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Revision of Canadian Eurytomidae (Hymenoptera, Chalcidoidea) associated with galls induced by cynipid wasps of the genus *Diplolepis* Geoffroy (Hymenoptera, Cynipidae) and description of a new species

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Abstract

Eurytomids are small parasitic wasps associated with many communities of phytophagous insects. In most cases, the accurate identification of eurytomids is impeded by inadequate species descriptions that do not include figures of diagnostic features, and keys that are difficult to use. Here, diagnostic features and redescriptions are provided for both sexes of the eurytomids associated with galls induced by cynipid wasps of the genus *Diplolepis* Geoffroy found on shrub roses across Canada. Consequently, six species of *Eurytoma* Illiger, along with *Tenuipetiolus ruber* Bugbee, are dealt with. One new species, *Eurytoma shorthousei* Zhang & Gates, **sp. n.**, is described. Two species are synonymized, *E. hebes* Bugbee, 1973 and *E. spina* Bugbee, 1951 under *E. longavena* Bugbee, 1951, **syn. n.** Several new host and distribution records are reported. A dichotomous key is provided for both sexes of all seven species using photographs and scanning electron microscopy images.

Keywords

Eurytomidae, *Diplolepis*, *Eurytoma*, *Tenuipetiolus*, Canada

Introduction

The interaction between insect herbivores and their associated natural enemies is one of the key factors in understanding the origin and evolution of multi-trophic systems. One particularly species-rich, ecologically-closed model system for studies of host-parasitoid relationships is the community of gall wasps (Hymenoptera: Cynipidae) and their associated inquilines (e.g. *Periclistus* spp., Cynipidae: Diastrophini) and parasitoids (primarily Hymenoptera: Ichneumonoidea, Chalcidoidea) on oaks and roses (Csóka et al. 2005, Nicholls et al. 2010, Ronquist et al. 2015). Inquilines have lost their ability to induce galls, but still retain the ability to modify gall tissue (Brooks and Shorthouse 1997, Ronquist et al. 2015, Pujade-Villar et al. 2016). While entirely phytophagous, inquilines usually result in the death of inducers either through adult oviposition, or through competition for the same resources in the gall (Shorthouse 1973, 2010, Pujade-Villar et al. 2016). Parasitoids associated with cynipid galls feed either internally or externally as the host continues to develop (koinobionts), or when development of the host has been arrested by stinging prior to oviposition as for idiobionts (Csóka et al. 2005). Approximately 200 species of hymenopteran parasitoids are known from cynipid galls in Europe and North America, most of which are gall-specific (Csóka et al. 2005). For instance, parasitoids associated with galls induced by *Diplolepis* Geoffroy, in particular the European species *D. rosae* L. (Stille 1984, Lázsló and Tóthmérész 2006, 2011, Lotfalizadeh et al. 2007c), the North American species *D. polita* (Ashmead), *D. nodulosa* (Beuttenmüller) (Brooks and Shorthouse 1997, Shorthouse 1973, 2010), and *Diplolepis fructuum* (Rübsaamen) in Iran (Lotfalizadeh et al. 2012) have been well studied. However, the taxonomy and ecology of many of these inquilines and parasitoids associated with *Diplolepis* are poorly known due to their small size and morphological conservatism (Shorthouse 2010).

Members of the family Eurytomidae (Hymenoptera: Chalcidoidea) are one of the most common parasitoids associated with cynipid galls on roses in Canada, often comprising up to 40% of the component community (Shorthouse 2010). Bugbee (1951a, b) reported 12 species of *Eurytoma* Illiger and one species of *Tenuipetiolus* Bugbee known from galls of *Diplolepis*, and suggested that most species are monophagous. Little is known about the host specificity of eurytomids in galls of the 14 species of *Diplolepis* found in Canada, but all species of *Diplolepis* are host to at least one species of *Eurytoma* (Shorthouse 2010, Zhang et al. 2014).

Recent phylogenetic analyses redefined Eurytomidae as a monophyletic group (Lotfalizadeh et al. 2007b, Heraty et al. 2013). A gradual and mosaic evolution with large levels of homoplasy was observed within Eurytominae based on the study by Lotfalizadeh et al. (2007b). The genus *Tenuipetiolus* Bugbee was grouped with *Prodecatoma* Ashmead based on the following derived states: 1) Adscrobal area with a dorsal depression or areola; 2) Epicnemium with a large and circular median areola dorsally; 3) Precoxal carinae close to anterior margin of metapleuron; 4) Submedian carinae close to each other. However, no formal synonymization has been proposed and all

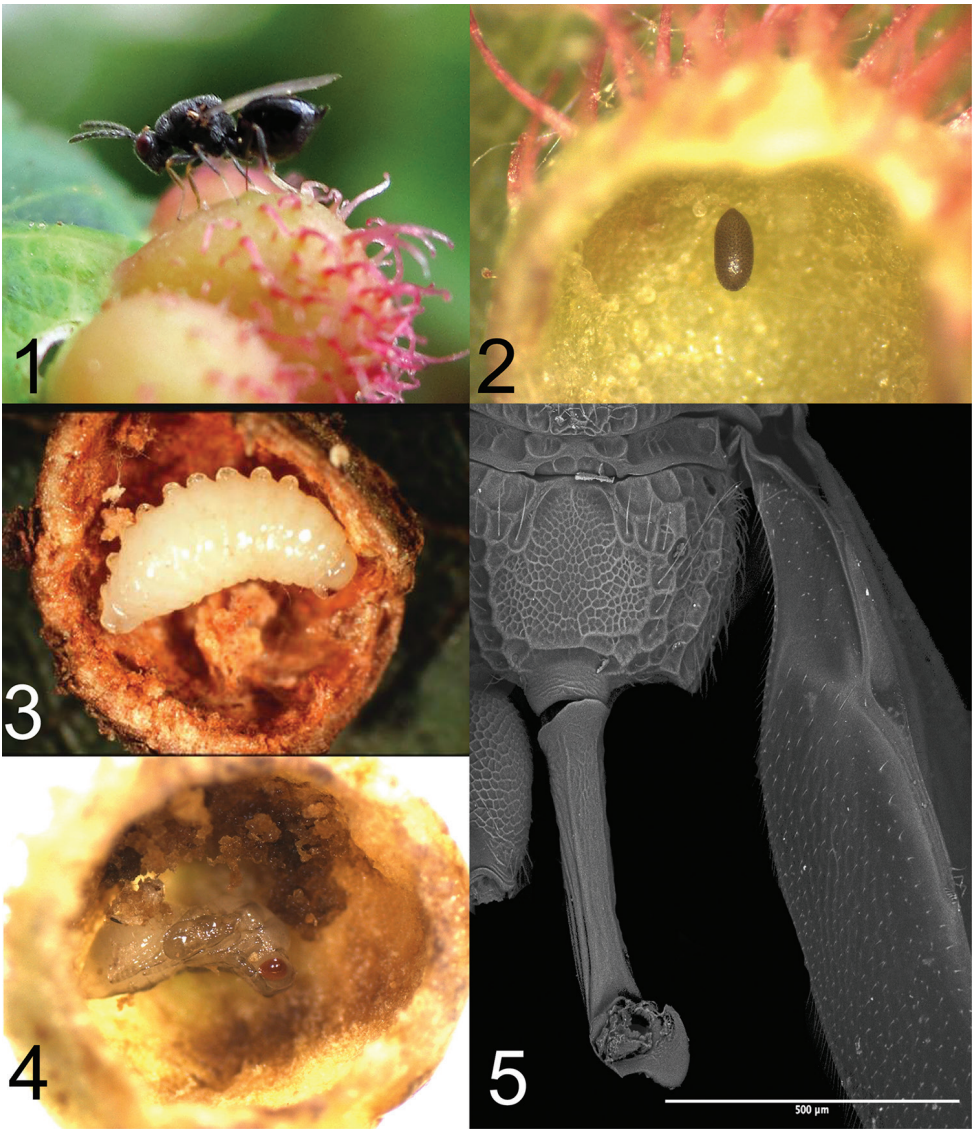
four species of *Tenuipetiolus* are found restricted within Nearctic, associated with galls of cynipids and cecidomyiids (Bugbee 1951a).

All species with a carinate gena and showing no other outstanding characters were redefined as *Eurytoma sensu stricto* (*s.s.*) with the following derived states: 1) Postgenal lamina present and raised ventrally over the surface of the postgena; 2) Postgena with a ventral depression between the posterior margin of the gena and the hypostomal fossa, with the depression delimited dorsally by a ridge or a step; 3) Gena with posterior margin slightly angulate above oral fossa (Lotfalizadeh et al. 2007b). *Eurytoma s.s.* is divided into 11 species groups including 700 nominal species worldwide, with ~100 Nearctic species north of Mexico (Lotfalizadeh et al. 2007b). *Eurytoma* associated with cynipid gall inducers have been placed under the *rosae* group, characterized by the presence of a precoxal tooth formed by the adscrobal carina (Lotfalizadeh et al. 2007b, see arrow in Fig. 11). Members of the *rosae* group often include cryptic species, which were morphologically indistinct or similar but with genetic and biological differences (Claridge and Askew 1960, Ács et al. 2002, Lotfalizadeh et al. 2007a, Gómez et al. 2011). The most recent published key to Nearctic *Tenuipetiolus* (Bugbee 1951a) and *Eurytoma* (Bugbee 1951b, 1967) is difficult to use due to the overlapping character states and the lack of illustrations. Additionally, current identification keys are limited to females, and thus the males are unidentifiable to species level.

Biology of eurytomids associated with galls induced by Diplolepis

Most eurytomids associated with galls induced by *Diplolepis* are univoltine. They feed throughout the summer on larvae of the gall inducer, inquilines, or on other parasitoids, overwinter as larvae within gall chambers, pupate in the spring and turn into adults (Shorthouse 1973). The emergence period of adults is synchronized with that of their host, which occurs soon after the immature galls appear such that the ovipositing females (Fig. 1) can reach the chambers of developing galls in this narrow window of opportunity (Shorthouse 2010). Eurytomid eggs are brown to black, and with an elongated egg body, and a curved peduncle which may be used to attach the egg to the inside surface of the developing gall chambers or the body of its host (Fig. 2) (Vårdal et al. 2016).

Eurytomid larvae in gall chambers with immature *Diplolepis* feed as koinobionts, keeping the inducer alive until the larva is fully grown and then consume it. This is necessary since the eurytomid larva grows to the same size as its single host. Eurytomids commonly feed on gall tissues along the inside surface of galls after the inducer is consumed (Fig. 3), and as a result, maturing galls become lined with frass (Fig. 4), a characteristic sign of this parasitoid (Shorthouse 1973). Eurytomid larvae having emerged from eggs deposited in galls with immature *Periclistus* larvae feed as predators consuming many inquilines before the inquiline form chambers (Shorthouse 1973, Brooks and Shorthouse 1997). Eurytomids in *Periclistus*-modified galls then chew into the *Periclistus* chambers to consume larvae.



Figures 1–5. *Eurtyoma longavena* **1** Female ovipositing into immature gall **2** Egg deposited on the inside surface of gall chamber **3** Mature larva inside a gall showing frass as a result of feeding on gall tissue **4** Pupa overwintering inside the gall before exiting the following year. *Tenuipetiolus ruber* **5** Propodeum + petiole. Photos 1–4 credit Brandy L. Fenwick.

Fully grown eurytomid larvae can be distinguished from larvae of other parasitoids in *Diplolepis* galls by their cylindrical body shape and the presence of dorsal protuberances (Shorthouse 1973). While the larvae of Ormyridae also have protuberances, they can be readily separated by their single toothed mandible that is not externally visible, as opposed to the bidentate, partially visible external mandibles of eurytomids (Fig. 3)

(Gómez et al. 2011). In late summer, eurytomids overwinter within the gall chamber at the pupal stage (Fig. 4). The coloration of the pupa darkens with the approach of adult emergence, the imago chewing through the gall wall to exit and repeat the life cycle.

The objective of this study is to describe both male and female eurytomids associated with rose galls in Canada, as well as updating morphological characters, hosts, and distributional records following the molecular study using *COI* (Zhang et al. 2014). Additionally, a dichotomous key is provided for both sexes of all seven species.

Materials and methods

The eurytomids used for this study were from the collection of J. D. Shorthouse (JDS), previously deposited at Laurentian University in Sudbury, Ontario. Upon JDS's retirement, pin-mounted specimens were deposited in the Canadian National Collections of Insects, Arachnids, and Nematodes (CNCI) in Ottawa. Specimens stored in alcohol and emerged from thousands of galls that were collected across Canada over the past 45 years, are deposited at Edinburgh University in Scotland in the laboratory of Graham Stone. In most cases, the eurytomids, along with all other gall inhabitants, were obtained by storing mature galls in glass jars in the laboratory and aspirating adults daily when they appeared. In other cases, the larvae of gall inhabitants were removed from mature galls either in autumn or spring and placed in pin-mounted gelatin capsules. Adults obtained in this manner could be associated with the larval stage and were cleaner than those that had chewed their way out of galls. Most specimens from these collections for this study were chemically dried using hexamethyldisilazane (HMDS), following the protocol of Heraty and Hawks (1998), before they were point- or card- mounted. A full list of specimens examined is listed under each redescription. Additional specimens were also borrowed from the following institutions:

CNCI Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada (John T. Huber, curator);

DEBU University of Guelph Insect Collection, Guelph, Ontario, Canada (Stephen A. Marshall, curator);

USNM National Museum of Natural History, Washington D.C., USA (Michael W. Gates, curator).

The specimens were photographed using a Canon 7D Mark II with either a Canon MP-E 65mm F/2.8 Macro Photo Lens, or with a Mitutoyo M Plan Apo 10x objective mounted onto the Canon EF Telephoto 70–200 mm zoom lens, and the Canon MT-24EX Macro Twin Lite Flash with custom made diffusers to minimize hot spots. Scanning electron microscopy (SEM) micrographs were taken using methods described by Gates and Pérez-Lachaud (2012). Composite descriptions were based on a combination of all examined specimens with DNA vouchers. Terminologies used for surface sculptures follow Harris (1979), while the morphology follows Gibson (1997), Lotfalizadeh et al. (2007b), and Gates and Pérez-Lachaud (2012). The following acro-

nyms are used: **LOL** (Lateral ocellar line), **OOL** (Ocello-ocular line), **POL** (Posterior ocellar line), $\mathbf{F_n}$ (Funicular segment #), $\mathbf{Gt_n}$ (Gastral tergite #). Measurements were taken using an ocular micrometer, and size range given is based on the largest and smallest specimens in the material examined. Image processing and plate assembly was completed with Photoshop CC and Illustrator CC. Distribution maps were produced using Simplemappr (Shorthouse 2017, www.Simplemappr.net).

Taxonomy

Key to species of Eurytomidae associated with galls induced by *Diplolepis* in Canada

1 Female. Gt_1 and Gt_2 fused dorsally. Petiole longer than metacoxa (Fig. 5). Male. F_3–F_5 with one row of setae . Petiole about 2× as long as metacoxa ..... ***Tenuipetiolus ruber***

– Female. Gt_1 and Gt_2 not fused dorsally. Petiole subequal in length to metacoxa (Fig. 11). Male. F_3–F_5 with 2–3 rows of setae (Figs 29, 30). Petiole less than 2× as long as metacoxa ..... ***Eurytoma* Illiger 2**

2 Tegula, scape and pedicel yellow (Figs 12, 13), propodeal spiracle with raised rim anteriorly (Fig. 19) ..... ***E. shorthousei* sp. n.**

– Tegula black to brown, scape and pedicel black with yellow restricted to basal region (Fig. 9), propodeal spiracle not without raised rim anteriorly **3**

3 Pro- and mesocoxa yellow to brown, never entirely black (Fig. 7) ..... ***E. iniquus***

– Pro- and mesocoxa entirely black (Fig. 8) **4**

4 Female. Gaster dorsal outline S-curve shaped in lateral view, longer than head plus mesosoma, ovipositor sheath upturned (Fig. 27). Male. Funicular segments longer than wide, with 2 rows of longitudinal sensilla and adpressed setae (Fig. 29) ..... ***E. discordans***

– Female. Gaster not S-curve shaped (Fig. 28), shorter or equal to head plus mesosoma, ovipositor sheath not upturned. Male. Funicular segments as long as wide, with 1 row of longitudinal sensilla and erect setae (Fig. 30) **5**

5 Scape entirely black (Fig. 8) ..... ***E. longavena***

– Scape black with yellow at extreme base or along entire anterior surface **6**

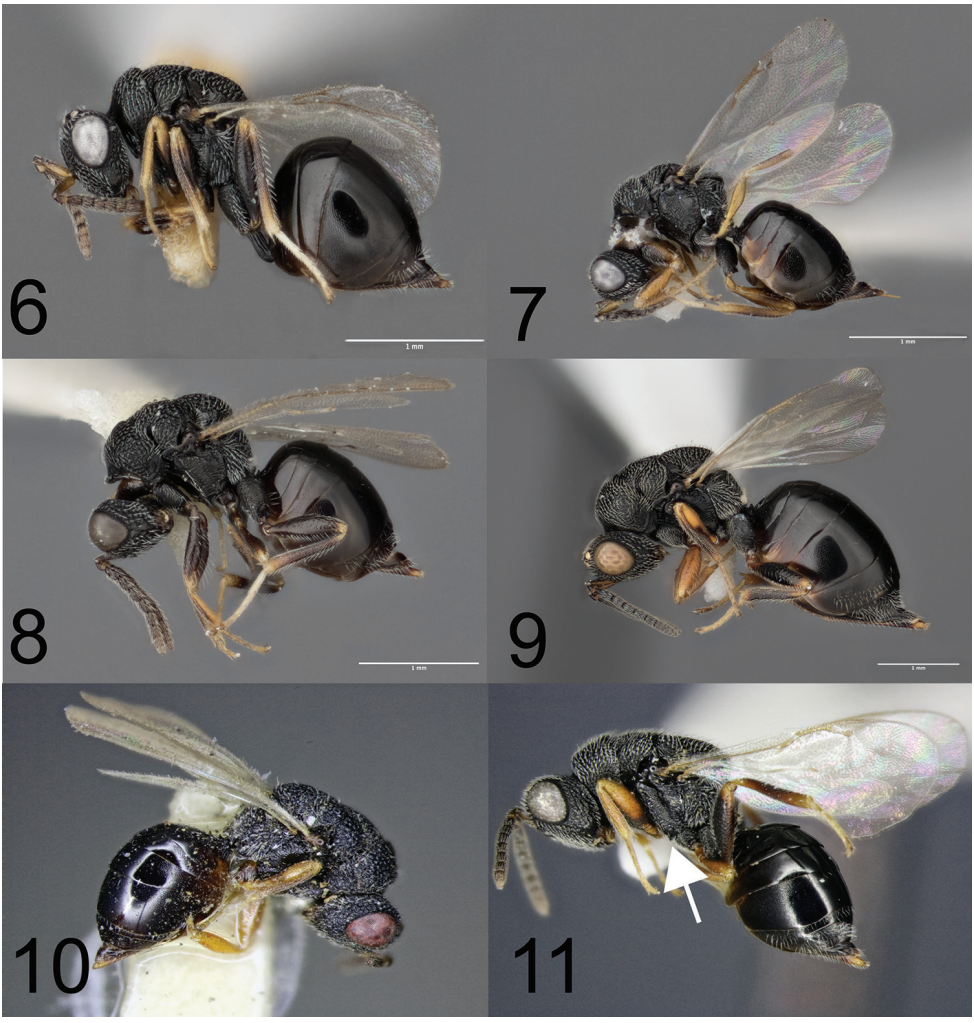
6 Female metasoma small, oval shaped (Fig. 10) ..... ***E. imminuta***

– Female metasoma large, elongate (Fig. 11) ..... ***E. spongiosa***

Tenuipetiolus ruber Bugbee, 1951

Figs 5, 6, 31

Tenuipetiolus rubra Bugbee, 1951a: 39–42. Holotype female (USNM). Type data: USA, Indiana [Bloomington]; reared from galls induced by *Diplolepis rosae* (L.) on species of *Rosa*, March 28, 1939.



Figures 6–11. *Tenuipetiolus ruber* **6** Female habitus. *Eurytoma iniquus* **7** Female habitus. *E. longavena* **8** Female habitus. *E. discordans* **9** Female habitus. *E. imminuta* **10** Female habitus (length 2.0 mm). *E. spongiosa* **11** Female habitus (length 3.2 mm), arrow pointing to precoxal tooth formed by the adscrobal carina.

Females. Body length 2.0–3.6 mm. Color: Black except yellow to brown on basal half of scape, pedicel, and funicular segments, apices of all femora, pro-, meso- and metatibia, tip of ovipositor sheath, tegula, wing venation; all tarsomeres 1–4 white (Fig. 6).

Head. Head 1.2× as broad as high, umbilicate punctured with small tentorial pits. Genal carina present. Malar space 0.8× eye height, clypeus emarginate and supraclypeal area superficially rugose. Toruli positioned dorsad lower ocular line. Antenna with funicular segments subequal in length; pedicel chalice-shaped; funiculars fusiform with one row longitudinal sensilla and two whorls of setae; F_1 slightly narrowed

basally. Ratio LOL:OOL:POL as 1:1:2.5. Head posteriorly without postgenal lamina or postgenal depression. Postgena sparsely setose.

Mesosoma. About 1.2× as long as broad; notauli incomplete, shallow. Epicnemium imbricate, flattened. Mesepisternum anterior to femoral depression umbilicate; mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating from the posterior margin. Propodeum concave, superficially punctate, bordered mediolaterally by numerous carinae forming irregular setose cells, median furrow not delimited (Fig. 5). Procoxa imbricate, lacking setation proximally. Metacoxa asetose anteriorly and one row of setae on the posterior apical margin. Forewing hyaline, marginal vein distinctly longer than postmarginal vein.

Metasoma. Gaster 1.5× as long as mesosoma in lateral view; smooth, anterior edge of gastral tergites microreticulate. Petiole 2× length of metacoxa (Fig. 5). Gaster laterally compressed, triangular shaped and strongly convex in lateral view, ovipositor parallel to horizontal axis. Gt_1 and Gt_2 fused dorsally, $Gt_{1–4}$ glabrate, $Gt_{5–8}$ and apex of ovipositor sheaths setose.

Male. Body length: 1.4–2.5 mm. Color as described for female. Sculpture as described for female. Antennae with funicular segments pedunculate, F_2–F_5 each with 2 rows of erect setae and 1 row of longitudinal sensilla; scape without ventral plaque. Petiole in lateral view cylindrical, in dorsal view about 3× as long as greatest width, 2× as long as metacoxa; strigose laterally.

Remarks. This species is likely a generalist that is not restricted only to *Diplolepis* galls. Rearing records reported in the original description include cynipids of the genus *Diastrophus*.

Biology. Reared from field populations of galls induced by *Diplolepis bassetti* on *Rosa woodsii* Lindl.; *D. polita*, *D. nodulosa*, and *D. triforma* on *Rosa acicularis* Lindl.

Material examined (27 females, 12 males). CANADA: British Columbia: Osoyoos, 14.V.2003, J.D. & M.R. Shorthouse, ex *Diplolepis bassetti* on *Rosa woodsii* (3F, 3M, CNCI). **Ontario**: Chelmsford, 5.V.1994, S.E. Brooks, ex *Periclistus pirata*-modified galls of *Diplolepis nodulosa* (3F, 1M, CNCI); Cochrane, 24.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis triforma* on *Rosa acicularis* (9F, 2M, CNCI); Manitoulin Island, 2.V.2009, J.D. Shorthouse & J.D. Renelli, ex *Diplolepis triforma* on *Rosa acicularis* (5F, 1M, CNCI). **Québec:** La Sarre, 13.VII.2010, B.L. Smallwood & Y.M. Zhang, ex *Diplolepis polita* on *Rosa acicularis* (7F, 5M, CNCI).

Distribution. Disjunctive populations have been found in Western Canada in British Columbia and Eastern Canada in Ontario and Québec (Fig. 31).

Eurytoma shorthousei Zhang & Gates, sp. n.

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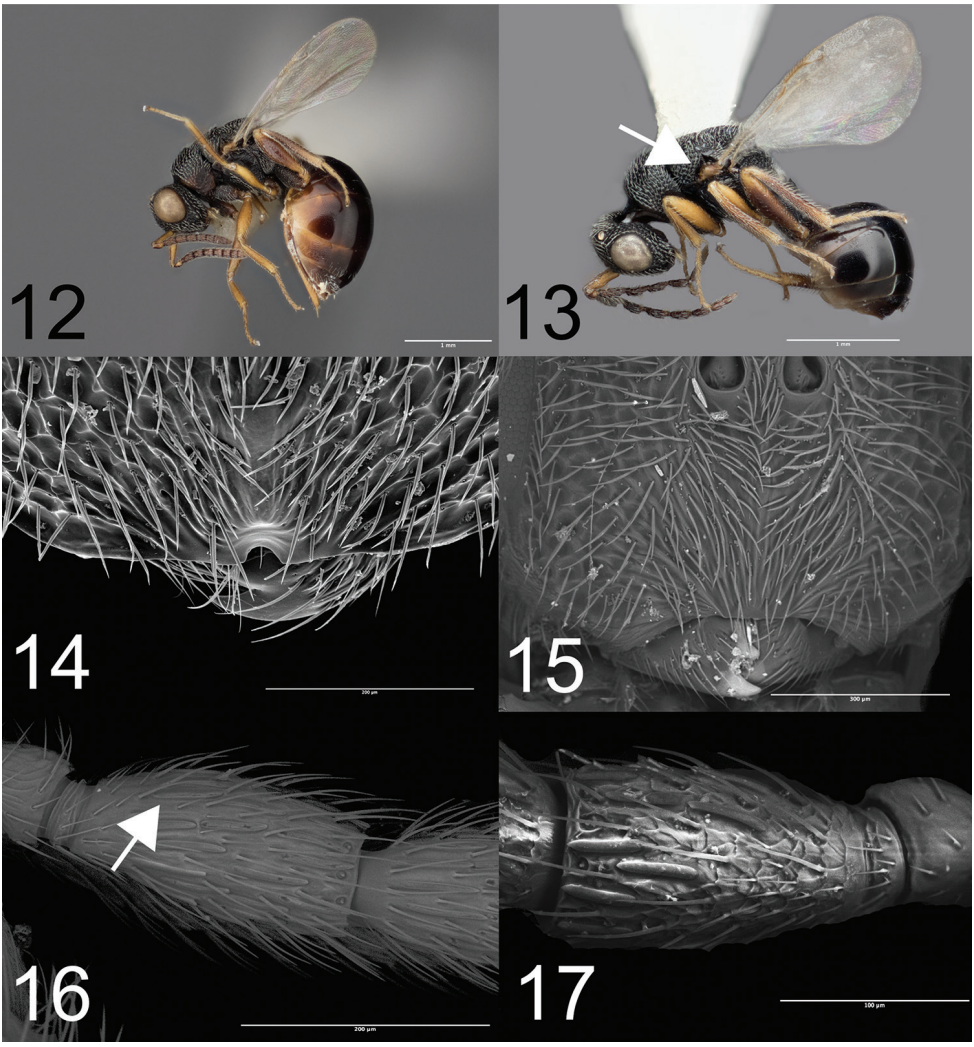
Figs 12, 13, 15, 17, 19, 21, 32

Etymology. This species is named for Joseph D. Shorthouse, honoring his contribution to the understanding of *Diplolepis* galls and their associated inhabitants, as well as the collector of the type specimens.



Figures 12–17. *Eurytoma shorthousei* sp. n. **12** Female habitus **13** Male habitus, arrow pointing to tegula **14** Clypeus **17** Female funicular segment 1. *E. obtusilobae* **15** Clypeus **16** Female funicular segment 1, arrow pointing to multiporous plate sensilla (MPS).

Diagnosis. This species differs from other eurytomids studied in the yellow or brown scape and tegula, with supraclypeal area strigose (Fig. 15). Propodeal spiracle with raised rim anteriorly (Fig. 19).

Holotype female. Body length 3.2 mm. Color: Black except brown funicular segments, apices of procoxa and metafemur, metatibia excluding apex, and yellow scape, pedicel, pro- and mesotibia, mesofemur, apices of metatibia and metafemur, all tarsomeres 1–4, tip of ovipositor sheath, tegula, wing venation (Fig. 12).

Head. 1.3× as broad as high, 2.5× as broad as long in dorsal view, umbilicate punctured. Malar space 0.5× eye height, malar carina present, raised in ventral half,

becoming impressed line in dorsal half (Fig. 24). Gena entirely umbilicate punctured, minutely strigose posterad malar carina in ventral half, umbilicate posterad dorsal half (Fig. 24). Genal carina raised, forming blunt angle above oral fossa. Clypeus receding to median emargination and lower face strigose (Fig. 14), median longitudinal glabrous supraclypeal area (Fig. 14). Toruli positioned about ~1.5 torular diameters above lower ocular line. Lateral margin of antennal scrobes carinate, forming a raised lobe just above toruli. Intertorular projection approximately quadrate, dorsally truncate, with 2 rows of setae. LOL:OOL:POL is 1:1.4:2.3. Antennal segment ratios as: 55:15:3:25:20:18:15:15:35; pedicel chalice-shaped; funicular segments fusiform, subequal, with 2 rows of longitudinal sensilla and 2–3 rows adpressed setae; F1 lacking longitudinal sensilla in the basal third (Fig. 17).

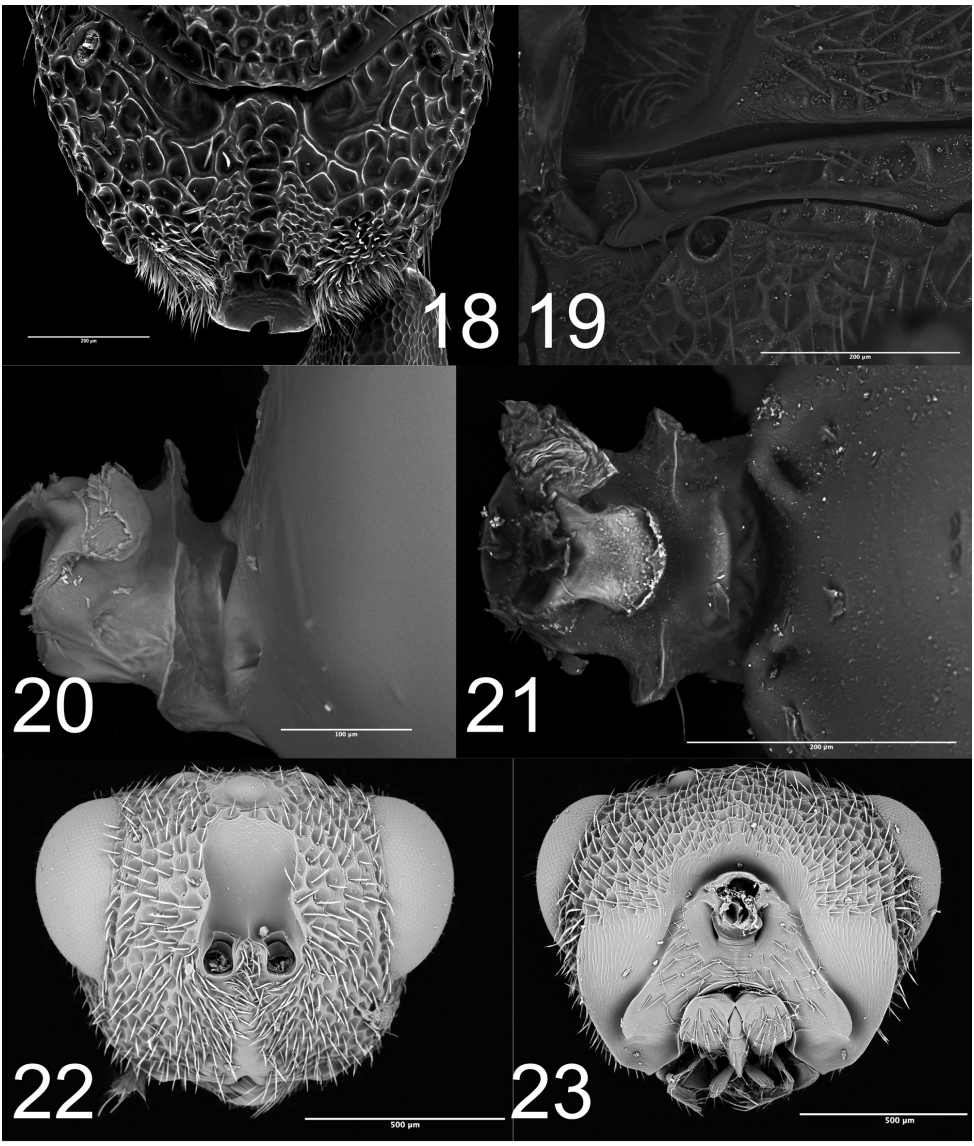
Mesosoma. About 1.2× as long as broad; notauli impressed, shallow. Epicnemium imbricate, flattened. Mesepisternum anterior to femoral depression, umbilicate; mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating from the posterior margin. Precoxal tooth formed by raised adscrobal carina present in lateral view. Procoxa imbricate, lacking setation proximally, with oblique groove and S-like basal ridge. Metacoxa sparsely setose anteriorly and one row of setae on the posterior apical margin. Mesocoxal lamella absent. Lateral panels of propodeum and callus with umbilicate punctures distinctly delimited from median area by carinae forming irregular asetose cells, median furrow delimited, forming 1–2 rows of irregular foveae. Propodeal spiracle with raised rim anteriorly (Fig. 19). Forewing hyaline, setation dark, marginal vein as long as postmarginal vein, basal cell bounded by distinct basal and cubital setal lines, with sparse row setae parallel to submarginal vein; costal cell with single row of setae dorsally in apical half, speculum present and approximates width parastigma.

Metasoma. Gaster 1.5× as long as mesosoma in lateral view. Length 81 (valvulae excluded), height 55, relative lengths of $Gt_{1–4}$ measured along dorsomedial line: 8:9:20:25; syntergum 7. Smooth, anterior edge of gastral tergites microreticulate. Petiole with three separate protuberances, one dorsomedial and two anterolateral (Fig. 21). Gaster laterally compressed, oval shaped and convex in lateral view, ovipositor parallel to horizontal axis. $Gt_{1–4}$ glabrate, $Gt_{5–8}$ and apex of ovipositor sheaths setose. Posterior margin of Gt_4 convex ventrally, straight dorsally. Posterior margin of Gt_5 weakly emarginate.

Male. Body length 3.0 mm. Color: Black, yellow and brown areas as described for female. Sculpture as described for female. Antennal segment ratios as: 52:14:3:36:27:31:27:27:42; funicular segments longer than wide, pedunculate, F_2–F_5 each with 3 irregular rows of appressed setae and two irregular rows of longitudinal sensilla; scape with ventral plaque in apical half (Fig. 13). Gaster 0.9× as long as mesosoma in lateral view. Length 40, height 30, relative lengths of $Gt_{1–4}$ measured along dorsomedial line: 7:10:34:10; syntergum 1. Petiole 2.0× as long as broad, rugulose dorsally, mostly glabrous laterally and ventrally.

Variation. Body length ranges from 2.5–3.2 mm in females, 1.7–3.0 mm for males. Occasionally, brownish area on anterior pronotum extends laterally onto collar.

Remarks. This species was originally mistakenly identified as *Eurytoma obtusilobae*, described by Ashmead in 1885 based on four specimens, "bred from an unidentified



Figures 18–23. *Eurytoma obtusilobae* **18** Propodeum **20** Petiole, lateral view. *E. shorthousei* sp. n. **19** Propodeal spiracle **21** Petiole, dorsal view. *E. discordans*: **22** Head, anterior view **23** Head, posterior view.

cynips gall on *Quercus obtusiloba* [now *stellata*; post oak]" from Jacksonville, Florida. The only specimen remaining from this series is a female designated and labeled as a lectotype by Bugbee (1967). Bugbee (1951b) had previously redescribed "*obtusilobae*" based on the types and included 5 females and 10 males collected by J. C. Bridwell in Vienna, Virginia 1941 (ex *Rhodites radicum* on *Rosa palustris*), but the latter belong to *E. shorthousei*. Only 4 pointed females and males could be located, though there is a gelatin capsule with 30 individuals from the same collecting event were not examined.

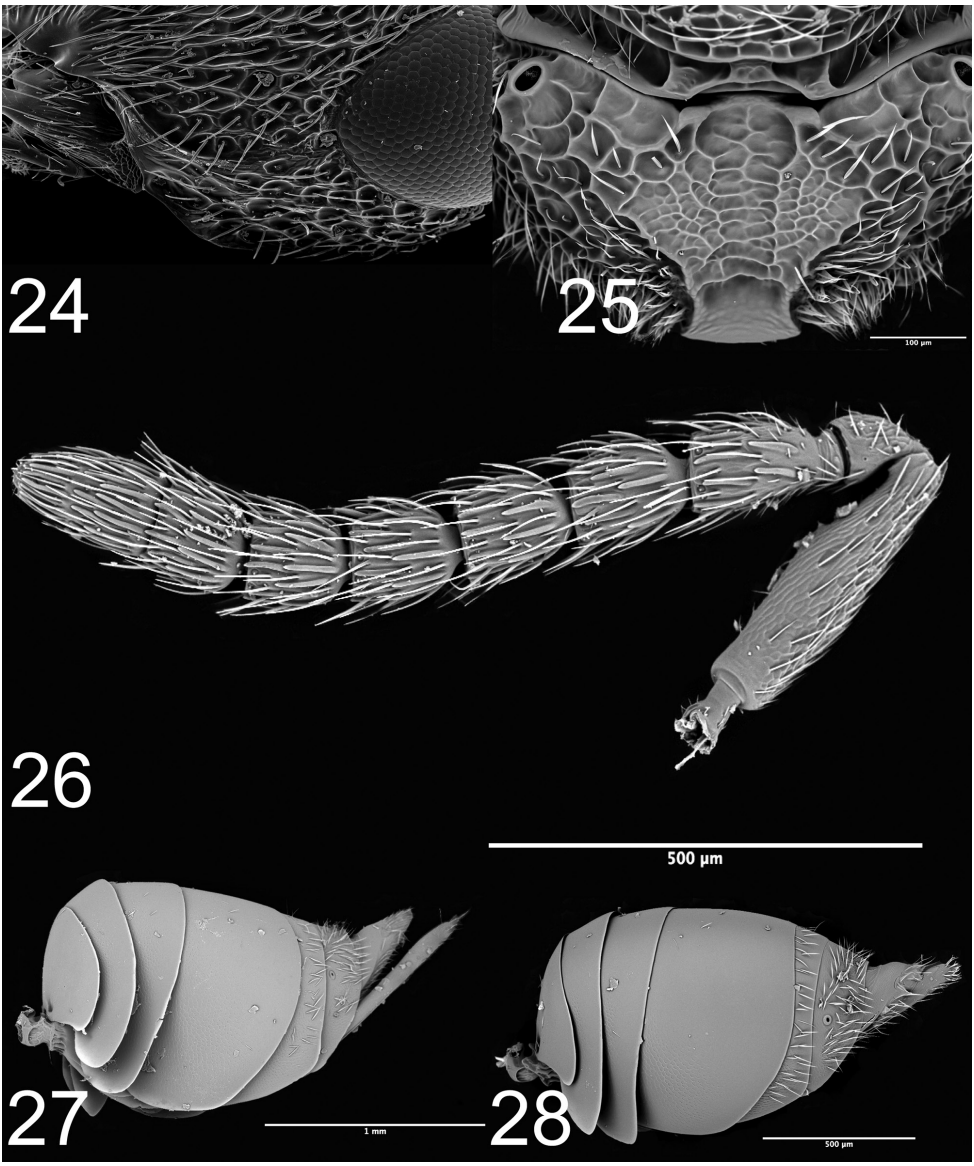


Figure 24–28. *Eurytoma shorthousei* **24** Face in lateral view. *E. longavena* **25** Propodeum **28** Female metasoma, lateral view. *E. discordans* **26** Female antenna **27** Female metasoma.

Despite the fact that the lectotype from Florida was reared from cynips on post oak, Bugbee (1967: 460) refers to *E. obtusilobae* as being restricted to *Diplolepis* galls on rose. He speculated that Ashmead erred either in gall determination or incorrectly associated *E. obtusilobae* with oak. We suspect that *E. shorthousei* was incorrectly identified as conspecific with the *E. obtusilobae* type series, given the affinities of the latter (petiole, F_1 MPS, propodeal spiracular rim, etc.) with oak associated *Eurytoma*, namely *E. sphaera*

Bugbee. Further, it appears that *E. obtusilobae* falls within the range of variation of *E. sphaera*, a species associated with post oak throughout the eastern United States. Bugbee (1951b) incorrectly referred to a holotype and neotypes of both sexes (of *E. obtusilobae*) deposited in the USNM and the Bugbee Collection (now at USNM).

The lectotype of *E. obtusilobae* is not conspecific with *E. shorthousei* as noted below although the two species do resemble each other in general habitus. They were confused due because sharing the supraclypeal striae and similar sculpture and coloration. They may be separated as *E. shorthousei* has medially notched clypeal margin (Fig. 14) versus un-notched (Fig. 15); MPS lacking in basal half F1 (Fig. 17) versus present (Fig. 16); propodeal spiracle with raised rim anteriorly (Fig. 19) versus not raised (Fig. 18); petiole anteriorly with three separate protuberances, one dorsomedial and two anterolateral (Fig. 21) versus anterodorsally produced as sharp lamina (Fig. 20). The three separate petiolar protuberances are commonly encountered in various forms across *Eurytoma* (and Eurytomidae) so are seen in all *Eurytoma* treated herein. The petiolar production as in the *E. obtusilobae* lectotype is common in Eurytomidae and is germane given it is seen in other species attacking oak-associated cynipids (e.g. *Quercus californica*, *Q. querciglobuli*, and *Q. studiosa*). However, much additional work across all *Eurytoma* associated with cynipids on oaks must be done before morphological trends are solidified.

Found at only one site in this study, *E. shorthousei*'s distribution is wide in North America given the specimens reported by Bugbee (1951b) as *E. obtusilobae*: VA, King George; MA, Gloucester; OR, La Grange; UT, Price; and CAN: Manitoba. The series Bugbee reported from New York and Minnesota could not be located. The series from Glencoe, Illinois is not *E. shorthousei*. The overall dearth of rearing records corresponds to the difficulty in locating their host galls induced by *D. radicum*, which are at ground level and often covered with soil and detritus (Shorthouse 2010). *Eurytoma shorthousei* resembles *E. discordans* in gaster shape, but can be distinguished from the latter by coloration patterns and shape and size of female gaster.

Biology. Reared from field populations of galls induced by *Diplolepis radicum* on *Rosa carolina*, *R. palustris,* and *R. woodsii*.

Material examined. Holotype. Female, **CANADA: British Columbia:** Central Okanagan; Kelowna 2 km S.E. of Kelowna airport 49.952N – 119.381W; 344m; J.D. Shorthouse & R.G. Lalonde; 14/10/1999. ex *Diplolepis radicum* on *Rosa woodsii* (USNM). Paratypes. 6F, 3M; 4M, 3F, same label data as holotype (all USNM); 2F, **CANADA: British Columbia:** Sandilands, 15–V–1967, J.C. Melvin, host gall on rose (CNCI).

Distribution. Collected in British Columbia and Manitoba (Fig. 32).

Eurytoma iniquus **Bugbee**

Figs 7, 33

Eurytoma iniquus Bugbee, 1951b: 253–254. Holotype female (USNM). Type data: USA, Colorado [Manitou]; associated with galls induced by *Diplolepis neglectus* (Gillette) on species of *Rosa*, April 24, 1920.

Diagnosis. This species is similar to *E. discordans*, it can be distinguished by the yellow infuscation on the inner side of the pro- and mesocoxae (Fig. 7), whereas all other species have entirely black coxae.

Females. Body length 2.2–3.0 mm. Color: Brown to black except for the following yellow to brown: inner faces of procoxa, pro- and mesofemur and tibia, apices of hindleg, protibia laterally, tip of ovipositor sheaths, all tarsomeres 1–4, wing veins (Fig. 7).

Head. 1.3× as broad as high, umbilicate punctured with small tentorial pits. Genal carina present; malar space 0.8× eye height; clypeus truncate and supraclypeal area smooth (Fig. 22). Toruli positioned about half way above lower ocular line. Intertorular space acute dorsally, with 2 rows setae. Ratio of LOL:OOL:POL is 1:1:2. Funiculars subequal in size; pedicel chalice-shaped; funicular segments fusiform; F1 slightly narrowed basally, funiculars with 2 rows of longitudinal sensilla and 3 whorls of setae; clava 2-segmented.

Mesosoma. Largely umbilicate, 1.4× as long as broad; notauli complete, shallow. Epicnemium imbricate, flattened. Mesepisternum anterior to femoral depression umbilicate; mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating from the posterior margin. Precoxal tooth formed by raised adscrobal carina present in lateral view. Lateral panels of propodeum and callus umbilicately punctate, distinctly delimited from median area by carinae forming irregular setose cells, median furrow delimited, forming 2 rows of irregular foveae (Fig. 25). Procoxa imbricate, lacking setation proximally. Mesocoxal lamella absent. Metacoxa sparsely setose anteriorly and one row of setae on the posterior apical margin. Forewing hyaline, marginal vein subequal to postmarginal vein in length. Basal cell with one row of setae.

Metasoma. Gaster 1.8× as long as mesosoma in lateral view; smooth, anterior edge of gastral tergites microreticulate (Fig. 7). Petiole 0.5× as long as broad in dorsal view, with projecting lateral teeth as well as mediodorsal prong. Gaster laterally compressed, oval shaped and convex in lateral view, ovipositor slightly upturned dorsad the horizontal axis. $Gt_{1–4}$ glabrate, $Gt_{5–8}$ and apex of ovipositor sheaths setose. Gt_4 strongly emarginate on posterior margin dorsally.

Male. Body length: 1.7–2.8 mm. Color: Black, yellow areas as described for female. Sculpture as described for female. Antennae with funicular segments pedunculate, F_2–F_5 each with 2 rows of erect setae and 1 row of longitudinal sensilla (Fig. 30); scape with ventral plate in apical half. Gastral petiole in lateral view cylindrical, in dorsal view length about 1.8× as long as greatest width, 0.6× times length of metacoxa; evenly reticulate dorsally and ventrally, obliterated laterally.

Remarks. This species is likely a predator of inquiline *Periclistus* rather than the gall inducer, as they are reared from hosts that have a high rate of inquilism (Zhang et al. 2014). *Eurytoma iniquus* is particularly abundant in *Periclistus*-modified galls induced by *D. nodulosa*, which are morphologically distinct from unmodified galls (Shorthouse 2010). As the inducer larvae are killed during oviposition by the inquiline, the only inhabitants that are abundant within these galls are inquiline larvae. *Eurytoma iniquus* are morphologically distinct from the lectotype of *Eurytoma nigri-*

coxa Provancher, which has yellow coxae. The type of *E. nigricoxa* has the front and middle coxae orange-yellow similar to the remainder of the legs. The hindleg has the coxa darkish brown or dark orange-brown, somewhat lighter than the black meso- and metasoma, but much darker than the rest of the hindleg, which is similar in color to the fore- and midlegs (Gibson, pers. comm.). The CNCI has a single specimen with a Bugbee determination label as *E. nigricoxa* from Aylmer, Quebec that is reared from *Periclistus*-modified gall, but it has all the coxae black (Gibson, pers. comm.). *Eurytoma nigricoxa* is the only Nearctic species recorded in association with *Periclistus*, however this is likely an error as the lectotype lacks any biological information. Specimens from CNCI identified as *E. nigricoxa* are actually *E. iniquus* (Bugbee 1967). Closely resembles *E. longavena*, but can be distinguished from the latter by the yellow infuscation on of the pro- and mesocoxae.

Biology. Reared from galls induced by *Diplolepis bicolor* on *Rosa blanda*; *D. nodulosa* on *R. virginiana*; *D. polita, D. rosaefolii* on *R. acicularis*; and *D. variabilis* on *R. woodsii*.

Material examined (33 females, 20 males). CANADA: Alberta: Peace River, 16.VIII.1970, J.D. & M.R. Shorthouse, ex *Diplolepis polita* fall/spring emergence (4F, 2M, CNCI); Waterton Lakes National Park, 11.V.2011, J.D. & M.R. Shorthouse, ex *Diplolepis biocolor* on *Rosa blanda* (2F, CNCI). **British Columbia:** Kelowna, 20.V.2008, R.G. Lalonde, ex *Diplolepis variabilis* on *Rosa woodsii* (1M, CNCI). **Ontario:** Chelmsford, 5.V.1994, S.E. Brooks, ex *Periclistus pirata*-modified galls of *Diplolepis nodulosa* (6F, CNCI); Manitoulin Island, 29.IV.2011, J.D. Shorthouse, B.L. Smallwood & Y.M. Zhang, ex *Diplolepis nodulosa* modified by *Periclistus* sp. (4F, 2M, CNCI); Red Lake, 18.V.2002, J.D. Shorthouse & S.T. Offman, ex *Diplolepis rosaefolii* on *Rosa acicularis* (2M, CNCI); Thunder Bay, 15.V.2002, J.D. Shorthouse & S.T. Offman, ex *Diplolepis bicolor* on *Rosa blanda* (14F, 10M, CNCI). **Prince Edward Island:** Eldon, J.D. & M.R. Shorthouse, 23.VIII.1992, ex *Periclistus pirata*-modified galls of *Diplolepis nodulosa* on *Rosa virginiana* (3F, 3M, CNCI).

Distribution. British Columbia, Alberta, Ontario, Québec, and Prince Edward Island (Fig. 33).

Eurytoma longavena **Bugbee**

Figs 8, 25, 28, 30, 34

Eurytoma longavena Bugbee, 1951b: 249–250. Holotype female (USNM). Type data: CANADA, British Columbia [Terrance]; associated with galls induced by *Diplolepis bicolor* (Ashmead) on species of *Rosa*, 1927.

Eurytoma hebes Bugbee, 1973: 13–14. Holotype female (USNM). Type data: CANADA, Alberta [Peace River]; associated with galls induced by *Diplolepis polita* (Ashmead) on species of *Rosa*, August 16, 1970. **Syn. n.**

Eurytoma spina Bugbee, 1951b: 250–251. Holotype female (USNM). Type data: USA, Oregon [La Grande]; bred from *Diplolepis tuberculatrix versicolor* on *Rosa* species, April 12, 1920. **Syn. n.**

Diagnosis. This species differs from other eurytomids in the wholly brown to black scape, legs (except apices of femora and tibiae) (Fig. 8). Additionally, the females have large Gt_4 that covers most of Gt_5.

Females. Body length 3.0–3.7 mm. Color: Black, except for the following yellow to brown: apices of all legs, protibia laterally, tip of ovipositor sheaths, tarsomeres, wing venation (Fig. 8).

Head. 1.25× as broad as high, umbilicate punctured with small tentorial pits. Genal carina present; malar space 0.8× eye height; clypeus weakly emarginate and supraclypeal area smooth (Fig. 22). Ratio of LOL:OOL:POL is 1:1.6:2.5. Head posteriorly with postgenal lamina and postgenal grooves ridged, delimited ventrally by postgenal depression. Postgena sparsely setose. Toruli dorsad, positioned about dorsad to lower ocular line. Funicular segments subequal in size; pedicel chalice-shaped; funicular segments fusiform; F_1 slightly narrowed basally, funicular segments with 2 rows of longitudinal sensilla and 3 whorls of setae.

Mesosoma. Largely umbilicate, 1.2× as long as broad; notauli complete, shallow. Epicnemium imbricate, flattened. Mesepisternum anterior to femoral depression umbilicate; mesepimeron mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating from the posterior margin. Precoxal tooth formed by raised adscrobal carina present in lateral view. Lateral panels of propodeum and callus umbilicately punctate, distinctly delimited from median area by carinae forming irregular setose cells, median furrow delimited, forming 2 rows of irregular foveae (Fig. 25). Procoxa imbricate, lacking setation proximally. Mesocoxal lamella absent. Metacoxa sparsely setose anteriorly and one row of setae on the posterior apical margin. Forewing hyaline, marginal vein subequal to postmarginal vein in length. Basal cell with one row of setae.

Metasoma. Gaster 1.3× as long as mesosoma in lateral view; smooth, anterior edge of gastral tergites microreticulate (Fig. 28). Petiole 0.6× as long as broad in dorsal view, with projecting lateral teeth as well as mediodorsal prong. Gaster laterally compressed, oval shaped and convex in lateral view, ovipositor parallel to horizontal axis. $Gt_{1–4}$ glabrate, $Gt_{5–8}$ and apex of ovipositor sheaths setose. Gt_5 emarginate to expose Gt_6 spiracle. Gt_4 weakly emarginate in dorsal view.

Male. Body length: 1.7–2.2 mm. Color: Black, yellow areas as described for female. Sculpture as described for female. Antennae with funicular segments pedunculate, F_2–F_5 each with 2 rows of erect setae and 1 row of longitudinal sensilla (Fig. 30); scape with ventral plate in apical half. Gastral petiole in lateral view cylindrical, in dorsal view length about 1.5× as long as greatest width, 0.6× times length of metacoxa; evenly reticulate dorsally and ventrally, obliterated laterally.

Remarks. This widespread species is found from galls of 7 native species of *Diplolepis* that induce galls on leaves. Additionally, it is collected from stem galls of *D. fusiformans*, a species that is closely related to *D. rosaefolii*, which induces galls on leaves (Shorthouse 2010, Plantard et al. 1998). Two generations of *E. longavena* have been recorded as "fall emergents" exit spring-induced galls (e.g. *D. polita*) as early as mid-summer to early fall, while "spring emergents" overwinter and exit from galls the following year (Shorthouse 1973, 2010). It is likely that fall emergents attack late-summer induced galls

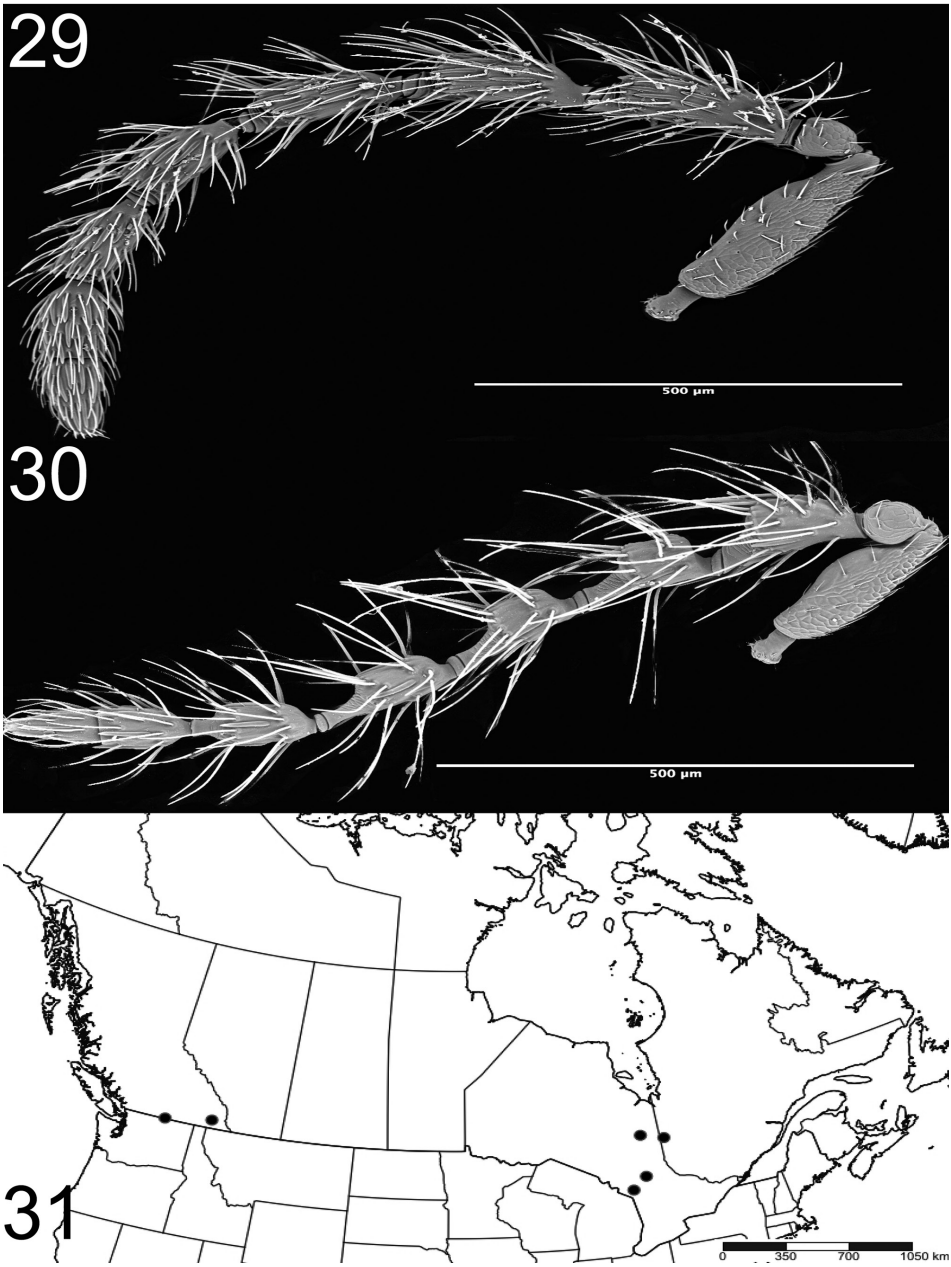


Figure 29–31. *Eurytoma discordans* **29** Male antenna. *E. longavena* **30** Male antenna **31** Known localities of *Tenuipetiolus ruber* in Canada.

(e.g. *D. nebulosa*), or late appearing galls of *D. polita* (Shorthouse 1973); however, it is unknown what factors determine this bivoltinism. *E. hebes* shares all the distinguishing characters of *E. longavena* but are smaller and brown, thus they are synonymized under

the latter. This species closely resembles *E. iniquus*, but can be distinguished by the wholly black pro- and mesocoxae.

Biology. Reared from galls induced by *Diplolepis bassetti*, *D. bicolor*, *D. fusiformans* on *R. blanda*; *D. gracilis* on *R. woodsii*; *D. nebulosa* on *R. blanda*; *D. polita*, *D. rosaefolii* on *R. acicularis* and *R. woodsii*; and *D. variabilis* on *Rosa* sp.

Material examined (52 females, 22 males). CANADA: Alberta: Coaldale, 24.X.2002, J.D. Shorthouse, ex *Diplolepis nebulosa* on *Rosa woodsii* (2F, 1M, CNCI); Peace River, 16.VIII.1970, J.D. & M.R. Shorthouse, ex *Diplolepis polita* fall/spring emergence (19F, 3M, CNCI). **British Columbia:** Kelowna, 19.X.1999, R.G. Lalonde, ex *Diplolepis rosaefolii* on *Rosa woodsii* (7F, 3M, CNCI). **Ontario:** Cochrane, 24.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis rosaefolii* on *Rosa acicularis* (8F, 7M, CNCI); Chelmsford, 1.X.1995, J.D.Shorthouse (2F, CNC); Manitoulin Island, 4.IX. 2010, J.D. & M.R. Shorthouse, ex *D. nebulosa* on *Rosa blanda* (2F, 4M, CNCI); Moose Factory Island, J.D. Shorthouse & M.G. St. John, ex *Diplolepis polita* on *Rosa acicularis* (4F, CNCI); Renfrew, 15.IV.2000, J.D. Shorthouse, ex *Diplolepis fusiformans* on *Rosa blanda* (2M, CNCI). **Québec:** La Sarre, B.L. Smallwood & Y.M. Zhang, 13.VII.2010, ex *D. polita* on *R. acicularis* (5F, 1M, CNCI). **Saskatchewan:** Douglas Provincial Park, J.D. & M.R. Shorthouse, 26.IX.1999, ex *D. gracilis* on *Rosa woodsii* (2F, 1M, CNCI); Pike Lake Provincial Park, J.D. & M.R. Shorthouse, 29.IX.1999, ex *D. gracilis* on *Rosa woodsii* (1F, CNCI).

Distribution. Widespread, from British Columbia, Alberta, Saskatchewan, Ontario, and Québec (Fig. 34).

Eurytoma discordans Bugbee

Figs 9, 22, 23, 26, 27, 29, 35

Eurytoma discordans Bugbee, 1951b: 220–223. Holotype female (USNM). Type data: USA, Indiana [Howe]; associated with galls induced by *Diplolepis globuloides* (Beutenmuller) = (*Diplolepis variabilis* (Bassett)) on species of *Rosa*, Dec 20, 1930.

Eurytoma acuta Bugbee, 1951b: 223–234. Holotype female (USNM). Type data: USA, Utah [Price]; associated with galls induced by *Diplolepis tuberculatrix xerophila* (Cockerell) on *Rosa*, April 20, 1920. Zhang et al. 2014 (synonymy under *Eurytoma discordans*).

Eurytoma calcarea Bugbee, 1951b: 240–249. Holotype female (USNM). Type data: USA, Utah [Wellsville]; associated with galls induced by *Diplolepis variabilis* (Bassett), September 6, 1927. Zhang et al. 2014 (synonymy under *Eurytoma discordans*).

Diagnosis. Females are distinguished from other species by the S-curved metasoma that is larger than head plus mesosoma (Fig. 27) and the sharply upturned ovipositor dorsad the horizontal axis of the metasoma. Males have elongated funicular segments and yellow fore- and midlegs similar to *E. obtusilobae*, however, it differs in the black pedicle and tegulae.

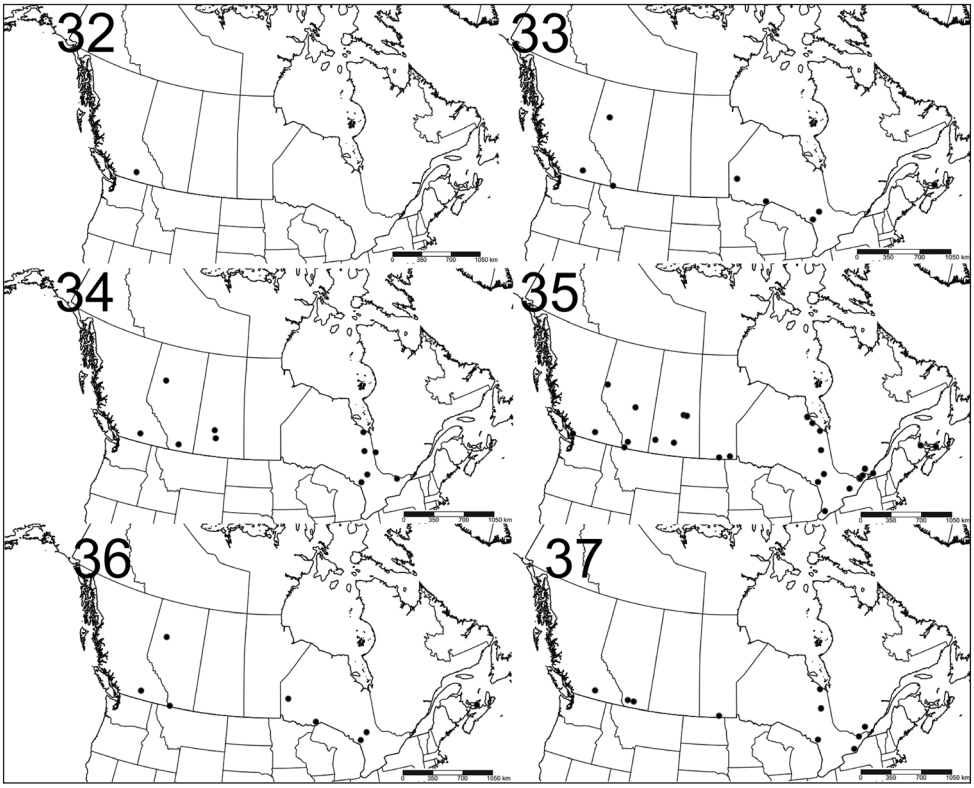


Figure 32–37. 32 Known localities of *Eurytoma shorthousei* in Canada **33** Known localities of *E. iniquus* in Canada **34** Known localities of *E. longavena* in Canada **35** Known localities of *E. discordans* in Canada. **36.** Known localities of *E. imminuta* in Canada **37** Known localities of *E. spongiosa* in Canada.

Females. Body length 2.1–5.0 mm. Color: Black except for the following yellow – basal half of scape, pro- and mesofemur, basal pro- and mesotibia, apex of metatibia, tip of ovipositor sheaths, tarsomeres 1–4, wing veins (Fig. 9).

Head. 1.2× as broad as high, umbilicate punctured (Fig. 22). Genal carina present, evenly sculptured; malar space 0.7× eye height, clypeus strongly emarginate and supraclypeal area smooth (Fig. 22). Toruli positioned slightly above lower ocular line. Intertorular space acute dorsally, with 2 rows setae. Ratio of LOL:OOL:POL is 1:1.3:2. Head posteriorly with postgenal lamina and postgenal grooves ridged, delimited ventrally by postgenal depression. Postgena evenly setose (Fig. 23). Funicular segments subequal in size, longer than wide; pedicel chalice-shaped; funicular segments fusiform; F_1 slightly narrowed basally, funicular segments with 2 rows of longitudinal sensilla and 3 whorls of setae (Fig. 26).

Mesosoma. Largely umbilicate, 1.5× as long as broad; notauli complete, shallow. Epicnemium imbricate, flattened, with superficial submedial, shallow depressions to receive procoxa. Mesepisternum anterior to femoral depression umbilicate; mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating

from the posterior margin. Precoxal tooth formed by raised adscrobal carina present in lateral view. Lateral panel of propodeum and callus with umbilic punctures, distinctly delimited from median area by carinae forming irregular setose cells, median furrow delimited, forming 2 rows of irregular foveae (Fig. 25). Procoxa imbricate, lacking setation proximally. Mesocoxal lamella absent. Metacoxa densely setose along anterior margins, glabrate with one row of setae along posterior distal margin. Forewing hyaline, marginal vein and postmarginal vein subequal in length. Basal cell evenly setose.

Metasoma. Gaster 1.8× as long as mesosoma in lateral view; smooth, anterior edge of gastral tergites microreticulate (Fig. 27). Petiole 0.7× as long as broad in dorsal view, with projecting lateral teeth as well as mediodorsal prong. Gaster laterally compressed, S-curve shaped and not convex in lateral view, ovipositor upturned dorsad horizontal axis. $Gt_{1–3}$ glabrate, Gt_4 with 1–4 setae lateromedially, $Gt_{5–8}$ and apex of ovipositor sheath densely setose. Gt_4 strongly emarginate on posterior margin dorsally.

Male. Body length: 1.7–3.1 mm. Color: Black, yellow areas as described for female. Sculpture as described for female (Fig. 29). Antennae with funicular segments longer than wide, pedunculate, F_2–F_5 each with 2 or more rows of apressed setae and 2 rows of longitudinal sensillae (Fig. 29); scape with ventral plaque in apical half. Gastral petiole in lateral view cylindrical, in dorsal view length about 1.5× as long as greatest width, 0.7× times length of metacoxa; evenly reticulate dorsally and ventrally, obliterated laterally.

Remarks. This is a widespread and morphologically variable species. Bugbee (1951b) originally divided this species into 3 based on subtle morphological differences and distribution: the Eastern populations as *E. discordans* and western populations as *E. acuta* (5 subspecies), and those smaller in size as *E. calcarea* (6 subspecies). Upon examining additional materials it was noted that the degree of infuscation on legs and scape are variable within this species and thus cannot be used as reliable distinguishing characters. The molecular evidence presented in Zhang et al. (2014) also support the monophyly of this group, albeit with the highest intra-specific divergence compared to other eurytomids. Considering there are no distinct geographical or host differences that support three distinct species, *E. acuta* and *E. calcarea* along with their associated subspecies were synonymized under *E. discordans* pending further molecular or ecological studies. It is also likely that *Eurytoma incerta* Fullaway is the senior synonym of *E. discordans* given the similar description by Bugbee (1951b). Closely resembles *E. obtusilobae*, but can be distinguished from the latter by the coloration of the tegulae, scape, and shape of the female metasoma.

Biology. Reared from field populations of galls induced by *D. bicolor* on *R. blanda*; *D. nodulosa* on *R. woodsii*; *D. spinosa* on *R. blanda* and *Rosa rugosa* Thunb.; *D. radicum* on *R. acicularis*; *D. tumida* on *R. woodsii*; *D. variabilis* on *R. woodsii*. Also reared from galls of *Diastrophus nebulosus* (Osten Sacken) on *Rubus* spp..

Material examined (197 females, 120 males). CANADA: Alberta: Beaverlodge, 1933 (1F, CNC); Head-Smashed-In Buffalo Jump, 10.V.2011, J.D. & M.R. Shorthouse, ex *Diplolepis tumida* on *Rosa woodsii* (3F, 4M, CNCI); Edmonton, 20.IV.1942, R.W.Salt (1F, CNC); Edmonton, 6.VI.1946, R.M.Mason, ex rose gall (5F, CNC); Waterton Lakes National Park, 9.V.2007, J.D. & M.R. Shorthouse, ex *Diplolepis bicolor*/*Diplolepis nodulosa* modified by *Periclistus* sp. on *Rosa woodsii* (24F, 20M, CNCI). **British**

Columbia: Kelowna airport, 20.V.2008, R.G. Lalonde, ex *Diplolepis variabilis* on *Rosa woodsii* (2F, 1M, CNCI); Summerland, 2.V.1959, R.E. Leech, ex *Rosa* (3F, CNC); Surrey, 9.IV.1954. K. Yamanaka, ex *Rubus* (4F, 2M, CNC). **Manitoba:** Morden, 1.IX.1986, J.D. Shorthouse, ex *Rosa woodsii* (7F, 3M, CNCI); Sandlands F.R., em 1.VI.1944, F.I.Survey, stem gall on raspberry (2F, CNC). **New Brunswick:** Kouchibouguac National Park, 8.VIII.1977, S.J. Miller (3F, 9M, CNC). **Ontario:** Attawapiskat, 18.V.2005, M.J.T. Bodnar, ex *Diplolepis spinosa* on *Rosa blanda* (22F, 20M, CNCI); Bell's Corners, 13.V.1940. O. Peck, Host *Diastrophus nebulosus* (1F, CNC); Chelmsford, 5.V.1994, S.E. Brooks, ex *Periclistus pirata*-modified galls of *Diplolepis nodulosa* (4F, 2M, CNCI); Cochrane, 24.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis spinosa* on *Rosa blanda* (5F, 5M, CNCI); Fort Albany, 28.V.2005, M.J.T. Bodnar, ex *Diplolepis radicum* on *Rosa acicularis* (4F, 2M, CNCI); Jockvale, 8–27.V.1955, O. Peck, *Rosa blanda*/*rugosa* (42F, 19M, CNC); Manitoulin Island, 29.IV.2011, J.D. Shorthouse, B.L. Smallwood & Y. M. Zhang, ex *Diplolepis nodulosa* modified by *Periclistus* sp. (2F, 1M, CNCI); Marmora, 20.VI.1945. G.R.Hammond. Cynipid gall on wild rose (4F, CNC); Merivale, 17.VI.1954. O. Peck, Host gall *Periclistus pirata* ex *Rosa blanda* (3F, 1M, CNC); Moose Factory Island, 23.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis spinosa* on *Rosa blanda* (5F, 5M, CNCI); One Sided Lake, em XII.1960. S.M. Clark (2F, CNC); Ottawa, 17–25.V.1955, O. Peck, ex *Rosa rugosa* (19F, 4M, CNC); Thamesville, 4.VII.1962. S.M.Clark, ex gall of wild rose (3F, CNC); Rockcliffe, 27.V.1959. S.M.Clark. gall on *Rosa* sp. (3M, CNC). **Prince Edward Island:** Eldon, J.D. & M.R. Shorthouse, 23.VIII.1992, ex *Periclistus pirata*-modified galls of *Diplolepis nodulosa* on *Rosa virginiana* (4F, 3M, CNCI). **Québec:** Aylmer, VIII.1939. E.G. Lester, Host *Periclistus sylvestris* (2F, 5M, CNC); Chrysostome, 23.VI.1986, ex Cynipidae on *Rosa* sp. (1F, CNC); Lac Mercier, 7.VIII.1937. G.S. Walley. (1F, CNC); Montréal, O. Peck, 22.V–11.VI.1962, ex *D. radicum* (6F, 2M, CNC). **Saskatchewan:** Caron, em 20–23.II.1951, F.I.Survey, rose gall (1F, 3M, CNC); Great Sand Hills, 22.IX.1999, J.D. & M.R. Shorthouse, ex *Diplolepis radicum* on *Rosa woodsii* (6F, 6M, CNCI); Snowden, 18.VII.1944, O. Peck (1F, CNC); White Fox, 17.VI.1944, O. Peck (3F, CNC).

Distribution. Widespread, from British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Québec, New Brunswick, and Prince Edward Island (Fig. 35).

Eurytoma imminuta **Bugbee**

Figs 10, 36

Eurytoma imminuta Bugbee, 1951b: 259–260. Holotype female (USNM). Type data: USA, Nevada [Pyramid Lake]; associated with galls induced by *Diplolepis variabilis* (Bassett) on *Rosa puberulenta*, May 20, 1929.

Diagnosis. *Eurytoma imminuta* can be distinguished from most *Eurytoma* species by black tegula and scape. *E. imminuta* differs from *E. spongiosa* by their small, oval metasoma that is not laterally compressed (Fig. 10).

Females. Body length 1.9–4.0 mm. Color: Black except for the following yellow – basal half of scape, apical fifth of pro- and mesofemur, basal pro- and mesotibia, apex of hindlegs, tip of ovipositor sheaths, tarsomeres 1–4, wing veination (Fig. 10).

Head. 1.2× as broad as high, umbilicate punctured with small tentorial pits. Genal carina present; malar space 0.8× eye height, supraclypeal area smooth (Fig. 22). Toruli positioned slightly above lower ocular line. Intertorular space obtuse dorsally, with 2 rows setae. Ratio of LOL:OOL:POL is 1:1.2:2.4. Head posteriorly with postgenal lamina and postgenal grooves ridged, delimited ventrally by postgenal depression. Postgena sparsely setose. Funicular segments subequal in size, fusiform; pedicel chalice-shaped; F_1 slightly narrowed basally, funicular segments with 2 rows of longitudinal sensilla and 3 whorls of setae; clava 2-segmented.

Mesosoma. Largely umbilicate, 1.5× as long as broad; notauli complete, shallow. Epicnemium imbricate, flattened. Mesepisternum anterior to femoral depression umbilicate; mesepimeron mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating from the posterior margin. Precoxal tooth formed by raised adscrobal carina present in lateral view. Lateral panel of propodeum and callus with umbilicate punctures, distinctly delimited from median area by carinae forming irregular setose cells, median furrow delimited, forming 2 rows of irregular foveae (Fig. 25). Procoxa imbricate, lacking setation proximally. Mesocoxal lamella absent. Metacoxa densely setose along anterior margins, glabrate with one row of setae along posterior distal margin. Forewing hyaline, marginal vein and postmarginal vein subequal in length.

Metasoma. Gaster 1.2× as long as mesosoma in lateral view; smooth, anterior edge of gastral tergites microreticulate (Fig. 10). Petiole 0.5× as long as broad in dorsal view, with projecting lateral teeth as well as mediodorsal prong. Gaster not laterally compressed, oval shaped and convex in lateral view, ovipositor parallel to horizontal axis. $Gt_{1–3}$ glabrate, Gt_4 with 1–4 setae lateromedially, $Gt_{5–7}$ and apex of ovipositor sheath densely setose. Gt_4 strongly emarginate on posterior margin dorsally.

Male. Body length: 1.7–2.0 mm. Color: Black, yellow areas as described for female. Sculpture as described for female. Antennae with funicular segments pedunculate, F_2–F_5 each with 2 rows of erect setae and 1 row of longitudinal sensilla (Fig. 30); scape with ventral plate in apical half. Gastral petiole in lateral view cylindrical, in dorsal view length about 1.5× as long as greatest width, 0.5× times length of metacoxa; irregularly reticulate dorsally and ventrally, obliterated laterally.

Remarks. *E. imminuta* in the USNM collection can be separated from *E. spongiosa* by the metasomal character noted. It is best to keep them as separate species based on the examination of hundreds of *E. spongiosa* in the collection in which there are smaller specimens resembles the *E. imminuta* in metasomal shape. The profemur leg coloration character is inconsistent within *E. spongiosa*.

Biology. Reared from galls induced by *Diplolepis ignota* on *R. woodsii*, *D. nebulosa*, *D. polita*, *D. spinosa* on *R. blanda*, *R. rugosa*; *D. rosae* on *R. canina*, *D. triforma* on *R canina*; *D. tumida* on *R. woodsii*, and *D. variabilis*.

Material examined (101 females, 50 males): CANADA: Alberta: Coaldale, 12.V.2007, J.D. & M.R. Shorthouse, ex *Diplolepis ignota* on *Rosa woodsii* (2F, CNCI);

Head-Smashed-In Buffalo Jump, 10.V.2011, J.D. & M.R. Shorthouse, ex *Diplolepis tumida* on *Rosa woodsii* (3F, 2M, CNCI). **British Columbia:** Kelowna, 20.V.2008, R.G. Lalonde, ex *Diplolepis variabilis* on *Rosa woodsii* (3F, 1M, CNCI). **Ontario:** Cochrane, 24.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis spinosa* on *Rosa blanda*, (5F, CNCI); Kanata, 19.IV.2006, J.D. & M.R. Shorthouse, ex *Diplolepis spinosa* on *Rosa rugosa* (2F, 6M, CNCI); Manitoulin Island, 2.V.2009, J.D. Shorthouse & J.D. Renelli, ex *Diplolepis triforma* on *Rosa canina* (7F, 3M, CNCI); Manitoulin Island, 3.V.2009, J.D. Shorthouse & J.D. Renelli, ex *Diplolepis rosae* on *Rosa canina* (5F, 1M, CNCI); Manitoulin Island, 6.V.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis triforma* on *Rosa canina* (9F, 5M, CNCI); Moose Factory Island, 23.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis spinosa* on *Rosa blanda*, (5F, 5M, CNCI); Picton, 28.IV.2003, J.D. Shorthouse, ex *Diplolepis mayri/D. rosae* on *Rosa canina* (12F, 7M, CNCI). **Manitoba:** Mordon, 1.IX.1986, J.D. Shorthouse, ex *Diplolepis spinosa* on *Rosa woodsii* (31F, 18M, CNCI). **Québec:** Mt. Tremblant, 23.XII.2004, M.J.T. Bodnar, ex *Diplolepis spinosa* on *Rosa rugosa* (17F, 2M, CNCI).

Distribution. Widespread, from British Columbia, Alberta, Manitoba, Ontario, and Québec (Fig. 36).

Eurytoma spongiosa Bugbee

Figs 11, 37

Eurytoma spongiosa Bugbee, 1951b: 254–258. Holotype female (USNM). Type data: USA, Indiana [Bloomington]; associated with galls induced by *Diplolepis rosae* (L.) on species of *Rosa*, April 14, 1933.

Diagnosis. Similar to *E. imminuta*, but metasoma larger and more elongated (Fig. 11).

Females. Body length 1.0–4.0 mm. Color: Black except for the following yellow - basal half of scape, posterior half profemur, mesofemur, basal pro- and mesotibia, apex of hindlegs, tip of ovipositor sheaths, tarsomeres 1–4, wing veination (Fig. 11).

Head. 1.3× as broad as high, with umbilicate punctures with small tentorial pits. Genal carina present; malar space 0.8× eye height; supraclypeal area smooth (Fig. 22). Toruli positioned slightly above lower ocular line. Intertorular space obtuse dorsally, with 2 rows setae. Funicular segments subequal in size, fusiform; pedicel chalice-shaped; F_1 slightly narrowed basally, funicular segments with 2 rows of longitudinal sensillae and 3 whorls of setae; clava 2-segmented. Ratio of LOL:OOL:POL is 1:1.2:2.5. Head posteriorly with postgenal lamina and postgenal grooves ridged, delimited ventrally by postgenal depression. Postgena sparsely setose.

Mesosoma. Largely umbilicate, 1.5× as long as broad; notauli complete, shallow. Epicnemium imbricate, flattened. Mesepisternum anterior to femoral depression umbilicate; mesepimeron reticulate ventrally, striolate or smooth dorsally, with longitudinal rugae originating from the posterior margin. Precoxal tooth formed by raised adscrobal carina present in lateral view. Lateral panels of propodeum and callus with

umbilicate punctures, distinctly delimited from median area by carinae forming irregular setose cells, median furrow delimited, forming 2 rows of irregular foveae (Fig. 25). Procoxa imbricate, lacking setation proximally. Mesocoxal lamella absent. Metacoxa densely setose along anterior margins, glabrate with one row of setae along posterior distal margin. Forewing hyaline, marginal vein and postmarginal vein subequal in length.

Metasoma. Gaster 1.2× as long as mesosoma in lateral view; smooth, anterior edge of gastral tergites microreticulate (Fig. 11). Petiole 0.5× as long as broad in dorsal view, with projecting lateral teeth as well as mediodorsal prong. Gaster not laterally compressed, oval shaped and convex in lateral view, ovipositor parallel to horizontal axis. $Gt_{1–3}$ glabrate, Gt_4 with 1–4 setae lateromedially, $Gt_{5–8}$ and apex of ovipositor sheath densely setose. Gt_4 strongly emarginate on posterior margin dorsally.

Male. Body length: 1.7–2.2 mm. Color: Black, yellow areas as described for female. Sculpture as described for female. Antennae with funicular segments pedunculate, F_2–F_5 each with 2 rows of erect setae and 1 row of longitudinal sensillae (Fig. 30); scape with ventral plaque in apical half. Gastral petiole in lateral view cylindrical, in dorsal view length about 1.5× as long as greatest width, 0.6× times length of metacoxa; irregularly reticulate dorsally and ventrally, obliterated laterally.

Remarks. Few consistent morphological differences were found between *E. imminuta* and *E. spongiosa* (identified in Zhang et al. 2014 as *E. spongiosa* 1, and *E. spongiosa* 2, respectively) despite deep divergence in *COI* sequences and differences in host records (Zhang et al. 2014). Considering there are examples of other members of the *Eurytoma rosae* species group having been identified as genetically distinct but morphologically indistinguishable (Ács et al. 2002, Gómez et al. 2011), the two species are therefore considered as distinct. Variation in size and degrees of infuscation on legs. Bugbee (1951b: 259) indicated that *E. flavicruensa* may represent "the extreme western equivalent of *E. spongiosa*." Only the holotype is intact and all of the paratypes are lacking metasoma, much of their legs, and antennae. He indicates the pro- and mesocoxae are yellow, but they are actually blackish on their lateral surfaces. Given the paucity of material of *E. flavicruensa*, evaluation of its species status must await the collection of additional topotypical material.

Biology. Reared from galls induced by *D. fusiformans* on *R. blanda*; *Diplolepis ignota* on *R. arkansana* Porter; *D. nebulosa* on *R. blanda*; *D. polita* on *R. acicularis*; *D. triforma* on *R. acicularis* and *R. canina*; and *D. variabilis*.

Material examined (28 females, 25 males). CANADA: Alberta: Coaldale, 12.V.2007, J.D. & M.R. Shorthouse, ex *Diplolepis ignota* on *Rosa arkansana* (4F, 2M, CNCI). **Ontario:** Cochrane, 24.IV.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis triforma* on *Rosa acicularis*, (11F, 7M, CNCI); Manitoulin Island, 2.V.2009, J.D. Shorthouse & J.D. Renelli, ex *Diplolepis triforma* on *Rosa acicularis*, (1F, 3M, CNCI); Manitoulin Island, 6.V.2010, J.D. Shorthouse & Y.M. Zhang, ex *Diplolepis triforma* on *Rosa canina*, (1F, 5M, CNCI); Manitoulin Island, 4.IX.2010, J.D. & M.R. Shorthouse, ex *Diplolepis nebulosa* on *Rosa blanda*, (1F, CNCI); Moose Factory Island, 13.VIII.1998, J.D. Shorthouse & M.G. St. John, ex *Diplolepis polita* on *Rosa acicularis* (1M, CNCI);

Renfrew, 15.IV.2000, J.D. Shorthouse, ex *Diplolepis fusiformans* on *Rosa blanda* (1M, CNCI). **Québec:** La Sarre, 13.VII.2010, B.L. Smallwood & Y.M. Zhang, ex *Diplolepis polita* on *Rosa acicularis* (5F, 1M, CNCI). **Saskatchewan:** Maple Creek, 10.V.2003, J.D. & M.R. Shorthouse, ex *Diplolepis ignota* on *Rosa arkansana* (5F, 5M, CNCI).

Distribution. From Alberta, Saskatchewan, Ontario, and Québec (Fig. 37).

Discussion

Taxonomic recognition of chalcid wasps of the family Eurytomidae is notoriously difficult, as is the case with members within the genus *Eurytoma* associated with galls of *Diplolepis* (Shorthouse 2010). All species associated with galls of *Diplolepis* are conservative in regards to adult morphology. The distinguishing features presented by Bugbee (1951a, 1951b, 1967, 1973) are unfortunately often ambiguous due to overlapping measurements and intermediate character states. While the results of the current study indicate that morphological characters on the posterior head capsule, male antennae, and petiole are particularly useful in species delimitation, they are often obscured on intact specimens and cannot be seen clearly unless dissections are performed.

The overall morphological similarities between the Canadian species of *Eurytoma* with other members of the *rosae* species group found in Europe suggest that these species shared a common evolutionary line. As the *rosae* group is most diverse in Europe (Lotfalizadeh et al. 2007b, Delvare pers. comm.), it seems likely that the six *Eurytoma* species found in Canada represent an extension of this species group, although the low number of Nearctic *rosae* group species could simply be the result of insufficient taxonomic study.

Although eurytomids are known from a wide variety of hosts (Lotfalizadeh et al. 2007b), those examined as part of this project were only found associated with galls induced by *Diplolepis* on native wild rose species and the introduced Japanese rose *Rosa rugosa* and the European rose *R. canina*. It is difficult to see overall patterns of host specificity by eurytomids associated with rose galls, as recorded in this paper; however, now that the species are more clearly delineated, a more detailed examination of the specimens collected from across Canada can be undertaken. A good start would be the wet collections of JDS now stored at Edinburgh University. There are thousands of eurytomids in this collection all associated with host galls, the host wild rose, and collection localities.

Even without this more extensive analysis, some trends are already apparent. Firstly, the abundance of eurytomids in the galls of all species of *Diplolepis* from across Canada indicate that eurytomids are so closely associated with galls of *Diplolepis* that some species, or certain populations of these species, are now restricted to rose galls. Eurytomids attack both galls initiated in the spring (*D. polita* and *D. spinosa*) and those initiated later in the season (*D. nebulosa* and *D. ignota*) indicating that the emergence periods of eurytomids are lengthy enabling them to track different periods of gall initiation. Some species such as *T. ruber* and *E. discordans* attack both leaf and stem galls.

Eurytoma iniquus and *E. discordans* attack both galls inhabited only by an inducer where they feed as koinobionts, along with inquiline-modified galls of the same *Diplolepis* where they feed as predators on immature *Periclistus* and then chew into several *Periclistus*-induced chambers to consume larvae (Shorthouse 1973). Some species such as *T. ruber*, *E. imminuta* and *E. spongiosa* feed on inhabitants of the *D. rosae* gall which is a species introduced from Europe (Shorthouse 2001). All three species of *Diplolepis* introduced from Europe are naturalized in Canada, along with their European host roses (Shorthouse 2001) and are inhabited by eurytomids. It is not known if these eurytomids came from Europe with galled host plants or if the endemic eurytomids have moved onto the European galls once they became established in Canada. We suspect *E. imminuta* and *E. discordans* have followed *D. spinosa* and *D. triforma* onto introduced *R. rugosa* which are grown in urban gardens where they are just as heavily attacked by eurytomids as are galls growing on wild roses in their natural habitat.

Three of the most widely distributed galls in Canada are those induced by *D. polita*, *D. spinosa* and *D. triforma* and all are heavily attacked by eurytomids. These observations suggest that eurytomids are highly plastic in their choice of hosts, ability to locate roses and their galls in all parts of the range of each, feed as predators or koinobionts on all species of gall inhabitants, tolerate cold and dry conditions of northern Canada, and in the case of *E. longavena*, have two generations per year when populations of the same gall appear both in the spring and mid-summer (Shorthouse 1973). Obtaining large numbers of eurytomids from rose galls over long distances is easy for once the mature galls are collected in the spring, gall inhabitants are emerged in the laboratory. Collecting galls induced by one species of *Diplolepis* in one habitat and emerging the adults, accurately establishes the species of inhabitants at that locality.

While the distribution of eurytomids in this study only includes localities within Canada, it is likely representative of the Nearctic fauna even though most diversity of wild roses occurs within Canada (Shorthouse 2010). As part of the contribution of this study, we have reported an expansion of known localities for seven species of eurytomids. While the full ranges of these eurytomids are still to be determined, we suspect their distribution mirrors that of their hosts. The exceptions are *E. obtusilobae* and *T. ruber* which apparently are only found in disjunctive populations in Canada, although past literature suggests it is widespread within USA (Bugbee 1951a, 1951b). As a result of our study, new provincial records were made from British Columbia to Prince Edward Island since the last revision (Bugbee 1951a, 1951b). Bugbee (1951b, 1967 and 1973) used distributions as an important criterion for delimiting species of *Eurytoma*. The range of expansions in our study joins the previously disjunctive populations and along with molecular data (Zhang et al. 2014) supports the synonymization of these species. In addition to the galls of *Diplolepis*, *E. discordans* and *T. ruber* have also been collected from galls of *Diastrophus* spp. on raspberry. Given the polyphagous nature of many of these eurytomid species, the full host range is likely much wider than currently known. Thus, using host records alone to distinguish morphologically similar species is error-prone and a source of confusion when identifying eurytomids (Lotfalizadeh et al. 2007b).

The systematic placement of the Eurytomidae within the superfamily Chalcidoidea has been controversial in past studies (Lotfalizadeh et al. 2007b, Gates 2008, Munro et al. 2011, Heraty et al. 2013). The species treated by Bugbee (e.g. 1951a, 1951b, 1967) undoubtedly includes many synonymous species, and a revision of all Nearctic eurytomids is needed. Details of the evolutionary relationships of *Diplolepis* with their host roses and the relationships between *Eurytoma* and other gall inhabitants using modern molecular techniques, remain to be undertaken. With further insight into the taxonomy of eurytomids associated with cynipid rose galls, a new and exciting approach has been provided for future phylogenetic studies of the whole superfamily Chalcidoidea.

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