

A revision of *Choleva agilis* (Illiger, 1798) and related species (Coleoptera: Staphylinoidea: Cholevidae)

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The *Choleva agilis*-group is revised. The three species are redescribed and their zoogeography is discussed. The phylogeny of the three species is hypothesized. *Choleva jailensis* Jeannel, 1923 and *C. agilis clermonti* van der Wiel, 1931 are new synonyms of *C. agilis* (Illiger, 1798). *C. lederiana* var. *brevicollis* Krogerus, 1926, is a new synonym of *C. lederiana* Reitter, 1901. The cavernicolous taxon *gracilenta* Szymczakowski, 1957, formerly regarded as a subspecies of *C. lederiana*, is transferred to *C. septentrionalis* Jeannel, 1923.

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Introduction

The taxonomy and distribution of the several species in the *Choleva agilis* (Illiger)-group sensu stricto have been obscure till this moment, due to misinterpretations and underestimations of the variability of sexual and other characters in these species. In this paper, the distinguishing characters of the taxa have been revised and an account of their geographical distribution is presented.

In his "Monographie des Catopidae" Jeannel (1936) divided the subgenus *Choleva* Latreille s. str. into eight species-groups. As in his earlier work on this genus (Jeannel, 1923), he based his classification mainly on differences in the structure of

primary and secondary sexual characters, of both males and females. His general classification of *Choleva* has never been contradicted since. What gave rise to doubts, however, was the invariability that these characters were thought to have. For instance, Van der Wiel (1931) demonstrated a substantial variation in the shape of both aedeagus and male metatrochanter of *Choleva reitteri* Petri. Szymczakowski (1963) did the same for the metatrochanter of male *Choleva glauca* (Britten) and many other examples may be given.

Choleva agilis, a well known European species, is another one that shows a considerable instability of the sexual characters, especially the male metatrochanter and the female genital tergite. This instability must have struck several authors, who as a result began to doubt the taxonomic status of two species, closely related to *C. agilis*, and differing in (among other things) the shape of these structures. These species were *C. aquilonia* Krogerus, 1926 (now known as *C. lederiana* Reitter, 1901) and *C. septentrionis* Jeannel, 1923.

After having seen a few specimens of *C. aquilonia* sent to him by Krogerus, Van der Wiel (1931) observed: "the differences are less clear in these specimens than would be expected from the description and the pictures: the tooth on the hind trochanter for instance, is rather narrow and almost straight [...] Considering the variability in *C. agilis* Ill. I consider *C. aquilonia* Krog. to be a subspec. of this species. Mr. Jeannel, whom I sent the Finnish specimens, completely agreed with my view" (my translation). Jeannel (1936) however, apparently changed his opinion on this matter and reported *C. aquilonia* as a distinct species in his monograph. Meanwhile, Krogerus seemed to have decided that *C. septentrionis* were a mere variation of his *C. aquilonia*, for several *C. septentrionis* specimens from the collection of the Bergen Zoologisk Museum (Norway) bear his identification labels: "*C. aquilonia* Krog. v. *septentrionis* Jeann.". Palmqvist (1949) spoke of "*Choleva septentrionis* v. *aquilonia*" and reported mixed forms of this species and *C. agilis*. For that reason he revealed the suspicion of his colleague Palm that *C. agilis* merges into *C. aquilonia* via transitional forms.

It is evident that the matter has become quite complicated, especially since several other taxa (species, subspecies and variations, some of which cavernicolous), closely related to *C. agilis* should also be taken into consideration. Szymczakowski (1957) dwelled at length on this entire problem, and concluded: "because of the great variability of *C. agilis* (Ill.) [...], it is doubtful if one could maintain the rank of species, not only in *C. aquilonia* Krog., that has more than once been disputed, but also in *C. septentrionis*, that has been invariably recognized: I cannot solve this problem, before having obtained ample material from different areas, especially of *C. agilis* (Ill.)" (my translation). Since Szymczakowski has never again returned to the matter of *C. agilis* and its related species, in this paper I will try to present an analysis of the variability, taxonomy, biogeography and phylogeny of these species.

General morphology of the *Choleva agilis*-group

Externally, *Choleva agilis* and its related species form a distinct group within the genus. They can easily be recognized by their relatively robust habitus, by the prono-

tum, that has its greatest width in the caudal part, and by the metatrochanter of the male, that bears a short tooth. Internally, they can be characterized by the paired armature of the internal sack of the aedeagus, consisting of several rows of short, similarly shaped spines, and one large ventral tooth that is caudally crenated or indented. The genital tergite of the female is square or subtriangular (Jeannel, 1936).

Definitions of the sexual characters are given below:

Male.— Primary sexual characters. The male genitalia consist of a tube-like, unpaired structure, the aedeagus, at the ventral side with an orifice, that is covered by the two ligulae. The aedeagus is connected at its base to the two parameres, situated on either side of the aedeagus. In copulation, both aedeagus and parameres remain partly outside the female body. The actual copulative organ is the internal sack, that, in rest, is inside the aedeagus but, in action, may bulge through the orifice and enter the female sexual organs. The internal sack jams in the internal sexual structures of the female as it is armed with several rows of spines. At its base a large tooth is present, the ventral tooth, that articulates with the ventral side of the genital tergite of the female (Jeannel, 1936).

Secondary sexual characters. Most secondary sexual characters can be found on the legs of the male. The protarsus is usually widened in males, when compared to females. The mesotibia is peculiarly modified: flattened and tortuous. The proximo-caudal corner of the metatrochanter bears a sharp tooth.

Female.— Primary sexual characters. The only primary sexual structure dealt with in this paper is part of the genital segment, viz. the genital tergite. When in rest, this sclerite is situated inside the abdomen, beneath the pygidium.

Secondary sexual characters. The only striking secondary sexual structure in certain taxa in the *C. agilis*-group s. str. is the elongation of the elytral apex. This feature is found in many other female Coleoptera of the Staphylinoidea. Within the genus *Choleva* a similar character is present in females of the *C. nivalis*-group and the *C. sturmi*-group (Jeannel, 1936).

Abbreviations

- BMNH: The Natural History Museum, London.
- ITZ: Instituut voor Taxonomische Zoölogie, Amsterdam.
- MP: Muséum National d'Histoire Naturelle, Paris.
- NMI: National Museum of Ireland, Dublin.
- NNM: Nationaal Natuurhistorisch Museum, Leiden.
- NRS: Naturhistoriska Riksmuseet, Stockholm.
- RMS: Royal Museum of Scotland, Edinburgh.
- TMB: Természettudományi Múzeum Allatára, Budapest.
- UZMH: Universitetets Zoologiska Museum, Helsinki.
- ZIL: Zoologicheski Institut, Leningrad.
- ZMB: Zoologisches Museum der Humboldt-Universität, Berlin.
- ZMBG: Zoologisk Museum, Bergen.

Species accounts

Choleva agilis (Illiger, 1798)

(fig. 1)

Ptomaphagus agilis Illiger, 1798: 88.

Choleva agilis agilis; Jeannel, 1936: 262, 264, figs. 506, 551-555.

Choleva jailensis Jeannel, 1923: 68, figs. 32, 85. *Syn. nov.*

Choleva agilis forma clermonti van der Wiel, 1931: 203, figs. 44-48. *Stat. nov.*

Material.—1 ♂ holotype: "7403", "[illegible abbreviation] Königsberg (Pr.) Kugelann leg.", "agilis Ill. Typus 1798" (red label), "agilis Ill. Ptomaph. ag. Pr. Choleva a. Spence Catops fuscus Gyll. Chol. testacea Latr.", "Zool. Mus. Berlin". "Umpräpariert vii.1940 K. Sokolowski-Hbg.", "Choleva agilis (Illiger) det. Schilthuizen 1987", ZMB. 1 ♂ paratype: "7403", "[illegible abbreviation] Königsberg (Pr.) Kugelann leg.", "Paratypus Ill." (red label), "Umpräpariert vii.1940 K. Sokolowski-Hbg.", "agilis Ill. det. K. Sokolowski", "Zool. Mus. Berlin", "Choleva agilis (Illiger) det. Schilthuizen 1987", ZMB. 1 ♂ paratype: "49", "7403", "1 original zu agilis Sturm (Berlin, Sauppel)", "Paratypus" (red label), "Umpräpariert vii.1940 K. Sokolowski-Hbg.", "agilis Ill. det. K. Sokolowski", "Zool. Mus. Berlin", "Choleva agilis (Illiger) det. Schilthuizen 1987", ZMB. 1 ♀ paratype: "49", "7403", "2 original zu agilis Sturm (Berlin, Sauppel)", "Paratypus" (red label), "Umpräpariert vii.1940 K. Sokolowski-Hbg.", "agilis Ill. det. K. Sokolowski", "Choleva agilis (Illiger) det. Schilthuizen 1987", ZMB. 1 ♀ lectotype of *C. jailensis* Jeannel (here designated): "Iaila-Gebirge Krim, Moczarski", "TYPE" (red label), "Muséum Paris Coll. R. Jeannel 1931", "Breit", "jailensis m. R. Jeannel det.", "Choleva agilis (Illiger) det. Schilthuizen 1987", MP. 1 ♂ holotype of *C. agilis clermonti* van der Wiel: "Type: 1930 Choleva agilis Ill. subsp. *Clermonti* v.d. W.", "Choleva agilis Ill. det. v.d. W. 1931", "♂", "coll. J. Clermont", "5", "Pyrén. or.", "Choleva agilis (Illiger) det. Schilthuizen 1983", ITZ. 2 ♀♀ paratypes of *C. agilis clermonti* van der Wiel: "Cotype: 1930, Choleva agilis Ill. ♀ subsp. *Clermonti* v.d. W.", "agilis subsp. nov. R. Jeannel det.", "Coll. van der Wiel", "♀", "Samatan, Gers, J. Clermont", "Choleva agilis (Illiger) det. Schilthuizen 1983"

Additionally examined about 300 specimens from France, Italy, Yugoslavia, U.S.S.R., Switzerland, Austria, Poland, DDR, BRD, Belgium, Great Britain, Ireland, The Netherlands, Denmark and Sweden (ITZ, NNM, RMS, BMNH, NMI, UZMH, ZIL, ZMB, ZMBG, ZMK, collection of B.J. van Vondel, collection of G. Stobbe, author's collection).

Males.—The aedeagus (figs. 3, 5) is apically narrowed and bent ventrad (fig. 3), but not as strongly as in *C. lederiana* and *C. septentrionis*. In a few of the examined specimens, the apical part of the aedeagus is more elongated, in dorsal view almost equal to *C. lederiana* and *C. septentrionis*. In lateral view however, the relatively slight downward bend is always recognizable in such specimens (figs. 6-9).

The ventral tooth of the internal sack is apically rather broad and bears three or more teeth. It is slightly asymmetric and there is a tendency to a leftward bend (figs. 21, 22).

The tooth on the metatrochanter is rather variable in size and shape (figs. 23-27). It may be short and straight or large and hook-like. The most frequent form is the one shown in fig. 25.

Females.—The shape of the genital tergite (fig. 32) varies from elongate triangular to diamond-shaped (figs. 41-48). Its caudal border may be almost straight (fig. 41) or sharply angular (figs. 44-46); it may also be supplied with a curious lobe as in fig. 42. Although most of these shapes are not found in *C. lederiana* and *C. septentrionis*, it is hard to present a comprehensive definition of the genital tergite in *C. agilis*. Two features however, appear to be characteristic in this species: the genital tergite has its

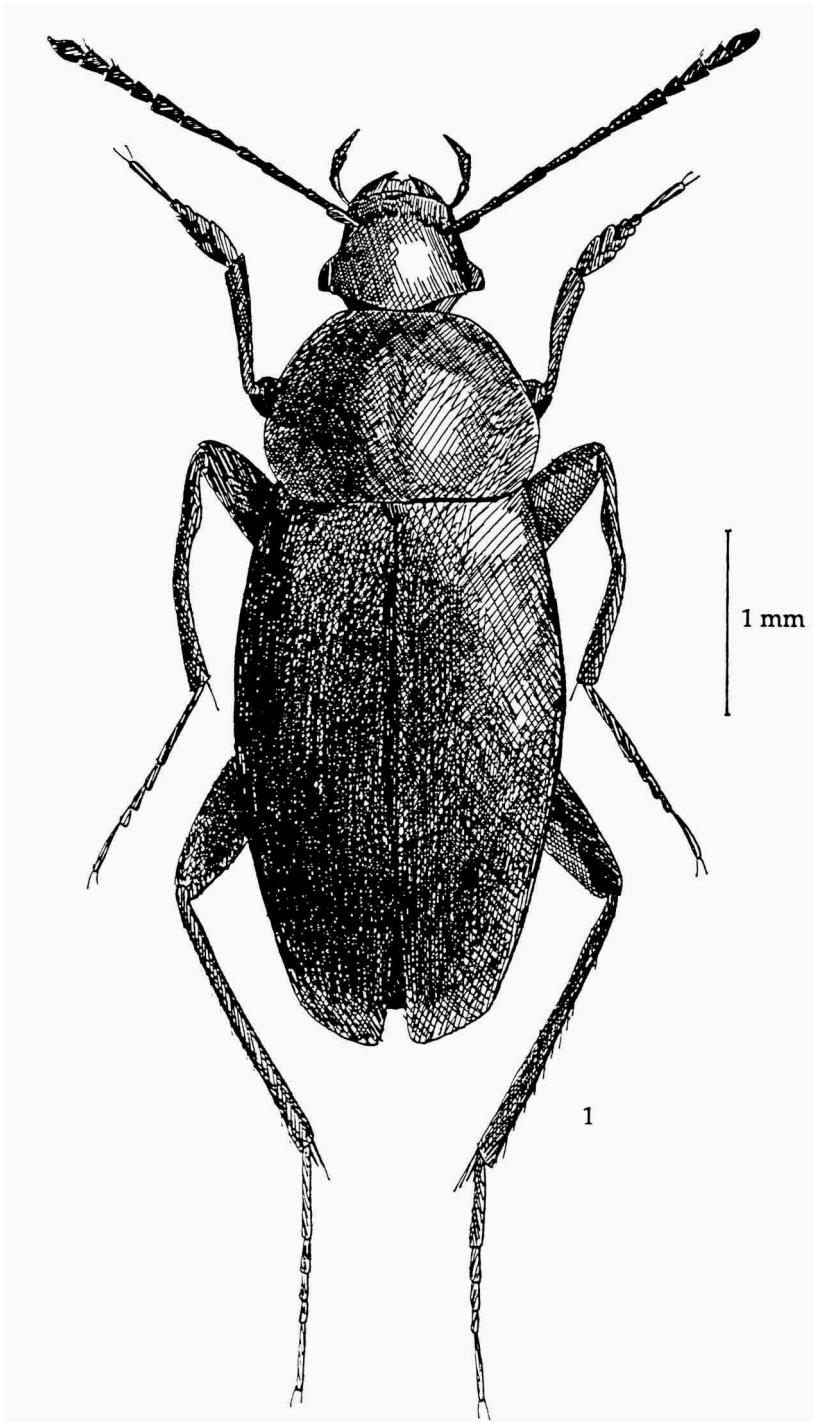


Fig. 1. *Choleva agilis* (Illiger, 1798), ♂, habitus, dorsal aspect; Netherlands, Oostvoorne (author's collection).

greatest width in its caudal part and has caudolateral corners that are rounded, not angular.

The apex of each elytron is rounded, though in the female it is less so than in the male. Still, the elytral apices are not angular or elongated as in females of *C. septentrionis*.

In 1923 Jeannel described *C. jailensis*, on the basis of two females from Jaila Mountains (Crimea). In his key to the species Jeannel (1936) characterized *C. jailensis* as having the pronotum 1.7 times as wide as long (versus 1.5 times in *C. agilis*), the 9th antennal segment 1.5 times as long as wide (versus hardly longer than wide in *C. agilis*), and the apical border of the genital tergite straight (versus convex in *C. agilis*).

After having seen other material from the Crimea, namely a female of *C. agilis* from Jalta (ZIL), I started to doubt the taxonomic status of *C. jailensis*. One of the type-specimens (MP), appeared to be a female of *C. agilis*, with no exceptional features, apart from its rather robust habitus. The pronotal index is 1.5, which is normal in *C. agilis*. The apical border of the genital tergite is not, as Jeannel reported, straight, but slightly convex, and shows a shape that is found in many females of *C. agilis*. I think its robustness is what caused Jeannel to believe it represents a distinct species. Southeastern-European specimens tend to be more thick-set, but I have not seen enough material from these areas to conclude whether this form has subspecific status or not. At the moment, *C. jailensis* must be considered a new synonym of *C. agilis*.

The subspecies *C. agilis clermonti* Van der Wiel was described in 1931 on the basis of five specimens from Samatan (France). Van der Wiel gave three features by which *C. agilis clermonti* was supposed to differ from the typical *C. agilis*: the elongated genital tergite, the relatively slender aedeagus, and the very large and hooked tooth on the male metatrochanter.

I studied the "type" (female) and two "cotypes" (males) of this subspecies. Of these, the female and one male show no exceptionalities: the elongated genital tergite is not an uncommon feature in *C. agilis* and is found all over its area of distribution. The aedeagi of both males are normally shaped, and so is the metatrochanter of one male. In the other one however, this segment is rather abnormal: its tooth is quite large and hooked (fig. 27). I have not found such an extreme development of the metatrochanter in any other male of *C. agilis* I studied. However, since this character is somewhat variable, and since the other specimen from the same locality shows no such aberration, the rank of subspecies, in my opinion, can not be maintained. The name *clermonti* should apply to a "forma" rather than a subspecies, viz. to such abnormal males as described above.

Immature stages.— Larval stages and pupa have been described by Casale (1975).

Ecology.— *C. agilis* is a rather common species in Western Europe. Towards the east its rarity increases (Horion, 1949). It seems to prefer a wet environment (Van der Wiel, 1931; Sokolowski, 1942; Szymczakowski, 1971). Apparently, it lives in the burrows of mole (*Talpa europaea*), rabbit (*Oryctolagus cuniculus*) and several species of

mice (Sokolowski, 1942). Szymczakowski (1959) reported epigean captures from litter at the banks of streams. In mountainous areas it is, like most *Choleva*, sometimes found in caves (Jeannel, 1936); Coiffait (1955) qualified *C. agilis* as "troglophil". I would like to observe here, that *C. agilis* chooses similar habitats as *C. glauca* with which it is often found together.

Geographical distribution.—In fig. 85 all traceable localities of the studied material have been indicated. Apparently, *C. agilis* is found all over Europe. In the west it reaches Southwestern France. It has not been found at the Iberian side of the Pyrenees. Jeannel (1923a) said: "I do not know it from peninsular Italy, where, however, it must be present" (my translation). Still, no records from Central or Southern Italy are known to me, although it has been reported from Greece (Coiffait, 1955). In the north, it reaches the central part of Great Britain. Since the only Scottish specimen I saw was in fact a *C. septentrionis* (see below), possibly all earlier reports of Scottish captures (Jeannel, 1936) actually refer to this species. It is present in Denmark and in the southern part of Sweden (Halland). Palmqvist (1949) reported a specimen from Helsingborg. To the east the distribution becomes less clear: it is present on the Crimea, in Prussia (Königsberg, type locality), near Jaroslavl (U.S.S.R.) and in Turkey (Anatolia: Amasia, type locality of *Choleva adusta* Reitter, 1899, which is an old synonym of *C. agilis*, see Jeannel, 1936). Several authors (Jeannel, 1936; Szymczakowski, 1959) also named the Caucasus. Probably, it is widely distributed over the U.S.S.R.

Choleva lederiana Reitter, 1901

Choleva lederiana Reitter, 1901: 177.

Choleva aquilonia Krogerus, 1926: 5-6, fig. 2.

Choleva aquilonia var. *brevicollis* Krogerus, 1926: 6. *Syn. nov.*

Material.—1 ♂ holotype: "Altai centr. Leder", "coll. Reitter", "Holotypus [red ink] 1901 *Choleva lederiana* Reitter", "*Ch. lederiana* m. n. sp. 1901", "*Choleva lederiana* Reitter det. Schilthuizen 1987", TMB. 2 ♀♀ paratypes: "Altai centr. Leder", "coll. Reitter", "Paratypus [red ink] 1901 *Choleva lederiana* Reitter", "*Choleva lederiana* Reitter det. Schilthuizen 1987", TMB. 1 ♂ lectotype of *C. aquilonia* Krogerus (here designated): "Lojo", "Krogerus", "*Choleva aquilonia* Krog. m. Krogerus det.", "Mus. Zool. H:fors Spec. typ. No 1599 *Choleva aquilonia* Krog m", "Mus. Zool. Helsinki Loan No. C 7828", "Zool. Mus. Helsinki Loan No C-87 230", "*Choleva lederiana* Rtt. det. M. Schilthuizen 1987", "Lectotype Schilthuizen des. 1987", UZMH. 1 ♀ paralectotype of *C. aquilonia* (here designated): "Lojo", "Krogerus", "637", "*Choleva aquilonia* Krog. ♀ Krogerus det.", "Mus. Zool. H:fors Spec. typ. No. 1560 *Choleva aquilonia* Krog. ♀", "Mus. Zool. Helsinki Loan No. C 7827", "Zool. Mus. Helsinki Loan No C-87 229", "*Choleva lederiana* Rtt. det. M. Schilthuizen 1987", "Paralectotype Schilthuizen des. 1987", UZMH. 2 ♀♀ syntypes of *C. aquilonia* var. *brevicollis* Krogerius from Fischer Peninsula (U.S.S.R.), UZMH.

Additionally examined 99 specimens from Finland, U.S.S.R., Norway and Sweden (ITZ, UZMH, ZIL, ZMB, ZMBG, ZMK, author's collection).

Males.—The aedeagus (figs. 2, 4) is apically more elongated and narrow than in *C. agilis*. The curvature of the apex is strong. The aedeagal shape is quite constant in all studied material. Jeannel (1936) mentioned the existence of a terminal "petit bouton cylindrique" at the extreme apex of the aedeagus. In reality, this "bouton" is the

tip of the bent aedeagus, that shows a sudden bend in the opposite direction. In the strongly curved aedeagus of *C. lederiana*, this feature is more striking than in the slightly curved aedeagus of *C. agilis*, where it is present as well (figs. 14, 15).

The ventral tooth of the internal sack is slender and at the apex rather narrow. Its apex bears one to three (rarely more) teeth. It is slightly asymmetric and tends to be bent to the right (figs. 18-20).

Metatrochanter (fig. 28); Krogerus (1926) described the short and obtuse tooth on the metatrochanter of *C. aquilonia* as a major distinguishing character. As has been observed already by Van der Wiel (1931) and Szymczakowski (1957), this is not a stable character. In a vast material from the type locality of *C. aquilonia* (Torhola Cave near Lohja, Finland, see below) I found males having a "normal", *C. agilis*-like metatrochanter as well as males with a more obtuse tooth on the metatrochanter (figs. 67-70).

A few authors (e. g., Szymczakowski, 1957) have presented the unusually slight modification of the mesotibia as an important character, useful for distinction between *C. lederiana* on the one hand and *C. agilis* and *C. septentrionis* on the other. Reitter (1901) was the first to mention this character. However, after much comparative research I think it is hardly possible to use the mesotibia for recognizing *C. lederiana*. Again, it seems to be a variable character. Moreover, it is hard to establish a measure for this modification, because the impression of its shape depends highly on the angle of view.

Females.—In the shape of the genital tergite, *C. lederiana* seems less variable than *C. agilis*. The shape is mostly clearly ovoid (fig. 33). Sometimes genital tergites as in figs. 38, 39 are found.

Generally, like *C. agilis*, *C. lederiana* shows hardly any sexual dimorphism in the shape of the elytral apices. Some female specimens from the area of the Pallastunturi (one of the old, eroded and rather isolated mountains in the northwest of Finland) show elytra that are apically truncate (fig. 54), whereas those of the males are separately rounded.

Together with the description of *C. aquilonia*, Krogerus (1926) defined a form, occurring on the "Fischer"-Peninsula (U.S.S.R.), as var. *brevicollis*, having quite a broad pronotum (two times as wide as long). I studied these specimens, two females, one of which badly damaged, only consisting of an abdomen with elytra. The pronotal index of the one undamaged specimen is 1.5, which is an almost normal width/length relation, since the pronotal index of females usually is approximately 1.4, as measured in some 20 other females of *C. lederiana* from several localities. Consequently, I do not think that *brevicollis* is a recognizable variety, and the name should be synonymized with *C. lederiana*.

Immature stages.—The larval stages and pupa of *C. aquilonia* have been described by Krogerus (1927). Some differences in number and site of insertion of setae on the mouthparts exist between the drawings by Krogerus and those of the *C. agilis* larva by Casale (1975). Still, without extensive comparison between *C. lederiana* and *C. agilis* larvae, it is impossible to say if any such morphological differences are

of importance.

Ecology.—Very little is known about the ecology of *C. lederiana*. It is known from the Torhola Cave near Lohja, Finland, where it was found feeding on fungi and carrion (Krogerus, 1927). The specimens from other localities apparently were not captured in caves.

Geographical distribution.—In Europe, *C. lederiana* occurs in Finland and in the extreme north of Norway and Sweden. In the U.S.S.R., it has been found on the peninsula of Kola (Jeannel, 1936) and in Carelia. The holotype however, was captured in the Central Altai Mountains, near the Mongolian border. Possibly, *C. lederiana* occurs in large parts of the northern U.S.S.R., reaching Scandinavia in the west. More records from the U.S.S.R. might clarify its actual pattern of distribution. In fig. 82 the European localities of *C. lederiana* are indicated.

Choleva septentrionis septentrionis Jeannel, 1923

Choleva septentrionis Jeannel 1923: 68, fig. 84.

Material.—1 ♀ holotype: "Norvegia Hermann Otto", "Tromsø 1888.vi.23", "Holotypus [red ink] 1923 *Choleva septentrionis* Jeannel", "septentrionis m. R. Jeannel det.", "TYPE [red ink]", "Choleva septentrionis Jeannel det. Schilthuizen 1987", TMB.

Additionally examined 40 specimens from Ireland, Great Britain, Sweden and Norway (NMI, BMNH, ITZ, NRS, UZMH, ZMB, ZMBG).

Males.—The shape of the aedeagus is exactly as in *C. lederiana* (figs. 2, 4). No constant differences could be detected.

The ventral tooth of the internal sack was extracted from two specimens, one of which is shown in fig. 16. As only two specimens were examined for this character, it is impossible to give general remarks on any characteristic properties of the ventral tooth in this species.

No reports in the literature are present on the shape of the metatrochanter. In the specimens that were examined in this study, the tooth on the metatrochanter is short and straight, like in *C. agilis*.

As mentioned before, the modification of the mesotibia is rather variable and hard to judge in all species. In my opinion, it is not useful for distinction between *C. lederiana* and *C. septentrionis septentrionis*.

Females.—The genital tergite is usually characteristically shaped, as shown in fig. 34. Its angular caudal border and the centrally parallel lateral borders are constant features. Generally, its shape resembles fig. 34, but aberrant forms may also be found (figs. 37, 40).

The elongated elytral apices are one of the most striking features. Still, this character is variable, too: a number of females from Loos, Sweden show elytral apices that range from only slightly sinuate to strongly elongate (figs. 49, 50). Two females from Fokstua, Norway could not even be recognized by means of the elytra, which

in these specimens are apically normally rounded.

Non sexual characters.— *C. septentrionis septentrionis* has been characterized by Jeannel (1923, 1936) and by Szymczakowski (1957) on two non-sexual characters: its relatively small eyes and its relatively sharp caudolateral angles of the pronotum. These characters were first presented by Jeannel (1923), who based them on the type specimen from Tromsø, Norway.

The pronotal form undoubtedly is an individual feature of the type-specimen, that has indeed the left caudolateral angle accented; the other angle however is normally rounded. The pronotal shape of all other studied specimens is equal to *C. agilis* and *C. lederiana*.

The supposedly smaller eyes however, may be more useful. In figs. 59 and 60 the orbital part of the head of *C. septentrionis septentrionis* is compared with the same part in a *C. lederiana* specimen. In many *C. septentrionis septentrionis* specimens such relatively small eyes are found, and a tendency toward eye-restriction seems to exist in *C. septentrionis septentrionis*. It is not, however, a constant character. I saw many normally large eyes in specimens from different localities.

Immature stages.— As far as I know, neither larval nor pupal stages have been described for *C. septentrionis septentrionis*. Those of *C. septentrionis holsatica* however, are known (see below).

Ecology.— Several authors have given ecological reports on *C. septentrionis septentrionis*. Strand (1944) said: "v, vi, viii-x. Under plant-remains and in sap of birches (also in caves, barns and in rotting fungi)" (my translation). It should be noted, that in Strand's opinion the name *C. septentrionis* comprises *C. lederiana* too. His mentioning caves probably refers to the *C. lederiana* population in Torhola Cave. Palmqvist (1949) reported some ecological circumstances to the capture of several *C. septentrionis septentrionis* specimens in Sweden: "poor grassland, [...] near a rich foliage thicket, in a tunnel of a rodent under a large stone/ large sandpit, stony field; grass, herbs, foliage thickets; running under a large stone with rodent tunnel [...]. Rather moist ditch; xerophilous, firm grass; [...] in tunnels, partly under small *Salix fragilis*-bushes [...]. Humus, gravel and stones in soil, shady beech forest, poor of vegetation; many mostly superficial rodent tunnels." (my translation).

Some specimens from the ZMBG, captured in the communities of Eidfjord and Ullensvang, Norway, bear labels concerning the altitude: 490, 580, 1150 and 1240 m above sea-level. Greve Jensen (in litt.) from the ZMBG reported some ecological information on one of these localities (Ullensvang: Veivann, 1150 m, 13.vii.1968): "a lake in a broad alpine valley upon the Hardangervidda mountain plateau in a phyllitic zone with rich flora".

Geographic distribution.— In his monograph, Jeannel (1936) discussed the probable distribution of *C. septentrionis septentrionis* (of which only the holotype from Tromsø was known at that time): "species that appears to be special to the extreme north of Scandinavia. Perhaps, like *Catops alpinus* Gyll., it exists in Western Siberia too" (my translation). Since by then, the male (that is indistinguishable from male *C.*

lederiana) was not known yet, probably all Norwegian and Swedish localities of *C. lederiana*, as cited by Sahlberg and Krogerus (Jeannel, 1936) must in reality have been records of *C. septentrionis septentrionis*. As we know now, it is not an extremely boreal species at all. Its distribution (fig. 84) is mainly Western Scandinavian, and it touches the area of distribution of *C. agilis* in Southern Sweden. Also, it appears to be present in Scotland, Ireland and Wales. Therefore, the distribution of *C. septentrionis septentrionis* corresponds to what Lindroth (1935) called "boreo-British". This has some consequences on the interpretation of its distributional history and its Central-European subspecies (see below)

Choleva septentrionis gracilenta Szymczakowski, 1957

Choleva aquilonia gracilenta Szymczakowski, 1957: 65-85, figs. x1-x2, x4-x8, xii1-xii2.

Choleva lederiana gracilenta; Szymczakowski, 1971: 215.

Material.—1 ♂ paratype, "Polonia centr. 16.v.1954 caverna "Pod Sokola Góra" W. Szymczakowski leg.", "Paratypus *Choleva aquilonia* ssp. *gracilenta* m. Szymczakowski det. 1955", "Mus. H:fors Spec. typ. No 2739 *Choleva aquilonia* ssp. *gracilenta* Szymcz.", "Zool. Mus. Helsinki Loan No. c-87 228", "*Choleva septentrionis gracilenta* Szymcz. Schilthuizen det. 1987". UZMH. 1 ♀ paratype with the same labels, but: 15.x.1954 and: Spec. typ. No. 2740. UZMH. 2 ♂♂, 1 ♀, "Poland: Czestochowa, in Sokole Mts., Jaskinia, Studnisko Cave", "A. Skalski, 9.ix.1961, B.M. 1964-'75". BMNH.

Males.—The aedeagus is in ventral view slightly more slender than in *C. septentrionis septentrionis* (fig. 12), but in lateral view it shows the same features (fig. 13).

Szymczakowski (1957) reported the presence of a "ventral tooth, shaped as an elongated letter V, apically pointed" (my translation). In the one (juvenile) male of which I extracted the aedeagus, I unfortunately could not distinguish the exact structure of its tooth.

Like the rest of the legs, the metatrochanter is elongated, when compared to the nominal subspecies (fig. 29). Its tooth is narrow and short.

The male protarsus is less dilated than in other taxa (figs. 30, 31).

Females.—In shape, the genital tergite is unmistakably *C. septentrionis*-like (fig. 35), instead of *C. lederiana*-like, as is stated by Szymczakowski (1957). Both in the studied specimens and in the drawings by Szymczakowski (1957) of the genital tergite of the allotype, the features of *C. septentrionis* are recognizable. Mainly for this reason I have transferred this taxon from *C. lederiana* to *C. septentrionis*.

Although not as obvious as in *C. septentrionis*, the female elytral apex is more angular than its male equivalent (figs. 52, 53). This too, is an argument for placing *gracilenta* in the relationship of *C. septentrionis* rather than *C. lederiana*.

Non-sexual characters.—This subspecies is much more slenderly built than *C. septentrionis septentrionis*. Its average quotient of bodylength and greatest bodywidth is 2.72, whereas the same in *C. septentrionis septentrionis* amounts to 2.46 (Szymczakowski, 1957).

Its legs are more slender than in *C. septentrionis septentrionis* (fig. 56). All tarsi are,

in relation to the bodylength, longer than those in the nominal subspecies (Szymczakowski, 1957).

The antennae (figs. 65, 66) are longer and more slender than in *C. septentrionis septentrionis* (figs. 61, 62).

Immature stages.— No descriptions of larval stages and pupa have been published so far.

Ecology.— No reports on the ecology of this subspecies are known to me, apart from its cavernicolous mode of life. Szymczakowski (1957) gave some notes on the geography and climate of the caves in which it dwells.

Geographical distribution (fig. 84).— *C. septentrionis gracilenta* is known to live in only two caves, the "Pod Sokola Góra" and "Studnisko", that are close to each other and are connected by numerous crevices. They both are situated some 12 km north-east of Częstochowa, Poland, about 800 km south of the nearest known localities of *C. septentrionis septentrionis* in Sweden.

Choleva septentrionis holsatica Benick & Ihssen, 1937

Choleva holsatica Benick, 1937: 154-167.

Choleva septentrionis holsatica; Szymczakowski, 1957: 65-85.

Material.—1 ♂ lectotype: "Lübeck 16.ix.35 Segeberg. Höhle.", "Coll. Dr. Ihssen", "♂", [red label without text], "holsatica", "Zool. Mus. Berlin", "lectotype M. Schilthuizen des. 1987", "Choleva septentrionis holsatica Schilthuizen det. 1987". ZMB. 11 paralectotypes (here designated) with the same labels, but: "Paralectotype M. Schilthuizen des. 1987". ZMB. 4 paralectotypes (here designated) with the same labels, but: 9.ii.35, and: "Paralectotype M. Schilthuizen des. 1987". ZMB. 3 paralectotypes (here designated) with the same labels, but: 5.vii.35 and "Paralectotype M. Schilthuizen des. 1987". ZMB. Furthermore 41 specimens from the same locality (ZMB, ZMK, MF, author's collection): 40 adults and 1 larva.

Males.—In aedeagal shape (figs. 10, 11), *C. septentrionis holsatica* is indistinguishable from *C. septentrionis septentrionis*.

The ventral tooth of the internal sack is similar in shape and dentation to the two ventral teeth that were studied in *C. septentrionis septentrionis*.

The tooth on the metatrochanter is short and narrow, as in the nominal subspecies.

Females.—The genital tergite of *C. septentrionis holsatica* shows the typical shape of the nominal subspecies (fig. 36).

All females of *C. septentrionis holsatica* have apically dented elytra, some equal to *C. septentrionis septentrionis*, but mostly with an even stronger elongation (fig. 51).

Non-sexual characters.— As in *C. septentrionis gracilenta*, its Polish equivalent, the habitus of *C. septentrionis holsatica* is slender and flattened. Its quotient of bodylength and greatest bodywidth is about 2.6 (my measurement) whereas it is 2.72 in *C.*

septentrionis gracilenta. Hence, the elongation of its body is less than in the latter subspecies.

In the original description, Benick (1937) emphasizes the extremely long tarsi of *C. septentrionis holsatica*, when compared to *C. lederiana* and *C. agilis*. Indeed, by the relative length of the tarsi the general elongation of the legs is best recognizable (table 1, fig. 55).

Table 1. Relative lengths of the tarsi in *C. agilis* and *C. septentrionis holsatica* (after Benick, 1937).

	<i>C. agilis</i>		<i>C. septentrionis holsatica</i>	
	♂♂	♀♀	♂♂	♀♀
protarsal length/bodylength	0.157	0.158	0.177	0.163
mesotarsal length/bodylength	0.215	0.219	0.238	0.244
metatarsal length/bodylength	0.275	0.276	0.311	0.306

The antennae are long and slender (figs. 63, 64). A good measure is the length/width-relation of the 8th antennal segment: 1.6 in the male. These proportions are never encountered in *C. septentrionis septentrionis*.

The eyes of most *C. septentrionis holsatica* are relatively small. Heun (1955) counted the number of facets and demonstrated that there are less facets in an eye of *C. septentrionis holsatica* (some 200) than there are in an eye of *C. agilis* (some 270). However, Heun did not analyse the often small eyes in *C. septentrionis septentrionis*, so it is as yet unknown whether the small eyes in *C. septentrionis holsatica* are a species-character or a result of the cave environment.

Immature stages.— Larval stages and pupa were described by Heun (1955). A comparison between his drawings and those by Krogerus (1927) of the larvae and pupa of *C. aquilonia* and by Casale (1975) of the larvae and pupa of *C. agilis* shows, that the habitus is more slender in *C. septentrionis holsatica*. The same applies to the adult habitus (see above). Also, the number of setae on the body and extremities seems to be different in number and position, but the degree of variability in this respect is unknown.

Ecology.— *C. septentrionis holsatica* is a cavernicolous subspecies, that is found only in one cave near Bad Segeberg, Schleswig-Holstein, BRD. Benick (1937) reports many characteristics of the Segeberger Höhle. It is dark, it has three small entrances, it is humid, "the walls are covered with water everywhere" (my translation). The temperature in the cave is constantly 8°-9°C (Zwick, 1966). Benick (1937) believes the menu of the beetles to consist of dead Diptera, Isopoda, bats and batdung.

Zwick (1966) extensively studied the reproduction of captive specimens and reported, apart from many observations on larvae and pupae, a short diapause of some three months old adults in small, self-made holes. A similar behaviour has been reported from *Choleva angustata* (Fabricius) and *Choleva fagniezi* Jeannel (Deleurance, 1959). Also, Zwick (1966) demonstrated, that the beetles are capable of normal reproduction and survival in different, non-cave conditions.

Geographical distribution (fig. 84).— The only known locality is the Segeberger Höhle in Schleswig-Holstein, some 400 km from Sokole Góry Mountains, where *C. septentrionis gracilenta* is found, and some 250 km from the nearest known locality of *C. septentrionis septentrionis*, in southern Sweden.

The Irish and Welsh populations.— A strange observation was made while studying material from Ireland and Wales: all males examined seem to belong to *C. septentrionis septentrionis*, but all females certainly belong to *C. agilis*. I am at a loss how to explain these records. Possibly both species occur sympatrically in this area and by coincidence only females of the one and males of the other species were collected. Another explanation would be the existence of a hybrid zone between *C. agilis* (that is present in Southern and Central England) and *C. septentrionis septentrionis* (that occurs in Scotland), in which the females bear characters of the former species and the males bear characters of the latter. The following specimens were studied:

C. septentrionis septentrionis: 1 ♂ Harlech (Wales), 22.vi.1906, leg. Donisthorpe, BMNH. The ventral tooth of the internal sack of this specimen is shown in fig. 17; 1 ♂ Armagh (Northern Ireland), 10.v.1894, leg. Johnson, NMI; 1 ♂ Dublin, 2.ii.1947, NMI; 1 ♂ Deer Park Killarney (Ireland), ix.1924, NMI.

C. agilis: 6 ♀ ♀: Killarney (Ireland), iv.1915, x. 1929, 21.viii.1931, 26.ix.1931, 18.vi.1932, and 7.ii.1935, NMI; 1 ♀ Limerick (Ireland), 1901, NMI; 1 ♀ Glencree (near Wicklow, Ireland), iv.1915, leg. May, RMS.

All the localities of these specimens have been mapped in fig. 77.

A simple key to the non-cavernicolous species

1. Males: Protarsi dilated (fig. 30) 2
- Females: Protarsi narrow 3
2. Aedeagus little elongated with a reduced ventrad bend (figs. 3, 5) *C. agilis*
- Aedeagus elongated, apically with a strong ventrad bend (figs. 2, 4); two virtually indistinguishable species *C. septentrionis septentrionis* & *C. lederiana*
3. Elytral apex rounded 4
- Elytral apex elongated (figs. 59, 60) *C. septentrionis septentrionis*
4. Genital tergite ovoid, its caudal angles rounded (fig. 33) *C. lederiana*
- Genital tergite subtriangular, its caudal angles accented (fig. 32) *C. agilis*

The variability of several characters within a populations of *C. lederiana*

As demonstrated in this paper, a considerable variability in several characters usually exists in the species of the *C. agilis*-group s. str. Due to a lack of sufficient material, it was until now impossible to conclude whether the observed variability is geographically distributed or that it is present within a small population too. Several hundreds of specimens of *C. lederiana* could be studied, taken between 22.viii. and

30.x.1985 in Torhola Cave, near Lohja, Finland; the type locality of *C. aquilonia* (UZMH, in ethanol 70%, Biström & Hippa leg.). This material may be considered as a random sample from one or two generations of a deme, and can be used to establish the extent of variability within such a population. Some 20 specimens of each sex were randomly taken and studied for several sexual and non-sexual characters. The results are listed below. It is important to notice, that we are dealing with a cavernicolous population, which may not be simply comparable to a population in the open country.

1. Shape of aedeagus. The aedeagal shape is strikingly constant in the studied specimens. All show exactly the same elongation and curvature.
2. Shape of the genital tergite. In figs. 71-73 the three categories of shapes that were found are shown.
3. Shape of the male metatrochanter. In figs. 67-70 the four distinguishable categories of shapes that were found are given.
4. Elytral apex. All males and females have clearly separately rounded elytral apices.
5. Male mesotibia. I have mentioned above, that it is difficult to establish a measure for the modification of the male mesotibia. In this analysis, I have used the following measure, the relation of which might give an indication of the degree of modification: A= Distance between femur/tibia joint and basis of the largest apical spine on the tibia; B= Distance between line A and the point, most remote from A, on the outside of the tibia. In fig. 74 the positions of lines A and B are given. In fig. 75 the distribution of several values of A:B over 13 males is given.
6. Pronotal index. The pronotal index is here used as: the quotient of the greatest width (a), and the length, measured over the longitudinal axis, when the specimen has been positioned in such a way, that the rostral border of the pronotum resembles a straight line (b). The distribution of several classes of values of a:b is shown in fig. 79 for 19 males and for 20 females.
7. Length. In 18 males and 20 females the body length was measured from the mandibulae of the extended head to the elytral apex. The distribution of several classes of length is given in fig. 77. The extremes and averages in length for these specimens are: males: 5.0-5.8 mm, average length: 5.4 mm; females: 4.7-5.8 mm, average length: 5.3 mm.
8. Relation between pronotal length and elytral length. This relation is given by: p: pronotal length, measured along the longitudinal axis, when the specimen has been positioned in such a way, that the rostral border of the pronotum resembles a straight line; e: elytral length, measured from the caudal tip of the scutellum to the elytral apex, when the specimen has been positioned in such a way, that the rostral half of the elytral disc has an approximately right angle with the line of view. In fig. 78 the distribution of classes of values of e:p is given for 19 males and for 20 females.
9. Elytral index. When the specimen has been positioned in such a way, that the rostral half of the elytral disc has an approximately right angle with the line of view, the elytral index is given by l:w, where: l= elytral length, measured from the caudal tip of the scutellum to the apex; w= the largest width of the elytra, if both elytra are

joined. In fig. 76 the distribution of classes of values of l:w is given for 15 males and 17 females.

Conclusions.— 1. Among the characters examined, only the shape of the aedeagus seems to be constant within this population. The other sexual characters, viz. shape of male metatrochanter, female genital tergite and male mesotibia, show a considerable variability, which is consistent with observations on *C. lederiana* material from other localities.

2. In this population, males have less wide pronota and elytra: they are more slender than the females. This statement is a general rule in Cholevidae.

Discussion on phylogeny and zoogeography

Phylogeny.— In establishing the phylogeny of the taxa, the following morphological characters are considered most important, as they show a minimal intraspecific variability.

Character	Character state
1. apical bend of aedeagus	bend is strong (+)/bend is weak (-)
2. elongation of aedeagus	elongation is strong (+)/elongation is weak (-)
3. elytral apex of female	dent-like elongated (+)/separately rounded (-)

(+) indicates a supposed apomorphous character state; (-) indicates a supposed plesiomorphous character state. In fig. 81 these characters have been used for a cladogram of the three species.

The original argument on the taxonomic rank of the several taxa, as discussed in the introduction, still remains to be discussed. To begin with, the epigean taxa *C. agilis*, *C. lederiana* and *C. septentrionis* have a parapatric distribution. To give an account on the reproductive isolation of the taxa it is necessary to study more closely the areas where sympatric populations might be present. These areas are presented in fig. 83.

Below specimens from these areas that were studied are discussed. Two things have been assumed:

— if specimens occur, showing intermediate features, this can be taken as evidence for the presence of hybridization.

— if specimens occur, showing no intermediate features or even more strongly developed species-characters (character displacement), this can be taken as evidence for reproductive isolation.

1. *C. agilis* versus *C. lederiana*.— Since scarce material from the U.S.S.R. is known from either species, it is hard to say where the areas of both species make contact. The only specimens that might originate from the contact region are: 1 ♀: near Berdetsino (U.S.S.R., Jaroslawl region), 17.vi.1900, leg. Jakowlev, ZIL. This is a typical *C. agilis*; 2 ♂♂: Königsberg (U.S.S.R.: Kaliningrad), leg. Kugelann, ZMB. Both speci-

mens show an unusually strong bend in the apical part of the aedeagus. The same goes for a specimen from Sorau, in Western Poland (ZMB); 2 ♀♀: Osterjärvi (U.S.S.R.), leg. Thuneberg, UZMH. Both typical *C. lederiana*.

2. *C. lederiana* versus *C. septentrionis*.— Since plenty Scandinavian material of both species is present, it is possible to define the exact region where the areas of these two species adjoin (see figs. 82 and 84). Because males of both species are virtually indistinguishable, only females are mentioned in the list below.

1 ♀ (holotype of *C. septentrionis*): Tromsø (Norway), 23.vi.1888, leg. Otto, TMB; 1 ♀: Mortensnes (Norway), ZMK. A typical *C. lederiana*; 1 ♀: Pallastunturi (Finland), 7.vii.1957, leg. Wegelius, UZMH, 8 ♀♀: Pallasjärvi (Finland), 19.vi., 23.vi., 2.vii.1953 and 13.vii.1951, UZMH. These last 9 females from Finland all show a genital tergite that is typical for *C. lederiana*. The elytral apices however, are for several of these specimens somewhat angular, and cannot be distinguished from the elytral shape of the females of *C. septentrionis* from Fokstua, Norway (see above).

3. *C. septentrionis* versus *C. agilis*.— Two regions are of importance: — Southern Sweden (Halland) where populations of both *C. agilis* and *C. septentrionis* seem to be present; — Ireland and Central Great Britain (see above).

1 ♀: Sarö, leg. Thomson, ZMB. A typical *C. agilis*; 1 ♀: Hal., ZMB. A typical *C. septentrionis*. Palmqvist (1949) reported the capture of a mixed form "*C. agilis-aquilonia*" from Hälsingborg. I have not seen this specimen. As mentioned above, the situation in Ireland and Great Britain is not clear. Possibly a hybrid zone is present.

4. *C. septentrionis holsatica* versus *C. agilis*.— 1 ♂: Holstein, Segeberg Höhle, 28.i.1928, leg. Arndt, ZMB. A typical *C. agilis*; 1 ♂ with the same labels, ZMB. A typical *C. septentrionis holsatica*. These records indicate, that *C. agilis* occasionally enters the area of *C. septentrionis holsatica*. Still, among the vast material of the latter, no intermediates could be found. It may be concluded, that *C. agilis* and this subspecies of *C. septentrionis* are reproductively isolated.

Clearly, more material from the contact regions should be studied before the taxonomic status of each of the several forms can be established with certainty. At the moment, evidence both for and against hybridization is present. For the time being it is best to remain treating *C. agilis*, *C. septentrionis* and *C. lederiana* as distinct species. Still, considering the above-mentioned circumstantial evidence, and the parapatric distribution, we are probably dealing here with three species that have not yet gained full reproductive isolation: the species do interbreed in some places, whereas they do not elsewhere.

Distributional history.— Only *C. septentrionis* shows features in its present geographical pattern, which may serve as clues to its history of distribution. It is the only one that presents a disjunct distribution: it exists in Western Scandinavia, from 57° N to 70° N, in Scotland (about 57° N) and has two subspecies in caves in Central Europe. This distributional pattern of Scandinavian and British colonies is sometimes called "boreo-British", and its discontinuity can be explained by viewing the distribution of land and sea during the glacials (Lindroth, 1935). During the Weichselian (the

last major ice-age) for instance, land must have connected the British Isles to the European mainland, while Scandinavia was completely covered with ice. The climate was colder too, so most of the present Central Europe was tundra and steppe or at least a type of terrain that is now found only in northern regions (Zagwijn et al., 1985). Probably *C. septentrionis*, if it had the same ecological preferences in those days as it has today, was widely spread over Europe. During interglacials, like the one we are experiencing nowadays, it must take its refuge to the northern parts of Europe, meaning Scandinavia and Scotland, that became separated during the warming of the climate, thus forming the disjunction. This also may account for the isolated subspecies in Central-European caves. These caves retain the low temperature and humidity throughout the year, and may therefore have presented the only places where the glacial *C. septentrionis* populations could survive as the climate was slowly getting warmer and the epigean *C. septentrionis* gradually disappeared from Central Europe. This is probably the most plausible explanation for the existence of *C. septentrionis gracilenta*. The same explanation was presented by Szymczakowski (1957), except that he regarded *gracilenta* as a descendant of the boreal *C. lederiana*. The other subspecies, *C. septentrionis holsatica*, inhabits a young cave that some 14,000 to 17,000 years ago was filled with water (Zwick, i.l.). During this time, the Weichselian was on its retreat again (Zagwijn et al., 1985). It is possible that the *C. septentrionis* colony was founded in that time, as Benick (1950) said. It is also possible, since the present *C. septentrionis septentrionis* reaches south to some 250 km distance from Segeberg, that it is a much more recent subspecies, formed during a temporarily cooler climate somewhere within the last few thousands of years. Selective pressure in a cave may be regarded as high, and a modified habitus as *C. septentrionis holsatica* shows, may have been formed in such a short period.

Conclusions

1. Males of *Choleva lederiana* Reitter and *Choleva septentrionis septentrionis* Jeannel are indistinguishable; females of *Choleva agilis* (Illiger) and *Choleva lederiana* Reitter are hardly distinguishable. All other males and females can be identified.
2. *Choleva jailensis* Jeannel and *Choleva agilis clermonti* Van der Wiel are synonyms of *Choleva agilis* (Illiger). *Choleva lederiana* var. *brevicollis* Krogerus is a synonym of *Choleva lederiana* Reitter.
3. The subspecies *gracilenta* Szymczakowski is transferred from *Choleva lederiana* Reitter to *Choleva septentrionis* Jeannel.
4. The variability of several characters, both sexual and non-sexual, is remarkably high within a cavernicolous deme of *Choleva lederiana* Reitter. Only the shape of the aedeagus seems constant.
5. *Choleva lederiana* Reitter, *Choleva agilis* (Illiger) and *Choleva septentrionis* Jeannel are best regarded as parapatric species that may have not yet reached full reproductive isolation in all their contact regions.
6. *Choleva septentrionis* Jeannel has a discontinuous distribution, that can be explained by its (hypothetical) distribution during the ice-ages.

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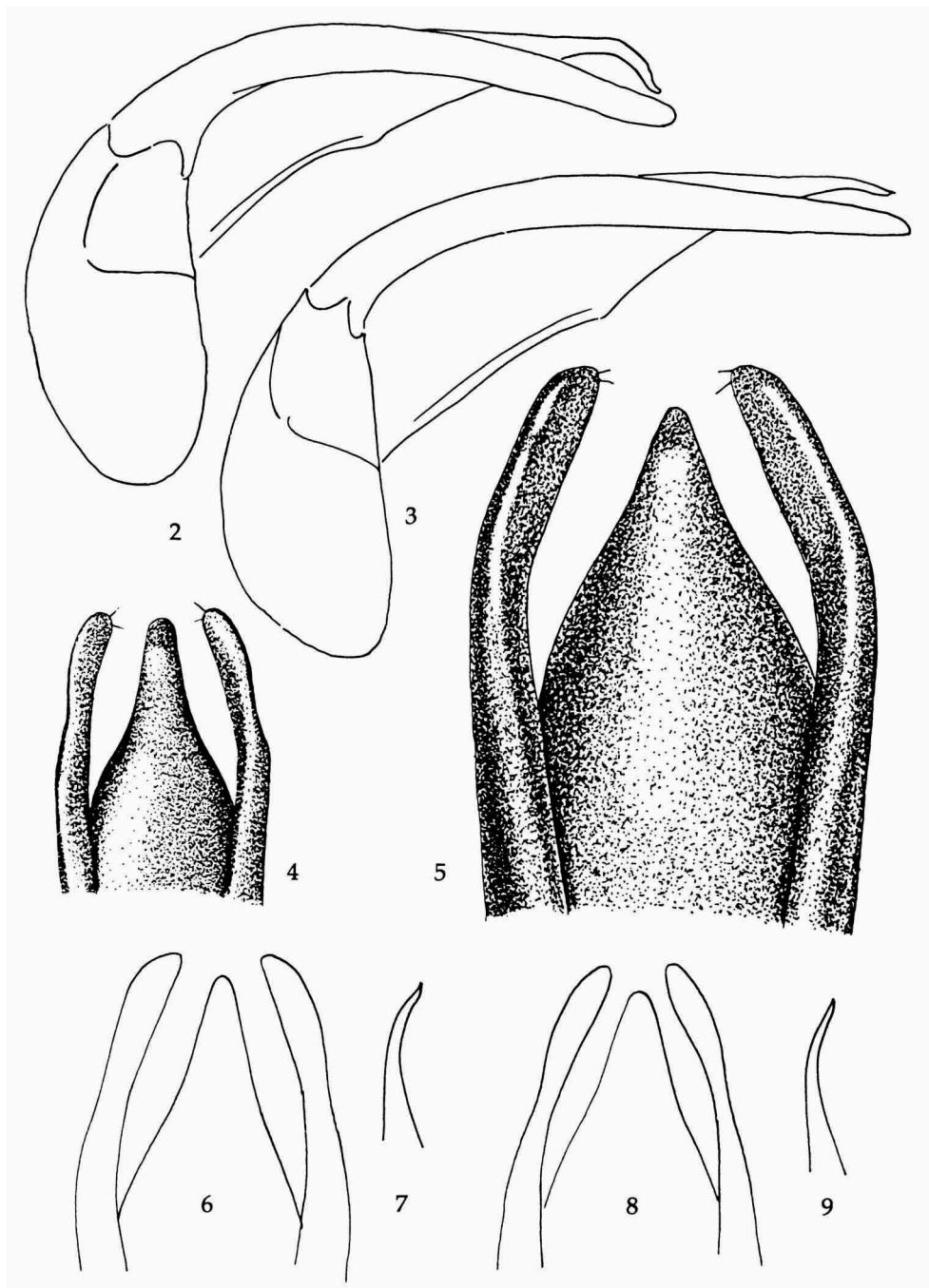
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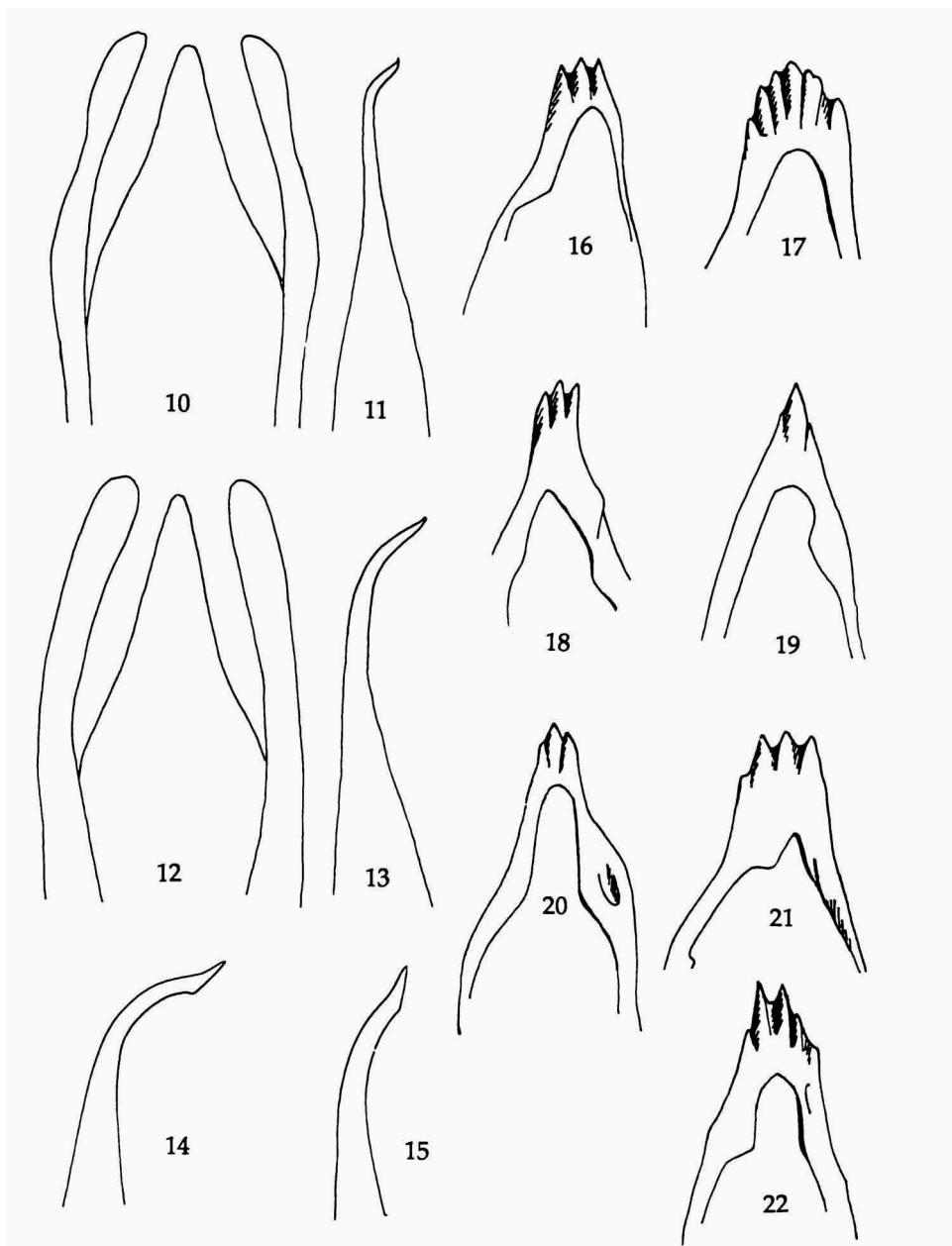
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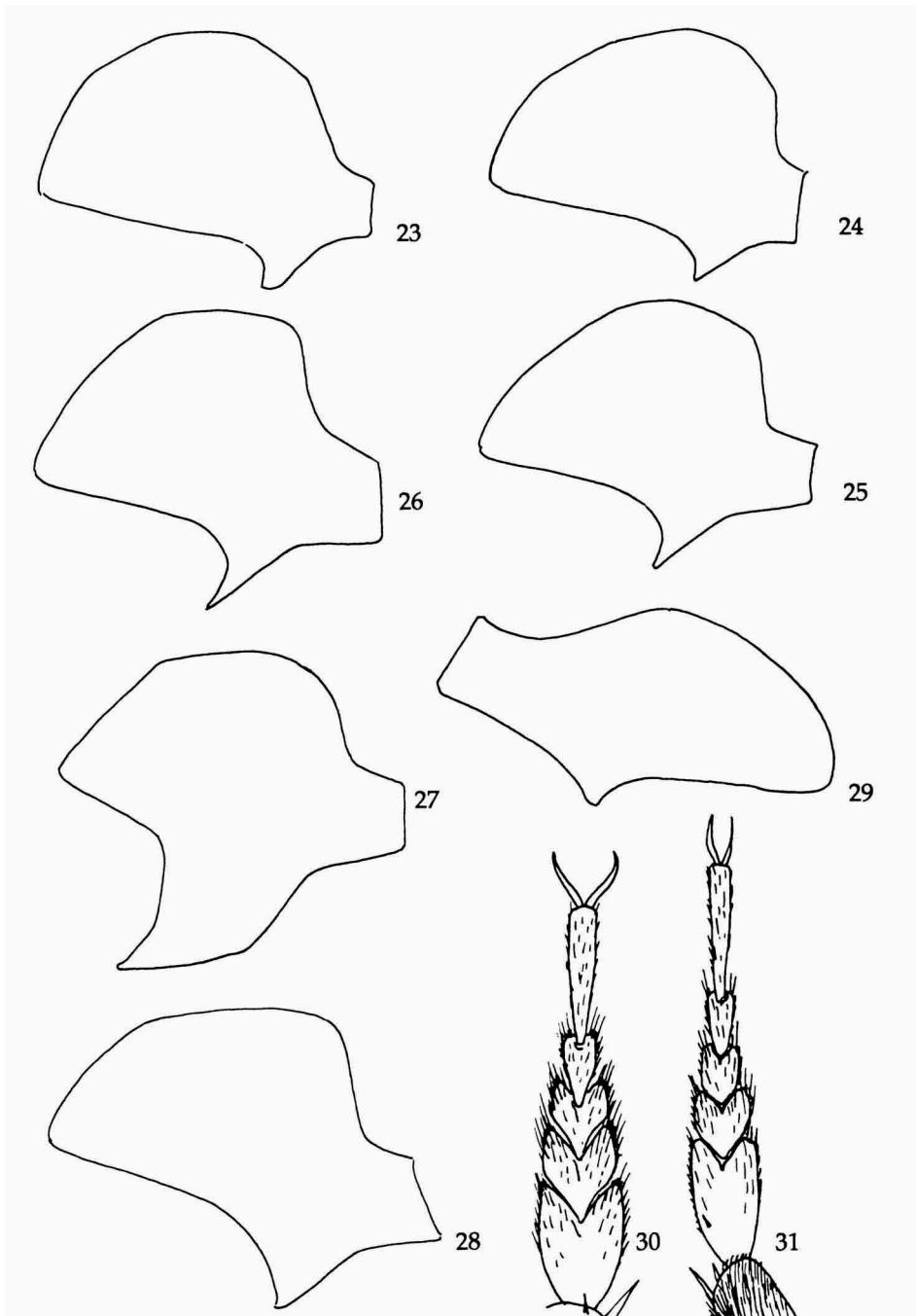
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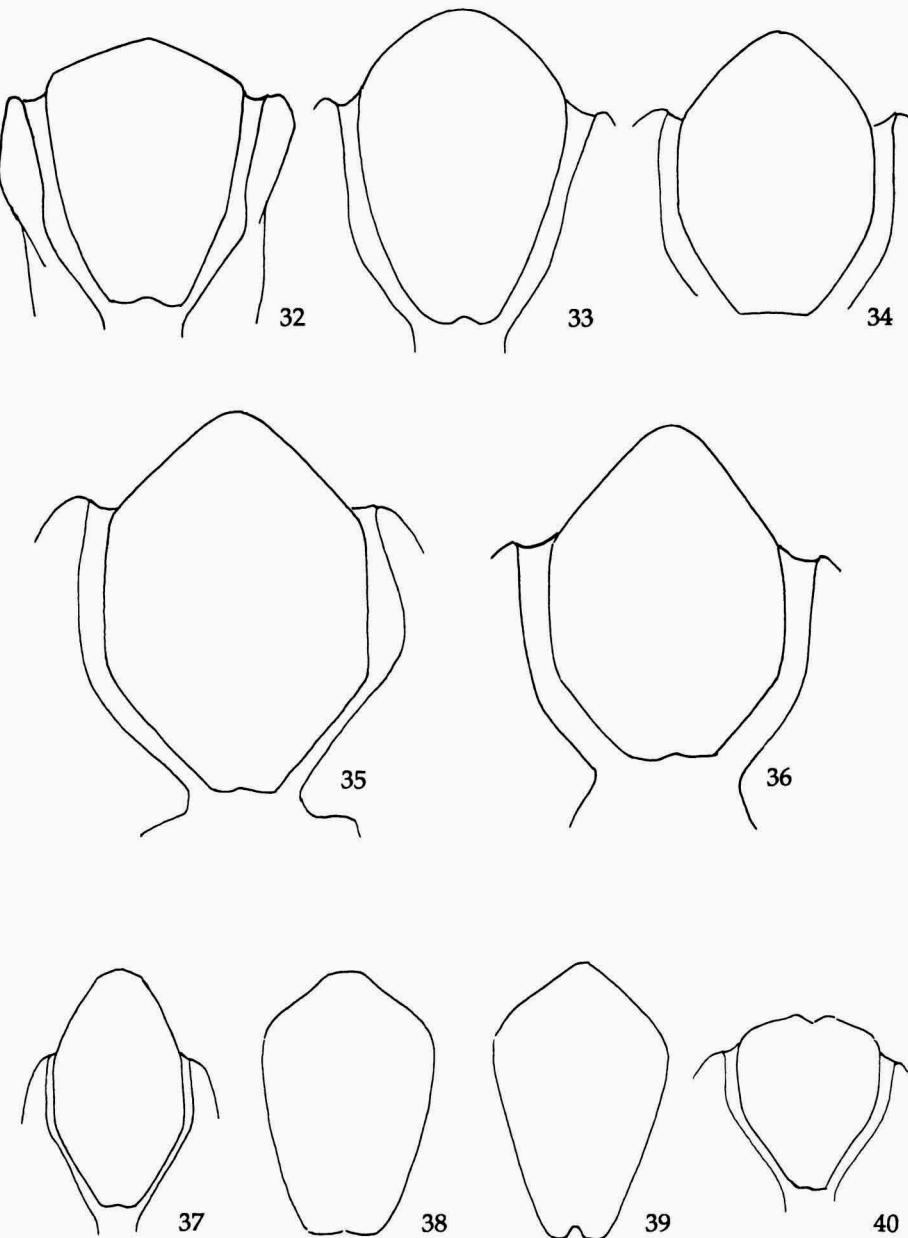
Figs. 2-9; 2, *Choleva lederiana* Reitter, 1901, ♂, Finland, Lohja (UZMH); 3, *C. agilis* (Illiger, 1798), ♂, Netherlands, Schiedam (author's collection); 4, *C. lederiana* Reitter, 1901, ♂, Norway, Vardø (ZMK); 5, *C. agilis* (Illiger, 1798), ♂, Netherlands, Oostvoorne (author's collection); 6-9, id., ♂, Great Britain, New Forest (BMNH). 2, 3, 7, 9, aedeagal apex, lateral aspect; 4-6, 8, aedeagal apex, dorsal aspect.



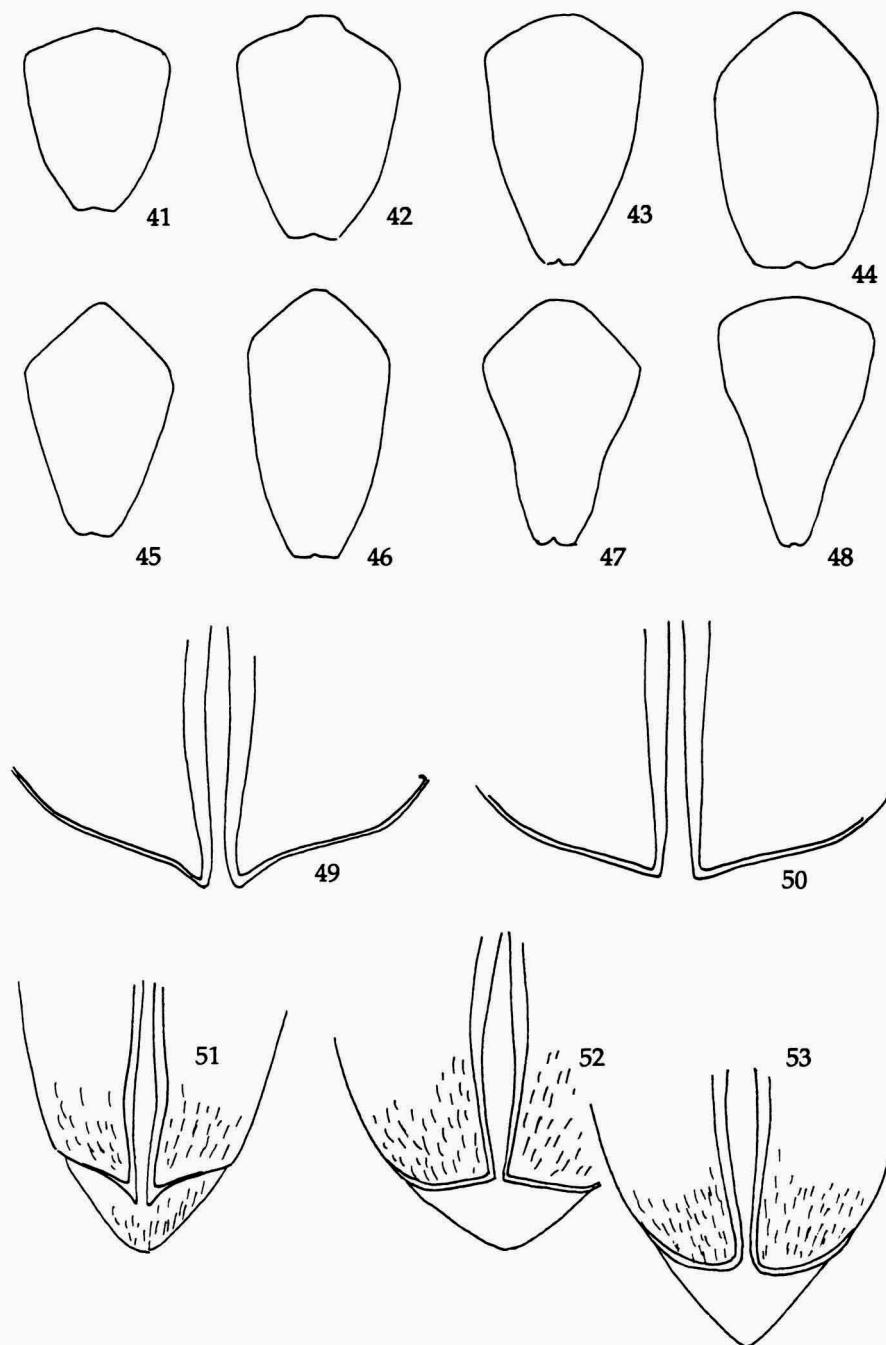
Figs. 10-22; 10,11, *Choleva septentrionis holsatica* Benick & Ihssen, 1937, ♂, BRD, Segeberg (author's collection); 12,13, *C. septentrionis gracilenta* Szymczakowski, 1957, ♂, Poland, Pod Sokola Góra (UZMH); 14, 19, *C. lederiana* Reitter, 1901, ♂, Finland, Lohja (UZMH); 15, *C. agilis* (Illiger, 1798), ♂, Netherlands, Velsen (ITZ); 16, *C. septentrionis septentrionis* Jeannel, 1923, ♂, Norway, Haus (ZMBG); 17, id., ♂, Great Britain, Harlech (BMNH); 18, *C. lederiana* Reitter, 1901, ♂, U.S.S.R., Varniechny (ZIL); 20, id., ♂, Norway, Nordkapp (ZMB); 21, *C. agilis* (Illiger, 1798), ♂, France, Vélizy (BMNH). 22, id., ♂, Netherlands, Schiedam (author's collection). 10, 12, aedeagal apex, dorsal aspect; 11, 13-15, aedeagal apex, lateral aspect; 16-22, ventral tooth of the internal sack, dorsal aspect.



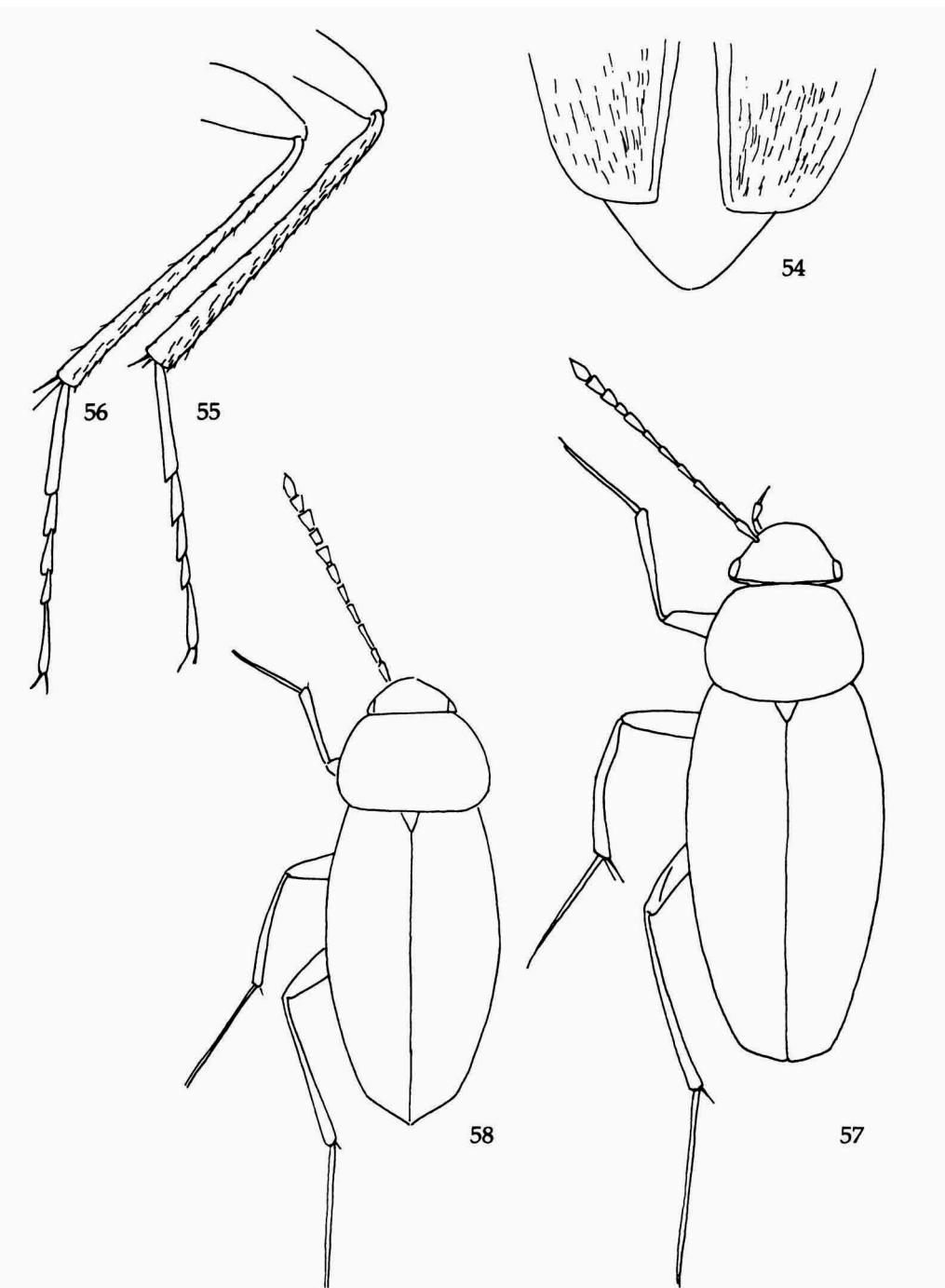
Figs. 23-31; 23, *Choleva agilis* (Illiger, 1798), ♂, Austria, Hard Fussanz (ITZ); 24, id., ♂, Netherlands, Haarlem (NNM); 25, id., ♂, Netherlands, Kolhorn (NNM); 26, id., ♂, Great Britain, Lancastershire (BMNH). 27, *C. agilis* forma *clermonti* Van der Wiel, 1931 ♂, France, Samatan (ITZ); 28, *C. lederiana* Reitter, 1901, ♂, Finland, Lohja (UZMH). 29, 31, *C. septentrionis gracilenta* Szymczakowski, 1957, ♂, Poland, Pod Sokola Góra (UZMH); 30, *C. agilis* (Illiger, 1798), ♂, Netherlands, Oostvoorne (author's collection). 23-29, metatrochanter, dorsal aspect; 30, 31, protarsus, dorsal aspect.



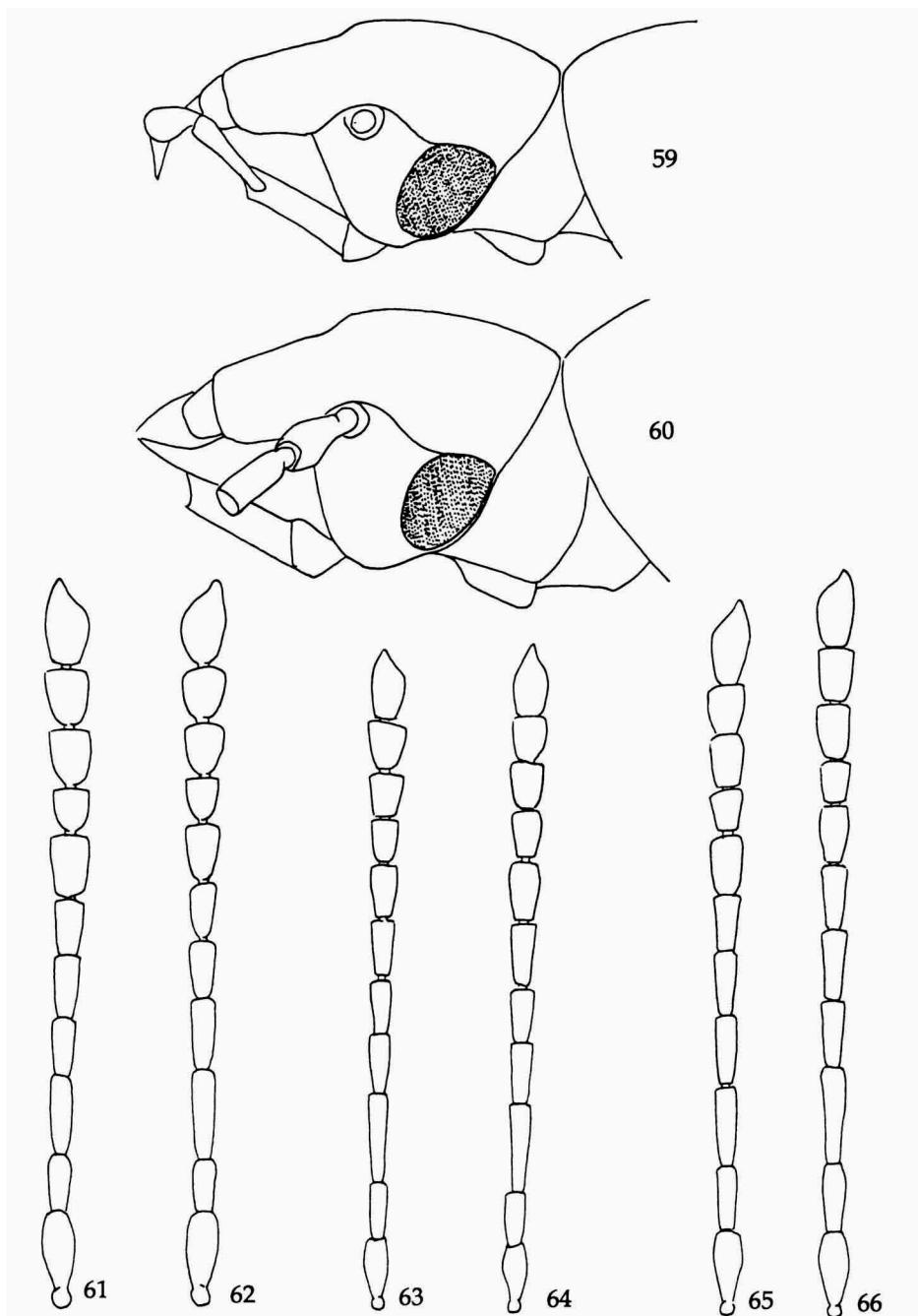
Figs. 32-40; 32, *Choleva agilis* (Illiger, 1798), ♀, Netherlands, Schiedam (author's collection); 33, *C. lederiana* Reitter, 1901, ♀, Finland, Lohja (UZMH); 34, *C. septentrionis septentrionis* Jeannel, 1923, ♀, Sweden, Ragunda (UZMH); 35, *C. septentrionis gracilenta* Szymczakowski, 1957, ♀, Poland, Pod Sokola Góra (UZMH); 36, *C. septentrionis holsatica* Benick & Ihssen, 1957, ♀, BRD, Bad Segeberg (author's collection); 37, *C. septentrionis septentrionis* Jeannel, 1923, ♀, Sweden, Loos (ITZ); 38, *C. lederiana* Reitter, 1901, ♀, Finland, Lohja (UZMH); 39, id., ♀, Finland, Pallastunturi (UZMH); 40, *C. septentrionis septentrionis* Jeannel, 1923, ♀, Norway, Veivann (ZMBG). 32-40, genital tergite, dorsal aspect.



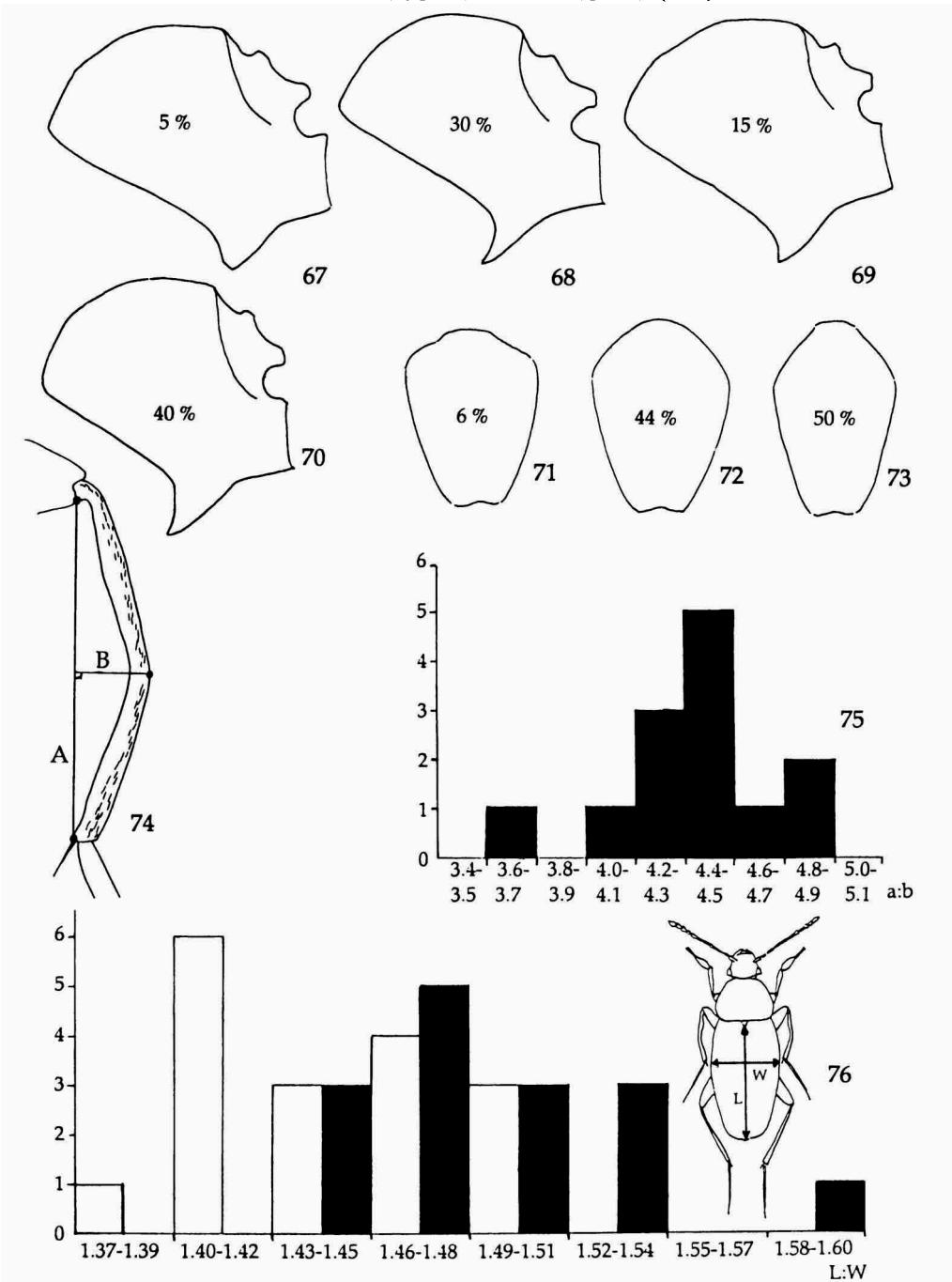
Figs. 41-53; 41, *Choleva agilis* (Illiger, 1798), ♀, France, Lille (ITZ); 42, 46, id., ♀, Denmark, Herlev (ZMK); 43, id., ♀, Netherlands, Haamstede (NNM); 44, id., ♀, Great Britain, Cowley (BMNH); 45, id., ♀, France, St. Germain (ITZ); 47, id., ♀, Great Britain, New Forest (BMNH); 48, id., ♀, Netherlands, Brummen (NNM); 49, 50, *C. septentrionis septentrionis* Jeannel, 1923, ♀, Sweden, Ragunda (UZMH); 51, *C. septentrionis holsatica* Benick & Ihssen, 1937, ♀, BRD, Bad Segeberg (author's collection); 52, *C. septentrionis gracilenta* Szymczakowski, 1957, ♀, Poland, Pod Sokola Góra (UZMH). 53, id., ♂, Poland, Studnisko (BMNH). 41-48, genital tergite, dorsal aspect; 49-53, elytral apices, dorso-caudal aspect.



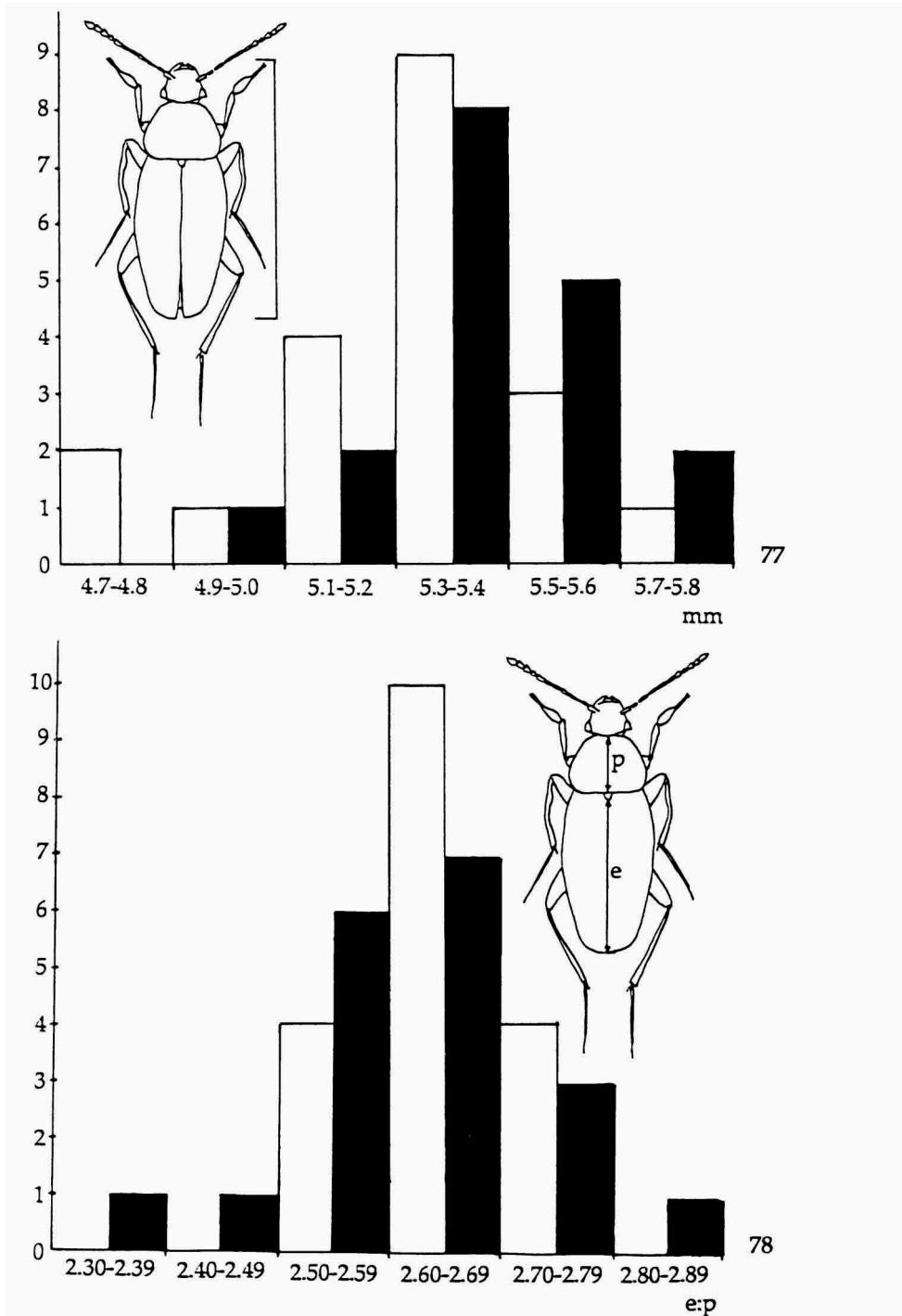
Figs. 54-58; 54, *Choleva lederiana* Reitter, 1901, ♀, Finland, Pallastunturi (UZMH); 55, *C. septentrionis holsatica* Benick & Ihssen, 1937, ♂, BRD, Bad Segeberg (author's collection); 56, 57, *C. septentrionis gracilenta* Szymczakowski, 1957, ♂, Poland, Pod Sokola Góra (UZMH); 58, *C. septentrionis holsatica* Benick & Ihssen, 1937, ♀, BRD, Bad Segeberg (ZMB). 55, 56, hindleg; 57, 58, habitus, dorsal aspect.



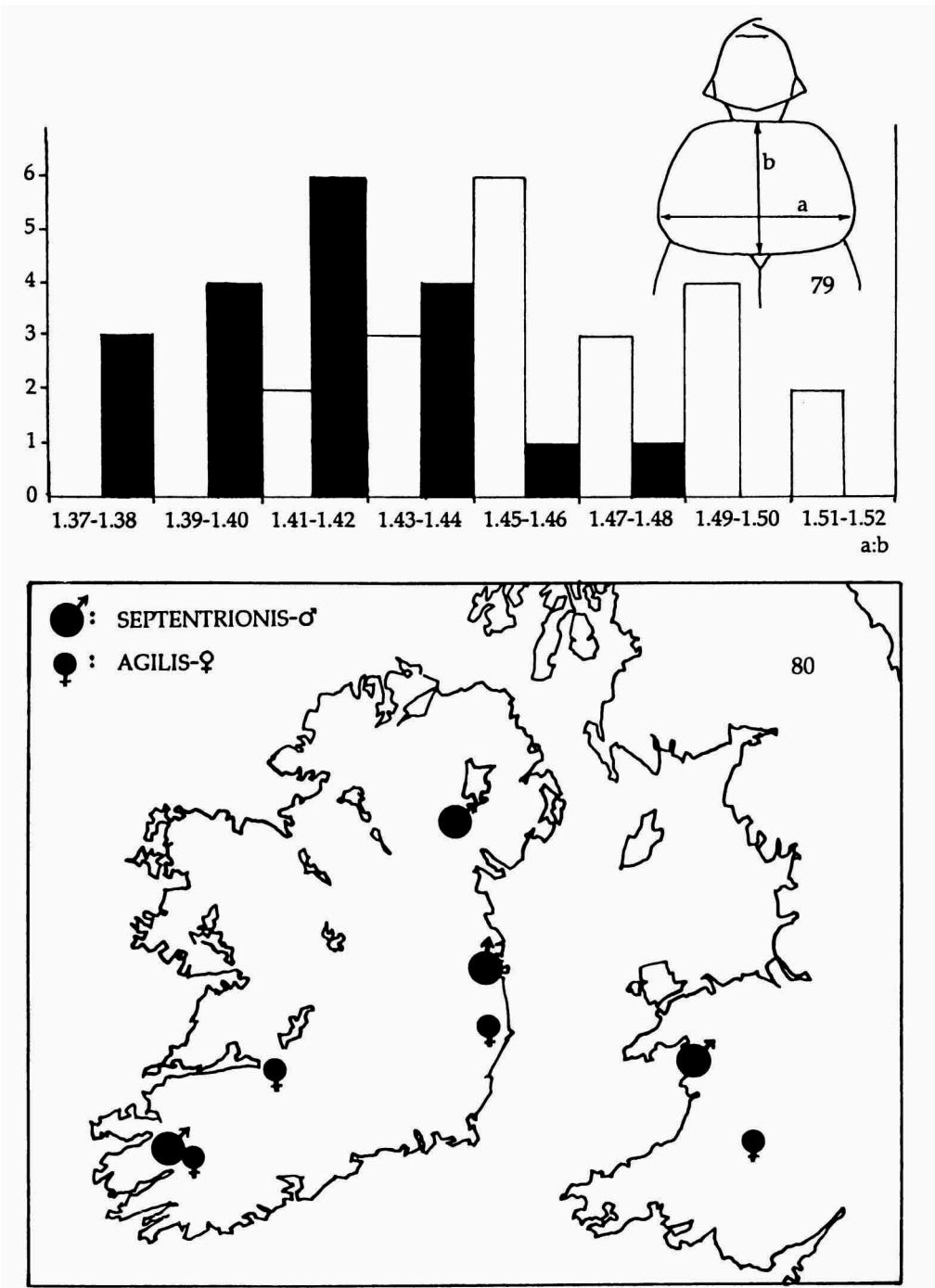
Figs. 59-66; 59, *Choleva lederiana* Reitter, 1901, ♀, Finland, Ruissalo (UZMH); 60, *C. septentrionis septentrionis* Jeannel, 1923, ♀, Sweden, Loos (UZMH); 61, id., ♀, Norway, Mabødalen (ZMBG); 62, id., ♂, Norway, Majastua (ZMBG); 63, *C. septentrionis holsatica* Benick & Ihssen, 1937, ♀, BRD, Bad Segeberg (ZMB); 64, id., ♂, BRD, Bad Segeberg (ZMB); 65, *C. septentrionis gracilenta* Szymczakowski, 1957, ♀, Poland, Pod Sokola Góra (UZMH); 66, id., ♂, Poland, Studnisko (BMNH). 59, 60, head, dorso-lateral aspect; 61-66, antenna.



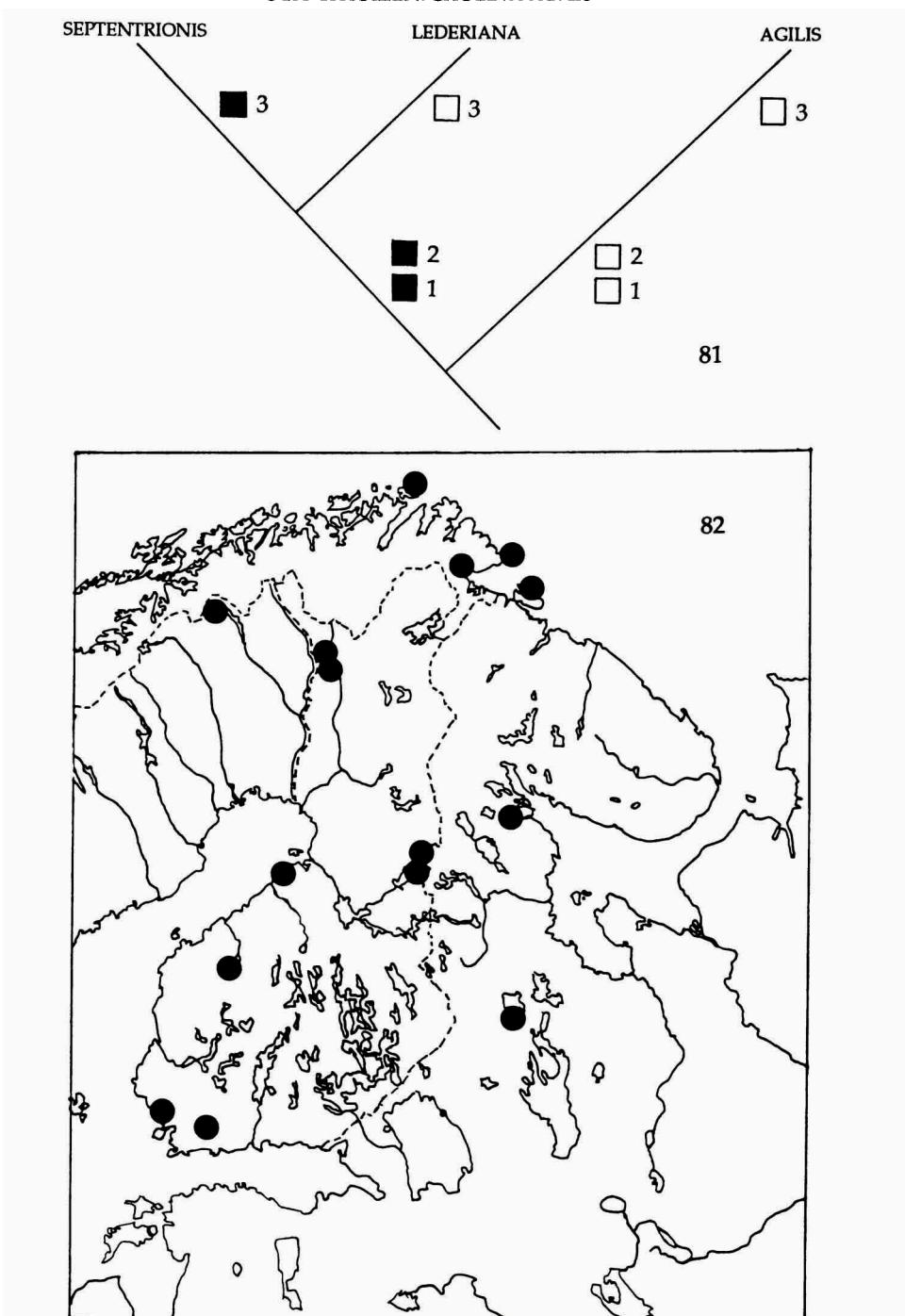
Figs. 67-76, *Choleva lederiana* Reitter, 1901, Finland, Lohja, Torhola Cave (UZMH). 67-70, ♂♂, metatrochanter, dorsal aspect; percentages indicating the proportion of the studied specimens that show a similar shape; 71-73, ♀♀, genital tergite, dorsal aspect; percentages indicating the proportion of the studied specimens that show a similar shape. 74, ♂♂, mesotibia; indicated are the positions of A and B; 75, ♂♂, distribution of values of A:B among the studied specimens; black bars represent ♂♂, white bars represent ♀♀.



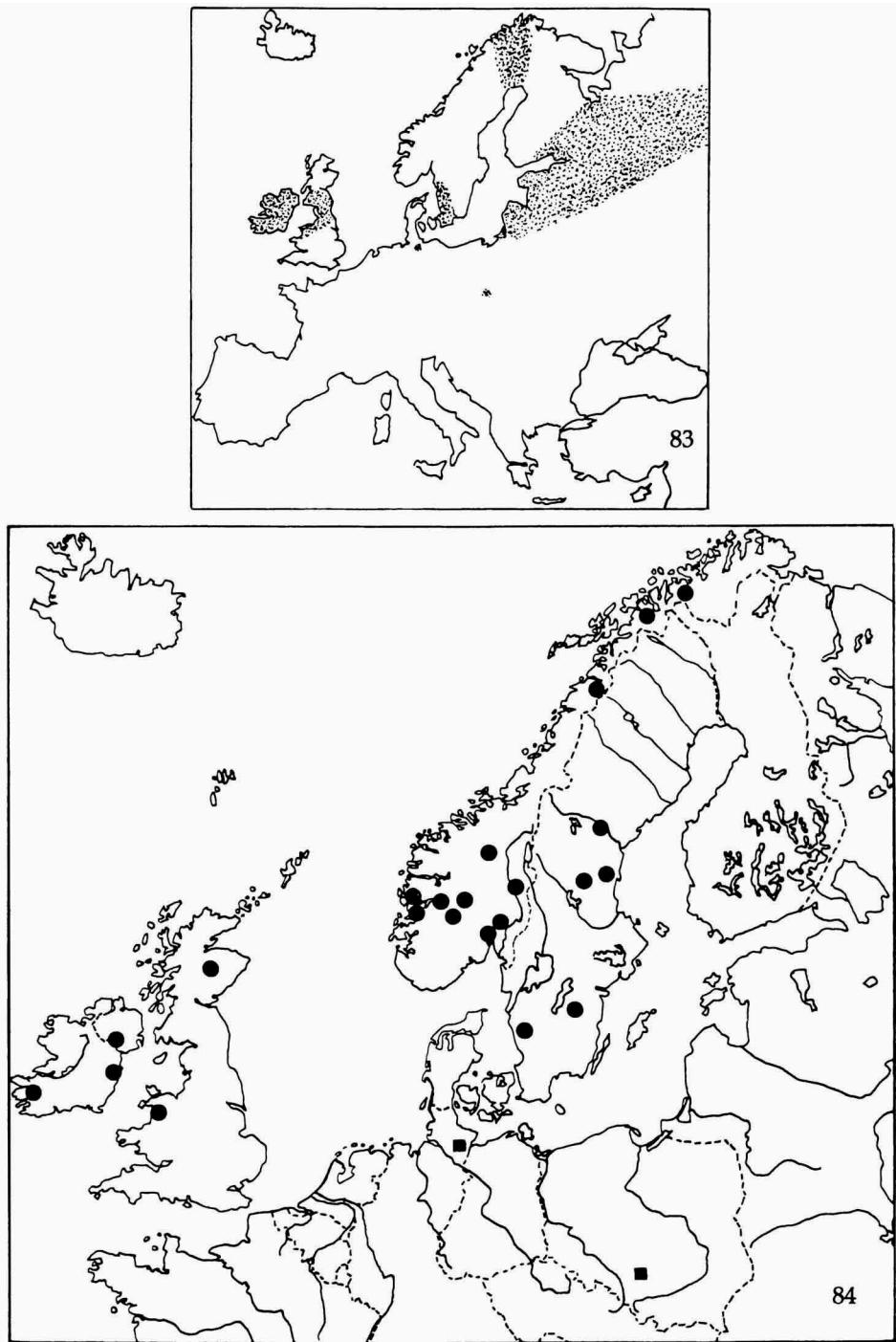
Figs. 77-78, *Choleva lederiana* Reitter, 1901, Finland, Lohja, Torhola Cave (UZMH). 77, distribution of bodylength among the studied specimens; black bars represent ♂♂, white bars represent ♀♀; 78, distribution of values of elytral length:pronotal length among the studied specimens; black bars represent ♂♂, white bars represent ♀♀.



Figs. 79-80. 79, *Choleva lederiana* Reitter, 1901, Finland, Lohja, Torhola Cave (UZMH); distribution of pronotal indices among the studied specimens; black bars represent ♂♂, white bars represent ♀♀; 80, geographical distribution of ♂♂ *C. septentrionis septentrionis* Jeannel, 1923 and ♀♀ *C. agilis* (Illiger, 1798) in Ireland and Wales.



Figs. 81-82. 81, cladogram showing the proposed phylogeny of *Choleva agilis* (Illiger, 1798), *C. lederiana* Reitter, 1901 and *C. septentrionis* Jeannel, 1923. White squares represent supposed plesiomorphous character states, black squares represent supposed apomorphic character states; 82, geographical distribution of *C. lederiana* Reitter, 1901 in Europe.



Figs. 83-84. 83, stippled areas indicate possible areas of contact between two species; 84, geographical distribution of *Choleva septentrionis* Jeannel, 1923; squares indicate the localities of the two cavernicolous subspecies: *C. septentrionis holsatica* Benick & Ihssen, 1937 in Germany and *C. septentrionis gracilenta* Szymczakowski, 1957 in Poland.

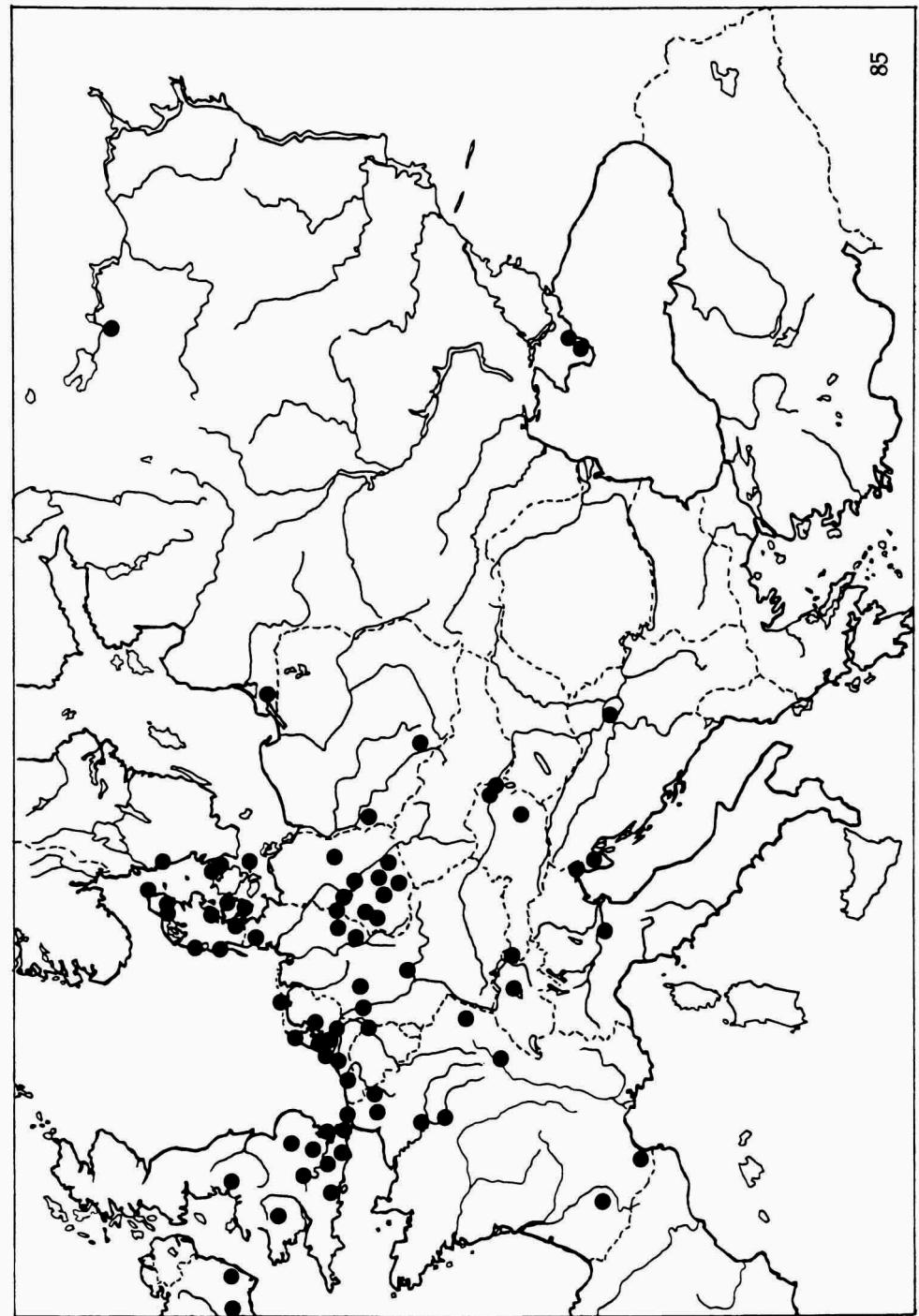


Fig. 85. Geographical distribution of *Choleva agilis* (Illiger, 1798).