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ADAPTATION OF THE MOUTHPARTS IN SOME SUBTERRANEAN CHOLEVINAE (COLEOPTERA, LEIODIDAE)

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Cholevinae are a group of beetles with many cave representatives that are mainly detritivorous or saprophagous. Some species show modifications of the mouthparts on account of their dietary niche, being adapted to a semi-aquatic way of life, or on account of the degree of adaptation to the life in caves. Differences are obvious also among the genera, and cave species that are at the same level of adaptation. The main modifications concern the shape and structure of the different parts, as well as their length and the disposal of hairs, bristles and setae. The adaptation to an aquatic dietary niche has modified the mandibles, which acquired a spoon-like form to bring water near the mouth, the lacinia taking on the role of stirring and the galea of filtering the organic particles with its fine and very dense hairs. The apparent uniformity of the subterranean environmental conditions and of the trophic resources, together with the scarcity of the latter, might mistakenly lead to the conclusion of a one-way evolution for the underground colonizers. The observed differences between the mouthparts of the studied species can be good material for taxonomists, who can include some of these features in their studies, often difficult due to the homogenous morphology of many inhabitants of the underground. As a contribution to the comparative study of the mouthparts at some representatives of cholevin beetles, we can also highlight the effect of adaptation to cave life on the mouthparts and the evidence of a divergent evolution in a relatively constant environment in terms of climate and food input.

Key words: Cholevinae, cave beetles, mouthparts, scanning microscopy, adaptation

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Holevine su skupina kornjaša s mnogo podzemnih predstavnika koji su pretežno detritivorni ili saprofagni. Neke vrste pokazuju modifikacije usnih organa zbog svoje prehrambene niše, prilago-

đavajući se poluakvatičkom načinu života, ili zbog stupnja adaptacije na život u špilji. Razlike su očite i među rodovima i špiljskim vrstama koje su na istom stupnju adaptacije. Glavne modifikacije tiču se oblika i strukture različitih dijelova, kao i njihove duljine, i rasporeda dlaka, čekinja i seta. Prilagodba na akvatičku prehrambenu nišu modificirala je čeljusti, koje su dobile oblik žlice kojom se voda prinosi ustima; lacinia preuzima ulogu miješanja, a galea filtriranja organskih čestica svojim finim i vrlo gustim dlačicama. Očita jednoličnost uvjeta u podzemnom okolišu, te izvora hrane, zajedno s njenom rijetkošću, mogu pogrešno upućivati na jednosmjernu evoluciju stanovnika podzemlja. Uočene razlike između usnih organa proučavanih vrsta mogu biti dobar materijal za taksonomiste koji neke od tih osobina mogu uključiti u svoj rad, obično težak zbog homogene morfologije mnogih stanovnika podzemlja. Kao doprinos komparativnoj studiji usnih organa nekih predstavnika holevina, na temelju usnih organa naglašavamo efekt prilagodbe na špiljski život te dokaz divergentne evolucije u relativno konstantnom okolišu, u smislu klime i dotoka hrane.

Ključne riječi: holevine, podzemni kornjaši, usni organi, skenirajući mikroskop, prilagodba

INTRODUCTION

The Leiodidae Cholevinae (NEWTON, 1998; PERREAU, 2000) are numerous in the subterranean environment, representing 30% of all known underground beetles (DECU & JUBERTHIE, 1998). They populate caves, as well as the fissure network and even the layers of the soil. The subfamily shows a mixture of archaic, plesiomorphic and derivate together with ultra-specialized, autapomorphic features (GIACHINO *et al*., 1998a). Some of these evolved features refer to the parts of the mouth, like the maxillary palpi with 3 articles, the last becoming very small and conical to the ultra-specialized species, or the mandibles, generally very regular in form that are modified as adaptation to the semi-aquatic way of life. This mixture of new and old features is also the consequence of the presence in this group of species with different degrees of adaptation to the underground life, from endogean to hypogean species, or from species that can be encountered only at the entrance of the caves to those that are found exclusively in the deepest passages (CASALE *et al.*, 2000).

Cholevinae representatives are detritivorous or saprophagous, feeding on organic matter more or less decomposed, deposited on the substrate (walls and stalagmites of the caves) or stored in the sediment deposits of the caves or the cracks, and decayed epigean or subterranean animals. Therefore the mouthparts show an adaptation relevant to these trophic niches. Generally, the mouthparts were ignored in descriptions of taxa, excepting the very modified, such as those of species in a semi-aquatic habitat (JEANNEL, 1924; PAOLETTI, 1973, 1980; CASALE & JALŽIĆ, 1988; CASALE *et al*., 2000). Observing the modification of the antennae, tarsus and exocrine glands as a result of underground adaptation (MOLDOVAN & JUBERTHIE, 1994; MOLDOVAN, 1998; BUZILA & MOLDOVAN, 2000) we focused, this time, on the mouthparts and their diversity among cholevin representatives. Therefore, several species with different degrees of adaptation to and exploitation of different subterranean habitats have been studied to emphasize the mouthparts structure adaptation.

JEANNEL (1923) described the mouthparts of *Choleva cisteloides*, as basic morphological structure of the Cholevinae, taken as the starting point of our study, a pattern that was taken into account for the analysis: the labrum is transverse, with a

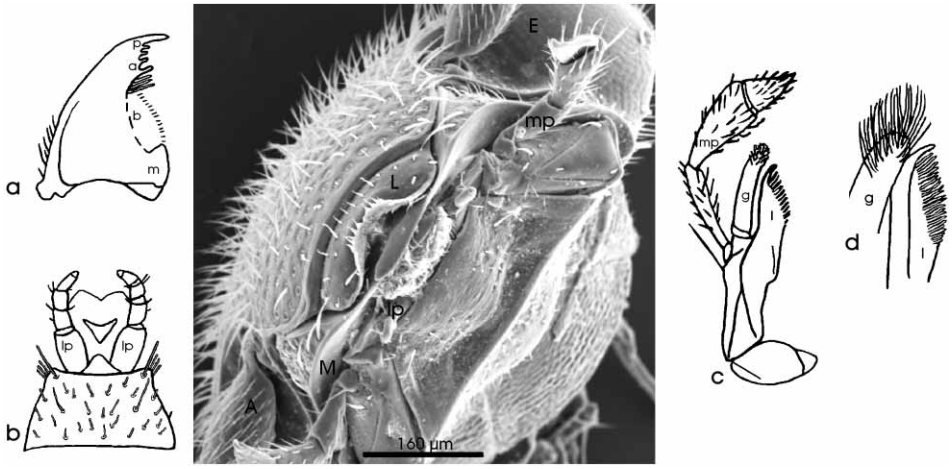

Fig. 1. Frontal view of the mouth of *Choleva cisteloides*. a. Left mandible, dorsal view; b. Labium with labial palpi, ventral view; c. Left maxilla, ventral view; d. Detail of the lobes of the left maxilla, ventral view: A = antenna, a = accessory tooth, b = masticator border, E = eye, g = galea, L = labrum, l = lacinia, lp = labial palp, M = mandible, m = mola, mp = maxillary palp, p = principal tooth.

membranous superior lip; mandibles are short and thick, their tip is bent, with two teeth and 2–3 smaller teeth in between, the mola is asymmetrical, the masticator border has hairs and the external face is convex, large and pubescent; the maxilla is long, the galea is bi-articulated with a terminal article with numerous small hairs; the lacinia is shorter than the galea, ending as a robust crochet, its masticator border with very numerous bristles; the maxillary palpi are pubescent, with the 1st article very small, the 2nd long and thin and the 3rd inflated and the apical article conical, short, and sharp; the labium is trapezoid, pubescent, the mentum and prementum are fused; the labial palpi are short, with 4 articles, the 2nd has one external and one internal sensilla, the 3rd has two external sensilla.

MATERIALS AND METHODS

The mouthparts of 9 species, all collected in caves, have been studied and compared with those of *Choleva cisteloides*:

Subfamily Cholevinae

Choleva cisteloides Froelich 1799 (Fig. 1)

Catops longulus Kellner, 1846

Subfamily Leptodirinae

Speonomus phyletic lineage

Speonomus infernus Dieck, 1869

Drimeotus phyletic lineage
Pholeuon proserpinae Knirsch, 1913

Sophrochaeta phyletic lineage
Closania orghidani Decu, 1959
Sophrochaeta (Cernella) reitteri retezati Mallasz, 1928
Tismanella chappuisi Jeannel, 1928

Spelaeodromus-Speoplanes phyletic lineage
Radziella styx Casale et Jalžić, 1988

Antroherpon phyletic lineage
Hadesia vasiceki Müller, 1911 (Jeannel, 1924)
Croatodirus bozicevici Casale, Giachino et Jalžić, 2000

The first two species are troglophilous, encountered at the entrance of the caves or on bat guano. The others are troglobiontic, showing adaptation for life in caves: lack of eyes, long or very long and slender antennae and legs. Among the troglobiontic species some, like those belonging to the genus *Speonomus*, are less adapted to the subterranean life, with no eyes but shorter legs and antennae. The most specialized are the last three species from the above list. These also live in a very different habitat in caves, walking and climbing exclusively on vertical flooded stones and rocks (a hygropetric habitat, after SKET, 2001), where they probably feed on organic matter or bacteria brought by water percolating from the surface.

Catops longulus has a holarctic and *Choleva cisteloides* a palearctic distribution, while the other species are endemic, with very reduced distribution areas. *Catops*, *Choleva*, *Pholeuon*, *Closania*, *Sophrochaeta* and *Tismanella* specimens were collected in Romanian caves, *Speonomus* specimens in a French cave, *Radziella* and *Croatodirus* specimens are from Croatian caves and *Hadesia* specimens from a cave in Bosnia – Herzegovina.

Two individuals of each species were dissected under the microscope, and entire heads or detached pieces of the mouth were prepared for scanning electronic microscopy. They were cleaned in a 15% KOH solution, dried and covered with gold-palladium. Observations were made under a JEOL SEM 6400 in the Laboratory of Electronic Microscopy of the University of Bergen (Norway), and under a JEOL JSM 5510 LV in the Center of Electronic Microscopy of the »Babes-Bolyai« University of Cluj (Romania).

RESULTS

Catops longulus

Maxilla is shorter and more robust, wider dorso-ventrally. It has maxillary palpi very like those of *Choleva* sp., with the third article inflated, and the apex under a conical form, but slightly longer and with lesser sensilla (Fig. 2a). The galea has nu-

merous hairs not only at the apex (like *Choleva*) but also laterally, while the lacinia has many apical bristles (Fig. 2b). The mandibles are short and wide (Fig. 2c), with the masticator border very rich in dense hairs. The apex has one tooth. The labial palpi are shorter and thicker (Fig. 2d), and the apical article has, like the apical arti-

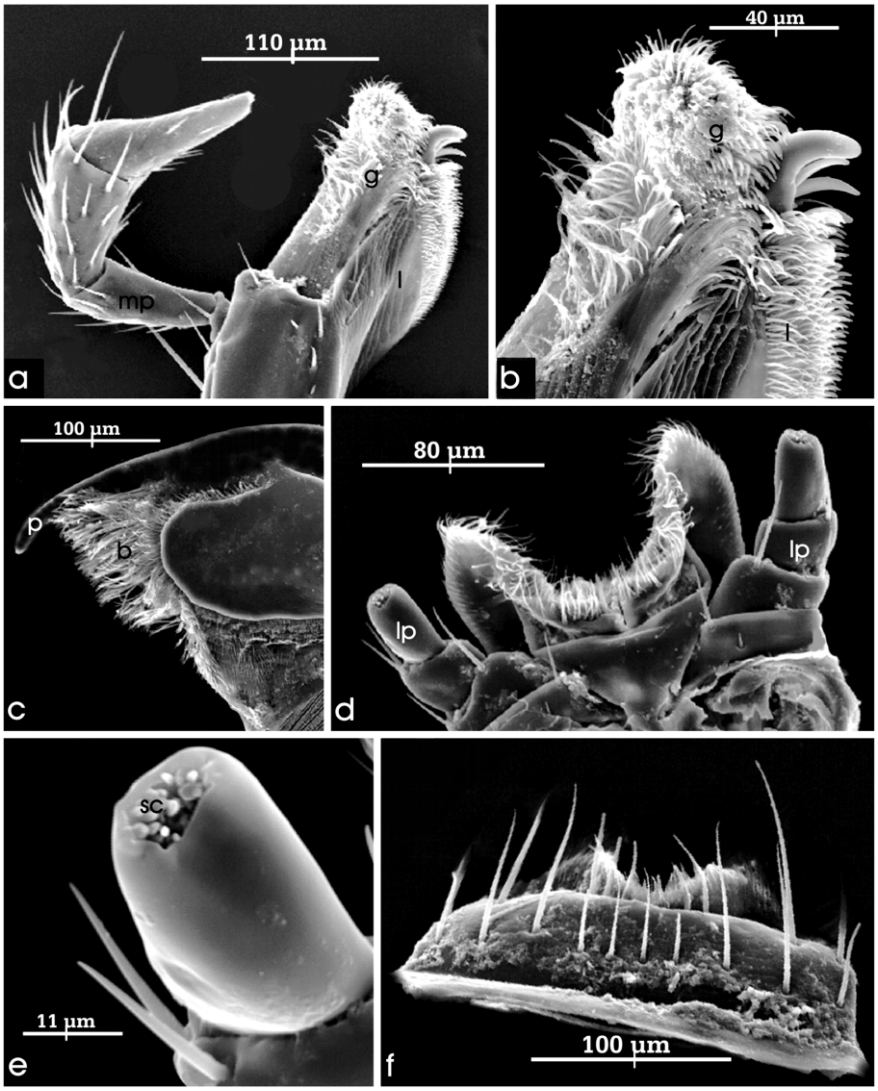

Fig. 2. Mouthparts of *Catops longulus*. a. Right maxilla, ventral view; b. Detail with lobes of the maxilla; c. Left mandible, ventral view; d. Labium with labial palpi, dorsal view; f. Detail of the labial palp; g. Labrum, dorsal view: b = masticator border, g = galea, l = lacinia, lp = labial palp, mp = maxillary palp, p = principal tooth, sc = sensory complex.

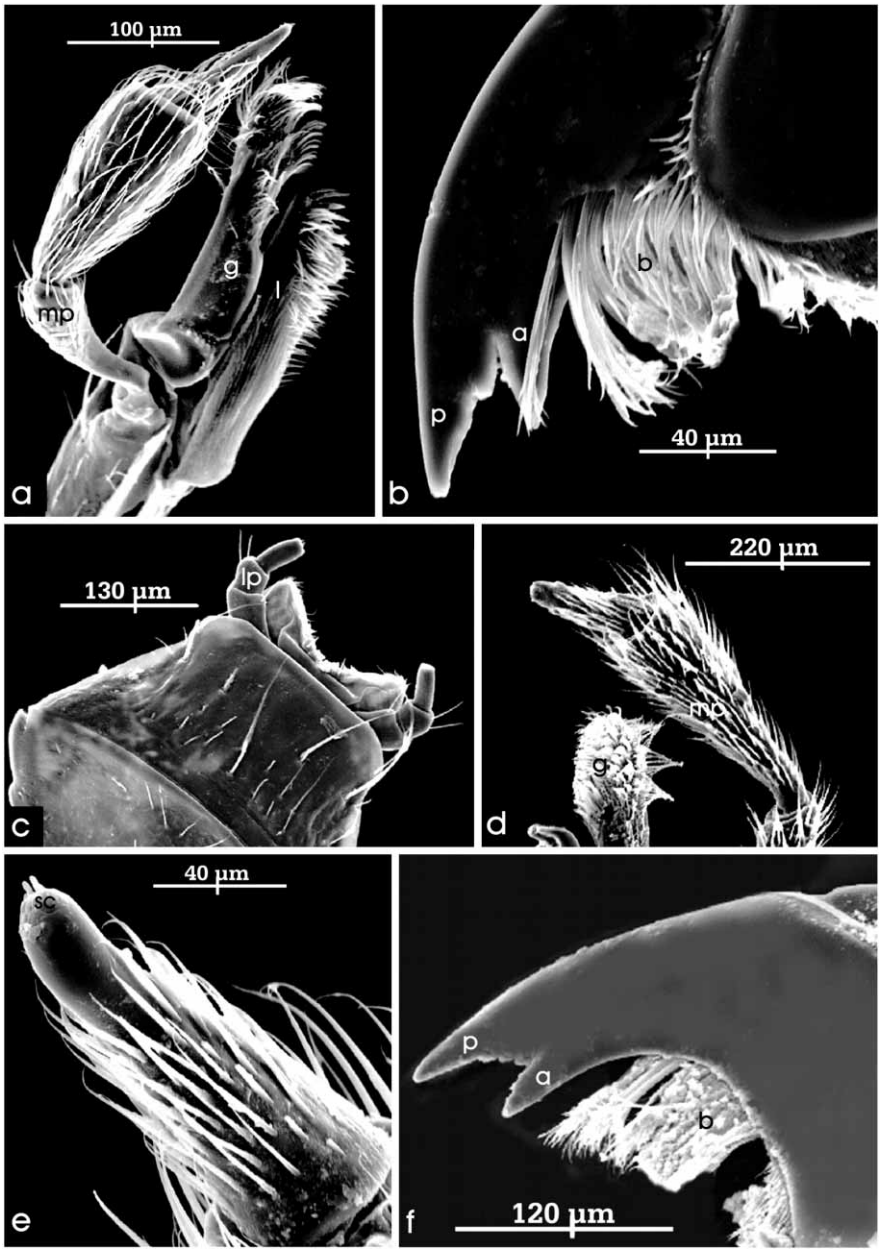

Fig. 3. Mouthparts of *Speonomus infernus* (a – c) and *Pholeuon proserpinae* (d – g). a. Right maxilla, ventral view; b. Left mandible, ventral view; c. Labium, ventral view; d. Left maxilla, dorsal view; e. Detail of the 3rd article of the maxillary palpi; f. Dorsal view of the right mandible: a = accessory tooth, b = masticator border, g = galea, l = lacinia, lp = labial palp, mp = maxillary palp, p = principal tooth, sc = sensory complex.

cle of the maxillary palpi, the receptors in a concavity at the apex (Fig. 2e). The labrum is narrow and wide with many hairs, long especially laterally and shorter in the median part (Fig. 2f).

Speonomus infernus

The maxillary palpi have a thin terminal article, but are similar to those of *Choleva* in respect to the number and position of the hairs (Fig. 3a). The galea is much longer than the lacinia, unlike the previous species, and covered with dense and long bristle while the last one has strong and curved bristle, much thinner than in *Catops*, continuing toward the inferior end with a strip of long and not very dense setae. The mandible has a wide, curved apex with two teeth and a smaller denticule between them (Fig. 3b). The masticator border has very long hairs. The labial palpi are long and flattened dorso-ventrally with the third article much lon-

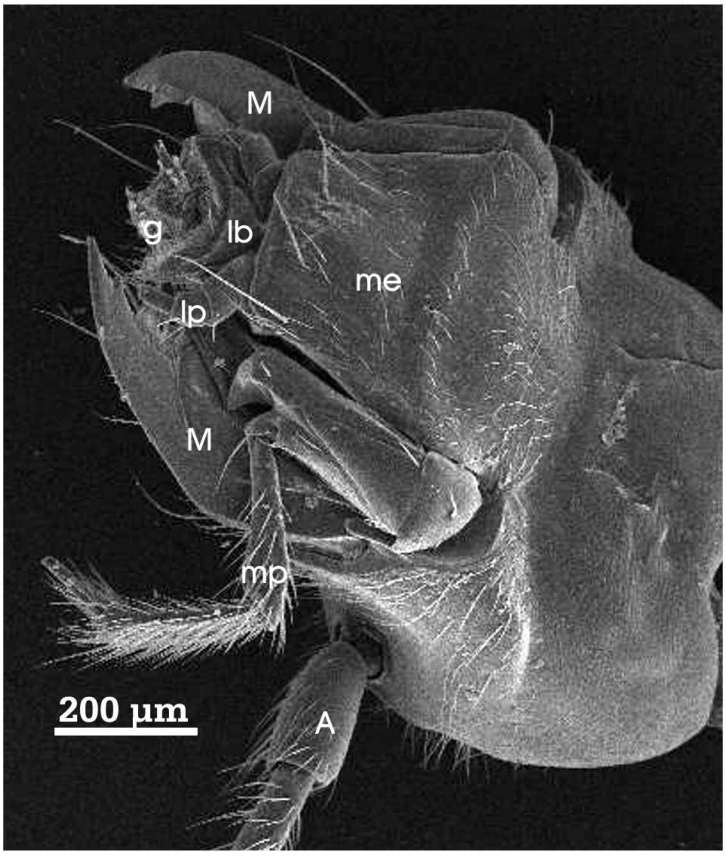

Fig. 4. Ventral view of the head of *Tismanella chappuisi*: A = antenna, g = galea, lb = labium, lp = labial palp, M = mandible, me = metasternum, mp = maxillary palp,

ger compared to the troglophilous species (Fig. 3c). The end of the article is represented by numerous receptors in a concavity, similar to *Choleva*. The labrum is wide with finer hairs.

Pholeuon proserpinae

The maxillary palpi are much thinner than in the previous species, especially the first and the second articles (Fig. 3d), and the apical are very similar to those of the previous species (Fig. 3e). The galea, flattened and covered with dense hairs looks like a hair-brush, is longer than the lacinia, and is very similar to that observed in *Speonomus*. The mandible has also two teeth with no denticule between them (Fig. 3f). The hairs of the masticator border have ramified ends, as at the previous species.

Closania orghidani, Sophrochaeta reitteri, Tismanella chappuisi

The three species have similar mouthparts (Fig. 4) to those of the two previously described species. *Tismanella* and *Closania* have thin maxillary palpi, with long articles and a third article of conical form (Figs. 5a, 5b); a sensilla basiconica can be observed on the external surface of this article. In *Sophrochaeta* the first article is shorter. The galea in all these species has a similar disposition of hairs on the apex (Figs. 5c, 5d, 5e). Small differences are in the length of the galea by comparison to the lacinia, the first being always longer, but much longer in *Closania*, and almost equal in *Tismanella*. The lacinia has several small teeth at its apex; the number of them differs slightly among these species. The mandibles have two teeth, one principal and one accessory (Figs. 5f, 5g, 5h); the masticator border is represented by hairs, shorter that those of the previously described species. The labrum is narrow, with long hairs and small differences between the species (Figs. 6a, 6b). The apex of the labrum is covered by one row of sensilla, probably basiconica, as in Fig. 6c, and the apex of the labium with mechanical and chemical receptors, very dense at *Closania orghidani*, sparse and long at *Tismanella chappuisi* (Fig. 6d, 6e). As in all the species there is a sensorial complex on the apex of the labial palpi (Fig. 6f).

Hadesia vasiceki, Radziella styx and *Croatodirus bozicevici* (Figs. 7,8,9)

The morphological features of these species were first illustrated by JEANNEL (1924), CASALE & JALŽIĆ (1988) and respectively, CASALE *et al.*, 2000.

These species present similar adaptations of the mouthparts (Fig. 10), but with some particularities. The maxillary palpi are very long without being filiform as in *Pholeuon*, covered with dense pubescence made by very long hairs in *Radziella*. This species differs from *Hadesia* and *Croatodirus* also in the very small terminal article, and also in having a much thicker second article. The lacinia is shorter than the galea in all these species. Its masticator border is covered with short and dense bristles in *Hadesia* (Fig. 11a), short and stronger in *Radziella* (Figs. 11b, 11c) and longer and denser in *Croatodirus* (Fig. 11d). The apex of the lacinia ends with strong and slightly curved spines. In *Croatodirus* and *Hadesia* the lacinia is much thinner than in *Radziella*. Very modified is especially the galea, which has a spoon form, pointed

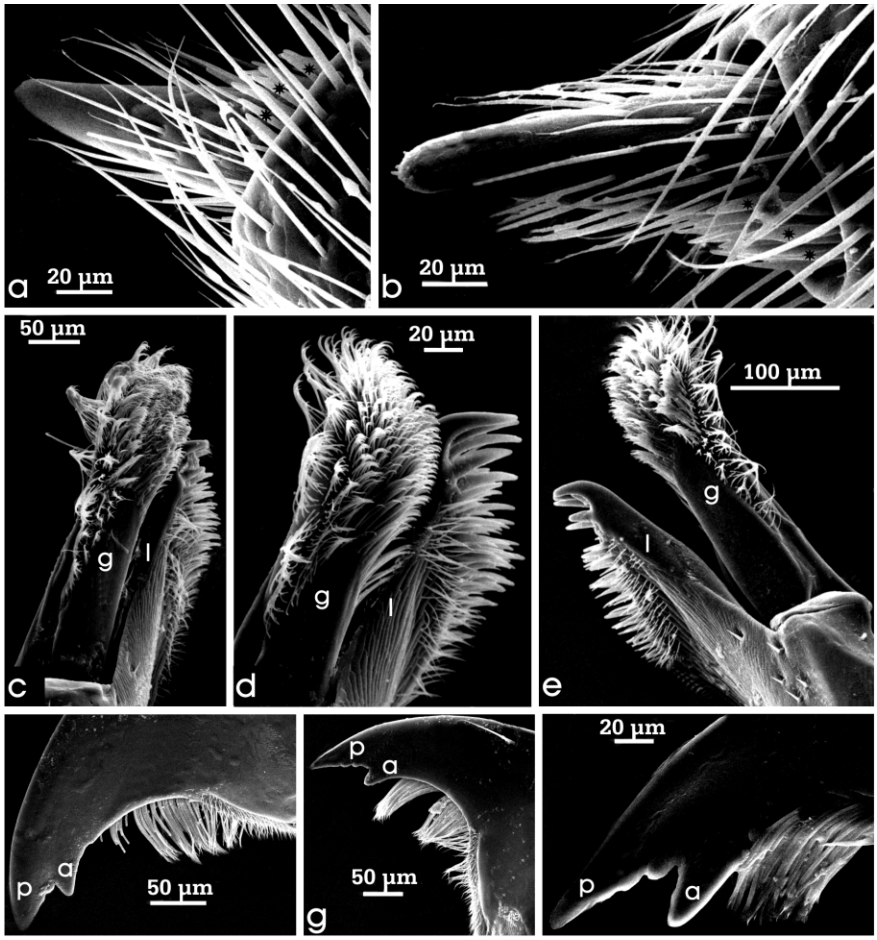

Fig. 5. Mouthparts at *Closania orghidani* (a, e, f), *Sophrochaeta reitteri* (b, c, g), *Tismanella chappuisi* (d, h): a., b. Apex of the maxillary palp, dorsal view, with sensilla basiconica (H); c., d., e. Galea and lacinia, dorsal view; f., g., h. Apex of the right mandible in ventral view: a = accessory tooth, g = galea, l = lacinia, p = principal tooth.

in *Hadesia*, which has this part completely covered by very short and fine hairs disposed in parallel lines (Fig. 11f). These hairs are longer and less dense in *Radziella* (Fig. 11c) and long, dense and thick at *Croatodirus* (Fig. 11e). The mandible is very much modified compared with other species, in which it has a curved and much widened apex. The mandible has 6–7 teeth in *Hadesia* (Fig. 12a), 2 in *Radziella* (Fig. 12b) and 3 in *Croatodirus* (Fig. 12c). These three species have very long masticator border, with sparse setae, much more developed on the external side.

The labial palpi are almost identical in *Hadesia* and *Radziella*, excepting the apex of the terminal article which is concave in the first (Fig. 12d), bearing numerous re-

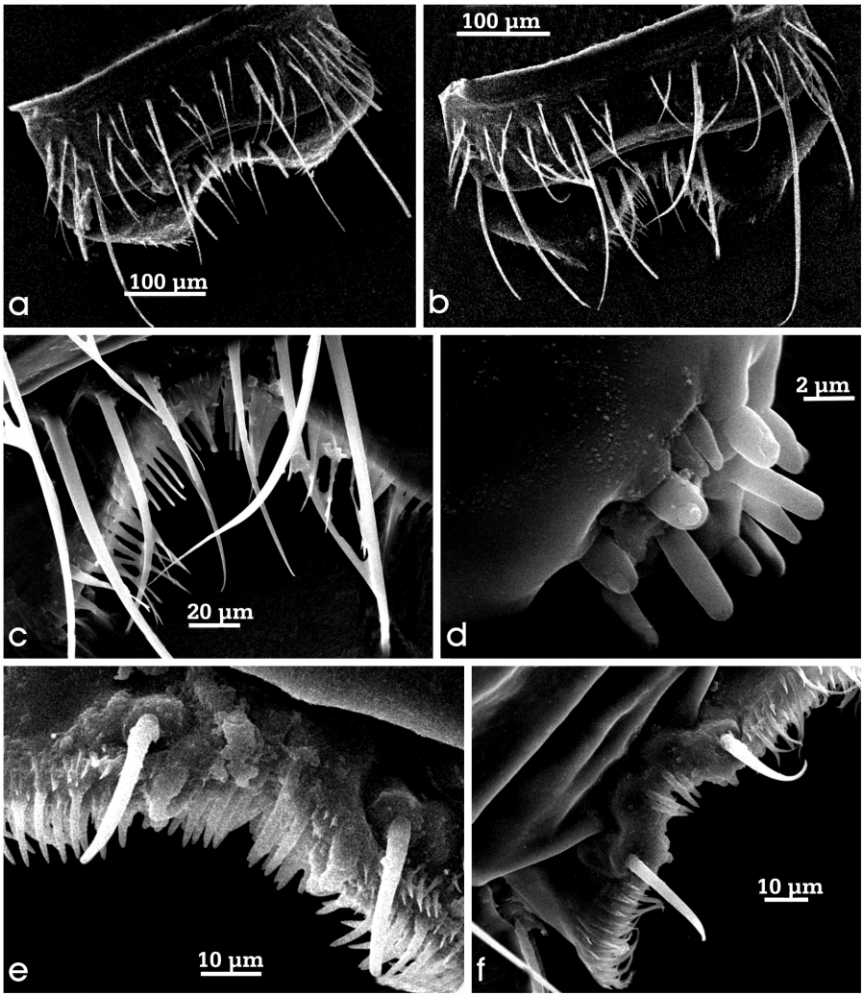

Fig. 6. Dorsal view of the labrum (a, b, c) and details of the labium (d, e, f) at *Closania orghidani* (a, e), *Sophrochaeta reitteri* (b, c) and *Tismanella chappuisi* (d, f); c. Apex of the labrum; d. Apex of the labial palp with the sensory complex; e, f. Apex of the labium with mechanical and gustatory sensilla.

ceptors, and laterally flattened in the second species with receptors distributed also toward the inferior end of the article (Fig. 12e). *Croatodirus* has a completely different morphology of the labial palpi, with a flattened and widened apex that has many receptors surrounded by a circle of long and flattened setae; some are also present on the second article, in the superior half (Fig. 12f).

The labrum is much modified, rather squared in *Croatodirus* (Fig. 13a) and *Hadesia* (Fig. 13c) and covered by numerous long hydrophilous pubescences, extremely

Fig. 7. *Hadesia vasiceki*, Vjetrenica cave in Popovo Polje (Bosna and Herzegovina) (Photo: I. Sivec)

Fig. 8. *Radziella styx*, Stara Škola pothole, Mt Biokovo, Croatia (Photo: B. Jalžić)

Fig. 9. *Croatodirus bozicevici*, the Cavern in the Učka Tunnel, Croatia (Photo: B. Jalžić)

dense in *Croatodirus*. *Radziella* has a semi circled labrum (Fig. 13e) covered with very long hairs. The labium of these three species is narrow and long in *Croatodirus* and *Hadesia*, covered with long hairs (Figs. 13b, 13d). *Radziella* has a shorter labium (Fig. 13f).

DISCUSSION

The study of some troglophilous and troglobiontic representatives of the Cholevinae in scanning electronic microscopy pointed out two types of morphological modifications of the mouthparts:

1. Determined by the colonization of an environment where the lack of eyes needs to be compensated by development of the other senses, such as touch, taste and smell during the search for food or for a partner. This type of modification can be observed in *Speonomus infernus*, *Pholeuon proserpinae*, *Closania orghidani*, *Sophrochaeta reitteri* and *Tismanella chappuisi* as compared to the *Choleva* and *Catops* species. The lengthening of the maxillary and labial palpi fits the long-known general trend as affecting the antennae and the legs. It also produces the lengthening of these mouthparts' sensilla providing better reception and differentiation of the chemical stimuli. The number of labial sensilla also increases in the cave species.

2. Determined by different trophic niches, such as terrestrial versus aquatic. *Radziella styx*, *Hadesia vasiceki* and *Croatodirus bozicevici* are species that have made a remarkable adaptation to taking organic matter or microorganisms directly from dripping water. The widening of maxilla and the mandibles recall Copepod mouthparts (STAMHUIS *et al.*, 1998; GARM & HØEG, 2000), used as a kind of spoon to stir sediments and filter food particles; the maxillipeds have »woolly hair«-like plumose setae and spoon-tipped setae for particle selection. As in the case of the species we studied, where the mandibles with their spoon-like form bring the water near the mouth, the lacinia has the role of stirring, the apex of the galea filters the organic particles with its fine and very dense hair. The apparent uniformity of the environmental features and of the trophic resources together with the scarcity of the latter can wrongly adduce the conclusion of one-way evolution for colonizers of the underground, whether only the general evolutionary trends as the features used for orientation and survival in darkness and 100% relative humidity are convergent.

The differences observed among the mouthparts of the species studied can be a good start for taxonomists, and also, with care, for phylogenists, who can include

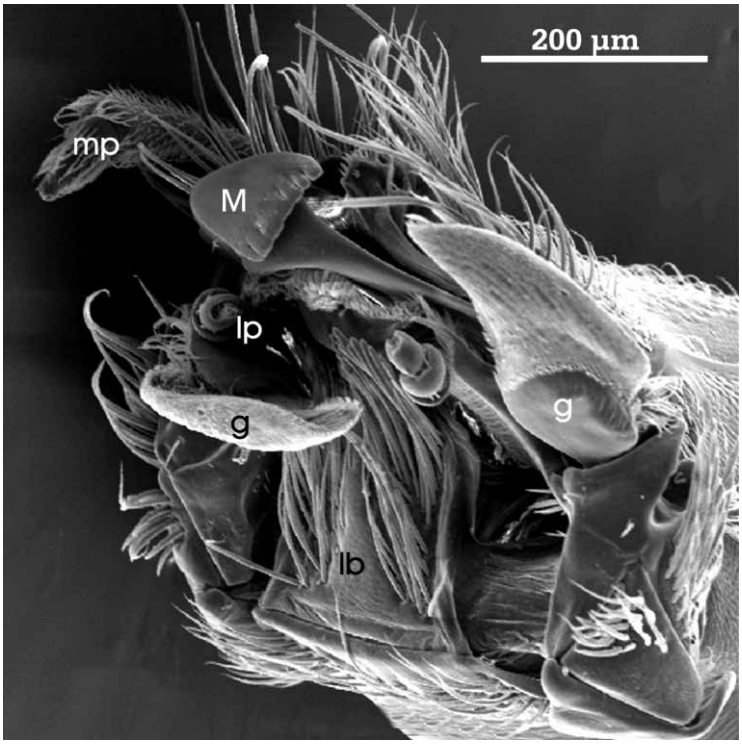

Fig. 10. Frontal view of the mouth of *Hadesia vasiceki*: g = galea, lb = labium, lp = labial palp, M = mandible, mp = maxillary palp,

some of these features in their studies, often very difficult because the apparent similarities in the morphologies of the denizens of the underground. ASHE (2000) uses the mouthparts, among other morphological features, for a cladistic reanalysis of the phylogenetic position of the genus *Stylogymnusa* (Coleoptera: Staphylynidae: Aleocharinae). For Leiodidae, in most cases the mouthparts were ignored and this paper is an attempt to compare their adaptation to different environments and different habitats. In 1911 JEANNEL made a first thorough description of the mouthparts in the formerly Bathysciinae (Leptodirinae). He insisted on the differences that can be observed in the structure of the mouth among the species, emphasizing the impossibility to use some of the characters in taxonomy, such as the number of the mandible denticules and the length of the maxillary palpi. GIACHINO *et al.* (1998) discussed the use or misuse of the mouthparts in cladistic studies in a review of the phylogeny and biogeography of the Cholevidae.

Anyway, in some cases the phylogenetic relationship between species can be emphasized by consideration of the mouthparts. For example, in the case of the cave species *S. infernus* and *P. proserpinae* the phylogenetic relationships are stronger with the troglophilous *C. cisteloides* than with *C. longulus*. Differences presented above especially in the number and the length of the sensilla and of the mouthparts

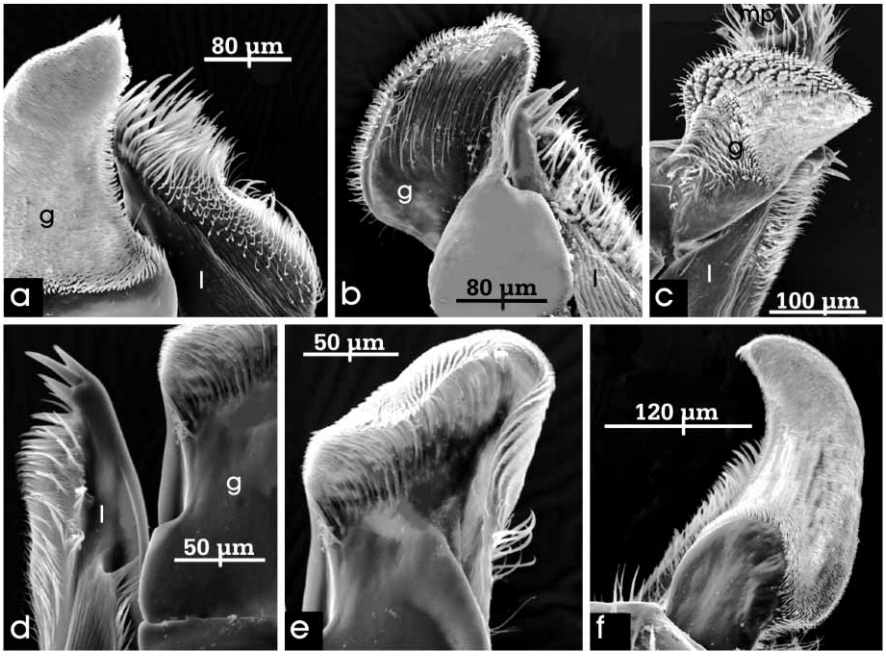

Fig 11. Mouthparts of *Hadesia vasiceki* (a, f) *Radziella styx* (b, c) and *Croatodirus bozicevici* (d, e): a., b., c. Detail of the apex of the maxilla lobes; d. Detail of lacinia; e., f. Detail of galea: g = galea, l = lacinia, mp = maxillary palp.

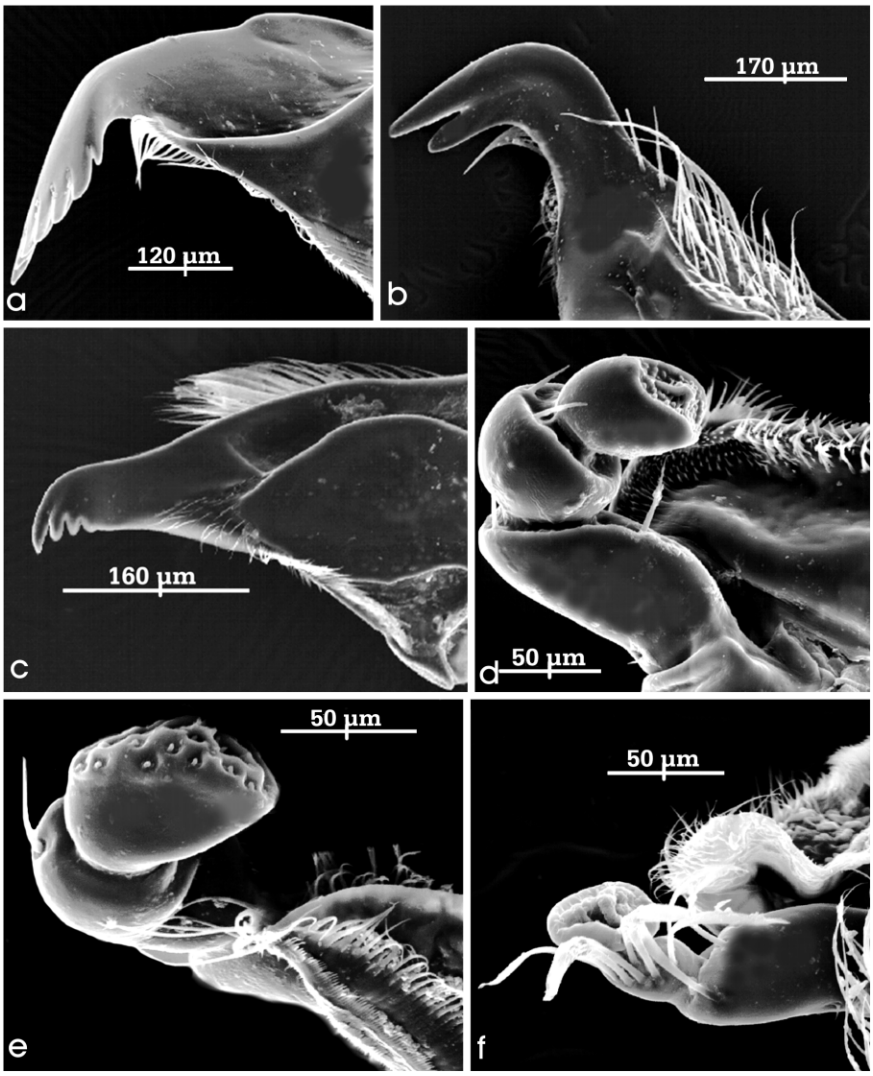

Fig. 12. Ventral view of the left mandible at *Hadesia vasiceki* (a), *Radziella styx* (b), *Croatodirus bozicevici* (c); Labial palpi, dorsal view, at *Hadesia vasiceki* (d), *Radziella styx* (e), *Croatodirus bozicevici* (f).

are opposed to some similarities, such as the length of the galea related to the lacinia, the apex of the mandibles, the disposition of the hairs of the galea.

For troglobiontic species it is likely that the number and especially the surface of chemical receptors on the mouthparts increase, as is the case of the antennae. It is very possible that in the species using aquatic sources of food, rough, finely dis-

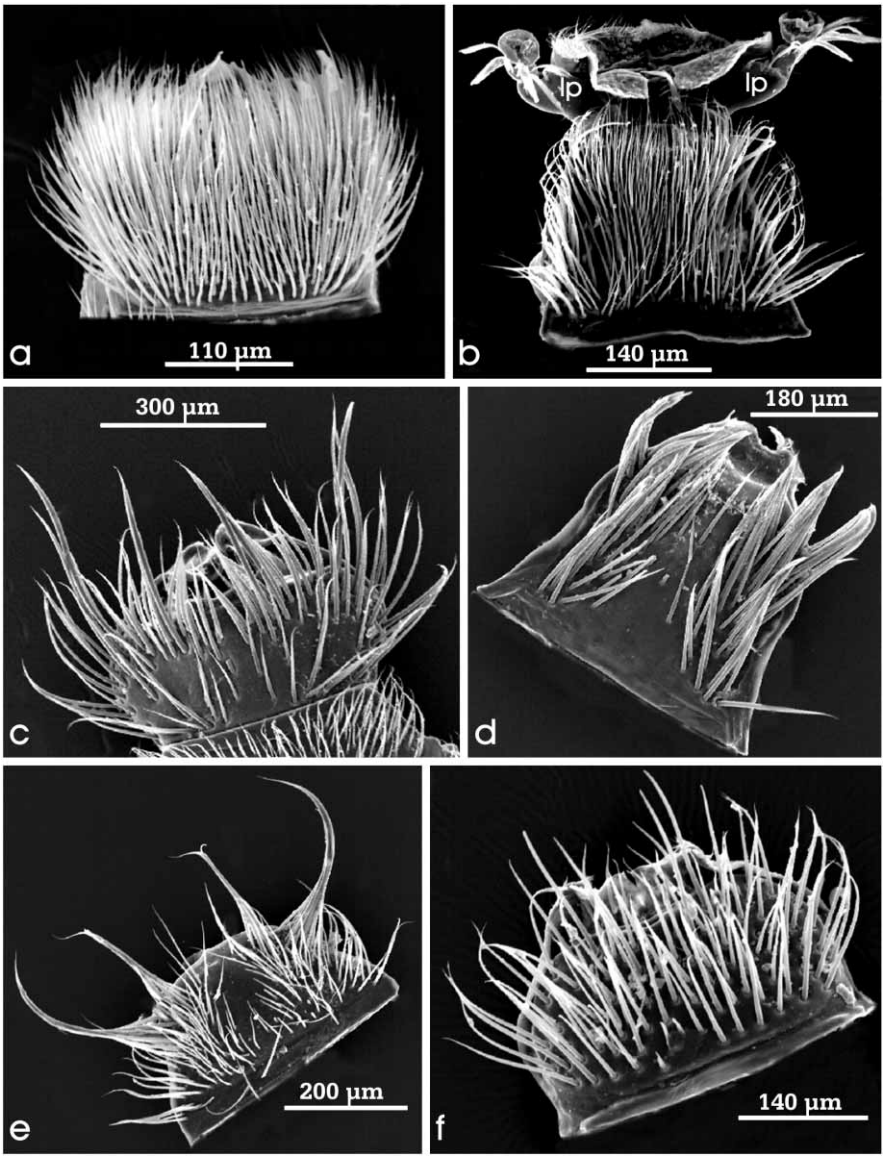

Fig. 13. Dorsal view of the labrum and labium at *Croatodirus bozicevici* (a, b), *Hadesia vasiceki* (c, d) and *Radziella styx* (e, f): lp = labial palp.

solved organic matter or microorganisms induced differentiation. GARM & HØEG (2000) mentioned that the Copepod *Munida sarsi* can select sediment not only by size, but also by quality, thanks to their maxilla. STAMHUIS *et al.* (1998) compared the sediments and the different setae morphology and found out that species forag-

ing on coarser sediments have more spoon-tipped and less plumose setae than the species feeding on finer substrates. For the species we studied there are no obvious differences in the substrate they live on, but at least some of the species are able to use organic particles of various sizes from the water, being thus adapted to a narrow and extremely specialized trophic niche.

Among cave animals there are also representatives in other terrestrial groups, such as Diplopoda and Collembola, adapted to take food from the water with modified mouthparts, especially structures evolving toward the spoon-like form (DEHARVENG & CHRISTIAN, 1984; ENGHOFF, 1985a, 1985b; ADIS *et al*., 1997; ENGHOFF *et al*., 1997).

In this first attempt at a comparative study of the mouthparts in representatives of Cholevinae beetles, we can emphasize the effect of adaptation to cave life on the mouthparts and evidence of divergent evolution within an environment relatively constant in terms of climate and food input.

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