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Comparative morphology of the larval stages of Cholevinae (Coleoptera: Leiodidae), with special reference to those in the Netherlands

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Among insects, the description of the morphology of immature life stages is often less extensive than that of adults. This is also the case with the subfamily Cholevinae (Coleoptera: Leiodidae). Of the 39 species of Cholevinae known to occur in the Netherlands, only the larvae of 15 species are described in the literature, often insufficiently. To develop new descriptions and identification keys for the larvae, specimens from Germany and the Netherlands, mainly collected by Peter Zwick and Menno Schilthuizen respectively, were examined. In addition, an extensive inventory of the literature was carried out. From this, keys were constructed and descriptions were made covering all three larval stages of all four tribes occurring in the Netherlands, consisting of 28 Dutch species as well as five other species. For distinction of tribes, mandible shape and the relative length of urogomphomere I were primarily used, whereas for distinction of species, chaetotaxy of the mandible, maxilla, antenna, tergite, and urogomphus was primarily used. More specimens should be collected to confirm the characteristics used in the keys and the descriptions, as the existing specimens may not represent the full range of intraspecific variation, some specimens may be worn down, and some specimens appear to have been misidentified. Although the keys are currently not usable for the full identification to species, they do provide a scaffold for the further development of a key to the species of Northwestern Europe. Additionally, the morphological characteristics used in the keys may be related to the diets of the larvae and be used to further investigate the phylogeny of the group, such as the paraphyly of *Catops* Paykull, 1798 and the delineation of the *Catops fuscus*-group.
Keywords: larval taxonomy, chaetotaxy, Anemadini, Cholevini, Leptodirini, Oritocatopini, Ptomaphagini.
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Introduction

Taxonomic knowledge and the ability to identify organisms is fundamental to ecological research. Traditionally, organisms are identified by comparing them to morphological descriptions or by using identification keys. Although much progress has been made on the use of DNA sequencing and barcoding as alternative methods for identification (Kloeke et al. 2022), those methods are not always feasible. Apart from the resource cost, specimens are not always collected. This is the case for opportunistically collected, photo-based records, including those on citizen science nature observation platforms like iNaturalist and Observation.org. However, even in certain systematic recording schemes such as DIOPSIS (van Klink et al. 2022), no specimens are collected. In these situations, other methods of identification are necessary, such as morphology-based identification keys. Knowledge gaps in the comparative morphology of animals therefore pose a challenge to ecological research.

Among insects, the description of the morphology of immature life stages is often less extensive than that of adults (van Emden 1957, Meier & Lim 2009). One reason is that since new species are generally first described based on adult specimens, finding immature specimens to base a morphological description on requires rearing them from adult individuals which can be reliably identified. Some authors avoid this requirement by identifying larvae *ex societate imaginis*, i.e. by proximity to identifiable adults (e.g. Paulian 1941, p. 87). However, by making the assumption both the larvae and adults belong to the same species, this yields less accurate identifications. In modern research, DNA barcoding may also offer an alternative method of identifying specimens for use in descriptions, but this method is often unavailable for older, existing specimens. Even having collected immature specimens of known species, creating descriptions that can be used to differentiate species is not straightforward. Depending on the taxonomic group, the morphology of the different species might not yet be as differentiated in early stages, and whereas morphologically identical adults can often still be identified by genital characteristics, in most cases these characteristics are not yet visible in larvae.

One of the many groups where descriptions of the larval morphology are scarcely available is Cholevinae (Giachino & Vailati 1993, Schilthuizen et al. 2011, Ledesma et al. 2022), and no comprehensive comparison of Cholevinae species has been carried out. Cholevinae is a subfamily of beetles in the Leiodidae family (Coleoptera: Staphylinoidea) with a global distribution. Many species are mainly found on decaying matter (Schilthuizen et al. 2011), although there are several specialized subtaxa that are either troglobites (Jeannel 1922) or live in nests or burrows of birds or mammals (Falcoz 1914). The subfamily has an uncommon phenology, with many species undergoing larval development during winter (Schilthuizen et al. 2011). This combination of uncommon phenology and feeding on decaying matter makes the species of the group of potential forensic importance but their use is hampered by underdeveloped methods of species identification, although early results on DNA barcoding look promising (Schilthuizen et al. 2011).

Of the 39 species of Cholevinae known to occur in the Netherlands, only the larvae of 15 species are described in the literature (Fig. 1). In many cases the identification of the specimens on which the description is based is inaccurate, and regardless many descriptions are not sufficient for comparative morphology. As is the case for entomology in general, this poses a problem for research into the distribution and biology of the group. For example, during a recent biodiversity inventory of Cholevinae in the Sierra de Guadarrama National Park in Spain, researchers collected more than 900 larvae but were unable to identify them (Ledesma et al. 2022).

To fill the knowledge gaps in comparative morphology of Cholevinae species, a complete inventory of the literature was carried out. In addition, specimens from Naturalis Biodiversity Center, mainly collected by Peter Zwick and Menno Schilthuizen, were examined. Based on these specimens, generic and specific characteristics were identified and applied to produce diagnoses and identification keys. These diagnoses and keys were mainly intended to cover the fauna in the Netherlands, as well as five additional species with sufficient material or descriptions: two species occurring close to the Netherlands were included (*Dreposcia umbrina* (Erichson, 1837) and *Choleva lederiana* Reitter, 1902); additionally, three New-World species in the Ptomaphagini tribe were included to distinguish the generic characteristics of *Ptomaphagus* Hellwig, 1795 from the tribal characteristics of Ptomaphagini and lay groundwork for a global key to the genera (*Adelopsis leo* Gnaspini, 1993, *Ptomaphagus hirtus* (Tellkampf, 1844), and *Proptomaphaginus apodemus* Szymczakowski, 1969).

History

The first known description of the larval morphology of Cholevinae appears in 1861, when Jørgen M. C. Schiødte published a description and figures of the larval stage of *Choleua* [sic!] *fusca* Panz. (= *Catops fuscus* (Panzer, 1794)) (Schiødte 1861). The next descriptions appeared in two works on findings in Mammoth Cave in Kentucky, United States, from 1880 (Hubbard 1880) and 1888 (Packard 1888),

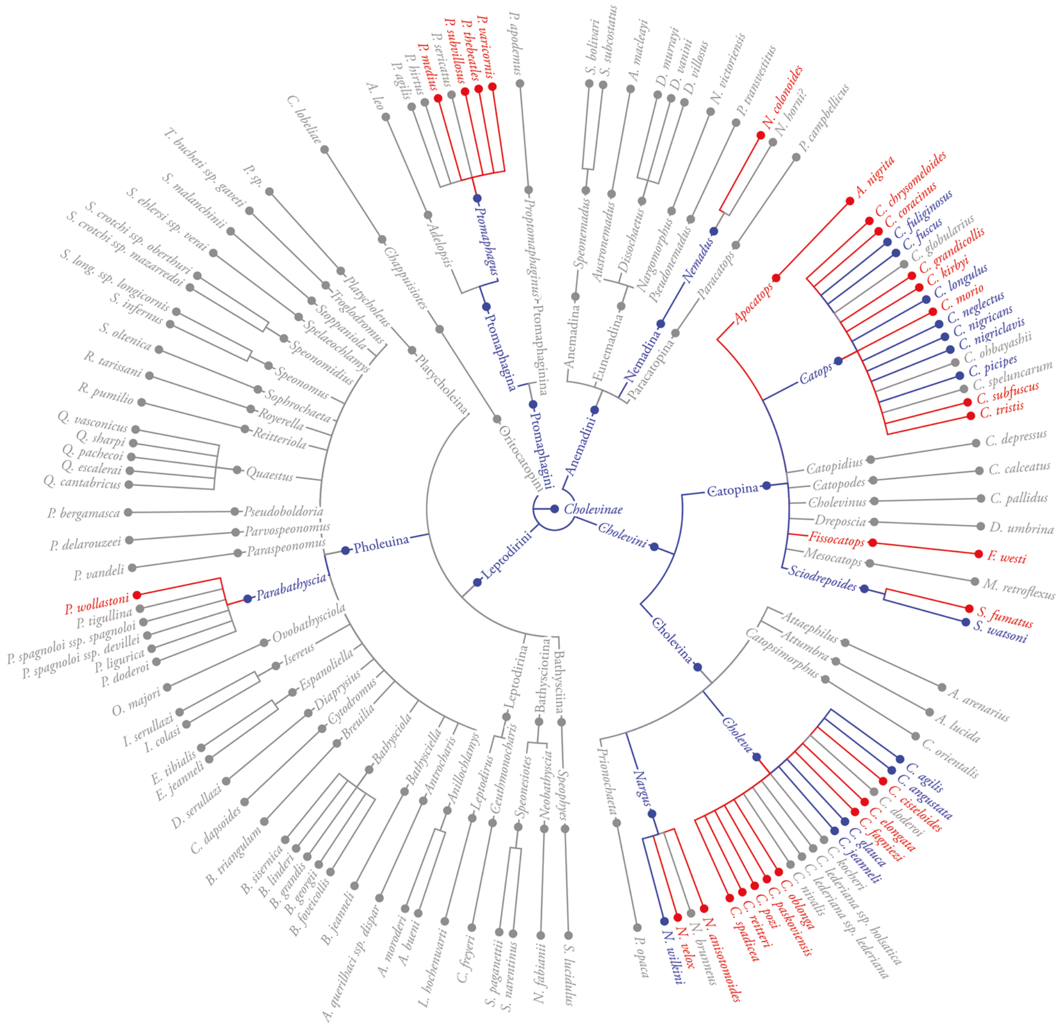


Fig. 1. Radial visualization of the taxonomic tree. – Lines and labels in blue indicate taxa that occur in the Netherlands and are described in literature; lines and labels in red indicate taxa that occur in the Netherlands but are not described, other than in a previous attempt to produce descriptions of the larval morphology from the same material in 2015 (Pinto 2015, Renkens 2015). Other taxa are described in literature or available as material, but do not occur in the Netherlands.

and were followed by a French series of publications by Le Capitaine (Pierre Joseph Vincent) Xambeu (Xambeu 1889, 1892, 1899, 1900, 1903, 1904, 1916). Another description was published in 1901 (Eichelbaum 1901). These descriptions were all largely lacking in detail, as there was little material or literature of related species available at the time to identify diagnostic characteristics. Notably the descriptions of Xambeu, who described a number of species across all insect groups every few months, contained no comparisons to closely related species.

The first identification key for the larvae of Cholevinae was published a few years later along with a number of species descriptions (Peyerimhoff 1906, 1907). This key only distinguished some specialized (sub)genera from a paraphyletic group consisting of *Catops* Paykull, 1798, *Sciodrepoides* Hatch, 1933, and *Ptomaphagus* (s. str.), which were not distinguished from each other in the key. In addition, it is clear that only the characteristics of later instars were considered, as instar I of *Catops* and *Sciodrepoides* gets misidentified based on the shape of the galeae. This was a broader problem at the time, as none of the contemporary descriptions made a distinction between the larval instars yet and were often too unclear to determine the instar *post hoc*. Knowing the larval instar is important for almost all species-specific characteristics, including size, chaetotaxy, and mandible shape (see e.g., Zwick 1978).

At the same time as these publications, interest in cave fauna arose in France (Schut & Delalandre 2015). Starting in 1908, René Jeannel published a number of works revising the cave-inhabiting beetles in the Bathysciinae (= Cholevinae: Leptodirini) and Trechinae (Carabidae) subfamilies (Jeannel 1908, 1911, 1922). In 1937 and 1941, Renaud Paulian published two works describing a large number of larvae of both Leptodirini and non-Leptodirini species (Paulian 1937, 1941), and noted problems with earlier descriptions, calling the descriptions of Xambeu "unusable" (Paulian 1941, p. 86). In 1945 Jeannel suggested creating an underground laboratory in France, dedicated to biospeleological research (Vandel 1953). He then also played a large part in the start of the research of Sylvie Deleurance (née Glaçon) at the new *Laboratoire souterrain de Moulis*. She went on to publish several detailed descriptions of the morphology of Leptodirini larvae (Glaçon 1953, 1955, Deleurance 1957a, 1957b, 1957c, 1958a, 1958c, 1961), as well as insights into the development of Cholevinae in general (Deleurance 1958b, 1959). This work culminated in her 1963 thesis containing the first major analysis of comparative morphology of the larvae of the group (Deleurance-Glaçon 1963). This work also showed the major differences that can be found between the different larval instars.

Deleurance then moved to the new Institut de neurophysiologie et psychophysiologie (INP) in Marseille, where the work on the larval morphology and development of Cholevinae was continued by Colette Strambi (Strambi 1963, 1964), Christine Fieffé (Fieffé 1965a, 1965b), and Gisèle Corbière-Tichané (Corbière 1967, 1969, Corbière-Tichané 1969), producing among other things some of the first detailed descriptions for the larvae of *Choleva* Latreille, 1796 species.

In the same decade, Peter Zwick started collecting adults and larvae of Cholevinae in Germany and breeding the adults (Zwick 1966), obtaining larvae with verified species identifications. In 1978, this work yielded a key to the larvae of most northwestern European genera of Cholevinae (Zwick 1978). He also examined the larvae of several Australian species, but the material was not complete enough to create detailed descriptions (Zwick 1979).

Descriptions of larval morphology also started appearing from different parts of the world, including Japan (Tanaka 1972, Hayashi 1986), Nepal (Szymczakowski & Plath 1976), Cuba (Decou 1973), Brazil (Gnaspini 1993a, 1993b), Spain (Blas & Vives 1978, Sendra et al. 1985, 1987), Italy (Casale 1975a, 1975b), and Morocco (Perreau 1987). The broader interest in the larval morphology meant that descriptions were less standardized, and no attempts were published comparing the morphological characters of the different genera. Several descriptions did not treat the entire larva, but for example only the thorax and abdomen (Szymczakowski & Plath 1976).

More recently, however, new terminology and a new system for chaetotaxy was developed by Kilian (1998, 2007, 2012) based on earlier work on chaetotaxy of related Coleoptera larvae (Ashe & Watrous 1984, Wheeler 1990). These works are the modern standard for morphological descriptions of Cholevinae larvae and have been used since (Kilian & Mądra 2015, Kilian & Newton 2017, 2021, Kilian et al. 2023).

Material and methods

Taxonomy

Cholevinae is a subfamily of Leiodidae (Coleoptera: Staphylinoidea) (Cai et al. 2022). Previously, it has also been considered a family of its own (Schilthuizen et al. 2011). The taxonomy and synonymy of Perreau is used (Perreau 2000), in combination with https://cholevidae.myspecies.info/ and with updates from more recent taxonomic literature. The distribution of species is based on Perreau (2000, pers. comm.) as well, unless stated otherwise. For the list of species occurring in the Netherlands, the *Nederlandse Soortenregister* is used (Creuwels & Pieterse 2024). See Fig. 1 for an overview, and Table 1 for the full list of species.

The subfamily is divided into seven tribes, of which five are included in this analysis (Fig. 1). The two remaining tribes, Sciaphyini and Eucatopini, are relatively small and were not included, as no literature or material was available on their larval morphology. Of the five tribes that are included, Leptodirini is the most speciose and has the most extensively described larval morphology. However, as only a single species occurs in the Netherlands, no material was available of this taxon, and an extensive comparative analysis of other species in the group had already been carried out (Deleurance-Glaçon 1963), only the tribe is included in the keys and descriptions, without a distinction between further subtaxa.

Examined material

Material from Naturalis Biodiversity Center was examined. The specimens were collected by Peter Zwick and Wolfgang Zimmermann in Germany in the 1960s and by Menno Schilthuizen in the Netherlands in the 1980's, mostly from baited traps but also in bird and mole nests and on carrion. Of the individuals found on carrion, *Catops* was found mostly on mammals and birds, whereas *Ptomaphagus*, *Nargus* Thomson, 1867, and others were also found on other vertebrate carrion. A large part of these specimens was caught as adults, and could therefore be reliably identified to species. From these adults, larvae were then raised. Some specimens were caught as larvae, and the identification of those specimens is therefore less precise (see Discussion) or less accurate, being only identified to subfamily or genus level.

The examined material was preserved as microscope slides of whole larvae and larval exuviae, for a large part in Euparal or Canada balsam. Though most microscope slides contained a single individual, around a third contained multiple individuals, sometimes of different species. Around a fifth of the slides were created in 2015 by students of Menno Schilthuizen (Pinto 2015, Renkens 2015). Some additional material was preserved in 70% ethanol. A cursory examination revealed much of the material belonged to species for which enough material was already available as microscope slides. The material was not examined further due to time constraints and is not included in this analysis.

The specimens were photographed with a Leica DFC450 digital camera on a Leica DMRBE trinocular microscope, using LAS X Core software (Leica Camera AG, Wetzlar, Germany), which recorded the scale of the images. From these images, illustrations were made in Inkscape. Features of dorsal and ventral surfaces were generally drawn in the same illustration, in which case the ventral features were drawn with dotted lines.

In the same LAS X Core software, the sizes of certain morphological features were also measured in Catopina and certain *Choleva* species. Total body length or head length could not be measured directly as the material consists of a mix of exuviae and whole larvae, and in many cases the abdomen and the head capsule were strongly deformed or contracted by the preparation process. For an indicator of total size, instead the lengths of the three antennomeres and the posterior femur, tibia, and tarsungulus were measured. Especially the second antennomere and the tibia can be measured consistently and can be related to overall size, though it should be noted this cannot be compared between Catopina and *Choleva* as relative appendage lengths differ. To validate the identifying characteristics of Catopina, the lengths of abdominal tergite X and urogomphomere I were measured. Abdominal tergite X often appeared to start under tergite IX and was measured from there to the carina just after setae pair D1 (Kilian & Mądra 2015, see Figs 52 and 55 below). To validate characteristics in the key to species of Catopina, the length of the dorsal medial seta and ventral apical seta on urogomphomere I were measured and related to the total length of the urogomphomere. Additional species or species group characteristics were explored by measuring the length of urogomphomere II and its apical seta. Additional measurements were made in 2015 (Pinto 2015, Renkens 2015), but were not always usable as the instar of the larvae was not always recorded and not many individuals were measured.

Literature

Literature searches were first performed in Google Scholar and similar platforms. Based on this initial set, supplemented by 5–10 articles known to be relevant, additional literature was found by systematically going through the reference lists of found articles. For a taxonomy-based index of the literature, see Table 1.

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•).

Anemadini Hatch, 1928	†		
Anemadina Hatch, 1928			
Speonemadus Jeannel, 1922			
bolivari (Jeannel, 1922)			(Jeannel 1922)
subcostatus (Reiche, 1864)			(Peyerimhoff 1907, Jeannel 1922)
Eunemadina Newton, 1998			
Austronemadus Zwick, 1979			
macleayi (Blackburn, 1903)			(Zwick 1979)
Dissochaetus Reitter, 1884			
murrayi Reitter, 1884			(Gnaspini 1993a)
vanini Gnaspini, 1991			(Gnaspini 1993a)
villosus Szymczakowski, 1961			(Gnaspini 1993a)

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•). (*cont.*)

Nargomorphus (Jeannel, 1936)		
victoriensis (Blackburn, 1891)		(Zwick 1979)
Pseudonemadus Portevin, 1914		
(*Leptonemadus* Zwick, 1979)		
transvestitus Zwick, 1979		(Zwick 1979)
Nemadina Jeannel, 1936	†	
Nemadus Thomson, 1867	†	(Tanaka 1972, Zwick 1978)
(*Nemadus* Thomson, 1867)	†	
colonoides (Kraatz, 1851)	†•	(Pinto 2015)
horni Hatch, 1933		(Lawrence 1991,?)
Paracatopina Jeannel, 1936		
Paracatops Portevin, 1907		
campbellicus (Brookes, 1951)		(Samuelson 1964)
Cholevini Kirby, 1837	†	
Catopina Chaudoir, 1845	†	(Zwick 1978)
Apocatops Zwick, 1968	†	
nigrita (Erichson, 1837)	†•	(Renkens 2015)
Catopidius Jeannel, 1922		
depressus (Murray, 1856)		(Falcoz 1914, Paulian 1941)
Catopodes Portevin, 1914		
calceatus Szymczakowski & Plath, 1976		(Szymczakowski & Plath 1976)
Catops Paykull, 1798	†	(Paulian 1941, Beutel & Molenda 1997)
chrysomeloides (Panzer, 1798)	†•	(Renkens 2015)
coracinus Kellner, 1846	†•	(Renkens 2015)
fuliginosus Erichson, 1837	†•	(Paulian 1941, Renkens 2015)
fuscus (Panzer, 1794)	†•	(Schiødte 1861, Xambeu 1899, Renkens 2015)
globularius Szymczakowski & Plath, 1976		(Szymczakowski & Plath 1976)
grandicollis Erichson, 1837	†•	(Renkens 2015)
kirbyi (Spence, 1815)	†•	(Renkens 2015)
longulus Kellner, 1846	•	(Xambeu 1916, Paulian 1941)
morio (Fabricius, 1787)	†•	(Renkens 2015)
neglectus Kraatz, 1852	†•	(Paulian 1941, Renkens 2015)
nigricans (Spence, 1815)	†•	(Xambeu 1900b, Renkens 2015)
nigriclavis Gerhardt, 1900	†•	(Paulian 1941, Casale 1975a, Renkens 2015)
ohbayashii Jeannel, 1954		(Tanaka 1972, Hayashi 1986)
picipes (Fabricius, 1787)	†•	(Eichelbaum 1901, Renkens 2015)

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•). (*cont.*)

speluncarum (Reitter, 1884)		(Casale 1975a)
subfuscus Kellner, 1846	†•	(Renkens 2015)
tristis (Panzer, 1794)	†•	(Renkens 2015)
Cholevinus Reitter, 1901		
pallidus (Ménétries, 1832)		(Blas & Vives 1978)
Dreposcia Jeannel, 1922	†	(Zwick 1978)
umbrina (Erichson, 1837)	†	(Pinto 2015)
Fissocatops Zwick, 1968	†	
westi (Krogerus, 1931)	†•	(Renkens 2015)
Mesocatops Szymczakowski, 1961		
retroflexus Szymczakowski & Plath, 1976		(Szymczakowski & Plath 1976)
Sciodrepoides Hatch, 1933	†	
fumatus (Spence, 1815)	†•	(Pinto 2015)
watsoni (Spence, 1815)	†•	(Eichelbaum 1901, Paulian 1941, Kilian & Mądra 2015, Pinto 2015, Jakubec 2016)
Cholevina Kirby, 1837	†	(Zwick 1978)
Attaephilus Motschulsky, 1844	†	
arenarius (H. Hampe, 1852)	†	(Xambeu 1889, 1892, Peyerimhoff 1907, Jeannel 1922)
Attumbra Gozis, 1886		
lucida (Kraatz, 1852)		(Silvestri 1912)
Catopsimorphus Aubé, 1850		
(*Catopsimorphus* Aubé, 1850)		
orientalis (Aubé, 1850)		(Antunes-Carvalho et al. 2019)
Choleva Latreille, 1796	†	(Böving & Craighead 1930, Paulian 1941, Zwick 1978)
(*Choleva* Latreille, 1796)	†	
agilis (Illiger, 1798)	†•	(Casale 1975a, Pinto 2015)
angustata (Fabricius, 1781)	†•	(Strambi 1963, 1964)
cisteloides (Frölich, 1799)	•	
doderoi Breit, 1903		(Casale 1975a)
elongata (Paykull, 1798)	•	
fagniezi Jeannel, 1922	†•	(Pinto 2015)
glauca Britten, 1918	•	(Paulian 1937, 1941)
jeanneli (Jeannel, 1922)	•	(Paulian 1937, 1941)
kocheri Henrot, 1962		(Perreau 1987)
lederiana ssp. *holsatica* Benick & Ihssen, 1937	†	(Heun 1955, Zwick 1966, Pinto 2015)
lederiana ssp. *lederiana* Reitter, 1902		(Krogerus 1927)

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•). (*cont.*)

nivalis (Kraatz, 1856)		(Paulian 1937, 1941)
oblonga Latreille, 1807	†•	(Pinto 2015)
pozi Roubal, 1916	•	
reitteri Petri, 1915	•	
(*Cholevopsis* Jeannel, 1922)		(Zwick 1978)
paskovensis Reitter, 1913	•	
spadicea (Sturm, 1839)	†•	(Pinto 2015)
Nargus Thomson, 1867	†	(Zwick 1978)
(*Demochrus* Thomson, 1867)		
anisotomoides (Spence, 1815)	•	
brunneus (Sturm, 1839)		(Xambeu 1904)
wilkini (Spence, 1815)	•	(Paulian 1941)
(*Nargus* Thomson, 1867)	†	
velox (Spence, 1815)	†•	(Pinto 2015)
Prionochaeta Horn, 1880	†	
opaca (Say, 1825)	†	(Böving & Craighead 1930, Kilian & Newton 2021)
Leptodirini Lacordaire, 1854	†	
Bathysciina Horn, 1880		(Jeannel 1911, Deleurance-Glaçon 1963)
Speophyes Jeannel, 1910		
lucidulus (Delarouzée, 1860)		(Fieffé 1965a, Corbière 1967, 1969, Corbière-Tichané 1969)
Bathysciotina V. B. Guéorguiev, 1974		
Neobathyscia Müller, 1917		(Brasavola de Massa 1931, Deleurance-Glaçon 1963)
fabianii (Dodero, 1904)		(Paulian 1941)
Speonesiotes Jeannel, 1910		
(*Speonesiotes* Jeannel, 1910)		
narentinus (L. Miller, 1861)		(Paulian 1941)
paganettii (Ganglbauer, 1902)		(Weber 1902, Jeannel 1911, Deleurance-Glaçon 1963)
Leptodirina Lacordaire, 1854		
Ceuthmonocharis Jeannel, 1914		
(*Ceuthmonocharis* Jeannel, 1914)		
freyeri (L. Miller, 1855)		(Weber 1899, Jeannel 1911, Deleurance-Glaçon 1963)
Leptodirus F. J. Schmidt, 1832		
hochenwarti F. J. Schmidt, 1832		(Deleurance 1961, Deleurance-Glaçon 1963)

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•). (*cont.*)

Pholeuina Reitter, 1886	†	
Anillochlamys Jeannel, 1909		
bueni Jeannel, 1909		(Paulian 1941)
moroderi Bolívar, 1923		(Sendra et al. 1985)
Antrocharis Abeille de Perrin, 1878		
querilhaci (Lespès, 1857) ssp. *dispar* Abeille de Perrin, 1878		(Deleurance 1957a, Deleurance-Glaçon 1963)
Bathysciella Jeannel, 1906		
jeanneli (Abeille de Perrin, 1904)		(Deleurance 1957b, 1958c, Deleurance-Glaçon 1963)
Bathysciola Jeannel, 1910		
(*Bathysciola* Jeannel, 1910)		
foveicollis Peyerimhoff, 1904		(Peyerimhoff 1906, Jeannel 1911)
georgii Cerruti & Patrizi, 1952		(Cerruti 1955)
grandis (Fairmaire, 1856)		(Jeannel 1908, 1911, Deleurance-Glaçon 1963)
linderi (Abeille de Perrin, 1875)		(Jeannel 1911, Paulian 1941)
sisernica Cerruti & Patrizi, 1952		(Cerruti 1955)
Breuilia Jeannel, 1909		(Paulian 1941)
triangulum (Sharp, 1872)		(Jeannel 1911)
Cytodromus Abeille de Perrin, 1876		
dapsoides (Abeille de Perrin, 1875)		(Deleurance 1958a, Deleurance-Glaçon 1963)
Diaprysius Abeille de Perrin, 1878		
serullazi Peyerimhoff, 1904		(Deleurance 1957b, 1957c, Deleurance-Glaçon 1963)
Espanoliella V. B. Guéorguiev, 1976		
jeanneli (Bolívar, 1917)		(Paulian 1941)
tibialis (Jeannel, 1909)		(Paulian 1941)
Isereus Reitter, 1886		
colasi Bonadona, 1955		(Deleurance 1958a, Deleurance-Glaçon 1963)
serullazi Fagniez, 1914		(Deleurance 1958a, Deleurance-Glaçon 1963)
Ovobathysciola Jeannel, 1924		
majori (Reitter, 1884)		(Casale 1975b)
Parabathyscia Jeannel, 1908	†	(Franciscolo 1953)
(*Parabathyscia* Jeannel, 1908)	†	
doderoi (Fairmaire, 1882)		(Menozzi 1939, Franciscolo 1953)
ligurica (Reitter, 1889)		(Xambeu 1903, Franciscolo 1953)
spagnoloi ssp. *spagnoloi* (Fairmaire, 1882)		(Peyerimhoff 1906, Jeannel 1911, Franciscolo 1948)
spagnoloi ssp. *devillei* Jeannel, 1911		(Paulian 1941)

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•). (*cont.*)

tigullina Binaghi, 1940		(Franciscolo 1948, 1953)
wollastoni (Janson, 1857)	†•	
Paraspeonomus Coiffait, 1952		
vandeli Coiffait, 1952		(Deleurance 1965)
Parvospeonomus Bellés & Escolà, 1977		
delarouzeei (Fairmaire, 1863)		(Jeannel 1909, 1911, Paulian 1941)
Pseudoboldoria Ghidini, 1937		
bergamasca (Jeannel, 1914)		(Rossi 1976)
Quaestus Schaufuss, 1861		(Paulian 1941)
(*Amphogeus* Salgado Costas, 2000)		
cantabricus (Uhagón, 1881)		(Paulian 1941)
escalerai (Jeannel, 1909)		(Jeannel 1911)
(*Quaesticulus* Schaufuss, 1861)		
pachecoi (Bolívar, 1915)		(Adamczyk et al. 2011)
sharpi (Escalera, 1898)		(Jeannel 1911, Paulian 1941)
vasconicus (Piochard de la Brûlerie, 1872)		(Paulian 1941)
Reitteriola Giachino & Vailati, 2019		
pumilio (Reitter, 1884)		(Franciscolo 1950)
Royerella Jeannel, 1910		(Brasavola de Massa 1931)
tarissani (Bedel, 1878)		(Deleurance 1961, Deleurance-Glaçon 1963)
Sophrochaeta Reitter, 1884		
(*Sophrochaeta* Reitter, 1884)		
oltenica Jeannel & Mallász, 1930		(Decou & Juberthie 1969)
Speonomidius Jeannel, 1924		
crotchi (Sharp, 1872) ssp. *mazarredoi* (Uhagón, 1881)		(Paulian 1941)
crotchi (Sharp, 1872) ssp. *oberthuri* (Jeannel, 1909)		(Paulian 1941)
Speonomus Jeannel, 1908		(Glaçon 1955)
(*Machaeroscelis* Jeannel, 1924)		
infernus (Dieck, 1869)		(Jeannel 1909, 1911, Deleurance-Glaçon 1963)
(*Speonomus* Jeannel, 1908)		
longicornis (Saulcy, 1872)		(Glaçon 1953, Deleurance-Glaçon 1963)
Spelaeochlamys Dieck, 1870		
ehlersi Dieck, 1870 ssp. *verai* Comas, 1977		(Sendra et al. 1987)

Table 1. Taxonomic index of literature. Species covered in this article are indicated with a dagger (†). Species found in the Netherlands are indicated with a bullet (•). (*cont.*)

Stoppaniola Vailati, 2017		
malanchinii (Pavan & Ronchetti, 1949)		(Rossi 1976)
Troglodromus Sainte Claire Deville, 1901		
bucheti (Sainte Claire Deville, 1898) ssp. *gaveti* Sainte Claire Deville, 1901		(Deleurance 1957b, Deleurance-Glaçon 1963)
Platycholeina Horn, 1880		
Platycholeus Horn, 1880		(Kilian & Newton 2017)
Oritocatopini Jeannel, 1936	†	
Chappuisiotes Jeannel, 1957		
lobeliae (Jeannel, 1936)		(Paulian 1937, 1941)
Ptomaphagini Jeannel, 1911	†	
Ptomaphagina Jeannel, 1911	†	
Adelopsis Portevin, 1907	†	
leo Gnaspini, 1993	†	(Gnaspini 1993b)
Ptomaphagus Hellwig, 1795	†	(Zwick 1978, Peck & Gnaspini 1997)
(*Adelops* Tellkampf, 1844)	†	
hirtus (Tellkampf, 1844)	†	(Hubbard 1880, Packard 1888, Peyerimhoff 1906, Böving & Craighead 1930)
(*Ptomaphagus* Hellwig, 1795)	†	
medius (Rey, 1889)	†	(Pinto 2015)
sericatus (Chaudoir, 1845)	†•	(Jeannel 1922, Paulian 1941, Pinto 2015)
subvillosus (Goeze, 1777)	†•	(Xambeu 1894, Pinto 2015)
thebeatles Schilthuizen, Latella & Njunjić, 2021	†•	(Pinto 2015)
varicornis (Rosenhauer, 1847)	†•	(Pinto 2015)
(*Synaulus* Portevin, 1903)		
agilis (Lucas, 1846)		(Peyerimhoff 1907)
Ptomaphaginina Szymczakowski, 1964	†	
Proptomaphaginus Szymczakowski, 1969	†	
apodemus Szymczakowski, 1969	†	(Decou 1973)

Descriptions

The identification keys and descriptions were written using the morphological terminology and the chaetotaxy system used by Kilian (1998, 2007, 2012), with special reference to the description of *Sciodrepoides watsoni* (Spence, 1815) using that terminology and system (Kilian & Mądra 2015).

Abbreviations used in key, descriptions, and figures are as follows:

AI, AII, AIII	Antennomere I, II, II
AIX, AX	Abdominal segments
Cdo	Cardo
Da1, Da2, Db2, Dc2, Dd1*, Dd2	Dorsal setae
ds1	Dorsal sensillum

Ga	Galea
Gp	Pretergal gland
IIs1, IIs2	Sensilla 1 and 2 on AII
L, Lb	Lateral setae
La	Lacinia
Lg	Ligula
L1, L2, L3	Larval instar 1, 2, 3
LPI, LPII	Labial palpomeres I and II
ls1	Lateral sensillum
M1, M2, M3', M4'	Mandibular setae
Ma	Mala
Mnt	Mentum
Mo	Mola
MPI, MPII, MPIII	Maxillary palpomeres I, II, and III
P1, P2, P5	Posterior setae
Pmnt	Prementum
Pr	Prostheca
PS	Paracercal seta
ps1, ps2	Posterior sensilla
R (abdomen)	Reservoir
R (mandible)	Retinaculum
SA	Sensory appendage
SF	Setal field
Smnt	Submentum
Stp	Stipes
URI, URII	Urogomphomere I, II

Prostheca vs retinaculum. The terms "prostheca" and "retinaculum" are used inconsistently in the literature, and this is regularly acknowledged by the authors themselves. Jeannel is the first to use both terms in the description of a single Cholevinae species, and uses "retinaculum" for the thin, bristle- or tooth-like appendage (depending on the species) on the inner edge of the mandible and "prostheca" for the sometimes absent broad tooth between the retinaculum and the mola (Jeannel 1911, 1922). This seems to follow the terminology used by Schiødte (1861), who uses "retinaculum" in the same way as Jeannel but who does not describe a prostheca.

Other authors, however, reverse these terms, and use "prostheca" for the bristle- or tooth-like appendage instead (Böving & Craighead 1930, Menozzi 1939, Paulian 1941). Böving and Craighead (1930, pp. 83–84) define "prostheca" and "retinaculum" as follows:

lm, lacinia mandibulae (= prostheca = lacinia mobilis, a fleshy or membranous process from the interior face of the mandible; see r, retinaculum)

r, retinaculum (a hard, pointed, and tooth shaped process usually near or at the middle of the inner edge of the mandible; never jointed).

Krogerus (1927) only uses "retinaculum", in the same way as Böving and Craighead, and instead uses "Zahn" for the "prostheca". Strouhal circumvents the issue by using "Zahn" for both features (Beier & Strouhal 1928).

Deleurance and Franciscolo conserve the terminology of Jeannel (cf. Franciscolo 1950, Deleurance-Glaçon 1963), and are followed by other authors (Strambi 1963, Fieffé 1965b, Corbière 1967). It should be noted that Deleurance worked in the same institutes as Jeannel (Laboratoire d'évolution des êtres organisés de Paris, Laboratoire souterrain de Moulis), and later Strambi, Fieffé, and Corbière in the same institute as Deleurance (Institut de neurophysiologie et psychophysiologie de Marseille). Deleurance explicitly acknowledges the difference with other authors, stating:

> Comme Franciscolo, nous avons conservé la terminologie de Jeannel concernant le *rétinacle:* lobe membraneux s'insérant sur la *mola*. On réserve le nom de *prostheca* à la dent qui s'implante entre le rétinacle et les dents molaires. Böving et Craighead, de même Paulian, intervertissent les termes. — Deleurance-Glaçon 1963, p. 118

In later years, the usage of Böving and Craighead seems more prevalent (Zwick 1978, Kilian 2007, Kilian & Mądra 2015, Kilian & Newton 2017, 2021). This usage seems to be compatible with Lawrence (1991), who also acknowledges the present confusion, albeit without specific reference to these authors. Because of this, and because the terminology used by Jeannel, Deleurance, Franciscolo, and Strambi can be traced back to a single source, this work uses the currently prevalent terminology.

Results

Development

Generally, species of Cholevinae go through three larval instars (L1, L2, and L3). The larvae increase in size between instars (Fig. 2). Additionally, secondary setae develop between L1 and L2. Zwick (1978) lists several differences between the instars: (1) differences in size, (2) differences in chaetotaxy and (for Catopina) the shape of the mandible, (3) antennomere II not polytrichic (except *D. umbrina* and *Catops* *picipes* (Fabricius, 1787)), and (4) a straight paracercal seta (except *D. umbrina* and certain *Catops*). However, these differences are all either variable between species (size, chaetotaxy, mandible shape), or have many exceptions. A more general characteristic is also presented, in that in L1, the tergites I–VIII have "eight chaeta". As opposed to the former characteristics, this one seems to apply to all the L1 material seen by the author, with a few caveats listed in the key to instars below.

The Leptodirini are an exception to this, with many species only going through two or even just one larval instar before pupating (Deleurance-Glaçon 1963). In all the species found to have just one or two larval instars, Deleurance-Glaçon (1963) found the first of these instars to be equivalent to L1 in other Cholevinae based on chaetotaxy, as opposed to L3 or L2 respectively. However, in those species L1 (and L2, where applicable) is generally larger than the same instar in species with more instars (Fig. 3).

In some Catopina species the antennae and legs are relatively elongated and straight-edged in L3 compared to L2. Some species already have these secondary setae and elongated antennae and legs in L1, making the determination of larval instars difficult without already knowing the exact species. Similarly, in smaller species the change in shape of the antennae and legs is not observed. At first glance, *Catops neglectus* Kraatz, 1852 might represent a possible exception among Catopina. Based on L1, it seems to be a small species, of similar size to *Catops coracinus* Kellner, 1846 and *Fissocatops westi* (Krogerus, 1931). However, the specimen labelled L2 (II.52 = RMNH.INS.967946) is relatively very large (Fig. 2). Leg shape is more indicative of L2, but as seen in other small species this is not a consistent characteristic. Based on trends of size in Leptodirini species with one or two larval instars, it seems improbable that this is also the case in *C. neglectus*, and as such the specimen has been interpreted as L3 instead.

Key to the larval instars of Cholevinae

1. The posterior row on the tergites, between the medial suture and the spiracle, consisting of 3 macrosetae (P1, P2, P4/P5) and one small seta (P4'/P5'). Laterally, on the other side of the spiracle, an additional seta (L). Some polytrichic Catopina species are known to have additional setae on the hind edge, but inconsistently so, often only on one half of a single tergite .... Instar I

– The posterior row on the tergites, between the medial suture and the spiracle, consistently with additional, sometimes smaller setae (Instar II and III) 2

2. [This step is valid only for *Apocatops* Zwick, 1968, *Fissocatops*, *Sciodrepoides*, and *Catops* except for *C. picipes*.]
Lateral edges of AII rounded, AII widest before the sensory appendage. Sides of femurs and tibiae rounded, or straight but the posterior tibia not longer than 350 µm .... Instar II

– Lateral edges of AII straight, edges divergent until a sharp bend near the sensory appendage, AII widest near the sensory appendage. Sides of femurs and tibiae straight. Larger individuals, the posterior tibia longer than 330 µm .... Instar III

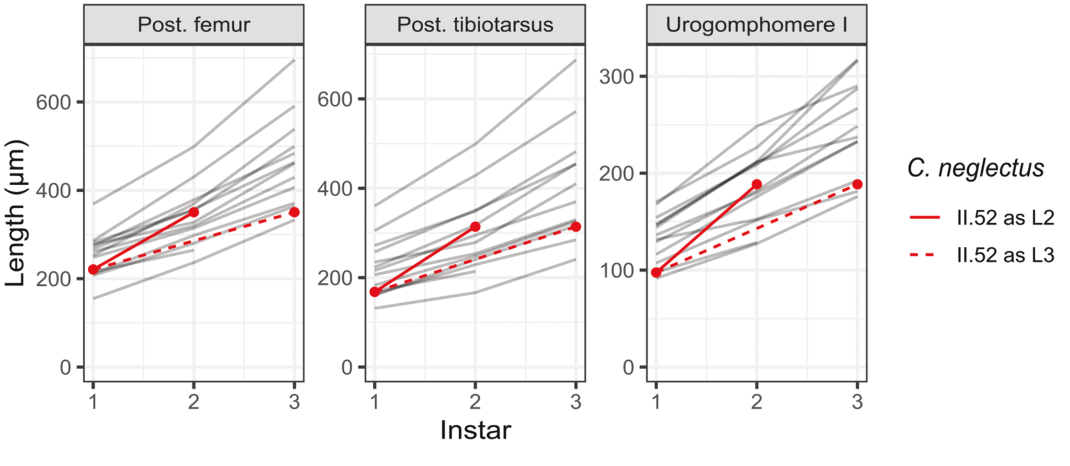


Fig. 2. Size progression across instars in Catopina species, based on the lengths of the posterior femur, the posterior tibia, and URI. – The red lines indicate the size progression of *C. neglectus*, with specimen II.52 interpreted as L2 (solid) or L3 (dashed).

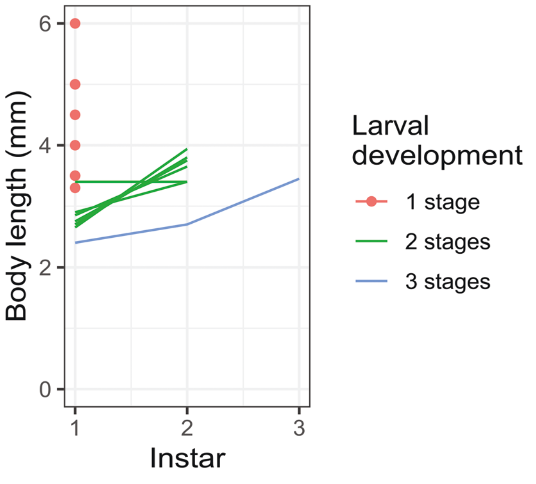


Fig. 3. Size progression across instars in Leptodirini species, based on total body length data from the literature (Deleurance-Glaçon 1963, Decou & Juberthie 1969, Sendra et al. 1985, Adamczyk et al. 2011). – Line and point colours indicate the number of larval instars that the species goes through.

Morphology

Head

The head consists of the head capsule, a pair of antennae, the labrum, the mandibles, the maxillae, and the labium. The head capsule may have one or more pairs of ocelli, usually behind the antennae, but certain troglobitic species have none. The mandibles often have mola, as well as a retinaculum, a prostheca, both, or neither. The maxillae consist of a stipes and lacinia and have a three-segmented palp. These segments are numbered MPI, MPII, and MPIII. The labium consists of the submentum, mentum, prementum, ligula, and two-segmented labial palps (Fig. 4).

Antennae. *Instar I* — Antennae consist of three segments (antennomeres), numbered AI, AII, AIII from the basal to the distal end, with AII being the largest one. In larger species, AIII is generally shorter relative to AII compared to in smaller species. AI usually has 4–5 campaniform sensilla (c.s.), two dorsally in the basal half of the segment, and 2–3 along the distal edge. AII usually has dorsally a campaniform sensillum and a large seta, laterally a large sensory appendage (SA), and ventrally two large setae and two sensilla (IIs1 and IIs2), respectively "peg-like" and setiform. AIII has subapically four setae, three large and one small, a campaniform sensillum or a small SA next to the small seta, and apically a central "peg-like" sensillum (IIIs1) and a setiform one (IIIs2). Across species, additional setae may occur on AI and AII. Several Catopina species have a single additional seta on AI, and some *Choleva* species have varying amounts of additional setae on AI and AII. Some species also have microtrichia or microsetae, mainly on AII and AIII. In addition, in some species the antennae, specifically AI and AII, are polytrichic even in instar I. Leptodirini have an additional, long, setiform appendage on AIII, between the four subapical setae and the two apical sensilla. In several Leptodirini species, AIII features a characteristic pigmented band.

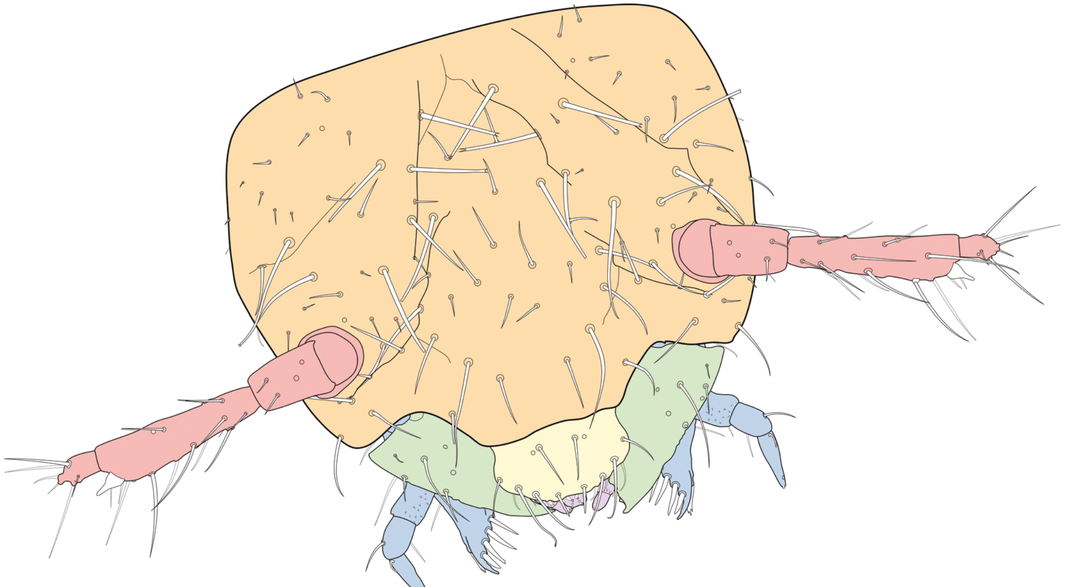


Fig. 4. Head of the larva of *Catops morio* (Fabricius, 1787), dorsally, schematically coloured to indicate different parts of the morphology. – Antennae in red, head capsule in orange, labrum in yellow, mandibles in green, maxillae in blue, and labium in purple.

Instar II — In instar II and instar III, AI and AII gain secondary setae that are not present in instar I. The number of secondary setae is variable and differs between individuals and between antennae of the same individual. The microtrichia and microsetae on AII are sometimes lost in instars II and III.

Instar III — In instar III, the shape of AIII changes in many Catopina species, with straight edges and the segment being widest at the base of the SA. Several species that have additional setae in instar I, including *C. picipes*, have that shape in all instars.

Thorax

The thorax consists of the prothorax, mesothorax, and metathorax, each with a pair of legs. All three segments are similar, but the prothorax has a more extensive chaetotaxy. The legs consist of a coxa, a trochanter, a femur, a tibia, and a tarsungulus. The legs are also similar, though the hind legs are generally slightly longer.

Abdomen

The abdomen consists of 10 abdominal segments. Abdominal segments I–IX each have two sclerites, one dorsal and one ventral. The spiracle is located on the posterior margin of the dorsal sclerite, similar in position to those in the larvae of *Nodynus leucofasciatus* Lewis, 1879 (Coleoptera: Silphidae), where the epipleurite is nonetheless a distinct sclerite in the first abdominal segments (Zaitsev & Tokareva 2021). Here, the dorsal sclerite seems to result from the merging of the tergite, the precoxa, and the epipleurite (see Deuve 2018). The first eight tergites are generally very similar to each other in chaetotaxy, though the shape and length of setae in the posterior row can differ. The chaetotaxy of the sternites is relatively conserved across species. Abdominal segment IX has a different, simpler chaetotaxy but also has a pair of urogomphi and a pair of paracercal setae (Dl3). Abdominal segment X is reduced even further and ends in an anal membrane.

Urogomphi. *Instar I* — The urogomphi consist of two segments (urogomphomeres), URI and URII. Across Cholevinae, the chaetotaxy of urogomphomere I is fairly conserved, and the main variation comes down to the relative length of the setae and the relative position of the medial dorsolateral seta, which can be located dorsally or laterally, from the proximal half to the distal end of the segment. In addition to the medial dorsolateral seta, most species have seven other setae: five proximal setae, of which three dorsal, one lateral, and one ventral; and two distal setae, one dorsal and one ventral. An exception are the Ptomaphagini, which have a shorter urogomphomere I with only six setae, and some of the Leptodirini, which also can have reduced urogomphi. In addition to the eight setae, urogomphomere I generally has five campaniform sensilla, all dorsolateral: two proximal, one medial, and two distal. A known exception occurs in Anemadini, where an elliptical structure similar to the medial sensillum can be found in largely the same location, albeit more distal; whether this structure is homologous to the medial sensillum is unclear. The two distal sensilla are usually adjacent, lined up in the direction of the urogomphomere, with the more distal of the pair appearing to be located on urogomphomere II. In all cited literature, both are considered to be located on urogomphomere I. Whereas Ptomaphagini do have all five campaniform sensilla, not all Leptodirini do, even in the less specialized species (Deleurance-Glaçon 1963). The chaetotaxy of urogomphomere II is trivial, consisting of a single apical seta in almost all species, bar a few specialized troglobitic species in Leptodirini.

Instar II and III — The chaetotaxy of URI and URII is generally conserved in later instars, though the relative lengths of the medial dorsolateral seta and the ventral distal seta may differ.

Key to the tribes of Cholevinae larvae

Adapted from Zwick (1978). Leptodirini was added based on various descriptions of larvae across several genera (Deleurance-Glaçon 1963, Adamczyk et al. 2011). Oritocatopini could not be added based on the description by Paulian (1937, 1941). The larval morphology of Sciaphyini and Eucatopini is not known, and so the two tribes are not included in the key.

1. Apex of mandible long, curved, and pointed; inner edge of mandible clearly concave (Figs 48–54) 2
– Apex of mandible different; inner edge of mandible straight, not with a singular notch wider than the apex of the mandible (Figs 5, 24–26) 5
2. URI shorter or barely longer than abdominal segment X, excluding the anal membrane … 3
– URI at least 1.5 times as long as abdominal segment X .... Cholevini (Cholevina)
3. URI with 6 setae. URI at most 2 times as long as wide, URII 4–5 times as long as URI. Prostheca frayed, bristled........... Ptomaphagini
– URI with 8 setae, or URI absent. URII variable or absent. Prostheca tooth-like, simple or with 1–3 teeth, or absent 4
4. AIII with 2 apical sensilla, 1 subapical campaniform sensillum, and 4 setae. Prostheca tooth-like. Retinaculum absent. URI short but slender. URII at most 3 times as long as URI .... Cholevini (Catopina, L1)
– AIII with 2 apical sensilla, 1 subapical often pigmented setiform sensillum, and 4 or more setae. Larvae variable, morphology in various stages of reduction. Prostheca absent, or tooth-like with 1–3 teeth. Retinaculum only on right mandible or absent, in some species

on both mandibles. Some species with URI short but slender, some with URI reduced with the base much wider than the apex, and in some species URI completely absent .... Leptodirini

5. URI at most 1.5 times as long as abdominal segment X 6
– URI 2–3 times as long as abdominal segment X .... Cholevini (Catopina, *Dreposcia* Jeannel, 1922)
6. URII 3–5 times as long as URI. Mandibles asymmetrical, like Fig. 5 .... Anemadini (Nemadina, *Nemadus* Thomson, 1867)
– URII less than 3 times as long as URI. Mandibles like Figs 48, 49 .... Cholevini (Catopina, L2/L3)

Anemadini

Nemadina

Nemadus Thomson, 1867

Nemadus (*Nemadus*) *colonoides* (Kraatz, 1851)

(Fig. 5)
Catops colonoides Kraatz, 1851.
Nemadus colonoides (Kraatz, 1851): Pinto 2015.

Material examined. Germany [8 ex.]: Berlin, Berlin Zoo, x.1968, 2 ex. (RMNH.INS.5069515, RMNH.INS.5069517); 1968, 6 ex. (RMNH.INS.5069516).

Diagnosis
Inner edge of the mandible straight, mandibles asymmetrical (Fig. 5). URI at most 1.5 times as long as abdominal segment X, URII 3–5 times as long as URI. **Instar I:** Prostheca pointed, simple.

Distribution
Throughout Europe.

Cholevini Kirby, 1837

Catopina Chaudoir, 1845

Diagnosis
AIII with 2 apical sensilla and 4 setae, as well as 1 subapical campaniform sensillum. URI at most 1.5 times as long as abdominal segment X. URI with 8 setae. URII at most 3 times as long as URI. Apex of mandible long, curved, and pointed, and inner edge of mandible concave (L1); or inner edge of mandible straight (L2, L3). In L3, the galea is reduced from a double fringe to a simple brush shape (Fig. 31) or a singular fringe.

Key to the species of larval instar I of Catopina
The phylogeny of Cholevini species presented in 2016 (Schilthuizen et al. 2016) has been used as a rough guideline for the construction of this key, though the exact structure has been changed to improve the usability.

1. URI 2–3 times as long as abdominal segment X. URI ventrally with many small setae (Fig. 6). Apex of mandible short; inner edge of mandible straight … *Dreposcia umbrina* (Erichson, 1837)
– URI does not extend or barely extends beyond abdominal segment X. URI ventrally with two setae (Figs 7–11). Apex of mandible long; inner edge of mandible concave 2
2. Medial seta on URI long, 0.4–0.6 times as long as URI. AI without setae (Figs 32, 35)......... 3
– Medial seta on URI less than 0.4 times as long as URI (Figs 7–11), or if more than 0.4 times as long as URI (*Catops tristis* (Panzer, 1794)), then with a seta on AI (Fig. 36) 6

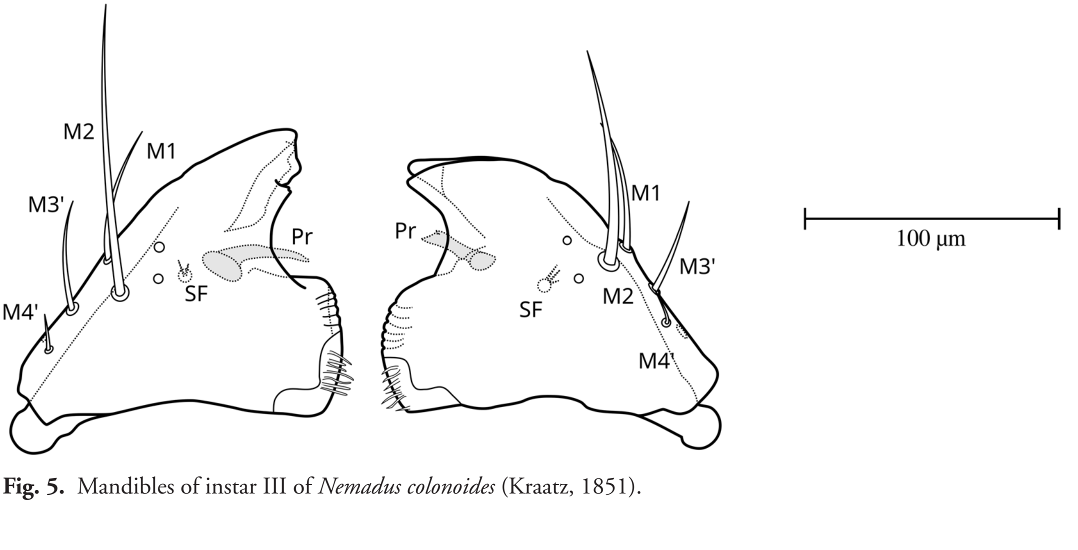
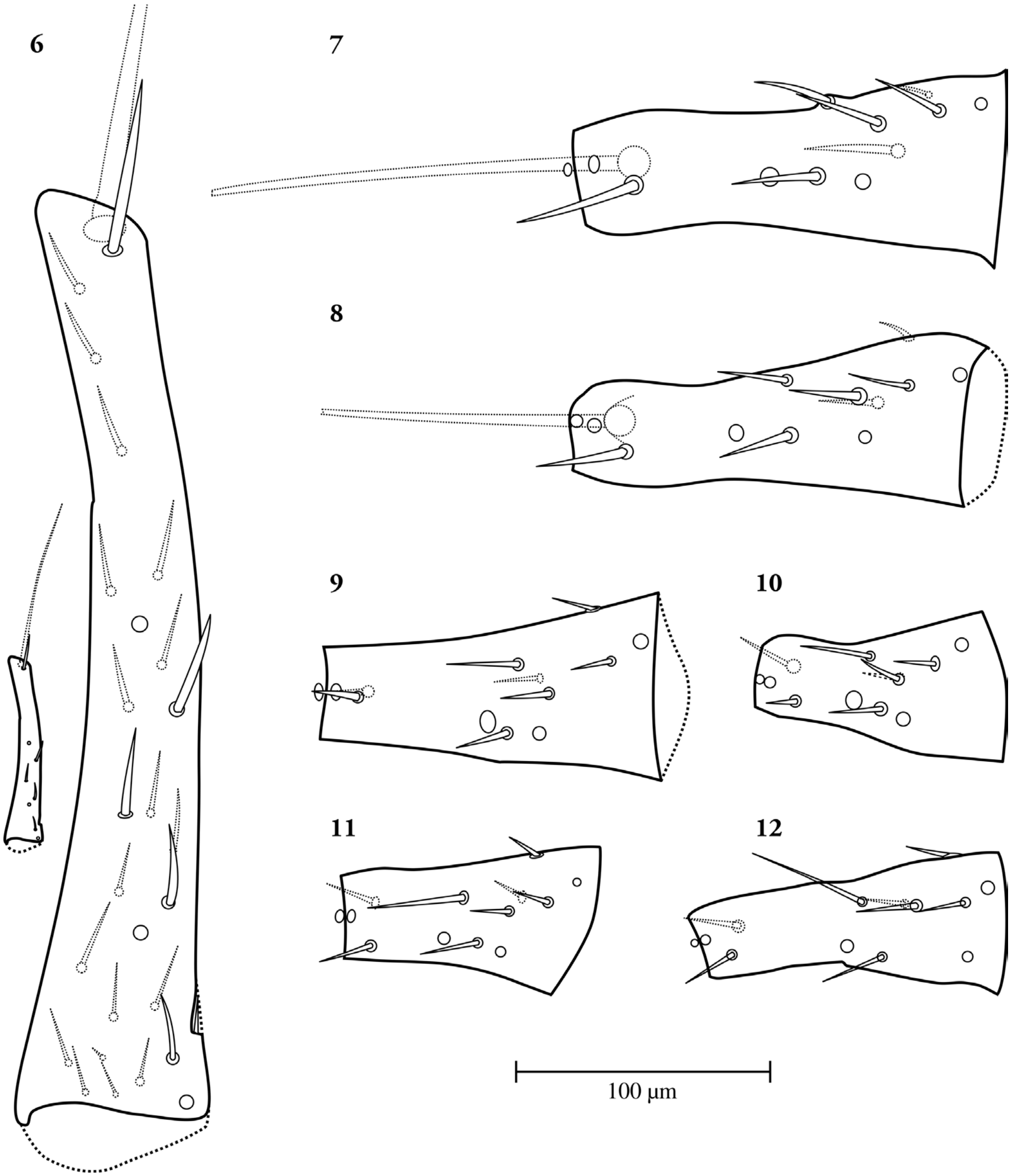


Fig. 5. Mandibles of instar III of *Nemadus colonoides* (Kraatz, 1851).

3. Subapical, ventral seta on URI much longer, 0.8–1 times as long URI. Position of the middle c.s. usually relatively distal. Posterior tibia 170–190 µm… *Catops morio* (Fabricius, 1787)
– Subapical, ventral seta on URI much shorter, 0.15–0.5 times as long as URI. Position of the middle c.s. variable.............................4

4. Larger species, posterior tibia 200–220 µm. Position of the middle c.s. usually relatively distal. Subapical, ventral seta on URI 0.25–0.5 times as long as URI.................................. *Catops subfuscus* Kellner, 1846
– Small species, posterior tibia 150–170 µm. Position of the middle c.s. usually relatively proximal.



Figs 6–12. Urogomphomere I of instar I. – 6, *Dreposcia umbrina* (Erichson, 1837), with 0.2x scale inset; 7, *Catops nigricans* (Spence, 1815); 8, *Catops fuscus* (Panzer, 1794); 9, *Apocatops nigrita* (Erichson, 1837); 10, *Catops grandicollis* Erichson, 1837; 11, *Fissocatops westi* (Krogerus, 1931); 12, *Sciodrepoides fumatus* (Spence, 1815).

Subapical, ventral seta on URI variable (*Sciodrepoides* Hatch, 1933)…………………5

5. Subapical, ventral seta on URI short, 0.15–0.25 times as long as URI……………………………… *Sciodrepoides fumatus* (Spence, 1815)

– Subapical, ventral seta on URI less short, 0.3–0.5 times as long as URI………………………… *Sciodrepoides watsoni* (Spence, 1815)

6. Tergites on each lateral half with more than 3 setae between anterior carina and P1–P5 of the posterior row (Figs 13, 15, 16); exact amount usually variable between tergites and left/right……………………………………7

– Tergites on each lateral half consistently with 3 setae between anterior carina and P1–P5 of the posterior row………………………………9

7. AI and AII polytrichic. P2 of tergites longer than P5. Usually not more than 7 setae between anterior carina and posterior row (Fig. 13) ……………*Catops picipes* (Fabricius, 1787)

– AI and AII with normal setae (Fig. 30). P2 of tergites shorter than P5 (Figs 15, 16)………8

8. 4–7, usually 5–6 setae between anterior carina and posterior row (Fig. 15). P2 is 0.3–0.5 times as short as P5. P1 and P2 are frayed for one third of the length. Antennomere II dorsally with multiple rows of microtrichia (Fig. 30) …………… *Catops grandicollis* Erichson, 1837

– 11–16, usually 13–14 setae between anterior carina and posterior row (Fig. 16). P2 is 0.6–0.7 times as short as P5. P1 and P2 are barely frayed. Antennomere II dorsally without multiple rows of microtrichia ………………………… *Catops kirbyi* (Spence, 1815)

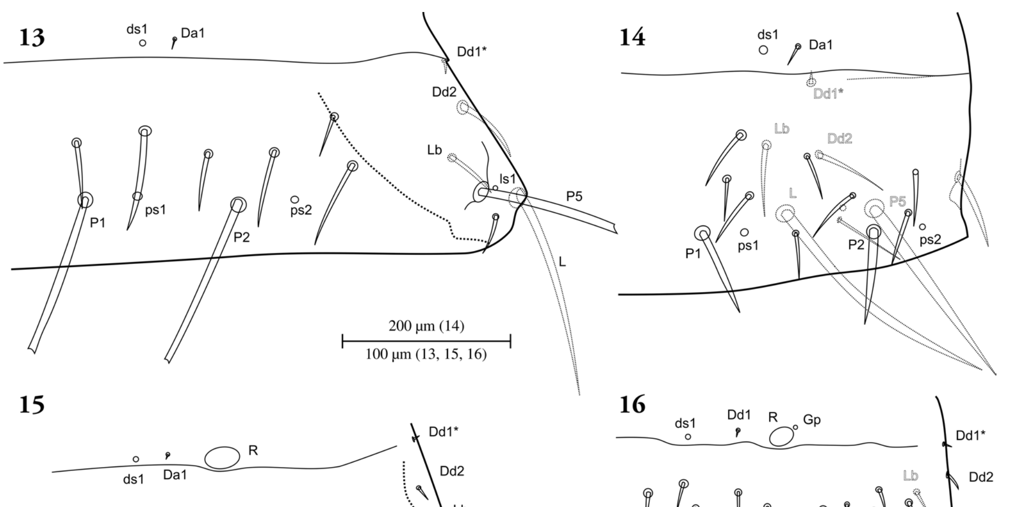
9. Antennomere II with microsetae (Fig. 34). Subapical, ventral seta on URI long, 0.5–1 times as long as URI (Figs 7, 8). Setae Da2–Dc2 on abdominal tergites tubular, with flat or frayed ends: *Catops fuscus*-group ……… 10

– Antennomere II without microsetae (Figs 27–29, 33, 36, 37). Subapical, ventral seta on URI much shorter, up to 0.45 times as long as URI (Figs 9, 11). Setae Da2–Dc2 on abdominal tergites pointed, sometimes shortly frayed; not tubular……………………………………13

10. P1 of tergites shorter than or barely as long as the distance to the anterior carina of the same tergite. Setae P1–P5 with nearly flat ends, only shortly frayed. No seta on AI ……………………………… *Catops nigriclavis* Gerhardt, 1900

– P1 of tergites longer than the distance to the anterior carina of the same tergite. Setae P1–P5 with frayed ends. AI variable …… 11

11. Smaller species, antennomere II 170–185 µm, posterior tibia 0.26 ± 0.01 mm. No seta on AI …………………*fuliginosus* Erichson, 1837

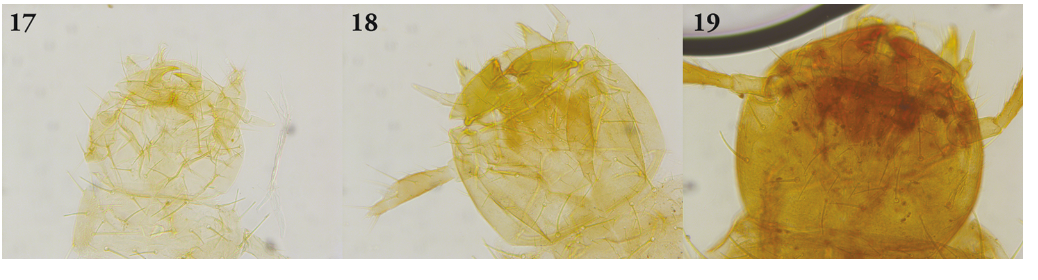


Figs 13–16. Right half of tergite V of instar I. Certain elements (lateral edge of the tergite, R, Gp) were omitted from the figure when they were not seen, but this does not necessarily imply absence. – 13, *Catops picipes* (Fabricius, 1787); 14, *Dreposcia umbrina* (Erichson, 1837), folded in half; 15, *Catops grandicollis* Erichson, 1837; 16, *Catops kirbyi* (Spence, 1815).

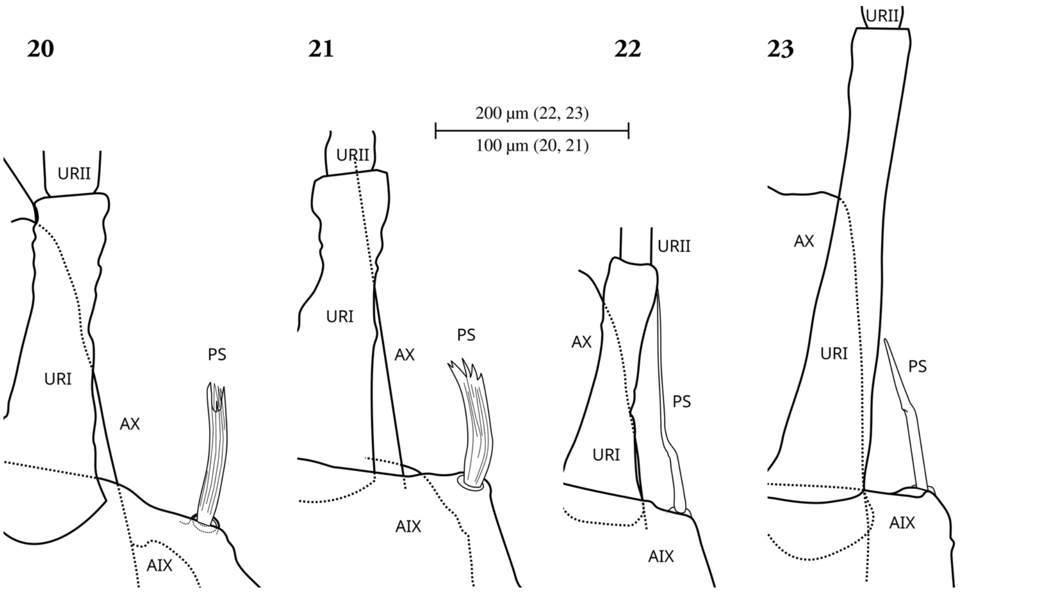
– Larger species, antennomere II longer than 185 µm, posterior tibia longer than 0.29 mm. AI variable 12
12. No seta on AI. Smaller species, antennomere II 185–205 µm, posterior tibia 0.31 ± 0.01 mm .... *Catops fuscus* (Panzer, 1794)
– AI with seta (Fig. 34). Larger species, antennomere II 215–225 µm, posterior tibia 0.36 ± 0.01 mm ...... *Catops nigricans* (Spence, 1815)
13. AI with seta. Larger species, posterior tibia 200–250 µm 14
– AI without seta. Smaller species, posterior tibia 120–200 µm 16
14. Medial seta on URI short, 0.15–0.3 times as long as URI. Setae Da2–Dc2 on abdominal tergites tubular, with flat or frayed ends. P2 about as long as P5 .... *Catops chrysomeloides* (Panzer, 1798)
– Medial seta on URI longer, 0.3–0.6 times as long as URI. Setae Da2–Dc2 on abdominal tergites with pointed ends. P2 shorter than P5 15
15. P2 on abdominal tergite shorter, 0.3–0.5 times as long as the space between the anterior carina and the posterior edge of the tergite. Antennomere III relatively short, 50–65 µm, 0.3–0.4 times as long as antennomere II (Fig. 27). Posterior tibia longer, 225–245 µm .... *Apocatops nigrita* (Erichson, 1837)
– P2 on abdominal tergite longer, 0.75–1 times as long as the space between the anterior carina and the posterior edge of the tergite. Antennomere III relatively long, 65–75 µm, 0.35–0.5 times as long as antennomere II (Fig. 36). Posterior tibia shorter, 200–225 µm .... *Catops tristis* (Panzer, 1794)
16. Antennomere II 90–110 µm (Fig. 29), posterior tibia shorter than 150 µm (usually 120–140 µm) .... *Catops coracinus* Kellner, 1846
– Antennomere II at least 120 µm (Figs 33, 37), posterior tibia longer than 150 µm (usually 160–180 µm) 17
17. Medial seta on URI is 0.1–0.2 times as long as URI*Catops neglectus* Kraatz, 1852
– Medial seta on URI is 0.3–0.4 times as long as URI (Fig. 11) .... *Fissocatops westi* (Krogerus, 1931)

Key to the species of larval instars II and III of Catopina

1. 1. URI at most 1.5 as long as abdominal segment X. URI ventrally with two setae (Figs 7–11) ... 2
– URI 2–3 as long as abdominal segment X. URI ventrally with many small setae (Fig. 6) .... *Dreposcia umbrina* (Erichson, 1837)
2. Prementum with two pairs of setae and one pair of campaniform sensilla 3
– Prementum with two pairs of setae and no sensilla (Fig. 31) .... *Catops morio* (Fabricius, 1787)
3. Medial seta on URI long, 0.38–0.6 times as long as URI. Tergites on each lateral half with a posterior row consisting of 5 large setae and 6 smaller setae 4
– Medial seta on URI short, up to 0.37 times as long as URI. If longer, posterior row consisting of 4 large setae (*Catops tristis* (Panzer, 1794)) 6
4. Tergites on each lateral half above the posterior row with 18 setae, arranged in two rows of 9 .... *Catops subfuscus* Kellner, 1846
– Tergites on each lateral half above the posterior row with 20–30 (L2) or 30–40 (L3) setae, not in two neat rows: *Sciodrepoides* Hatch, 1933 5
5. Faint (L2) or clear (L3) brown spot on head (Figs 18, 19). URII about 1.5 times as long as URI. Galea usually extends beyond tip of maxilla ...... *Sciodrepoides watsoni* (Spence, 1815)
– No brown spot on head. URII nearly 2 times as long as URI. Galea usually does not extend beyond tip of maxilla .... *Sciodrepoides fumatus* (Spence, 1815)
6. AI with 4–6 setae. MPII with 2 setae. Malae with 4 lacinia and dorsally 2–3 additional setae. Mandible with 4–5 setae. Subapical ventral seta short 7



Figs 17–19. Head of *Sciodrepoides watsoni* (Spence, 1815). – 17, Instar I; 18, Instar II; 19, Instar III.



Figs 20–23. Paracercal setae of instar III. – 20, *Catops grandicollis* Erichson, 1837; 21, *Catops kirbyi* (Spence, 1815); 22, *Catops morio* (Fabricius, 1787); 23, *Catops picipes* (Fabricius, 1787).

– AI polytrichic, with 20+ setae. MPII with 4–5 setae. Malae with 7 lacinia and dorsally 4+ additional setae. Mandible with 6 setae. Labrum with additional pair of setae dorsally. Subapical ventral seta long .... *Catops picipes* (Fabricius, 1787)

7. Paracercal setae less than half as long as URI, straight or curved, with frayed ends (Figs 20, 21) 8

– Paracercal setae shorter or longer than URI, the base somewhat flattened and then bent, with pointed ends (cf. Figs 22, 23) 9

8. Tergite on each lateral half with a posterior row of 4 major and 4 minor setae, about 20–25 setae on the rest of the tergite half. Subapical ventral seta on URI relatively proximal .... *Catops grandicollis* Erichson, 1837

– Tergite on each lateral half with a posterior row of 4 major and 9 minor setae, about 40–50 setae on the rest of the tergite half .... *Catops kirbyi* (Spence, 1815)

9. Subapical, ventral seta on URI long, at least 0.3 times as long as URI (cf. Figs 7, 8): *Catops fuscus*-group 10

– Subapical, ventral seta on URI short, at most 0.25 times as long as URI (cf. Figs 9, 11) ... 13

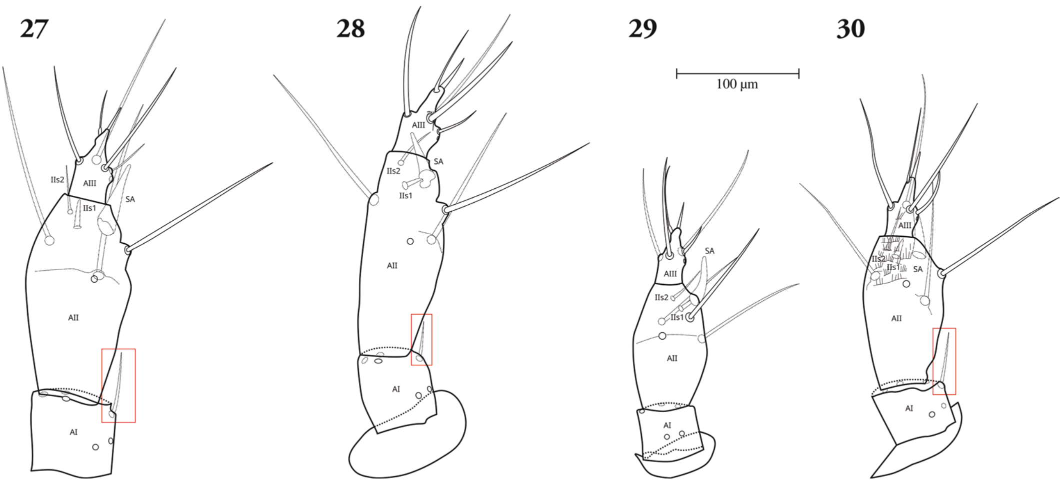
10. AI with 11+ setae. Tergites on each lateral half between the posterior row and anterior carina with more than 40 setae .... *Catops nigriclavis* Gerhardt, 1900

– AI with 7–10 setae. Tergites on each lateral half between the posterior row and anterior carina with less than 30 setae 11

11. Mandible with 3 larger and 3 smaller setae. Larger: AII is 310–330 µm (L2) or 380–400 µm (L3) and posterior tibia is 490–510 µm (L2) or 675–700 µm (L3) .... *Catops nigricans* (Spence, 1815)

– Mandible with 3 larger and 4 smaller setae. Smaller: AII at most 290 µm (L2) or 360 µm (L3) and posterior tibia is at most 440 µm (L2) or 600 µm (L3) 12

Figs 24–26. Mandibles of instar III. – 24, *Catops coracinus* Kellner, 1846; 25, *Catops morio* (Fabricius, 1787); 26, *Dreposcia umbrina* (Erichson, 1837).



Figs 27–30. Antennae of instar I. Red rectangles indicate the diagnostic setae. – 27, *Apocatops nigrita* (Erichson, 1837); 28, *Catops chrysomeloides* (Panzer, 1798); 29, *Catops coracinus* Kellner, 1846; 30, *Catops grandicollis* Erichson, 1837.

12. Larger: AII is 270–290 µm (L2) or 340–360 µm (L3) and posterior tibia is 420–440 µm (L2) or 550–600 µm (L3) ………………… ………………… *Catops fuscus* (Panzer, 1794)
– Smaller: AII is 240–260 µm (L2) or 300–310 µm (L3) and posterior tibia is 340–370 (L2) or 440–480 µm (L3) ……………………… ………….. *Catops fuliginosus* Erichson, 1837
13. Larger: AII is longer than 185 µm (L2) or longer than 220 µm (L3) and posterior tibia longer than 260 µm (L2) or longer than 335 µm (L3) …… 14
– Smaller: AII is shorter than 160 µm (L2) or shorter than 200 µm (L3) and posterior tibia shorter than 240 µm (L2) or shorter than 325 µm (L3) ………………………………… 16
14. Tergites on each lateral half with a posterior row with 5 major setae. P5 shorter than P2 ……… *Catops chrysomeloides* (Panzer, 1798)
– Tergites on each lateral half with a posterior row with 4 major setae. P5 longer than all other seta in the posterior row ……………… 15
15. Tergites on each lateral half between the posterior row and anterior carina with more than 35 setae. URII more than 2.5 times as long as URI ……….. *Apocatops nigrita* (Erichson, 1837)
– Tergites on each lateral half between the posterior row and anterior carina with less than 30 setae. URII less than 2.3 times as long as URI ………………… *Catops tristis* (Panzer, 1794)
16. Medial dorsal seta on URI very short, less than 0.2 times as long as URI. Small, posterior tibia 150–180 µm (L2) or 230–250 µm (L3) ……………… *Catops coracinus* Kellner, 1846
– Medial dorsal seta on URI longer, at least 0.25 times as long as URI ……………………… 17
17. Apical seta on urogomphomere II longer, 65–75 µm, more than 0.2 times as long as urogomphomere II ………………………… ………………… *Catops neglectus* Kraatz, 1852
– Apical seta on urogomphomere II shorter, up to 55 µm, less than 0.2 times as long as urogomphomere II ………………………… ………….. *Fissocatops westi* (Krogerus, 1931)

Apocatops Zwick, 1968

Apocatops nigrita (Erichson, 1837)

(Figs 9, 27)
Catops nigrita Erichson, 1837
Apocatops nigrita (Erichson, 1837): Renkens 2015

Material examined: Germany [16 ex.]: Berlin, Berlin-Grunewald, 1963–1964, 1 ex. (RMNH.INS.5069650); Hessen, Schlitz, x.1965, 2 ex. (RMNH.INS.967963); 1965, 11 ex. (RMNH.INS.967949, RMNH.INS.967960); 1966, 1 ex. (RMNH.INS.5069649); 1960s, 1 ex. (RMNH.INS.5069660).

Diagnosis

Instar I: Antennomere I with a seta (Fig. 27). Antennomere II with typical setae, without microsetae (Fig. 27). P1–P5 on tergites are pointed, but with short frays, and are relatively short, with P2 0.3–0.5 times as long as the tergite; Da2 on tergites pointed. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi slightly longer than

Fig. 31. Dorsal view of maxillae and labium of instar III of *Catops morio* (Fabricius, 1787).

typical, 0.3–0.4 times as long as urogomphomere I (Fig. 9). Distal ventral seta short, 0.1–0.2 times as long as urogomphomere I (Fig. 9).
Instar II & III: Antennomere I with 8 setae. Mandible with 5 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with more than 35 setae. Medial dorsolateral seta on urogomphi 0.15–0.3 times as long as urogomphomere I. Distal ventral seta short, 0.1–0.2 times as long as urogomphomere I. Urogomphomere I 0.3–0.4 times as long as urogomphomere II.

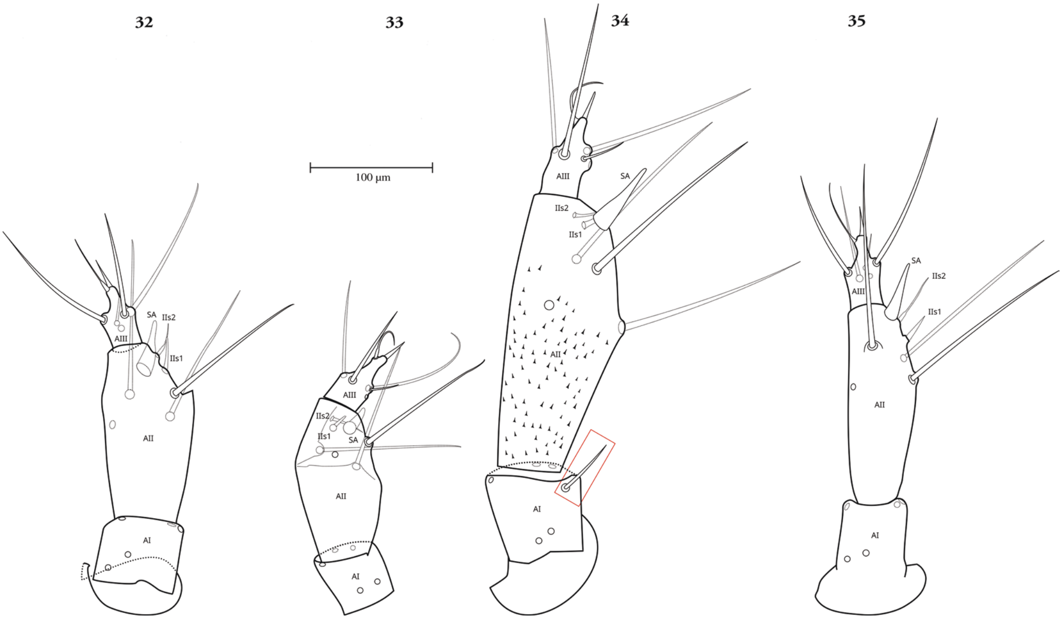
Distribution
Throughout Europe.

Catops Paykull, 1798

Catops chrysomeloides (Panzer, 1798)
(Fig. 28)
Helops chrysomeloides Panzer, 1798
Catops chrysomeloides (Panzer, 1789): Renkens 2015

Material examined: Germany [11 ex.]: Hessen, Schlitz, 1965, 4 ex. (RMNH.INS.5069628, RMNH.INS.967933); xi.1965, 4 ex. (RMNH.INS.967954); Rheinland-Pfalz, Ingelheim, viii.1970–v.1971, 3 ex. (RMNH.INS.967957); **Netherlands** [7 ex.]: Zuid-Holland, Oostvoorne, n.d., 7 ex. (RMNH.INS.5069544, RMNH.INS.5069549, RMNH.INS.5069551, RMNH.INS.5069552, RMNH.INS.5069553, RMNH.INS.5069554).

Diagnosis
Instar I: Antennomere I with a seta (Fig. 28). Antennomere II with typical setae, without microsetae (Fig. 28). P1–P5 on tergites are frayed, and are relatively short, P2 0.5–0.7 times as long as the tergite; Da2 on tergites tubular. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi short, 0.15–0.3 times as long as urogomphomere I. Distal ventral seta short, 0.15–0.3 times as long as urogomphomere I.
Instar II & III: Antennomere I with around 6 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 20–30 setae. Medial dorsolateral seta on urogomphi 0.15–0.3 times as long as urogomphomere I. Distal ventral seta short, 0.1–0.25 times as long as urogomphomere I. Urogomphomere I 0.5–0.65 times as long as urogomphomere II.



Figs 32–35. Antennae of instar I. Red rectangles indicate the diagnostic setae. – 32, *Catops morio* (Fabricius, 1787); 33, *Catops neglectus* Kraatz, 1852; 34, *Catops nigricans* (Spence, 1815); 35, *Catops subfuscus* Kellner, 1846.

Distribution
Central, western, southern, and eastern Europe, up to Denmark; Turkey; Armenia.

Catops coracinus Kellner, 1846

(Figs 24, 29)
Catops (Catops) coracinus Kelln[er]. [, 1846]: Beier and Strouhal 1928
Catops coracinus (Kellner, 1846) [sic]: Renkens 2015

Material examined: Germany [13 ex.]: Hessen, Schlitz, 1966, 11 ex. (RMNH.INS.5069630, RMNH.INS.967932, RMNH.INS.967951, RMNH.INS.967955, RMNH.INS.967964); Hessen, Schlitz, Eisenberg, Altes Gerölle, 4.vii.1971, 1 ex. (RMNH.INS.5069629); Hessen, Schlitz, Tempelberg, 21.viii.1966, 1 ex. (RMNH.INS.947578).

Diagnosis
Instar I: Antennomere I without setae (Fig. 29). Antennomere II with typical setae, without microsetae (Fig. 29). P1–P5 on tergites are frayed, and are relatively short, P2 0.4–0.5 times as long as the tergite; Da2 on tergites pointed. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi short, 0.15–0.25 times as long as urogomphomere I. Distal ventral seta short, 0.15–0.3 times as long as urogomphomere I.

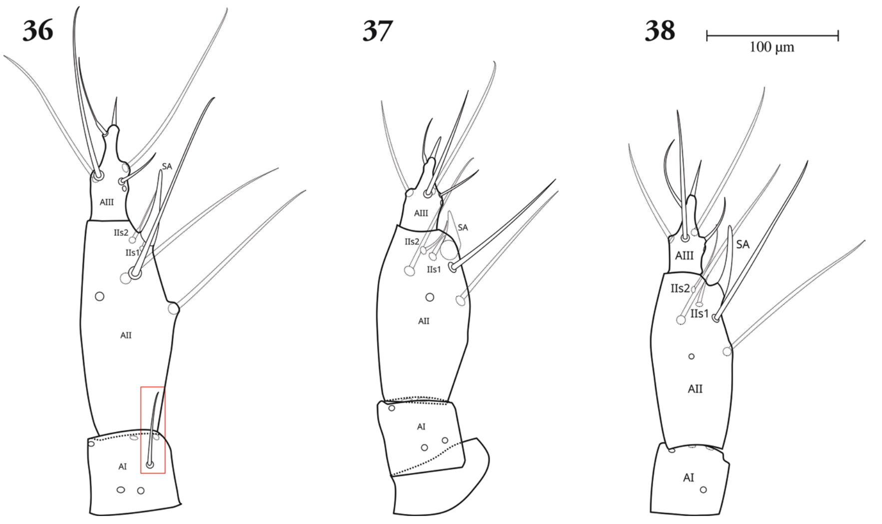
Instar II & III: Antennomere I with 4 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 20–25 setae. Medial dorsolateral seta on urogomphi 0.1–0.15 times as long as urogomphomere I. Distal ventral seta short, 0.1–0.2 times as long as urogomphomere I. Urogomphomere I 0.45–0.65 times as long as urogomphomere II.

Distribution
Throughout Europe; North Africa; Middle East; Central Asia.

Catops fuliginosus Erichson, 1837

Catops fuliginosus Erichson [, 1837]: Paulian 1941
Catops fuliginosus (Erichson, 1837) [sic]: Renkens 2015

Material examined: Germany [43 ex.]: Berlin, Berlin-Grunewald, 1963–1964, 3 ex. (RMNH.INS.5069633, RMNH.INS.5069634, RMNH.INS.5069635); 30.ix.–8.x.1963, 1 ex. (RMNH.INS.947581); x.1963, 6 ex. (RMNH.INS.947579, RMNH.INS.947585); n.d., 2 ex. (RMNH.INS.947584); Berlin, Berlin-Grunewald, Jagen 86, x.1963, 17 ex. (RMNH.INS.947583, RMNH.INS.947586, RMNH.INS.947587, RMNH.INS.947588); Berlin, Berlin-Tiefwerder, 29.ii.1964, 1 ex. (RMNH.INS.947582); Schleswig-Holstein,



Figs 36–38. Antennae of instar I. Red rectangles indicate the diagnostic setae. – 36, *Catops tristis* (Panzer, 1794); 37, *Fissocatops westi* (Krogerus, 1931); 38, *Sciodrepoides fumatus* (Spence, 1815).

Plön, iv.1965, 4 ex. (RMNH.INS.947589); unknown location, n.d., 9 ex. (RMNH.INS.947580, RMNH.INS.947590, RMNH.INS.947594, RMNH.INS.967977).

Diagnosis

Instar I: Antennomere I without setae. Antennomere II with microsetae, setae otherwise typical.

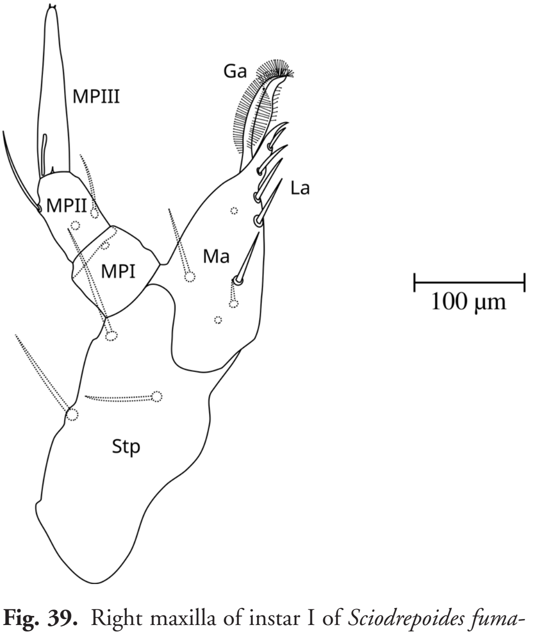


Fig. 39. Right maxilla of instar I of *Sciodrepoides fumatus* (Spence, 1815).

P1–P5 on tergites are frayed, and are typical, P2 0.75–1 times as long as the tergite; Da2 on tergites tubular. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi short, 0.2–0.25 times as long as urogomphomere I. Distal ventral seta long, 0.5–0.8 times as long as urogomphomere I.

Instar II & III: Antennomere I with 7–10 setae. Mandible with 7 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 25–30 setae. Distal ventral seta long.

Habitat

Found in mouse nests.

Distribution

Throughout Europe; Middle East.

Catops fuscus fuscus (Panzer, 1794)

(Fig. 8)

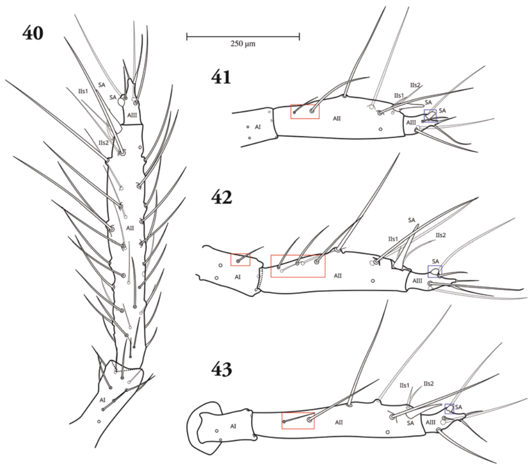
Helops fuscus Panzer, 1794

Choleua [sic] *fusca* Panz. [(Panzer, 1794)]: Schiødte 1861

Catops fuscus Panzer [(Panzer, 1794)]: Xambeu 1899

Catops fuscus (Panzer, 1794): Renkens 2015

Material examined: Germany [34 ex.]: Berlin, Berlin-Schöneberg, x.1963, 1 ex. (RMNH.INS.967925); ix.–xi.1963, 22 ex. (RMNH.INS.947600, RMNH.INS.967928); x.–xi.1963, 2 ex. (RMNH.INS.967927); unknown location, n.d., 9 ex. (RMNH.INS.947590, RMNH.INS.947594, RMNH.INS.967926, RMNH.INS.967977).



Figs 40–43. Antennae of instar I. Red rectangles indicate the diagnostic setae, blue rectangles indicate the SA on AIII. – 40, *Choleva fagniezi* Jeannel, 1922; 41, *Choleva agilis* (Illiger, 1798); 42, *Choleva lederiana* Reitter, 1902; 43, *Choleva oblonga* Latreille, 1807.

Diagnosis

Instar I: Antennomere I without setae. Antennomere II with microsetae, setae otherwise typical. P1–P5 on tergites are frayed, and are typical, P2 0.7–1 times as long as the tergite; Da2 on tergites tubular. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi short, 0.1–0.25 times as long as urogomphomere I (Fig. 8). Distal ventral seta long, 0.6–0.9 times as long as urogomphomere I (Fig. 8).
Instar II & III: Antennomere I with 7–10 setae. Mandible with 7 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 25–30 setae. Distal ventral seta long.

Distribution

Throughout Europe; Western Siberia.

Catops grandicollis Erichson, 1837

(Figs 9, 15, 20, 30)
Catops grandicollis (Erichson, 1837) [sic]: Renkens 2015

Material examined: Germany [15 ex.]: Hessen, Schlitz, 1965, 6 ex. (RMNH.INS.5069638, RMNH.INS.967939); 1960s, 2 ex. (RMNH.INS.5069636, RMNH.INS.5069637); n.d., 7 ex. (RMNH.INS.967937, RMNH.INS.967938).

Diagnosis

Instar I: Antennomere I with a seta (Fig. 30). Antennomere II dorsally with multiple rows of microtrichia, setae otherwise typical (Fig. 30). P1–P5 on tergites are short, broad, and frayed for one third of the length, P2 0.05–0.2 times as long as the tergite; Da2 on tergites pointed (Fig. 15). Between the anterior carina and P1–P5 there are 4–7 setae, usually 5–6, in a single row (Fig. 15). Medial dorsolateral seta and distal ventral seta on urogomphi short (Fig. 10).
Instar II & III: Antennomere I with 4–6 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 20–25 setae. Paracercal setae curved, not bent. Medial dorsolateral seta on urogomphi short. Distal ventral seta short.

Distribution

Throughout Europe; Turkey.

Catops kirbyi kirbyi (Spence, 1815)

(Figs 16, 21)
Choleva Kirbii Spence, 1815
Catops kirbyi (Spence, 1815): Renkens 2015

Material examined: Germany [19 ex.]: Hessen, Schlitz, x.1965, 12 ex. (RMNH.INS.967935); 1965, 2 ex. (RMNH.INS.5069639, RMNH.INS.967934); 15.ii.1965, 1 ex. (RMNH.INS.5069659); 27.x.1965, 1 ex. (RMNH.INS.5069640); n.d., 3 ex. (RMNH.INS.967936).

Diagnosis

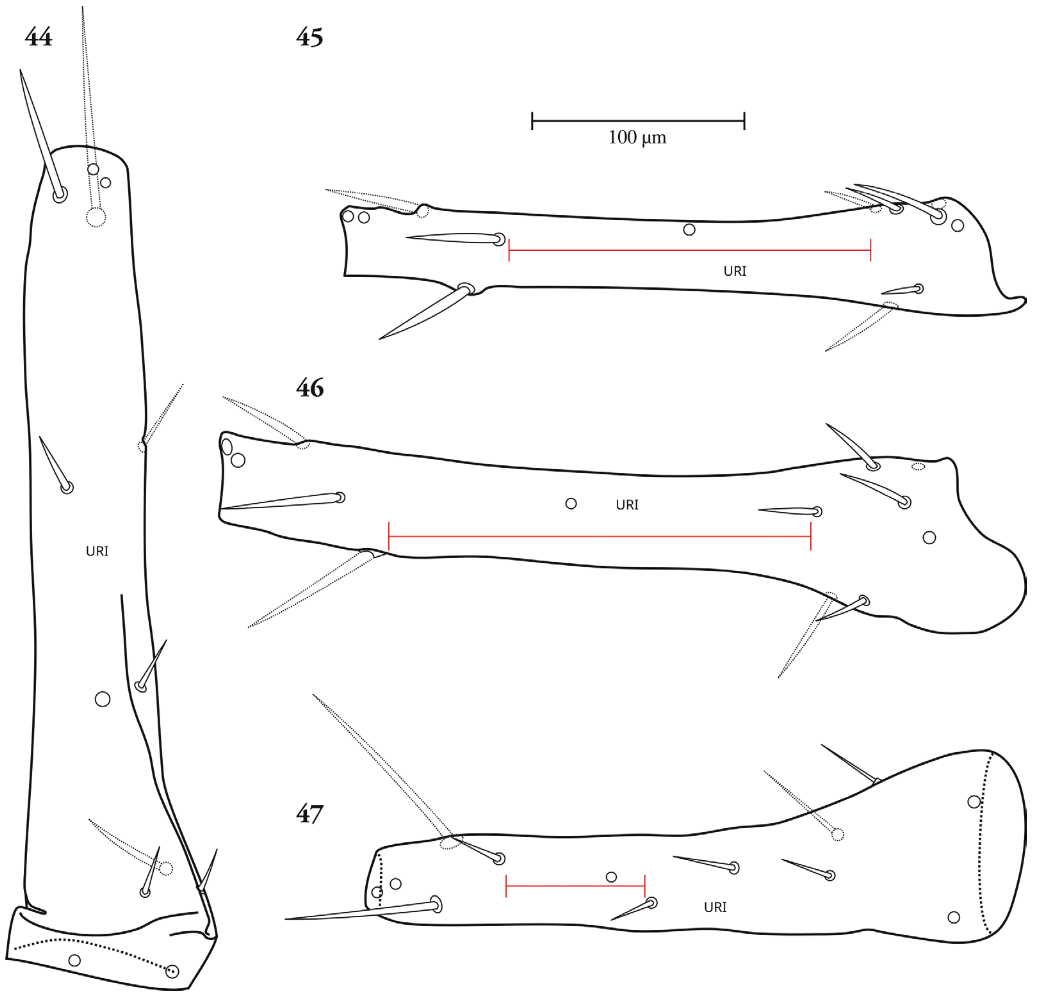
Instar I: Antennomere I with a seta. Antennomere II with typical setae, no microsetae. P1–P5 on tergites are short, broad, barely frayed, P2 0.05–0.2 times as long as the tergite; Da2 on tergites pointed. Between the anterior carina and P1–P5 there are 11–16 setae, usually 13–14, in two rows. Medial dorsolateral seta and distal ventral seta on urogomphi short.
Instar II & III: Antennomere I with 4–6 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 40–50 setae. Paracercal setae curved, not bent. Medial dorsolateral seta on urogomphi short. Distal ventral seta short.

Distribution

Central, western, and southern Europe; Caucasus; Central Asia.

Catops morio (Fabricius, 1787)

(Figs 4, 22, 25, 31, 32)
Tritoma morio Fabricius, 1787
Catops morio (Fabricius, 1787): Renkens 2015



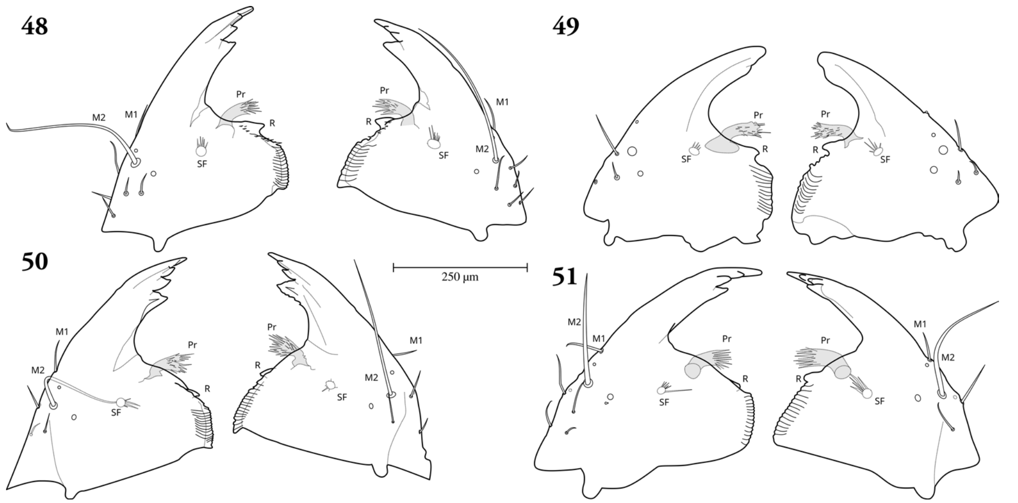
Figs 44–47. Urogomphomere I of instar I. Red lines indicate the gap between the most proximal 5 setae and the most distal 3 setae. – 44, *Choleva fagniezi* Jeannel, 1922; 45, *Choleva agilis* (Illiger, 1798); 46, *Choleva lederiana* Reitter, 1902; 47, *Choleva oblonga* Latreille, 1807.

Material examined: Germany [47 ex.]: Berlin, Berlin-Tiefwerder, x.1963, 38 ex. (RMNH.INS.967971, RMNH.INS.967972, RMNH.INS.967973, RMNH.INS.967975); x.–xi.1963, 2 ex. (RMNH.INS.947571, RMNH.INS.967970); x.1963–01.iii.1964, 1 ex. (RMNH.INS.5069642); Schleswig-Holstein, Plön, 1965, 1 ex. (RMNH.INS.5069641); vii.–x.1965, 4 ex. (RMNH.INS.967961, RMNH.INS.967974); unknown location, 1960s, 1 ex. (RMNH.INS.5069643); **Netherlands** [11 ex.]: Zuid-Holland, Leiden, 1980s, 8 ex. (RMNH.INS.5069564, RMNH.INS.5069565, RMNH.INS.5069568, RMNH.INS.5069569, RMNH.INS.5069575, RMNH.INS.5069579, RMNH.INS.5069580); Zuid-Holland, Leiden, Cronesteijn, n.d., 3 ex. (RMNH.INS.5069543, RMNH.INS.5069548).

Diagnosis

Instar I: Antennomere I without setae (Fig. 32). Antennomere II with typical setae, no microsetae (Fig. 32). P1–P5 on tergites are frayed, and of typical length, P2 0.8–1 times as long as the tergite; Da2 on tergites pointed. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta long, 0.4–0.6 times as long as urogomphomere I. Distal ventral seta also long, 0.8–1 times as long as urogomphomere I.

Instar II & III: Antennomere I with 6 setae. Mandible with 4 setae (Fig. 25). Maxillary palpomere II with 2 setae (Fig. 31). Tergites between posterior row and anterior carina with 18 setae. Medial dorsolateral seta on urogomphi 0.25–0.4 times as long as urogomphomere I. Distal ventral seta 0.35–0.55 times as long as urogomphomere I. Urogomphomere I 0.45–0.65 times as long as urogomphomere II.



Figs 48–51. Mandibles of instar III. – 48, *Choleva fagniezi* Jeannel, 1922; 49, *Choleva spadicea* (Sturm, 1839); 50, *Choleva oblonga* Latreille, 1807; 51, *Choleva lederiana* Reitter, 1902.

Distribution

Throughout Europe; Siberia; Central Asia.

Catops neglectus Kraatz, 1852

(Figs 2, 33)
Catops neglectus (Kraatz, 1852) [sic]: Renkens 2015

Material examined: Germany [5 ex.]: Hessen, Schlitz, 1966, 5 ex. (RMNH.INS.967945, RMNH. INS.967946).

Diagnosis

Instar I: Antennomere I without setae (Fig. 33). Antennomere II with typical setae, no microsetae (Fig. 33). P1–P5 on tergites have flat ends, are frayed, and relatively short, P2 0.5–0.7 times as long as the tergite; Da2 on tergites pointed. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta short, 0.1–0.2 times as long as urogomphomere I.

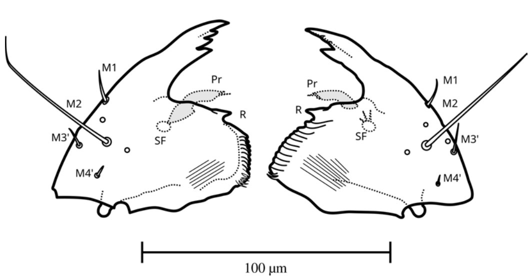


Fig. 52. Mandibles of instar II of *Nargus* sp.

Distal ventral seta also short, 0.1–0.25 times as long as urogomphomere I.
Instar II: Unknown.
Instar III: Antennomere I with 6 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 25–30 setae. Medial dorsolateral seta on urogomphi 0.3–0.4 times as long as urogomphomere I. Distal ventral seta 0.05–0.2 times as long as urogomphomere I. Urogomphomere I 0.6–0.7 times as long as urogomphomere II.

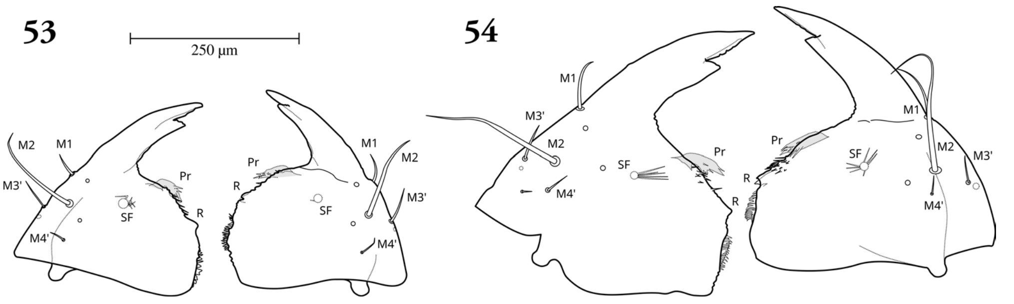
Distribution

Throughout Europe.

Catops nigricans (Spence, 1815)

(Figs 7, 34)
Choleva nigricans Spence, 1815
Catops nigricans Spence [(Spence, 1815)]: Xambeu 1900
Catops nigricans (Spence, 1815): Renkens 2015

Material examined: Germany [46 ex.]: Berlin, Berlin-Grunewald, 1963–1964, 1 ex. (RMNH. INS.5069644); x.1963, 22 ex. (RMNH. INS.947595); Berlin, Berlin-Grunewald, Jagen 86, x.1963, 8 ex. (RMNH.INS.947596, RMNH. INS.947598); 06.–16.x.1963, 2 ex. (RMNH. INS.947597); Hessen, Schlitz, 1960s, 2 ex. (RMNH.INS.5069645, RMNH.INS.5069646); unknown location, n.d., 11 ex. (RMNH. INS.947575, RMNH.INS.947590, RMNH. INS.947594, RMNH.INS.967930, RMNH.



Figs 53, 54. Mandibles of instar III. – 53, *Ptomaphagus medius* (Rey, 1889); 54, *Ptomaphagus varicornis* (Rosenhauer, 1847).

INS.967977); **Netherlands** [13 ex.]: Zuid-Holland, Leiden, 1980s, 7 ex. (RMNH.INS.5069581, RMNH.INS.5069582, RMNH.INS.5069583, RMNH.INS.5069584, RMNH.INS.5069585, RMNH.INS.5069586, RMNH.INS.5069587); Zuid-Holland, Leiden, Cronesteijn, xii.1988, 3 ex. (RMNH.INS.5069536); n.d., 3 ex. (RMNH.INS.5069542, RMNH.INS.5069547).

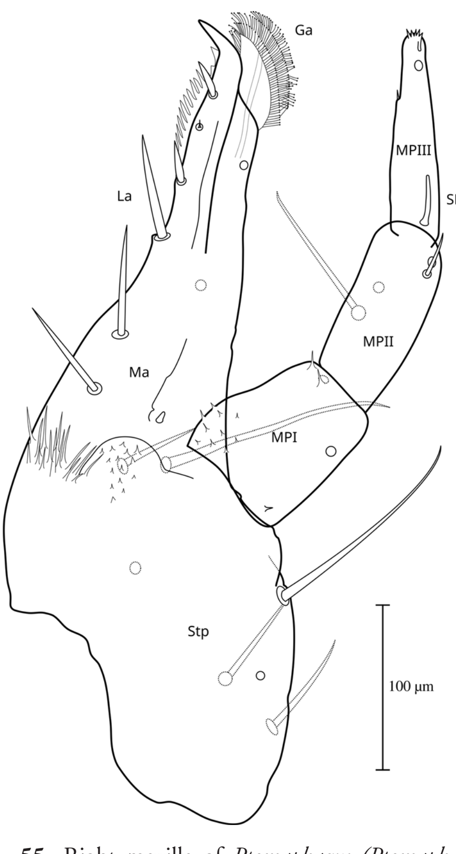


Fig. 55. Right maxilla of *Ptomaphagus (Ptomaphagus) varicornis* (Rosenhauer, 1847).

Diagnosis

Instar I: Antennomere I with a seta (Fig. 34). Antennomere II with microsetae, setae otherwise typical (Fig. 34). P1–P5 on tergites are frayed, and are typical, P2 about as long as the tergite; Da2 on tergites tubular. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi short, 0.15–0.25 times as long as urogomphomere I (Fig. 7). Distal ventral seta long, 0.8–1.1 times as long as urogomphomere I (Fig. 7).

Instar II & III: Antennomere I with 8–9 setae. Mandible with 6 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 20–30 setae. Distal ventral seta long.

Distribution

Central and western Europe; Northern Asia up to China.

Catops nigriclavis Gerhardt, 1900

Catops Dorni Reitter, 1913

Catops nigriclavis Gerhardt [, 1900]: Paulian 1941

Catops nigriclavis (Gerhardt, 1900) [sic]: Renkens 2015

Material examined: Germany [15 ex.]: Hessen, Schlitz, 1960s, 2 ex. (RMNH.INS.5069647, RMNH.INS.5069648); xi.1965, 6 ex. (RMNH.INS.947592, RMNH.INS.947593); 16.iii.1963, 1 ex. (RMNH.INS.947599); 30.x.1965, 2 ex. (RMNH.INS.5069631, RMNH.INS.5069632); 28.xi.1965, 3 ex. (RMNH.INS.967929); unknown location, n.d., 1 ex. (RMNH.INS.967976).

Diagnosis

Instar I: Antennomere I without setae. Antennomere II with microsetae, setae otherwise typical. P1–P5 on tergites have flat ends, are frayed, and are short, P2 about half as long as the tergite; Da2 on tergites tubular. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi

short, 0.10–0.25 times as long as urogomphomere I. Distal ventral seta long, 0.4–0.9 times as long as urogomphomere I.
Instar II & III: Antennomere I with 11 setae. Mandible with 7 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 40–50 setae. Distal ventral seta long.

Habitat
Found in mole nests.

Distribution
Throughout Europe; Armenia; Iran; Central Asia.

Catops picipes (Fabricius, 1787)

(Figs 13, 23)
Hydrophilus picipes Fabricius, 1787
Catops picipes (?) Fbr. [(Fabricius, 1787)]: Eichelbaum 1901
Catops picipes (Fabricius, 1787): Renkens 2015

Material examined: Germany [8 ex.]: Hessen, Schlitz, xi.1965, 1 ex. (RMNH.INS.947577); 12.i.1966, 1 ex. (RMNH.INS.967967); xi.1966, 2 ex. (RMNH.INS.967968, RMNH.INS.967969); 26.vii.1969, 1 ex. (RMNH.INS.5069651); Hessen, Schlitz, Institutsgarten, 31.x.1965–1965, 1 ex. (RMNH.INS.5069652); Hessen, Schlitz, Weg zur ”Kahl”, 20.x.1974, 1 ex. (RMNH.INS.5069653); Schleswig-Holstein, Hamburg, Dassendorf, 1.i.1965, 1 ex. (RMNH.INS.967966).

Diagnosis
Instar I: Antennomeres I and II polytrichic, each with multiple additional setae. Antennomere II also with microsetae. P1–P5 on tergites are long and frayed, P2 about as long as the tergite; Da2 on tergites variable, usually pointed but tubular on anterior tergites (Fig. 13). Between the anterior carina and P1–P5 there are 5–7 setae, usually 6–7, in a single row (Fig. 13). Medial dorsolateral seta on urogomphi short, distal ventral seta on urogomphi relatively longer than typical.
Instar II & III: Antennomere I with more than 20 setae. Mandible with 6 setae. Maxillary palpomere II with 4–5 setae. Tergites between posterior row and anterior carina with around 20 setae. Paracercal setae bent. Medial dorsolateral seta on urogomphi short. Distal ventral seta longer.

Habitat
Found in mouse nests, oak tree hollow.

Distribution
Central and western Europe.

Catops subfuscus Kellner, 1846

(Fig. 35)
Catops subfuscus (Kellner, 1846) [sic]: Renkens 2015

Material examined: Germany [19 ex.]: Hessen, Schlitz, 1966, 11 ex. (RMNH.INS.5069654, RMNH.INS.967965); 1960s, 2 ex. (RMNH.INS.5069655, RMNH.INS.5069656); Schleswig-Holstein, Plön, 1965, 6 ex. (RMNH.INS.967948, RMNH.INS.967956).

Diagnosis
Instar I: Antennomere I without setae (Fig. 35). Antennomere II with typical setae, no microsetae (Fig. 35). P1–P5 on tergites are frayed, and of typical length, P2 0.75–1 times as long as the tergite; Da2 on tergites pointed with frays. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta long, 0.4–0.5 times as long as urogomphomere I. Distal ventral seta also long, 0.25–0.5 times as long as urogomphomere I.
Instar II & III: Antennomere I with 4–6 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 18 setae. Medial dorsolateral seta on urogomphi 0.45–0.55 times as long as urogomphomere I. Distal ventral seta 0.15–0.3 times as long as urogomphomere I. Urogomphomere I 0.4–0.55 times as long as urogomphomere II.

Distribution
Europe, except British Isles; Armenia.

Catops tristis tristis (Panzer, 1794)

(Fig. 36)
= *Helops tristis* Panzer, 1794
Catops tristis (Panzer, 1794): Renkens 2015

Material examined: Germany [11 ex.]: Hessen, Schlitz, 1965, 2 ex. (RMNH.INS.967952); x.–xi.1965, 5 ex. (RMNH.INS.967959); unknown location, 15.ii.1965, 2 ex. (RMNH.INS.5069657, RMNH.INS.5069658).

Diagnosis
Instar I: Antennomere I with a seta (Fig. 36). Antennomere II with typical setae, without microsetae (Fig. 36). P1–P5 on tergites are frayed, and are of typical length, P2 0.75–1 times as long as the tergite; Da2 on tergites pointed. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi relatively long, 0.35–0.55 times as long as urogomphomere I. Distal ventral seta short, 0.1–0.4 times as long as urogomphomere I.
Instar II & III: Antennomere I with 7 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior

carina with 20–25 setae. Medial dorsolateral seta on urogomphi 0.25–0.35 times as long as urogomphomere I. Distal ventral seta 0.1–0.2 times as long as urogomphomere I. Urogomphomere I 0.4–0.65 times as long as urogomphomere II.

Distribution
All of Europe.

Dreposcia Jeannel, 1922

Dreposcia umbrina (Erichson, 1837)
(Figs 6, 14, 26)
= *Catops umbrinus* Erichson, 1837
Dreposcia umbrina (Erichson, 1837): Pinto 2015

Material examined: Germany [23 ex.]: Berlin, Berlin, 1966, 12 ex. (RMNH.INS.967940, RMNH.INS.967941, RMNH.INS.967942, RMNH.INS.967943); Berlin, Berlin-Grunewald, 1966, 9 ex. (RMNH.INS.947576); 1960s, 2 ex. (RMNH.INS.5069661, RMNH.INS.5069662).

Diagnosis
Instar I: Apex of mandible short. Antennomeres I and II polytrichic, each with multiple additional setae. P1–P5 on tergites are short and pointed, P2 0.1–0.3 times as long as the tergite; Da2 on tergites pointed (Fig. 14). Between the anterior carina and P1–P5 there are 7–12 setae, usually 8–9, in three rows (Fig. 14). Urogomphomere I polytrichic, especially ventrally; long, 2–3 times as long as abdominal segment X (Fig. 6). Medial dorsolateral seta on urogomphi short (Fig. 6). Distal ventral seta on urogomphi very long, about two thirds of the length of urogomphomere II (Fig. 6).
Instar II & III: Antennomere I with around 30 setae. Mandible with more than 8 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 40–50 setae. Paracercal seta straight, short. Urogomphomere I polytrichic. Medial dorsolateral seta on urogomphi short. Distal ventral seta long.

Distribution
Central and western Europe, up to Romania in the east and Denmark in the north.

Fissocatops Zwick, 1968

Fissocatops westi (Krogerus, 1931)
(Figs 11, 37)
Catops Westi Krogerus, 1931
Fissocatops westi (Krogerus, 1931): Renkens 2015

Material examined: Germany [7 ex.]: Hessen, Schlitz, 1966, 7 ex. (RMNH.INS.5069627, RMNH.INS.967944, RMNH.INS.967947, RMNH.INS.967950).

Diagnosis
Instar I: Antennomere I without setae (Fig. 37). Antennomere II with typical setae, without microsetae (Fig. 37). P1–P5 on tergites are frayed, and are of typical length, P2 0.6–0.8 times as long as the tergite; Da2 on tergites pointed, frayed. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta on urogomphi relatively longer than typical, 0.3–0.4 times as long as urogomphomere I (Fig. 11). Distal ventral seta short, 0.15–0.2 times as long as urogomphomere I (Fig. 11).
Instar II: Antennomere I with 5 setae. Mandible with 3 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 20–25 setae. Medial dorsolateral seta on urogomphi 0.275–0.4 times as long as urogomphomere I. Distal ventral seta 0.05–0.15 times as long as urogomphomere I. Urogomphomere I 0.425–0.5 times as long as urogomphomere II.
Instar III: Unknown.

Distribution
Northern and western Europe.

Sciodrepoides Hatch, 1933

Sciodrepoides fumatus (Spence, 1815)
(Figs 12, 38, 39)
Choleva fumata Spence, 1815
Sciodrepoides fumatus (Spence, 1837) [sic]: Pinto 2015

Material examined: Germany [9 ex.]: Hessen, Schlitz, 1966, 7 ex. (RMNH.INS.947591); 1960s, 2 ex. (RMNH.INS.5069667, RMNH.INS.5069668).

Diagnosis
Instar I: Antennomere I without setae (Fig. 38). Antennomere II with typical setae, no microsetae (Fig. 38). P1–P5 on tergites are frayed, relatively short, P2 0.5–0.75 times as long as the tergite; Da2 on tergites pointed with frays. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta long, 0.4–0.6 times as long as urogomphomere I (Fig. 12). Distal ventral seta short, 0.15–0.25 times as long as urogomphomere I (Fig. 12).
Instar II & III: Antennomere I with 6 setae. Mandible with 4 setae. Maxillary palpomere II with 2 setae (cf. Fig. 39). Tergites betwee essen, Schlitz,

30.xi.196 n posterior row and anterior carina with 30–40 setae. Medial dorsolateral seta on urogomphi 0.35–0.55 times as long as urogomphomere I. Distal ventral seta 0.05–0.2 times as long as urogomphomere I. Urogomphomere I 0.35–0.55 times as long as urogomphomere II.

Distribution

All of Europe and Asia, up to Japan.

Sciodrepoides watsoni watsoni (Spence, 1815)

(Figs 17–19)
Choleva Watsoni Spence, 1815
Catops Watsoni Spence [(Spence, 1815)]: Eichelbaum 1901
Sciodrepoides Watsoni Spencer [sic]: Paulian 1941
Sciodrepoides watsoni watsoni (Spence, 1813): Kilian and Mądra 2015
Sciodrepoides watsoni (Spence, 1815): Pinto 2015
Sciodrepoides watsoni (Spence, 1813): Jakubec 2016

Nomenclature

The author citation "Spence, 1813" refers to the same publication as "Spence, 1815", namely that in *Transactions of the Linnean Society of London* vol. 11, issue 1, pp. 123–160. The cover page of the volume lists the year of publication as 1815, but the first issue may have been published at an earlier date. The author citations used in (Perreau 2000) are used here.

Material examined: Germany [34 ex.]: Berlin, Berlin-Böttcherberg, v.1964, 12 ex. (RMNH.INS.967962); Berlin, Berlin-Tiefwerder, 1963–1964, 1 ex. (RMNH.INS.5069663); n.d., 6 ex. (RMNH.INS.947574); Hessen, Obernhausen Rhön, vii.1960, 1 ex. (RMNH.INS.947573); Hessen, Schlitz, 1966, 11 ex. (RMNH.INS.967953); unknown location, n.d., 3 ex. (RMNH.INS.947572); **Netherlands** [9 ex.]: Overijssel, Enschede, 01.v.2012, 1 ex. (RMNH.INS.5069666); Zuid-Holland, Katwijk aan Zee, x.1987, 1 ex. (RMNH.INS.5069540); Zuid-Holland, Leiden, 1980s, 7 ex. (RMNH.INS.5069566, RMNH.INS.5069570, RMNH.INS.5069573, RMNH.INS.5069574, RMNH.INS.5069576, RMNH.INS.5069577, RMNH.INS.5069578) [labelled *Catops morio*].

Diagnosis

Instar I: Antennomere I without setae. Antennomere II with typical setae, no microsetae. P1–P5 on tergites are frayed, of typical length, P2 0.75–1 times as long as the tergite; Da2 on tergites pointed with frays. Chaetotaxy of tergites otherwise typical. Medial dorsolateral seta long, 0.4–0.6 times as long as urogomphomere I. Distal ventral seta relatively long, 0.3–0.5 times as long as urogomphomere I.
Instar II & III: Antennomere I with 5–6 setae. Head dorsally with a brown spot. Mandible with 4 setae. Maxillary palpomere II with 2 setae. Tergites between posterior row and anterior carina with 30–40 setae. Medial dorsolateral seta on urogomphi 0.35–0.55 times as long as urogomphomere I. Distal ventral seta 0.05–0.2 times as long as urogomphomere I. Urogomphomere I 0.35–0.55 times as long as urogomphomere II.

Distribution

All of Europe and Asia; North America.

Cholevina Kirby, 1837

Diagnosis

Mandibles symmetrical, each with two or four apical teeth. Prostheca frayed, bristle-like.

Key to the genera of Cholevina larvae

Xambeu (1892) describes the larva of *Attaephilus arenarius* (H. Hampe, 1852) but does not go into enough detail as to determine which instar is being described, and size is too variable between genera to use as a comparison. If it is assumed that the ratio of the length of the first and second segments of the maxillary palps does not differ between instars, as it does not in *Choleva* and *Nargus*, *Attaephilus* Motschulsky, 1870 can be distinguished from other Cholevina by the second segment of the maxillary palps being twice as long as the first, instead of the same size, or at most slightly longer.

Kilian and Newton (2021) describe third-instar larvae of *Prionochaeta opaca* (Say, 1825), which have a unique morphological characteristic in that antennomere II consists of two separate segments AIIa and AIIb. Since the larvae of the first and second instars are unknown, this characteristic cannot be incorporated in the full key.

1. Tibia 2–3 times as long as tergite. Epipharynx with 18–21 sensilla … *Choleva* Latreille, 1796
– Tibia less than 2 times as long as tergite. Epipharynx with 12 sensilla ………………… ……………………… *Nargus* Thomson, 1867

Attaephilus Motschulsky, 1870

Attaephilus arenarius (H. Hampe, 1852)

Catops arenarius H. Hampe, 1852

Catopsimorphus pilosus Muls[ant & Rey, 1853]: Xambeu 1892

Habitat
Myrmecophile, in nests of *Atta structor* (Latreille, 1798) (= *Messor structor* (Latreille, 1798)) (Xambeu 1892).

Distribution
Central and western Europe.

Choleva Latreille, 1796

Diagnosis
Tibia 2–3 times as long as tergite. Epipharynx with 18–21 sensilla.

Key to the species of larval instar I of *Choleva*
1. Dd2 on tergites very close to end of carina and Dd1*. Appendage on antennomere III longer than wide. 2 extra dorsal setae on antennomere II (Figs 41, 42). On urogomphomere I, gap between proximal group of 5 setae and distal group of 3 setae more than half the length of urogomphomere I (Figs 45, 46) (*Choleva agilis*-group) 2
– Dd2 on tergites lower. Appendage on antennomere III as long as wide, or shorter. More than 2 extra setae on antennomere II (Fig. 43). Gap on urogomphomere I less than half of the length of urogomphomere I (Figs 44, 47) 3
2. Smaller, stouter species. Posterior tibia 0.44 ± 0.02 mm .... *C. (C.) agilis* (Illiger, 1798)
– Larger, more slender species. Posterior tibia 0.58 ± 0.02 mm ... *C. (C.) lederiana* Reitter, 1902
3. Antennae polytrichic, antennomeres I and II with multiple additional setae. Lateral end of the anterior carina on tergites with single seta 4
– Antennomere I with 1 seta, antennomere II with 2 extra setae ventrally and 3–4 extra setae dorsally. Lateral end of the anterior carina on tergites with group of 3 minute setae .... *C. (C.) oblonga* Latreille, 1807
4. Maxillary palpomere II with 3 setae .... *C. (C.) angustata* (Fabricius, 1781)
– Maxillary palpomere II with 4–5 setae .... *C. (C.) fagniezi* Jeannel, 1922

Key to the species of larval instars II and III of *Choleva*
1. On urogomphomere I, gap between proximal group of 5 setae and distal group of 3 setae more than half of the length of urogomphomere I. Maxillary palpomere II with 4 setae in L2 and L3 .... *Choleva agilis*-group 2
– Gap on urogomphomere I less than half of the length of urogomphomere I. Maxillary palpomere II not always with exactly 4 setaeand L3 3
2. Apex of mandible with 2–3 rounded teethand L3.....................*C. (C.) agilis* (Illiger, 1798)
– Apex of mandible with 4 pointed teeth (Fig. 51)and L3......*C. (C.) lederiana* Reitter, 1902
3. Apex of mandible with 4 pointed teeth (Figs 48, 50)and L3......................................4
– Apex of mandible with 2 rounded teeth (Fig. 49)and L3..............*C. (Cholevopsis) spadicea*
4. Dorsal-proximal tooth on mandible apex with an entirely smooth or slightly serrated bottom edge (Fig. 48). Retinaculum pointed (L2) or rounded (L3, Fig. 48). Lacinia with 6 or 7 teethandL3......................................5
– Dorsal-proximal tooth on mandible apex with a strongly serrated bottom edge (Fig. 50). Retinaculum pointed (Fig. 50). Lacinia with 5 teeth ....*C. (C.) oblonga* Latreille, 1807
5. Maxillary palpomere II with 4 (L2) or 6 (L3) setae. Mandible with 5 setae and L3 .... *C.) angustata* (Fabricius, 1781)
– Maxillary palpomere II with 7 (L2 & 3) setae. Mandible with 7 setae (Fig. 48)and L3 .... *C. (C.) fagniezi* Jeannel, 1922

Choleva (Choleva) agilis (Illiger, 1798)
(Figs 41, 45)
Ptomaphagus agilis Illiger, 1798
Choleva agilis (Illiger[,] 1798): Casale 1975a
Choleva agilis (Illiger, 1798): Pinto 2015

Material examined: Germany [16 ex.]: Berlin, Berlin-Tiefwerder, x.1965, 2 ex. (RMNH.INS.5069524); 19.x.1964, 13 ex. (RMNH.INS.5069518, RMNH.INS.5069519, RMNH.INS.5069522, RMNH.INS.5069523); unknown location, n.d., 1 ex. (RMNH.INS.5069521).

Diagnosis
Instar I: Epipharynx with 18–21 sensilla. Mala with row of 5–6 setae. Maxillary palpomere II with 2 setae. Antennomere I without setae, antennomere II with 2 additional setae dorsally (Fig. 41). Appendage on antennomere III long (Fig. 41). Tergites with P1, P2, P5, P5’, L, Lb, Dd2; Da1 and Dd1*; and 5 additional setae between P1, P5, and the anterior carina. Position of Dd2 high, near Dd1*. Urogomphomere I with 8 setae, 5 campaniform sensilla (Fig.

45). Large gap between the 5 most proximal setae and the 3 most distal setae (Fig. 45). Posterior tibia 0.44 ± 0.02 mm (Pinto 2015).
Instar II & III: Mandible with 2–3 smooth apical teeth. Maxillary palpomere II with 4 setae. Tergites between the posterior row and the anterior carina with 10–20 setae. Urogomphomere I with 8 setae, 5 campaniform sensilla, large gap.

Distribution
Central and western Europe except Spain, up to the Netherlands in the north; Turkey.

Choleva (Choleva) angustata (Fabricius, 1781)
Cistela angustata Fabricius, 1781
Choleva angustata Fabricius [(Fabricius, 1781)]: Strambi 1963, 1964

Diagnosis
Instar I: Epipharynx with 20–21 sensilla. Mala with row of 7 setae. Maxillary palpomere II with 3 setae. Antennae polytrichic, antennomeres I and II with many more setae. Appendage on antennomere III short. Tergites with P1, P2, P5, P5', L, Lb, Dd2; Da1 and Dd1*; and 5 additional setae between P1, P5, and the anterior carina. Position of Dd2 regular, between L and Dd1*. Urogomphomere I with 8 setae, 5 campaniform sensilla. No gap between the 5 most proximal setae and the 3 most distal setae.
Instar II & III: Mandible with 5 setae, apex with 4 pointed apical teeth. On right mandible, most proximal tooth with a smooth bottom edge. Maxillary palpomere with 5 (L2) or 6 (L3) setae. Tergites between the posterior row and the anterior carina with 28–30 setae. Urogomphomere I with 8 setae, 5 campaniform sensilla, no gap.

Distribution
Central and western Europe, up to Greece.

Choleva (Choleva) fagniezi Jeannel, 1922
(Figs 40, 44, 48)
Choleva fagniezi Jeannel (1922) [sic]: Pinto 2015

Material examined: Germany [55 ex.]: Berlin, Berlin-Grunewald, x.1963, 34 ex. (RMNH.INS.5069677, RMNH.INS.5069678, RMNH.INS.967982, RMNH.INS.967985, RMNH.INS.967990, RMNH.INS.967996); Berlin, Berlin-Grunewald, Jagen 86, x.1963, 21 ex. (RMNH.INS.967981, RMNH.INS.967983, RMNH.INS.967984, RMNH.INS.967986, RMNH.INS.967987, RMNH.INS.967989).

Diagnosis
Instar I: Epipharynx with 20–21 sensilla. Mala with row of 7–8 setae. Maxillary palpomere II with 4–5 setae. Antennae polytrichic, antennomeres I and II with many more setae (Fig. 40). Appendage on antennomere III short (Fig. 40). Tergites with P1, P2, P5, P5', L, Lb, Dd2; Da1 and Dd1*; and 4–5 additional setae between P1, P5, and the anterior carina. Position of Dd2 regular, between L and Dd1*. Urogomphomere I with 8 setae, 5 campaniform sensilla (Fig. 44). Small gap between the 5 most proximal setae and the 3 most distal setae (Fig. 44).
Instar II & III: Mandible with 7 setae, apex with 4 pointed apical teeth (Fig. 48). On right mandible, most proximal tooth with a weakly serrated bottom edge (Fig. 48). Maxillary palpomere with 7 setae. Tergites between the posterior row and the anterior carina with 20–30 setae. Urogomphomere I with 8 setae, 5 campaniform sensilla, no gap.

Distribution
Southwestern France; Spain.

Choleva (Choleva) lederiana holsatica Benick & Ihssen, 1937
(Figs 42, 51)
Choleva holsatica Benick & Ihssen, 1937
Choleva septentrionis holsatica Benick & Ihssen, 1937
Choleva holsatica Benick & Ihssen [, 1937]: Heun 1955
Choleva holsatica B[eni]ck. & Ihss[en]. [, 1937]: Zwick 1966 *Choleva holsatica* Benick & Ihssen (1937) [sic]: Pinto 2015

Material examined: Germany [33 ex.]: Schleswig-Holstein, Bad Segeberg, ii.1963, 31 ex. (RMNH.INS.967988, RMNH.INS.967991, RMNH.INS.967992, RMNH.INS.967993, RMNH.INS.967994, RMNH.INS.967995); 1963, 2 ex. (RMNH.INS.5069675, RMNH.INS.5069676).

Diagnosis
Instar I: Epipharynx with 20–21 sensilla. Mala with row of 5–6 setae. Maxillary palpomere II with 2 setae. Antennomere I without setae, antennomere II with 2 additional setae dorsally (Fig. 42). Appendage on antennomere III long (Fig. 42). Tergites with P1, P2, P5, P5', L, Lb, Dd2; Da1 and Dd1*; and 5 additional setae between P1, P5, and the anterior carina. Position of Dd2 high, near Dd1*. Urogomphomere I with 8 setae, 5 campaniform sensilla (Fig. 46). Large gap between the 5 most proximal setae and the 3 most distal setae (Fig. 46). Posterior tibia 0.58 ± 0.02 mm (Pinto 2015).

Instar II & III: Mandible with 4–6 setae, apex with 4 pointed apical teeth (Fig. 51). On right mandible, most proximal tooth with a smooth bottom edge (Fig. 51). Maxillary palpomere with 4 setae. Tergites between the posterior row and the anterior carina with 10–20 setae. Urogomphomere I with 8 setae, 5 campaniform sensilla, large gap.

Distribution

Endemic to Bad Segeberg, Germany.

Choleva (Choleva) oblonga oblonga Latreille, 1807

(Figs 43, 47, 50)
Choleva oblonga (Latreille, 1807) [sic]: Pinto 2015

Material examined: Germany [8 ex.]: Hessen, Schlitz, ii.1969, 1 ex. (RMNH.INS.5069510); 02.iii.1969, 2 ex. (RMNH.INS.5069514); ii.–iii.1969, 1 ex. (RMNH.INS.5069511); ii.–v.1969, 2 ex. (RMNH.INS.5069512); 1969, 2 ex. (RMNH.INS.5069673, RMNH.INS.5069674).

Diagnosis

Instar I: Epipharynx with 18 sensilla. Mala with row of 6 setae. Maxillary palpomere II with 2 setae. Antennomere I with 1 seta, antennomere with 3–4 additional setae dorsally and 2 additional setae ventrally (Fig. 43). Appendage on antennomere III short (Fig. 43). Tergites with P1, P2, P5, P5', L, Lb, Dd2; Da1; and 5 (5–6) additional setae between P1, P5, and the anterior carina. Near the lateral ends of the anterior carina, three minute setae instead of just Dd1*. Position of Dd2 regular, between L and lateral end of the anterior carina. Urogomphomere I with 8 setae, 5 campaniform sensilla (Fig. 47). Small gap between the 5 most proximal setae and the 3 most distal setae (Fig. 47).
Instar II & III: Mandible with 5 setae, apex with 4 pointed apical teeth (Fig. 50). On right mandible, most proximal tooth with a serrated bottom edge (Fig. 50). Maxillary palpomere with 2 setae. Urogomphomere I with 8 setae, 5 campaniform sensilla, small gap.

Distribution

Central and western Europe; Middle East.

Choleva (Cholevopsis) spadicea (Sturm, 1839)

(Fig. 49)
= Catops spadiceus Sturm, 1839
Choleva spadicea (Sturm, 1839): Pinto 2015

Material examined: Germany [1 ex.]: Hessen, Schlitz, Eisenberg, iv.–v.1971, 1 ex. (RMNH.INS.5069513).

Diagnosis

Instar I & II: Morphology unknown.
Instar III: Apical teeth of mandible rounded (Fig. 49). Maxillary palpomere with 2 setae. Posterior row of tergites with 9 setae. Tergites between the posterior row and the anterior carina with 20–25 setae. Urogomphomere I with 8 setae, 5 campaniform sensilla, small gap.

Distribution

Central and western Europe, up to the Netherlands in the north, up to Romania in the east.

Nargus Thomson, 1867

Diagnosis

Tibia at most 2 times as long as tergite. Epipharynx with 12 sensilla. Maxillary palpomere II with 2 setae.
Instar I: Antennomere I without setae.

Nargus (Nargus) velox velox (Spence, 1815)

= *Choleva velox* Spence, 1815
Nargus velox (Spence, 1815): Pinto 2015

Material examined: Netherlands [1 ex.]: Zuid-Holland, Leiden, Cronesteijn, n.d., 1 ex. (RMNH.INS.5069541).

Diagnosis

Instar I: Antennomere II without additional setae.

Distribution

Central and western Europe.

Nargus sp.

(Fig. 52)

Material examined: Germany [2 ex.]: Hessen, Schlitz, 30.xi.1968, 2 ex. (RMNH.INS.967978, RMNH.INS.967979).

Diagnosis

Instar II: Mandible with 4 setae. Mandible with 4 pointed apical teeth. On right mandible, most proximal tooth with a smooth bottom edge (Fig. 52). Maxillary palpomere with 2 setae.

Prionochaeta Horn, 1880

Prionochaeta opaca (Say, 1825)

= *Catops opacus* Say, 1825
Prionochaeta opaca (Say, 1825): Kilian and Newton 2021

Diagnosis Antenna with 4 segments.

Distribution
Eastern and central North America.

Leptodirini Lacordaire, 1854

One species occurring in the Netherlands, *Parabathyscia wollastoni* (Janson, 1857).

Diagnosis
Apex of mandible long. Prostheca tooth-like, with 1, 2, or 3 teeth, sometimes only present on the left mandible, or completely absent. Retinaculum often only on the right mandible, often completely absent; rarely on both mandibles. Antennomere III in L1 often with a pigmented band, faint in some species and always absent in L2. Antennomere III also with third additional setiform sensillum, replacing the campaniform sensillum in Catopina and the shorter SA in Cholevina. Urogomphi often strongly reduced, even absent, but if present, URI always has 8 setae and 5 campaniform sensilla.

Pholeuina Reitter, 1886

Parabathyscia Jeannel,1908

Diagnosis
Extensively described by Franciscolo (Franciscolo 1948, 1953), who also provides a key to four of the species in the genus. The genus can be distinguished from many other Leptodirini by an additional pair of dorsal setae on the labrum (Franciscolo 1953).

Parabathyscia (Parabathyscia) wollastoni (Janson, 1857)

= *Adelops Wollastoni* Janson, 1857

Diagnosis
Larval morphology not known.

Distribution
Western Europe.

Oritocatopini Jeannel, 1936

Paulian (1937, 1941) lists a number of characteristics that set apart Oritocatopini from other Cholevinae, namely (1) galea with three fringes, (2) elongated ligula with an enlarged apex, and (3) labial palps with an enlarged apex with spinules. However, based on currently available information, those characteristics are not unique to Oritocatopini.

Ptomaphagini Jeannel, 1911

Key to the genera of Ptomaphagini larvae

1. Both mandibles with a prostheca. URI at least as long as wide. (Ptomaphagina) … 2
– Right mandible without prostheca, retinaculum long. URI very short, wider than long; urogomphomere II much longer (Ptomaphaginina) …………………… *Proptomaphaginus*
2. Mandible with pointed apical teeth ………………… *Ptomaphagus* Hellwig, 1795
– Mandible with rounded apical teeth …………………… *Adelopsis* Portevin, 1907

Ptomaphagina Jeannel, 1911
Adelopsis Portevin, 1907

Adelopsis leo Gnaspini, 1993

Adelopsis (Iuturutica) leo: Gnaspini 1993b

Diagnosis
Extensively described by Gnaspini (1993b).

Distribution
Brazil.

Ptomaphagus Hellwig, 1795

Diagnosis
Epipharynx with 8 c.s. and 2 pairs of sensilla. Prementum without c.s. Apices of mandibles symmetrical, bidentate. Prostheca frayed, bristle-like. Mala with a row of 5–6 setae. Maxillary palpomere II with 1–2 setae, 3 in *P. hirtus*. Urogomphomere I with 6 setae, 5 campaniform sensilla.
Instar I: Tergites with chaetotaxy like Catopina, with P1, P2, P5, P5', L, Lb, Dd2; Da1 and Dd1*; and Da2–Dc2. Position of Dd2 high, near Dd1*.
Instar II & III: Tergites with 4 large and 4 secondary setae in the posterior row, and 5–10 secondary setae between the posterior row and anterior carina.

Key to the species of larval instar I of *Ptomaphagus*

1. Maxillary palpomere II with 1 seta .... *P. (P.) thebeatles* Schilthuizen, Latella & Njunjić, 2021
– Maxillary palpomere II with 2 setae 2
2. Maxilla with 5 setae ... *P. (P.) medius* (Rey, 1889)
– Maxilla with 6 setae .... *P. (P.) subvillosus* (Goeze, 1777)

Key to the species of larval instar II and III of *Ptomaphagus*

1. Mandibles with retinaculum. Maxillary palpomere II with 2 setae (subgenus *Ptomaphagus*) 2
– Mandibles without retinaculum. Maxillary palpomere II with 3+ setae .... *P. (Adelops) hirtus* (Tellkampf, 1844)
2. Mala and lacinia not elongated (cf. 31). Maxillary palpomere III nearly twice as long as maxillary palpomere II 3
– Mala elongated, teeth of lacinia far apart (Fig. 55). Maxillary palpomere II just longer than maxillary palpomere III ....*P. (P.) varicornis* (Rosenhauer, 1847)
3. No ocelli. Antennomere I with 2 setae 4
– One pair of crescent-shaped ocelli. Antennomere I with 2 (L2) or 3 (L3) setae ....*P. (P.) subvillosus* (Goeze, 1777)
4. Front edge of dorsal-proximal tooth on mandible apex smooth (Fig. 53) .... *P. (P.) medius* (Rey, 1889)
– Front edge of dorsal-proximal tooth on mandible apex with a bump (c.f. Fig 54) ... *P. (P.) thebeatles* Schilthuizen, Latella & Njunjić, 2021

Ptomaphagus (Adelops) hirtus (Tellkampf, 1844)

= *Adelops hirtus* Tellkampf, 1844
Adelops hirtus Tellk[ampf]. [, 1844]: Hubbard 1880
Adelops hirtus Tellk[amp]f. [, 1844]: Packard 1888
Adelops hirtus Tellk[am]p[f]. [, 1844]: Peyerimhoff 1906
Adelops hirtus Tellk[ampf]. [, 1844]: Böving and Craighead 1930

Diagnosis
No description of instar I. Instar II and III have mandibles without retinacula and maxillary palpomeres II with 3 or more setae.

Habitat
Caves.

Distribution
Midwestern United States.

Ptomaphagus (Ptomaphagus) medius (Rey, 1889)

(Fig. 53)
= *Catops medius* Rey, 1889
Ptomaphagus medius (Rey, 1889): Pinto 2015

Material examined: Germany [31 ex.]: Berlin, Böttcherberg, v.1965, 29 ex. (RMNH.INS.5069527, RMNH.INS.5069528, RMNH.INS.5069529, RMNH.INS.5069530); unknown location, n.d., 2 ex. (RMNH.INS.5069671, RMNH.INS.5069672).

Diagnosis
Maxillary palpomere II with 2 seta.
Instar I: Maxilla with 5 setae.
Instar II & III: Maxilla with 6 setae. Mandibles with retinaculum, on right mandible the retinaculum is bifurcated, rounded (Fig. 53). Front edge of dorsal-proximal tooth on mandible apex smooth (Fig. 53).

Distribution
Northern and western Europe, recently expanding to Central Europe; Canada (Schilthuizen et al. 2021).

Ptomaphagus (*Ptomaphagus*) *sericatus* (Chaudoir, 1845)

= *Catops sericatus* Chaudoir, 1845
Pt[omaphagus]. subvillosus sericatus Chaud. [(Chaudoir, 1845)]: Jeannel 1922 *Ptomaphagus sericatus* Chaudoir [(Chaudoir, 1845)]: Paulian 1941

Habitat Found in old nests of *Lasius* Fabricius, 1804 (Hymenoptera: Formicidae) (Jeannel 1922).

Distribution
Central, southern, and eastern Europe (Schilthuizen et al. 2021).

Ptomaphagus (Ptomaphagus) thebeatles Schilthuizen, Latella & Njunjić, 2021

Ptomaphagus sericatus auct.: Pinto 2015 (misidentification)

Material examined: Netherlands [6 ex.]: Zuid-Holland, Schiedam, n.d., 6 ex. (RMNH.INS.5069537, RMNH.INS.5069555, RMNH.INS.5069556, RMNH.INS.5069557).

Diagnosis
Maxilla with 6 setae. No ocelli.

Instar I: Maxillary palpomere II with 1 seta.
Instar II & III: Maxillary palpomere II with 2 seta. Mandibles with retinaculum, on right mandible the retinaculum is bifurcated, rounded. Front edge of dorsal-proximal tooth on mandible apex with a bump.

Distribution
Western and southern Europe, reaching southern Russia in the east, and recently expanding northwards (Schilthuizen et al. 2021).

Ptomaphagus (Ptomaphagus) subvillosus (Goeze, 1777)

= *Peltis nigro-fusca subvillosa* Geoffroy, 1762 (nomen nudum)
= *Silpha subvillosa* Goeze, 1777
Catops sericeus, Panz[er]. [sic]: Xambeu 1894
Ptomaphagus subvillosus (Goeze, 1777): Pinto 2015

Material examined: Germany [4 ex.]: Hessen, Schlitz, 1965, 2 ex. (RMNH.INS.5069525); Schleswig-Holstein, Plön, 1960s, 2 ex. (RMNH.INS.5069664, RMNH.INS.5069665).

Diagnosis
Maxilla with 6 setae. Maxillary palpomere II with 2 seta. One pair of crescent-shaped ocelli.
Instar III: Antennomere I with 3 setae.

Distribution
Central and western Europe.

Ptomaphagus (Ptomaphagus) varicornis (Rosenhauer, 1847)

(Figs 54, 55)
= *Catops varicornis* Rosenhauer, 1847
Ptomaphagus varicornis (Rosenhauer, 1847): Pinto 2015

Material examined: Germany [3 ex.]: Schleswig-Holstein, Plön, vii.1965, 1 ex. (RMNH.INS.5069526); 1965–1966, 2 ex. (RMNH.INS.5069669, RMNH.INS.5069670).

Diagnosis
Morphology of instar I is unknown.
Instar II & III: Mala elongated, teeth of lacinia far apart (Fig. 55). Maxillary palpomere II is just longer than maxillary palpomere III (Fig. 55). Mandibles with retinaculum, on right mandible the retinaculum is bifurcated, pointed (Fig. 54).

Distribution
Europe, up to Denmark in the north, up to Russia in the east.

Ptomaphaginina Jeannel, 1911
Proptomaphaginus Szymczakowski, 1969
Proptomaphaginus apodemus Szymczakowski, 1969

Proptomaphaginus apodemus Szymczakowski, 1969: Decou 1973

Diagnosis
Right mandible without prostheca, retinaculum long. Urogomphomere I very short, wider than long.

Distribution
Cuba.

Discussion

A key was constructed of all larval stages of 28 of 39 species of Cholevinae in the Netherlands, representing all species for which sufficient literature or material was available to the authors. *Catops longulus*, *Choleva cisteloides*, *C. elongata*, *C. glauca*, *C. jeanneli*, *C. paskovensis*, *C. pozi*, *C. reitteri*, *Nargus anisotomoides*, *N. wilkini*, and *Parabathyscia wollastoni* were excluded as no material specimens or descriptions of the larval morphology were available. One tribe presently occurring in Europe, Oritocatopini, was excluded as the only literature did not contain distinguishing characteristics.

Accuracy
More specimens should be collected of the species that were included, especially from different regions, to confirm the characteristics presented in this study. Firstly, even though care was taken to only implement characteristics without overlap, chaetotaxy was found to be variable in several areas of the larva. This could mean more extreme outliers exist that would be identified incorrectly using this key. Secondly, the rounded mandible shape of *Choleva spadicea* could be caused by wear, though no similar wear was found in other species. Thirdly, a specific set of specimens available to the authors are possibly misidentified. Seven of the 14 specimens labelled *C. morio* that were collected in Leiden, The Netherlands in the 1980s have both the brown spot characteristic for *S. watsoni*, and the pair of campaniform

sensilla on the prementum uncharacteristic for *C. morio*. Of the remaining seven larval specimens, none of which have the brown spot, the prementum is visible in three and in all of these the pair of campaniform sensilla is missing as expected. This strongly indicates the former seven species are misidentified or mislabelled, and the latter seven are labelled correctly. A larger set of larval specimens with confirmed identifications could indicate whether this is indeed the case, or whether those characteristics (brown spot, c.s. on prementum) are variable.

Key to the tribes. Kilian and Mądra (2015) questions the validity of the key to genera for larvae of Cholevinae by Zwick (1978), used here as a base for the key to tribe, stating: "characters leading to *Sciodrepoides* are, from evidence produced during the present study, incorrect." However, based on our reading of their publication, the key correctly identifies *Sciodrepoides*: in instar I, the inner edge of the mandible is concave (Kilian & Mądra 2015, Fig. 23), URI is drawn as approx. 97 µm (Kilian & Mądra 2015, Fig. 54) and abdominal tergite X as approx. 112 µm (Kilian & Mądra 2015, Fig. 50), URII not more than three times as long as URI (Kilian & Mądra 2015, Fig. 54), and the prostheca is described as a "simple lobe"; in instar III, the inner edge of the mandible is straight (Kilian & Mądra 2015, Figs 24, 25), URI is drawn as approx. 159 µm (Kilian & Mądra 2015, Fig. 55) and abdominal tergite X as approx. 178 µm (Kilian & Mądra 2015, Fig. 52), URII not more than three times as long as URI (Kilian & Mądra 2015, Fig. 55), and the mean length of L2 is listed as 2.79 mm. The discrepancy possibly arises from counting the anal membrane as part of abdominal segment X or not.

Chaetotaxy of *Sciodrepoides watsoni*. *Sciodrepoides watsoni* had recently been described with modern terminology in great detail (Kilian & Mądra 2015), meaning the species was suitable for a comparison with the material of *S. watsoni* and other species in Catopina available to the author. This comparison revealed a number of significant differences in the chaetotaxy of instar I, where setae found in the material of *S. watsoni* and other Catopina species were not included in the descriptions by Kilian and Mądra.

Head. Both *S. watsoni* and *S. fumatus* show an additional frayed seta on the lateral granulated areas behind the antennae, as well as a line of 3–7 setae extending from the larger one to the ventral surface, all seemingly homologous to the L' setae in the later instars. An additional seta can be found on the ventral surface, between Vl1 and L. None of these setae seem to be present in the description by Kilian and Mądra (2015).

Antennae. The antennae are mostly similar apart from the campaniform sensilla on AI. In instar I, all Cholevini including both *Sciodrepoides* species, have two campaniform sensilla in the basal half of the segment, whereas the figure in their description shows four sensilla along the distal edge of the segment (Kilian & Mądra 2015, Fig. 21). The figure for instar III does show these sensilla (Kilian & Mądra 2015, Fig. 22).

Abdominal segments. In instar I, most Catopina have an additional seta on both halves of each tergite between Dd1* and P5, not present in their description (Kilian & Mądra 2015, Fig. 42), and tentatively labelled Dd2 in these descriptions.

Urogomphi. Kilian and Mądra (2015) include for instar I of *Sciodrepoides watsoni* a figure with seven setae and four campaniform sensilla, the difference consisting of the proximal ventral seta and one of the proximal sensilla (Kilian & Mądra 2015, Fig. 54). The text only mentions six setae, and it is unclear which seta from the figure is not included in that count. Furthermore, the figure shows two *dorsal* distal setae, as opposed to one dorsal and one ventral seta, which does not match the present findings.

It is unclear to the authors what these differences signify, as Kilian and Mądra confirmed the identity of their specimens using both molecular and morphological methods. The presence of these setae and sensilla across Catopina species may suggest that the specimens examined by Kilian and Mądra display strong local variation. However, this interpopulation variation would be larger than many interspecific differences.

Identifying characteristics

The resulting key primarily uses mandible shape and the relative length of urogomphomere I for the distinction of tribes, and size as well as the chaetoxy of the mandible, maxilla, antenna, tergite, and urogomphi for distinction of species within genera. In future studies, chaetotaxy of the head capsule, thorax, and legs could be explored for further identifying characteristics. Microsculpture, glands, and reservoirs were also found to be potentially useful sources of identification characteristics for other subfamilies in Leiodidae (Kilian 2012). Further, the width of the labrum could be used as a measure of overall size instead of tibia length, as it is not dependent on the relevant length of appendages.

Application

The keys are currently not usable for the full identification to species of unknown specimens as the key is incomplete even for the Dutch fauna. To improve the taxonomic and geographical coverage of the key, specimens of additional species are required. However, these keys do provide a scaffold for the further development of a key to the species of (Northwestern) Europe.

The morphological characteristics used in the keys may also be used to further investigate the phylogeny of the group. Even though in general existing taxonomic divisions were used to structure the keys, this was not feasible for *Catops* sensu lato, i.e., *Apocatops*, *Catops*, *Fissocatops*, *Sciodrepoides*, with the characteristics used in this study. This concurs with a phylogenetic reconstruction of Catopina which shows *Catops* as a paraphyletic genus (Schilthuizen et al. 2016). Conversely, some taxonomic groups were found to be strongly delineated by larval morphology as well as phylogeny, such as the *Catops fuscus*-group (Schilthuizen et al. 2016).

The same morphological characteristics can also be related to ecological traits of the larvae. For example, the less concave mandibles found in later instars of *Catops* larvae could be suitable for clipping the feather rami and pieces of hair found in the guts of some of the larvae.

Conclusion

Existing specimens and literature on the larval morphology of European Cholevinae species were comprehensively re-examined. The results validate an existing key to tribes (Zwick 1978), and were used to create further keys to species for each of the tribes for which material or descriptions were available. In addition, diagnostic descriptions for the species were made where possible. The resulting keys and descriptions cover 28 of the 39 species in the Netherlands, giving pointers to the phylogeny and the ecology of the subfamily as well as providing a suitable framework for a complete identification key. To validate and finish such a key, additional specimens from different populations of described species, and of previously undescribed species are necessary.

References

Adamczyk, B., A. Kilian & J. M. S. Costas, 2011. Description of the larva of *Quaestus (Quaesticulus) Pachecoi* (Bolivar, 1915) (Coleoptera: Leiodidae: Cholevinae). – Annales Zoologici 61: 691–708. https://doi.org/10.3161/000345411X622534.

Antunes-Carvalho, C., I. Ribera, R. G. Beutel & P. Gnaspini, 2019. Morphology-based phylogenetic reconstruction of Cholevinae (Coleoptera: Leiodidae): a new view on higher-level relationships. – Cladistics 35: 1–41. https://doi.org/10.1111/cla.12230.

Ashe, J. S. & L. E. Watrous, 1984. Larval chaetotaxy of Aleocharinae (Staphylinidae) based on a description of *Atheta coriaria* Kraatz. – The Coleopterists Bulletin 38: 165–179. https://www.jstor.org/stable/4008166.

Beier, M. W. P. & H. Strouhal, 1928. Käferlarven und Käferpuppen aus Maulwurfsnestern. – Zeitschrift für wissenschaftliche Insektenbiologie 23: 1–34.

Beutel, R. G. & R. Molenda, 1997. Comparative morphology of selected larvae of Staphylinoidea (Coleoptera, Polyphaga) with phylogenetic implications. – Zoologischer Anzeiger 236 (1): 37–67.

Blas, M. & E. Vives, 1978. A proposito de la biología y desarrollo de *Cholevinus pallidus* (Ménétries, 1832) (Col. Catopidae). – Miscelanea Zoologica 4 (2): 147–159. https://other.museucienciesjournals.cat/en/other/mz/mz-volum-04-2-1978/a-proposito-de-la-biologia-y-desarrollo-de-cholevinus-pallidus-menetries-1832-col-catopidae.

Böving, A. G. & F. C. Craighead, 1930. An illustrated synopsis of the principal larval forms of the order Coleoptera. – Entomologica Americana 11 (1): 1–351. https://www.biodiversitylibrary.org/page/50669874.

Brasavola de Massa, A., 1931. Note sulle larve dei generi *Neobathyscia* Müll. e *Royerella* Jeann. (con 1 tav.). – In: Esplorazione Scientifica delle grotte dei dintorni di Rovereto, Vol. 58: pp. 13–15. Museo Civico di Rovereto.

Cai, C., E. Tihelka, M. Giacomelli, J. F. Lawrence, A. Ślipiński, R. Kundrata, S. Yamamoto, M. K. Thayer, A. F. Newton, R. A. B. Leschen, M. L. Gimmel, L. Lü, M. S. Engel, P. Bouchard, D. Huang, D. Pisani & P. C. J. Donoghue, 2022. Integrated phylogenomics and fossil data illuminate the evolution of beetles. – Royal Society Open Science 9 (3): 211771. https://doi.org/10.1098/rsos.211771.

Casale, A., 1975a. Ciclo biologico e morfologia preimmaginale di Coleoptera Staphylinoidea delle famiglie Leptinidae e Catopidae. – Redia 56: 199–230.

Casale, A., 1975b. Morfologia larvale di *Ovobathysciola majori* (Reitter) specie cavernicola di un genere endemico sardo (III Nota sui Coleoptera Catopidae). – Bollettino della Società sarda di Scienze naturali 9: 193–202.

Cerruti, M., 1955. Morfologia ed ecologia comparate di due *Bathysciinae* speleobii (Coleopt. Catopidae). – Fragmenta Entomologica 2 (1): 1–15.

Corbière, G., 1967. Anatomie sensorielle des appendices céphaliques de la larve du *Speophyes lucidulus* (Delar.) (Colèopteré cavernicole de la sous-famille des Bathysciinae). – Annales de Spéléologie 22: 417–431.

Corbière, G., 1969. Ultrastructure des sensilles trichoïdes de l'antenne chez les larves de *Speophyes lucidulus* (Delar.) (Col. Bathysc.). – Comptes rendus de l'Académie des sciences. Série D 268 (1): 387–388.

Corbière-Tichané, G., 1969. Ultrastructure du labium de la larve du *Speophyes lucidulus* Delarouzeei (Coleoptera, Catopidae). – Zeitschrift für Morphologie der Tiere 66 (1): 73–86. https://doi.org/10.1007/BF00298714.

Creuwels, J. & S. Pieterse, 2024. Checklist Dutch Species Register - Nederlands Soortenregister. – https://doi.org/10.15468/rjdpzy.

Decou, V.Gh., 1973. Recherches sur les Coléoptères hypogés de Cuba. III. Catopidae-Catopinae: *Proptomaphaginus apodemus* Szymczakowski. – Résultats Des Expéditions Biospéologiques Cubano-roumaines à Cuba 1: 367–372.

Decou, V.Gh. & C. Juberthie, 1969. Sur l'élevage et le développement de *Sophrochaeta oltenica* Jeann. et Mall: description de la larve du premier stade. – Annales de Spéléologie 24 (3): 579–593.

Deleurance, S., 1957a. Biologie larvaire et morphologie externe nymphale d'*Antrocharis querilhaci* L. – Notes biospéologiques 12: 13–16.

Deleurance, S., 1957b. Description de la morphologie externe larvaire de *Diaprysius serullazi* Peyer. (Col. Bathysciitae). – Notes biospéologiques 12 (1): 17–22.

Deleurance, S., 1957c. Cycle évolutif des larves de *Troglodromus bucheti gaveti* (S. C. D.), *Bathysciella jeanneli* (Ab.) et *Diaprysius serullazi* (P.). – Comptes rendus hebdomadaires des séances de l'Académie des sciences 244 (2): 2318–2319. https://gallica.bnf.fr/ark:/12148/bpt6k7215/f478.item.

Deleurance, S., 1958a. Biologie et morphologie larvaire d'*Isereus serullazi* F., *Isereus colasi* Bon. et *Cytodromus dapsoïdes* Ab. – Comptes rendus hebdomadaires des séances de l'Académie des sciences 246 (23): 3286–3287. https://gallica.bnf.fr/ark:/12148/bpt6k723q/f1244.item.

Deleurance, S., 1958b. Morphologie de la larve de *Bathysciella jeanneli* Ab. (Coléoptère Bathyscinae). – Comptes rendus hebdomadaires des séances de l'Académie des sciences 246 (12): 1925–1927.

Deleurance, S., 1958c. La contraction du cycle évolutif des Coléoptères *Bathysciinae* et *Trechinae* en millieu souterreain. – Comptes rendus hebdomadaires des séances de l'Académie des sciences 247 (1): 752–753. https://gallica.bnf.fr/ark:/12148/bpt6k31993/f772.item.

Deleurance, S., 1959. Sur l'écologie et le cycle évolutif des *Choleva angustata* Fab. et *fagniezi* Jeann. (Coléoptères Catopides). – Annales de Spéléologie 14 (3): 339–341.

Deleurance, S., 1961. Morphologie des larves de *Royerella tarissani* Bedel et *Leptodirus hochenwarti* Schm. – Annales de Spéléologie 16 (2): 193–198.

Deleurance, S., 1965. Biologie et morphologie larvaire du *Paraspeonomus vandeli* Coiff. (Coléoptères *Bathysciinæ*). – Comptes rendus hebdomadaires des séances de l'Académie des sciences 260: 701–703. https://gallica.bnf.fr/ark:/12148/bpt6k4016x/f731.item.

Deleurance-Glaçon, S., 1963. Recherches sur les coléoptères troglobies de la sous-famille des Bathysciinae. – Annales des Sciences Naturelles, Zoologie 12 (5): 1–172.

Deuve, T., 2018. What is the epipleurite? A contribution to the subcoxal theory as applied to the insect abdomen. – Annales de la Société entomologique de France (N.S.) 54 (1): 1–26. https://doi.org/10.1080/00379271.2018.1431568.

Eichelbaum, F., 1901. Die Larven von *Catops Watsoni* Spence und *Catops picipes* (?) Fbr. – Berliner entomologische Zeitschrift 46: 9–14. https://www.biodiversitylibrary.org/page/32650596.

Emden, F.I. van, 1957. The taxonomic significance of the characters of immature insects. – Annual Review of Entomology 2 (1): 91–106.

Falcoz, L., 1914. Contribution à l'étude de la faune des microcavernes.–Faune des terriers et des nids.. – Université de Lyon, Lyon, 185 p. https://doi.org/10.5962/bhl.title.2479.

Fieffé, C., 1965a. Morphologie externe de la nymphe de *Speophyes lucidulus* Delarouzée (Coléoptère Bathysciinae de la tribu des Bathysciae groupe des Théléomorphes). – Annales de Spéléologie 20 (2): 295–299.

Fieffé, C., 1965b. Morphologie de la larve de *Speophyes lucidulus* Delarouzée (Coléoptère Bathysciinae de la tribu des Bathysciini, groupe des Théléomorphes). – Annales de Spéléologie 20 (3): 401–407.

Franciscolo, M. E., 1948. Nota preliminare sulla Larva della *Parabathyscia tigullina* Binaghi e notizie sulla Tana delle Streghe preso Rapallo. – Bollettino della Società Entomologica Italiana 77 (7): 51–54.

Franciscolo, M. E., 1950. Res Ligusticae LXXI. La Fauna della Tann-a do Balou No. ll. LI e descrizione della Larva di *Bathysciola pumilio* Reitter. – Annali del Museo civico di storia naturale 64: 111–129. https://www.biodiversitylibrary.org/page/35422546.

Franciscolo, M. E., 1953. Studio comparativo sulle larve mature delle specie liguri cavernicole del genere *Parabathyscia* Jeann. – In: Communications, Vols. Section III - Biologie: pp. 95–112. Premier Congrès International de Spéléologie.

Giachino, P. M. & D. Vailati, 1993. Monografie di Natura Bresciana 18: Revisione degli Anemadinae Hatch, 1928 (Coleoptera Cholevidae), 314 p. – Museo Civico di Scienze Naturali di Brescia, Brescia, 314 p. https://www.comune.brescia.it/sites/default/files/2023-12/mono18-completa.pdf.

Glaçon, S., 1953. Description des larves jeunes de *Speonomus longicornis* Saulcy et *Speonomus pyreneaus* Lespès. – Notes Biospéologiques 8: 17–25.

Glaçon, S., 1955. Remarques sur la morphologie et la biologie de quelques larves de Bathysciinæ cavernicoles. – Comptes rendus hebdomadaires des séances de l'Académie des sciences 240 (1): 679–681. https://gallica.bnf.fr/ark:/12148/bpt6k3192x/f679.item.

Gnaspini, P., 1993a. Brazilian Cholevidae (Coleoptera), with emphasis on cavernicolous species. IV. *Adelopsis (Iutururuca)* - Biology and description of larvae. – Mémoires de Biospéologie 20: 91–99. https://repositorio.icmbio.gov.br/handle/cecav/733.

Gnaspini, P., 1993b. Brazilian Cholevidae (Coleoptera), with emphasis on cavernicolous species. III. *Dissochaetus* larvae, with description of a new feature. – Revista Brasileira de Entomologia 37 (3): 545–553.

Hayashi, N., 1986. Larvae. – In: K. Morimoto & N. Hayashi (Eds), The Coleoptera of Japan in color, Vol. 1: pp. 202–218. Hoikusha Publishing Company, Osaka.

Heun, C., 1955. Biologie und Ökologie von *Choleva holsatica* Ihss. & Ben. – Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museum Hamburg 1 (7): 195–234.

Hubbard, H. G., 1880. Two day's collecting in Mammoth Cave. – American Entomologist 3: 34–40, 79–84.

Jakubec, P., 2016. Thermal summation model and instar determination of all developmental stages of necrophagous beetle, *Sciodrepoides watsoni* (Spence) (Coleoptera: Leiodidae: Cholevinae). – PeerJ 4: e1944. https://doi.org/10.7717/peerj.1944.

Jeannel, R., 1908. Biospéologica V. Coléoptères (première série). – Archives de Zoologie Expérimentale et Générale (4) 8: 267–326. https://hdl.handle.net/2027/hvd.hc4k3y?urlappend=%253Bseq=393%253Bownerid=27021597765591829-411.

Jeannel, R., 1909. Biospéologica X. Coléoptères (seconde série). – Archives de Zoologie Expérimentale et Générale (5) 1: 447–532. https://hdl.handle.net/2027/hvd.hc4k42?urlappend=%253Bseq=553%253Bownerid=27021597765584803-575.

Jeannel, R., 1911. Revision des Bathysciinae (Coleopteres silphides): morphologie, distribution géographique, systématique, 798 p. – Libraire A. Schulz, Paris, 798 p. https://doi.org/10.5962/bhl.title.63151.

Jeannel, R., 1922. Biospeologica 47. Silphidae Catopinae (Coléopterès) (deuxième série) avec une étude phylogénique et paléogéographique de la sous-famille. – Archives de Zoologie Expérimentale et Générale 61 (1): 1–98. https://hdl.handle.net/2027/wu.89098735533?urlappend=%253Bseq=149%253Bownerid=13510798897836617-155.

Kilian, A., 1998. Morphology and phylogeny of the larval stages of the tribe Agathidiini (Coleoptera: Leiodidae: Leiodinae). – Annales Zoologici 48 (3): 125–220.

Kilian, A., 2007. Comparative morphology of larval Camiarinae (Coleoptera: Leiodidae). Part I. Genus *Paragyrtodes* Szymczakowski 1966. – Zootaxa 1640 (1): 1–39. https://doi.org/10.11646/zootaxa.1640.1.1.

Kilian, A., 2012. Phylogenetic analysis of Camiarinae (Coleoptera: Leiodidae) based on larval morphology. – Annales Zoologici 62 (1): 11–68. https://doi.org/10.3161/000345412X633667.

Kilian, A. & A. Mądra, 2015. Comments on the biology of *Sciodrepoides watsoni watsoni* (Spence, 1813) with descriptions of larvae and pupa (Coleoptera: Leiodidae: Cholevinae). – Zootaxa 3955 (1): 45–64. https://doi.org/10.11646/zootaxa.3955.1.2.

Kilian, A. & A. F. Newton, 2017. Morphology of the immature stages of *Platycholeus* Horn, 1880 (Coleoptera: Leiodidae: Cholevinae: Leptodirini). – Zoologischer Anzeiger 266: 158–168. https://doi.org/10.1016/j.jcz.2016.11.007.

Kilian, A. & A. F. Newton, 2021. Unique larval morphology of *Prionochaeta opaca* (Say, 1825) (Coleoptera: Leiodidae: Cholevinae: Cholevini), the only Nearctic representative of Cholevina. – Zoologischer Anzeiger 292: 111–125. https://doi.org/10.1016/j.jcz.2021.03.005.

Kilian, A., J. Růžička & L. P. Sandoval Salinas, 2023. Morphology of very unusually modified larva of myrmecophilous Cholevinae (Coleoptera: Leiodidae). – In: Abstracts of the Immature Beetles Meeting 2023, Vol. 63: pp. 479–483. Immature Beetles Meeting 2023. https://www.biotaxa.org/AEMNP/article/view/84927.

Klink, R. van, T. August, Y. Bas, P. Bodesheim, A. Bonn, F. Fossøy, T. T. Høye, E. Jongejans, M. H. M. Menz, A. Miraldo, T. Roslin, H. E. Roy, I. Ruczyński, D. Schigel, L. Schäffler, J. K. Sheard, C. Svenningsen, G. F. Tschan, J. Wäldchen, V. M. A. Zizka, J. Åström & D. E. Bowler, 2022. Emerging technologies revolutionise insect ecology and monitoring. – Trends in Ecology & Evolution 37 (10): 872–885. https://doi.org/10.1016/j.tree.2022.06.001.

Kloeke, E. van O., C. Huijbers, K. Beentjes, J. Kamminga, P. Bakker & W. Kissling, 2022. ARISE: Building an infrastructure for species recognition and biodiversity monitoring in the Netherlands. – Biodiversity Information Science and Standards 6: e93613. https://doi.org/10.3897/biss.6.93613.

Krogerus, R., 1927. Studien über *Choleva*-Arten. II. Lebensweise und Entwicklung von *Choleva aquilonia* Krog. – Notulae entomologicae 7: 1–7.

Lawrence, J. F., 1991. Order Coleoptera. – In: F.W. Stehr (Ed), Immature insects, Vol. 2: pp. 144–658. Kendall/Hunt Publishing Co., Dubuque, Iowa.

Ledesma, E., A. Jiménez-Valverde, J. M. Salgado & V. M. Ortuño, 2022. Cholevinae (Coleoptera: Leiodidae) of the Sierra de Guadarrama National Park, Spain: occurrence in the MSS of a siliceous landscape. – Zoosystema 44 (4): 125–149. https://doi.org/10.5252/zoosystema2022v44a4.

Meier, R. & G. S. Lim, 2009. Conflict, convergent evolution, and the relative importance of immature and adult characters in endopterygote phylogenetics. – Annual Review of Entomology 54: 85–104. https://doi.org/10.1146/annurev.ento.54.110807.090459.

Menozzi, C., 1939. La fauna della Grotta della Suja sul Monte fascie (Genova) ed osservazioni biologiche sulla *Parabathyscia doderoi* Fairm. (Coleopt. Catopidae), con descrizione della larva e delle caratteristiche morfologiche del suo intestino e di quello dell'adulto. – Memorie della Società Entomologica Italiana 18: 129–154.

Packard, A. S., 1888. The cave fauna of North America, with remarks on the anatomy of the brain and origin of the blind species. – Memoirs of National Academy of Sciences 4 (1): 1–228. https://doi.org/10.5962/bhl.title.51841.

Paulian, R., 1937. Contribution a l'etude des larves de Staphylinoidea (3 note). Sur quelques larves de Catopides. – Revue Francaise d'Entomologie 4: 239–245.

Paulian, R., 1941. Les premiers états des Staphylinoidea. Etude de morphologie comparée. – Mémoires du Muséum national d'histoire naturelle: Nouvelle série 15 (1): 1–361.

Peck, S. B. & P. Gnaspini, 1997. Review of the myrmecophilous *Ptomaphagus*, subgenus *Echinocoleus* (new status), of North America (Coleoptera Leriodidae Cholevinae Ptomaphagini). – The Canadian Entomologist 129 (1): 93–104. https://doi.org/10.4039/Ent12993-1.

Perreau, M., 1987. Description de la larve de *Choleva kocheri* Henrot (Coleoptera Catopidae). – Biocosme mésogéen 4 (1): 37–41.

Perreau, M., 2000. Mémoires de la Société entomologique de France 4: Catalogue des Coléoptères Leiodidae Cholevinae et Platypsyllinae, 460 p. – Société entomologique de France, Paris, 460 p.

Peyerimhoff, P. de, 1906. Sur quelques larves de Coléoptères cavernicoles. – Bulletin de la Société entomologique de France 11 (8): 109–118. https://doi.org/10.3406/bsef.1906.23904.

Peyerimhoff, P. de, 1907. Deux types nouveaux de larves Silphidae (Col.). – Annales de la Société Entomologique de France 76: 83–88. https://www.biodiversitylibrary.org/page/8242847.

Pinto, S., 2015. Characteristics for identification of larval Cholevinae (Coleoptera: Leiodidae). – Leiden University, Leiden, Netherlands, 23 p. https://cholevidae.myspecies.info/sites/cholevidae.myspecies.info/files/2015_Pinto_Susanne_BSc%20report_Terrestrial%20zoology.pdf.

Renkens, K., 2015. Characters for identification of larval Cholevinae (Coleoptera): a study on 13 *Catops*, 1 *Apocatops*, and 1 *Fissocatops* species. – Leiden University, Leiden, Netherlands, 7 p.

Rossi, R. V., 1976. Biology and external morphology of the larvae of *Boldoria (Pseudoboldoria) bergamasca* Jeannel and of *B. malanchinii* Pavan. – Annales de Spéléologie 31: 253–262.

Samuelson, G. A., 1964. Coleoptera: Hydraenidae, Leptodiridae (larvae). – In: Pacific Insects Monograph 7: Insects of Campbell Island: pp. 624–627. Bishop Museum, Hawaii, US. http://hbs.bishopmuseum.org/pim/pim7.htm.

Schilthuizen, M., C. Scholte, R. E. J. van Wijk, J. Dommershuijzen, D. van der Horst, M. M. zu Schlochtern, R. Lievers & D. S. J. Groenenberg, 2011. Using DNA-barcoding to make the necrobiont beetle family Cholevidae accessible for forensic entomology. – Forensic Science International 210 (1): 91–95. https://doi.org/10.1016/j.forsciint.2011.02.003.

Schilthuizen, M., P. de Jong, R. van Beek, T. Hoogenboom & M. M. zu Schlochtern, 2016. The evolution of asymmetric genitalia in Coleoptera. – Philosophical Transactions of the Royal Society B: Biological Sciences 371 (1710): 20150400. https://doi.org/10.1098/rstb.2015.0400.

Schilthuizen, M., W. van Oostenbrugge, S. Visser, M. van der Meer, R. Delval, C. Dias, H. Köster, R. Maarschall, N. Peeters, P. Venema, R. Zaremba, C. Beltrami, M. Rossato, L. Latella, F. Nieuwenhuis, N. de Rop, I. Njunjić, M. Perreau & J. M. Koene, 2021. *Ptomaphagus thebeatles* n. sp., a previously unrecognized beetle from Europe, with remarks on urban taxonomy and recent range expansion (Coleoptera: Leiodidae). – Contributions to Zoology 90 (1): 1–20. https://doi.org/10.1163/18759866-BJA10007.

Schiødte, J. C., 1861. De metamorphosi eleutheratorum observationes: bidrag til insekternes udviklingshistorie, 558 p. – Thieles Bogtrykkeri, Copenhagen, Denmark. https://doi.org/10.5962/bhl.title.8797.

Schut, P.-O. & M. Delalandre, 2015. L'échec d'une discipline: Montée et déclin de la spéléologie en France (1888-1978). – Revue d'histoire des sciences 68 (1): 81–107. https://doi.org/10.3917/rhs.681.0081.

Sendra, A., J. Tormos & X. Pardo, 1985. Morfología larval de *Anillochlamys moroderi* Bol. (Col., Catopidae, Bathysciinae). – Boletín de la Asociación española de Entomología 9: 279–284. https://www.entomologica.es/publicaciones-boletin/en/art290.

Sendra, A., J. Tormos & X. Pardo, 1987. El desarrollo postembrionario de *Spelaeochlamys verai* (Col., Catopidae, Bathysciinae). – Boletín de la Asociación española de Entomología 11: 287–292. https://www.entomologica.es/publicaciones-boletin/art364.

Silvestri, F., 1912. Contribuzioni alla conoscenza dei Mirmecofili. ii. Di alcuni Mirmecofili dell'Italia meridionali e della Sicilia. – Bollettino del Laboratorio di Zoologia Generale e Agraria della Facoltà Agraria in Portici 6: 222–245. https://biostor.org/reference/58546.

Strambi, C., 1963. Étude de la morphologie larvaire d'un Coléoptère de la famille des Catopidae (sousfamille des Catopinae) *Choleva angustata* Fabricius. – Annales de Spéléologie 18 (4): 495–510.

Strambi, C., 1964. Morphologie nymphale de *Choleva angustata* Fabricius (Coleoptera Catopide de la sous famille des Catopinae). – Annales de Spéléologie 19 (3): 581–585.

Szymczakowski, W. & D. Plath, 1976. Catopidae aus dem Nepal-Himalaya (Ins., Col.). – Senckenbergiana Biologica 57 (1): 35–48.

Tanaka, M., 1972. Descriptions of two larvae and a pupa of Catopidae from Japan (Coleoptera). – Bulletin of the Japan Entomological Academy 6 (2): 41–46.

Vandel, A., 1953. Le laboratoire souterrain du C.N.R.S. à Moulis (Ariège). – La Nature (3224): 353–356. https://cnum.cnam.fr/pgi/fpage.php?4KY28.148/357/100/396/5/387.

Weber, L., 1899. Über Larven von Höhlenkäfer. – Illustrierte Zeitschrift für Entomologie 4 (1): 1–2. https://www.biodiversitylibrary.org/page/31664061.

Weber, L., 1902. Die Larve von *Aphaobius Paganettii* Gglb. – Allgemeine Zeitschrift für Entomologie 7: 17–19. https://www.biodiversitylibrary.org/page/25327505.

Wheeler, Q. D., 1990. Morphology and ontogeny of postembryonic larval *Agathidium* and *Anisotoma* (Coleoptera, Leiodidae). – American Museum Novitates 2986: 1–46. https://digitallibrary.amnh.org/handle/2246/5076.

Xambeu, V., 1889. Description de deux larves de coléoptères. – Revue d'entomologie, Caen 8: 332–334.

Xambeu, V., 1892. Moeurs et métamorphoses d'insectes. Suite. – Annales de la Société Linnéenne de Lyon 39: 135–194. https://doi.org/10.3406/linly.1892.4029.

Xambeu, V., 1894. Moeurs et métamorphoses d'insectes. Cinquième mémoire. – Annales de la Société Linnéenne de Lyon 41: 107–156. https://doi.org/10.3406/linly.1894.4048.

Xambeu, V., 1899. Moeurs et métamorphoses d'insectes (suite). – Annales de la Société Linnéenne de Lyon 45: 157–211. https://www.biodiversitylibrary.org/page/54607679.

Xambeu, V., 1900. Moeurs et métamorphoses des insectes (9e mémoire, 2e partie) (suite et fin). – Revue d'entomologie, Caen 19 (3): 29–56.

Xambeu, V., 1903. Moeurs et métamorphoses des insectes (suite). Mélanges entomologiques. – Annales de la Société Linnéenne de Lyon 49: 95–160. https://doi.org/10.3406/linly.1903.4135.

Xambeu, V., 1904. Moeurs et métamorphoses des insectes (suite). Mélanges entomologiques. – Annales de la Société Linnéenne de Lyon 50: 79–129. https://doi.org/10.3406/linly.1904.4147.

Xambeu, V., 1916. Moeurs et métamorphoses des insectes. 16e mémoire. 4e fascicule. – Annales de la Société Linnéenne de Lyon 62: 25–42. https://doi.org/10.3406/linly.1916.4242.

Zaitsev, A. A. & A. S. Tokareva, 2021. Larval description of *Nodynus leucofasciatus* Lewis, 1879 (Coleoptera: Staphylinidae: Apateticinae) with discussion of Staphylinidae chaetotaxy. – Russian Entomological Journal 30 (4): 482–499. https://doi.org/10.15298/rusentj.30.4.10.

Zwick, P., 1966. Fortpflanzung von *Choleva holsatica* Bck. & Ihss. in Gefangenschaft. – Entomologische Blätter 62 (2): 70–77.

Zwick, P., 1978. Bestimmungstabelle für die Larven der Catopidae. – In: B. Klausnitzer, Bestimmungsbücher zur Boden-Fauna Europeas: Ordnung Coleoptera (Larven), Vol. 10. Springer Netherlands, Dordrecht. https://doi.org/10.1007/978-94-009-9975-6.

Zwick, P., 1979. Contributions to the knowledge of Australian Cholevidae (Catoptidae auct.: Coleoptera). – Australian Journal of Zoology Supplementary Series 27 (70): 1–56. https://doi.org/10.1071/ajzs070.