

***Harpalus* larvae (Coleoptera: Carabidae: Harpalina): description of several species and taxonomic remarks**

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Abstract. Three larval instars of *Harpalus* (*Harpalus*) *atratus* Latreille, 1804, *H. (H.) cisteloides hurkai* Divoký, Pulpán et Rébl, 1990, *H. (H.) picipennis* (Duftschmid, 1812), *H. (H.) saxicola* Dejean, 1829, *H. (H.) servus* (Duftschmid, 1812), first and third larval instars of *H. (H.) luteicornis* (Duftschmid, 1812) and third larval instar of *H. (H.) solitarius* Dejean, 1829 and *H. (H.) xanthopus winkleri* Schaubberger, 1923 are described and illustrated. Differential diagnosis of the nominotypical subgenus *Harpalus* Latreille, 1802, based on larval characters, is given. Taxonomic significance of species aggregates and subgenera are discussed. Some new larval characters (detailed additional chaetotaxy of femora) are used.

Larval taxonomy, preimaginal characters, Coleoptera, Carabidae, *Harpalus*

INTRODUCTION

The subgenus *Harpalus* Latreille, 1802 consists of about 300 species world-wide (Lorenz 1998). The more or less superficial and incomplete notes on about 30 species of larvae of this subgenus are mentioned in the literature (Schiodte 1867, Gardner 1938, van Emden 1942, Chu 1945, Larsson 1941, 1968, Sharova 1958, 1964, Habu & Sadanaga 1963, 1965, 1970a, b, Kirk 1972, Habu 1973, Hůrka 1975, Brandmayr, Ferrero & Zeto Brandmayr 1980, Arndt 1991, Luff 1993). Only the works by Habu & Sadanaga (1963, 1965, 1970a, b), Habu (1973) and Arndt (1991) deal with more than one larval instar and consider the chaetotaxy.

The purposes of the paper are to describe to date undescribed larvae of *Harpalus*, discuss possible relationships between the taxa studied, and provide the differential diagnosis of the subgenus *Harpalus* in the larval stage.

MATERIAL AND METHODS

Three larval instars of *Harpalus* (*Harpalus*) *atratus* (5 L₁, 2 L₂, 6 L₃), *H. (H.) cisteloides hurkai* (5 L₁, 5 L₂, 6 L₃), *H. (H.) luteicornis* (5 L₁, 5 L₃), *H. (H.) picipennis* (6 L₁, 4 L₂, 6 L₃), *H. (H.) saxicola* (2 L₁, 1 L₂, 2 L₃), *H. (H.) servus* (18 L₁, 3 L₂, 6 L₃) and the third instar of *H. (H.) solitarius* (1 L₃) and *H. (H.) xanthopus winkleri* (1 exuvia of L₁, 1 L₃) are reared ex ovo during years 1989 and 1999 following the technique described by Hůrka (1996).

The parental pairs are found as follows: *H. (H.) atratus* – Bohemia centr., Praha-Kunratice (code of mapping square 5952, for details see Pruner & Míka 1996), 24.4.1998, Z. Papoušek leg.; *H. (H.) cisteloides hurkai* – Bohemia, České středohoří, Pisečný vrch, (5548), 11.9.1993, P. Veselý leg.; *H. (H.) luteicornis* – Bohemia centr., Praha-Radotín, Cikánka env. (6051), fallow, 20.4.1999, K. Hůrka leg.; *H. (H.) picipennis* – Bohemia centr., Tuhaň nr. Neratovice (5753), 21.6.1995, K. Hůrka leg.; *H. (H.) saxicola* – Slovakia mer., Avaš hill nr. Sírnik (7497), 8.4.1989, J. Hejkal leg.; *H. (H.) servus* – Moravia, Bzenec-střelnice (7069), 28.9.1997, Z. Papoušek leg.; *H. (H.) solitarius* Bohemia, Český les, Čerchov 1000m, (6642), 29.7.1993, K. Hůrka leg.; *H. (H.) xanthopus winkleri* – Bohemia centr., Travčice (5451), 15.5.1997, K. Hůrka leg.

For comparative purpose larvae of following taxa have been studied: *H. (Acardystus) flavescens* (Piller et Mitterpacher, 1783), *H. (Harpalus) anxius* (Duftschmid, 1812), *H. (H.) autumnalis* (Duftschmid, 1812), *H. (H.) distinguendus* (Duftschmid, 1812), *H. (H.) froelichii* Sturm, 1818, *H. (H.) honestus* (Duftschmid, 1812), *H. (H.) latus* (Linnaeus, 1758), *H. (H.) pumilus* Sturm, 1818, *H. (H.) subcylindricus* Dejean, 1829, *H. (H.) tardus* (Panzer, 1797) and *H. (Semiophonus) signaticornis* (Duftschmid, 1812).

All material is deposited in the Collectio Hürka of the Charles University Praha, Department of Zoology. The notation of setae and pores follows the papers by Bousquet & Goulet (1984) and Bousquet (1985).

DESCRIPTION OF LARVAE

Harpalus (Harpalus) atratus Latreille, 1804

(Figs 1–10)

First instar

HABITUS AND COLOR. Head capsule and pronotum conspicuously broad and transverse; body yellow, head and pronotum pale brown, retinaculum and apex of mandible dark brown. Width of head capsule 1.44–1.50 mm ($x = 1.47$ mm, $n = 5$).

MICROSCULPTURE. Isodiametric microsculpture absent, granulated microsculpture on pronotal prescutum and postscutum.

CHAETOTAXY. Only one additional pair of spines on anterior femora; seta PA₄ very fine, but distinctly longer than setae PA₁–PA₃; setae FR₁ and FR₃ obviously reduced; group gMX consists of 5–6 thicker and more than 70 thinner, long setae.

HEAD (Fig. 1) distinctly transverse (index width/length 1.35); nasale (Fig. 2) not or slightly prominent, distinctly toothed throughout, with 13–16 teeth, two lateral on each side larger, ventral row with 30–32 teeth; adnasalia moderately sloping; cervical grooves clearly bent, almost reaching the level of seta PA₇ on dorsal side, don't reaching the ventral side; coronal suture very long, distinctly longer than length of antennomere II; egg burster consists of 5–6 small teeth on each side of frontale. Antennae as long as mandibles; mandible (Fig. 3) triangular, 3 times as long as basal width, with one larger and one smaller teeth in front of retinaculum; seta MB₁ short, only a little longer than retinaculum, penicillus present; maxillae (Fig. 4) slender, stipes more than 3 times as long as wide; labium (Fig. 5) very short and rounded on lateral borders, ligula reaching the level of one quarter of palpomere I, distinctly bifid at apex.

THORAX. Pronotum transverse, as wide as head, notal carina indistinct, seta PR₁ reduced up to pore; legs (Fig. 6) normally developed, claws unequal, anterior curved, almost twice as long as posterior on the first pair and only a little longer than posterior on the other pairs.

ABDOMEN. Urogomphi subparallel, longer than width of tergum IX and of anal tube.

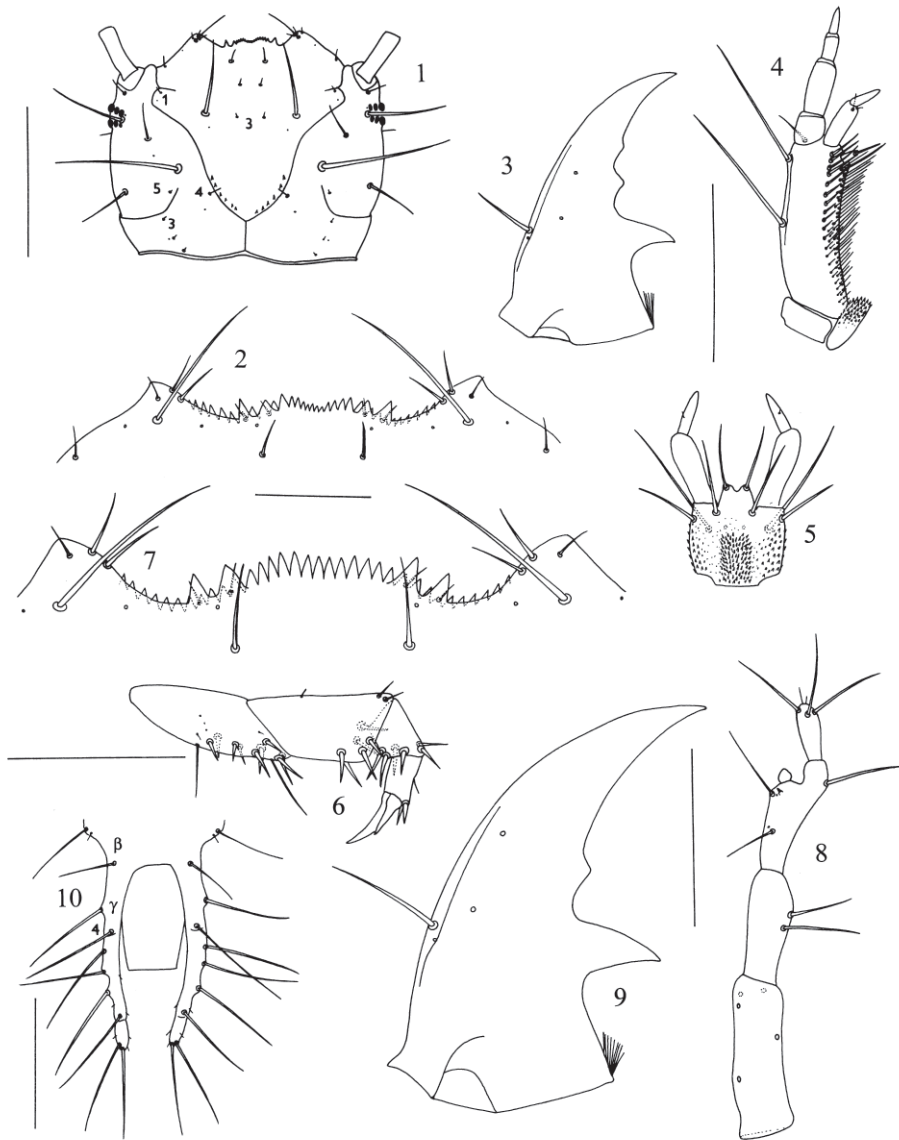
Second and third instars

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 1.89 and 2.07 mm in the second and 2.45–2.59 mm ($x = 2.52$ mm, $n = 6$) in the third instar.

MICROSCULPTURE. Isodiametric microsculpture on head and pronotum, granulated microsculpture on pronotal prescutum and postscutum and on postscutum of meso- and metanotum.

CHAETOTAXY. Head: 2 secondary setae on inner side of antennomere II, 2 setae on outer side of stipes, 1–2 setae near apex of palpomere I, 8 pairs of setae (10 pairs in L₃) on dorso-lateral surface of prementum, 1–2 setae on place of inner and outer stemmatal furrows. Thorax: pronotum with 2–3 secondary setae along notal carina, several setae on lateral margin and between setae PR₁₁ and PR₁₂; 9–11 secondary spines on each side of anterior femora. Abdomen: abdominal tergites with 1 secondary seta between TE₁ and TE₆, 2 setae between TE₆ and TE₇ and 1–2 setae between TE₉



Figs 1–10. *Harpalus (Harpalus) atratus* Latreille. First instar larva: 1 – head capsule (dorsal view). 2 – nasale. 3 – mandible. 4 – maxilla. 5 – labium. 6 – first leg. Third instar larva: 7 – nasale. 8 – antenna. 9 – mandible. 10 – urogomphi. Scales: 1 mm (Figs 1, 10), 0.5 mm (Figs 3, 4, 5, 6, 8, 9), 0.2 mm (Figs 2, 7).

and TE₁₀, 2–3 small setae on lateral margin; 4 long and many small secondary setae on surface of urogomphi, length of UR_β 0.65 times that of UR₄, UR₇ about as long as UR₄.

HEAD AND NASALE (Fig. 7) similar as in L₁, nasale more prominent, lateral teeth larger; cervical grooves reaching the level of PA₅; coronal suture longer than antennomere II; seta PA₄ as long as antennomere II or III; setae PA_{1,2,3} very small; antenna (Fig. 8); mandible with only one extra tooth (Fig. 9).

THORAX. Claws unequal as in first instar.

ABDOMEN. Urogomphi (Fig. 10) long and subparallel, twice as long as width of tergum IX, distinctly longer than anal tube.

***Harpalus (Harpalus) cisteloides hurkai* Divoký, Pulpán et Rébl, 1990**
(Figs 11–19)

First instar

HABITUS AND COLOR. Body yellow white, head and pronotum pale brown, retinaculum and apex of mandible dark brown. Width of head capsule 1.14–1.20 mm (\bar{x} = 1.16 mm, n = 5).

MICROSCULPTURE. Isodiametric microsculpture on frontale and parietale, granulated microsculpture on prescutum and postscutum of pronotum and on postscutum of mesonotum, pointed microsculpture on metanotum and on abdominal terga.

CHAETOTAXY. Excepting ancestral chaetotaxy one additional seta on dorso-lateral surface of prementum and 4 pairs of additional spines on anterior femora; seta PA₄ slightly longer than coronal suture, as long as antennomere IV and distinctly longer than setae PA₁–PA₃; the majority of setae on frontale, except FR₂, relatively short, especially setae FR_{8,9} and one additional neighbouring seta; group gMX consists of 4–5 thicker and more than 50 thinner, long setae.

HEAD (Fig. 11) distinctly transverse (index width/length 1.3); nasale (Fig. 12) protruding, with triangular central incision and with 5–6 teeth on each side, two lateral only a little larger, ventral row consists of 18–22 teeth, adnasalia moderately sloping; cervical grooves clearly bent, almost reaching the level between setae PA₇ and PA₄ on dorsal side, don't reaching the level of seta PA₁₆ on ventral side; coronal suture distinctly longer than width of antennomere I; egg burster consists of 2 smaller teeth on the level of seta PA₄ on each side. Antennae slightly longer than mandibles; mandible (Fig. 13) strongly curved and robust, twice as long as basal width, with only a slight swelling in front of retinaculum, penicillus present; maxillae (Fig. 14) slender, stipes almost 3.5 times as long as wide; labium (Fig. 15) rather short, with slender labial palpi; ligula reaching the level of one third of palpomere I and distinctly bifid apically.

THORAX. Pronotum transverse, wider than head, with very distinct notal carina, reaching the level of seta PR₂; legs normally developed, claws unequal, anterior twice as long as posterior in the first pair.

ABDOMEN. Urogomphi parallel and longer than width of tergum IX, with ancestral setae as long as urogomphi; anal tube long and slender, reaching the level between setae UR₅ and UR₆.

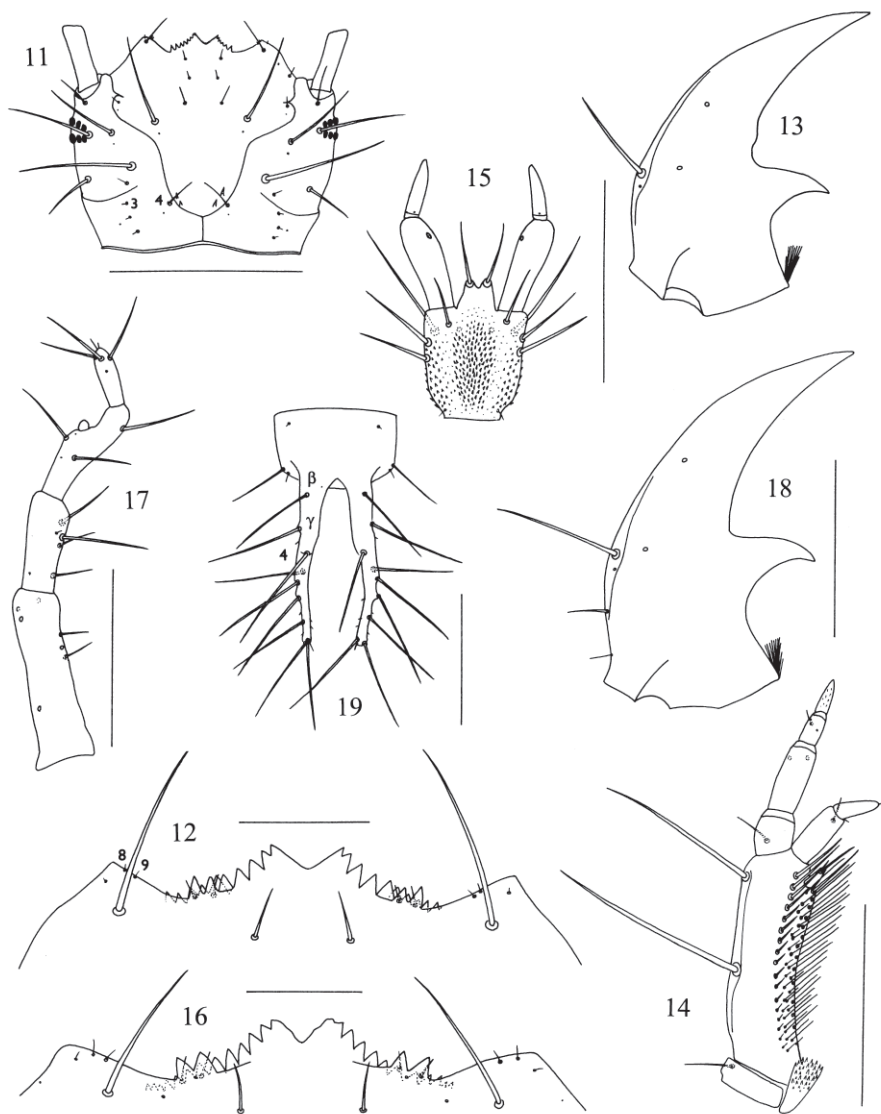
Second and third instars

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 1.38–1.57 mm (\bar{x} = 1.50 mm, n = 5) in the second and 1.84–1.98 mm (\bar{x} = 1.90 mm, n = 6) in the third instar.

MICROSCULPTURE. Granulated microsculpture also on postscuta of metanotum and abdominal terga, pointed microsculpture on urogomphi.

CHAETOTAXY. Head: 2 additional setae on inner side of antennomere I, 4–6 setae on inner side of antennomere II, 2–3 setae on outer side of stipes, 2 setae near base of mandible, 2–3 setae near



Figs 11–19. *Harpalus (Harpalus) cisteloides hurkai* Divoký, Pulpán et Rébl. First instar larva: 11 – head capsule (dorsal view). 12 – nasale. 13 – mandible. 14 – maxilla. 15 – labium. Third instar larva: 16 – nasale. 17 – antenna. 18 – mandible. 19 – urogomphi. Scales: 1 mm (Figs 11, 19), 0.5 mm (Figs 13, 14, 15, 17, 18), 0.2 mm (Figs 12, 16).

apex of palpomere I, 5–7 pairs of setae (8–9 pairs in L_3) on lateral side of prementum; 2 setae on place of inner and outer stemmatal furrows, many diminutive setae or sensillae on dorsal surface of head capsule. Thorax: Pronotum with 2–3 additional setae along notal carina, number of setae on lateral margin and between setae PR_{11} and PR_{12} , more than 8 additional spines on each side of anterior femora. Abdomen: 1 additional seta between TE_1 and TE_6 , 2 setae between TE_6 and TE_7 , 1–2 setae between TE_9 and TE_{10} and 2–3 small setae on lateral margin. Length of UR_β 0.75 times that of UR_4 , UR_7 about as long as UR_4 .

HEAD. Nasale (Fig. 16) with larger lateral teeth; coronal suture longer than antennomere II; seta PA_4 as long as antennomeres II or III; setae PA_1 – PA_3 very small; antenna (Fig. 17); mandible (Fig. 18).

THORAX. Legs long and slender, claws unequal as in first instar.

ABDOMEN. Urogomphi (Fig. 19) subparallel and long, twice as long as width of tergum IX and longer than anal tube.

Harpalus (Harpalus) luteicornis (Duftschmid, 1812)

(Figs 20–27)

First instar

HABITUS AND COLOR. Body yellow-white, retinaculum and apex of mandible brown. Width of head capsule 1.04–1.14 mm ($x = 1.08$ mm, $n = 5$).

MICROSCULPTURE. Isodiametric microsculpture on anterior part of frontale, granulated microsculpture on prescutum and postsutum of pronotum.

CHAETOTAXY. Head: Setae PA_4 , PA_5 and especially PA_1 – PA_3 very fine and small, setae PA_6 and PA_8 markedly fine and reduced; group gMX consists of 4–5 thicker and more than 50 thinner and rather short setae. Thorax: Except for ancestral chaetotaxy 6 or 7 additional spines on either side of anterior femora.

HEAD (Fig. 20) transverse (index width/length 1.3); nasale (Fig. 21) protruding, with fine but distinct central incision and 6–7 teeth on each side, two lateral slightly longer, adnasalia moderately sloping, ventral row consists of 22–24 teeth; cervical grooves clearly bent, almost reaching the level of seta PA_7 on dorsal side, don't reaching the level of seta PA_{16} on ventral side; coronal suture as long as width of antennomere I; egg-burster consists of 4–5 teeth, being larger caudad, along frontal suture on each side. Antennae slightly longer than mandibles; mandible (Fig. 22) strongly curved and robust, twice as long as basal width, with a toothlike swelling in front of retinaculum, penicillus present; maxillae (Fig. 23) slender, stipes almost 3 times as long as wide; labium (Fig. 24) short, with slender labial palpi; ligula reaching the level of one fourth or fifth of palpomere I and weakly bifid at apex.

THORAX. Pronotum narrower than head, with indistinct notal carina; legs normally developed, claws unequal, anterior as long as or a little longer than posterior.

ABDOMEN. Abdominal tergites transverse; urogomphi weakly curved, twice as long as width of tergum IX and about one third of anal tube length.

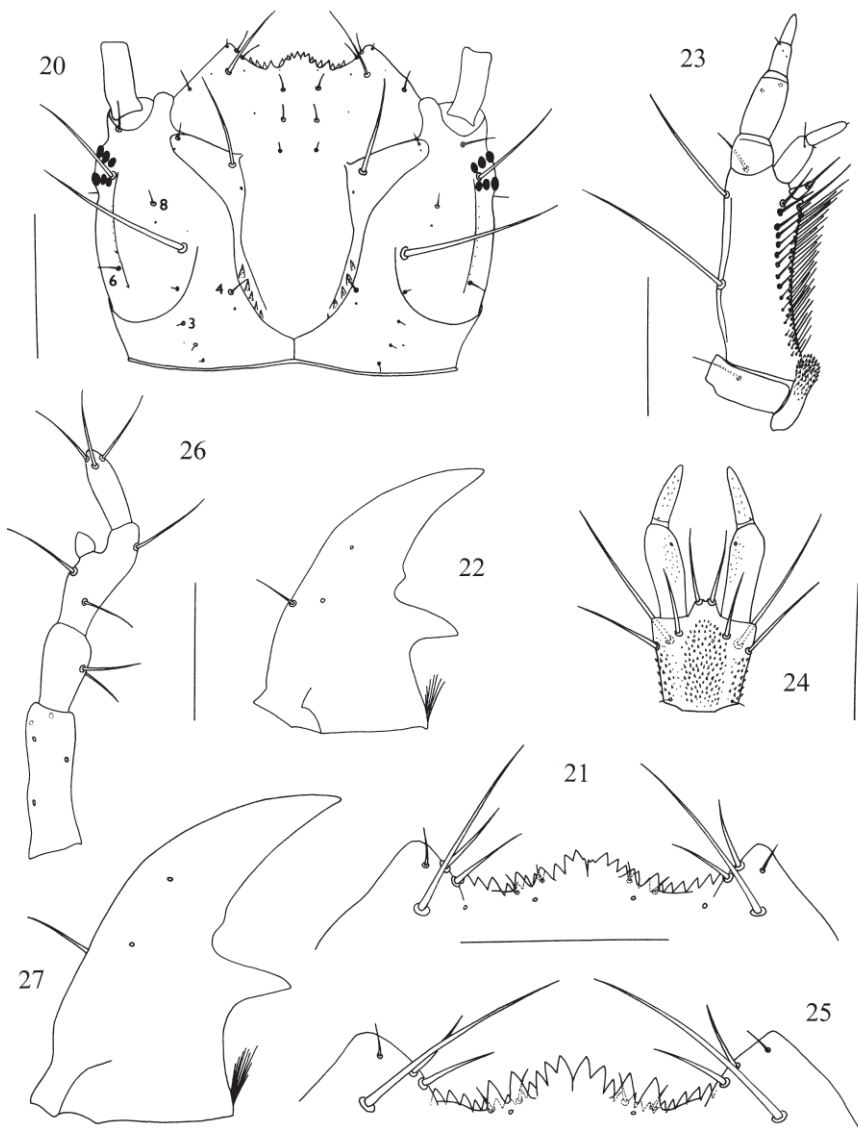
Third instar

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 1.30–1.40 mm ($x = 1.34$ mm, $n = 5$).

MICROSCULPTURE. Isodiametric microsculpture weakly distinct.

CHAETOTAXY. Head: 2 additional setae on inner side of antennomere II, 2 setae on outer side of stipes, 1–2 seta near apex of palpomere I, 7–9 pairs of setae on dorso-lateral surface of prementum; 2–3 small setae on place of outer stemmatal furrows. Thorax: 1 (2) secondary setae on either side of



Figs 20–27. *Harpalus (Harpalus) luteicornis* (Duftschmid). First instar larva: 20 – head capsule (dorsal view). 21 – nasale. 22 – mandible. 23 – maxilla. 24 – labium. Third instar larva: 25 – nasale. 26 – antenna. 27 – mandible. Scales: 0.5 mm (Fig. 20), 0.3 mm (Figs 21, 22, 23, 24, 25, 26, 27).

anterior femora. Only diminutive setae on dorsal surface of head capsule, thoracic and abdominal tergites. Length of seta UR_β about 0.5 times, of UR_γ 0.75 times that of UR₄.

HEAD similar to L₁, nasale (Fig. 25) more prominent and with larger lateral teeth; cervical grooves very distinct and bent; well developed outer stemmatal furrows; antenna (Fig. 26), mandible (Fig. 27).

THORAX. Pronotum with weakly developed notal carina; legs similar to L₁; claws unequal, anterior about one fourth longer than posterior.

ABDOMEN. Urogomphi slender and long, more than twice as long as width of tergum IX and length of anal tube.

Harpalus (Harpalus) picipennis (Duftschmid, 1812)

(Figs 28–35)

First instar

HABITUS AND COLOR. Small larvae with transverse, angular head capsule and shortened extremities; body yellow-white, head and pronotum yellow-brown, retinaculum and apex of mandibles dark brown. Width of head capsule 0.70–0.78 mm ($x = 0.73$ mm, $n = 6$).

MICROSCULPTURE. Isodiametric microsculpture absent, granulated microsculpture on pronotal pre-scutum and postscutum.

CHAETOTAXY. Except for ancestral chaetotaxy 4 additional setae on either side of anterior femora; seta PA₄ distinctly longer than setae PA₁–PA₃ and PA₅.

HEAD. (Fig. 28) transverse (index width/length 1.4); nasale (Fig. 29) slightly prominent, with 7–9 central and 2, slightly longer, lateral teeth on each side, ventral row consists of 19–23 teeth, adnasalia moderately sloping; cervical grooves bent, almost reaching the level of seta PA₃; coronal suture very short, as long as half of width of antennomere I; egg burster consists mostly of 2 teeth, one larger on the level of seta PA₄, one smaller on the level of seta PA₃; group gMX consists of only 1–2 thick and more than 40 thinner, very fine and short setae. Antennae short and thickset, less than 6.5 times as long as wide; mandibles (Fig. 30) strongly curved and robust, twice as long as basal width, with a fine swelling in front of retinaculum, penicillus present; maxillae (Fig. 31) thickset, stipes only 2.3 times as long as wide; labium (Fig. 32) short with slender labial palpi, ligula reaching the level of one third of palpomere I.

THORAX. Pronotum transverse, with distinct notal carina; legs short and robust.

ABDOMEN. Abdominal tergites transverse; urogomphi very short and divergent, only slightly longer than width of tergum IX and length of anal tube.

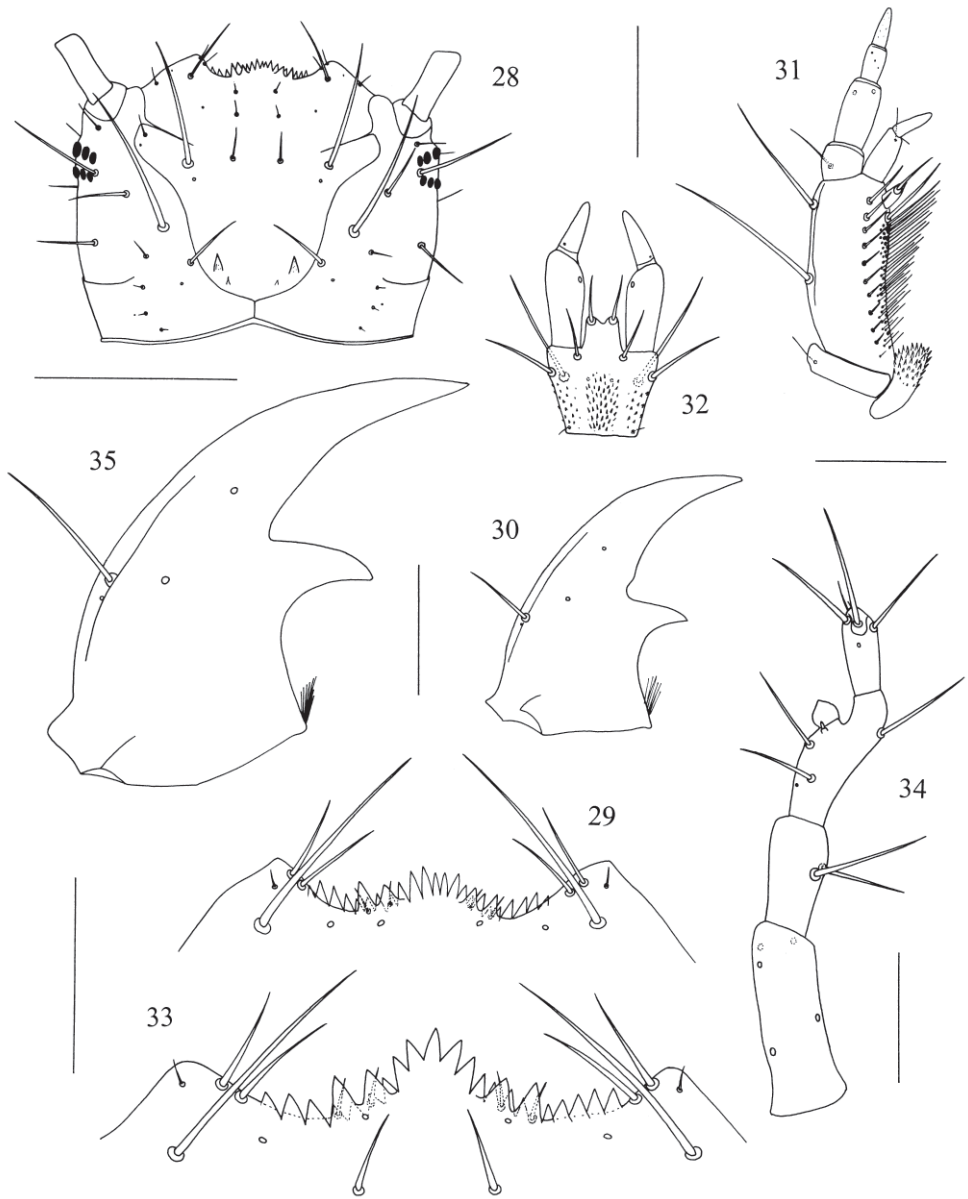
Second and third instars

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 0.83–0.97 mm ($x = 0.92$ mm, $n = 3$) in the second and 0.94–1.20 mm ($x = 1.06$ mm, $n = 6$) in the third instar.

MICROSCULPTURE. Weakly distinct isodiametric microsculpture on head capsule, granulated microsculpture also on postscuta of meso- and metanotum.

CHAETOTAXY. Head: 2 additional setae on inner side of antennomere II, 2 setae on outer side of stipes, 2 setae near apex of palpomere I, 5–6 pairs of setae (8–9 pairs in L₃) on dorso-lateral surface of prementum; 1–2 small setae on place of inner and outer stemmatal furrows. Thorax: 6 additional setae on each side of anterior femora. Abdomen: On abdominal terga 1 additional seta between TE₁ and TE₆, 2 setae between TE₆ and TE₇ and 1 seta between TE₉ and TE₁₀; 4 long secondary setae on urogomphi. Several very small setae on surface of thoracic and abdominal terga and urogomphi. Length of both UR_β and UR_γ about 0.80 times that of UR₄.



Figs 28–35. *Harpalus (Harpalus) picipennis* (Duftschmid). First instar larva: 28 – head capsule (dorsal view). 29 – nasale. 30 – mandible. 31 – maxilla. 32 – labium. Third instar larva: 33 – nasale. 34 – antenna. 35 – mandible. Scales: 0.5 mm (Fig. 28), 0.2 mm (Figs 29, 30, 31, 32, 33, 34, 35).

HEAD. Similar to L₁; nasale (Fig. 33) more protruding; coronal suture longer; cervical grooves deeper; outer stemmatal furrows weakly distinct. Extremities slightly longer: antenna (Fig. 34); mandible (Fig. 35).

THORAX. Pronotum with weakly determined notal carina; legs a little longer.

ABDOMEN. Urogomphi a little longer than width of tergum IX and the length of anal tube.

Harpalus (Harpalus) saxicola Dejean, 1829

(Figs 36–44)

First instar

HABITUS AND COLOR. Body pale, retinaculum and apex of mandible dark brown. Width of head capsule 1.42 and 1.46 mm.

MICROSCULPTURE. Isodiametric microsculpture absent, granulated microsculpture on prescurum and postscutum of pronotum and on postscuta of mesonotum, metanotum and of abdominal tergites I–III.

CHAETOTAXY. Except for ancestral chaetotaxy one additional seta on dorso-lateral surface of prementum and 7 additional setae on either side of anterior femora; group gMX consists of 10–11 thick and more than 60 thinner, rather short setae; seta PA₄ very long, as long as antennomere I and 3–4 times as long as seta PA₅, setae PA₁ – PA₃ very short.

HEAD (Fig. 36) transverse (index width/length 1.3); nasale (Fig. 37) protruding, almost reaching the top of adnasalia, with 8–10 central teeth and two lateral on each side twice as long as the others, ventral row consists of 25–27 teeth; cervical grooves bent, reaching the level of seta PA₅; coronal suture as long as antennomere II; egg burster consists of 1 small teeth behind the level of seta PA₇. Antennae as long as mandibles; mandible (Fig. 38) strongly curved and robust, 1.8 times as long as basal width, with only a fine swelling in front of retinaculum; maxilla (Fig. 39) with stipes 3 times as long as wide; labium (Fig. 40) slender, ligula reaching the level of one fourth of palpomere I.

THORAX. Pronotum transverse, wider than head, with well developed notal carina, reaching the level of seta PR₂; legs (Fig. 41) short and robust, claws unequal, anterior distinctly shorter than posterior.

ABDOMEN. Abdominal terga transverse with ancestral setae; urogomphi very short and weakly divergent, only a little longer than width of tergum IX and length of anal tube. Setae UR_{4–8} longer than urogomphi, shifted apicad.

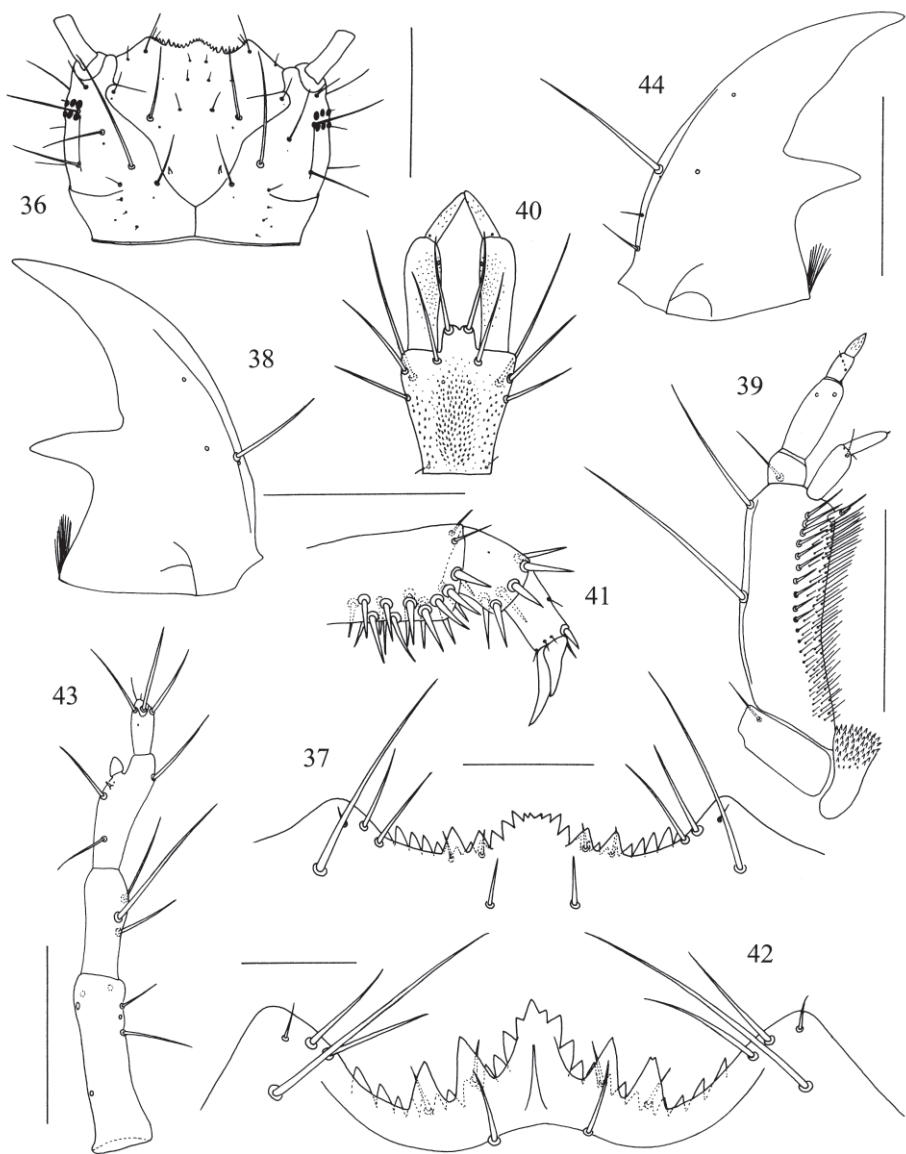
Second and third instar

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 1.57 mm in L₂ and 1.95 and 1.98 mm in L₃.

MICROSCULPTURE. Isodiametric microsculpture on head and pronotum.

CHAETOTAXY. 1 additional seta on inner side of antennomere I (2 setae in L₃), 3 setae on inner side of antennomere II, 1 long and 1 short setae on outer side of stipes (2 long and 2 short setae in L₃), 2 setae near base of mandible, 1 seta near apex of palpomere I (2 setae in L₃), 6–10 pair of setae on dorso-lateral side of prementum; 2 setae on place of inner and outer stemmatal furrows, 1–2 setae near very long seta PA₄, 2 pairs of small setae on the level of seta FR₄. Thorax: 2–3 secondary setae in both anterior and posterior rows, 5–7 setae on lateral margin, 2 setae near prothoracic notal carina; 2 secondary spines and 2–3 setae on either side of anterior femora. Numerous very small setae on head capsule, thoracic and abdominal terga and urogomphi. Length of seta UR_β about 0.75 times that of UR₄, UR_γ about as long as UR₄.



Figs 36–44. *Harpalus (Harpalus) saxicola* Dejean. First instar larva: 36–head capsule (dorsal view). 37 – nasale. 38 – mandible. 39 – maxilla. 40 – labium. 41 – first leg. Third instar larva: 42 – nasale. 43 – antenna. 44 – mandible. Scales: 1 mm (Fig. 36), 0.5 mm (Figs 38, 39, 40, 41, 43, 44), 0.2 mm (Figs 37, 42).

HEAD similar to L₁; nasale (Fig. 42) more protruding, overlapping top of adnasalia, with 9–10 central teeth, two lateral on each side very large, ventral row consists of about 26 teeth, adnasalia moderately sloping; cervical grooves more bent; antennae slender (Fig. 43); mandible (Fig. 44).

ABDOBEN. Urogomphi very short and divergent, shorter than width of tergum IX and only slightly longer than anal tube.

Harpalus servus (Harpalus) (Duftschmid, 1812)
(Figs 45–53)

First instar

HABITUS AND COLOR. Body yellow-brown, head capsule, apex of mandibles, retinaculum, thoracic and abdominal sclerites dark brown. Width of head capsule 0.84–1.02 mm ($x = 0.94$ mm, $n = 18$).

MICROSCULPTURE. Isodiametric microsculpture absent, granulated microsculpture on prescutum and postscutum of pronotum and of postscuta of mesonotum, metanotum and abdominal tergites I–III.

CHAETOTAXY. Except for ancestral chaetotaxy 2 additional spines on either side of anterior femora; seta PA₄ relatively long, more than twice as long as PA₅ and more longer than PA₁–PA₃; group gMX consists of two or three thick and more than 50 thinner, rather short setae.

HEAD (Fig. 45) transverse (index width/length less than 1.3); nasale (Fig. 46) protruding and weakly bifurcate at apex, with 7–8 central teeth, two lateral teeth only a little longer; ventral row consists of 16–18 teeth; cervical grooves clearly bent, almost reaching the level of seta PA₅; coronal suture very short, as long as length of setae PA₁–PA₃; egg burster consists on each side of only one larger tooth. Extremities short and robust; antennae as long as mandibles; mandible (Fig. 47) strongly curved, twice as long as basal width, with one small swelling in front of retinaculum, penicillus present; maxilla (Fig. 48) stout and robust, stipes 2.4 times as long as wide; labium (Fig. 49) short with ligula reaching the level of one third of palpomere I and slightly bifid at apex.

THORAX. Pronotum distinctly transverse, wider than head, with distinct notal carina, reaching the level of seta PR₁₄; legs (Fig. 50) robust, claws unequal, anterior twice as long as posterior in first pair, anterior a little longer in other pairs.

ABDOMEN. Urogomphi very short and curved, a little longer than width of tergum IX and slightly longer than anal tube.

Second and third instars

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 1.05–1.27 mm ($x = 1.18$ mm, $n = 4$) in the second and 1.50–1.64 mm ($x = 1.59$ mm, $n = 6$) in the third instar.

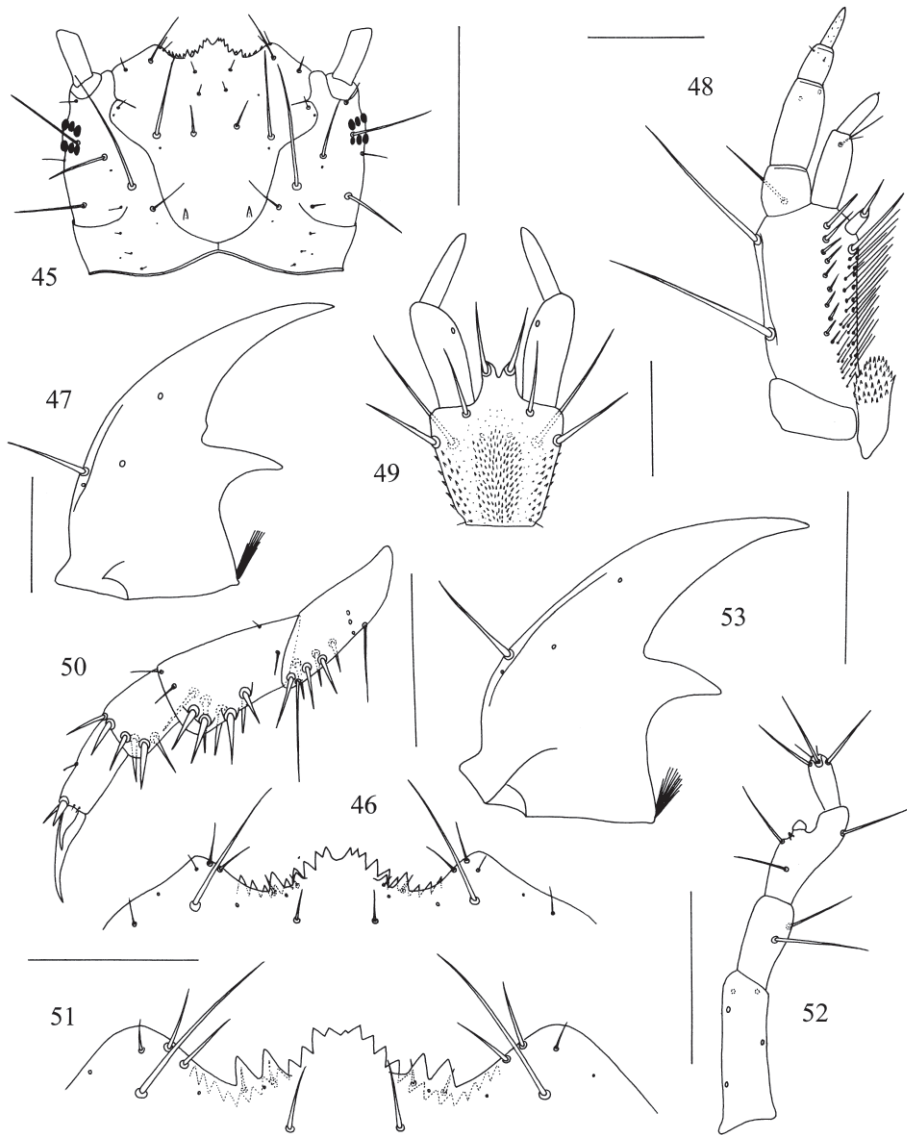
MICROSCULPTURE. Isodiametric microsculpture on head and pronotum.

CHAETOTAXY. Head: 2 additional setae on inner side of antennomere II, 2 setae on outer side of stipes, 1–2 setae near apex of palpomere I, more than 10 pairs of setae on dorso-lateral surface of prementum; 1 or 2 setae on places of inner and outer stemmatal furrows. Thorax: pronotum with 2 secondary setae near notal carina and 4–5 setae on lateral and 2 setae on posterior margin; 6 secondary spines on either side of anterior femora. Abdomen: 1 seta between TE₁ and TE₆, between TE₆ and TE₇ and between TE₉ and TE₁₀. Length of seta UR_β about 0.75 that of UR₄, seta UR_γ about as long as UR₄.

HEAD similar to L₁; nasale (Fig. 51) more prominent and with larger lateral teeth; antenna (Fig. 52); mandible (Fig. 53); maxilla longer than in first instar, stipes more than 3.5 times as long as wide.

THORAX. Legs with unequal tarsal claws.

ABDOBEN. Urogomphi parallel, slightly longer than width of tergum IX and distinctly longer than anal tube.



Figs 45–53. *Harpalus (Harpalus) servus* (Duftschmid). First instar larva: 45–head capsule (dorsal view). 46 – nasale. 47 – mandible. 48 – maxilla. 49 – labium. 50 – first leg. Third instar larva: 51 – nasale. 52 – antenna. 53 – mandible. Scales: 0.5 mm (Fig. 45), 0.3 mm (Figs 47, 48, 49, 50, 52, 53), 0.2 mm (Figs 46, 51).

Harpalus (Harpalus) solitarius Dejean, 1829

(Figs 54–61)

Third instar

HABITUS AND COLOR. Body yellow-white, head and pronotum yellow-brown, retinaculum and apex of mandible dark brown. Width of head capsule 1.91 mm in one specimen.

MICROSCULPTURE. Isodiametric microsculpture on parietale and pronotum, granulated microsculpture on prescutum and postscutum of pronotum and on postscuta of mesonotum, metanotum and abdominal terga I–III.

CHAETOTAXY. Head: 2 additional setae on inner side of antennomere II, 2 setae on outer side of stipes, 2 setae near apex of palpomere I, 7–11 pairs of setae on dorso-lateral surface of prementum; 2–3 setae on place of inner and number of setae or sensillae on place of outer stemmatal furrows, one small seta along cervical grooves, group gMX consists of only two or three thicker and more than 70 thinner, long setae; seta PA₅ and especially PA₁ – PA₃ small, seta PA₄ three times as long as seta PA₅ and as long as antennomere I, the majority of setae on frontale, except for FR₂ and FR₇, relatively fine. Thorax: several small secondary setae on thoracic tergites; 9–10 spines on each side of anterior femora. Abdomen: tergites transverse (Fig. 60) with 2 secondary setae neighbouring TE₁ and TE₁₀ and one seta neighbouring TE₆. Length of seta UR_β 0.6 times that of UR₄, seta UR_γ about as long as UR₄.

HEAD (Fig. 54) distinctly transverse (index width/length 1.3–1.4); nasale (Fig. 55) slightly protruding, with only 5–6 large central teeth and two slightly larger lateral teeth on each side, ventral row consists of about 25 teeth; adnasalia strongly sloping; cervical grooves long and bent, reaching the level of seta PA₇ dorsally and the level of seta PA₁₅ on ventral side; coronal suture slightly longer than width of antennomere I. Antennae (Fig. 56) as long as mandibles; mandible (Fig. 57) triangular and robust, 1.9 times as long as basal width, with two distinct additional teeth in front of retinaculum, penicillus present; maxillae (Fig. 58) slender, stipes almost 3.3 times as long as wide; labium (Fig. 59), ligula reaching the level of one fourth of palpomere I.

THORAX. Pronotum transverse, notal carina weakly developed; legs normally developed, claws unequal, anterior twice as long as posterior in first pair, a little longer in other pairs.

ABDOMEN. Urogomphi (Fig. 61) relatively long and weakly curved, twice as long as width of tergum IX, about one third as long as length of slender anal tube.

Harpalus (Harpalus) xanthopus winkleri Schauberger, 1923

(Figs 62–70)

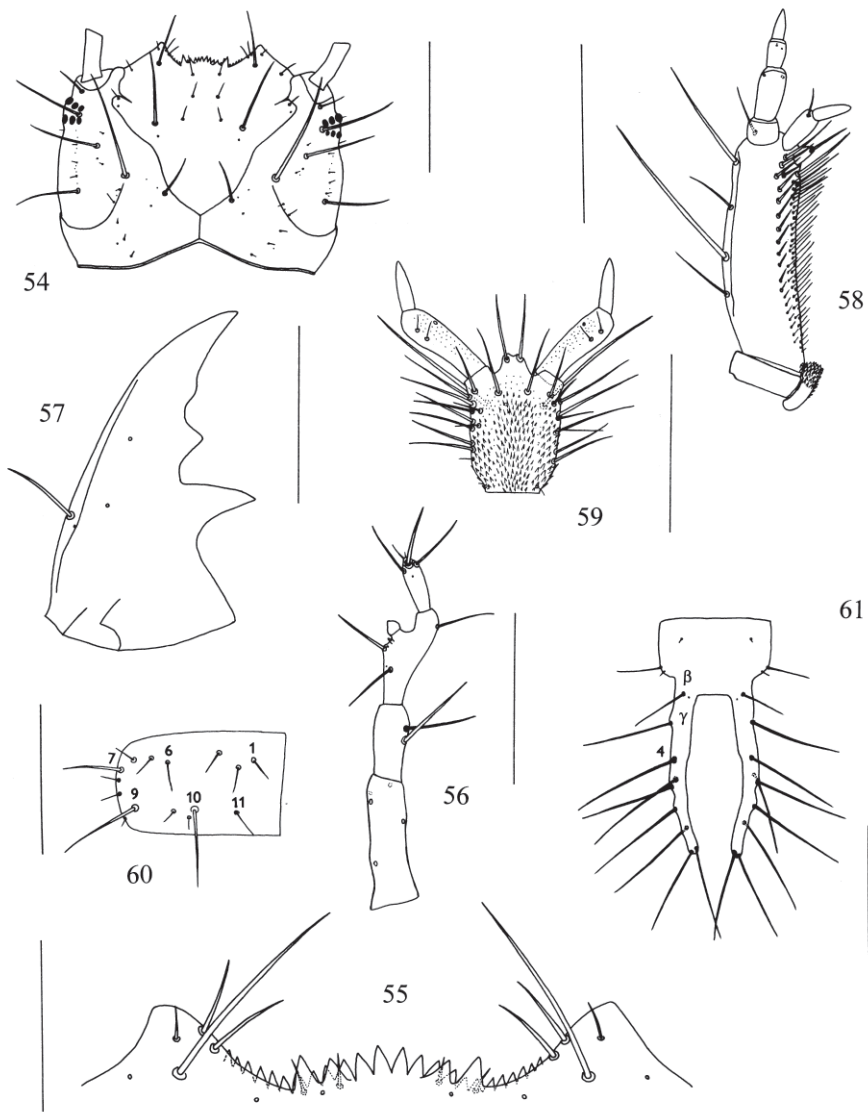
First instar

HABITUS AND COLOR. Body yellow-brown, head and pronotum pale brown, retinaculum and apex of mandible dark brown. Width of head capsule 0.98 mm in one specimen.

MICROSCULPTURE. Isodiametric microsculpture on head very distinct.

CHAETOTAXY. Ancestral chaetotaxy on head capsule and extremities; seta PA₄ and especially setae PA₅, PA₆ and PA₈ short and reduced.

HEAD distinctly transverse; nasale (Fig. 62) only slightly protruding, with 10 central teeth and two a little larger lateral teeth on each side, ventral row consists of 25–26 teeth, adnasalia moderately sloping; cervical grooves short and weakly bent, almost reaching the level of seta PA₅; coronal suture as long as width of antennomere I; egg burster consists of 5 small teeth along frontal suture on each side. Extremities, especially antennae and mandibles, short and robust; mandible (Fig. 63) triangular, 1.9 times as long as basal width, with only one small tooth in front of retinaculum,



Figs 54–61. *Harpalus (Harpalus) solitarius* Dejean. Third instar larva: 54–head capsule (dorsal view). 55–nasale. 56–antenna. 57–mandible. 58–maxilla. 59–labium. 60–tergum I. 61–urogomphi. Scales: 1 mm (Figs 54, 60, 61), 0.5 mm (Figs 56, 57, 58, 59), 0.3 mm (Fig. 55).

penicillus present; maxilla slender, stipes more than 3 times as long as wide; labium short and rather robust.

THORAX AND ABDOMEN. Not available.

Third instar

Same character states as in the first instar except for following:

HABITUS. Width of head capsule 1.37 mm in one specimen.

MICROSCULPTURE. Isodiametric microsculpture on head, thoracic and abdominal tergites. Granulated microsculpture on pronotal prescutum and postscutum and on postscuta of mesonotum, metanotum and abdominal tergites I–II(III).

CHAETOTAXY. Head: 2 secondary setae on inner side of antennomere II, 2 setae on outer side of stipes, 1 seta near apex of labial palpomere I, 8 pairs of setae on dorso-lateral surface of prementum, 4 setae near outer stemmatal furrow. Thorax: 2 small secondary setae along notal carina on prothorax; 8 additional spines on either side of anterior femora. Abdomen: seta TE₁₁ on abdominal terga very reduced or rudimental. Length of seta UR β only about 0.2 times that of UR₄ and about 0.3 times that of UR γ .

HEAD (Fig. 64) transverse (index weight/length 1.4); nasale (Fig. 65) more prominent, with 9–10 central teeth, two lateral on each side distinctly longer, ventral row consists of 25 teeth, adnasalia more sloping; cervical grooves more deepened and bent; coronal suture longer than width of antennomere I; outer stemmatal furrow developed. Extremities more slender; antenna (Fig. 66); mandible (Fig. 67) with one distinct additional tooth in front of retinaculum; maxilla (Fig. 68); labium (Fig. 69).

THORAX. Legs with unequal claws, anterior distinctly shorter than posterior.

ABDOMEN. Urogomphi (Fig. 70) long and parallel, 1.8 times as long as width of tergum IX and about one third longer than anal tube.

LARVAL DIAGNOSIS OF SUBGENUS *HARPALUS*

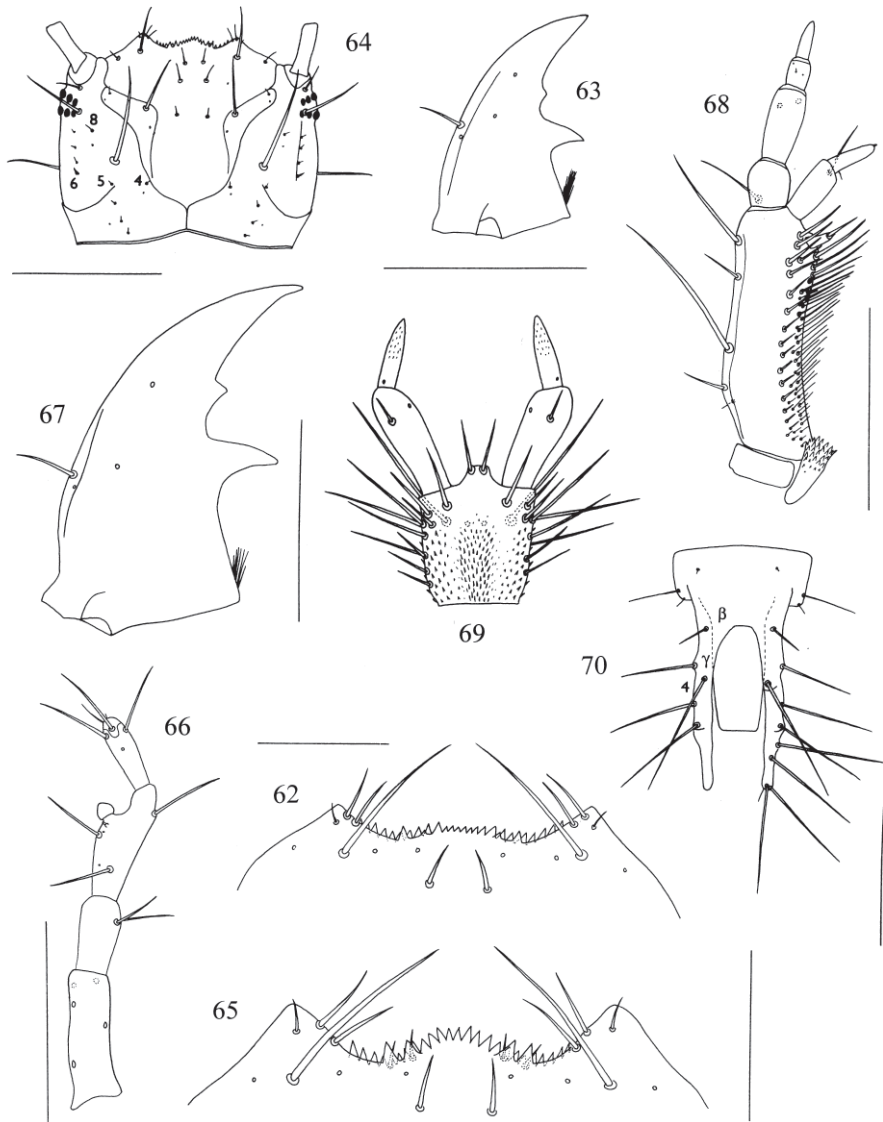
First instar

HABITUS. Typical Harpalini larva with great and transverse head capsule and pronotum, body being narrower caudad.

MICROSCULPTURE. Mostly only parts of frontale and parietale and lateral sides of pronotum with isodiametric microsculpture. Granulated microsculpture on pronotal prescutum and postscutum and on the postscuta of mesonotum, metanotum and of anterior abdominal tergites. Pointed microsculpture sometimes on tergite IX, on base of urogomphi and on antero-lateral parts of abdominal scuta.

CHAETOTAXY. All ancestral setae and pores, except for seta LA₄ on prementum, present; one additional seta of ancestral origin on adnasalia, and mostly one additional pair of spiniform setae or spines on all pairs of femora.

HEAD. Distinctly transverse (index width/length more than 1.1), nasale diverse but frequently prominent and always with central protuberance and one pair of lateral teeth on each side; cervical grooves and coronal suture always present; egg-bursters consist of 2 rows of 1–10 teeth along frontal suture. Antennae mostly a little longer than mandibles; mandible more or less incurvate and stout, as a rule twice as long as wide, frequently with only one or none tooth in front of retinaculum, exceptionally with three extra teeth, penicillus present; six stemmata well-developed; maxillary stipes different in length, 1.5 to 5 times as long as wide, lacinia distinct, with stout lateral seta MX₆; prementum longer than wide, ligula at least as wide as base of palpomere I, frequently bifid at apex.



Figs 62–70. *Harpalus (Harpalus) xanthopus winkleri* Schaubeger. First instar larva: 62 – nasale. 63 – mandible. Third instar larva: 64 – head capsule (dorsal view). 65 – nasale. 66 – antenna. 67 – mandible. 68 – maxilla. 69 – labium. 70 – urogomphi. Scales: 1 mm (Figs 64, 70), 0.5 mm (Figs 63, 66, 67, 68, 69), 0.3 mm (Fig. 65), 0.2 mm (Fig. 62).

THORAX. Pronotum transverse, mostly wider than head, often with well developed notal carina above half of pronotum; legs stout, spiny, claws frequently unequal.

ABDOMEN. Abdominal tergites transverse, sometimes with a fine keel separating prescutum and scutum; urogomphi parallel or divergent, mostly longer than both width of tergite IX and length of anal tube.

Second and third instars

Same character states as in the first instar except the following:

HABITUS. Head capsule wider than in first instar.

MICROSCULPTURE. In some species isodiametric microsculpture also on abdominal tergites. Pointed microsculpture on posterior abdominal tergites and on base of urogomphi.

CHAETOTAXY. Secondary chaetotaxy regularly represented by these setae: Head. 2–3 (1–6) setae on inner side of antennomere II, 2–3 setae on outer side of stipes, 2–3 (1) setae near apex of palpomere I, a number pairs of setae (5–6 pairs in L₂, 8–9 pairs in L₃) on dorso-lateral surface of prementum; 2 setae on place of inner and outer stemmatal furrows; many diminutive setae or sensillae on dorsal surface of head capsule. Thorax. Some setae around notal carina, on lateral border and between setae PR₁₁ and PR₁₂; legs often with many secondary setae. Abdomen. Abdominal tergites with several setae; urogomphi with 4 long secondary setae and often with many diminutive setae or sensillae on the surface; seta UR_α small or absent, seta UR_β more or less shorter than setae UR_γ and UR₄.

HEAD and nasale mostly similar to L₁, nasale with rather larger lateral teeth and more distinct central protuberance. Cervical grooves and stemmatal furrows more deepened, extremities rather longer.

THORAX AND ABDOMEN similar to L₁, urogomphi regularly longer.

DISCUSSION

The fundamental paper on the taxonomy of the larvae of Harpalina was published by Brandmayr, Ferrero & Zetto Brandmayr, 1980. In this paper, they separated within the genus *Harpalus* Latreille, 1802 sensu lato, the “ophonoid” and “harpaloid” lineages, based on distinctive, morphological larval characters. They also presented differential diagnoses and the key of all described taxa within the genus group, and a list of more or less well described species, including the authors of the descriptions.

The taxonomy of the genus *Harpalus* is far of being stabilised at present. Based on the combination of both adult and larval characters we consider *Ophonus* Dejean, 1821, *Cryptophonus* Brandmayr & Zetto Brandmayr, 1982, *Pseudoophonus* Motschulsky, 1844 and *Nipponoharpalus* Habu, 1973 as generic level taxa.

The last monographic treatments of Carabidae larvae (Arndt 1991, Luff 1993) offer morphological data for 17 species (11 species respectively) within the genus *Harpalus* in our concept. After adding data from additional sources (Brandmayr et al. 1980, Gardner 1938, Habu 1973, Hürka 1975, 1992, Kirk 1972, Puchkov 1992, Zetto Brandmayr & Brandmayr 1978), the number of species raises to 32, of which 29 are in the subgenus *Harpalus*. In this paper we are adding larval descriptions of further 8 species of the subgenus *Harpalus*. Most papers published so far are based on incomplete and insufficient material that does not fully take in consideration the variability of the larval characters of the studied species. With the increased number of described taxa, it is becoming obvious that the variability of larval characters is considerably higher than previously thought. It is also necessary to increase the spectrum of the characters used in larval taxonomy, particularly by the characters concerning the chaetotaxy of the head and appendages.

Based on the study of our larval material, as well as on data in the literature, the genus *Harpalus* in our concept may be characterised mainly by the following characters: (1) Nasale deepened between adnasalia; (2) Labial palpomere I in both second and third instars with 2 (1–4) short setae near apex; (3) Mandible with 0–4 teeth in front of retinaculum, mandibular apex never bifid; (4) Antennomere II in instars II and III with (1)2–5(6) large subapical setae directed inwards; (5) Inner side of stipes with a setal group gMX consisting of more than 40 setae.

A slightly more than 10 subgenera are mentioned world-wide in the genus *Harpalus* in our concept (Lorenz 1998), several tens of species aggregates are recognised in the subgenus *Harpalus* (Kataev 1995). In addition to the subgenus *Harpalus*, some of the larval characters are available also for species of the subgenera *Acardystus* Reitter, 1908 (Habu 1973), *Artabas* Des Gozis, 1882 (Puchkov 1992), *Harpalophonus* Ganglbauer, 1892 (Zeto Brandmayr & Brandmayr 1978), *Megapangus* Casey, 1914 (Kirk 1972), *Plectralidus* Casey, 1914 (Kirk 1972) and *Semio-phonus* Schaubberger, 1933 (Hůrka 1992). Taxonomic–morphological differences between the larvae of the species aggregates of the subgenus *Harpalus* are often more significant than those between the larvae of conventional subgenera.

The results of our study of both larval and adult characters within the subgenus *Harpalus* sensu novo mostly quite support the Kataev's division in species aggregates that was established using adult characters, as it can be documented by the following examples:

Harpalus (Harpalus) atratus

Kataev 1995 established the separate species aggregate “*atratus*” for this species. This is fully supported by the larval characters. Unique is the form of nasale (Figs 2, 7), the shape of mandible with two additional teeth in front of retinaculum (Fig. 3), the shape of first instar labium (Fig. 5), as well as the general habitus of the larva.

Harpalus (Harpalus) cisteloides hurkai

A separate “*cisteloides*” species aggregate was established for this and three additional species by Kataev 1995. This is fully supported by the larval morphology, particularly by the following: details in the development of the nasale, with the wide V-shaped medial emargination (Figs 12, 16), the development of the ancestral chaetotaxy, the minute setae PA₂ and PA₃, and particularly the reduced setae FR₈, FR₉ and an additional seta near them. Some of these characters are similar to those of *H. autumnalis* from the next species aggregate, in particular the similar shape of the mandible and of the egg-bursters, similar arrangement of the additional chaetotaxy of the labium and of the legs (particularly of the femora), the similar development of the secondary chaetotaxy of the antennae, mandibles and of the maxillae. The actual relationships are not clear at present.

Harpalus (Harpalus) picipennis

A well defined “*pumilus*” species aggregate was established for this and seven additional species (= *Actephilus* Stephens, 1833). This is entirely supported by the larval morphology, especially after a comparison with the larva of *H. pumilus*. The larvae of this group are characterised particularly by the shape of the nasale (Figs 29, 33), by the markedly shortened head appendages, by the arrangement of the egg-bursters (Fig. 28), and by the shortened urogomphi. The shortened head appendages and urogomphi and the basic shape of the nasale, are similar to those of the “*anxius*” species aggregate, but in the latter the arrangement of the egg-bursters, the additional chaetotaxy of the legs and the details in the shape of the nasale are different.

Harpalus (Harpalus) saxicola

Based on adult characters, the species was assigned, together with *H. angulatus* Putzeys and *H. distinguendus* (Duftschmid), to the “*distinguendus*” species aggregate. This taxonomical action is fully supported by the larval morphology, particularly after a comparison with the larva of *H. distinguendus*. The species aggregate is characterised by the sagittiform nasale (Figs 37, 42), the shortened urogomphi, as well as by the secondary chaetotaxy of the antennae (Fig. 43), mandibles (Fig. 44) and the maxillae. Some of the characters, e.g. the somewhat similar shape of the nasale and the secondary chaetotaxy may suggest a possible relationships to the “*affinis*” and “*hospes*” species aggregates.

Harpalus (Harpalus) servus

Based on adult characters, the species was assigned by Kataev 1995, together with 8 additional species, to the “*anxius*” species aggregate. The larval morphology of *H. anxius*, *H. servus* and *H. subcylindricus* fully supports this action. The larvae of the named species are very difficult to distinguish. The species aggregate is mainly defined by the shape of the nasale with a small apical emargination (Figs 46, 51), by the arrangement of the egg-bursters (Fig. 45), the shortened head appendages and urogomphi, and by the chaetotaxy of the legs (namely of the femora). Some of the characters are shared with the “*pumilus*” species aggregate (see above).

The “*latus*” species aggregate

Kataev assigned 10 Palearctic species to this species aggregate. About half of the species are described in the larval stage in more or less details: *H. latus*, *H. luteicornis*, *H. marginellus*, *H. solitarius* and *H. xanthopus winkleri*. The larval features of this five species indicate that the species aggregate is likely not homogeneous. *Harpalus luteicornis* and *H. xanthopus winkleri* are related. *Harpalus latus* and *H. solitarius* differ by the shape of the mandible and nasale, the larva of *H. latus* in addition by the conspicuously transverse head. The arrangement of the egg-bursters is similar in all species examined. The species aggregate requires a taxonomic revision based on sufficient material of all larval instars.

The comparison of both larval and adult characters of species of the genus *Harpalus* indicates that it is at present more proper to assign the related species to the species aggregates rather than to separate subgenera. However, some of the species aggregates established by Kataev 1995 should be re-examined.

A c k n o w l e d g e m e n t

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