Description of the Mature Larva of the Sand Wasp Bembix bidentata and Its Parasitoids (Hymenoptera: Crabronidae, Chrysididae, Mutillidae)

Authors: Tormos, Josep, Asís, Josep Daniel, Beneitez, Amparo, and Gayubo, S. F.

Source: Florida Entomologist, 92(1) : 43-53

Published By: Florida Entomological Society

URL: https://doi.org/10.1653/024.092.0108
DESCRIPTION OF THE MATURE LARVA OF THE SAND WASP BEMBIX BIDENTATA AND ITS PARASITOIDS (HYMENOPTERA: CRABRONIDAE, CHRYSIDIDAE, MUTILLIDAE)

JOSEP TORMOS, JOSEP DANIEL ASÍS, AMPARO BENEITEZ AND S. F. GAYUBO
Unidad de Zoología, Facultad de Biología, Universidad de Salamanca, 37071-Salamanca, Spain
E-mail: tormos@usal.es

ABSTRACT
The mature larvae of Bembix bidentata and one of its chrysidid and mutillid parasitoids are described and illustrated, and structures of phylogenetic value are discussed. The mature larva of B. bidentata is characterized by an integument with short setae (< 40 μm) and scanty microspinules. The ratio between the length of the antennal papilla and the width of the antennal orbit is a character state that can be used in the separation of the final instar of European Bembix species. The mature larva of Chrysidea disclusa is characterized by a combination of two character states: (1) an atrium without asperities or weak lines on the circumference, and (2) antennal papillae longer than broad; the larval morphology of Chrysidea previously was unknown. The mature larva of Chrysura hybrida is characterized, within the genus Chrysura, by the autapomorphy "maxillary palpus with 4 sensilla at apex." The range of hosts of Chrysura spp. is broadened to the Crabronidae. The mature larva of Smicromyrmex rufipes is characterized, within the Mutillinae, by having more than 8 apical setae and no apical papillae on the labium.

Key Words: Preimaginal stages, Bembix, Chrysidea, Chrysura, Smicromyrmex

RESUMEN
Se describen e ilustran, a la vez que se discuten estructuras de valor filogenético, la larva madura de Bembix bidentata y las de sus crisididos y mutílidos parasitoides. La larva madura de B. bidentata se caracteriza por presentar el tegumento con setas cortas (< 40 μm) y escasas microespinulas. La relación entre la longitud de la papila antenal y la anchura de la órbita antenal es un estado de carácter que podría utilizarse en la separación de los estados larvarios de las especies europeas de Bembix. La larva madura de Chrysidea disclusa se caracteriza por presentar la combinación de los siguientes estados de carácter: (1) atrium sin asperidades o líneas sobre la circunferencia y (2) papila antenal más larga que ancha; la morfología larvaria de Chrysidea era desconocida. La larva madura de Chrysura hybrida se caracteriza, dentro del género Chrysura, por presentar la autapomorfia: palpos maxilares con 4 sensilas en el ápice; el rango de hospedadores de Chrysura se amplía a los Crabonídeos. La larva madura de Smicromyrmex rufipes se caracteriza, dentro de los Mutillíneos, por presentar más de 8 setas, y no presentar papilas, sobre la zona apical del labio.

Translation by the authors.

From a study on parasitoid-host interactions within the Hymenoptera, carried out in Soria (Spain) since 1999, we collected data on 2 species of Chrysididae and 2 species of Mutillidae that act as parasitoids of a species of Crabronidae. The following host/parasitoid combinations were found: Bembix bidentata Vander Linden, 1829 (host)/parasitoids: (a) Chrysididae: Chrysidea disclusa (Linsenmaier, 1959) and Chrysura hybrida (Lepeletier, 1806); (b) Mutillidae: Smicromyrmex rufipes (Fabricius, 1787) and Nemka viduata (Pallas, 1773). Additionally, we obtained the mature larvae of the host and of the 4 parasitoid species.

The Crabronidae (sensu Melo 1999) form a broad family of Hymenoptera Aculeata in which the Bembicininae, with more than 1700 species (Pulawski 2007), represent one of the most numerous subfamilies. Although several authors (among them Evans & Lin 1956; and Evans 1959; 1964, 1987 are relevant) have studied the preimaginal stages of this subfamily, the number of species for which the mature larva has been described is very low, with larvae of a fair number of genera remaining unknown.

Bembix Fabricius includes around 350 species (Pulawski 2007), more than 50 being present in the Paleartic Region (Asís et al. 1992). Nevertheless, studies on larval morphology are scarce, and descriptions of the mature larva have been provided only for 24 species, of which 9 are Paleartic (Grandi 1926a, b, 1928; Evans & Lin 1956; Evans 1959; 1964; Iida 1979; Asís et al. 1989, 1992, 1997). In this paper we describe the morphology of the last instar of B. bidentata. This instar is il-
illustrated and compared with the previously described mature larvae of European species of this genus.

“Cuckoo wasps” (Chrysididae) are very common parasitoids or kleptoparasites of many fosorial Hymenoptera. Of this family, which includes about 2430 species (Kimsey & Bohart 1990), the mature larvae of 25 species have been described appropriately (Tormos et al. 2001, 2003, 2006, 2007), of which 2 belong to the genus Chrysura Dahlbom (Tormos et al. 2001). The larval morphology of Chrysidea Bischoff was unknown. In the present work the mature larvae of C. disclosa and Ch. hybrida are described, illustrated, and compared with the previously described mature larvae of the closest taxa.

The Mutillidae are ectoparasitoids of larval insects and they usually attack the postdefecated larvae or pupae of other insects, generally aculeate Hymenoptera (Brothers et al. 2000). Although the family includes more than 9000 species (Pitts & Matthews 2000), few studies have addressed its preimaginal stages and biology. Thus, with respect to their larval phases, only the mature larvae of 7 species or subspecies have been described accurately enough to be used for comparative purposes (Tormos et al. 2003). In this paper, we report the morphological character states corresponding to the postdefecating mature larva of S. rufipes that are essential for assessing the greater or lesser affinity of this genus with the closest genera. The prepupa of this species had been described by Grandi (1961). A description of the mature larva of N. viduata, of which specimens were also obtained in the present study, has been given in Tormos et al. (2003).

MATERIALS AND METHODS

Mature larvae of B. bidentata and of its parasitoids C. disclosa, Ch. hybrida, and S. rufipes were obtained at Rabanera del Campo (Soria, Spain) in Jun, 2003 (larvae of Ch. hybrida); Sep, 2003 (prepupae of S. rufipes); Jun, 2004 (larvae of C. disclosa), and Jun, 2006 (larvae of B. bidentata). The material for morphological studies was fixed and preserved in 70% EtOH. The remaining larvae and cocoons were placed in terraria with a sandy bed and with cells similar to the original ones from which they had been obtained. In the terraria, kept under environmental conditions of temperature, RH and photoperiod, we obtained adults to determine the species. The method employed for preparing the larval specimens and the terminology of larval morphology and format used in the descriptions follow those of Asís et al. (1997) and Tormos et al. (2001). The following abbreviations are used: d = diameter, h = height, l = length, and w = width. The descriptions are based on 2 mature larva (Bembix bidentata) and 1 mature larva (one each of the species of Chrysidae and Mutillidae). Voucher specimens are deposited at the “Torres-Sala” Entomological Foundation (Valencia, Spain).

RESULTS

Descriptions of Larvae

Bembix bidentata Vander Linden, 1829, (Figs. 1-5)

General Aspect (Fig. 1). Fusiform body (l = 2.20 cm, w (maximum) = 1 cm), thinner towards the anterior end. Anus terminal, as a transverse slit, with the supra-anal lobe slightly larger than intra-anal one. Pleural lobes well developed. Integument with scantly and disperse setae (l = 25 μm) and microspinules (l = 5 μm). Spiracles (Fig. 2) (d = 170-180 μm, n = 12) with atrium walls lined with concentric rows of asperities; the prothoracic ones slightly larger than the others. Opening to subatrium with branched spinules. Cranium (Fig. 3) (w = 1.4 mm, h (from the apex of clypeus) = 1.5 mm) with scattered, small setae (l = 10 μm); placoid sensilla close to the insertion of the mandibles. Coronal suture very conspicuous; parietal bands absent. Antennal orbits circular (d = 95 μm); antennal papillae (l = 32 × 30 μm) well developed, with 3 apical sensilla. Clypeus with setae (l = 10 μm) and sensilla (d = 5-10 μm). Labrum (Fig. 4a) (w = 650 μm; h = 190 μm) slightly emarginate, with around 28 setae (l = 20-30 μm) and 38 placoid (w = 20 μm) and 10-12 cupuliform (15-20 μm) sensilla, the latter located on the apical margin. Epipharynx (Fig. 4b) spinulose (l of spinules = 20 μm), with 2 central sensory areas, one on each side, without spinules and pigmented, with 6 placoid sensilla; 4 sensilla in the central anterior region. Mouthparts. Mandibles (Fig. 3) (l = 600 μm, w at the base = 400 μm) tri-quadridentate, without setae. Maxillae (Fig. 5b) (l = 380 × 360 μm) with a very spinulose lacinial area, and a setose (l of setae = 25 μm) external side. Galeae (170 × 35 μm) horn-shaped, slightly smaller than maxillary palpi (l = 175, w = 60 μm). Maxillary palpus with 5 sensilla at apex, 4 cupuliform and one placoid. Labium (Fig. 5a) (w = 340 μm) spinulose on oral face, and with setae on lower part. Labial palpi (l = 140, w = 40 μm) shorter than salivary orifice (l = 160 μm), with 5 sensilla at apex, 4 cupuliform and one placoid.

Chrysidea disclosa (Linsenmaier, 1959), (Figs. 6-13)

General Aspect (Figs. 6, 10): Body robust (l = 0.5 cm, w = 0.2 cm; abdominal segments divided into 2 annulet by a transverse crease. Anus terminal, as a transverse slit. Pleural lobes developed. Integument with scattered setae (l = 9 μm).
Spiracles (Figs. 7, 11, 12): (d first pair = 60 μm, rest = 40-55 μm, × (rest) = 52 μm, n = 12) with peritreme; atrium and opening into subatrium simple, naked; subatrium with 9-15 swellings. Cranium (Figs. 8, 13): (w = 650 μm, h = 500 μm) with scarce setae (l = 10-15 μm) arranged symmetrically. Coronal suture very well developed, parietal bands absent. Antennal orbits inconspicuous; antennal papillae (Fig. 13a) (l = 50 μm, w = 10 μm) long, below middle of cranium, with three apical sensilla. Clypeus with 10 setae (l = 10-20 μm) and 2 sensilla (w = 5 μm). Labrum (Figs. 9a, 13b) (w = 400 μm; h = 170 μm) emarginate, with around 26 setae (l = 10-20 μm). Epipharynx (Fig. 9b) with 12 sensilla (d = 5 μm). Mouthparts: Mandible (Fig. 8) (l = 450 μm, w = 200 μm) quadridentate, with teeth on different planes. Maxilla (l = 270 μm, w = 100 μm) with 3 setae (l = 15 μm) on external part. Maxillary palpus (12 × 8 μm) with 2 sensilla at apex, 1 of them larger; galeae differentiated (10 × 25 μm). Labium (w = 180 μm) with 2 setae (l = 12 μm) behind palpi; labial palpus (14 × 12 μm) with 4 sensilla at apex, one of them larger; salivary orifice (Fig. 13c) as a transverse slit (w = 85 μm).

Chrysura hybrida (Lepeletier, 1806),
(Figs. 14-19, 21-26)

General Aspect (Fig. 14): Body robust (l = 0.8 cm, w = 0.3 cm); abdominal segments divided into 2 annulets by a transverse crease. Anus terminal, as a transverse slit. Pleural lobes (Figs. 20, 21) developed, with a seta on apex. Integument (Figs. 21, 22) with setae on each segment, arranged in a transversal row (l = 3-4 μm). Spiracles (Figs. 15, 23): (d first pair = 60 μm, rest = 43-58 μm, × (rest) = 51.9 μm, n = 12) with peritreme; atrium simple, naked. Cranium with sparse setae (l = 8 μm). Coronal suture scarcely developed, parietal bands absent. Antennal orbits (Fig. 16) (d = 16 μm) circular, with 3 sensilla at centre. Clypeus (Fig. 24a) differentiated, with 22 setae (l = 7 μm) regularly distributed. Labrum (Figs. 17a, 23, 24b) (w = 350 μm; h = 120 μm) emarginate, with around 28 setae (l = 7 μm). Epipharynx (Fig. 17b) with 6 sensilla. Mouthparts: Mandible (Fig. 18) (l = 260 μm, w = 140 μm) tridentate. Maxilla (Fig. 19a) (w = 120 μm) with setae (l = 14 μm) on external part. Maxillary palpus (Fig. 25) (20 × 40 μm) with 4...
sensilla at apex; galeae (10 × 10 μm). Labium (Fig. 19b) (h = 280 μm, w = 160 μm) with 4 setae (l = 12 μm) behind palpi; labial palpus (Fig. 26) (40 × 40 μm) with 4 sensilla at apex; salivary orifice (Figs. 23, 24c) as a transverse slit (w = 90 μm).

Smicromyrmex rufipes (Fabricius, 1787), (Fig. 20)

The description agrees with that offered by Grandi (1961), to which the following aspects should be added:

General Aspect: Integument with scattered spinules (l of spinules = 12 μm) and setae (l = 20-30 μm). Abdominal and metathoracic spiracles with the atrium lined with ridges; opening into subatrium large and unarmed; subatrium long and expanded (d = 80 μm), with 6 swellings (Fig. 20).

DISCUSSION

The larval morphology of the European species belonging to the genus Bembix has been studied by Asís et al. (1989, 1992, 1997) and Grandi (1926a, b; 1928). On the basis of the body chaetotaxy, Asís et al. (1997) separated the 8 European species of this genus, of which the mature larvae were known, into 2 fairly well defined groups: (1) a first group characterized by showing well-developed setae (l > 65 μm) and numerous spinules on the integument (Bembix flavescens bolivari Hendlirsch, 1893, B. oculata Panzer, 1801, and B. rostrata (Linnaeus, 1758)), and (2) a second group in which the setae of the integument are much smaller (<40 μm) and the spinules are either absent or very scanty (Bembix merceti Parker, 1929, B. olivacea Fabricius, 1778, B. sinuata Panzer, 1804, B. tarsata Latreille, 1809, and B. zonata Klug, 1835). This second group would include B. bidentata, the species described here.

Regarding other character states that could be used in the separation of the mature larvae of European species of Bembix (Asís et al. 1992; 1997), it should be mentioned that in the larvae of B. bidentata described here a certain variability was observed in the number of teeth on the mandibles,

Figs. 6-9. Mature larva of Chrysidea disclusa: (6) general aspect: lateral view; (7) 2nd left spiracle (atrium, subatrium, and tracheal trunk); (8) cranium (frontal view); (9a) labrum and tegumental differentiations of the clypeus. In this illustration the setae and sensilla of the clypeus are shown surrounded by a circle; (9b) epiharynx.
and the number of cupuliform sensilla on the margin of the labrum. In contrast, the ratio length of the antennal papilla: width of the antennal orbit is constant (without variability). Despite this, since only 2 mature larvae were studied, it would be advisable to study a greater number of specimens of this and other species of the genus to determine whether this character state can be used to differentiate the final larval instar of *Bembix* species.

The biology of the Chrysididae is poorly known. Most information refers only to host identity, and even this is scanty (Evans 1966; Krombein 1967; Kimsey & Bohart 1990). It is therefore not surprising that to date all known hosts of *Chrysura* have been bees of the family Megachilidae (Hicks 1934; Kimsey & Bohart 1990). Here, we expand the range of hosts into the Crabronidae.

The description of the mature larvae of 2 Chrysidini (1 of them belonging to a genus whose final

---

Figs. 10-13. Mature larva of *Chrysidea disclusa*: (10) general aspect: ventral view; (11) 1st left spiracle; (12) 2nd left spiracle (detail); (13) head (frontal view) showing the antennal papilla (a), labrum emarginate (b), and salivary orifice (c).
larval stage morphology was unknown), provides new information that underscores the importance of larval characters when establishing the phylogenetic relationships of the Chrysididae.

The mature larvae of *C. disclusa* and *Ch. hybrida* share the character states that define the last instar of Chrysidae, Chrysidinae, and Chrysidini. The family Chrysididae is defined by dis-
playing the labrum with sensilla, and a well-developed peritreme. The subfamily Chrysidinae can be characterized by the following autapomorphies: (1) an integument with setae, and (2) a labrum with more than 2 setae. The mature larvae of the tribe Chrysidini are defined by showing abdominal segments divided into 2 annulets, and having cranium with 5 or more pairs of setae.

Following the analysis in the larvae already studied of the 15 characters that seem to be important to clarify the phylogeny of the group (Tormos et al. 2001; 2006), we observe that there are no autapomorphies within the Chrysidini that characterize the genus Chrysidea (Table 1). Accordingly, this taxon can be characterized by a combination of the 2 characters (Table 1), as follows: (1) an atrium without asperities or weak lines on the circumference (a character state shared with the genera Chrysis Linnaeus, Chrysura, Stilbum Spinola, and Trichrysis Lichtenstein), and (2) antennal papillae longer than broader (a character state shared with the genus Caenochrysis Kimsey & Bohart). Chrysura hybrida is characterized, within its genus, by display-
ing the autapomorphy “maxillary palpus with 4 sensilla at apex” (Table 1).

Bearing in mind the character states provided in this study, the mature larva of *S. rufipes*, unlike other species of Smicromyrmini described, exhibits the following traits (Table 2): (1) head without parietal bands, (2) frontoclypeal suture distinct, and (3) labium with more than 8 apical setae, and without apical papillae. Although there is no autapomorphy that allows the mature larva of *Smicromyrme* Thomson to be characterized, within the set of the family Mutillidae, it may be affirmed that the mature larva of this genus is characterized within the Mutillinae, by displaying more than 8 apical setae and no apical papillae on labium.

**ACKNOWLEDGMENTS**

We are indebted to Franco Strumia (Museo di Storia Naturale e del Territorio, Pisa, Italy) and Guido Pagliano (Museo Regionale Scienze Naturali, Torino, Italy) for helping in the determination of the chrysidid and mutillid parasitoids, respectively. Grants from the DGES (CGL2006-02568) and Junta de Castilla y León (SA010A06) supported the study.
TABLE 1. CHARACTERS USED IN THE TYPIFICATION OF THE MATURE LARVAE OF CHRYSIDIDAE. –

**ABDOMINAL SEGMENTS:** (1) ALL DIVIDED INTO 2 ANNULETS (+); NOT ALL DIVIDED INTO 2 ANNULETS (—). –
**INTEGUMENT:** (2) WITH SETAE (+); WITHOUT SETAE (—). (3) WITH SPINES (+); WITHOUT SPINES (—);
**Spiracles:** (4) atrium with asperities or weak lines on circumference (+); atrium without asperities or weak lines on circumference (—). (5) OPENING INTO SUBATRIUM WITH SPINES (+); OPENING INTO SUBATRIUM WITHOUT SPINES (—). **Cranium:** (6) WITH 5 OR MORE PAIRS OF SETAE (+); WITH 1 TO 4 PAIRS OF SETAE (—); WITHOUT SETAE (*). 
**Antennal Papillae:** (7) LONGER THAN BROADER (+); AS LONG AS BROAD OR BROADER THAN LONG (—). (8) WITH 3 SENSILLA AT APEX (+); WITH 2 SENSILLA (—); WITH 4 SENSILLA (*). 
**Labrum:** (9) EMARGINATED (+); NOT EMARGINATED (—). (10) WITH SENSILLA (+); WITHOUT SENSILLA (—). 
**Mandibles:** (11) WITH SETAE ON THE BASE (+); WITHOUT SETAE ON THE BASE (—). 
**Maxillae:** (12) WITH SPINULES (+); WITHOUT SPINULES (—). 
**Maxillary Palpi:** (13) WITH 5 SENSILLA AT APEX (+); WITH A DIFFERENT NUMBER OF SENSILLA (—). 
**Galeae:** (14) HIGHLY DEVELOPED (≥78 μM × 57 μM) (+); NORMALLY DEVELOPED (7-29 μM × 9-39 μM) (—); POORLY DEVELOPED (3-10 μM × 3-10 μM) (*); ABSENT (&). 
**Labium:** (15) WITH MARGIN PAPILLOSE (+); NOT PAPILLOSE (—).

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|
| **CHRYSIDIDAE, CHRYSIDINAE, CHRYSIDINI** | | | | | | | | | | | | | | |
| Caenochrysis doriae (Gribodo) | + | + | — | — | + | + | — | + | — | — | + | & | — |
| C. mucronata (Brullé) | + | + | + | + | + | — | — | + | — | — | * | — |
| C. sayi Bohart | + | + | — | + | + | + | + | — | — | — | + | — | + |
| Chrysidea disclosa (Linsenmaier) | + | + | — | — | + | — | — | + | — | — | — | — | + |
| Chrysis angustula Schenk | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. cembricola Krombein | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. fulgida Linnaeus | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. gracilis Förster | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. inaequidens Dahlbom | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. inflata Aaron | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. nitidula Fabricius | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. smaragdula Fabricius | + | + | — | — | + | — | — | + | — | — | — | — | + |
| Chrysura hybridra (Lepeltier) | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. pacifica (Say) | + | + | — | — | + | — | — | + | — | — | — | — | + |
| C. sonorensis (Cameron) | + | + | — | — | + | — | — | + | — | — | — | — | + |
| Exochrysis tolteca (Mocsáry) | + | + | + | + | — | — | + | — | — | — | — | — | + |
| Stilbum cyanura (Förster) | + | + | — | — | + | — | — | + | — | — | — | — | + |
| Trychrysis cyanea (Linnaeus) | + | + | — | — | + | — | — | + | — | — | — | — | + |

| **CHRYSIDIDAE, CHRYSIDINAE, ELAMPINI** | | | | | | | | | | | | | | |
| Hedychridium elegantulum Buysson | — | + | — | — | + | — | — | — | (4) | * | — |
| H. solierellae Bohart & Brumley | — | + | — | — | + | — | — | — | (4) | — | — |
| Philoctetes intermedius (Aaron) | — | + | — | — | + | — | — | — | (4) | — | — |
| Omalus biaccinctus (Buysson) | — | + | — | — | + | — | — | — | (4) | — | — |
| O. aeneus (Fabricius) | — | + | — | — | + | — | — | — | (4) | — | — |
| Pseudolopyga taylori (Bodenstein) | — | + | — | — | + | — | — | — | (4) | — | — |

| **CHRYSIDIDAE, AMISEGINAE** | | | | | | | | | | | | | | |
| Adelphe anisomorphae Krombein | — | — | — | — | + | — | — | — | (3) | — | — |
| Myrmecomimesis bispinosus (Riek) | — | — | — | — | + | — | — | — | (3) | — | — |

| **BETHYLIDAE** | | | | | | | | | | | | | | |
| — | — | — | + | — | — | + | — | — | — | + | & | — |
TABLE 2. CHARACTERS OF MATURE LARVAE OR PREPUPAE OF MUTILLIDAE.  

**Integument**: (1): with setae (+), without setae (—).  

**Abdomen**: (2) anal segment rounded above and below the transverse anal slit (+), abdominal segment elongate, produced above the anus (—).  

**Spiracles**: (3): with atrium lined with ridges (+), unarmed (—); (4) subatrium elongate (+), no differentiated subatrium (—).  

**Head**: parietal bands (5): present (+), absent (—); antennal orbits (6): located below middle of head (+), located on middle, or above middle, of head (—); frontoclypeal suture (7): distinct (+), indistinct (—).  

**Mandibles**: (8): with basal tooth smallest (+), with 4 apical teeth of about equal size (—).  

**Maxillae**: maxillary palpi (9): with 4 apical sensilla (+), with 3 apical sensilla (—).  

**Labium**: (10): with 8 apical setae (+), with a greater number of apical setae (—); (11): with 2 apical papillae (+), without apical papillae (—).

| Characters | Mutillinae Smicromyrmelini | Myrmosinae | Sphaeropthalminae |
|------------|----------------------------|------------|-------------------|
|            | Nemka                      | Smicromyrmelini | Myrmosula | Dasymutilla | Pseudomethoca | Sphaeropthalma | Odontophotopsis |
| N. viduata | +                          | +           | +                  | +          | +           | +           | —                  |
| S. rufipes | +                          | +           | +                  | +          | +           | +           | —                  |
| M. parvula | —                          | +           | +                  | +          | +           | +           | —                  |

**Taxa**

| Characters | Mutillinae Smicromyrmelini | Myrmosinae | Sphaeropthalminae |
|------------|----------------------------|------------|-------------------|
|            | Nemka                      | Smicromyrmelini | Myrmosula | Dasymutilla | Pseudomethoca | Sphaeropthalma | Odontophotopsis |
| 1          | +                          | +           | +                  | +          | +           | +           | —                  |
| 2          | +                          | +           | +                  | +          | +           | +           | —                  |
| 3          | +                          | +           | +                  | +          | +           | +           | —                  |
| 4          | +                          | +           | +                  | +          | +           | +           | —                  |
| 5          | +                          | —           | +                  | +          | +           | +           | —                  |
| 6          | +                          | +           | +                  | +          | +           | +           | —                  |
| 7          | —                          | +           | +                  | +          | +           | +           | —                  |
| 8          | +                          | +           | +                  | +          | +           | +           | —                  |
| 9          | +                          | +           | +                  | +          | +           | +           | —                  |
| 10         | +                          | —           | +                  | +          | +           | +           | —                  |
| 11         | +                          | —           | +                  | —          | —           | —           | —                  |
REFERENCES CITED

ASÍS J. D., GAYUBO, S. F., AND TORMOS, J. 1989. Notes on the preimaginal states of Iberian Sphecidae (IV). Description of larvae of *Bembix flavescens bolivari* Handlirsch, 1893 and *Bembix sinuata* Panzer, 1804 (Hymenoptera, Sphecidae). Nouv. Revue. Ent. (N.S.) 6: 313-319.

ASÍS J. D., GAYUBO, S. F., AND TORMOS, J. 1992. Data on the nesting behaviour of five European *Bembix* and description of the mature larvae of *B. merceti* and *B. rostrata* (Hymenoptera, Sphecidae). Dtsch. Ent. Z., N. F. 39: 221-231.

ASÍS J. D., GAYUBO, S. F., AND TORMOS, J. 1997. Descripción de las larvas maduras de *Hoplisoides punctuosus* (Eversmann) y *Bembix zonata* Klug. Doriana VI (299): 1-8.

BROTHERS D. J., TSCHUCH, G., AND BURGER, F. 2000. Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects. Insect. Soc. 47: 201-211.

EVANS, H. E. 1959. Studies on the larvae of digger wasps (Hymenoptera, Sphecidae). Part V. Conclusion. Trans. American Entomol. Soc. 85: 137-191.

EVANS, H. E. 1964. Further studies on the larvae of digger wasps. Trans. American Entomol. Soc. 90: 235-299.

EVANS, H. E. 1966. The Comparative Ethology and Evolution of the Sand Wasps. Cambridge, Mass.: Harvard University Press.

EVANS, H. E. 1987. Order Hymenoptera, pp. 597-710 In F. W. Stehr [ed.], Immature Insects. Vol. 2. Dubuque, Iowa: Kendall/Hunt, Publishing Company.

EVANS, H. E., AND LIN, C. S. 1956. Studies on the larvae of digger wasps (Hymenoptera, Sphecidae). Part II: Nyssoninae. Trans. American Entomol. Soc. 82: 32-65.

GRANDI, G. 1926a. Contributi a la conoscenza della biologia e della morfologia degli imenotteri melliferi e predatori III. Bol. Lab. Zool. Gen. 19: 269-327.

GRANDI, G. 1926b. Contributi a la conoscenza della biologia e della morfologia degli imenotteri melliferi e predatori IV. Mem. Soc. ent. Ital. 5: 187-213.

GRANDI, G. 1928. Contributi a la conoscenza biologica e morfologica degli imenotteri melliferi e predatori VI. Bol. Lab. Entom. R. Ist. sup. agr., 1: 8-31.

GRANDI, G. 1961. Studi di un entomologo sugli Imenotteri Superiori. Boll. Ist. Ent. Univ. Bologna 25: i-xvi, 397-400.

HICKS, C. H. 1934. Observations on a chrysidid parasite and its host. Entomol. News 44: 206-209.

IDA, T. 1979. Contributions to the knowledge on the sphecid larvae in Japan (Hymenoptera). Part II. Kontyu 37: 280-289.

KINSEY, L. S., AND BOHART, R. 1990. The Chrysidid Wasps of the World. New York: Oxford University Press.

KROMBEIN, K. V. 1967. Trap-Nesting Wasps and Bees: Life Histories, Nests, and Associates. Washington D.C.: Smithsonian Press.

MELO, G. A. R. 1999. Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera), with emphasis on the crabronid wasps. Scientific Papers, Nat. Hist. Mus. Univ. Kansas 14: 1-55.

PITTS J. P., AND MATTHEWS, R. W. 2000. Description of the larva of *Sphaerophalma pensylvanica* (Lepeletier) (Hymenoptera: Mutillidae: Sphaerophalminae). J. Entomol. Sci. 35: 334-337.

PULAWSKI, W. J. 2007. Catalog of Sphecidae. http://www.calacademy.org/research/entomology/Entomology_Resources/Hymenoptera/sphecidae/Genera_and_species_PDF/introduction.htm.

TORMOS, J., KROMBEIN, K. V., ASÍS, J. D., AND GAYUBO, S. F. 2001. A Systematic Study of Larvae of Chrysidini (Hymenoptera: Chrysididae). Ann. Entomol. Soc. America 94(6): 809-834.

TORMOS, J., ASÍS, J. D., AND GAYUBO, S. F. 2003. Description of the Mature Larva of *Nemka viduata* (Pallas) (Hymenoptera: Mutillidae: Mutillinae), a Parasitoid of *Stizus continuus* (Klug) (Hymenoptera: Crabronidae: Bembicine). J. Entomol. Sci. 38(4): 502-510.

TORMOS, J., POLIDORI, C., ASÍS J. D., AND FEDERICI, M. 2006. Description of the postdefecating larva of *Stilbum cyanura* (Forster) and observations on adult behavior. J. Entomol. Sci. 41(1): 1-8.

TORMOS J., ASÍS, J. D., POLIDORI, C., AND BOESI, R. 2007. Host association and description of the prepupa of *Chrysis fulgida* L. (Hymenoptera: Chrysididae). J. Entomol Sci. 42(1): 52-55.