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A Contribution to the Knowledge of the Biology of a Troglobiont Carabid Species, *Jeannelius birsteini* Ljovuschkin, 1963 (Coleoptera, Carabidae, Trechini)

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Abstract—Biology and larval stages of the carabid genus *Jeannelius* are described for the first time. *Jeannelius birsteini* lives at temperatures varying between 8.0 and 15.5°C, and its temperature tolerance is rather high for troglobiont forms. Larvae of *Jeannelius* exhibit many distinctive features (absence of sulci and carinae on the head capsule, presence of macrochaetae in the posterior part of the frons, shortening of setae LA_5, structure and arrangement of setae CO_1–CO_3, FR_4 and FR_5, etc.), being, however, very similar to larvae of the genus *Allegrettia*. Data on the larval morphology substantiate the placement of this species to the *Aphaenops* group of the tribe Trechini.

The large subtribe Trechina (about 2000 species of about 100 genera) is readily distinguished from other members of the tribe Trechini, as more than half (1060) of its species demonstrate distinct adaptations to soil and cave habitats (Casale *et al.*, 1998). The hidden mode of life complicates examination of these carabids, and their larvae have been studied worse than larvae of other carabids. Among the published reviews devoted to this subject, papers by Jeannel (1920) and Boldori (1932, 1958) are notable. In Hůrka's (1978) key to the carabid larvae of Europe, 28 genera of Trechini are indicated, with 11 of these inhabiting caves.

The genus *Jeannelius* Kurnakov, 1959 is endemic to the western Caucasus and includes no less than four species known from various caves (Kryzhanovskij *et al.*, 1995). In the present study, data on the biology of *Jeannelius birsteini* are given, 3rd-instar larva is described, and the taxonomic position of this species in the tribe Trechini is discussed.

MATERIALS AND METHODS

Jeannelius birsteini Ljovuschkin, 1963 was described from a material collected in 3 caves of the western Caucasus (Ljovuschkin, 1963). The holotype was collected in the Vorontsovskaya, and the paratypes, in the Akhunskaya and Beloskal'skaya Caves. Our researches have shown that *J. birsteini* is distributed in many caves of the Vorontsovskii and Akhunskii karst massifs in the zone of a low-mountain karst in Sochi. The temperature in these caves is rather stable (see table), and the relative air humidity varies between 90 and 100%. Such conditions are typical of many caves of the western Caucasus (Tintilozov, 1976).

About 1500 adult individuals and only three larvae of *J. birsteini* have been collected in these caves in 13 years (1988–2000). Adults were caught manually or by means of the traps similar to those used by Barber (1931). The material was collected from parts of caves with very moist clay sediments in which small pools and water-filled cavities were usually formed. These areas were the richest in collembolans, which apparently served a food for the carabids. Adult beetles rather quickly ran over horizontal surfaces and rather slowly moved over inclined and vertical formations (stalactites, stalagmites, etc.), and even over vertical surfaces. The beetles were found in caves under fragments of limestone and in cracks. In addition, adults of *J. birsteini* occurred in other underground voids and microvoids, most frequently, in isodiametric, irregular or elongate cavities in rock, varying in size from 1 mm to 50 cm (Sokolov, 1962; Dublyanskii and Andreichuk, 1991). Such cavities are situated in the zone of rock crushing and in the karstogenous filler in clays and brecciae. Owing to the properties of rock, *J. birsteini* can live not only in caves. In particular, adult individuals were found in spring and summer under deep-lying rock blocks (more frequently, limestone blocks) in the same locality (I.A. Belo-

Parameters of the caves inhabited by *Jeannelius birsteini* Ljovuschkin

Cave	Altitude above sea level, m	Temperature, °C
Vorontsovskii Karst Massif		
Vorontsobskaya	520	8.5–10.0
Labirintovaya	550	8.5–11.0
Dolgaya	720	8.5–10.9
Psakho	270	11.5–15.0
Akhunskii Karst Massif		
Akhunskaya	300	8.0–11.0
Beloskal'skaya	180	10.5–12.0
Chertova Nora (distant part)	55	13.0–15.5

lousov, verbal comm.). Thus, *J. birsteini* should be regarded as a cavernicolous species (Casale *et al.*, 1998).

However, the morphological adaptations of *J. birsteini* nearly exclude its emergence to the soil surface and characterize it as a troglobiont, according to Racovitza's (1907) classical study. A rather wide distribution range of *J. birsteini* is due to its rather high ecological plasticity, in comparison with that in other troglobionts. For example, according to observations of one of the present authors, another troglobiont carabid, *Pseudaphaenops tauricus* Winkler, dwells in caves of the Crimea, distinguished by a narrow temperature range (8–11°C), whereas *J. birsteini* inhabits caves near Sochi, in which the temperature varies between 8.0 and 15.5°C.

Larvae of *J. birsteini* prefer areas with dry aerated loamy sediments. All the larvae were found in such sediments at a depth of 20–40 cm. In the Vorontsovskaya Cave, larvae were found at a distance of about 900 m, and in Psakho Cave, 150 m away from the nearest entry. Attempts to caught larvae by traps failed, and this indicates that the larvae do not appear on the surface of cave sediments. The larvae probably feed on Enchytraeidae (Oligochaeta), which are frequently found in digging in these habitats, together with the larvae.

LARVAL MORPHOLOGY OF JEANNELIUS BIRSTEINI

Material. Three 3rd-instar larvae[1]: W Caucasus, Sochi, Vorontsovskaya Cave, 17.VIII.1999, leg. A.G. Koval; same locality, 17.VIII.2000, leg. A.G. Koval; W. Caucasus, Sochi, Psakho Cave, 24.VIII.1999, leg. A.G. Koval.

Description. Habitus. Body strongly elongate, cylindrical, slightly narrowed to the end, with rather short appendages and narrow head capsule (Fig. 1). Coloration pale, sclerites weakly pigmented; only thoracic tergites, legs, head, and appendages darker.

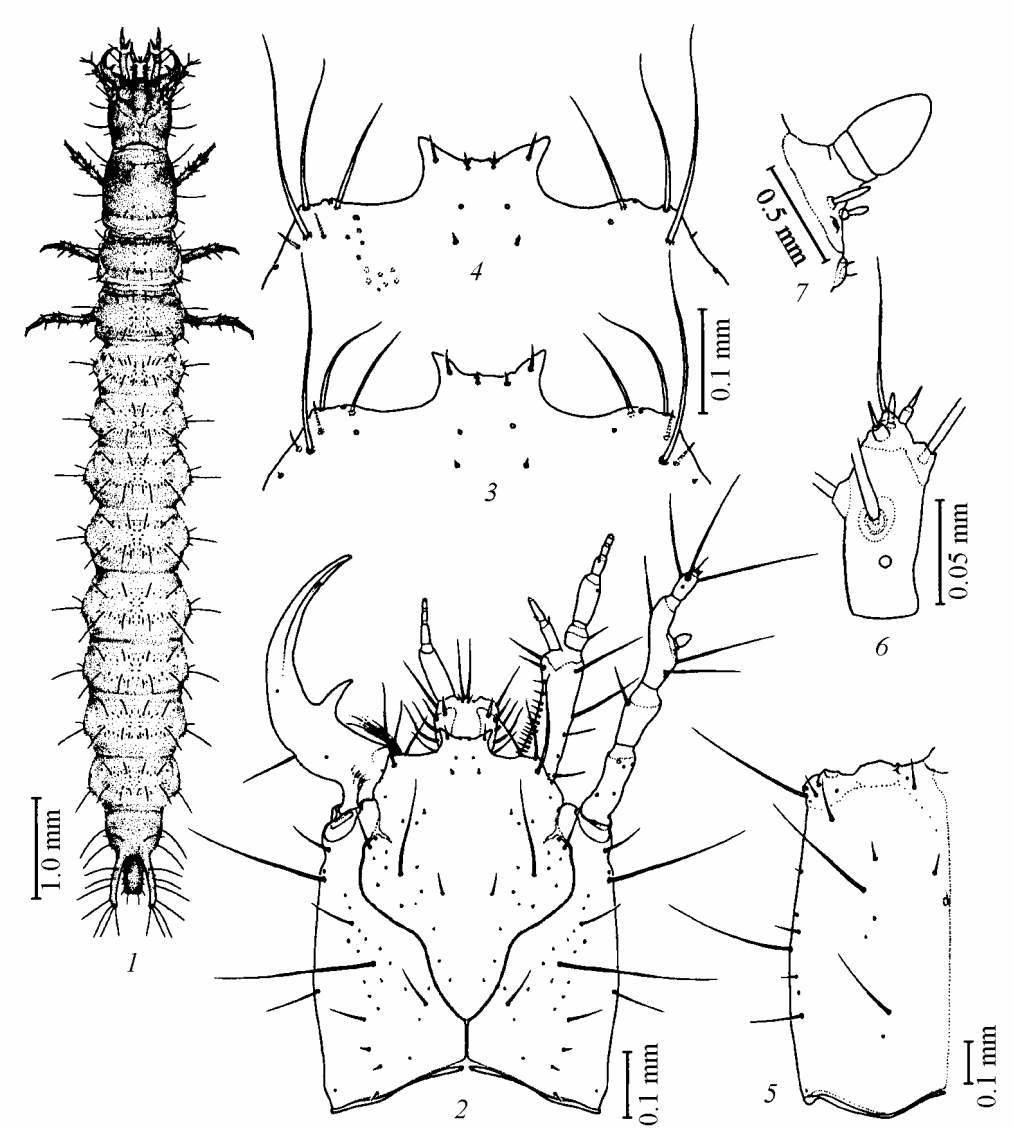
Microsculpture ill-defined. Head and appendages smooth, with group of spines only at base of maxilla and on cardo. Abdominal tergites and urogomphi with combs of minute teeth.

Head capsule nearly as long as wide (length to width ratio 1.00–1.05), with rather uniformly convex lateral margin, without distinct grooves or carinae (Fig. 2). Nasale slightly asymmetrical (Figs. 3, 4), projecting strongly forwards, about 0.75 times as wide as anterior margin of paraclypeus. Lateral teeth of nasale very large, forming common forked prominence; middle teeth inconspicuous. Outer angles of paraclypeus not projecting, weakly slanting. Antennal ring weakly separated, ocelli absent. Frontal sutures moderately curved, epicranial suture 0.23 times as long as frontal sclerite. Head with moderate heteropolychaetotaxy[2]: several additional conical sensilla present near FR_4 and FR_1–FR_2 and basally to FR_3, one more sensillum present basally to FR_f. Discal chaetae of frons (FR_4, FR_5) and median chaetae of nasale (FR_{11}) very short, usually shorter than diameter of apical segment of labial palp. FR_2 and FR_7 of subequal length, 0.4 times as long as frontal sclerite. FR_7 shifted toward anterior corners to such extent that distance FR_7–FR_9 not exceeding FR_8–FR_9. Sensilla FR_d shifted forwards and lying at the level of bases of chaetae FR_8 or even more distally; bases of chaetae FR_1, FR_2, and FR_3 lying nearly on one line. Dorsal chaetotaxy of parietal sclerites characterized by similar modifications (Fig. 2). Additional conical sensilla present near chaetae PA_4, PA_5, PA_7, and PA_8. Macrochaetae PA_7 and PA_9 up to 0.55 times as long as frontal sclerite. Sensilla PA_a and PA_b shifted sideways and toward base relative to the usual position.

Ventral surface of head (Fig. 5) with solitary additional microchaetae near PA_{14}, PA_{15}, PA_{17}, and PA_{12}. PA_{11}, PA_{17}, and PA_{14} about as long as PA_9. PA_{13} very short, distinctly shorter than PA_1. Sensillum PA_1 lying near margin of occipital suture.

[1] The larval instar is estimated preliminary, as larvae of the cave-inhabiting Trechini sometimes develop in a shorter period.

[2] Hereinafter, the nomenclature of the sensilla follows that by Bousquet and Goulet (1984).

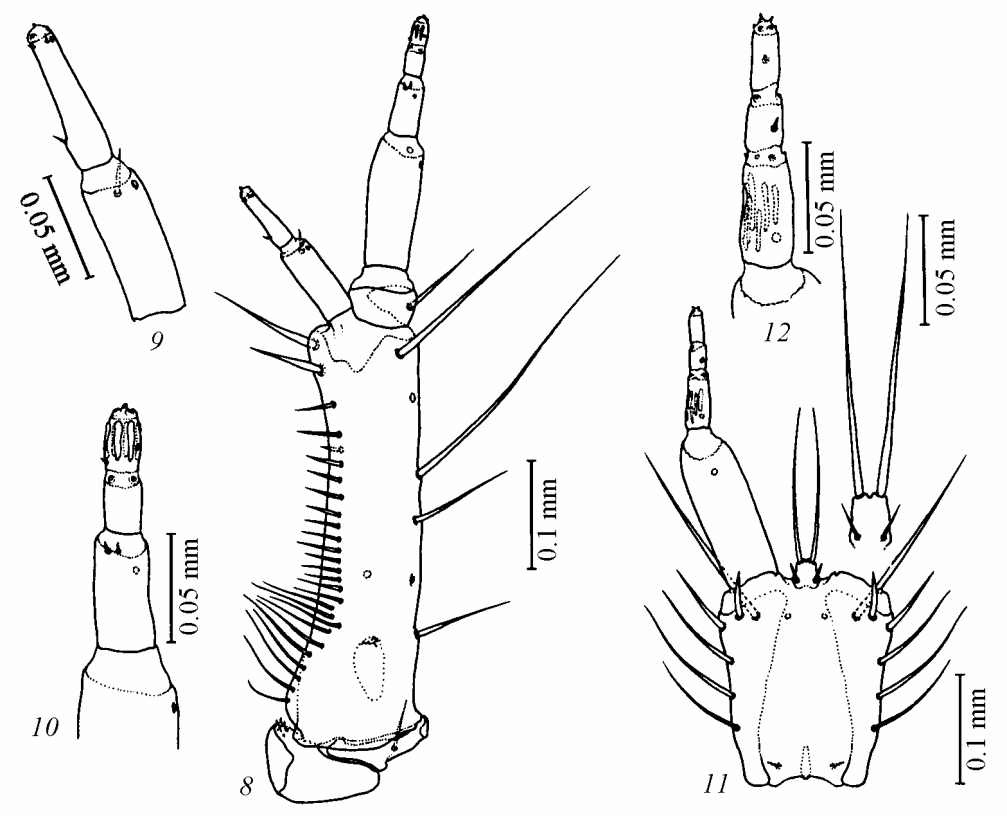


Figs. 1–7. *Jeannehus birsteini* Kurnakov, 3rd-instar larva: (*1*) habitus; (*2*) head, dorsal view (left antenna, maxilla, and right mandible not shown); (*3*, *4*) nasale and anterior margin of frons (an individual from Vorontsovskaya Cave), dorsal view; (*5*) right parietal sclerite of head, ventral view; (*6*) apical antennal segment, dorsal view; (*7*) apex of antennal segment, dorsal view.

Antennae 4-segmented (Fig. 2), length ratio of their segments (average measures) about 1.0 : 0.65 : 1.15 : 0.45. Second segment with subapical macrochaeta, chaetae AN_1–AN_5 moderately long, slightly longer than 3rd antennal segment. On apical segment, inner chaeta (AN_7) only slightly shorter than outer chaetae. Sensory complex of 3rd segment including 1 large oval, 2 baculiform, and 1 placoid sensilla (Fig. 7). Apex (Fig. 6) with 2 styloconical sensilla varied in shape and 1 slightly clavate sensillum, all surrounding chaeta AN_6.

Mandibles moderately curved, without additional teeth (Fig. 2) and microsculpture; their laterobasal surface without additional chaetae; MN_2 very short, in the form of conical sensillum. Penicillum nearly reaching base of retinaculum.

Maxillae (Fig. 8) moderately long. Stipes about 4.3 times as long as wide, uniformly sclerotized; only its dorsal surface forming at base small, weakly sclerotized area bearing cuticular teeth; apex of stipes slightly flattened and widened at inner margin. Palp about 0.72 times as long as stipes, its 2nd segment not shorter than 3rd and 4th segments combined. Apical segment distinctly divided into 2 pseudo-segments by ring of sensilla. Length ratio of segments (average measures) 1.0 : 3.1 : 1.3 : 1.4. Galea half as long as palp, with basal segment only slightly longer than apical one. Lacinia missing.

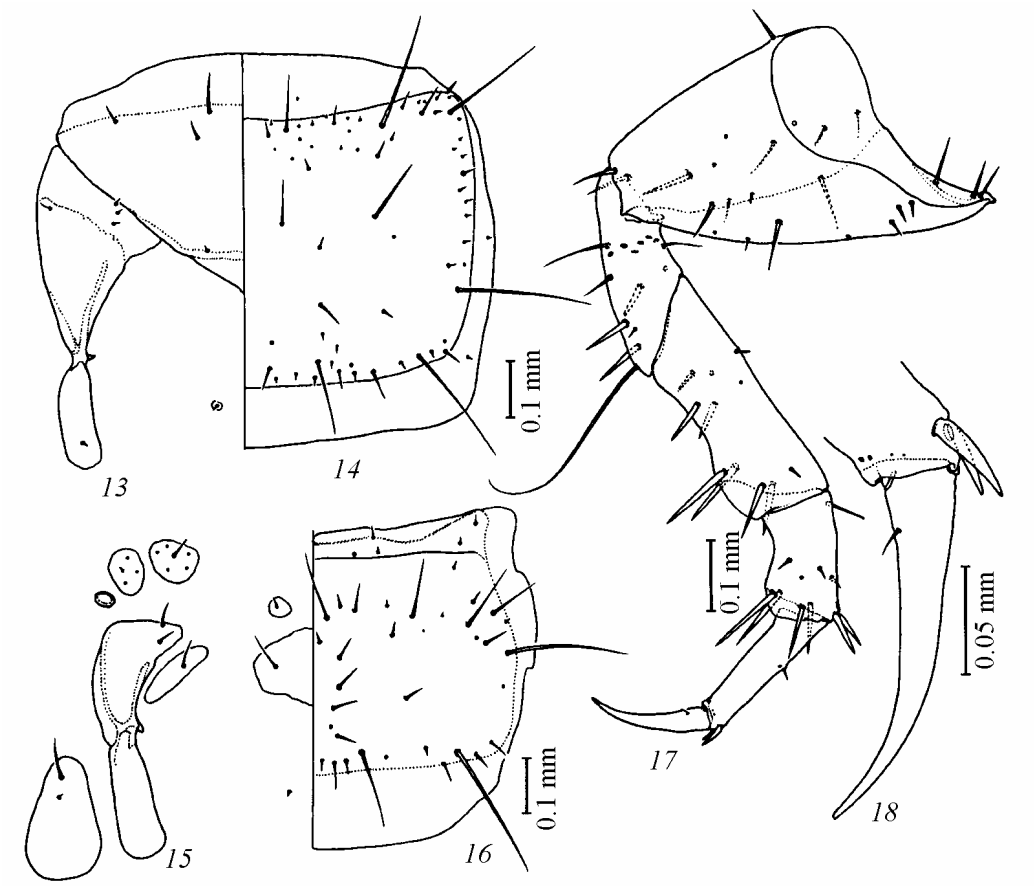


Figs. 8–12. *Jeannelius birsteim* Ljovuschkin, 3rd-instar larva: (*8*) right maxilla, dorsal view; (*9*) galea, dorsal view; (*10*) 3rd and 4th segments of maxillary palp, dorsal view; (*11*) labium (right palp not shown) and ligula, dorsal view; (*12*) apical segment of labial palp, dorsal view.

Chaetotaxy of maxilla close to typical one. Cardo with chaeta MX_1, length of chaeta not exceeding half of basal width of stipes. Inner margin of stipes with 24 chaetae arranged in row; basal 10 or 11 chaetae longer and noticeably curved; others rather short, slightly thickened. Chaeta MX_5 situated on dorsal, and MX_6, on ventral surface of stipes. MX_6 nearly twice as long as MX_5. Outer margin of stipes with long chaetae MX_2 and MX_3 (up to 0.7 times as long as stipes) and 2 additional basal mesochaetae (gMX_2) (Fig. 8). Arrangement of placoid sensilla of stipes usual. Chaetae MX_{11} and MX_{12} on palp very small, 0.25–0.33 times as long as diameter of ultimate segment. Apical complex formed by 3 campaniform and 1 conical sensilla; subapical complex, by 6 digitate, 1 placoid, 1 basoconical, and 3 or 4 campaniform sensilla in groove separating pseudo-segments (Fig. 10). On galea, chaeta MX_7 situated almost subapically; its length not exceeding diameter of 1st segment. Chaetae MX_8 and MX_9 very small. Apex of 2nd segment of galea with 3 campaniform and 1 conical apical sensilla and 1 conical subapical sensillum (Fig. 9).

Labium (Fig. 11) with weakly elongate mentum (1.2 times as long as wide) and well-developed sclerotized ligula. Palp 1.2–1.3 times as long as mentum; its 2nd segment 1.3 times as long as 1st one, subdivided into 3 pseudo-segments. Chaetae LA_6 about as long as 1st palpal segment, chaeta LA_2 1.3 times as long as it. LA_7 well developed, situated at base of ligula. Laterodorsal surface of mentum with thicker and shorter apical chaetae LA_4 and LA_5 and group LA_3 formed by 3 narrower longer chaetae. Sensory complex of 2nd palpal segment (Fig. 12) including, in addition to placoid sensillum LA_C, 7 or 8 digitate sensilla, 2 conical sensilla situated at midlength of 2nd and 3rd pseudo-segments, and apical complex formed by 2 conical and 4 or 5 campaniform sensilla. Each of grooves separating pseudo-segments bearing 3 or 4 campaniform sensilla.

Thoracic segments with rather heavily sclerotized tergites and prosternum. Pronotum (Fig. 14) 1.25 times as wide as long, lateral margins weakly uniformly rounded. Chaetotaxy characterized by absence of sen-



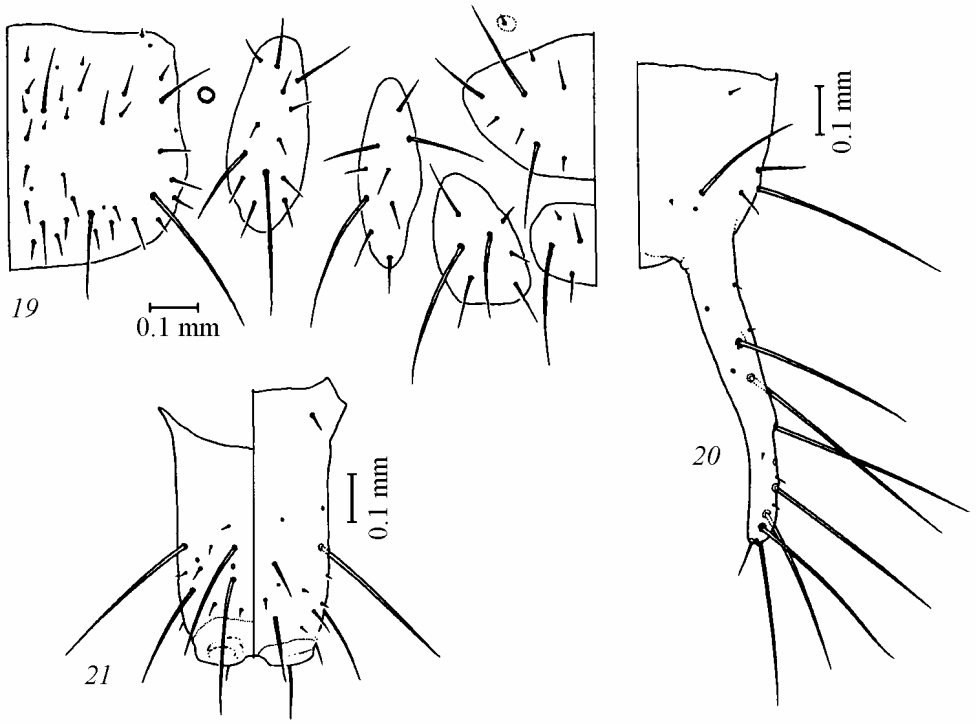
Figs. 13–18. *Jeannehus birsteim* Ljovuschkin, 3rd-instar larva: (*13*) right half of prothorax, ventral view; (*14*) right half of pronotum, dorsal view; (*15*) right half of mesothorax, ventral view; (*16*) right half of mesonotum, dorsal view; (*17*) right middle leg, posterior view; (*18*) apex of tarsus, posterior view.

silla PR_c., PR_e, PR_i, and PR_j and a small number of additional sensilla (for the most part, microchaetae and basoconical sensilla lying mainly at margins). Longitudinal row of 2 or 3 chaetae present only between chaetae PR_8 and PR_{14}. All lateral macrochaetae of subequal length, nearly 0.33 times as long as pronotum. Epipleura with 2 microchaetae: median and basal. Propleura with typical set of sensilla, and all chaetae small. Prosternum with group of 3 or 4 mesochaetae at anterior margin (Fig. 13).

Meso- and metanotum 1.4–1.5 times as wide as long. Anterior carina rather indistinct (Fig. 16). Sensilla ME_c and ME_e absent. In contrast to pronotum, secondary chaetom of meso- and metanotum consisting mostly of macrochaetae forming transverse row ME_1–ME_8 at posterior margin of sclerite and along medial suture. Epipleura without chaetae. Chaetotaxy of pleura and ventrites (Fig. 15) similar to generalized one; only chaeta EM_1 absent and MS_1 and ES_1 forming groups of 1 chaeta and 3–5 basoconical sensilla.

Legs rather short, rather heavily sclerotized, with 1 large claw (Fig. 17), which no less than 0.75 times as long as tarsus. Tarsus 0.5–0.6 times as wide as tibia and femur. Length ratio of leg segments (average measures) 1.0 : 0.53 : 0.69 : 0.34 : 0.41. Chaetotaxy of leg similar to generalized one. Coxa with microchaeta CO_{17}. Chaetae CO_1–CO_3 unusually large (length reaching diameter of tarsus), irregularly arranged: distance CO_2 between CO_3 6–7 times that between CO_1 and CO_2. Additional sensilla present only on femur and tibia (3 spiniform chaetae ventral to *FE* and 3 small setae girding tibia nearly middle). Claw with 1 chaeta (?UN_2); lateroapical chaetae of tarsus (TA_3, TA_4 and TA_5, TA_6) strongly reduced, in the form of conical sensilla visible only at large magnification (Fig. 18). Length of ventroapical chaetae of tibia (TI_4 and TI_5) and femur (FE_3 and FE_4) slightly exceeding diameter of tibial apex.

Abdominal segments with nearly membranous sclerites. Tergites without distinct carinae, with numerous additional mesochaetae (Fig. 19). Longitudinal



Figs. 19–21. *Jeannelius birsteini* Ljovuschkin, 3rd-instar larva: (*19*) sclerites of right half of abdominal segment IV; (*20*) right half of abdominal tergite IX, dorsal view; (*21*) abdominal segment X, ventral and dorsal view, respectively.

row of 6–8 chaetae usually running in parallel to median suture. Longest chaeta of tergites, TE_9, only 0.7 times as long as sclerite. Sensillum TE_b absent. Pleura and ventrites also with numerous additional mesochaetae (Fig. 19).

Tergite IX without carina and distinct posterior angles, smoothly turning into urogomphi (Fig. 20). Urogomphi only slightly longer than segment X, slightly curved, with weak nodules near chaetae UR_4 and UR_5. Chaetotaxy of urogomphi characterized by presence of additional mesochaetae near UR_2 and macrochaetae near UR_a and UR_5. In addition, urogomphi with inconspicuous 6–8 microchaetae irregularly distributed along their length. Macrochaetae 0.55–0.64 times as long as urogomphi.

Segment X weakly sclerotized, without lateral sutures, with minute teeth on eversible appendages (Fig. 21) and up to 12 pairs of microchaetae irregularly scattered closer to apex than chaetae *PY6*. Group RY_7 formed by 2 macrochaetae, additional mesochaeta present above PY_4. Macrochaetae up to 0.65 times as long as segment.

DISCUSSION

On the whole, the larval morphology of *Jeannelius* conforms to the diagnosis of the tribe Trechini in the traditional characters (Emden, 1942; Sharova, 1958, 1964; Luff, 1985, 1993) and chaetotaxy (Grebennikov, 1999; Arndt *et al.*, 1999). The macromorphological characters include the absence of the lacinia, presence of one claw, and division of the apical palpal segments into pseudo-segments. Such characters of the chaetotaxy as the absence of some sensilla on the thoracic and abdominal tergites ($PR_{c, e, i, j}$, $ME_{c, e}$, and TE_b) and chaeta EM_1 on the meso- and metapleura and the presence of an additional chaeta on 2nd antennal segment and 2 chaetae at the anterior corners of the cibarium agree with the modern diagnosis of the tribe (Grebennikov, 1999). In addition, larvae of *Jeannelius* have a set of apical and subapical sensilla on the antennae and chaetae on the abdominal sclerites, which are characteristic of the tribe.

At the same time, the larvae described clearly differ from most of the known larvae of Trechini in the absence of grooves and carinae on the head capsule, shape of the nasale, rather narrow and uniformly curved retinaculum, and details of the chaetotaxy. The larvae have a very poorly developed secondary chaetae, especially on the head and pronotum, where additional elements are not numerous, being represented by microchaetae and basoconical sensilla. The structure of chaetae CO_1–CO_3 (Fig. 17) is very specific; FR_3, FR_4, and FR_5 (Fig. 2) are very small; LA_5 is very short (less than 0.25 times as long as LA_6,

Fig. 11); MN_a and lateral sensilla of the urogomphi (UR_c and UR_e) are absent. The position of chaetae MX_5 and MX_6, separated by the projecting inner margin of the stipes (Fig. 8), is also distinctive.

Among the known larvae of Trechini, only the larva of *Allegrettia*, briefly described by Boldori (1924) and Jeannel (1926), is somewhat similar to the larva of *Jeannelius*. An examination of a larva of *Allegrettia boldorii* Jeann. from the collection of the Natural History Museum in Milan (Museo Civico di Storia Naturale di Milano) revealed some essential characters shared by these genera: primarily, a rather similar chaetotaxy of the head capsule (including the absence of the basal macrochaetae on the frons), ligula, and legs, and also a similar structure of the head capsule and mandibles. Probably, the most significant shared character (synapomorphy) is the absence of the macrochaetae in the basal part of the frons, which are typical of most other larvae of Trechini.

In addition, larvae of *Allegrettia* possess better developed secondary chaetae (for example, additional chaetae are present near PA_6, PA_{14}, PA_{16}, the disc of tergite IX bears the median macrochaeta, the urogomphi bear 8–10 additional microchaetae, etc.). Note that the outwardly similar structure is formed in *Jeannelius* by the nasale as a whole and the sensilla FR_d are situated on the nasale; whereas in *Allegrettia*, FR_d are present only in the middle part of the nasale, and, thus, FR_d retain the starting position on the frontal sclerite.

Two points of view on the position of the genus *Jeannelius* in the tribe Trechini exist. Describing *Jeannelius*, Kurnakov (1959) placed it in the *Aphaenops* phyletic series. This series comprises more than 140 species belonging to 22 genera of Trechini, mainly distributed in the Pyrenees, Alps, and Balkan Peninsula, and also three species of the Caucasian genus *Meganophthalmus* Kurn. and two species of the Crimean *Pseudaphaenops* Winkl. The small (comprising only four species) genus *Allegrettia* Jeann., inhabiting caves of the Alps of Brescia and Bergamo in northern Italy (Casale and Laneyrie, 1982; Casale *et al.*, 1998), is also among the Alpine representatives of this group. Describing the new genus, Kurnakov indicated its similarity to *Allegrettia* Jeannel, 1928 in the habitus and chaetotaxy. It should be noted that, although both genera exhibit the aggregated condition of the humeral group of the umbilical series, this character has been found only in several representatives of the *Aphaenops* series (e.g., *Allegrettia*) and can be regarded as an exemption.

However, adult *Jeannelius* clearly differ from all other members of the *Aphaenops* series in the unwidened fore tarsus of the male. This circumstance and the lack of information on the fauna of the Caucasus induced Jeannel (1960) to place the genus *Jeannelius*, together with *Nannotrechus* Jeann. and *Cimmerites* Jeann., in the *Neotrechus* phyletic series.

Previously, the *Neotrechus* phyletic series included more than 90 species belonging to 11 genera distributed mainly in the Balkan Peninsula, Caucasus, and Turkey (Casale and Laneyrie, 1982; Casale *et al.*, 1998). Seven more new genera and several tens of new species from the Caucasus and Crimea (Belousov, 1998, 1999; Belousov and Zamotajlov, 1997) have been added to the series only recently. The position of the genus *Jeannelius* in the tribe was clarified, after two new genera, *Caucasorites* Bel. et Zamot. and *Caucasaphaenops* Bel., were described (especially, *Caucasorites kovali* Belousov, 1999). The male of the last species, being similar to the male of *Jeannelius* in the chaetotaxy (aggregation of the humeral group of the umbilical series) and structure of the aedeagus, possesses two widened segments in the fore tarsus. Characters of this species relate *Jeannelius* to the other Caucasian representatives of the *Aphaenops* phyletic series (Belousov, 1999), and this circumstance substantiates Kurnakov' opinion.

Being rather similar in the chaetotaxy as a whole, larvae of the genera *Jeannelius* and *Allegrettia* clearly differ in details of the chaetotaxy and structure of the nasale. An outward similarity of the nasale (absence of additional teeth, not projecting hypodon) in these larvae is caused by the modification of various areas of the frontal sclerite. Possibly, some other variants of the structure of the frontal anterior margin will also be found in other genera of this line. A number of other larval features shared by *Jeannelius* and *Allegrettia* (shape of the mandibles, underdeveloped secondary chaetae) is probably caused only by their similar modes of life. The question cannot be answered yet, as the cave-inhabiting larvae of Trechini have been poorly studied. Judging from the range of the variability of larval morphological characters in Trechini, we can assume that at least three larval features: absence of macrochaetae in the basal part of the frons, shortening of chaetae LA_6, and reduction of the lateral sensilla (UR_c and UR_e) on the urogomphi are important for characterization of the *Aphaenops* series.

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