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Larvae of Pogonini (Coleoptera: Carabidae): genera *Pogonus*, *Pogonistes*, *Cardiaderus*, and *Thalassotrechus*

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Abstract. Larvae of the genera *Pogonus* Dejean, 1821, *Pogonistes* Chaudoir, 1871, *Cardiaderus* Dejean, 1828, and *Thalassotrechus* Van Dyke, 1918 of the tribe Pogonini are described. A key to the four genera and illustrations of the most important features are provided. Characters of larvae suggest that the tribe Pogonini represents a monophyletic lineage based on three synapomorphies: 1) presence of spindle-shaped setae on some parts of the body; 2) position of the seta FR_2 on frontale near FR_1; 3) absence of a relatively long secondary seta on each lateral margin of the ninth abdominal tergite (just anteriad to UR_2) in second and third instars. This study supports inclusion of Pogonini in the supertribe Trechitae together with Bembidiini, Trechini and Zolini. Both *Cardiaderus* and *Thalassotrechus* are very distinct and their relationships uncertain. Monophyly of *Pogonus* and *Pogonistes* is not evident; presumably these taxa are more related to each other than to the other two genera treated.

Morphology, phylogeny, description, key, larvae, Coleoptera, Carabidae, Pogonini, *Pogonus*, *Pogonistes*, *Cardiaderus*, *Thalassotrechus*

INTRODUCTION

The tribe Pogonini is represented in all major zoogeographical regions of the world but is most diverse in the Palaearctic, particularly in the Mediterranean area. This group includes about 70 species, which are classified in the genera *Bedeliolus* Semenov, 1900, *Cardiaderus* Dejean, 1828, *Diodercarus* Lutshnik, 1931, *Diplochaetus* Chaudoir, 1871, *Ochtozetus* Chaudoir, 1871, *Pogonistes* Chaudoir, 1871, *Pogonopsis* Bedel, 1898, *Pogonus* Dejean, 1821, *Syrdenus* Chaudoir, 1871, and *Thalassotrechus* Van Dyke, 1918 (Bousquet & Laplante 1997). In addition, Komarov (1996) recently described, as a pogonine, a genus with uncertain affinities (*Olegius*) based on a single female collected in southwestern Turkmenia. The tribe Pogonini is currently placed in the supertribe Trechitae along with Trechini, Zolini (Merizodini of some authors) and Bembidiini (including Tachyina) (Kryzhanovskij 1976, 1983; Erwin 1985, 1991). All species, except apparently those of *Ochtozetus* from South America (see Reichardt 1974), live in saline habitats and are found in littoral places or around inland salt lakes, ponds or pans.

Very little is known about Pogonini larvae. Morphological descriptions of older-instar larvae of only four species included in two genera have been published: *Pogonus cumanus* (Sharova 1958, 1964), *P. luridipennis* (Jeannel 1941; van Emden 1942; Sharova 1958, 1964; Larsson 1968; Raynaud 1976; Luff 1985, 1993; Arndt 1991), *P. chalceus* (Luff 1985, 1993; Arndt 1991), and *Thalassotrechus barbarae* (Moore 1956; Thompson 1979).

The main purpose of the present paper is to describe the larval features of four genera of the tribe Pogonini. In addition, relationships between these genera based on larval morphology will be briefly discussed.

MATERIALS AND METHODS

This work is based on the study of 46 slide-mounted larvae of Pogonini belonging to 11 species and four genera; 62 additional larvae were available in alcohol but not studied in detail. All larvae, except one specimen, were reared *ex ovo* from mature females kept in laboratory. Adults were collected during expeditions by the senior author along saline lakes in southern Ukraine (Dnestrovsky and Kuyalnisky Limans in the Odessa district), southern Russia (Sarepta in Volgograd area and Baskunchak Lake in the Astrakhan district), and southwestern Turkmenia (Uzboy Lakes system, southwestern part of the Kara Kum). Larvae of *Thalassotrechus barbarae* were borrowed from the Canadian National Collection of Insects, Ottawa, Canada (CNC). Most larvae are kept in the collection of the senior author (VVG); the remaining have been deposited in CNC, the British Museum of Natural History, London (BMNH), and Martin L. Luff collection, University of Newcastle upon Tyne (MLL).

Larvae were mounted on microscope slides in Hoyer's medium and studied with a compound microscope MBI-1 at magnifications up to 900×. Morphological drawings were prepared using a Reichert camera lucida. Notation of primary sensilla follows Bousquet & Goulet (1984), notation of secondary setae follows Bousquet (1985).

All measurements were made using an ocular micrometer. Measurements of antennomeres were taken along their medial side, including the membranous part. The abbreviations L_1, L_2, L_3 indicate first, second, and third instars respectively.

For comparative purpose, larvae of 22 genera belonging to the supertribe Trechitae have been studied: *Aepopsis* Jeannel, 1922, *Temnostega* Enderlein, 1905, *Perileptus* Schaum, 1860, *Thalassophilus* Wollaston, 1854, *Amblystogenium* Enderlein, 1905, *Trechus* Clairville, 1806, *Epaphius* Samouelle, 1827, and *Trechimorphus* Jeannel, 1927 of the tribe Trechini; *Bembidion* Latreille, 1802, *Asaphidion* Des Gozis, 1886, *Ocys* Stephens, 1828, *Phrypeus* Casey, 1924, *Tachys* Dejean, 1821, *Paratachys* Casey, 1918, *Sphaerotachys* G. Müller, 1926, *Elaphropus* Motschulsky, 1839, *Porotachys* Netolitzky, 1914, *Tachyta* Kirby, 1837, *Polyderis* Motschulsky, 1862, and *Mioptachys* Bates, 1882 of the tribe Bembidiini; *Oopterus* Guérin-Méneville, 1841 and *Idacarabus* Lea, 1910 of the tribe Zolini.

No descriptions of species are provided in this paper in part because the number of available larvae was low. A preliminary analysis indicates that differences among most pogonine species are slight, especially in the second and third instars.

Tribe Pogonini

DIAGNOSIS. Larvae of Pogonini differ from those of other groups included in the supertribe Trechitae by the presence of spindle-shaped setae (see Fig. 17) on some sclerites. In the first instar, at least setae ES_1 on pro- and mesothorax, EP_1 on ninth abdominal segment, and PY_2 on pygidium are spindle-shaped. In the second and third instars, there are numerous short, secondary, spindle-shaped setae on the dorsal surface of the cephalic capsule. Such modified setae are absent in larvae of other Trechitae examined. In addition to this character, we should mention (1) that the frontal sutures are less sinuate in larvae of Pogonini compared to those of other Trechitae groups, (2) that seta FR_2 on the frontale is closer to FR_1 than on average for Trechitae, and (3) that each lateral margin of the ninth abdominal tergite in second and third instars lacks a secondary seta (just anteriad to UR_2) present in most Trechitae larvae known to us.

DESCRIPTION. Head widths of specimens studied are indicated in Table 1. **First-instar larvae**. Moderately sclerotized; coloration varying from very light, almost colorless, to somewhat brown or grey. Cephalic capsule without basal constriction; parietale with 2 rows of 3 ocelli in most species, ocelli of posterior row small to absent in some species; postocellar and cervical grooves present or not. Frontal sutures only slightly sinuate (Figs 2–9); epicranial suture relatively long, 0.7–1.0× as long as antennomere 1 (Figs 2–9); nasale variable (Figs. 10–14), somewhat produced and denticulate, with a single row of denticles (Figs 10–14). Egg-bursters absent (Figs 2–5, 7–9) except in *Thalassotre-*

Tab. 1. Cephalic capsule width (mm) of pogonine larvae studied

	L1			L2		L3	
Species	n	M	Range	n	M	n	M
Pogonus luridipennis	2	0.56	0.55–0.56	1	0.75	1	1.35
Pogonus iridipennis	1	0.43		–		1	1.07
Pogonus transfuga	2	0.48	0.47–0.48	1	0.70	1	1.18
Pogonus meridionalis	4	0.46	0.45–0.48	1	0.69	1	1.13
Pogonus punctulatus	2	0.36	0.35–0.38	1	0.51	1	0.63
Pogonus cumanus	1	0.56		–		1	1.35
Pogonistes rufoaeneus	1	0.39		1	0.54	1	0.70
Pogonistes convexicollis	2	0.34	0.33–0.34	1	0.50	1	0.62
Pogonistes angustus	2	0.32	0.30–0.33	2	0.41	1	0.57
Cardiaderus chloroticus	2	0.50	0.47–0.52	1	0.81	1	1.10
Thalassotrechus barbarae	1	0.46		–		–	

chus (Fig. 6). Antennae slightly longer than mandibles in most species; second antennomere 0.7–1.0× as long as first; third antennomere 1.1–1.3× as long as first; fourth antennomere 0.6–0.9× as long as first; antennomere 3 with prominent sensorium (sensorial appendage of Van Emden 1942), two campaniform and one placoid sensilla laterally; antennomere 4 with two conical and one campaniform sensilla apically; lateral side of antennomere 3 not sclerotized between sensorium and base of antennomere 4. Mandible with single retinaculum; penicillus with more than 5 setae; cutting edges of terebra and retinaculum smooth, not serrate (Figs 2–9); dorsal surface between MN_b and MN_1 with or without microdenticles. Maxilla without lacinia; stipes about 2.2–3.0× as long as wide; dorsal surface of stipes membranous, not sclerotized; first galeomere 1.0–1.2× as long as second; maxillary palpomere 4 not subdivided. Labium with relatively long, conical ligula; second labial palpomere not subdivided, slightly shorter than first. Leg with single, relatively long claw (Figs. 15–16). Urogomphi fused to ninth tergite, rather long, not joined, without nodules.

Chaetotaxy. All primary sensilla, except pores PR_c, PR_e, PR_i, PR_j, in some taxa also PR_h, on pronotum, pores ME_d, ME_e on meso- and metanotum, seta ES_1 on metathorax, pore TE_b on abdominal tergites 1–8, and setae TA_3, TA_4, TA_5 and TA_6 on tarsus, present; no additional sensilla. Seta FR_1 close to FR_2; anterior angles of hypopharynx each with one seta; setal group gMX with 14–30 (usually less than 24) setae; setae MX_5 and MX_6 relatively long and subequal in length; seta MX_7 about half length of galeomere 2; seta MX_8 located at base of galeomere 2; seta LA_5 located on ligula, which is quadrisetose. Setae PR_7 and ME_{10} on thorax short, not longer than basal diameter of nearest long setae; length of setae PR_{13} and ME_{14} 0.4–0.7× that of PR_{12} and ME_{13} respectively; seta ES_1 spindle-shaped; seta EM_1 spindle-shaped except in *Pogonistes*. Seta TA_1 usually located at basal third of tarsus, rarely at middle. Abdomen with setae TE_6, TE_7, TE_{11} and ST_3 spindle-shaped in many taxa. Seta EP_1 on epipleurites of ninth abdominal segment and seta PY_2 on pygidium spindle-shaped.

Second- and third-instar larvae. Same character states as first instar except for the followings. Antennae with second antennomere 0.9–1.6× as long as first; third antennomere 1.1–1.5× as long as first; fourth antennomere 0.5–0.8× as long as first. Mandible without microdenticles on dorsal surface between pore MN_b and seta MN_1. Maxillae with dorsal surface of stipes partly sclerotized; stipes 3.5–5.5× as long as wide.

Chaetotaxy. Primary setae on frontale usually trichoid (FR_1 and FR_3 spindle-shaped in some specimens); frontale with numerous short, irregular, secondary setae, some of them spindle-shaped. Antenna without secondary setae (Figs 21, 24–25) or with secondary setae on antennomeres 1–3

(Figs 22–23), in some taxa on antennomere 2 only (Fig. 26). Mandible with 2 or 3 secondary setae laterally at base. Maxilla with group gMX consisting of 20–65 setae; lateral side of stipes with 5–7 setae (including MX_2 and MX_3); setae MX_5 and MX_6 long (length 1.5–2.5× width of stipes). Labium with 3–22 setae on each side (including LA_3 and LA_4). Leg without secondary setae in most species, rarely femur, tibia, and tarsus with short secondary setae. Seta UR_α on abdominal tergite IX distinct; urogomphi each with 7 long setae (UR_4–UR_8, UR_δ, UR_ϵ); lateral margins of tergite IX without secondary seta at middle (just anteriad to UR_2).

Bionomics. Although the habitat preferences of Pogonini larvae are inadequately known, one can assume that larvae of most species prefer saline places like the adults. In laboratory, we were able to obtain eggs of many species only after table salt was added to the substratum in the Petri dishes containing the adults. Most first-instar larvae were obtained in laboratory in June, usually right after the adults were brought from the field. It takes about three to four weeks for the larval development to be completed. All species collected in the field were successfully reared, except *Pogonus litoralis*.

Monophyly. Larval features suggest that the tribe Pogonini represents a monophyletic lineage. Known larvae possess three character states which are likely apomorphic. 1) Some setae on the body are spindle-shaped instead of trichoid. No other Trechitae larvae possess such setae and their occurrence is rare in other groups of Carabidae. 2) Seta FR_2 on frontale is located closer to FR_1 than on average for Trechitae and most other groups of Carabidae (our observations). 3) Pogonine larvae lack a relatively long, secondary seta on each lateral margin of the ninth abdominal tergite (just anteriad to UR_2) in second and third instars which is present in all other genera of Trechitae studied except *Ocys*, *Tachyta*, *Oopterus*, and *Idacarabus*. This character state has been little surveyed in other groups of Carabidae.

Phylogenetic Relationships. Larval features of Pogonini support their inclusion in the supertribe Trechitae. Pogonine larvae share with those of the remaining Trechitae groups the absence of pores PR_c, PR_e, PR_i, PR_j on pronotum, pores Me_d and ME_e on meso- and metanotum, seta ES_1 on metathorax, pore TE_b on abdominal tergites 1–8, and setae TA_3, TA_4, TA_5, TA_6 on tarsus. These structures are part of the ground plan of the family Carabidae (Bousquet & Goulet 1984) and their absence in Trechitae larvae is very likely a synapomorphic condition.

One additional character state should be mentioned: the presence of a single claw at the extremity of the leg. This state, which is undoubtedly derived for the family Carabidae, occurs in all Trechitae larvae except for those of the genera *Perileptus*, *Thalassophilus*, *Amblystogenium*, *Temnostega*, and *Kenodactylus* Broun, 1909 which have two claws (Boldori 1936, Womersley 1937, Johns 1974, Grebennikov 1996, our observations). These genera belong to the subtribes Perileptina, Trechodina, Plocamotrechina, and Aepina (last two) respectively of the tribe Trechini. Reversal from one to two claws within the Trechini is unlikely in our opinion. Therefore, we must assume that the presence of one claw has been derived at least twice in the Trechitae, once in the tribe Trechini and a second time in the remaining groups. In such case, the Pogonini may be more closely related to Bembidiini and Zolini. The fact that a few other groups of Carabidae, apparently not closely related to the Trechitae such as some genera of Clivinini and the Broscini, do possess a single claw suggests that this character state may be subject to convergence in carabids. Another possibility is that the tribe Trechini is not a monophyletic lineage. We cannot comment on this hypothesis at this point.

Müller (1975) postulated that the tribe Pogonini is the adelphotaxon of Bembidiini. This view was based, in our opinion, on "weak" synapomorphies and has not been corroborated. As properly stated by Maddison (1993: 196), relationships of the various tribes of Trechitae have not been adequately demonstrated.

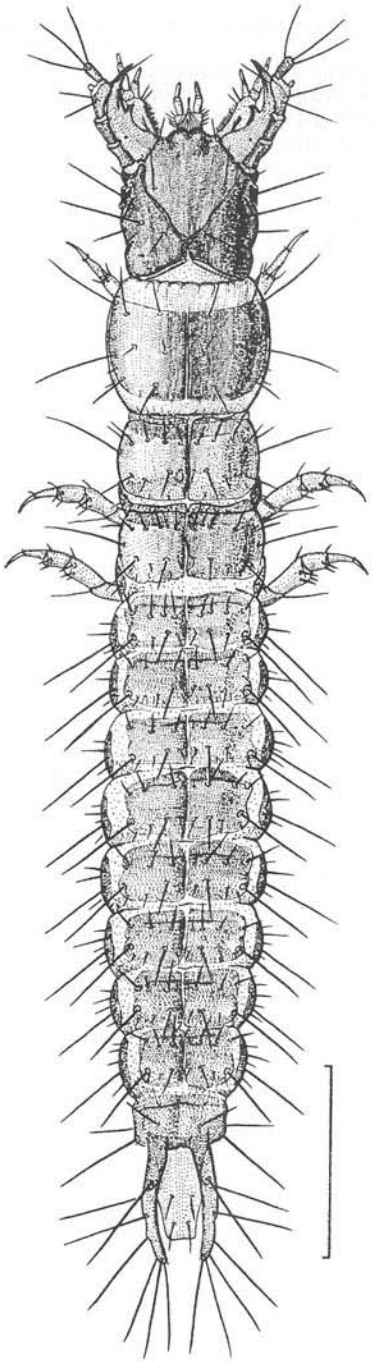


Fig. 1. Larva of *Pogonus meridionalis*, L_2, habitus. Scale bar = 1 mm.

Key to larvae of the tribe Pogonini

1. Urogomphus with 5 long setae (Figs 18–20). Mandible with one seta on basal half (Figs 2–9). Lateral side of stipes with 2 setae. Abdominal hypopleurites without setae. ..... First instar 2
– Urogomphus with 7 long setae (Fig. 1). Mandible with more than one seta on basal half (Figs 24–26). Lateral side of stipes with more than 2 setae. Abdominal hypopleurites with setae. ..... Second and third instars 5
2. Dorsal surface of mandible between MN_l and MN_b with at least one microdenticle, usually 3–6 (Figs 2–4). Seta PY_6 on pygidium spindle-shaped. ..... *Pogonus* Dejean
– Dorsal surface of mandible between MN_l and MN_b smooth, without microdenticles (Figs 5–9). Seta PY_6 on pygidium trichoid. 3
3. Length of setae MX_{11} and MX_{12} more than half diameter of maxillary palpomere 3. Parietale with posterior row of ocelli somewhat reduced or absent. ..... *Pogonistes* Chaudoir
– Length of setae MX_{11} and MX_{12} less than 1/4 diameter of maxillary palpomere 3. Parietale with posterior row of ocelli markedly developed. 4
4. Parietale with egg-bursters consisting of one large microspine on each side near epicranial suture (Fig. 6). Mandibular terebra slightly convex near base (Fig. 6). Pore PR_b on pronotum absent. Setae TE_7 on tergites spindle-shaped. ..... *Thalassotrechus* Van Dyke
– Parietale without egg-bursters (Fig. 5). Mandibular terebra regular, slightly concave (Fig. 5). Pore PR_b on pronotum present. Setae TE_7 on tergites normal, trichoid. ..... *Cardiaderus* Dejean
5. Antennae with secondary setae on antennomere 2 only (Fig. 26). Length of setae MX_{11} and MX_{12} less than 1/4 diameter of maxillary palpomere 3. Meso-, metanotum, and abdominal tergites 1–6 with numerous secondary setae on medial half (Fig. 27). ..... *Cardiaderus* Dejean
– Antennae without secondary setae (Figs 21, 25) or antennomeres 1–3 with secondary setae (Figs 22, 23). Length of setae MX_{11} and MX_{12} more than half diameter of maxillary palpomere 3. Meso-, metanotum, and abdominal tergites 1–6 with no or few secondary setae on medial half. ..... *Pogonus* Dejean and *Pogonistes* Chaudoir

Genus *Pogonus* Dejean, 1821
(Figs 1–4, 10, 19, 21–25)

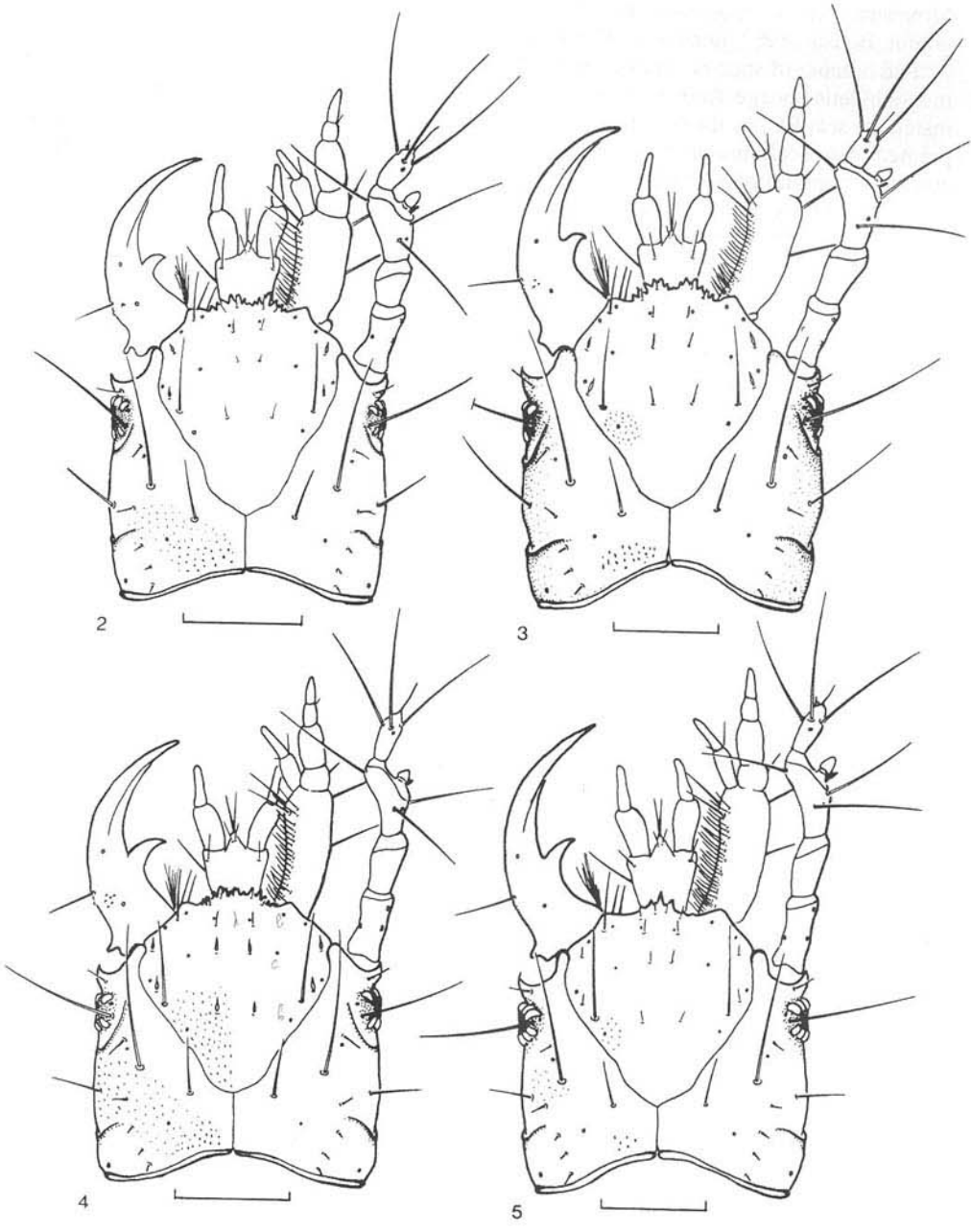
DIAGNOSIS. First-instar larvae of *Pogonus* differ from those of other genera by having microdenticles on the dorsal surface of the mandible between MN_b and MN_l and by having the seta PY_6 on the pygidium spindle-shaped. We have found no character state that would differentiate second- and third-instar larvae of *Pogonus* from those of *Pogonistes*.

DESCRIPTION. **First-instar larvae**. Cephalic capsule parallel-sided (Figs 2–4). Frontale with or without pointed microsculpture, if present, microsculpture developed on basal half of sclerite (Fig. 4) or near pore FR_b (Fig. 3); nasale rather straight or slightly notched at middle (Figs 10, 11). Parietale without egg-bursters (Figs 2–4); ocelli, postocellar and cervical grooves markedly developed (Figs 2–4). Mandible with pointed microsculpture between MN_b and MN_l consisting of 1–8, usually 3–6, sharp microdenticles (Figs 2–4); terebra regular, slightly concave (Figs 2–4). Claw 0.8–1.0× length of tarsus. Urogomphi relatively long, parallel (Fig. 19).

Chaetotaxy: Seta AN_6 1.0–2.0× as long as width of antennomere 4 (Figs 2–4). Frontale with at least 2 setae, FR_l and either FR_3, FR_4, or FR_6, spindle-shaped; seta EM_1 on prothorax and PY_6 on pygidium spindle-shaped; length of setae MX_{11} and MX_{12} more than half diameter of maxillary palpomere 3. Pore PR_b on pronotum present. Seta TA_1 located at basal third of tarsus (as in Fig. 15). Setae TE_7 on tergites normal, not spindle-shaped.

Second- and third-instar larvae. Postocellar and cervical grooves distinct.

Chaetotaxy: antennomeres 1–3 with (Figs 22, 23) or without secondary setae (Figs 21, 24). Leg without secondary setae on tarsus, tibia and femur in all species studied except *P. cumanus*. Meso-metanotum, and abdominal tergites 1–6 without numerous secondary setae on medial half of sclerites (Fig. 1).



Figs 2–5. Cephalic capsule, right antenna, left mandible, right maxilla, labium, L_1 (dorsal view). 2 – *Pogonus punctulatus*; 3 – *P. cumanus*; 4 – *P. luridipennis*; 5 – *Cardiaderus chloroticus*. Scale bars = 0.2 mm.

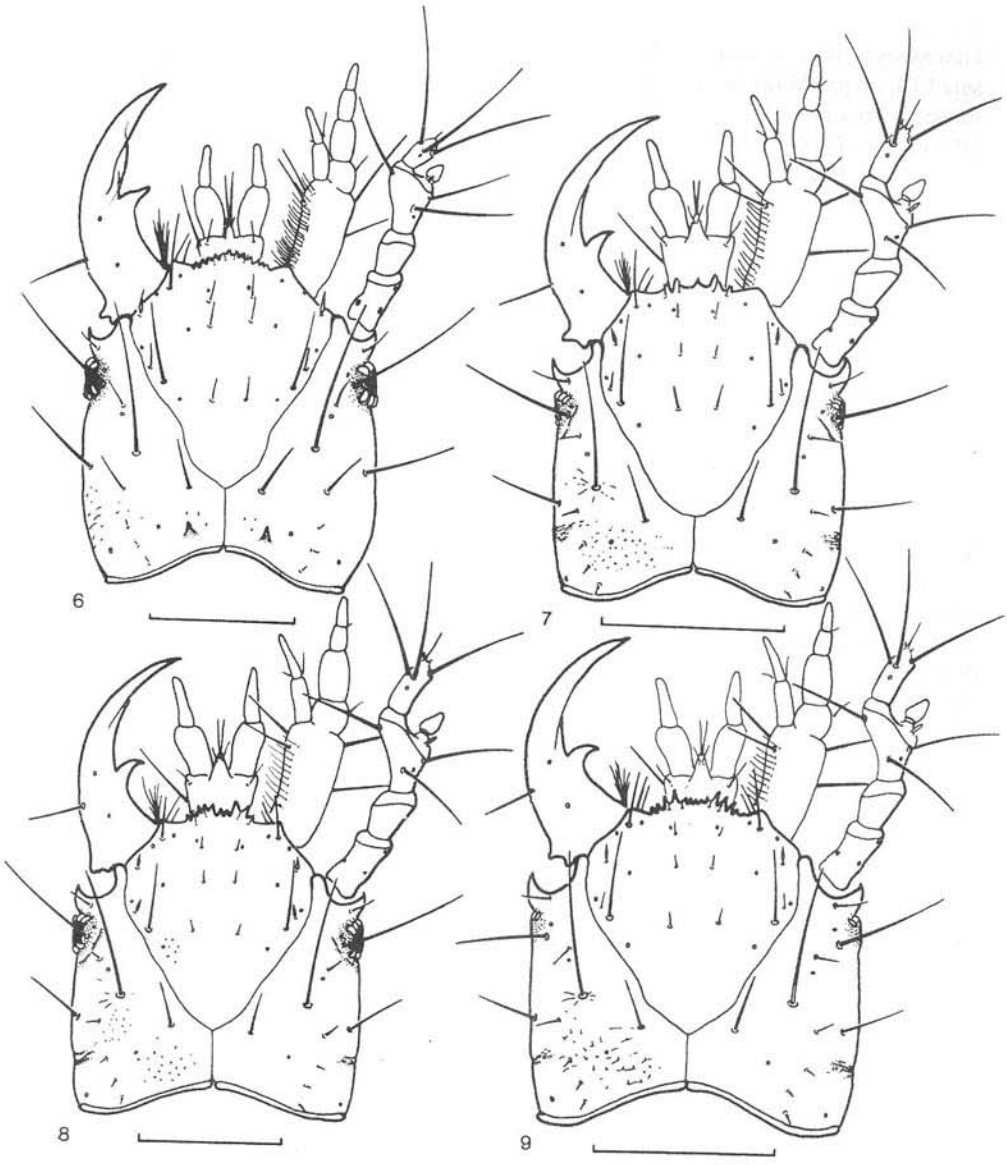
MONOPHYLY AND PHYLOGENETIC RELATIONSHIPS. In their taxonomic review of the New World Pogonini, Bousquet & Laplante (1997) found no synapomorphy for the genus *Pogonus* based on a limited number of species. They concluded that the genus, as presently conceived, may not be a monophyletic lineage. Known larvae of *Pogonus* share one apomorphic character state: in the first instar, the seta PY_6 on the pygidium is spindle-shaped instead of being trichoid. The presence of pointed microsculpture on the dorsal surface of the mandible of the first instar could represent another synapomorphy for the genus *Pogonus*. However, the transformation polarity of the character is difficult to assess. Presence of this feature occurs in several lineages within the supertribe Trechitae. Overall, evidence of monophyly for the genus *Pogonus* based on larval morphology is not overwhelming.

Among the genera treated here, *Pogonus* is probably more closely related to *Pogonistes* than to the other two genera. Larvae of *Pogonus* and *Pogonistes* have relatively long setae MX_{11} and MX_{12} on maxillary palpomere 3 (at least half width of the palpomere). This character state is rarely found in carabids, where these setae are extremely small. Relatively long setae MX_{11} and MX_{12} is likely the apomorphic state but its presence in the genus *Asaphidion* (see Maddison 1993: 153) suggests that it could be subject to convergence. The fact that no character state was found to separate second- and third-instar larvae of *Pogonus* from those of *Pogonistes* suggests also, in a way, that the two genera may be closely related.

MATERIAL STUDIED. *Pogonus luridipennis* (Germar, 1822): $2L_1$, $1L_2$, $1L_3$ (mounted on slide) reared from adults collected at Sarepta, Volgograd area, Russia on May 23, 1995 (VVG). *Pogonus iridipennis* Nicolai, 1822: $1L_1$, $1L_3$ (mounted on slide) reared from adults collected at Dnestrovsky Liman, Odessa distr., Ukraine on April 26, 1995 (VVG). *Pogonus transfuga* Chaudoir, 1870: $2L_1$, $1L_2$, $1L_3$ (mounted on slide) reared from adults collected at Baskunchak Lake, Astrakhan distr., Russia on May 25, 1995 (VVG); $1L_1$ (mounted on slide) reared from adults collected at Sarepta, Volgograd area, Russia on May 23, 1995 (VVG); additional material reared but not studied in detail includes $6L_1$, $2L_2$, and $1L_3$ (adults from Baskunchak Lake) (VVG). *Pogonus meridionalis* Dejean, 1828: $2L_1$, $1L_2$, (mounted on slide) reared from adults collected at Dnestrovsky Liman, Odessa distr., Ukraine on April 26, 1995 (VVG); $2L_1$, $1L_3$ (mounted on slide) reared from adults collected at Kuyalnisky Liman, Odessa distr., Ukraine on April 28, 1995 (VVG); additional material reared but not studied in detail includes $7L_1$, $3L_2$, $1L_3$ (BMNH, VVG). *Pogonus punctulatus* Dejean, 1828; $2L_1$, $1L_2$, $1L_3$ (mounted on slide) reared from adults collected at Dnestrovsky Liman, Odessa distr., Ukraine on April 26, 1995 (VVG); $4L_1$ (mounted on slide) reared from adults collected at Sarepta, Volgograd area, Russia on May 23, 1995 (VVG); additional material reared but not studied in detail includes $3L_1$ and $1L_3$ (VVG). *Pogonus cumanus* Lutshnik, 1916: $1L_1$ (mounted on slide) reared from adults collected at Kuyalnisky Liman, Odessa distr., Ukraine on April 28, 1995 (VVG); $1L_3$ (mounted on slide) collected with adults and identified by association (VVG).

GEOGRAPHICAL DISTRIBUTION AND DIVERSITY. The genus *Pogonus* includes about 45 species which are distributed worldwide, except in the Neotropical Region, but are most diverse in the Mediterranean area (Kryzhanovskij 1983; Bousquet & Laplante 1997) than anywhere else.

REMARKS. Second- and third-instar larvae of two species of *Pogonus*, namely *P. cumanus* and *P. punctulatus*, are easily recognized among the species studied in having secondary setae on antennomeres 1–3 (Figs 22, 23). Additionally, the single third-instar larva of *P. cumanus* we have studied is unique for the presence of secondary setae on the femur (8–9 setae), tibia (3–7 setae) and basal part of tarsus (2–4 setae). First-instar larvae of *P. punctulatus* differ readily from the other species studied by the absence of microsculpture on frontale and by the presence of only one microdenticle on the dorsal surface of the mandible between MN_b and MN_1. Larvae of other *Pogonus* species have pointed microsculpture in the basal part of the frontale and from 3 to 8 microdenticles on the dorsal surface of the mandible.



Figs 6–9. Cephalic capsule, right antenna, left mandible, right maxilla, labium, L_1 (dorsal view). 6 – *Thalassotrechus barbarae*; 7 – *Pogonistes angustus*; 8 – *P. rufoaeneus*; 9 – *P. convexicollis*. Scale bars = 0.2 mm.

Genus *Pogonistes* Chaudoir, 1871
(Figs 7–9, 11–12, 18)

DIAGNOSIS. First-instar larvae of *Pogonistes* differ from those of other genera treated in having the seta EM_1 on prothorax normal, trichoid. Second- and third-instar larvae cannot be separated from those of *Pogonus*.

DESCRIPTION. **First-instar larvae.** Cephalic capsule parallel-sided (Figs 7–9). Frontale without microsculpture (Figs. 7,9) or with pointed microsculpture restricted to near pore FR_b (Fig. 8); nasale rather straight at middle (Fig. 12). Parietale without egg-bursters (Figs 7–9); ocelli, postocellar and cervical grooves less distinct than in *Pogonus* (Figs 7–8) or posterior row of ocelli and postocellar groove absent (Fig. 9). Mandible without microdenticles between MN_b and MN_1 (Figs 7–9); terebra regular, slightly concave (Figs 7–9). Claw 0.9–1.0× length of tarsus. Urogomphi relatively short, parallel (Fig. 18).

Chaetotaxy: Seta AN_6 1.0–1.5× as long as width of antennomere 4 (Fig. 7). Frontale with at least seta FR_6 spindle-shaped; seta EM_1 on prothorax, TE_7 on abdominal tergites, and PY_6 on pygidium normal, trichoid; length of setae MX_{11} and MX_{12} at least half diameter of maxillary palpomere 3. Pore PR_h on pronotum present. Seta TA_1 located at basal third of tarsus (as in Fig. 15).

Second- and third-instar larvae. Postocellar and cervical grooves distinct.

Chaetotaxy: Antennae and legs without secondary setae. Meso-, metanotum, and abdominal tergites 1–6 without numerous secondary setae on medial half of sclerites.

MONOPHYLY AND PHYLOGENETIC RELATIONSHIP. We found no larval synapomorphy among the species studied to support the view that the genus is monophyletic. Second- and third-instar larvae of *Pogonistes* are similar to those of *Pogonus*. In addition, larvae of both genera share the presumably apomorphic condition of relatively long setae MX_{11} and MX_{12} on maxillary palpomere 3. As stated previously *Pogonistes* is probably more closely related to *Pogonus* than to the other genera treated.

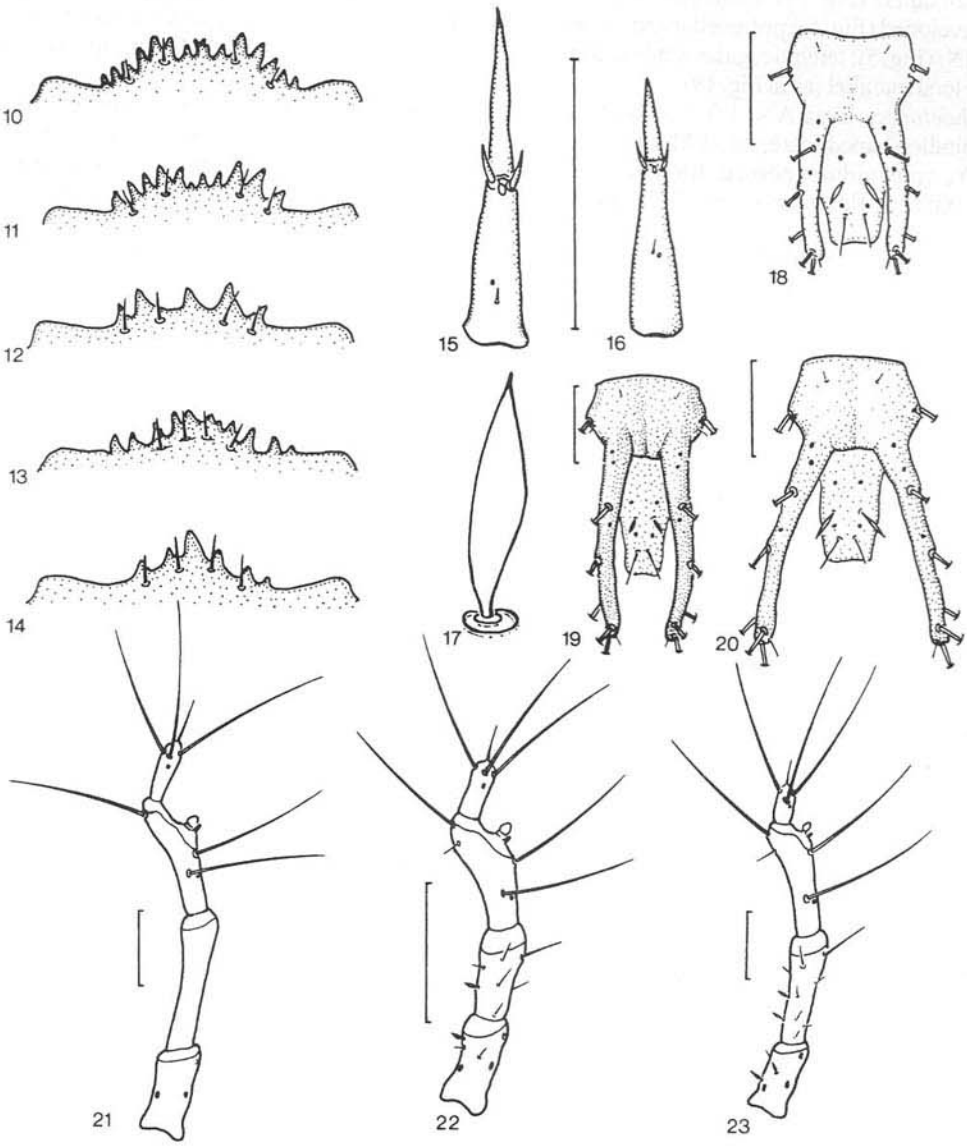
MATERIAL STUDIED. *Pogonistes rufoaeneus* (Dejean, 1828): $1L_1$, $2L_2$, $1L_3$ (mounted on slide) reared from adults collected at Sarepta, Volgograd area, Russia on May 23, 1995 (VVG); $2L_1$, $2L_2$, $1L_3$ reared from adults collected in the Kara Kum Desert, Uzboy Lakes system, Turkmenia on April 28, 1995 (CNC); additional material reared but not studied in detail includes $4L_1$ and $1L_2$ (VVG). *Pogonistes convexicollis* Chaudoir, 1871: $2L_1$, $1L_2$, $1L_3$ (mounted on slide) reared from adults collected at Kuyalnisky Liman, Odessa distr., Ukraine on April 28, 1995 (VVG); additional material reared but not studied in detail includes $1L_2$ (VVG). *Pogonistes angustus* (Gebler, 1830): $2L_1$, $2L_2$, $1L_3$ (mounted on slide) reared from adults collected at Kuyalnisky Liman, Odessa distr., Ukraine on April 28, 1995 (VVG); additional material reared but not studied in detail includes $8L_1$ and $4L_2$ (VVG).

GEOGRAPHICAL DISTRIBUTION AND DIVERSITY. The genus *Pogonistes* includes about 10 species in the Mediterranean area (Kryzhanovskij 1983).

Genus *Cardiaderus* Dejean, 1828
(Figs 5, 14, 15, 26, 27)

DIAGNOSIS. Larvae of *Cardiaderus* are differentiated from those of other members of Pogonini by the character states listed in the key and by having, in the second and third instars, numerous secondary setae located on the medial half of the meso-, metanotum, and abdominal tergites. Furthermore the antennomere 2 bears secondary setae while the antennomeres 1 and 3 have no such setae. Only some members of the genus *Pogonus* also possess secondary setae on antennomere 2 but in these species the antennomeres 1 and 3 bear secondary setae.

DESCRIPTION. **First-instar larvae.** Cephalic capsule parallel-sided (Fig. 5). Frontale with pointed microsculpture near pore FR_b (Fig. 5); nasale with 6–7 teeth, median one somewhat more protruding



Figs 10–23. 10–14, nasale, L_1 (dorsal view): 10 – *Pogonus luridipennis*; 11 – *Pogonistes rufoaeneus*; 12 – *P. angustus*; 13 – *Thalassotrechus barbarae*; 14 – *Cardiaderus chloroticus*. 15–16, tarsus and claw, L_1 (dorsal view): 15 – *Cardiaderus chloroticus*; 16 – *Thalassotrechus barbarae*. 17 – spindle-shaped seta. 18–20, urogomphi and pygidium, L_1 (dorsal view): 18 – *Pogonistes convexicollis*; 19 – *Pogonus luridipennis*; 20 – *Thalassotrechus barbarae*. 21–23, right antenna, L_3 (dorsal view). 21 – *Pogonus luridipennis*; 22 – *P. punctulatus*; 23 – *P. cumanus*. Scale bars = 0.2 mm.

than others (Fig. 14). Parietale without egg-bursters (Fig. 5); ocelli and cervical groove markedly developed (Fig. 5); postocellar groove absent. Mandible without microdenticles between MN_b and MN_1 (Fig. 5); terebra regular, slightly concave. Claw as long as tarsus (Fig. 15). Urogomphi relatively long, parallel (as in Fig. 19).

Chaetotaxy: Seta AN_6 1.0–1.3× as long as width of antennomere 4 (Fig. 5). Frontale without spindle-shaped setae; seta EM_1 on prothorax spindle-shaped; setae TE_7 on abdominal tergites and PY_6 on pygidium normal, trichoid; length of setae MX_{11} and MX_{12} less than 0.25× diameter of maxillary palpomere 3. Pore PR_h on pronotum present. Seta TA_1 located at basal third of tarsus (Fig. 15).

Second- and third-instar larvae. Postocellar groove distinct; cervical groove absent.

Chaetotaxy: Antenna with secondary setae on antennomere 2 only (Fig. 26). Legs without secondary setae on tarsus, tibia and femur. Meso-, metanotum, and abdominal tergites 1–6 with numerous, more or less long, secondary setae on medial half of sclerites (Fig. 27).

Phylogenetic Relationship. Second- and third-instar larvae of the genus *Cardiaderus* show two apomorphic character states: the meso-, metanotum, and abdominal tergites bear numerous secondary setae on the medial half of the tergites (Fig. 27) and the antennomere 2 has secondary setae (Fig. 26). The last feature is shared with some species of *Pogonus* (*P. cumanus* and *P. punctulatus*). However, we believe that the presence of this state in both taxa appeared independently. For example, presence of secondary setae on the antennomere 2 has appeared in several lineages within the tribes Pterostichini (Bousquet 1985), Bembidiini and Trechini (our observations). Relationships of the genus *Cardiaderus* are uncertain.

Material studied. *Cardiaderus chloroticus* (Fischer von Waldheim, 1823): $2L_1$, $1L_2$, $1L_3$ (mounted on slide) reared from adults collected at Kuyalnitsky Liman, Odessa distr., Ukraine on April 28, 1995 (VVG); additional material reared but not studied in detail includes $7L_1$, $4L_2$, $5L_3$ (VVG, CNC, BMNH).

Geographical distribution and Diversity. The genus *Cardiaderus* includes a single species, *C. chloroticus*, which is distributed throughout the steppe and semi-desert areas of Palaearctic Region from Romania and Bulgaria to eastern Kazakhstan and the Altai (Kryzhanovskij 1983).

Genus *Thalassotrechus* Van Dyke, 1918

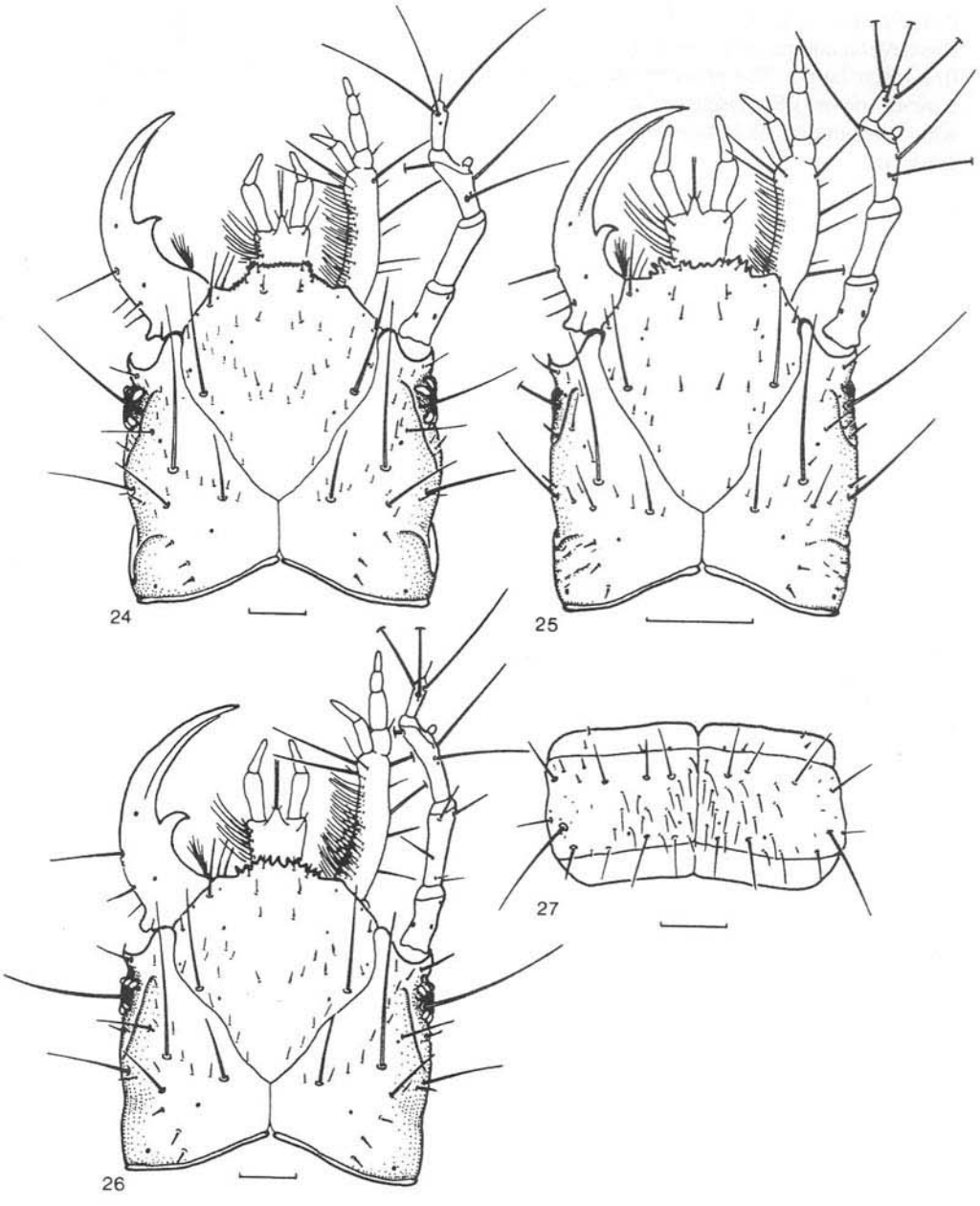
(Figs 6, 13, 16, 20)

Diagnosis. First-instar larvae of *Thalassotrechus* are unique among the species studied by the rounded lateral sides of the cephalic capsule, by the absence of cervical grooves; by the presence of egg-bursters on the parietale, by the absence of pore PR_h, by the short claw, by the position of the seta TA_1 which is at middle of the tarsus, and by the spindle-shaped setae TE_7 on tergites 1–8.

Description. **First instar larvae.** Cephalic capsule with rounded lateral sides (Fig. 6). Frontale without microsculpture (Fig. 6); nasale slightly protruding at middle (Fig. 13). Parietale with egg bursters consisting of one large tooth on each side near epicranial suture (Fig. 6); ocelli developed (Fig. 6); postocellar and cervical grooves absent (Fig. 6). Mandible without microdenticles between MN_b and MN_1; medial margin of terebra slightly convex near base (Fig. 6). Claw about 0.5× length of tarsus (Fig. 16). Urogomphi relatively long, divergent (Fig. 20).

Chaetotaxy: Length of seta AN_6 1/4–1/3 width of antennomere 4 (Fig. 6). Frontale with seta FR_6 spindle-shaped; seta EM_1 on prothorax spindle-shaped; length of setae MX_{11} and MX_{12} less than 0.25× diameter of maxillary palpomere 3. Pore PR_h on pronotum absent. Seta TA_1 located at middle of tarsus (Fig. 16). Setae TE_7 on tergites 1–8 spindle-shaped; seta PY_6 on pygidium normal, trichoid.

Second- and third-instar larvae. Unavailable. Superficially described by Moore (1956).



Figs 24–27. 24–26, cephalic capsule, right antenna, left mandible, right maxilla, labium, L_3 (dorsal view): 24 – *Pogonus transfuga*; 25 – *Pogonistes angustus*; 26 – *Cardiaderus chloroticus*. 27 – first abdominal segment of *Cardiaderus chloroticus*, L_3 (dorsal view). Scale bars = 0.2 mm.

PHYLOGENETIC RELATIONSHIP. Bousquet & Laplante (1997) indicate that adults of *T. barbarae* possess several autapomorphies within the tribe Pogonini. A similar statement could be made for the first instar larvae. The presence of egg-bursters on the parietale, comparatively short seta AN_6, absence of pore PR_h, absence of cervical grooves, and spindle-shaped setae TE_7 are character states which are unique, and probably apomorphic, to *T. barbarae*. Relationships of the genus remain uncertain.

MATERIAL STUDIED. *Thalassotrechus barbarae* (G. H. Horn, 1892): $2L_1$ (mounted on slide) reared by W.G. Evans from adults collected at Pacific Grove, Monterey Bay, California (CNC).

GEOGRAPHICAL DISTRIBUTION AND DIVERSITY. The genus *Thalassotrechus* includes a single species, *T. barbarae*, from the Pacific coast of USA and Baja California, Mexico (Bousquet & Laplante 1997).

CONCLUDING REMARKS

In general, immature stages of most groups of carabids are poorly known and the tribe Pogonini is no exception. Larvae of eleven species belonging to four genera were studied in the present paper, which account for only about 15% of the world fauna. Larvae of seven genera (*Bedeliolus*, *Dioedercarus*, *Diplochaetus*, *Ochtozetus*, *Pogonopsis*, *Syrdenus*, *Olegius*) remain unknown. We hope this modest contribution could stimulate others to study carabid larvae.

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