

The systematic position of *Alipumilio* and *Nausigaster* based on early stages (Diptera, Syrphidae)

[Zur systematischen Stellung von *Alipumilio* und *Nausigaster* im Ergebnis von Studien an ihren präimaginalen Stadien (Diptera, Syrphidae)]

by

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Abstract The larval and puparial stages of *Alipumilio femoratus* SHANNON, 1927, *Nausigaster texana* CURRAN, 1941 and *Nausigaster unimaculata* TOWNSEND, 1897 are described. Breeding sites and larval feeding modes are discussed. *Alipumilio* SHANNON, 1927 and *Nausigaster* WILLISTON, 1884 were both placed in the Eumerini by THOMPSON (1972). Larval structure supports such a position in *Alipumilio*, which may be the most plesiomorphic syrphid yet known. However, *Nausigaster* larvae were completely different and were closely related to *Criorhina* MEIGEN, 1822 in the Xylotini.

Key words Larva, puparium, phylogeny, head skeleton

Zusammenfassung Larven und Puparien von *Alipumilio femoratus* SHANNON, 1927, *Nausigaster texana* CURRAN, 1941 und *Nausigaster unimaculata* TOWNSEND, 1897 werden beschrieben. Es erfolgt eine Diskussion der Larvalhabitate und der Ernährungsweisen der Larven. *Alipumilio* SHANNON, 1927 und *Nausigaster* WILLISTON, 1884 wurden durch THOMPSON (1972) in die Tribus Eumerini eingeordnet. Strukturmerkmale der Larven von *Alipumilio*, die als diejenige Syrphidenlarve mit den ursprünglichsten Merkmalen unter den derzeit bekannten Larven gelten kann, unterstützen diese Zuordnung. Die *Nausigaster*-Larven erwiesen sich jedoch als völlig andersgestaltig und sind eng mit *Criorhina* MEIGEN, 1822 innerhalb der Xylotini verwandt.

Stichwörter Larve, Puparium, Phylogenie, Kopfskelett

Introduction

Building on HULL (1949) and STONE et al. (1965), THOMPSON'S (1972) influential study revised the supraspecific taxonomy of neotropical milesine Syrphidae and provided the means for future workers to make progress in this large and important fauna. THOMPSON (1972) suggested phylogenetic relationships based primarily on partial analyses of adult and some larval characters using the standard Hennigian methods of the time, and hence did not use parsimony methods. One supraspecific taxon proposed was the Eumerini which included six genera in the sequence: {*Psilota* MEIGEN, 1822 [*Eumerus* MEIGEN, 1822 (*Nausigaster* WILLISTON, 1884 + *Alipumilio* SHANNON, 1927)] [*Azpeytia* WALKER, 1865 + *Merodon* MEIGEN, 1803]}.

However using parsimony methods and larval characters, ROTHERAY & GILBERT (1999) found no support for suprageneric taxa such as subfamilies and tribes within Palearctic Syrphidae. Included in this latter analysis were three Eumerini (sensu THOMPSON 1972) genera: *Eumerus*, *Merodon* and *Psilota*. Of these *Eumerus* and *Merodon* formed a sister group and were basal within Syrphidae. However *Psilota* was placed in a much more derived position, close to *Sphagina* MEIGEN, 1822 and *Syrpitta* LEPELETIER & SERVILLE, 1828 (ROThERAY & GILBERT 1999).

In this paper we investigate larval morphology and breeding habits of species of two more of THOMPSON'S (1972) Eumerini genera, *Alipumilio* and *Nausigaster*. The early stages of *Alipumilio* are apparently undescribed and only the larva of one *Nausigaster* species has been described (CARRERA et al. 1947). We also examine the phylogenetic position of these genera using the character set previously developed by ROTHERAY & GILBERT (1999).

Materials and methods

Larvae of *Alipumilio femoratus* SHANNON, 1927 were borrowed from the Smithsonian Institution, Washington DC. Larvae of *Nausigaster* were obtained during fieldwork in Mexico in 1999. One species was reared from larvae found in decaying cacti (Cactaceae) and another in decaying bromeliads (Bromeliaceae). Larvae were reared by placing them in small amounts of decaying plant tissue in plastic tubs (about 10 cm diameter by 5 cm high) with part of the plastic lid replaced by netting for respiration. Small amounts of water were added every few days to keep conditions wet. Puparia were removed and placed individually in separate containers until adults emerged. One *Nausigaster* larva from cacti and one from bromeliads were fixed by placing in boiling water for several minutes and preserved in 70 % alcohol.

Larvae of all three species were examined by removing them from preservative, drying on tissue paper and studied using light microscopy. Head skeletons were studied by either soaking puparia (one per *Nausigaster* species) or the anterior end of a third stage *Alipumilio* larva in 10 % KOH for about 2 hours. Head skeletons were either removed from puparia or dissected from the larva and examined under light microscopy.

To investigate the phylogenetic position of *Alipumilio* and *Nausigaster*, the larva of each species was scored for 187 characters obtained from all over the body, the same characters described and used by ROTHERAY & GILBERT (1999). The results were run using Hennig86 with all the taxa of ROTHERAY & GILBERT (1999) but excluding aphidophages except *Melanostoma* SCHINER, 1860; *Pipiza* FALLÉN, 1810 and *Pipizella* RONDANI, 1856. Aphidophages were excluded to improve run times. All characters were treated as unordered. Initial trees were obtained using the command **mh***, and then others found using **bb***. A strict consensus tree was obtained using the command "**nelsen**". The successive weighting option was used to reduce the number of trees, and then a strict consensus tree was produced, as before.

Results

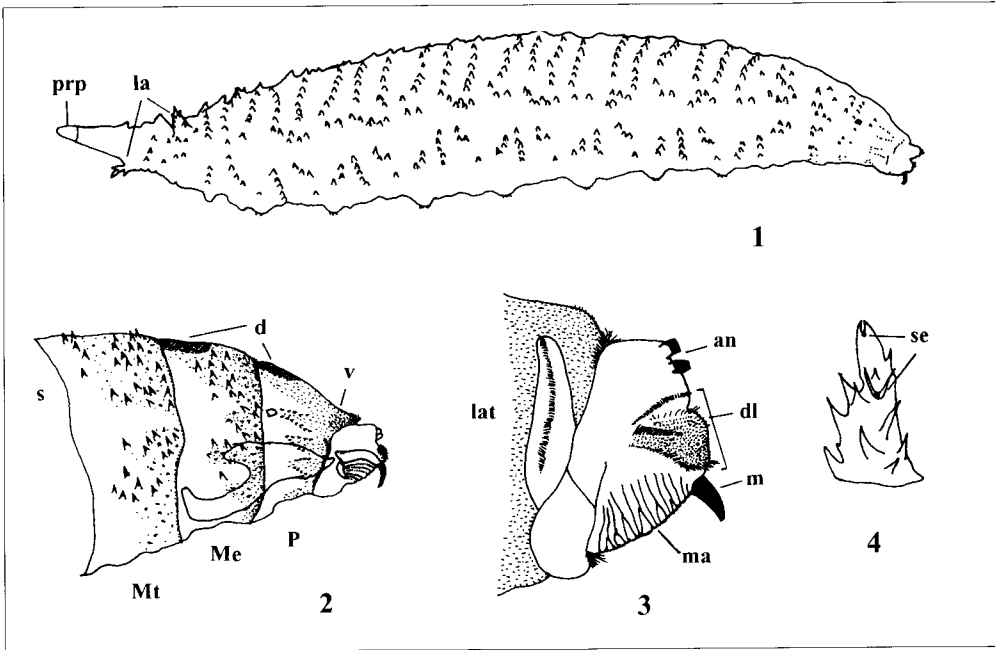
Descriptions of early stages

Alipumilio femoratus SHANNON, 1927

(Figs 1-11)

Third stage larva

Overall size and shape: length 12-14 mm; larva tapering posteriorly and anteriorly; maximum dorsal width = 2.2 mm; dorsal width of anal segment between the two pairs of lappets = 0.68 mm; dorsal width of prothorax anterior of spiracles = 0.73 mm (Fig. 1); subcylindrical in cross-section; larva translucent, lacking an obvious colour pattern except for the black hind gut and surrounding white fat body; vestiture over the entire body consisting of patchily distributed tapering orange-brown small and large spicules (Figs 1-2); sensilla accompanied by 2 or more pale setae; pattern of sensilla similar to other Syrphidae (ROTHERAY & GILBERT 1999) except on anal segment where lappet pair one (the anterior pair) has one sensillum at the tip and a second lower down towards the base (Fig. 4).

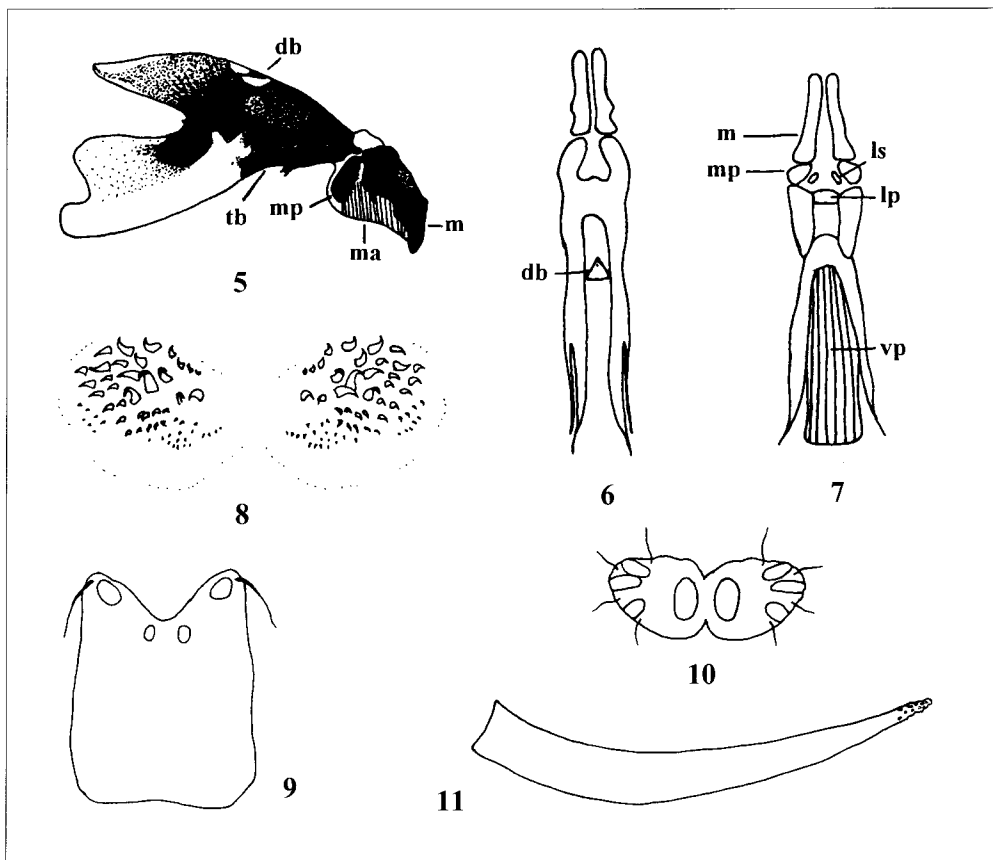


Figs 1-4: *Alipumilio femoratus* SHANNON, 1927, third stage larva. – 1: whole larva, lateral view, head to the right, length 12 mm; – 2: thorax and head, lateral view, head to the right; – 3: anterior part of prothorax and head; – 4: anterior lappet, lateral view, length 0.52 mm. Explanation of abbreviations: an = antennomaxillary organs; d = dorsal plate; dl = dorsal lip; la = lappets; lat = lateral lip; m = mouth-hook; ma = mandibular lobes; prp = posterior respiratory process; s = spicules; se = sensilla; v = vestiture; P = prothorax; Me = mesothorax; Mt = metathorax.

Head skeleton: mandibles large, conspicuous and heavily sclerotised with mouth-hooks projecting from the mouth (Figs 2-3); mandibular apodeme also well developed, about half as long as mandibular sclerite, heavily sclerotised and supporting the fleshy ridged mandibular lobes (Fig. 5); anterior part of the pharyngeal sclerite heavily sclerotised, tapering and produced forward to almost align with the apex of broad, heavily sclerotised tentorial bars fused with the anterior production of the pharyngeal sclerite (Fig. 5); apex of tentorial bars barely projecting forward; dorsal bridge sclerotised (Figs 5-6); tentorial strip broad and heavily sclerotised; labial plate opaque; labial sclerites inconspicuous and crescent-shaped (Fig. 7); epipharyngeal plate present and concealed within the heavily sclerotised anterior part of the pharyngeal sclerite; pharyngeal sclerite bearing a large oval-shaped depression (optic depression of ROBERTS, 1970); ventral pharyngeal ridges present, upturned at posterior end; grinding mill absent; ventral cornua truncate, without a dorsal apodeme.

Head: each of the two pairs of antennomaxillary organs mounted on a dome-shaped fleshy projection; dorsal lip brown; coated in upright micro-spicules and ridges formed from rows of upright spicules (Fig. 3); mandibular lobes ridged, fleshy and forming prominent lobes each side of the mouth (Fig. 3).

Prothorax: dorsal surface: anterior spiracles present, set in a recessed part of the integument, 0.80 mm long with about 6 apical respiratory openings; posterior margin of prothorax with a lightly sclerotised dorsal plate and longitudinal ridges (Fig. 2); lateral surface: anterior margin with a longitudinal row of upright spicules (Figs 2-3) and lateral lips little developed and having a longitudinal row of upright spicules (Fig. 3); ventral surface: anterior



Figs 5-11: *Alipumilio femoratus* SHANNON, 1927, third stage larva and pupal spiracles. – 5: head skeleton, lateral view; – 6: head skeleton, dorsal view; – 7: head skeleton, ventral view; – 8: locomotory organs, 3rd abdominal segment, apical view, anterior end towards top of page; – 9: posterior respiratory process, lateral view, length 0.34 mm; – 10: posterior respiratory process, apical view; – 11: pupal spiracle, lateral view, length 4 mm. Explanation of abbreviations: db = dorsal bridge; m = mouth-hook; ma = mandibular lobes; mp = mandibular apodeme; tb = tentorial bar; lp = labial plate; ls = labial sclerite; vp = ventral pharyngeal ridges.

margin raised slightly and projecting medially (Fig. 3). **Mesothorax:** antero-dorsal margin with a row of upright spicules; mid-dorsal part of mesothorax with a lightly sclerotised region, the dorsal plate (Fig. 2).

Abdomen: dorsal surface of abdomen coated in 3 transverse rows of large, upright, sclerotised orange-brown spicules up to 0.8 mm in length, similar spicules on the lateral margins of the body and thorax tending to be backwardly directed, more variable in size and more evenly coated, particularly dense on the anterior margins of each segment of the thorax (Figs 1&2); lower lateral margins of abdomen with interrupted lines of aggregated pale setae and becoming dense on the ventral surface of the 7th and 8th abdominal segments; 7th abdominal segment tapered with sensilla pair 2 almost directly posterior to sensilla pair 1; locomotory organs on abdominal segments 1-7 consisting of a pair of grouped crochets orientated in more than one direction and lacking a planta (indented region usually anterior to the crochets where muscles are attached) or planta little developed (Fig. 8); prolegs on 7th abdominal segment set close together and most crochets with tips facing anteriorly; two pairs of

about equal-sized lappets each about 0.52 mm long and two additional pairs of inconspicuous lappets barely projecting from the integument between them. **Posterior respiratory process:** length 0.34 mm, width 0.28 mm; apex bifurcated (Fig. 9); each bifurcation bearing 3 parallel, transverse spiracular openings, cuticular scar at base of bifurcation; interspiracular setae present (Fig. 10). **Pupal spiracles:** horn-like, 4 mm long and tapering with spiracular openings clustered at tip (Fig. 11).

Material examined: Ecuador, Past. Puyo, 29.i.1979, 20 larvae, 2 puparia, in Ipecac sap, *Psychotria* spec. (Rubiaceae), coll. Norm WHITTEN (Smithsonian Institution).

Nausigaster texana CURRAN, 1941

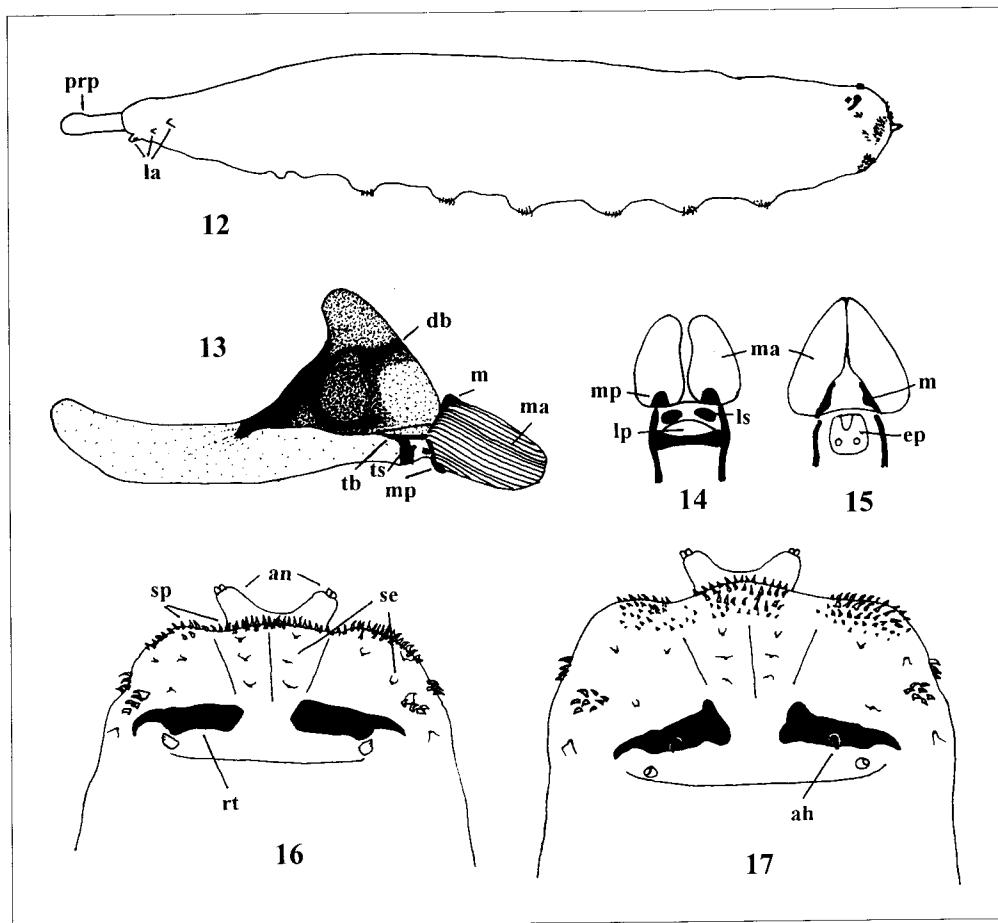
(Figs 12-16, 19)

Third stage larva

Overall size and shape: length 15 mm; larva tapering posteriorly and truncate anteriorly (Fig. 12); dorsal width between the two posterior pairs of lappets on the anal segment = 0.83 mm; dorsal width prothorax across the anterior spiracles = 0.9 mm; maximum dorsal width = 2.6 mm; subcylindrical in cross-section; larva white with a distinct blue coloured haemolymph; vestiture consisting of a few pale setae; sensilla accompanied by 2 or more pale setae; pattern of sensilla similar to other Syrphidae (ROTHERAY & GILBERT 1999). **Head skeleton:** similar to *Eristalis* (HARTLEY 1963) and *Myathropa* (ROBERTS 1970) (Fig. 13), mandibles reduced to supporting the expanded mandibular lobes (Figs 13-15); mandibular apodemes broad and flattened and supporting posterior margin of mandibular lobes (Fig. 14); tentorial bars shorter than tentorial strip, this strip heavily sclerotised (Fig. 13); labial plate opaque; labial sclerites crescent-shaped; epipharyngeal plate well developed with three opaque regions arranged in a triangular pattern (Fig. 15); anterior part of pharyngeal sclerite heavily sclerotised and bearing a large oval-shaped depression (optic depression of ROBERTS 1970); ventral pharyngeal ridges present; grinding mill absent; dorsal bridge heavily sclerotised; ventral cornua elongate, without a dorsal apodeme (Fig. 13). **Head:** each of the two pairs of antennomaxillary organs mounted on a two stage fleshy projection, shared basal stage wedge-shaped, upper separate stage cylindrical; dorsal lip with a few rows of micro-spicules; mandibular lobes ridged and entirely inside the mouth.

Prothorax: dorsal surface: anterior spiracles dark brown, 0.1 mm long with a crescent-shaped arrangement of up to six respiratory openings; in front of the anterior spiracles across the two longitudinal folds bearing sensilla 1-3 and 4-5, are a pair of rectangular dark brown sclerotised plates 0.4×0.15 mm with a lateral hook about 0.24 mm long; these plates are separate on their inner margins by 0.24 mm (Fig. 16); anterior margin with a narrow band of 4-5 longitudinal row of dark brown spicules (Fig. 16); lateral lips well developed and bearing broad flattened setae at the base and fine setae at the tip. **Mesothorax:** antero-lateral margin with two groups of dark brown spicules: lower group consisting of about 12 spicules varying in length from 0.015 mm to 0.045 mm, upper group consisting of about 8 spicules of which anterior four are larger and about 0.075 mm long and the posterior ones about 0.045 mm long; mesothoracic prolegs present with 8 primary crochets and up to 4 rows of smaller crochets.

Abdomen: 7th abdominal segment tapered with sensilla pair 2 almost directly posterior to sensilla pair 1; locomotory organs on abdominal segments 1-6 consisting of prolegs with planta and 10-12 primary crochets, longest crochets in middle of row, and up to 4 interrupted rows of smaller crochets (Fig. 18); crochets becoming more laterally orientated towards posterior end; anal segment with two pairs of equal-sized lappets, about 0.15 mm long and a



Figs 12-17: *Nausigaster* spp., third stage larvae. – **12:** *N. texana* CURRAN, 1941, whole larva, lateral view, head to the right, length 15 mm; – **13:** *N. texana*, head skeleton, lateral view; – **14:** *N. texana*, anterior part of head skeleton, ventral view; – **15:** *N. texana*, anterior part of head skeleton, dorsal view; – **16:** *N. texana*, prothorax, dorsal view; – **17:** *N. unimaculata* TOWNSEND, 1897, prothorax, dorsal view. Explanation of abbreviations: an = antennomaxillary organs; ah = accessory hook; db = dorsal bridge; ep = epipharyngeal plate; la = lappets; m = mouth-hook; ma = mandibular lobes; mp = mandibular apodeme; tb = tentorial bar; ts = tentorial strip; lp = labial plate; ls = labial sclerite; prp = posterior respiratory process; rt = rectangular sclerotised plate with lateral hook; se = sensilla; sp = spicules on anterior fold.

smaller (0.04 mm) pair of lappets between them. **Posterior respiratory process:** length 1.16 mm, width at base 0.45 mm, width at apex 0.3mm; dark brown, with a mid-point constriction; spiracular plate bearing 3 almost parallel, transverse spiracular openings; interspiracular setae present (Fig. 19).

Puparium: Length 6 mm; width 2.5 mm; inflated anteriorly, anal end inclined upwards; coated thickly in a white powdery material forming a cratered pattern; pupal spiracles reduced and inconspicuous, only 0.03 mm long.

Material examined: México, Puebla, Tehuacán, Zapotitlán Salinas, Jardín Botánico, 1590 m, 11.vii.1999, one of several larvae found in the wet, decayed centre of a small (about 16 × 16 cm) *Ferocactus latispinus* (HAW.) BRITTON and Rose cactus and in wet decaying platycades of an *Opuntia* cactus species, male emerged September 1999.

Nausigaster unimaculata TOWNSEND, 1897

(Figs 17, 20-21)

Third stage larva

Overall size and shape: length 18 mm; larva tapering posteriorly and truncate anteriorly; dorsal width between the two posterior pairs of lappets on the anal segment = 0.75 mm; dorsal width prothorax across the anterior spiracles = 1.03 mm; maximum dorsal width = 3mm; subcylindrical in cross-section; larva white with a distinct pale-blue coloured haemolymph; vestiture consisting of a few pale setae; sensilla accompanied by 2 or more pale setae; pattern of sensilla similar to other Syrphidae (ROTHERAY & GILBERT 1999).

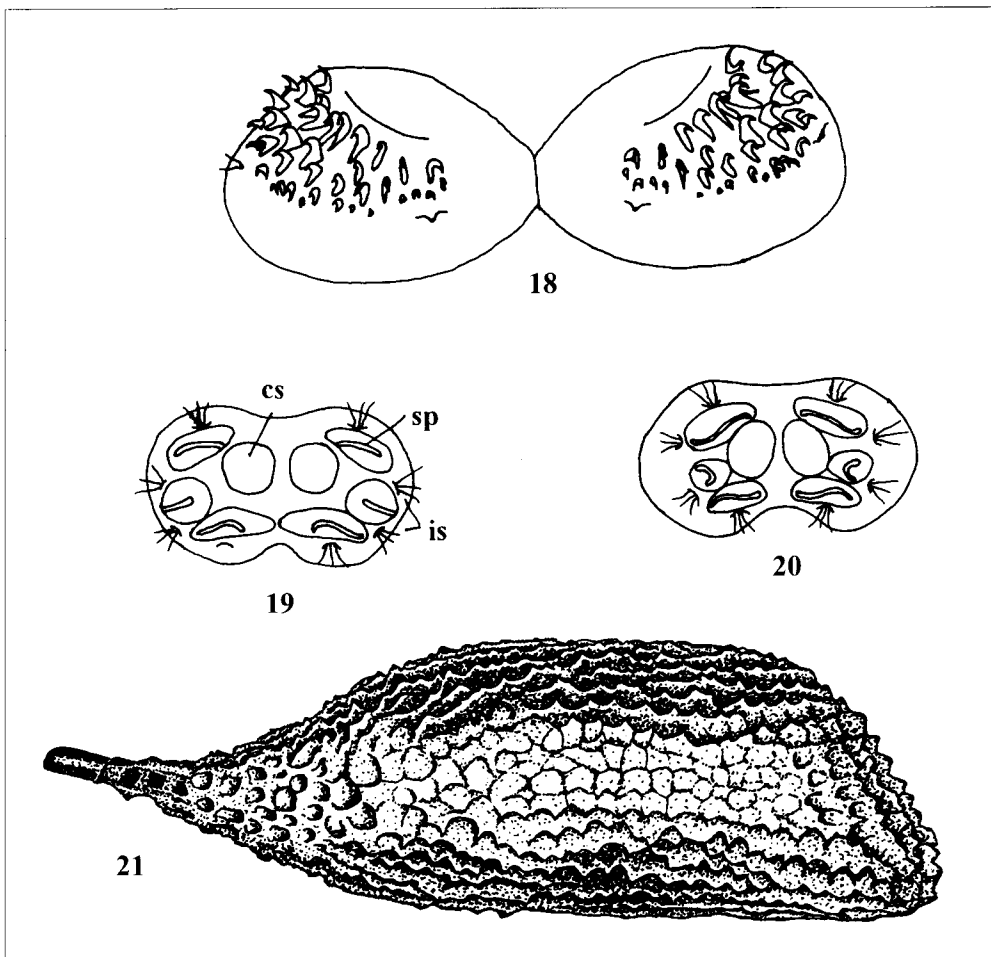
Head skeleton: almost identical to that of *N. texana* (Figs 13-15); mandibles reduced to supporting the expanded mandibular lobes; mandibular apodemes broad and flattened and supporting posterior margin of mandibular lobes; tentorial bars shorter than tentorial strip, this strip heavily sclerotised; labial plate opaque; labial sclerites crescent-shaped; epipharyngeal plate well developed with three opaque regions arranged in a triangular pattern; anterior part of pharyngeal sclerite heavily sclerotised and bearing a large oval-shaped depression (optic depression of ROBERTS 1970); ventral pharyngeal ridges present; grinding mill absent; dorsal bridge heavily sclerotised; ventral cornua without a dorsal apodeme.

Head: each of the two pairs of antennomaxillary organs mounted on a two stage fleshy projection, shared basal stage wedge-shaped, upper separate stage cylindrical; dorsal lip with a medial tuft of setae; mandibular lobes ridged and entirely inside the mouth.

Prothorax: dorsal surface: pale-brown anterior spiracles present, 0.07 mm long with two apical respiratory openings; in front of the anterior spiracles between the two longitudinal folds bearing sensilla 1-3 and 4-5, are a pair of pale-brown rectangular sclerotised plates with a broad inner margin 0.45×0.16 mm with a lateral hook about 0.24 mm long and, on the plate, a small hook about 0.03 mm long; these plates are separate on their inner margins by 0.42 mm (Fig. 17); anterior margin with a narrow band of 4-5 longitudinal row of spicules which are interrupted laterally at the groove separating the folds bearing sensilla 1-3 and 4-5 (Fig. 17); lateral lips well developed and bearing broad flattened setae at the base and fine setae at the tip. **Mesothorax:** antero-lateral margin with two groups of spicules: lower group consisting of about 12 spicules varying in length from 0.015 mm to 0.045 mm, upper group consisting of about 8 spicules of which anterior four are larger and about 0.05 long and the posterior ones about 0.025 mm long; mesothoracic prolegs present with 8 primary crochets and up to 4 rows of smaller crochets.

Abdomen: 7th abdominal segment tapered with sensilla pair 2 almost directly posterior to sensilla pair 1; locomotory organs on abdominal segments 1-6 consisting of prolegs with planta and 10-12 primary crochets, longest crochets in middle of row, and up to 4 interrupted rows of smaller crochets; crochets becoming more laterally orientated towards posterior end; anal segment with three pairs of lappets: anterior (basal) pair about 0.3 mm, middle pair short, about 0.075 mm long and the posterior lappets longest, about 0.53 mm. **Posterior respiratory process:** pale-brown, parallel-sided, length 1.68 mm, width 0.43 mm; spiracular plate bearing 3 almost parallel, transverse spiracular openings except middle pair curved; interspiracular setae present (Fig. 20).

Puparium: Length 8 mm; width 3 mm; inflated anteriorly, anal end upturned and tip of breathing tube is directed slightly upwards; coated thickly in a white powdery material forming a cratered pattern (Fig. 21); pupal spiracles reduced and obscured completely by the white material.



Figs 18-21: *Nausigaster* spp., third stage larva and puparium. – **18:** locomotory organs, 3rd abdominal segment, apical view, anterior end towards top of page; – **19:** *N. texana* CURRAN, 1941, posterior respiratory process, apical view; – **20:** *N. unimaculata* TOWNSEND, 1897, posterior respiratory process, apical view; – **21:** *N. unimaculata*, whole puparium, lateral view, anterior end to the right, length 8mm. cs = cuticular scar; is = interspiracular setae; sp = spiracular opening.

Material examined: México, Puebla, Tehuacán, Planede Fierro, 8.vii.1999, one of several larvae found in wet, decayed centres of *Hechtia podantha* Mez. plants (Bromeliaceae); a male and a female emerged September 1999.

Cladistic analysis

Using the commands **mh*** and **bb*** a total of 240 equally parsimonious trees were found with $ci=0.46$ and $ri=0.80$. The strict consensus tree showed that all trees placed *Alipumilio* as the first syrphid taxon, below *Eumerus* MEIGEN, 1822. *Nausigaster* was placed in a very derived position in relation to *Alipumilio* in a polytomy consisting of *Spilomyia* MEIGEN, 1803, *Milesia* Latreille, 1804, *Criorhina* MEIGEN, 1822, *Temnostoma* LEPELETIER & SERVILLE, 1828 and *Callicera* PANZER, 1809. The successive weighting option reduced the number of trees to 4. The consensus tree of these again had *Alipumilio* basal and placed *Nausigaster* as the sister group to *Criorhina*.

Tab. 1: Character states for *Alipumilio* and *Nausigaster* used to analyse phylogenetic position: 0 = primitive; 1, 2, 3, = derived; ? = unscorable
Each score follows the sequence of 187 larval characters described in Appendix 1 of ROTHERAY & GILBERT (1999)

<i>Alipumilio</i>					
1000000000	00?0001100	00001000?0	00000?????0	000000???0	010000???00
0000000000	0000010021	0000000000	0000002001	0???000000	1200000?00
0000000100	01?1010000	0???00???0	0000000000	0000020000	0000010000
0011001					
<i>Nausigaster</i>					
1002020000	2200011110	0000011211	1110100110	0001001120	0110001221
1010011120	1000020112	1000100000	0100212223	2???000000	0100000211
1011000100	01?1211110	0???00???0	0000000000	1000120000	0000010100
111111?					

Discussion

Alipumilio is a small genus of only about 12 species occurring from Argentina to Mexico (THOMPSON 1972). Apparently, the only data concerning breeding and early stages is THOMPSON'S (1972) statement that he had received a series of a new species reared from pitch of *Araucaria australis* (Pinaceae). The breeding record of *A. femoratus* detailed here also came from sap and suggests that exuded sap of woody plants is a major breeding site for species of this genus.

Thanks to F. C. THOMPSON we have also studied puparia of this new *Alipumilio* species. The head skeleton is almost identical to that of *A. femoratus* (Figs 5-7). However the two species can be separated on the size and shape of the pupal spiracles. The pupal spiracles of the new species are rounded at the tip, not tapered, and are only about half the length of those of *A. femoratus*. The pupal spiracles of both species shared the character of spiracular openings clustered at the tip (Fig. 11).

The larva of *A. femoratus* possessed the full range of syrphid apomorphies given in ROTHERAY & GILBERT (1999) such as the development of dorsal and lateral lips, longitudinal folds on the prothorax, anus on the posterior margin of the anal segment and fused posterior breathing tubes. Among syrphid larvae they are easily recognised by the following characters: anterior and posterior ends tapering with mouth-hooks protruding from the mouth (Fig. 1); dorsal surface of the abdomen with brown-tipped spicules in transverse rows (Fig. 1); locomotory organs consisting of two groups of crochet-like spines on each of the first seven abdominal segments (Fig. 8) and, dorsal and lateral lips with rows of upright spicules (Fig. 3).

In an analysis of larval characters, *Alipumilio* was basal within Syrphidae and placed immediately below *Eumerus* + *Merodon*, supporting a close relationship between these taxa. Living in exuded sap, the larva of *A. femoratus* is either a saprophage feeding on bacteria, yeasts and other micro-organisms present in the sap, or a phytophage feeding on cambial tissues obtained from the point where sap is exuded. Feeding on exuded tree sap has evolved several times in Syrphidae (ROTHERAY & GILBERT 1999) but feeding on cambial tissues is only known in certain species of *Cheilosia* MEIGEN, 1822 (ROTHERAY 1993).

The mandibular lobes surrounding the mouth and fringed lateral and dorsal lips are all structures that probably aid in gathering and imbibing semi-fluids. The heavily sclerotised head skeleton and large mouth-hooks suggest that food gathering is an active process. This is further indicated by the anterior part of the thorax being coated in sclerotised vestiture and

the possession of a lightly sclerotised dorsal plate which may reduce wear and tear. These are not autapomorphic features, being also found in *Cheilosia* larvae that tunnel their food plants (ROThERAY 1990). The possession of ventral pharyngeal ridges which are a feature of most saprophagous muscomorphan larvae, help separate micro-organisms from fluids. However the larva of *A. femoratus* does not possess the grinding mill seen in the head skeletons of some *Eumerus* and *Merodon* larvae (HARTLEY 1963; ROBERTS 1970).

Locomotory organs on seven, not six, abdominal segments is a feature of only certain *Eumerus* larvae possessing prolegs with crochets such as *E. obliquus* FABRICIUS, 1805 and *E. etnensis* VAN DER GOOT, 1964 (PÉREZ-BAÑÓN & MARCOS-GARCIA 1998) from the Afrotropical region and the Mediterranean Basin, respectively. All other syrphid taxa with crochets and prolegs lack them on the seventh abdominal segment (ROThERAY & GILBERT 1999). The apparent lack of a planta and orientation of crochets around almost all points of the compass are unusual features and may represent an early stage in the development of prolegs in Syrphidae.

The two puparia of *A. femoratus* examined were embedded in hard dry sap with the pupal spiracles directed forward and clear of the sap. This suggests a functional explanation for the remarkably elongate pupal spiracles, almost as long as the length of the puparium, with their clustered spiracular openings. Pupariation appears to take place within the sap close to the surface which may be advantageous in disguising and protecting the puparium. Protruded pupal spiracles enable respiration in this position. Spiracular openings clustered at the tip, rather than being distributed over the length of the pupal spiracles as in many other syrphids and other Aschiza larvae, minimises their potential to be blocked by sap.

Nausigaster is also a small genus of about 15 species from Argentina to California and Texas in the north (F. C. THOMPSON, pers. comm.). Previously *N. unimaculata* has been reared from *Opuntia* cacti in Texas (HUNTER et al. 1912). The only other breeding record and the only larval description is of *N. bonariensis* LYNCH ARRIBALZAGA, 1892 [= *shannoni* CARRERA, LOPES & LANE 1947 (F. C. THOMPSON, pers. comm.)] from a rain-filled decaying stem of papaya (CARRERA et al. 1947). Both cactus and bromeliad from which we reared *N. unimaculata*, are additional breeding substrates for this species.

Nausigaster larvae also share the apomorphies of other syrphid taxa and are easy to recognise by the following characters: anterior end truncate, posterior end tapering (Fig. 12); no mouth-hooks protruding from the mouth, (mandibles reduced and supporting the expanded mandibular lobes (Fig. 13) which coat the inside of the mouth); haemolymph blue in colour; dorsum of prothorax with a pair of rectangular sclerotised plates bearing a lateral hook (Figs. 16 and 17) and, prolegs with dark brown crochets and planta on abdominal segments 1-6 and the mesothorax (Fig. 18). The two species we reared can be told apart by characters of the prothorax. The rectangular plates bearing lateral hooks in *N. texana* lack the small accessory hook and anterior projection on the inner margin that are present in *N. unimaculata* (Figs. 16-17). Furthermore, the rows of spicules on the anterior fold are interrupted in *N. unimaculata* but are continuous in *N. texana* (Figs. 16 -17).

Possession of large hooks on the thorax is a derived feature within Syrphidae (ROThERAY & GILBERT 1999) where their function is to facilitate locomotion in particle-filled media (ROThERAY 1991). *Nausigaster* was placed among these derived genera in our phylogenetic analysis. Apart from thoracic hooks not being congruent with *Eumerus*, other characters include the head skeleton [similar to that of saprophagous Syrphidae, HARTLEY (1963); ROBERTS (1970)] and the locomotory organs which include mesothoracic, prolegs but lack prolegs on abdominal segment 7.

The decaying tissues of bromeliads and cacti varied in consistency from being like water to being relatively firm and filled with particles. Under these circumstances hooks are presumably an advantage in preventing wear and tear during locomotion. Other large syrphid larvae in decaying cacti belong to the genus *Copestylum* MACQUART, 1846 and of several species examined all had varying arrangements of sclerotised spicules on the thorax suggesting a common response to a shared problem.

However, no *Copestylum* larvae were coloured blue. The functional significance of coloured haemolymph is unclear. We found that *Nausigaster* larvae were resistant to fixing in hot water, suggesting great tolerance of heat. Although no measurements were taken, wet decaying tissues in cacti were often very hot to our bare hands. Fallen cacti were often lying in exposed places and received sunlight directly all day. Heat tolerance would be an advantage under these circumstances and perhaps blue haemolymph is part of the mechanism. Tolerance to temperatures of 45 °C was also observed in *E. etnensis* in *Opuntia platycades* (PÉREZ-BAÑÓN & MARCOS-GARCIA 1998). However these larvae are not blue. Another feature possibly involved with heat tolerance is the white material which coats *Nausigaster* puparia (Fig. 21). The only syrphids that pupariated on the outside of cacti were *Nausigaster*. *Copestylum* and *Eumerus* larvae appear to pupate in the soil and sand under the breeding site and are not coated in white material.

The origin of the white material was not resolved. It may be emitted as a fluid from either the anus or the mouth immediately prior to pupariation. The cratered appearance of this material is due to air; on emission the liquid is probably full of bubbles and sticky. Following pupariation it dries rapidly and becomes solid. This coating of material may protect the otherwise exposed puparium from heat, as well as natural enemies.

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