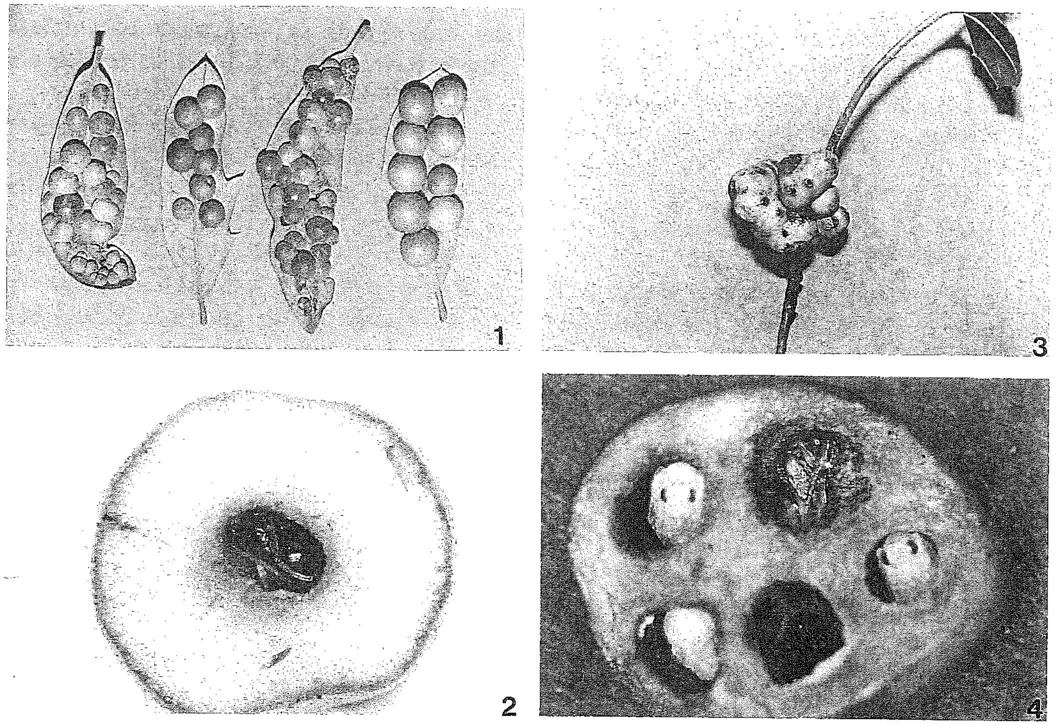
Here we demonstrate that two cynipid species, *Belonocnema treatae* Mayr 1881 and *B. kinseyi* Weld 1921, that are generally similar in morphology but produce morphologically dissimilar galls on their host plant, plateau live oak, *Quercus fusiformis* Small (formerly *Q. virginiana* var. *fusiformis*) represent alternate generations of a single species. This is the first demonstration of heterogony in North American Cynipidae outside the Pacific Slope region (Lyon 1996). The species name *B. treatae* has priority, thus *B. kinseyi* becomes a synonym, as is *Dryorhizoxenus floridanus* Ashmead 1881 (Ashmead 1886). We also provide a description of the life cycle of the species, a description of the galls induced by unisexual and bisexual females, and a list of the inquilines, parasitoids, and hyperparasitoids associated with galls produced by both generations. The observations and timing of events reported herein describe populations of *B. treatae* from Southwest Texas State University's Freeman Ranch located in Hays County, Texas. The experiments reported herein were conducted using wasps and plants from this same location.

Establishing Synonymy

Mayr (1881) described *B. treatae,* and Weld described *B. kinseyi* in 1921. Weld (1921) speculated that *B. kinseyi* and *B. treatae* could be alternate generations of a single species, but this relationship has only now been demonstrated. *Belonocnema kinseyi* emerges from pea-shaped galls on the leaves of *Quercus fusiformis* from mid-October through early November. No males have been described for this species. *Belonocnema treatae,* described from both male and female specimens, has been obtained from root galls on *Q. fusiformis* from mid-March through early April in both 1996 and 1997.

To link *B. treatae* emerging from root galls with the leaf galls from which *B. kinseyi* emerge, we performed a caging experiment in the field. Observations made in the spring of 1995 and 1996 showed that leaf galls on *Q. fusiformis* developed from oviposition events that occurred during and shortly after bud break. In the spring of 1997, prior to bud break and prior to emergence of *B. treatae,* exclusion cages constructed of fine-mesh, polyester-fiber cloth were placed over eight branches of a *Q. fusiformis* tree that had exhibited a high density of *B. kinseyi* leaf galls during the 1996 growing season. Four additional bags were placed over branches of a second tree that exhibited a moderate density of leaf galls in 1996. Clusters of root galls were then collected from rootlets underneath both trees, returned to the laboratory, and placed in collection traps. Emergent wasps were provided with nectar sources and allowed to mate for 2 days. From 4 to 15 female wasps were then introduced into each of 5 cages on tree # 1, and into each of 2 cages on tree # 2. Five cages (tree #1, $n = 3$; tree #2, $n = 2$) remained sealed as controls. Three months later all bagged branches were harvested and leaves were scored for the presence and number of oviposition scars and developing galls. In total, 2,378 oviposition scars and 207 developing *B. kinseyi* leaf galls were present among 1,356 leaves in cages in which *B. treatae* was introduced. No leaf galls were initiated in the 5 control cages. Thus, on plateau live oak, leaf galls that develop to produce the unisexual generation (i.e., *B. kinseyi*) are initiated by females of the bisexual generation (i.e., *B. treatae*) that emerge from root galls, confirming the synonymy of the two species.

In the laboratory we tested the oviposition preference of *B. treatae* reared from root galls of *Q. fusiformis* using both individual mated females and groups of mated females. Eight mated female *B. treatae* were placed separately in (3.2 × 9.6 cm) vials and presented with one shoot of *Q. fusiformis* and a second shoot from *Q. shumardii* Buckl. (southern red oak) for 24 hours. Four females oviposited exclusively



Figs. 1–4. Galls induced by *Belonocnema treatae.* 1, Unilocular leaf gall induced by bisexual generation (×1). 2, Sectioned leaf gall showing pre-emergent adult of the unisexual generation (×16). 3, Multilocular root gall induced by unisexual generation (×1). 4, Multilocular root gall, bisexual generation pupae exposed by cross section (×10).

on *Q. fusiformis* and four failed to oviposit. Three group cages, each containing 15 male and 15 female *B. treatae,* were established and wasps were provided with one shoot each of *Q. fusiformis, Q. shumardii,* and *Q. macrocarpa* Michx. (bur oak). Leaves were scored for oviposition scars after 3 and then 4.5 hours. In all cages, oviposition scars were evident on *Q. fusiformis* after 3 hours, whereas no oviposition scars were visible on *Q. shumardii* or *Q. macrocarpa* at 4.5 hours. A clear preference for oviposition on *Q. fusiformis* was demonstrated by both individual and groups of *B. treatae* females.

Description of Galls

Leaf galls.—Leaf galls produced by the bisexual generation develop following oviposition on buds and on newly unfurled leaves. Galls develop exclusively on the undersurface of leaves and are unilocular, smooth, and pea shaped. At maturity galls are lignified and range from 3 to 7 mm in diameter (Figs. 1, 2). Unisexual females emerged from lignified galls from mid-October through early November in both 1996 and 1997. No males have been recorded from the 115 wasps that have emerged from leaf galls in the laboratory.

Root galls.—Root galls induced by unisexual females grow in irregularly shaped, multilocular clusters on small rootlets just below the soil surface (Figs. 3, 4). Clusters appear fleshy and yellow and detach easily from the root surface. Sampled galls were composed of from 1 to 28 chambers and measured 5 to 28 mm in length. Developing root galls have been found in early January and at this stage appear yellow-green in color. Mature galls (those from which the bisexual generation has emerged in the laboratory) have been collected in mid-February. In the field, emergence holes in root galls were first observed in mid-March 1997, coincident with the appearance of oviposition scars on leaves of the host plant.

Host Plants

Weld (1921) gave *Quercus virginiana* Miller (Fagaceae) as the host plant for both *B. kinseyi* and *B. treatae* (unisexual and bisexual generations of *B. treatae* respectively). However, *Q. virginiana* has since been split into two species (Muller 1961). *Quercus fusiformis,* (formerly a variety of *Q. virginiana*) is common throughout the Edwards Plateau region of south-central Texas, while *Q. virginiana* (coastal live oak) is distributed from the Atlantic seaboard of the southeastern United States west to eastern Texas. *Quercus virginiana* reaches its western limit in coastal Texas east of the Brazos River (Nixon 1984). In the broad region bounded by the Brazos River and the Edwards Plateau, extensive hybridization between the two parent species has occurred (Nixon 1984). The type locality for *B. treatae* is given as Green Cove, Florida (Mayr 1881), whereas the type locality for *B. kinseyi* is given as Boerne, Texas (Weld 1921). We note that the type locality of *B. kinseyi* (Boerne, Texas) is located within the geographic range of *Q. fusiformis* well to the west of the recognized range of *Q. virginiana.* Thus the host plant species recorded by Weld for *B. kinseyi* should be amended to *Q. fusiformis. Belonocnema kinseyi* is not known outside of the geographic range of *Q. fusiformis.*

Weld (1921) also noted the presence of leaf galls on live oaks in Houston, Wharton, Victoria, Cuero, Austin, Sabinal, and Kerrville, Texas, galls he ascribed to *B. kinseyi* on the basis of morphology. We note that these sites span the entire range of the two parental oak species and their zone of hybridization in Texas. Thus, either the host range of the unisexual generation of *B. treatae* includes both parental oak species and their hybrid, or Weld's site east of the Brazos River, that is, Houston, represents leaf galls induced by a congeneric species, *B. quercusvirens* (Osten Sacken) (Osten Sacken 1861, Burks 1979) (= *B. fossoria* Weld) which is known to induce leaf galls on *Q. virginiana.* At the present time *B. quercusvirens* is known from only Florida and Georgia (E. Grissell and George Melika, pers. comm.). We have not reared *Belonocnema* sp. from either leaf or root galls collected from pure *Q. virginiana* populations located east of the Brazos River in Texas. Thus, on the basis of the available evidence the host plant range of the bisexual generation of *B. treatae* includes, *Q. virginiana,* and *Q. fusiformis* while the host range of the unisexual generation is restricted to *Q. fusiformis.*

Associated Hymenopteran Species

Thirteen hymenopteran species belonging to 7 families have been commonly reared from mature leaf galls in addition to the gall former. *Belonocnema treatae* larvae developing within leaf galls are frequently attacked by 3 species of parasitoids: *Acaenacis lausus* (Walker) (Pteromalidae), *Ormyrus labotus* Walker (Ormyridae), and *Torymus tubicola* (Osten Sacken) (Torymidae). Four species described as being inquilines—*Synergus* sp. (Cynipidae), *Sycophila flava* (Ashmead), *Eurytoma furva* Bugbee, and *Eurytoma* sp. (Eurytomidae)—and one hyperparasitoid, *Eurytoma bugbeei* Grissell, have also been reared from leaf galls. The trophic level of 5 other species, *Allorhogas* sp., (Braconidae), *Galeopsomyia* sp., and 3 unidentified *Brasema* (Eulophidae), reared from galls is presently unknown. An additional 10 species have been reared rarely from leaf galls to date and await identification. Root galls held in collection traps in the laboratory yielded several specimens of *Torymus tubicola* (Torymidae) from mid to late April. *Torymus tubicola* is the only species that appears to parasitize larval *B. treatae* in both leaf and root galls.

Description of Adults

Belonocnema treatae Mayr
(Figs. 5–7)

Belonocnema treatae Mayr 1881. Green Cove, Florida. 2 ♀ wasps mounted on a single pin, labeled *syntypes,* Natural History Museum, Vienna.

Dryorhizoxenus floridanus Ashmead 1882 (1881). Jacksonville, Florida. Holotype ♀ #2813 and 5 paratypes, National Museum of Natural History, Smithsonian Institution, Washington, D.C., describes ♂ and galls. Ashmead 1886 acknowledges priority of *Belonocnema* over *Dryorhizoxenus* and places the latter in synonymy.

Belonocnema kinseyi Weld 1921. Holotype ♀ #22832 and 27 paratypes, National Museum of Natural History, Smithsonian Institution, Washington, D.C. Examined by Lyon in 1961. **New synonymy.**

Type data.—Lewis Weld, in 1929, examined the 2 syntype females in the Natural History Museum, Vienna. The distinctive morphology was sketched and drawings were placed in Weld's personal notes now in the possession of R. Lyon. George Melika of the Systematic Parasitoid Laboratory, Hungary, examined the types at the Natural History Museum, Vienna, on April 27, 1998. One female syntype was selected and labeled as the lectotype. The other female was mounted on a separate pin with the label paratype. There were 17 specimens sent to Mayr by Ashmead. These were labeled *D. floridanus* Det. Ashmead and are synonyms of *B. treatae.*

Bisexual Generation
(Figs. 5, 7)

Redescription (Lyon)—*Female:* Uniformly yellow brown, scutellum and propodeum dark brown, almost black; abdomen light brown (Fig. 5E). Length 3.5 to 3.75 mm ($\bar{x}$ = 3.7 mm, n = 27 Weld specimens). Head as broad as mesosoma, transverse, coriaceous, gena not broadened behind eyes, malar space (Fig. 5C) 0.33× eye length with groove; frons tumescent; interlocular area broader than high. Antenna 14 segmented, filiform, segment 3 longer than 4, terminal segment 2× as long as 13. Scutum (Fig. 5B) slightly convex but flattened, smooth, shining, as broad as long; notauli percurrent, curving laterally at anterior portion with a few, scattered, setigerous punctures along lateral margins. Scutellum almost circular, nearly two-thirds length of scutum, coarsely rugose, roughly irregular along margin; foveae deep, separated with smooth, shining bottoms. Propodeum with irregular ridges, area between rugose. Mesopleuron bulging, slightly setose on lower portions. Forewing hyaline (Fig. 5A), short ciliate, longer on lower margins, pubescent; veins dark brown, R_{s2} heavy, curving toward wing margin forming a distinct club. Darkened areas around R_{s1} and R_{s2}, radial cell short. Legs bristly; foretibia with a distinctive spur (Fig. 5D), as long as furcula; tarsal claws edentate. Metasoma (Fig. 5E) longer than high with all terga visible along dorsal curvature. Hypopygeal spine short with bristles extending beyond apex.

Male: Similar to female but slightly smaller, length 3.4 to 3.75 mm ($\bar{x}$ = 3.6 mm, n = 5) (Fig. 7). Color light brown but blackened along margins of pronotum. Antenna 15 segmented, filiform, 3rd longer than others and deeply excavated, terminal segment equal in length to 14th. Forewing pubescent, ciliated, R_{s2} curving toward wing margin, slender and only slightly enlarged at tip. Foretibial spur much shorter than in female and sometimes not elongated. Tergite 2 oval and occupying most of abdomen, remaining terga visible along dorsal curvature but short.

Unisexual Generation
(Fig. 6)

Redescription (Lyon).—*Female:* Head and metasoma red brown; mesosoma very dark, almost black. Length 2.0 to 3.1 mm ($\bar{x}$ = 2.7 mm, n = 62 Weld specimens). Head transverse (Fig. 6B), slightly broader than mesosoma, coriaceous, gena not broadened behind eyes, malar space (Fig. 6E) less than

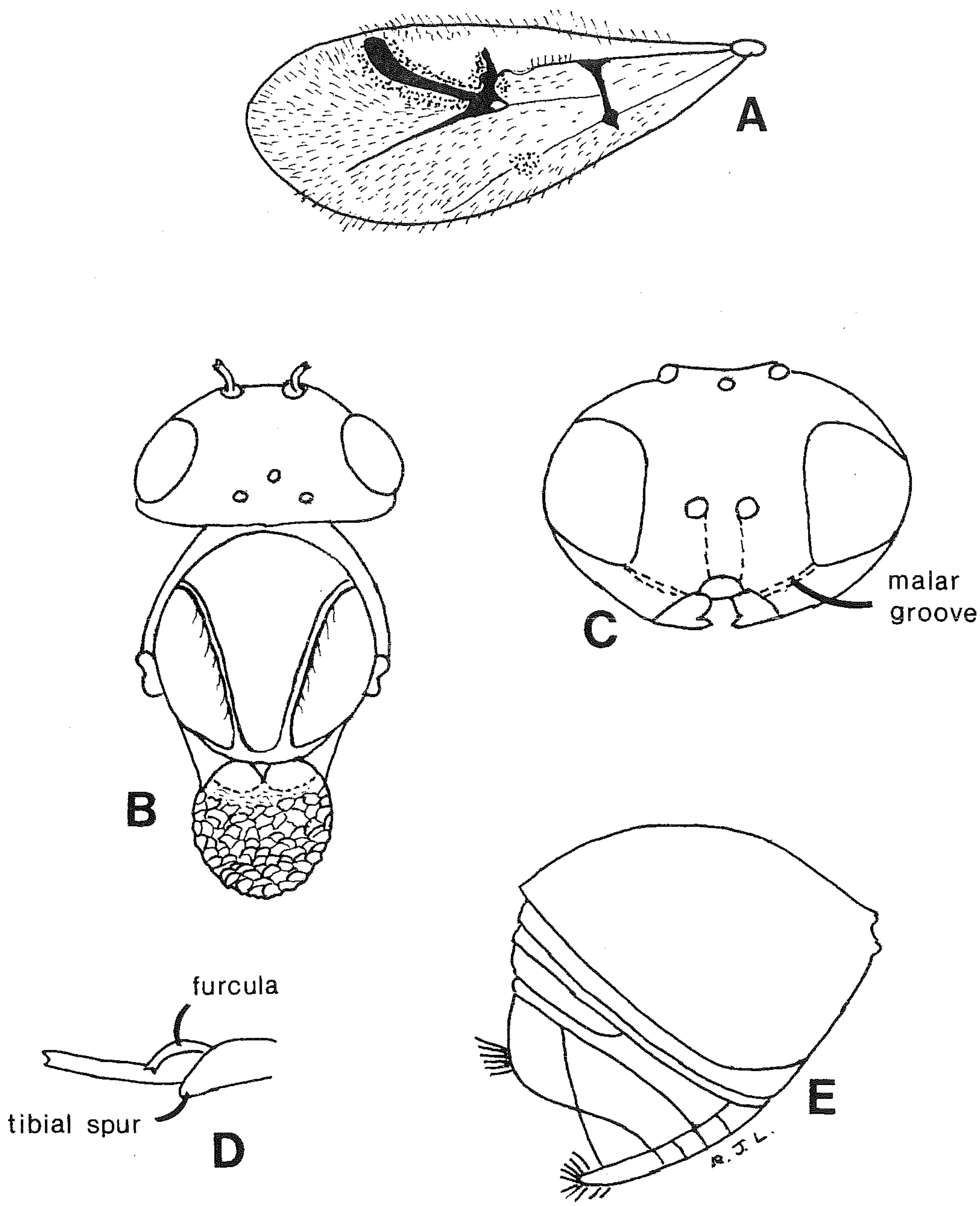


Fig. 5. *Belonocnema treatae* (bisexual female). A, Forewing venation, lateral view (×25). B, Head and mesosoma showing detailed morphology of scutum and scutellum, dorsal view (×40). C, Frontal view of head showing malar furrow (×60). D, Foretibia showing elongated, characteristic spur and furcula. E, Lateral view of metasoma showing shape of abdominal terga (×60).

half length of eye with groove; interocular space broader than high; frons tumescent. Antenna 13 segmented, 3rd nearly 2× length of 4th segment, 4–12 gradually shorter, terminal segment 2× length of preceding one. Scutum (Fig. 6B) slightly convex but flattened, smooth, bare, shining; notauli percurrent, deep, narrow, curving

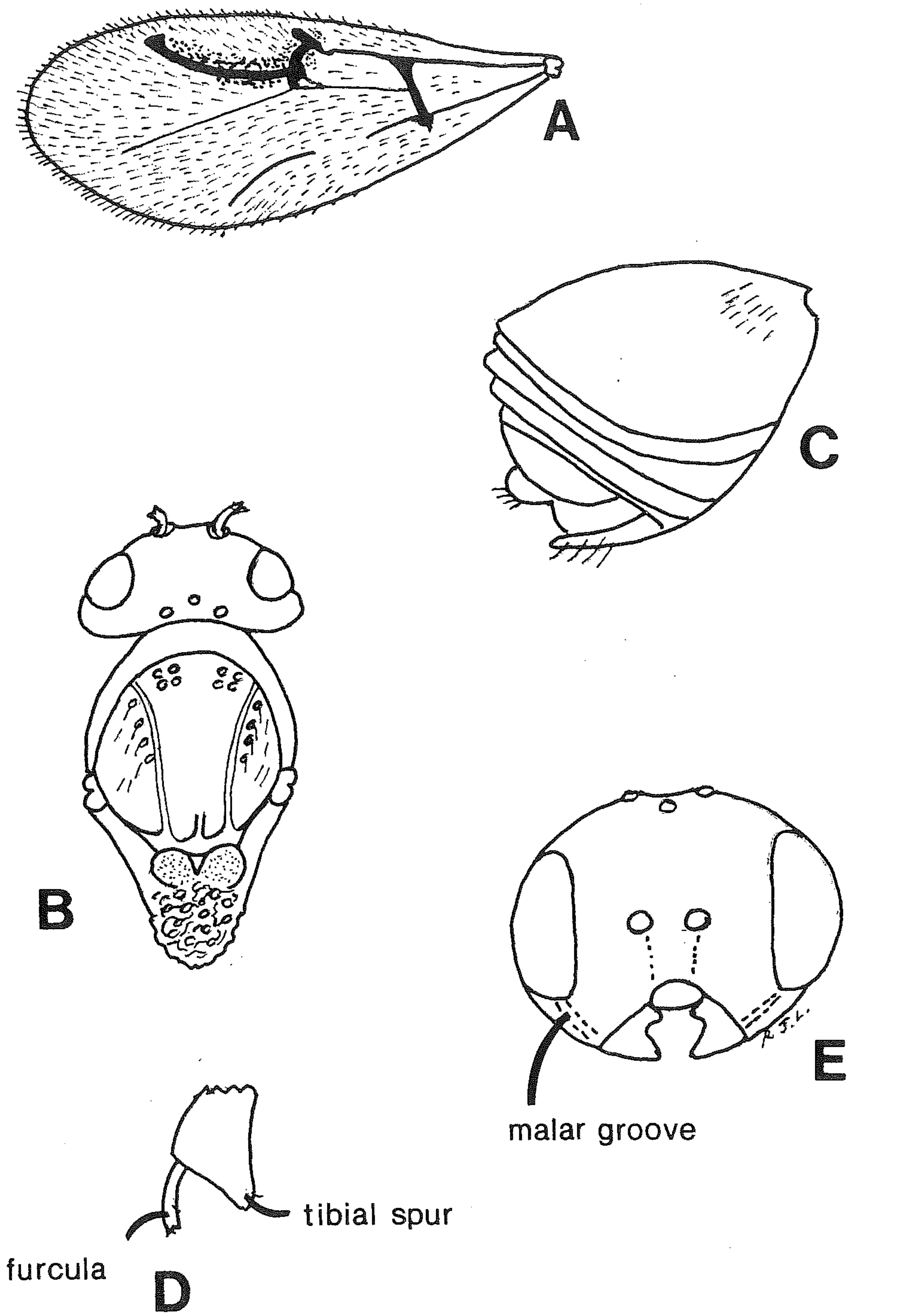


Fig. 6. *Belonocnema treatae* (unisexual generation female = *B. kinseyi*). A, Forewing venation, lateral view (×25). B, Head and mesosoma showing detailed morphology of scutum and scutellum, dorsal view (×40). C, Lateral view of metasoma showing shape of abdominal terga (×40). D, Foretibia showing elongated, characteristic spur and furcula. E, Frontal view of head showing malar furrow (×60).

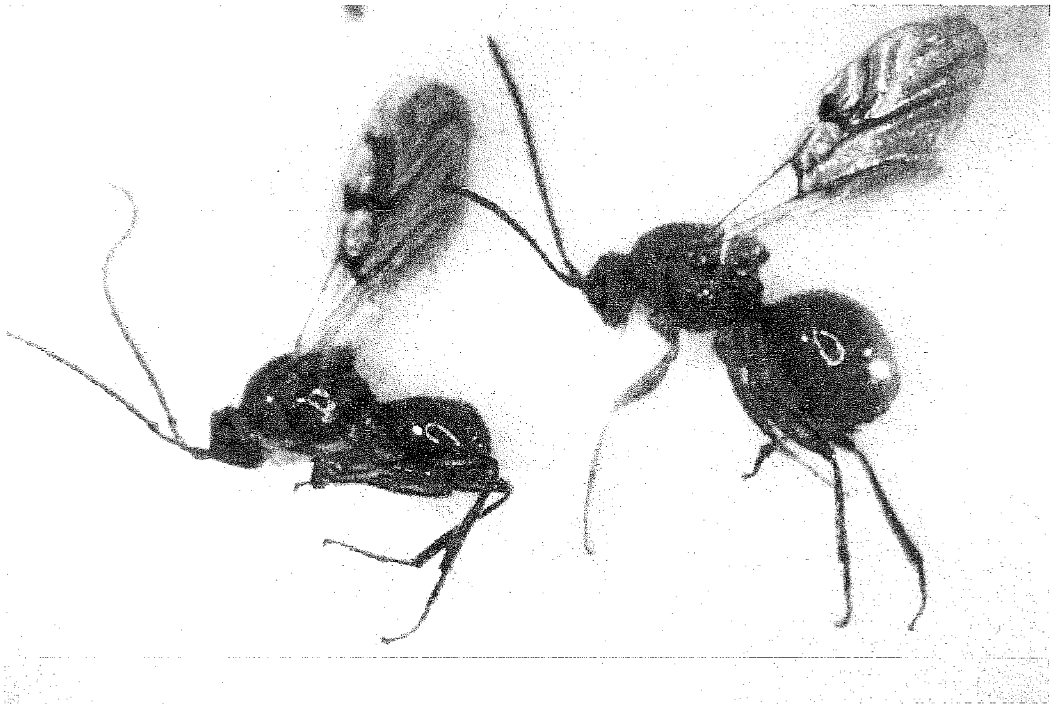


Fig. 7. *Belonocnema treatae* bisexual generation (×16); male (left), female (right).

slightly along upper lateral margins; a very short median posterior groove in some specimens. Scutellum sloping to a broad, rounded, roughened margin, slightly more than half length of scutum; foveal pits large, deep, separated with smooth, shining bottoms. Propodeum with two curved ridges, area between rugose. Mesopleuron bulging, shiny with setae along lower portion. Forewing hyaline (Fig. 6A), pubescent, short ciliate along anterior margin, longer on posterior margin; veins brown, R_{s1} with dark areas, R_{s2} curving toward wing margin with slightly flattened club at apex; radial cell short, 2× as long as broad. Metasoma (Fig. 6C) longer than high with all terga showing along dorsal margin. Hypopygeal spine with bristles extending beyond apex. Foretibia with an extended spine almost as long as furcula (Fig. 6D).

Comparison of the unisexual and bisexual generation females.—Average bisexual-generation females are larger than unisexual-generation females—3.6 mm versus 2.7 mm. This is unusual; unisexual-generation females are generally larger than those of the bisexual generation (R. Lyon, in litt.). Bisexual females are mostly light yellow brown with a dark scutellum and propodeum. Unisexual females are darker, with the mesosoma almost black and the head and metasoma red brown. The scutellum of bisexual females is broader and more rounded, appearing almost circular in outline, whereas the unisexual females have a narrower scutellum that slopes to a broad, more-rounded point. Bisexual females have 14 segmented antennae, unisexual females have 13 segmented antennae. Bisexual females have wing vein R_{s2} heavier, more sharply curving toward wing margin, and club at tip larger and more rounded than do unisexual females, for which R_{s2} is more slender and less sharply curved and the terminal club is smaller.

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