**A remarkable life strategy in the iberian endemic Acinipe segurensis (Bolívar, 1908) (Orthoptera, Pamphagidae)**

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**Abstract:**

The first data on the developmental life cycle of Acinipe segurensis (Bolivar, 1908) are provided as well as a morphological description of the nymphal stages. Data provided refer to the number of nymphal stages in the two sexes and their duration. The species hibernate in the egg stage. Males undergo four nymphal stages before reaching the adult stage while females undergo five, the extra stage being the third one. Morphological features studied concerning the number of antennal segments, the morphology of the wing rudiments on lateral lobes of the meso- and metanotum and the morphology of the external genitalia both in male and female, allowed to briefly describe and illustrate the different nymphal stages. The life cycle is different from other Pamphagini species as concerns the hibernation period and the rate of nymphal growth. A discussion on the possible causes of such divergences is given.
A remarkable life strategy in the Iberian endemic *Acinipe segurensis* (Bolívar, 1908) (Orthoptera: Pamphagidae)

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Abstract. The first data on the developmental life cycle of *Acinipe segurensis* (Bolívar, 1908) are provided as well as a morphological description of the nymphal stages. Data provided refer to the number of nymphal stages in the two sexes and their duration. The species hibernate in the egg stage. Males undergo four nymphal stages before reaching the adult stage while females undergo five, the extra stage being the third one. Morphological features studied concerning the number of antennal segments, the morphology of the wing rudiments on lateral lobes of the meso- and metanotum and the morphology of the external genitalia both in male and female, allowed to briefly describe and illustrate the different nymphal stages. The life cycle is different from other Pamphagini species as concerns the hibernation period and the rate of nymphal growth. A discussion on the possible causes of such divergences is given.

Résumé. Une stratégie de vie remarquable chez *Acinipe segurensis* (Bolívar, 1908), endémique ibérique (Orthoptera : Pamphagidae). Les premières données sur le cycle biologique de *Acinipe segurensis* (Bolívar, 1908) sont fournies, ainsi qu'une description morphologique des stades nymphaux. Les données fournies font référence au nombre de stades nymphaux chez les deux sexes et à leur durée. Cette espèce hiberne au stade œuf. Les mâles passent par quatre stades nymphaux avant d'atteindre le stade adulte tandis que les femelles passent par cinq stades, le stade supplémentaire étant le troisième. Les caractéristiques morphologiques étudiées concernant le nombre de segments antenaires, la morphologie des ébauches alaires sur les lobes latéraux du méso- et métanotum et la morphologie des organes génitaux externes chez le mâle et la femelle permettent de décrire et illustrer les différentes phases nymphales chez les deux sexes. Le cycle de vie observé est différent du reste des espèces de Pamphagini en ce qui concerne la période d'hibernation et le taux de développement des nymphes. Une discussion sur les causes possibles de telles divergences est présentée.

Keywords: life cycle, nymphal morphology, nymphal development, Pamphagini.

*Acinipe segurensis* (Bolívar, 1908) is a Pamphagidae species endemic to the Iberian Peninsula and restricted to its Southern Mediterranean area (Llorente & Presa 1997). It is typical in places abounding with rosemary, where it lives feeding almost exclusively on the leaves of *Rosmarinus officinalis* L.

As usual, the studies on the biology and development of Pamphagidae are very scarce, particularly in comparison with those devoted to orthopteran species of economic interest. Nevertheless, the biology and development features of certain species, such as *Pamphagus elephas* (Linnaeus, 1758), *Prionotropis rhodanica* Uvarov, 1923, *Euryaryphes sitifensis* Brisout, 1854, *Acinipe hesperica* Rambur, 1838, *Acrostira euphorbiae* García & Oromí, 1992 and *Pamphagus marmoratus* Burmeister, 1838 and *Pamphagus sardeus* (Herrich-Schäffer, 1840) are known (Aiouaz & Boufersaqui 1973; Foucart & Lecocq 1996; Korsakoff 1941; Llorente 1990; López et al. 2007; Massa & Cusimano 1979 respectively).
Concerning the biology and behaviour of *A. segurensis*, a recent work due to Gómez Ladrón de Guevara et al. (2009) described population abnormal outbreaks that can produce significant vegetation damages, an unusual phenomenon among Pamphagidae (Mendizábal 1948; Massa & LoVerde 1990; Foucart & Lecoq 1996; Llorente & Presa 1997; Bounechada & Doumandji 2003; Massa et al. 2012).

Gómez et al. (2010) studied the species in nature for two consecutive years and pointed that the eggs hatch during the following spring after oviposition; so the life cycle seems to suffer diapause during the egg stage instead of entering diapause in larval stage, a characteristic feature of Pamphagini (Korsakoff 1941; Aiouaz & Boufersaqui 1973; Massa & Cusimano 1979; Llorente 1990; Foucart & Lecocq 1996; López et al. 2007).

With reference to behavioral aspects, García et al. (2014) described its sound producing mechanism, which shows certain differences from those known up to now in other brachypterous species of Pamphagidae, as well as the physical song features of song produced by females.

Taking into account the peculiarities that the life cycle of *A. segurensis* seems to present besides the devastating effects that its populations sometimes have, a study in captivity was carried out to know the life cycle features of this species. The data here provided may be of great interest for a possible population control as well as for trying to explain the causes of divergences observed respect to other species of the same genus and the tribe Pamphagini.

**Materials and methods**

A total of 36 females and 44 males, in nymphal stage, were collected in Monte del Portillo (38°20' 25"N 2°19'20"W), Yeste's municipal area (Albacete), located 800 metres a.s.l. The vegetation is composed of pine forest of Aleppo (*Pinus halepensis* Mill.) with undergrowth of abundant rosemary (*Rosmarinus officinalis*) and thyme (*Thymus vulgaris* L.) belonging to the Sector Manchego-Murciano (Gómez et al. 2010). Captures were made by hand on the plants or with an entomological net in April-May of 2012 and 2013. As the first moult coincides with hatching and animals were collected in the field after hatching, developmental stages were recorded starting with the first mobile nymph (Foucart & Lecoq 1996; Schultner et al. 2012; Elamin et al. 2014).

After collection, each individual was placed in a small glass jars, identified with a number, with the top perforated. Individuals were fed with lettuce (*Lactuca sativa* L.) and rosemary (*R. officinalis*). Water was added by spraying food “*ad libitum*”. Heat was provided with 40 w light bulbs lit for 16 hours a day for all the period. Every jar was reviewed every two days; food was changed and water added at that moment.

The number of instars and instars duration were measured separately for each individual by recording the number of developmental stages and the days elapsed between successive moults. Data were analyzed with IBM® SPSS® Statistics 20 software.

Exuviae were kept independently by identifying the number of the specimen and the date of the moult. Faeces were collected after each moult and stored identifying the number of the specimen and the corresponding moult. In addition the feeding behaviour of individuals was studied by direct observation.

During the development period the temperature remained between 20°C and 32,2°C and the relative humidity between 31,2% and 60%.

According to Llorente (1990), three growth features were registered per individual and instar to describe it: 1) the number of antennal segments, 2) the morphology of the wing rudiments on lateral lobes of the meso- and metanotum (tegmina and wings of the adult) and 3) the morphology of the external genitalia both in male and female.

**Results**
Of the 80 nymphs collected (44 males, 36 females), only 18 males and 17 females reached the adult stage. The remaining nymphs died at different stages.

Males and females of *A. segurensis* pass through different number of nymphal stages before reaching the adult stage. Males pass through four stages and females through five, the extra stage of females being the third one. As usual among Pamphagidae, the reversal of the wing rudiments occurs in the antepenultimate stage, that is, the third (moul II-III) in males and the fourth (moul III-IV) in females.

On average, females developed from egg to adult in 44.3 days and males in 34.6 days (Table 1). As can be seen, the length of each intermoult period was very variable. Results of U-Mann-Whitney tests applied did not show significant differences between the length of each stage in both sexes except when comparing the stage IV of males and females, which offers a significant difference (Mann-Whitney U test, U=66.50, p=0.003). Nevertheless, when comparing data from the two consecutive years, the two first stages (I and II) showed differences concerning its duration, both in males (Mann-Whitney U test, U=17.50, p=0.043; U=18.00, p=0.055, respectively) and in females (Mann–Whitney U test, U = 16.0, p=0.059; U=2.50, p<0.001, respectively), although such differences are only marginally significant for stage II of males and for stage I of females.

From a morphological point of view, the different nymphal stages are easily recognizable in both sexes by the studied features.

**Nymph I**

**Male.** Ensiform and flattened antennae composed of seven flagellomeres (Figure 1A). Sometimes, the third flagellomere may show a transversal groove in the middle. Wing buds barely sketched, with rounded lower edge (Figure 1B). Subgenital plate narrowed to apex, which is V-notched, with short lobes (Figure 1C).

**Female.** Antennae as in the male, ensiform and flattened, composed of seven or eight flagellomeres depending on whether the third is divided (Figure 2A) or only presents a groove. Wing buds as in the male (Figure 2B). Upper ovipositor valves short and obtuse, separated by a nick at angle. Lower ovipositor valves widely triangular, occupying a third of the sternite (Figure 2C).

**Nymph II**

**Male.** Ensiform antennae composed of seven / eigth flagellomeres in which grooves already appear marking future divisions, especially in the segments 3, 6 and 7 (Figure 1D). Wing rudiments clearly differentiated, the mesothoracic one rounded directed backwards, the metathoracic one more clearly distinguishable than in the previous stage. Both wing buds and lateral lobes show longitudinal ridges that will later be the veins (Figure 1E). Subgenital plate, in ventral view, even more narrowed to apex, the notch smaller and more closed, slightly curve (Figure 1F).

**Female.** Antennae strongly ensiform, similar to those of stage I, although some grooves appear in flagellomeres 3, 6 and 7 (Figure 2D). Wing buds very weak. Mesothoracic lobe slightly directed obliquely downwards. Metathoracic lobe almost identical to that of previous stage (Figure 2E). Upper ovipositor valves more acute and long, their inner edges are parallels. The inner valves, small but distinguishable, are between them. Lower ovipositor valves reaching the middle of the sternite (Figure 2F).
**Nymph III**

**Male.** Antennae less ensiform than at nymph II, at least at the apical zone, composed of eleven flagellomeres with grooves, especially in the most basal segments (Figure 1G). In this stage, the reversal of the wing rudiments has already happened. Tegmen rudiment reversed upward, reaching beyond the mesothorax hind edge; wing located behind tegmen, well differentiable, occupying the lower part of metathorax, its upper edge curved (Figure 1H). Apex of subgenital plate parabolic, reaching beyond the middle of paraprocts (Figure 1I).

**Female.** Antennae less ensiform than at nymph II, composed of nine flagellomeres, some of them showing transversal grooves (Figure 2G). Mesothoracic wing rudiment better definite and well lobate, directed obliquely downwards, not reaching the middle of metathorax; metathoracic wing rudiments well differentiated, directed downwards. In both wing rudiments, outlines of future venation is distinguished (Figure 2H). Upper ovipositor valves longer and more slender, addressing with their inner edges parallels at the base. Between them the apex of inner valves can be observed. Lower valves more developed, reaching the base of the upper ones (Figure 2I).

**Nymph IV**

**Male.** Antennae less ensiform than at nymph III, at least at the apical zone, composed of fourteen flagellomeres, the basal ones featuring grooves (Figure 1J). Tegmen rudiment reversed upward, reaching beyond the middle of metathorax and reaching the wing tip, showing marks of future veins. Hindwings smaller than the tegmina, with weaker venation, their upper edge curved and thick (Figure 1K). Subgenital plate longer than at nymph III, clearly reaching beyond cerci. Paraprocts and epiproct not visible ventrally (Figure 1L).

**Female.** Antennae more elongated and less ensiform than at nymph III, composed of thirteen flagellomeres, the basal ones with some grooves (Figure 2J). Reversal of the wing rudiments has already happened. Tegmen rudiment directed upwards, reaching beyond the hind mesothoracic edge. Wing rudiment well differentiated, its upper edge curved; it is located behind the tegmen rudiment, occupying the metathorax lower part (Figure 2K). Upper ovipositor valves reaching the middle of the paraprocts. Lower valves reaching beyond the middle of the upper ones, not reaching the base of cerci. Inner valves no longer visible (Figure 2L).

**Nymph V**

**Female.** Antennae longer than at nymph IV, still slightly ensiform, at least at base, composed of fifteen flagellomeres, the basal ones with some grooves (Figure 2M). Reversed tegmina rudiment reaching beyond the middle of metathorax and reaching or exceeding the wing rudiment end. Wing rudiments smaller, the upper edge curve and thick; their venation weaker (Figure 2N). Upper ovipositor valves reaching beyond the cerci apex. Apex of lower valves reaching the base of cerci, clearly showing a transversal keel. Subgenital plate with hind edge similar to that of the adult (Figure 2O).

Both in male and female nymphs, sometimes appear individuals in which two-stage characteristics are combined, especially in relation to the antennae.
Discussion

Life cycle features

The Orthopteran Mediterranean species have a life cycle with hibernation in egg stage and a rapid larval development. These features are considered typical of Acridoidea although it is due without a doubt to the fact that most of the species studied live in temperate areas with cold winters (Uvarov 1977). Nevertheless, there is a group of species belonging to the Pamphagini tribe which have a cycle absolutely different. They suffer hibernation as nymph, both in nature and in captivity (Uvarov 1967; Massa & Cusimano 1979; Llorente 1990; Massa 1990; Massa & Lo Verde 1990; Llorente et al. 1995; Bounechada et al. 2006, among others).

Observations both in field (Gómez et al. 2010) and in laboratory (results here presented), have stated that A. segurensis has a life cycle with hibernation in egg stage and a rapid larval development. These features in principle separate it from the rest of Pamphagini species, which are characterized by a long egg incubation period and a low rate of larval growth (Uvarov 1967), their larval development ranging between 4 and 12.5 months (Llorente & Presa 1997).

Nevertheless, in some Pamphagini species it has been described or suggested that, under certain circumstances or in some areas, they can vary their life cycle in a way that would resemble that here described for A. segurensis. For example, some species of the genus Ocneridia Bolivar, 1912 inhabiting Italy hibernate at nymphal stage (Massa et al. 2012) while, in Algeria, they hibernate at egg stage (Boudegzdame 1980; Bounechada et al. 2006). But in different areas of Algeria, depending on the weather conditions throughout the year, it has been noted that such species may present one type of hibernation or another (Bounechada et al. 2006).

In other species, such as the Canary endemic Acrostira euphorbiae, a life cycle is presented with adults and nymphs interspersed throughout the year depending of the phenology of their nourishing plant (López et al. 2007). However, the life cycle is not related to the nourishment for other species of the same genus, Acrostira bellamyi (Uvarov, 1922), which presents the same type of life cycle, that is with interspersed adults and nymphs all-year round (Hernández-Teixidor et al. 2014).

The available data suggest that all the species belonging to the genus Acinipe Rambur, 1838 have a life cycle with nymphal diapause (Descamps & Mounassif 1972; Llorente 1990; Llorente & Presa 1997; Massa et al. 2012), but Bounechada et al. (2006) indicate that Acinipe tibialis (Fieber, 1853) falls among the species that may show egg diapause in an Algerian area, although they do not provide any further information.

The reasons for variations of the life cycle of the different species are diverse. In some cases, as commented above, they are related to the continuous food availability (López et al. 2007), in other cases they are related to the macroclimatic conditions, such as the case of the Ocneridia species inhabiting Italy (Massa et al. 2012) and Northern Africa (Bounechada et al. 2006), the annual climate fluctuations, especially humidity (Bounechada et al. 2006; Guendouz-Benrima et al. 2011), the local adaptations (Guendouz-Benrima et al. 2011) and, even, some peculiarities of the embryonic development, such as the presence of embryos with “late diapause” and embryos with “premature diapause” [diapause tardive and diapause précoce sensu
Boudegzdame (1980)]. Since in no case the authors find a clear determinant factor for these variations, Guendouz-Benrima et al. (2011) consider the possible interaction of some of them.

**Number and duration of nymphal stages**

Among the Caelifera, the number of nymphal stages varies between 4 and 9 due to different causes (Uvarov 1977). Available data on Pamphagini are also diverse (Table 2). In some cases, females have an additional stage or a longer duration of the last nymphal stage, probably related to their larger size (Uvarov 1977) (Table 2).

There are few data on the nymphal development duration as well as that of intermoult periods, and the available ones were all obtained in captivity. Taking into account that the environmental conditions have a strong influence in such duration, mainly humidity and temperature (Schädler & Witsack 1999; Guendouz-Benrima et al. 2011; Petit 2014), the results are difficult to compare (Table 2). For *A. segurensis* the intermoult periods and the duration of the whole larval development are much shorter (Table 1), more similar to that of some Pamphagidae of tribe Trinchini, as *Prionotropis rhodanica* Uvarov, 1923 (Foucart & Lecoq 1996) and that of Caelifera with embryonic diapause (Schädler & Witsack 1999).

The significant differences found regarding the duration of stage IV in males and females seem to be clearly related to that in males it is the preadult stage and in females there is still another nymphal stage. Concerning the significant differences found in the duration of stages I and II between the two years of the study, they can be due to the different experimental environmental conditions in both years; in 2012 the mean temperature was 6°C higher and the mean RH was 20% lower than in 2013. So, these parameters could have affected the duration of the stages (Uvarov 1966, 1977; Joern & Gaines 1990; Schultner et al. 2012).

**Causes of the life cycle features**

The differential features of the life cycle of *A. segurensis* (absence of nymphal diapause) that, in principle, separate this species from the rest of Pamphagini, may be due to all or just some of the causes cited above affecting the different species. Nevertheless, when examining in detail such causes it can be seen that some of them do not seem to affect especially this species.

Variations in life cycle due to changes in climate in the different geographical locations of the species or to interannual climate variation (Bounechada et al. 2006; Guendouz-Benrima et al. 2011; Massa et al. 2012) do not seem to be the cause for *A. segurensis*. Their populations have been followed in Hellin (Albacete) (unpublished data) for ten years and no changes in the cycle have been observed. Its phenology has been studied in three different locations, Sierra del Taibilla (Albacete) (Gómez Ladrón de Guevara et al. 1992), Sierra Espuña (Murcia) (García & Presa 1985) and Font Roja (Alicante) (Hernández et al. 1998); in all them the life cycle is the same. It is also interesting to point out that there is no reference to the capture of nymphs before April.

Telfer & Hassal (1999) propose the possibility of ecotypes with different life cycle depending on the different climates in the distribution area. However, many Mediterranean Pamphagidae species have developed physiological adaptations in nymphs and adults in harsh climates but have not changed their biological cycle. This indicates that such feature is firmly rooted in their genetic constitution (Uvarov 1967, 1977). Furthermore, other species of Pamphagini from the Iberian Peninsula, sympatric with *A. segurensis*,
such as Ocnerodes brunneri (Bolivar, 1876) (Hernández et al. 1998), Kurtharzia sulcata (Bolivar, 1912) (Gómez Ladrón de Guevara et al. 1992) or Eumigus monticola (Rambur, 1838) (García & Presa 1985), present nymphal diapause in their life cycle; thus, it is possible to consider these populations of A. segurensis with embryonic diapausas as an ecotype.

It has been mentioned that the vegetation and its phenology in the proliferation area might have a bearing in the species life cycle (Muralirangan et al. 1997). Chapman & Sword (1997) indicate that the insects use plants for food, shelter or as a roost. There are many references for orthopterans concerning it and, especially for Pamphagidae, there are two clear examples in Acrostira euphorbiae (López et al. 2007) and Prionotropis rhodanica (Foucart & Lecoq 1996).

Acinipe segurensis has been always related to presence of Rosmarinus officinalis in its habitat (García & Presa 1985; Gómez Ladrón de Guevara et al. 1992; Llorente & Presa 1997; Hernández et al. 1998; Gómez Ladrón de Guevara et al. 2009, among others). This plant serves it as a refuge, perch and food. Although A. segurensis is considered a polyphagous species (Gómez Ladrón de Guevara et al. 2009), as all grasshoppers (Chapman 1990), it has been always observed in nature feeding on rosemary. Even, sometimes a decline of its populations has been observed after collecting the rosemary for essential oils extraction (Gómez Ladrón de Guevara et al. 1992). In studies of food preference (unpublished data), all the stages except nymph I prefer the rosemary. Thus, it could be considered that its diet is governed by the abundance of the host plant as occurs in other species following Chapman (1990). It also could be considered as a polyphagous species related to a concrete plant due to different ecological reasons (Chapman & Sword 1997).

Conclusion

The results provided here contribute to enlarge the knowledge on the biology of A. segurensis. The identification of the different larval stages can facilitate control strategies when needed. Nevertheless, the possible causes of the peculiarities of its biological cycle remain unclear. Maybe such features can be due to a set of closely linked phenomena, as already suggested by Guendouz-Benrima et al. (2011).

Acknowledgments

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References


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Figure 1. Acinipe segurensis, male nymph. A–C, Stage I: A, antenna; B, meso- and metanotum in lateral view; C, external genitalia from below. D–F, Stage II: D, antenna; E, meso- and metanotum in lateral view; F, external genitalia from below. G–I, Stage III: G, antenna; H, meso- and metanotum in lateral view; I, external genitalia from below. J–L, Stage IV: J, antenna; K, meso- and metanotum in lateral view; L, external genitalia from below. Legend: E: epiproct; MsW: mesothoracic wing rudiment; MtW: metathoracic wing rudiment; P: paraproct; SG: subgenital plate; WR: wings rudiments.

Figure 2. Acinipe segurensis, female nymph. A–C, Stage I: A, antenna; B, meso- and metanotum in lateral view; C, external genitalia from below. D–F, Stage II: D, antenna; E, meso- and metanotum in lateral view; F, external genitalia from below. G–I, Stage III: G, antenna; H, meso- and metanotum in lateral view; I, external genitalia from below. J–L, Stage IV: J, antenna; K, meso- and metanotum in lateral view; L, external genitalia from below. M–O, Stage V: M, antenna; N, meso- and metanotum in lateral view; O, external genitalia from below. Legend: E: epiproct; IV: inner ovipositor valve; LV: lower ovipositor valve; MsW: mesothoracic wing rudiment; MtW: metathoracic wing rudiment; P: paraproct; SG: subgenital plate; UV: upper ovipositor valve; WR: wings rudiments.
Table 1. *Length-Duration* of the nympha stages of *Acinipe segurensis*. N: number of individuals studied.

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<tr>
<td>Female</td>
<td>17</td>
<td>Mean ± SD</td>
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<td></td>
<td>Minimum</td>
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Table 2. Data available for number of nymphal stages, diapause stage and length of intermoult periods in different Pamphagidae species.

<table>
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<th>Species</th>
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<td>Massa &amp; LoVerde (1990)</td>
</tr>
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Figure 1. Acinipe segurensis, male nymph. A–C, Stage I: A, antenna; B, meso- and metanotum in lateral view; C, external genitalia from below. D–F, Stage II: D, antenna; E, meso- and metanotum in lateral view; F, external genitalia from below. G–I, Stage III: G, antenna; H, meso- and metanotum in lateral view; I, external genitalia from below. J–L, Stage IV: J, antenna; K, meso- and metanotum in lateral view; L, external genitalia from below. Legend: E: epiproct; MsW: mesothoracic wing rudiment; MtW: metathoracic wing rudiment; P: paraproct; SG: subgenital plate; WR: wings rudiments.

170x194mm (300 x 300 DPI)
Figure 2. Acinipe segurensis, female nymph. A–C, Stage I: A, antenna; B, meso- and metanotum in lateral view; C, external genitalia from below. D–F, Stage II: D, antenna; E, meso- and metanotum in lateral view; F, external genitalia from below. G–I, Stage III: G, antenna; H, meso- and metanotum in lateral view; I, external genitalia from below. J–L, Stage IV: J, antenna; K, meso- and metanotum in lateral view; L, external genitalia from below. M–O, Stage V: M, antenna; N, meso- and metanotum in lateral view; O, external genitalia from below. Legend: E: epiproct; IV: inner ovipositor valve; LV: lower ovipositor valve; MsW: mesothoracic wing rudiment; MtW: metathoracic wing rudiment; P: paraproct; SG: subgenital plate; UV: upper ovipositor valve; WR: wings rudiments.

170x173mm (300 x 300 DPI)