Phylogenetic relationships between the genera *Aphidius* and *Lysaphidus* (Hymenoptera: Braconidae: Aphidiinae) with description of *Aphidius iranicus* sp. nov.

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Abstract—We analyzed the phylogenetic relationships between eight *Aphidius* Nees and six *Lysaphidus* Smith species on the basis of 12 morphological characters by parsimony analysis. The consensus tree does not support the generic status of *Lysaphidus*. *Aphidius iranicus*, **sp. nov.**, associated with *Titanosiphon bellicosum* Nevsky on *Artemisia absinthium* L. from Iran, is described. The new parasitoid species is described and illustrated by line drawings, and its diagnostic characters are discussed. The taxonomic position of the subgenus *Tremblayia* Tizado and Núñez-Pérez is also considered. *Tremblayia* and *Lysaphidus* are newly classified as synonyms of *Aphidius*. The following new or revised combinations are proposed: *Aphidius adelocarinus* Smith, **comb. rev.**, *A. ramythirus* Smith, **comb. rev.**, *A. rosaphidis* Smith, **comb. rev.**, *A. viaticus* (Sedlag), **comb. nov.**, *A. arvensis* (Starý), **comb. nov.**, and *A. erysimi* (Starý), **comb. nov.**

Résumé—Nous avons analysé les relations phylogénétiques entre huit espèces d'*Aphidius* Nees et six espèces de *Lysaphidus* Smith se basant sur 12 caractères morphologiques par analyse de parsimonie. L'arbre de consensus ne supporte pas le statut générique de *Lysaphidus*. *Aphidius iranicus* **sp. nov.**, provenant d' Iran et associé avec *Titanosiphon bellicosum* Nevsky sur *Artemisia absinthium* L., est décrit. Cette nouvelle espèce de parasitoïde est décrite et illustrée en dessin linéaire et ses caractères diagnostiques sont discutés. La position taxonomique du sous-genre *Tremblayia* Tizado et Núñez-Pérez est aussi considérée. *Lysaphidus* et *Tremblayia* sont récemment classifiés en tant que synonymes d'*Aphidius*. Les combinaisons suivantes nouvelles ou de révision sont donc proposées : *Aphidius adelocarinus* Smith, **comb. rev.**, *A. ramythirus* Smith, **comb. rev.**, *A. rosaphidis* Smith, **comb. rev.**, *A. viaticus* (Sedlag), **comb. nov.**, *A. arvensis* (Starý), **comb. nov.** et *A. erysimi* (Starý), **comb. nov.**

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Introduction

The genus *Aphidius* Nees is one of the most diverse taxa within the subfamily Aphidiinae (Hymenoptera: Braconidae). *Aphidius* species attack a wide range of aphid hosts (Starý 1981; Tomanović *et al.* 2003; Kavallieratos *et al.* 2004). To date, over 100 species have been described worldwide. The evolution of small body size in Aphidiinae resulted in the loss of many useful morphological characters compared with their larger braconid ancestors (Müller *et al.* 1999). Within the Aphidiinae, *Aphidius* represents the most problematic group taxonomically, with a very limited number of reliable characters relevant for species separation (Starý 1973; Pungerl 1986; Kambhampati and Mackauer 1988; Unruh *et al.* 1989; Tomanović *et al.* 2003). The taxonomic and phylogenetic relationships between *Aphidius* and the closely related genera *Lysaphidus* Smith, *Euaphidius* Mackauer, and *Diaeretiella* Starý are also still unresolved (Kambhampati *et al.* 2000; Sanchis *et al.* 2000).

Lysaphidus was originally described as a subgenus of *Aphidius* (Smith 1944). Starý (1960*a*) gave *Lysaphidus* generic status on the basis of wing venation and some head characters. Later, several new species were described from the Palaearctic region (Starý 1960*b*; Takada 1966). Recently, Smith *et al.* (1999), Kambhampati *et al.* (2000), Sanchis *et al.* (2000), and Shi and Chen (2005) studied several genes and found nothing to support the generic status of *Lysaphidus*.

Lysaphidus species (like many other aphidiines, including some *Aphidius* species) have been found in association with host aphids (Hemiptera: Aphididae) on species of *Artemisia* L. and related plants of the family Asteraceae in the Nearctic (Pike *et al.* 1997) and Palaearctic regions (Klausnitzer 1968; Takada 1968; Starý 1973, 2006; Tizado and Núñez-Pérez 1994; Shi and Chen 2005). An *Aphidius* species was reported from *Titanosiphon neoartemisiae* Takahashi from Taiwan (Gahan 1926). Tizado and Núñez-Pérez (1994) described *Aphidius* (*Tremblayia*) *artemisicola* from *Titanosiphon artemisiae* (Koch) in Spain. The other records of this species are from Serbia, where it was reared from *Macrosiphoniella* sp. on *Artemisia vulgaris* L. (Tomanović *et al.* 2003; Kavallieratos *et al.* 2004). Only a relatively limited number of Aphidiinae have so far been detected in the Middle and Far East (Starý 1975, 1979; Takada 1979; Raychaudhuri *et al.* 1982; Starý *et al.* 1998, 2000).

In the present paper we discuss the taxonomic position of and phylogenetic relationships between *Lysaphidus* and *Aphidius* species associated with host aphids on *Artemisia* spp. and related plants and the relationship between *Aphidius* and *Tremblayia* Tizado and Núñez-Pérez on the basis of morphological characters. We describe a new *Aphidius* species reared from the *Artemisia absinthium* L. – *Titanosiphon bellicosum* Nevsky association in Iran.

Materials and methods

Collection and deposition of specimens

Samples of plants supplying aphid colonies containing both live and mummified aphids were collected during 1960–2004. Live aphids were killed and preserved in a mixture of 90% ethanol and 75% lactic acid in a ratio of 2:1 (Eastop and van Emden 1972) for later identification. The remaining aphid colonies were maintained in the laboratory until parasitoid emergence. Dissected parasitoid specimens were mounted on slides in Canada balsam for later identification. The external structure of emerged parasitoids was studied using an Olympus BH2 phase-contrast microscope and illustrated with a drawing tube (Trdan 2002; Kavallieratos *et al.* 2005).

The material examined in this study is deposited in the collection of the Institute of Zoology, Faculty of Biology, University of Belgrade (Serbia and Montenegro); the collection of P. Starý (České Budějovicé, Czech Republic); and the collection of the Laboratory of Agricultural Zoology and Entomology, Agricultural University of Athens (Greece). In the course of our study we examined the paratype and topotypes of *Aphidius* (*Tremblayia*) *artemisicola* (deposited in the collection of the Department of Animal Biology, University of León, Spain).

Phylogenetic analysis

A cladistic parsimony analysis of *Aphidius* and *Lysaphidus* species parasitizing host aphids on *Artemisia* spp. and related plants was undertaken. Four additional *Aphidius* species (*A. aquilus* Mackauer, *A. hortensis* Marshall, *A. ervi* Haliday, and *A. matricariae* Haliday)

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were also included in the analysis. In total, we analyzed 14 species (eight species of *Aphidius* and six of *Lysaphidus*) (Table 1) on the basis of 12 morphological characters. Characters with two states were coded as polymorphic. *Ephedrus persicae* Froggatt and *Toxares deltiger* (Haliday) were designated as the outgroups because, based on morphology and life-history traits, both species can be considered basal among extant Aphidiinae (Mackauer 1961; Starý 1981; Gärdenfors 1986). The phylogenetic analyses proceeded from a maximum parsimony search using PAUP* 4.0b10 (Swofford 2003), with all positions equally weighted. We calculated the consistency index, retention index, and rescaled consistency index as indicators of the extent of homoplasy in the data as well as their consistency. We performed a bootstrap analysis with 1000 replicates. The tree was visualized and printed using TreeView (Page 1996).

Character description

The morphological terminology used in the phylogenetic analysis and the parasitoid species description is based on Huber and Sharkey (1993) and Kavallieratos *et al.* (2001). Twelve characters were coded using original coding strategies or coded characters compiled from the literature (Quicke and van Achterberg 1990; Quicke and Belshaw 1999) (Table 2). Plesiomorphic character states are coded as “0”.

1. Number of segments of maxillary palp: 0 = 4; 1 = 3 (Fig. 1).
2. Number of segments of labial palp: 0 = 3; 1 = 2; 2 = 1 (Fig. 1).
3. Flagellomere 1 (F_1): 0 = less than 3.0 times as long as wide (ratio between length of F_1 and its width basally); 1 = more than 3.0 times as long as wide (Figs. 2, 3). More elongated flagellomeres in general represent an adaptation for host searching.
4. Number of longitudinal placodes on flagellomere 1 (F_1): 0 = 1 or more (Fig. 4); 1 = 0 (Figs. 2, 3).
5. Number of longitudinal placodes on flagellomere 2 (F_2): 0 = 3 or more (Fig. 4); 1 = 0–2 (Figs. 2, 3).
6. Forewing stigma: 0 = less than 3.0 times as long as wide (ratio between length of forewing stigma and width at Radial sector (Rs)) (Fig. 5); 1 = elongated, more than 3.0 times as long as wide (Fig. 6).
7. Forewing vein R1: 0 = subequal or equal to length of stigma (Fig. 5); 1 = less than half length of stigma (Fig. 6).

Reduction of wing venation represents an apomorphic character state.

8. Forewing M+m-cu vein: 0 = developed throughout (Fig. 5); 1 = not developed or partly developed under r-m vein (Figs. 6, 7).
9. Propodeum: 0 = areolate (Fig. 8); 1 = carinate (Figs. 9, 10) ; 2 = smooth or with small divergent carina at the base (Fig. 11).
10. Petiole: 0 = subquadrate, less than 3.0 times as long as wide at spiracles (Fig. 12); 1 = more elongated, more than 3.0 times as long as wide at spiracles.
11. Ovipositor sheath: 0 = dorsal margin straight; 1 = dorsal margin clearly concave (Figs. 13, 14). We assumed that a curved and longer ovipositor sheath is an apomorphic character state that allows easy access to the host aphid during oviposition (Starý 1976).
12. Ovipositor sheath: 0 = short (Fig. 13); 1 = elongated (Fig. 14).

Results

Aphidius iranicus Rakhshani and Starý, sp. nov.

Type material

Holotype (female): Iran, Rostam-Abad (Guilan Province), 3.v.2004, reared from *Titanosiphon bellicosum* Nevsky on *Artemisia absinthium* L., coll. E. Rahkshani (Collection of the Institute of Zoology, University of Belgrade). **Paratype** (one female): same data as holotype, slide-mounted (Collection of the Institute of Zoology, University of Belgrade).

Etymology

The new species is named after the country of origin, Iran.

Diagnosis

The new species is similar to *Aphidius artemisicola* Tizado and Núñez-Pérez in having the propodeum with an incomplete central areola (Fig. 9) and two divergent distal carinae but differs clearly from it in the range of the tentorial index (0.35–0.40 in *A. iranicus vs.* 0.43–0.50 in *A. artemisicola*), the ratio between lengths of F_1 and F_2 (F_1 1.1–1.2 times as long as F_2 in

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Table 1. Aphidiinae species used in phylogenetic analysis.

Species	Aphid host	Country
Aphidius absinthii Marshall	*Macrosiphoniella* spp.	Serbia, Czech Republic, Russia
Aphidius artemisicola Tizado and Núñez-Pérez	*Titanosiphon artemisiae* (Koch), *Macrosiphoniella* sp.	Spain, Serbia
Aphidius aquilus Mackauer	*Callaphis flava* Mordvilko, *Euceraphis punctipennis* (Zetterstedt)	Serbia
Aphidius ervi Haliday	*Acyrthosiphon pisum* (Harris), *Sitobion avenae* (Fabricius)	Serbia, Greece
Aphidius iranicus sp. nov.	*Titanosiphon bellicosum* Nevsky	Iran
Aphidius hortensis Marshall	*Liosomaphis berberidis* (Kaltenbach)	Serbia, Russia
Aphidius matricariae Haliday	*Aphis gossypii* Glover, *Brachycaudus helichrysi* (Kaltenbach), *Myzus persicae* (Sulzer)	Serbia, Greece, Russia
Aphidius phalangomyzi Starý	*Macrosiphoniella oblonga* (Mordvilko)	Serbia
Aphidius ramithyrus (Smith)	*Pleotrichophorus cf. wasatchii* (Knowlton), *Pleotrichophorus* spp.	United States of America, Mexico
**Aphidius arvensis* Starý	*Coloradoa artemisiae* (del Guercio)	Czech Republic, Serbia
**Aphidius erysimi* Starý	*Pseudobrevicoryne erysimi* Holman	Czech Republic
**Aphidius adelocarinus* (Smith)	*Microsiphoniella artemisiae* Boyer de Fonscolombe	United States of America
**Aphidius viaticus* Sedlag	*Pleotrichophorus glandulosus* (Kaltenbach)	Germany, Serbia
**Aphidius rosaphidis* (Smith)	*Chaetosiphon fragaefolii* (Cockerell)	United States of America
Outgroup		
Ephedrus persicae Froggatt	*Myzus persicae* (Sulzer)	Serbia, France, Iran, Japan, Czech Republic, United States of America
Toxares deltiger (Haliday)	Unknown	Turkey

Note: Full data for all species are published in Kavallieratos *et al.* (2004) and are available from the authors.
*Previously placed in *Lysaphidus*.

Table 2. Character matrix used in cladistic analysis of *Aphidius* species.

	1	2	3	4	5	6	7	8	9	10	11	12
A. absinthii	0	1	1	1	1	1	0	0	0	1	1	1
A. artemisicola	1	1	1	1	1	1	1	0	1	0	1	1
A. aquilus	0	1	0	1	1	1	1	0,1	0	0	0	0
A. ervi	0	0	1	0	0	1	0	0	0	1	1	0
A. iranicus	1	2	1	1	1	0	0	0	1	0	1	0
A. hortensis	0	1	0	1	1	1	0	0	0	0	1	0
A. matricariae	1	1	0	0	0	1	0	0	0	1	1	0
A. phalangomyzi	0	0	1	1	1	1	0	0	0	1	1	0
**A. ramithyrus*	0	1	0	1	1	1	1	1	0	0	1	0
**A. arvensis*	1	2	0	1	1	1	0	1	0,1	0	1	1
**A. erysimi*	1	2	0	0	0	1	0	1	0	0	0	0
**A. adelocarinus*	1	1	0	1	1	0	0	1	2	0	1	1
**A. viaticus*	0	1	1	1	1	1	1	1	0	1	1	0
**A. rosaphidis*	0	1	1	1	1	0	1	1	0	0	1	1
E. persicae	0	0	1	0	0	1	0	0	0	0	0	1
T. deltiger	0	0	0	0	0	1	0	0	0	0	0	0

Note: *Ephedrus persicae* and *Toxares deltiger* were used as outgroups.
*Previously placed in *Lysaphidus*.

A. iranicus (Fig. 2) *vs.* F_1 as long as F_2 in *A. artemisicola*), the number of segments of labial palps (one-segmented in *A. iranicus* (Fig. 1) *vs.* two-segmented in *A. artemisicola*), the ratio between length of the stigma and length of the distal abscissa of R1 (stigma as long as distal abscissa of R1 in *A. iranicus* (Fig. 5) *vs.* 2.20 times as long in *A. artemisicola*), and coloration of the head (brown in *A. iranicus vs.* orange in *A. artemisicola*) and mesosoma (brown in *A. iranicus vs.* mostly yellow-orange in *A. artemisicola*).

Aphidius iranicus also resembles *A. absinthii* Marshall but differs clearly from it in the range of the tentorial index (0.35–0.40 in *A. iranicus vs.* 0.45–0.60 in *A. absinthii*), the ratio between malar space and longitudinal eye diameter (0.20 in *A. iranicus vs.* 0.25–0.33 in *A. absinthii*), the number of long setae on the clypeus (4–6 in *A. iranicus vs.* 7–13 in *A. absinthii*), the number of antennal segments (13–14 in *A. iranicus vs.* 15–17 in *A. absinthii*), the ratio between length of the stigma and length of the distal abscissa of R1 (stigma as long as distal abscissa of R1 in *A. iranicus vs.* 1.50–3.00 times as long in *A. absinthii*), the number of segments of maxillary and labial palps (three-segmented maxillary and one-segmented labial palps in *A. iranicus vs.* four-segmented maxillary and two-segmented labial palps in *A. absinthii*), and the ratio between length and width of the petiole at the spiracles (2.70–2.80 in *A. iranicus vs.* 3.00–3.50 in *A. absinthii*).

Description

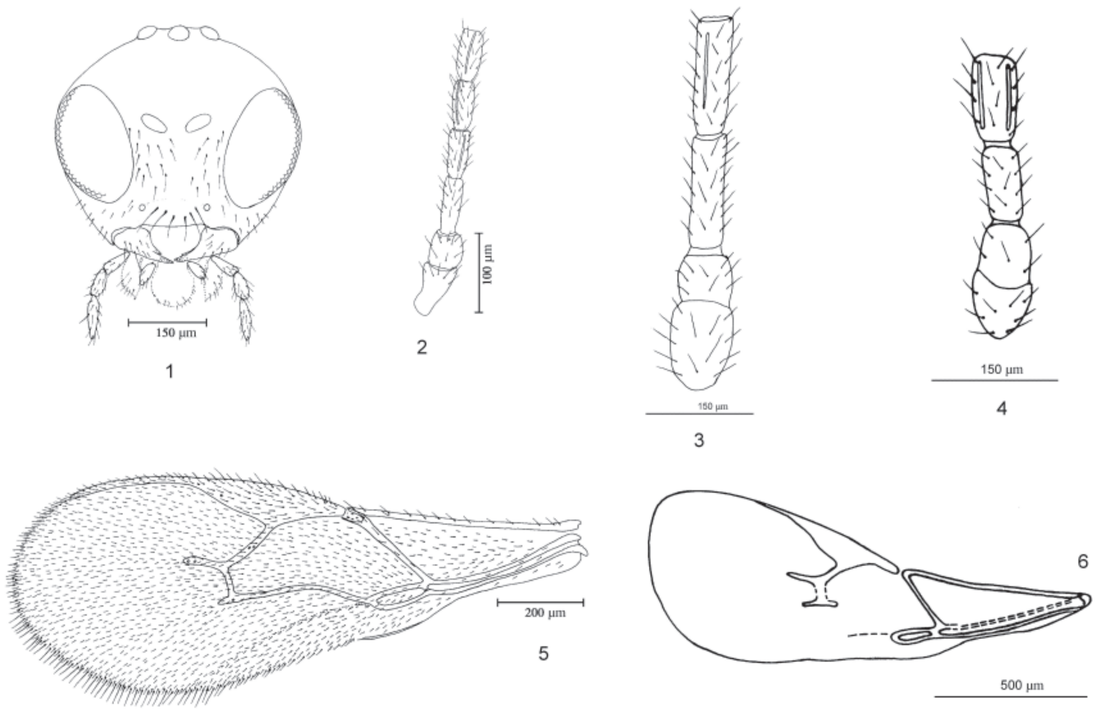
Female

Head (Fig. 1) wider than mesosoma at tegulae (ratio between width of head and width of mesoscutum, 1.40–1.45). Frons, vertex, and occipital area with sparse setae, face with narrow, bare band surrounded laterally by moderately long, regular, sparse setae. Tentorial index 0.35–0.40. Malar space equal to 0.20 of longitudinal eye diameter. Eyes oval, converging toward clypeus, with few short setae in posterior margin. Clypeus rounded, with 4–6 long setae. Antennae 13–14-segmented, moderately thickened at apex, with semierect and adpressed setae about as long as half of segment diameter. Scape and pedicel subglobular. Flagellar segments slender, with sparse, semierected setae. F_1 about 3.0 times as long as its maximum width, 1.1–1.2 times as long as F_2 and 1.3–1.4 times as long as F_3. $F_{1, 2, 3}$ with 0, 1–2, and 1–2 longitudinal placodes, respectively (Fig. 2). Maxillary palp 3-segmented (Fig. 1), apical segment distinctly longer than median and basal segments. Labial palp 1-segmented (Fig. 1).

Mesosoma

Mesonotum (Fig. 15) with notaulices in ascendant portion of anterolateral area, erased dorsally and outlined by 1–2 rows of long

Figs. 1–6. 1, *Aphidius iranicus*, holotype ♀: anterior aspect of head and maxillary and labial palps; 2, *Aphidius iranicus*, holotype ♀: flagellomeres 1–4; 3, *Aphidius absinthii* ♀: flagellomeres 1 and 2; 4, **Aphidius erysimi* ♀: flagellomeres 1 and 2; 5, *Aphidius iranicus*, holotype ♀: forewing; 6, **Aphidius ramythirus* ♀: forewing. (*, previously placed in *Lysaphidus*.)



sparse setae, which extend near to scutellum. Scutellum usually with 5–6 long setae laterally. Forewing (Fig. 5) stigma triangular, 2.70–3.00 times as long as its width, equal to or slightly longer than R1. Distal abscissa of R1 1.50 times as long as 3/Rs. Posterior margin of forewing with long setae. Propodeum (Fig. 9) with incomplete central areola bordered by two divergent posterocentral carinae extending transversely to the spiracles. Anterocentral carinae weakly developed, visible only in upper part, where united. Upper areola with 2–3 long setae laterally and lower areola with single seta in lower part. Upper areola about 1.50 times as long as lower areola. Hind femur and tibia with semierected, sparse setae, more dense near tibial spur.

Metasoma

Petiole (= metasomal tergum 1) (Fig. 12) parallel-sided, 2.70–2.80 times as long as its width at spiracle, anterolateral area with 6–8 costulae. Dorsal surface of petiole with fine rugosities and 6 long, erected lateromedial setae on basal portion. Genitalia: Ovipositor sheath (Fig. 13) short, distally truncated, with concave line at dorsal margin; ventral line straight. First valvula strongly convex ventrally and second valvula slightly concave (Fig. 13).

Coloration

Head brown, face and gena yellowish brown, mouthparts yellow, antenna uniformly brown. Mesosoma brown. Wings hyaline, slightly infumate; basal vein brown, stigma, R1, and radial veins yellow. Forewing surface covered with black, regular, short setae. Legs yellowish to brown. Petiole yellowish to brown; rest of metasoma and genitalia brown.

Body length

1.5–1.7 mm.

Male

Unknown.

Aphid mummy

Shiny white.

Host

Titanosiphon bellicosum Nevsky on *Artemisia absinthium* L.

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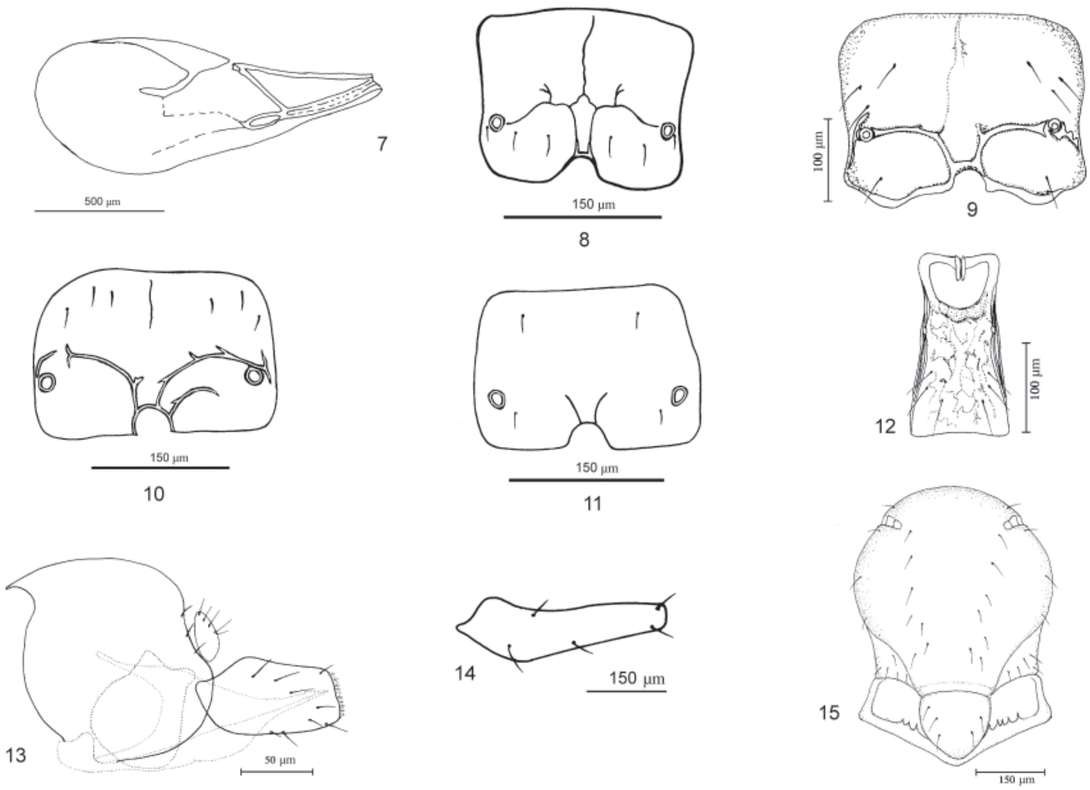
Figs. 7–15. 7, *Aphidius aquilus* ♀: forewing; 8, **Aphidius rosaphidis* ♀: dorsal aspect of propodeum; 9, *Aphidius iranicus*, holotype ♀: dorsal aspect of propodeum; 10, *Aphidius artemisicola* ♀: dorsal aspect of propodeum; 11, **Aphidius adelocarinus* ♀: dorsal aspect of propodeum; 12, *Aphidius iranicus*, holotype ♀: dorsal aspect of petiole; 13, *Aphidius iranicus*, holotype ♀: lateral aspect of ovipositor sheath; 14, **Aphidius adelocarinus* ♀: lateral aspect of ovipositor sheath; 15, *Aphidius iranicus*, holotype ♀: dorsal aspect of mesonotum. (*, previously placed in *Lysaphidus*.)



Distribution

Iran.

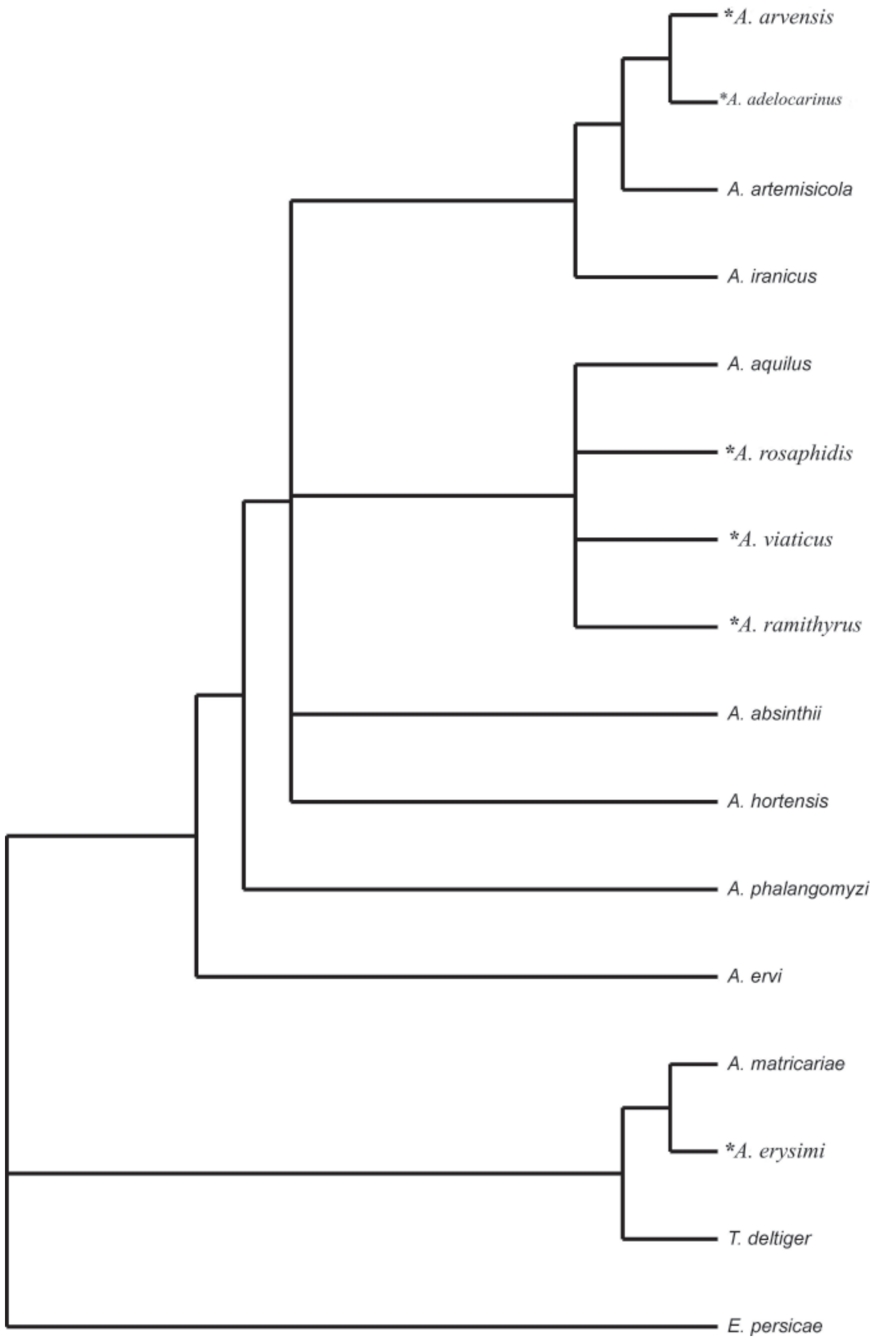
Phylogenetic inference

The consensus tree (Fig. 16) resulted from an unweighted parsimony analysis obtained from the six most parsimonious trees (tree length 34, consistency index 0.412, retention index 0.600, and rescaled consistency index 0.247).

Discussion

Tizado and Núñez-Pérez (1994) described the subgenus *Tremblayia* based on *Aphidius artemisicola* from the *Titanosiphon artemisiae* (Koch) – *Artemisia campestris* L. subsp. *glutinosa* (Gay *ex* Besser) Batt. association in Spain. The most important diagnostic character was "…propodeum with incomplete areola that is distinct as two divergent carinae in the lower portion…". After checking the paratype and topotypes we found that the propodeal areola in most specimens is not complete but has a clear indication of two upper carinae. Also, one topotype male has a complete propodeal areola. However, this character state is common in some small *Aphidius* species, probably because of allometry (Gärdenfors 1986). For example, some specimens of *A. urticae* Haliday emerged from the *Schizaphis scirpi* (Passerini) – *Typha latifolia* L. association also have an incomplete propodeal areola. Furthermore, some smaller *A. absinthii* specimens reared from the *Macrosiphoniella* spp. – *Artemisia* spp. association and *A. hortensis* specimens reared from the *Liosomaphis berberidis* (Kaltenbach) – *Berberis vulgaris* L. association have an incomplete propodeal areola, whereas larger ones have a complete pentagonal areola. *Aphidius iranicus* has an incomplete propodeal areola but a clear indication of two upper carinae. Although the

Fig. 16. Strict consensus tree of fourteen *Aphidius* taxa based on unweighted parsimony analysis of the six most parsimonious trees (tree length 34, consistency index 0.412, retention index 0.600, and rescaled consistency index 0.247). *Ephedrus persicae* and *Toxares deltiger* were used as outgroups. (*, previously placed in *Lysaphidus*.)



propodeal areola tends to be incomplete in parasitoids of small aphid hosts, as in the case of *A. artemisicola*, we expect to find additional *A. iranicus* specimens with a developed propodeal areola. We believe that there are no reliable characters justifying taxonomic separation of

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the subgenus *Tremblayia* and thus recognize *Tremblayia*, **syn. nov.** as a new synonym of *Aphidius*, not a subgenus.

Aphidius artemisicola has been found in associations with *Artemisia* species in Spain, Andorra, and Serbia (Tizado and Núñez-Pérez 1994; Tomanović *et al.* 2003; Kavallieratos *et al.* 2004). *Aphidius iranicus* was found in association with *Titanosiphon bellicosum* on *Artemisia absinthium* in Iran.

Lysaphidus species parasitize mainly small aphids (*e.g.*, species of *Titanosiphon* Nevsky, *Coloradoa* Wilson, *Microsiphoniella* Hille Ris Lambers, and *Lipaphis* Mordvilko) associated with *Artemisia* spp. and related plants of Asteraceae (Smith 1944; Starý 1960*b*; Pike *et al.* 1997). Owing to the small size of their aphid hosts, reductions in morphology occur. For example, *Lysaphidus* species have a one- or two-segmented labial palp, a reduced M+m-cu vein (only a small part is developed under the r-m vein), and an undeveloped propodeal areola in some species (*L. arvensis* Starý, *L. erysimi* Starý, and *L. adelocarinus* Smith) or even significantly reduced lower carinae (*L. adelocarinus* and *L. arvensis*). *Aphidius* species have two- or three-segmented labial palps, but *A. iranicus* has a one-segmented labial palp, like some *Lysaphidus* species (*L. arvensis*, *L. erysimi*). Also, forewing vein M+m-cu is usually developed in *Aphidius* species but is reduced in small *Aphidius aquilus* specimens. The propodeal areola is usually developed in all *Aphidius* species except *A. iranicus*, *A. artemisicola* (in certain cases, developed), and some small specimens of *A. absinthii*, *A. hortensis*, and *A. urticae*.

Lysaphidus arvensis, *L. adelocarinus*, *Aphidius artemisicola*, and *A. iranicus* form a clade (Fig. 16) sharing the following two synapomorphies: a small number of longitudinal placodes on F_1 and F_2 and a clearly concave dorsal margin of the ovipositor sheath. *Aphidius aquilus*, *L. rosaphidis* Smith, *L. viaticus* Sedlag, and *L. ramithyrus* Smith form another clade characterized by a two-segmented labial palp, a small number of longitudinal placodes on F_1 and F_2, and forewing vein R1 less than half the length of the forewing stigma as synapomorphies. Both clades are composed of species that parasitize small aphid hosts. The position of *Toxares deltiger* as sister group to the clade of *A. matricariae* + *L. erysimi* is probably due to the small number of species analyzed or the insufficient number of characters used. *Toxares deltiger* represents one of the basal lineages within Aphidiinae. It is characterized by several plesiomorphies, such as the braconid type of wing venation with seven closed cells in the forewing, a large number of longitudinal placodes on flagellomeres 1 and 2, and a short and triangular ovipositor sheath.

After bootstrap analysis with 1000 replicates, all *Aphidius* and *Lysaphidus* species studied form a polytomic tree (Fig. 16). Our tree is weakly supported because we analyzed closely related taxa with a restricted number of reliable characters for species separation. On the basis of the morphological characters examined, there is no clear distinction between *Aphidius* and *Lysaphidus*, and the tree does not support the generic status of *Lysaphidus*. *Lysaphidus*, **syn. nov.** is here synonymized with *Aphidius*, and the following new or revised combinations are proposed: *Aphidius adelocarinus* Smith, **comb. rev.**, *A. ramythirus* Smith, **comb. rev.**, *A. rosaphidis* Smith, **comb. rev.**, *A. viaticus* (Sedlag), **comb. nov.**, *A. arvensis* (Starý), **comb. nov.**, and *A. erysimi* (Starý), **comb. nov.**

We did not revise the following species attributed to *Lysaphidus* by various authors: *L. multiarticulatus* Ashmead (Smith 1944); *L. pleotrichophori* Takada, *L. matsuyamensis* Takada, and *L. callipterinellae* Takada (Takada 1966); *L. macrosiphoniella* Tamili and Raychaudhuri and *L. quadrii* Shujauddin (Raychaudhuri 1990); *L. santolinae* Michelena Saval and Sanchis Segovia (Michelena Saval and Sanchis Segovia 1995); and *L. kunmingensis* Wang and Dong (Wang and Dong 1997). These taxa are problematic and need further taxonomic treatment.

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