

Revision of the *Dicranotropis hamata* group (Auchenorrhyncha, Delphacidae) and remarks on the implication of chiral dimorphism in its history

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Abstract

A new species, *Dicranotropis remaniaca*, is described. Morphological differences between the new species and the closely related *D. hamata* (Boheman) and *D. zenata* Logvinenko are summarized. Chirality is discussed in view of hypothetical implications in the history of the *D. hamata* group and of the presence of the phenomenon in a supposed hybrid area between *D. hamata* and *D. remaniaca* in southwestern France. Zoogeographic and phylogenetic aspects are discussed using *D. sagata* Logvinenko as outgroup.

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Introduction

The genus *Dicranotropis* was established by Fieber (1866) for the type species *Delphax hamata* Boheman, 1847. It is widely distributed in the Palearctic region. Some species are recorded also from tropical Africa, Australia and the Neotropic region, but these records concern probably other genera with double or bifurcate carinae on the frons. No species of *Dicranotropis* is recorded from North America.

Kirkaldy (1907) established for *Dicranotropis beckeri* Fieber, 1866 the genus *Leimonodite* on the base of the morphology of the frontal carinae. Nowadays this taxon is considered a subgenus of *Dicranotropis*. In Europe are recorded: *Dicranotropis (Dicranotropis) hamata* (Boheman, 1847), *D. (Leimonodite) beckeri* Fieber, 1866, *D. (Leimonodite) divergens* Kirschbaum, 1868, *D. (Leimonodite) montana* (Horváth, 1897). *D. carpath-*

ica Horváth, 1884 is considered a synonym of *D. divergens* Kirschbaum (Wagner 1963).

D. hamata is recorded from vast parts of Europe, Turkey, Siberia and perhaps North Africa, *D. divergens* from most parts of Europe (except for Fennoscandia and the Iberian Peninsula) and some regions of Central Asia, *D. beckeri* primarily from the Balkan region and Eastern Europe with some relictary area in France and Spain, Turkey and Central Asia, and *D. montana* from some alpine regions (Germany, Austria, Italy) and Romania.

D. hamata is closely related to *D. (s. str.) zenata* Logvinenko, 1969, described from the Caucasus region (Georgia), and shares with it a similar genital morphology. *D. (s. str.) sagata* Logvinenko, 1976, a further species from the Caucasus region described from Georgia, displays a quite different morphology of pygofer and styles, but has some other characters in common with *D. hamata*

concerning for example the aedeagus shape in males and the shape of the genital scale in females.

The existence of a taxon slightly different from *D. hamata* and replacing it in Italy was discovered by Remane and independently by D'Urso already many years ago, but difficulties to obtain material also from the closely related species described by Logvinenko from the Caucasus delayed the publication of these data until today.

The aim of the present paper is to describe the new taxon, *D. remaniaca* sp. n., to outline the distribution of *D. hamata* and *D. remaniaca*, respectively, and to discuss the relationships between both taxa and *D. zenata*, and to debate the relevance of aedeagal chiral dimorphism in the history of this species group.

Material and methods

Measurements were made by using a Zeiss Stemi SV 11 Stereomicroscope with ocular micrometer. A camera lucida attachment was used for the drawings; pencil sketches were subsequently copied on cardboard by means of a light table and elaborated with drawing ink. Photographs were prepared with a digital camera Canon Eos70D supplied with lens 105 mm f/2,8 Macro Canon, extension tube 25 mm Canon, and ring flash Nikon SM-2.

We examined specimens of the following collections:

- Institute of Zoology, National Academy of Sciences of Ukraine (Kiev) (CIZ).
- Naturhistorisches Museum, Basel, Switzerland (NHMB)
- Museo Cantonale di Storia Naturale, Lugano, Switzerland (MCSN)
- Muséum d'Histoire Naturelle, Genève, Switzerland (MHNG)
- Muséum National d'Histoire Naturelle, Collection Ribaut, Paris, France (MNHN/CR)
- Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZIN)
- Museum für Naturkunde, Berlin, Germany (MNKB)
- Moravian Museum, Brno, Czech Republic (MMB)
- Museo Civico di Storia Naturale, Trieste (MCSNT)
- Museo di Storia Naturale, Collection Servadei, Verona (MSNV)
- Department of Agricultural and Forestry Sciences, University of Tuscia, Viterbo, Italy (collection Adalgisa Guglielmino) (CG)
- Department of Biological, Geological and Environmental Sciences, sec. Animal Biology, University of Catania (Collection Vera D'Urso) (CD)
- Private collection Ilia Gjonov, Sofia, Bulgaria (CIG)
- Private collection Christoph Bückle, Tübingen, Germany (CB)
- Private collection Gabrijel Seljak, Nova Gorica, Slovenia (CGS)
- Private collection Kees den Bieman, Ulvenhout, Netherlands (CDB)
- Private collection Werner Holzinger, Graz, Austria (CH)

The material of the Servadei collection is presently not available, but was checked and listed by our colleague Manfred Asche (Berlin) some years ago.

The locality numbers in parentheses in the examined material of the collection Guglielmino (CG) coincide with the locality number system used in our faunistic and zoogeographical papers.

Material examined

***Dicranotropis hamata* (Boheman):** 255 specimens from Albania, Austria, Bulgaria, Czech Republic, Denmark, Finland, France, Germany, Greece, Hungary, Italy, Macedonia, Montenegro, Poland, Russia, Serbia, Slovenia and Switzerland.

***Dicranotropis remaniaca* sp. n.** (see also the Type series below): 390 specimens from Germany, Italy, Slovenia, Spain and Switzerland.

***D. hamata*/*D. remaniaca* intermediate forms:** 86 specimens from France.

***Dicranotropis zenata* Logvinenko:** Eight specimens from Georgia.

***Dicranotropis sagata* Logvinenko:** Three specimens from Georgia.

For a detailed list of the material please see Suppl. material 1.

Results

Description of the new species

Dicranotropis remaniaca sp. n.

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Figs 9–26, 44–46

Measurements. Body length: 2.45–2.90 mm (brachypterous males), 3.85–4.20 mm (macropterous males), 2.90–3.40 mm (brachypterous females), 4.30–4.50 mm (macropterous females). Head length: 0.20–0.28 mm (males), 0.26–0.30 mm (females). Head width including eyes: 0.78–0.92 mm (males), 0.88–0.96 mm (females). Pronotum length: 0.20–0.25 mm (males), 0.22–0.26 mm (females). Mesonotum length: 0.40–0.50 mm (brachypterous males), 0.58–0.64 mm (macropterous males), 0.44–0.52 mm (brachypterous females), 0.66–0.80 mm (macropterous females). Length of fore wings from shoulder to wing tip: 1.15–1.48 mm (brachypterous males), 3.15–3.50 mm (macropterous males), 1.24–1.48 mm (brachypterous females), 3.65–3.75 mm (macropterous females).

Description. In size, coloration and shape very similar to *D. hamata*: Median carina of frons forked below junction with vertex (Figs 15, 16); lateral carinae of pronotum not reaching hind margin; wings of brachypterous specimens between 1.5 and 2 × longer than wide, apically rounded (Figs 9, 14).

Coloration. Males (Figs 9–12, 15): Face with carinae white and areas between carinae black or light brown bordered with black; vertex light brown, pronotum light brown with carinae white; mesonotum light brown or more or less dark with white central longitudinal stripe extending onto scutellum; upper side of abdomen black, often with central part and some spots on lateral parts more or less light brown; pygofer black with more or less extended light brown areas; anal tube white; anal style black; forewings (brachypterous) hyaline brown, in brachypterous specimens apical half of suture black with adjacent area of wing dark, basal half of suture and hind margin with adjacent veins white; in macropterous specimens forewings hyaline with apical half of clavus and narrow adjacent area dark; underside mostly black; legs black with knees, tibiae and tarsi light or dark brown, third tarsomere generally dark. Females (Figs 13, 14, 16): similar to males but generally lighter: areas between frontal carinae light brown narrowly bordered with black; dark spot on wing suture small; upper side of abdomen in great part light brown; ovipositor sheath light; femura often in part light brown.

Genital morphology. Males (Figs 17–26): Pygofer with distinctly protruding dorsocaudal protuberance on each side; protuberances apically with small and short spine in medioventral position (Figs 22–24); anal tube on each side with small tooth of variable size near the base in subbasal position (Figs 25, 26); styles subbasally on the mediocaudal side with scabrous surface and acute spine shaped process, in the middle distinctly curved mediocaudad and provided with preapical tooth (Fig. 21); aedeagus laterally depressed, ventrally bent, with phallosome on the right side, only in rare exceptions on the left side; on its dorsal margin in central position with carina comprised of varying number of fused teeth and in preapical position with large single tooth, both bent towards right side; on right side, close to ventral margin, with group of about three small teeth in preapical position and, basally of them, single large tooth curved somewhat dorsad; on left side very close to ventral margin with one or more series of small teeth, varying in size and number, and with group of about three teeth more apically and quite distant from each other and from ventral aedeagus margin (Figs 17–20). Females: Gonocoxae VIII wide, median margin equally convex (Fig. 46); genital scale distinct, \pm triangular, with narrow deep apical incision reaching about half length of genital scale (Figs 44, 45).

Remarks. The pygofer and aedeagus morphology (in males), e.g. width of the aedeagus, number of the aedeagal spines (Figs 159–188), and shape of pygofer protuberances (Figs 201–206, 219–224, 249–256), and the morphology of the genital scale (in females) is to some degree variable, and apparently there are also slight regional differences (e.g. aedeagi of specimens from northern Italy, southern Switzerland and Slovenia (Figs 167–180) are particularly slender). For the variability of the genital styles see Figs 84–97.

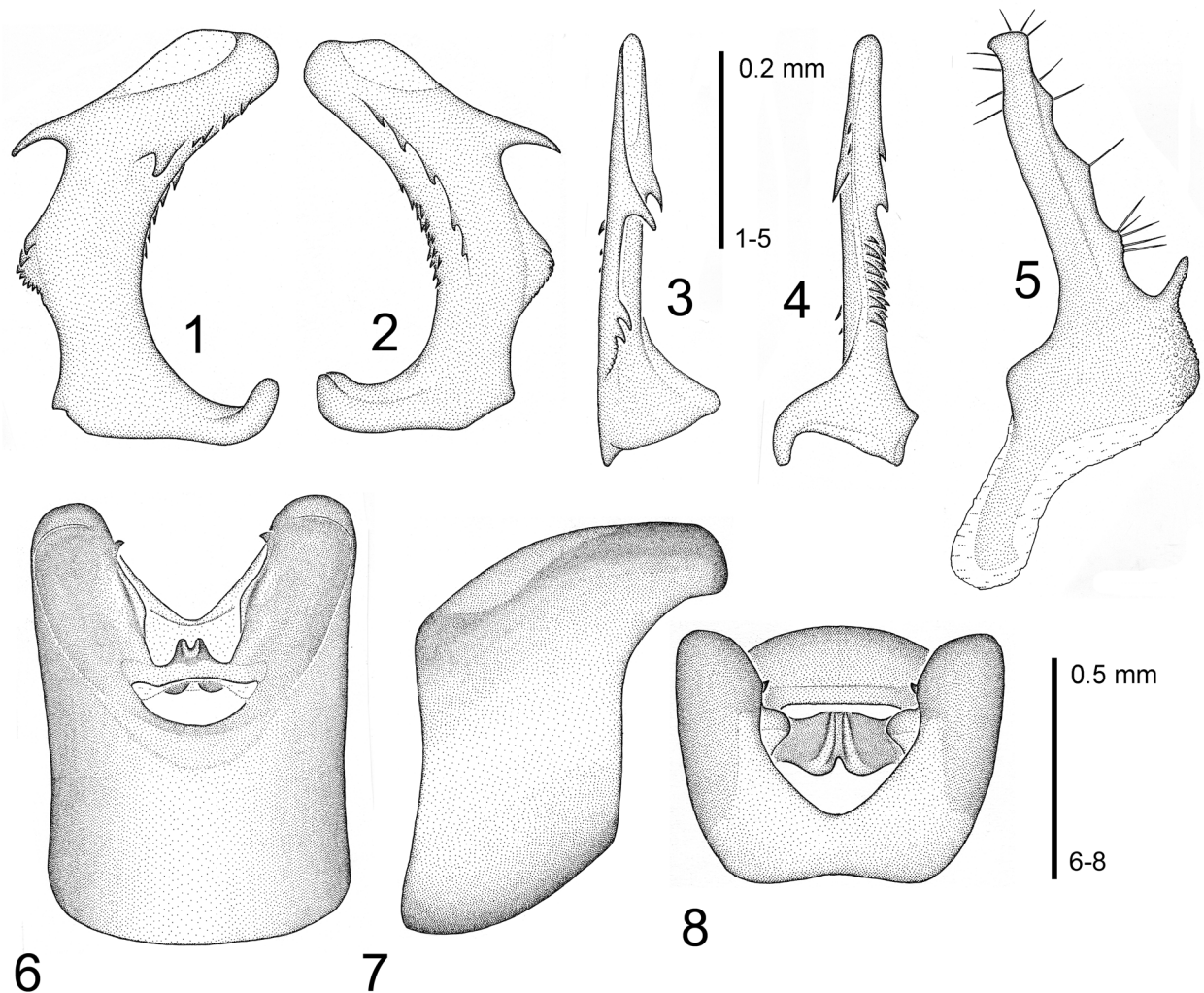
Diagnosis. Main differences to *D. hamata* consist in the shape of the genital styles and the aedeagus. The genital styles are stout, curved and provided with a preapical tooth in *D. remaniaca* while they are slender, straight, devoid of preapical tooth in *D. hamata* (Fig. 5). The aedeagus has its phallosome on the right side, only in rare exceptions on the left side, while it is typically on the left side in *D. hamata*, and also in all other characters of the aedeagus *D. remaniaca* is the mirror image to *D. hamata* (Figs 1–4). Other differences lie in the shape of the pygofer which is in *D. remaniaca* generally with a less protruding dorsocaudal portion and further caudally and dorsally located preapical teeth, therefore these are often visible in lateral view (Figs 22–24), while *D. hamata* has a more protruding dorsal portion of the pygofer and the preapical teeth are not visible in lateral view (Figs 6–8). However, the pygofer characters are rather variable and can be misleading in some cases.

Distribution (Fig. 257). Spain (Figs 84–86, 159–164); Switzerland south of the main Alpine chain (Canton Ticino) (Figs 88–90, 167–172); Italy except for Sicily and Sardinia and a small part in the northeastern Alpine region (Figs 94–97, 179–188); western Slovenia (Figs 91–93, 173–178); and some regions in Germany (southeastern Baden-Württemberg, southwestern Bavaria) (Figs 87, 165, 166).

Ecology. *D. remaniaca* shares its ecological characteristics with *D. hamata* and is found generally on not too dry meadows, often near forest margins or groups of bushes, from low to medium high altitude until about 1600m. Host plants are different species of Poaceae.

Biology. The species was mostly found from beginning of June until end of August, but one record from April (340m) indicates that the taxon may be bivoltine in lowlands. In mountain regions it has apparently only one generation.

Type series. **Holotype**, male: Lazio (Frosinone), Monti Ernici, road Collepardo-Vérolì, east of Civita; N41°45.596', E13°24.384'; 735m; 09/08/2012; St. 679; dry open area with Poaceae, thistles, *Thymus*, *Satureja* and shadowy path near dry brook with *Acer*, *Corylus* etc.; Guglielmino & Bückle leg. **Paratypes**: Same data as holotype, 6♂♂, 2♀♀. – Emilia-Romagna (Parma), SP 81 3,9km east (direction Bedonia) of Passo Tomarło (km 11,4); ~ 1200m; 09/06/2007; St.385; dry meadow and moderately moist meadow near beech wood, *Salix myrsinifolia*, *Urtica*, Poaceae; Guglielmino & Bückle leg.; 4♂♂, 6♀♀. – Same locality; 22/08/2008; St.444; Guglielmino & Bückle leg.; 12♂♂, 10♀♀. – Emilia-Romagna (Parma), road from Ponteceno to Anzola, 2,4km east of Anzola; ~ 850m; 21/08/2008; St.443; meadow with *Dactylis* surrounded by *Quercus*, *Acer*, *Corylus*, *Clematis*; Guglielmino & Bückle leg.; 7♂♂, 6♀♀. – Toscana (Massa), Alpi Apuane, ca. 3km south of Vinca; ~ 1000m; 05/06/2008; St.420; mixed forest with *Alnus cordata* (?), and undergrowth with *Rubus*, ferns, Poaceae; Guglielmino & Bückle leg.; 4♂♂, 2♀♀. – Same locality; 17/08/2008;

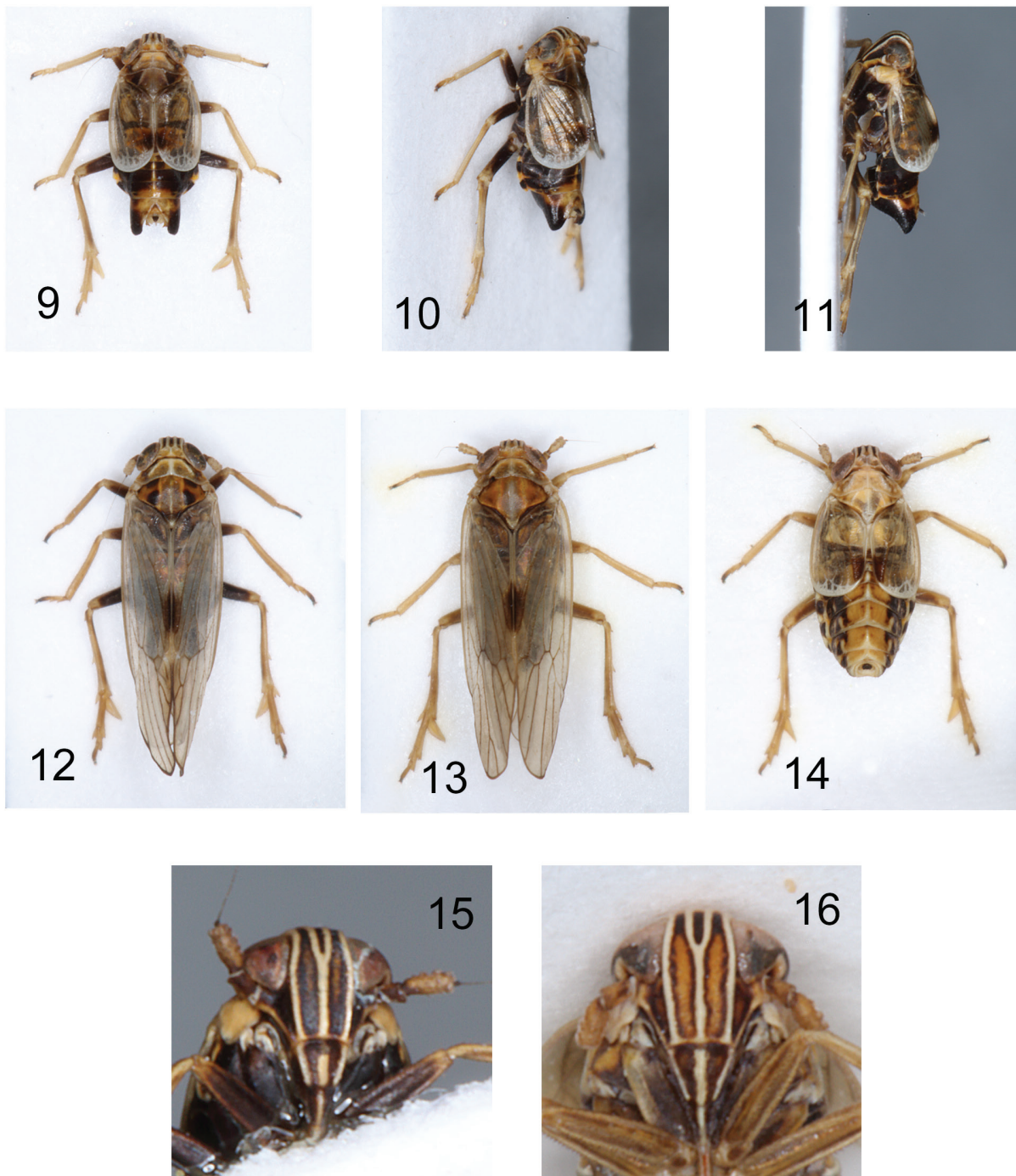


Figures 1–8. *Dicranotropis hamata* (Boheman), male. 1: Aedeagus, left lateral view. 2: Aedeagus, right lateral view. 3: Aedeagus, dorsal view. 4: Aedeagus, ventral view. 5: Right genital style from inside. 6: Pygofer, ventral view. 7: Pygofer, left lateral view. 8: Pygofer, caudal view. (1–5: Germany, Baden-Württemberg, Freudenstadt. 6–8: Germany, Bayern, Berchtesgaden).

St.435; Guglielmino & Bückle leg.; 5♂♂, 4♀♀. – Lazio (Rieti), Monti Reatini, M. Terminillo, S.P. 10, 4 Km from Leonessa; ~ 1200m; 22/8/1999; St. 36; vegetation along a brook; Guglielmino & Bückle leg.; 6♂♂, 15♀♀. – Lazio (Rieti), East of Lago di Piediluco, Madonna della Luce, SS 79 near fork Labro, Km 29,5; N42°31'15.0", E12°46'38.2"; 372m; 21/8/2000; St. 86; herbaceous vegetation with *Equisetum*, *Phragmites*, *Carex*, Cyperaceae, between *Ulmus*, *Salix*, *Quercus*; Guglielmino & Bückle leg.; 8♂♂, 5♀♀. – Lazio (Rieti), Amatrice, ca. 1km south of Preta, Tronto river; ~ 1150m; 18/6/2005; St.154; undergrowth of mixed forest with *Quercus cerris*, few *Ulmus*, *Salix*, *Populus tremula*; Guglielmino & Bückle leg.; 11♂♂, 12♀♀. – Lazio (Rieti), Rieti, Riserva Ripasottile-Lago Lungo, st. 3, 22/7/2009; St.454; Guglielmino & Bückle leg.; 8♂♂, 2♀♀. – Abruzzo (L'Aquila), slope south of Sella di Corno; ~ 1100m; 26/8/1999; St. 46; dry meadows with *Ostrya carpinifolia* Scop., *Quercus*,

Acer; Guglielmino & Bückle leg.; 7♂♂, 1♀. – Abruzzo (L'Aquila), slope south of Sella di Corno; ~ 1200m; 26/8/1999; St. 47; meadows on the borders of a mixed forest; Guglielmino & Bückle leg.; 8♂♂, 23♀♀. – Campania (Caserta), St.320: Strada da Gallo Matese a Fontegreca, prima del passo ~ 1,5 km a ovest di Gallo Matese, 850 m, 27/8/2006, prati fra siepi di *Acer monspessulanum*, *Rosa*, *Prunus spinosa*, *Crataegus* con Poaceae, Fabaceae ecc.; Guglielmino & Bückle leg.; 6♂♂, 8♀♀. – Basilicata (Potenza), Monte Sirino, road to Lauria, fountain 7,5km south of fork to Moliterno; ~ 1000m; 02/08/2009; St.470; forest with *Quercus*, *Crataegus*, *Alnus cordata*, *Spartium*, *Rubus* and small open pasture with Poaceae, Lamiaceae, *Holcus*; Guglielmino & Bückle leg.; 2♂♂, 3♀♀.

Type material deposited in Department of Agricultural and Forestry Sciences (DAFNE), University of Tuscia, Viterbo, Italy (Guglielmino's collection) (CG), two male and two female paratypes in Senckenberg Naturhistorische



Figures 9–16. *Dicranotropis remaniaca* sp. n. (Italy, Latium, Rieti). **9:** Brachypterous male, dorsal view. **10:** Brachypterous male, dorsolateral view. **11:** Brachypterous male, lateral view. **12:** Macropterous male, dorsal view. **13:** Macropterous female, dorsal view. **14:** Brachypterous female, dorsal view. **15:** Brachypterous male, frontal view. **16:** Brachypterous female, frontal view.

Sammlungen Dresden, Museum für Tierkunde, Dresden, Germany.

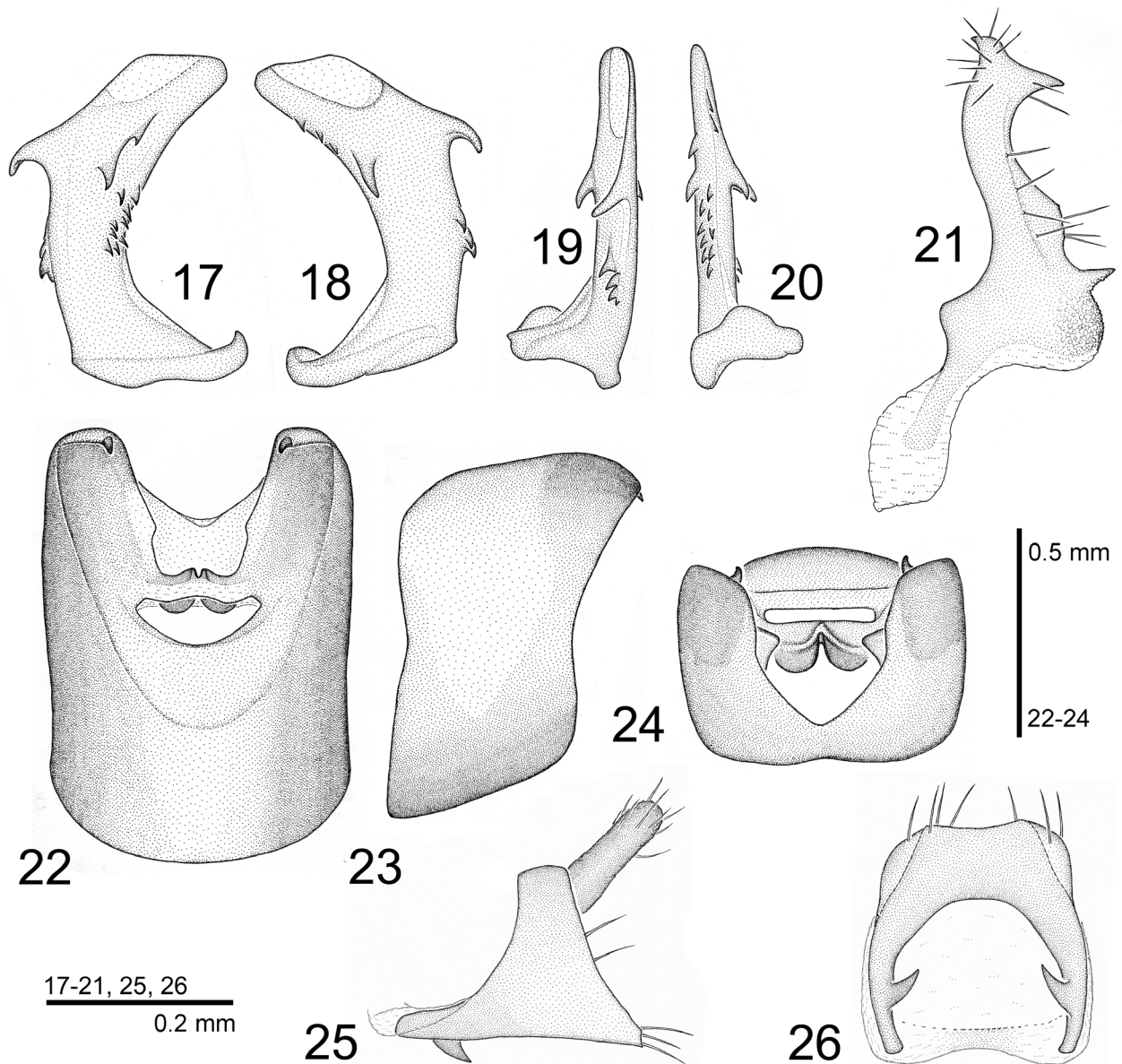
(For further material of this taxon see Suppl. material 1).

Redescription of genital morphology of related species

Dicranotropis hamata (Boheman): phallotreme on the left aedeagus side (Figs 1–4), only in some exceptions

on the right side, and slender, more or less straight styles without preapical tooth (Fig. 5), as figured e.g. in Ossianilsson (1978, Fig. 469). Females display the same type of triangular genital scale as *D. remaniaca* with narrow and deep caudal incision (Fig. 43), and have similar gonocoxae VIII without basal mediad protruding protuberance.

We examined specimens from Finland (Fig. 55), Denmark (Figs 56, 108, 109), most parts of France (Figs 50–54,



Figures 17–26. *Dicranotropis remaniaca* sp. n., male. **17:** Aedeagus, left lateral view. **18:** Aedeagus, right lateral view. **19:** Aedeagus, dorsal view. **20:** Aedeagus, ventral view. **21:** Right genital style from inside. **22:** Pygofer, ventral view. **23:** Pygofer, left lateral view. **24:** Pygofer, caudal view. **25:** Anal tube, lateral view. **26:** Anal tube, caudal view. (17–21: Italy, Emilia Romagna, Sologno. 22–24: Italy, Abruzzo, Campotosto. 25, 26: Italy, Abruzzo, Sella di Corno).

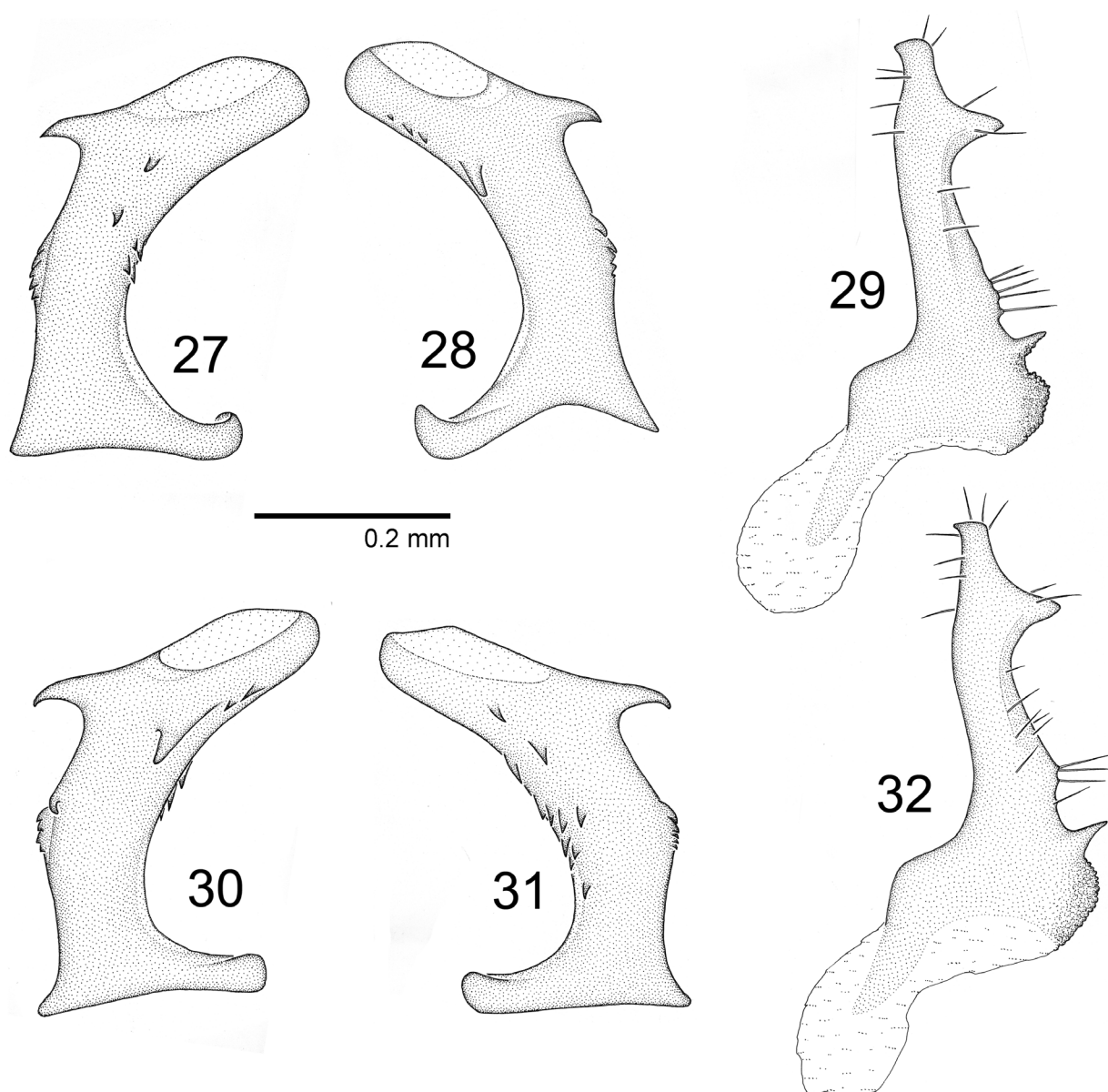
98–107) except for the southwestern regions, Germany (Figs 58, 59, 112–115) except for small areas in the southernmost parts, Czech Republic (Figs 63, 122, 123), Switzerland north of the main Alpine chain (Figs 57, 110, 111), Austria (Figs 60–62, 116–121), a small area in northeasternmost Italy, eastern Slovenia (Figs 65, 126, 127), Hungary (Figs 64, 124, 125), Ukraine (Crimea) (Figs 72, 140, 141), Russia (Krasnodar region) (Figs 73, 142, 143) and on the Balkan Peninsula: Serbia (Figs 66, 128, 129), Montenegro, Bulgaria (Figs 68, 69, 132–135), Macedonia (Figs 67, 130, 131), Albania, Greece (Figs 70, 71, 136–139).

Specimens from northern Poland display characters as those of other Central European regions, but have a small

preapical tooth on their styles (Fig. 74, see also fig. 470 in Ossiannilsson 1978).

The pygofer and aedeagus morphology (in males), e.g. width of the aedeagus, number of the aedeagal spines (Figs 98–143), and shape of pygofer protuberances (Figs 189–197, 207–215, 225–242), and the morphology of the genital scale (in females) is to some degree variable. For the variability of the genital styles see Figs 50–73.

D. hamata/*D. remaniaca* intermediate forms: intermediate style characters were found in specimens from southwestern France (Figs 29, 32, 75, 77–83). They display an aedeagus with phallotreme in some cases on



Figures 27–32. Transitional forms between *Dicranotropis hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?). 27: Aedeagus, left lateral view. 28: Aedeagus, right lateral view. 29: Right genital style from inside. 30: Aedeagus, left lateral view. 31: Aedeagus, right lateral view. 32: Right genital style from inside. (27–29: France, Haute-Garonne, Luchon. 30–32: France, Haute-Garonne, Luchon (other specimen)).

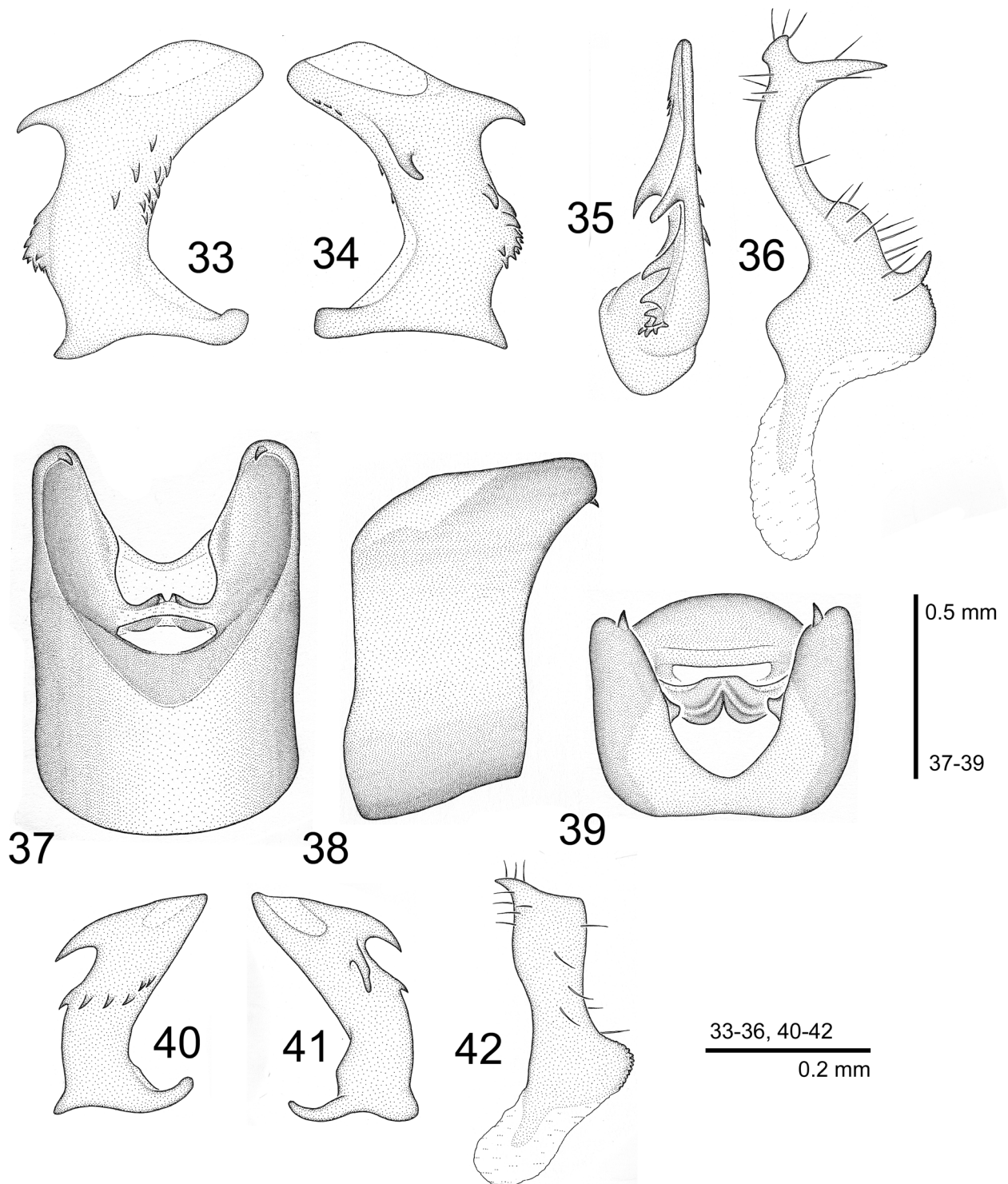
the left, in others on the right side (Figs 27, 28, 30, 31, 144–147, 150–158). One specimen is found also in a more northwestern region (Dep. Saone-et-Loire) (Figs 76, 148, 149). 40 specimens with intermediate characters were examined on the whole: 22 had an aedeagus with phallotreme on the left side and 18 an aedeagus with phallotreme on the right side. 31 specimens were from the same locality (St. Béat), 17 of which had an aedeagus with phallotreme on the left side and 14 with phallotreme on the right side.

The pygofer morphology is illustrated in Figs 198–200, 216–218, 243–248.

Females are undistinguishable from *D. remaniaca* and *D. hamata* females.

Dicranotropis zenata Logv.: stout, curved style shape with very long preapical tooth (Fig. 36), a robust aedeagus with phallotreme on the left side (Figs 33–35), and a pygofer similar to that of *D. remaniaca* (Figs 37–39; see also Fig. 1 in Logvinenko 1969). Females: The genital scale is quite large and displays a proportionally short and very narrow caudal incision (Fig. 47). Gonocoxae VIII similar to those of *D. hamata*.

Remark: The record of *D. hamata* from Caucasus (Georgia: Kodžori, two males) by Dlabola (1958, Figs 43, 44) refers apparently to this taxon. The figures of the styles show a long preapical tooth as is typical for this taxon (the lack of the subbasal thorn in these figures is probably due to the fact that Dlabola apparently did not

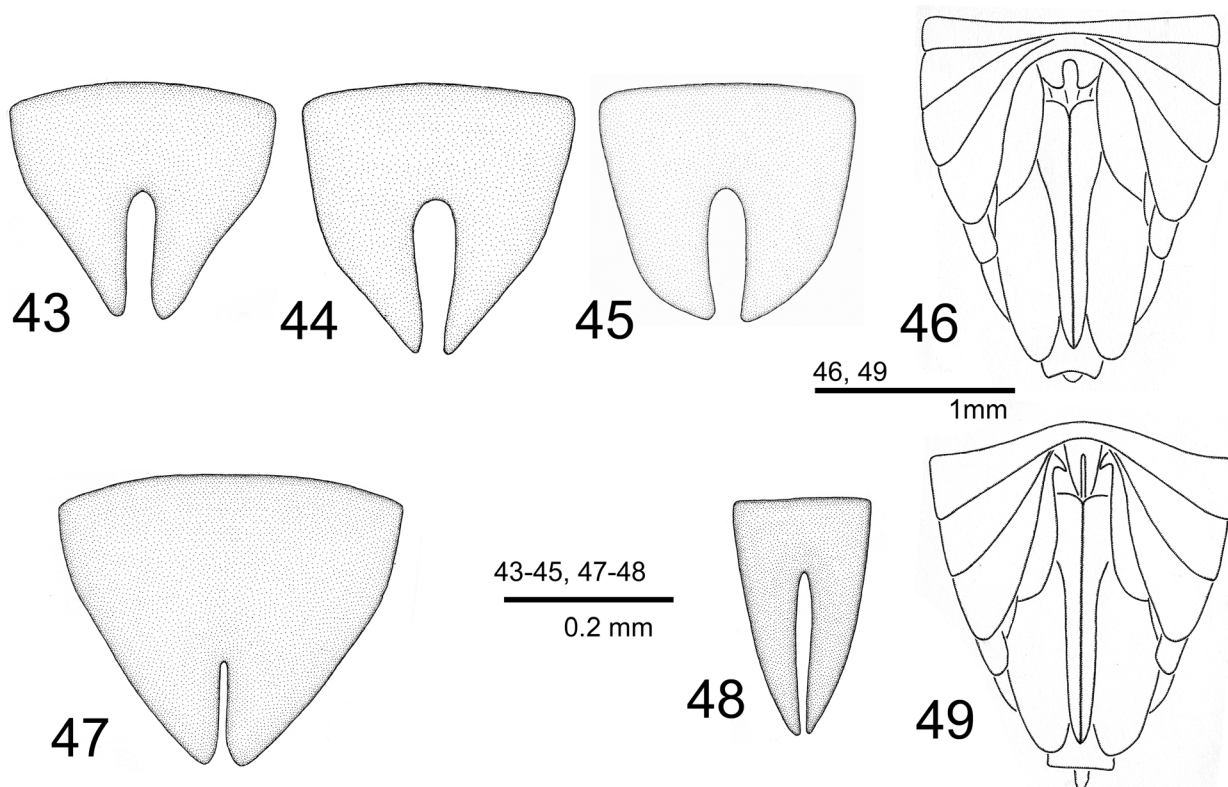


Figures 33–39. *Dicranotropis zenata* Logv. (Georgia, Goderdsi). **33:** Aedeagus, left lateral view. **34:** Aedeagus, right lateral view. **35:** Aedeagus, dorsal view. **36:** Right genital style from inside. **37:** Pygofer, ventral view. **38:** Pygofer, left lateral view. **39:** Pygofer, caudal view. **40–42.** *Dicranotropis sagata* Logv. (Georgia, Sasaredneo). **40:** Aedeagus, left lateral view. **41:** Aedeagus, right lateral view. **42:** Right genital style from inside.

dissect the genital apparatus and therefore the base of the styles were not well visible for him).

Dicranotropis sagata Logv.: small and short styles without preapical tooth and without basal spine shaped

protuberance (Fig. 42), and a small aedeagus with low number of teeth on both sides and phallotreme on the right side (Figs 40, 41, see also Figs 25–27 in Logvinenko 1976). The species lacks the large dorso-caudally protruding pygofer protuberances present in



Figures 43–49. *Dicranotropis hamata* group, females. **43:** *Dicranotropis hamata* (Boheman) (Bulgaria, Western Rhodopes, Elesh-nica), genital scale. **44:** *Dicranotropis remaniaca* sp. n. (Slovenia, Nova Gorica), genital scale. **45:** *Dicranotropis remaniaca* sp. n. (Italy, Umbria, Lago di Piediluco), genital scale. **46:** *Dicranotropis remaniaca* sp. n. (Italy, Basilicata, M. Sirino), abdomen, ventral view. **47:** *Dicranotropis zenata* Logv. (Georgia, Goderdsi, Advigeki), genital scale. **48:** *Dicranotropis sagata* Logv. (Georgia, Sasaredneo), genital scale. **49:** *Dicranotropis sagata* Logv. (Georgia, Sasaredneo), abdomen, ventral view.

D. hamata and *D. zenata*, but shares with these taxa the small tooth on the inner side of the dorsocaudal pygofer margin. Females display a small elongate genital scale with very long apical incision (Fig. 48). The gonocoxae VIII are narrowed basad and basally abruptly protruding mediad (Fig. 49).

Unfortunately, our knowledge on both taxa from the Caucasus region is based only on very few specimens, thus the range of variability in these taxa is unknown.

Discussion

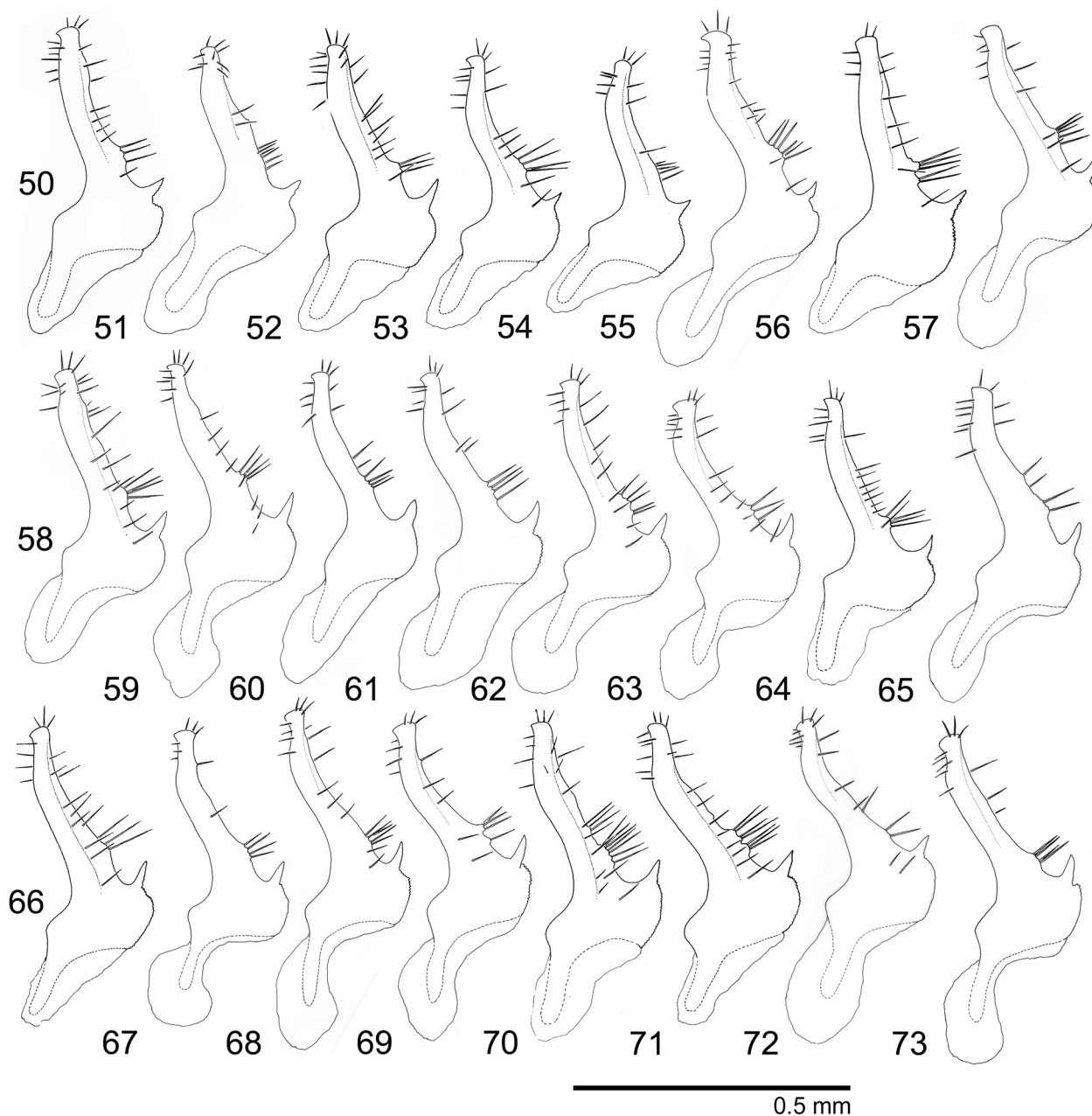
Chiral dimorphism (antisymmetry)

Besides the different shape of the genital styles in *D. hamata* and *D. remaniaca*, the most distinct difference between both taxa consists in their aedeagus morphology with this structure in one taxon being the mirror image of the other (Figs 1, 18). Exceptions, i.e. aedeagi with phallotreme on the right side in *D. hamata* (Fig. 118, 119, 138, 139) or with phallotreme on the left side in *D. remaniaca* (Figs 183, 184), are found in both taxa but they are not very common. It makes approximately 1% in *D. remaniaca*, and ca. 4% for *D. hamata*, but for the latter species should be considered that most of the

reverse specimens were from localities peripheric within the area of that species and not far from the area of *D. remaniaca*.

For the explanation of this situation we may go back to a period when the areas of the ancestors of both recent taxa were separated and speciation was in progress.

But before we have to make some considerations: The asymmetry of the aedeagus in Delphacidae (as in most of the other insect groups with asymmetric genital structures) is in most cases directional, i.e. only one of the two mirror symmetric possibilities is observed (rare exceptions are found in many taxa). There are, however, several cases in delphacids where the aedeagus asymmetry is not directional and both possible aedeagus types are present in a proportion of 50:50. This phenomenon was recorded for example for *Stiroma affinis* Fieber (De Jong 1985) and *Chloriona vasconica* Ribaut (Guglielmino and Bückle 2010). It is called chiral dimorphism, mirror image dimorphism or antisymmetry, and the two possible mirror images are termed enantiomorphs (Schilthuizen 2013). Apparently, this situation provides no disadvantage for the species and has no impact for the mating ability. In several taxa of insects, species of the same genus differ in the direction of chirality (Schilthuizen 2007, 2013; Huber et al. 2007). This implies that intermediate



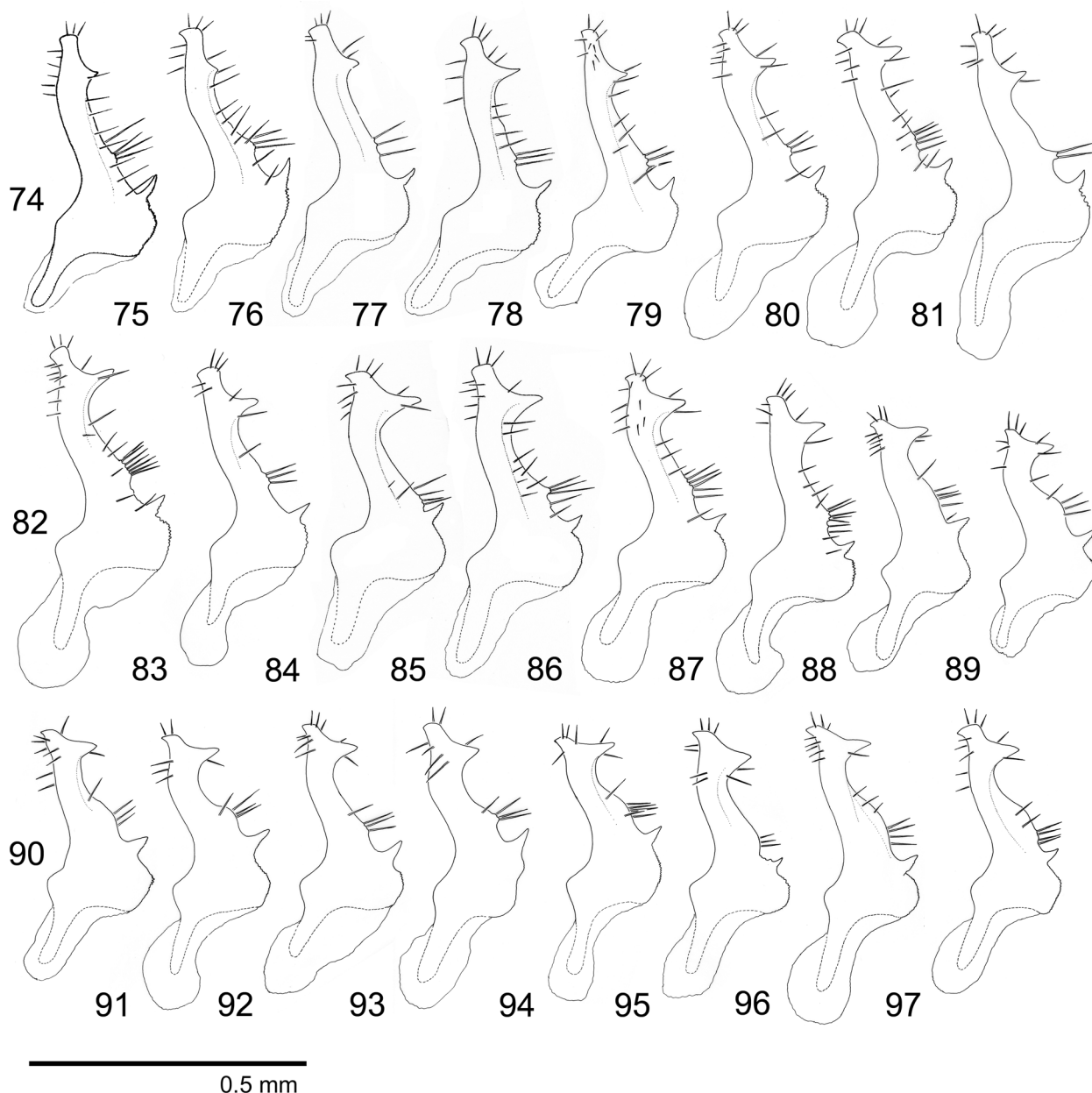
Figures 50–73. *Dicranotropis hamata* (Boheman), right genital style from inside. **50:** France, Hérault. **51:** France, Nantes. **52:** France, Jura. **53:** France, Ardèche. **54:** France, Vaucluse. **55:** Finland. **56:** Denmark. **57:** Switzerland, Jura. **58:** Germany, Baden-Württemberg, Tübingen. **59:** Germany, Bayern, Berchtesgaden. **60:** Austria, Kärnten, Woerthersee. **61:** Austria, Steiermark, Leibnitz. **62:** Austria, Niederösterreich, Himberg. **63:** Czech Republic, Moravia, Mikulov. **64:** Hungary, Velence. **65:** Slovenia, Zgornje Jezersko. **66:** Serbia, Džep. **67:** Macedonia, Strumica distr.. **68:** Bulgaria, Goce Delchev. **69:** Bulgaria, Western Rhodopes, Eleshnica. **70:** Greece, Katara region, Pindos. **71:** Greece, Katara region, Pindos (other specimen). **72:** Ukraine, Crimea. **73:** Russia, Krasnodar.

stages of chiral dimorphism must have existed, either during cladogenesis or during anagenesis.

The aedeagus morphology in *D. hamata* and *D. remaniaca* with one species representing the mirror image to the other may be interpreted in the same way, with a transitional stage of antisymmetry and a subsequent return to a directional asymmetry opposite to the original one. As such processes are more likely to occur in small populations, possibly this happened in the ancestor populations of one of the two taxa during a situation where

their area was distinctly more limited than now due to climate constraints.

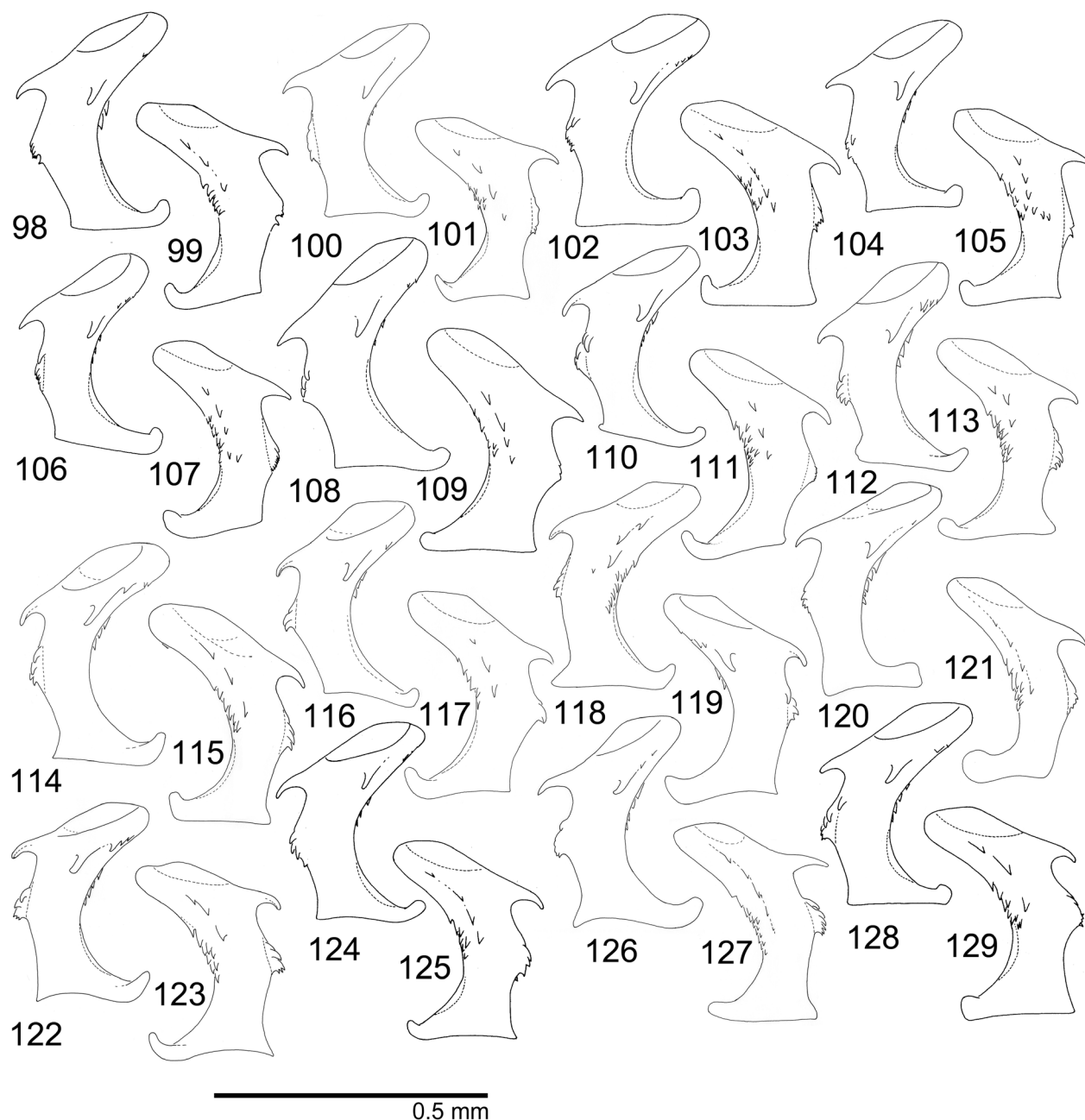
A striking parallel case is to be mentioned in another delphacid genus, *Chlorionidea* Löw. In central and eastern Europe and central Asia occurs *C. flava* Löw, on the Apennines *C. apenninica* Guglielmino and Bückle. Both species differ mostly by differences in the morphology of their anal tube and in their aedeagus morphology with this organ being in one species the mirror image in respect to the other (Guglielmino and Bückle 2010).



Figures 74–97. *Dicranotropis hamata* group, right genital style from inside. *Dicranotropis hamata* (?). **74:** Poland, Zdory. **75–83.** Transitional forms between *D. hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?). **75:** France, Gard. **76:** France, Saone-et-Loire. **77:** France, Ariège. **78:** France, Aude, Laroque de Fa. **79:** France, Toulouse. **80:** France, Haute-Garonne, St. B at. **81:** France, Tarn, Albi. **82:** France, Pyr enes Orientales, Mt. Louis. **83:** France, Haute-Garonne, Arlos. **84–97.** *Dicranotropis remaniaca* sp. n.. **84:** Spain, Teruel. **85:** Spain, Lerida. **86:** Spain, Girona, Ripoll. **87:** Germany, Bayern, F ussen, Trauchberg. **88:** Switzerland, Canton Ticino. **89:** Switzerland, Canton Ticino, Monteggio. **90:** Switzerland, Canton Ticino, Monteggio (other specimen). **91:** Slovenia, Bovec. **92:** Slovenia, Nova Gorica. **93:** Slovenia, Vogrsko. **94:** Italy, Valle d’Aosta, Monte Avic. **95:** Italy, Abruzzo, Sella di Corno. **96:** Italy, Abruzzo, Campotosto. **97:** Italy, Basilicata, Monte Sirino.

Chiral dimorphism is observed also in other groups of insects as in the mantid genus *Ciulfina*. Populations of four species belonging to this genus were investigated. In one of them a proportion near 50% between both enantiomorphs was observed, in a second one only one enantiomorph was present (directional asymmetry). For two species, however, the proportions of both enantiomorphs were far from 50:50 and unequal among the populations of the same species (Holwell and

Herberstein 2010). A completely different situation is found in the snail *Partula suturalis* Pfeiffer. This species is polymorphic for the direction of coiling. Populations with directional asymmetry are prevailing. Mixed populations are generally small and unstable. As mating between snails of opposite coil is difficult there is apparently a strong selection against chirally dimorphic populations which exist only under special conditions (Johnson et al. 1990).



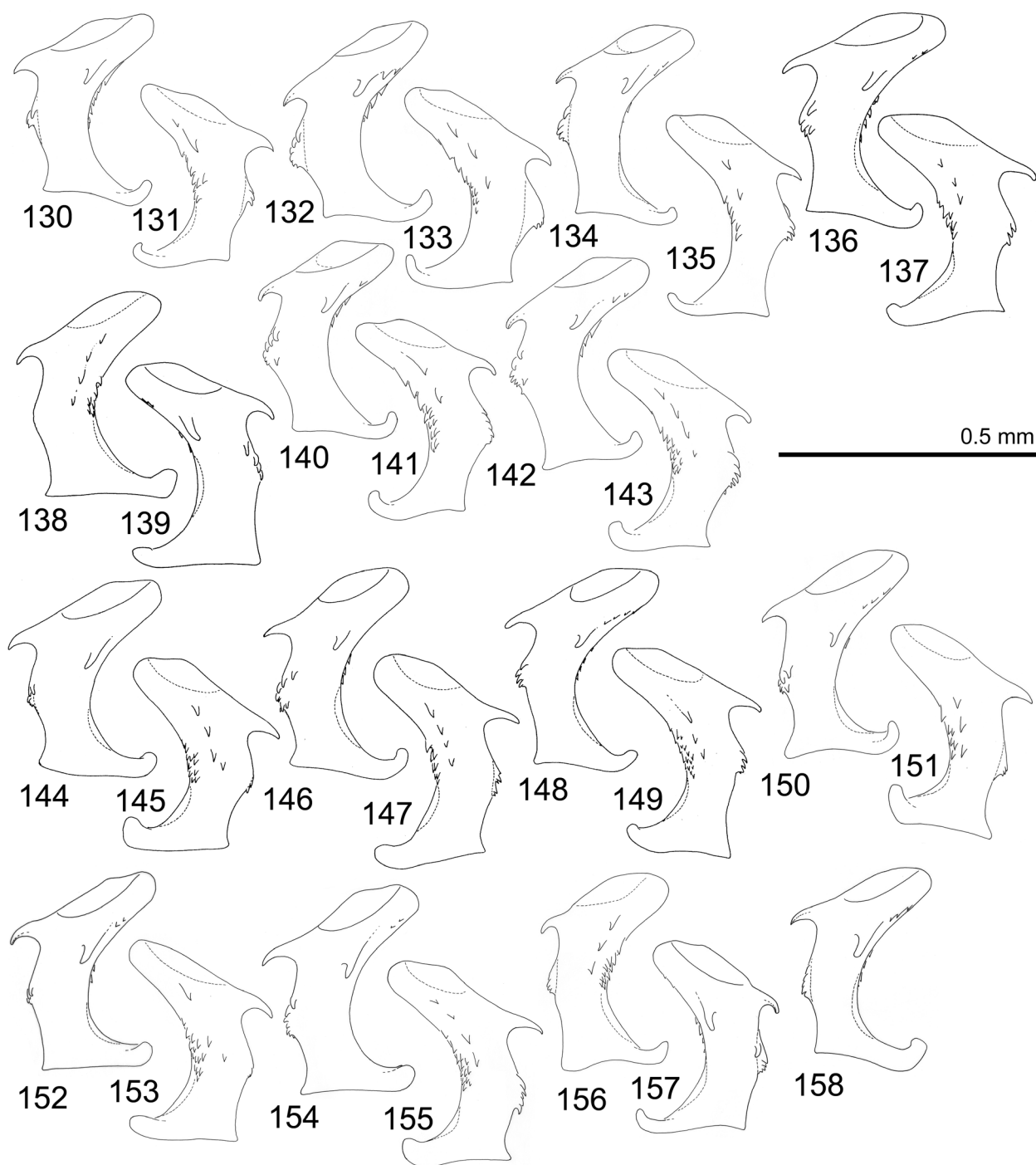
Figures 98–129. *Dicranotropis hamata* (Boheman), aedeagus, left and right lateral view. **98, 99:** France, Jura. **100, 101:** France, Nantes. **102, 103:** France, Hérault. **104, 105:** France, Ardèche. **106, 107:** France, Vaucluse. **108, 109:** Denmark. **110, 111:** Switzerland, Jura. **112, 113:** Germany, Baden-Württemberg, Tübingen. **114, 115:** Germany, Bayern, Berchtesgaden. **116, 117:** Austria, Niederösterreich, Himberg. **118, 119:** Austria, Steiermark, Leibnitz. **120, 121:** Austria, Kärnten, Woerthersee. **122, 123:** Czech Republik, Moravia, Mikulov. **124, 125:** Hungary, Velence. **126, 127:** Slovenia, Zgornje Jezersko. **128, 129:** Serbia, Džep.

Hybrid area in southwestern France?

Preliminary remark: The existence of supposed hybrids between *Dicranotropis hamata* and *D. remaniaca* taxa north of the Pyrenees may imply to describe them on a subspecies level. However, in other contact regions between both taxa (South Germany, Slovenia, Switzerland) to date no specimens were observed that present unequivocally intermediate characters in their genital

morphology or a mixture of both possible enantiomorphic aedeagus types. In those areas, the species show no signs of hybridisation.

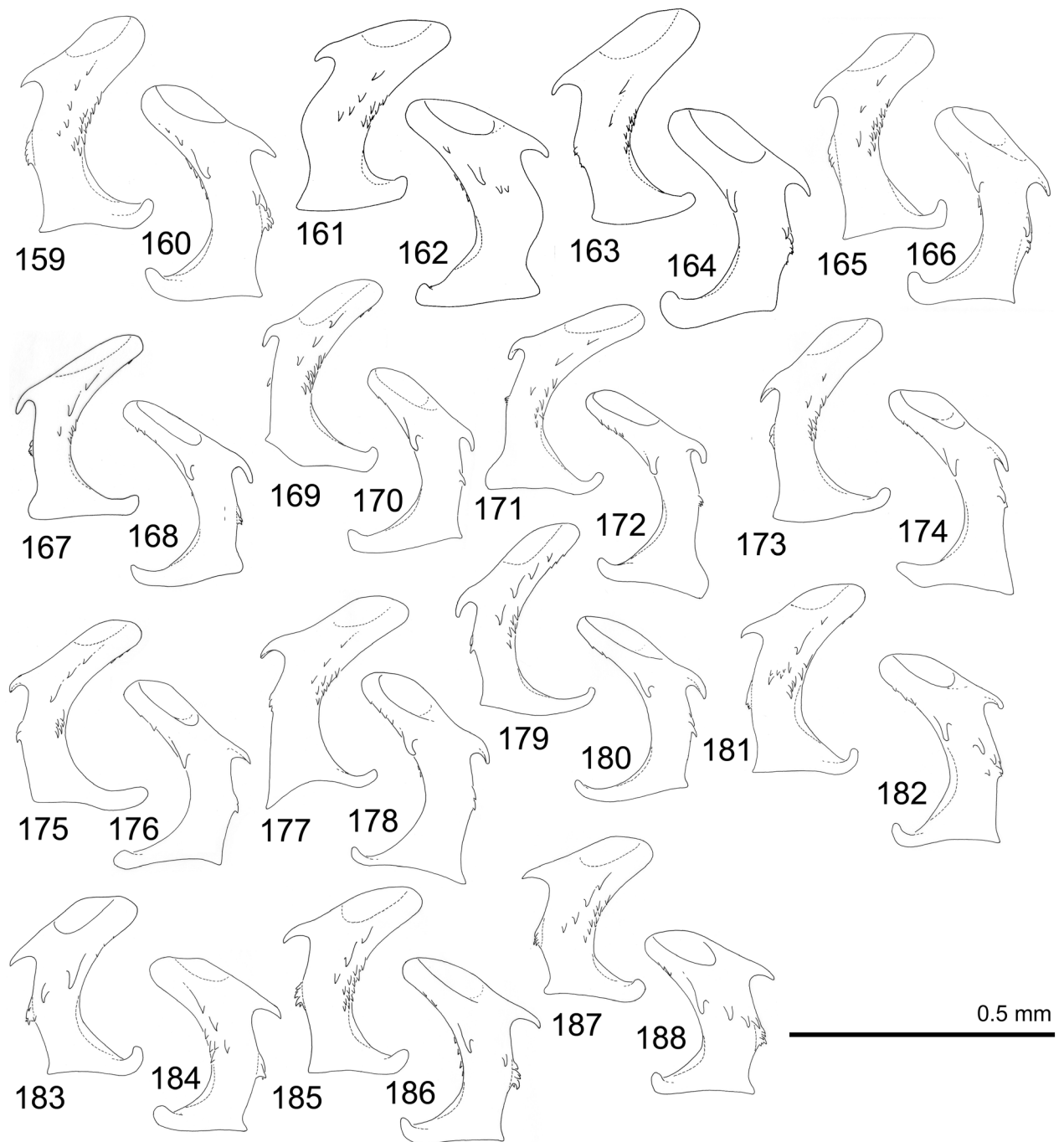
In southwestern France *Dicranotropis* specimens were found with genital styles (Figs 75, 77–83) that lie in between the shapes of *D. hamata* and *D. remaniaca*. Geographically, they are situated between an area with apparently pure *D. remaniaca* populations on the one side (the Iberian Peninsula, Figs 84–86) and pure *D. ha-*



Figures 130–157. *Dicranotropis hamata* group, aedeagus, left and right lateral view. **130–143.** *Dicranotropis hamata* (Boheman). **130, 131:** Macedonia, Strumica distr. **132, 133:** Bulgaria, Western Rhodopes, Eleshnica. **134, 135:** Bulgaria, Goce Delchev. **136, 137:** Greece, Katara region, Pindos. **138, 139:** Greece, Katara region, Pindos (other specimen). **140, 141:** Ukraine, Crimea. **142, 143:** Russia, Krasnodar. **144–157.** Transitional forms between *D. hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?). **144, 145:** France, Ariège. **146, 147:** France, Gard. **148, 149:** France, Saone-et-Loire. **150, 151:** France, Aude, Laroque de Fa. **152, 153:** France, Haute-Garonne, St. Béat. **154, 155:** France, Tarn, Albi. **156, 157:** France, Haute-Garonne, Arlos. **158:** Transitional forms between *D. hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?), aedeagus, left lateral view, France, Toulouse.

mata populations on the other (southeastern and central France, Figs 52–54). Of course, the Pyrenees were an interface between populations of numerous species which expanded from separate glacial refugia. During postglacial expansions, the Pyrenees formed a barrier for pop-

ulations on both sides of these mountains. The contact between southern *D. remaniaca* and northern *D. hamata* populations may have been hindered for a long time, until *D. remaniaca* populations from the South succeeded in surmounting this barrier and mixed with *D. hamata*



Figures 159–188. *Dicranotropis remaniaca* sp. n., aedeagus, left and right lateral view. **159, 160:** Spain, Girona, Ripoll. **161, 162:** Spain, Teruel. **163, 164:** Spain, Lerida. **165, 166:** Germany, Bayern, Füssen, Trauchberg. **167, 168:** Switzerland, Canton Ticino, Monteggio. **169, 170:** Switzerland, Canton Ticino, Monteggio. **171, 172:** Switzerland, Canton Ticino. **173, 174:** Slovenia, Bovec. **175, 176:** Slovenia, Nova Gorica. **177, 178:** Slovenia, Vogrsko. **179, 180:** Italy, Valle d’Aosta, Monte Avic. **181, 182:** Italy, Abruzzo, Campotosto. **183, 184:** Italy, Abruzzo, Sella di Corno. **185, 186:** Italy, Abruzzo, Sella di Corno (other specimen). **187, 188:** Italy, Basilicata, Monte Sirino.

populations from the North. Therefore, we interpret the intermediate characters in the genital morphology of the populations immediately north of the Pyrenees as due to hybridization of populations of both species.

In these supposed hybrid populations, aedeagi with phallotreme on the left side (Fig. 30, as in *D. hamata*) and with phallotreme on the right side (Fig. 28, as

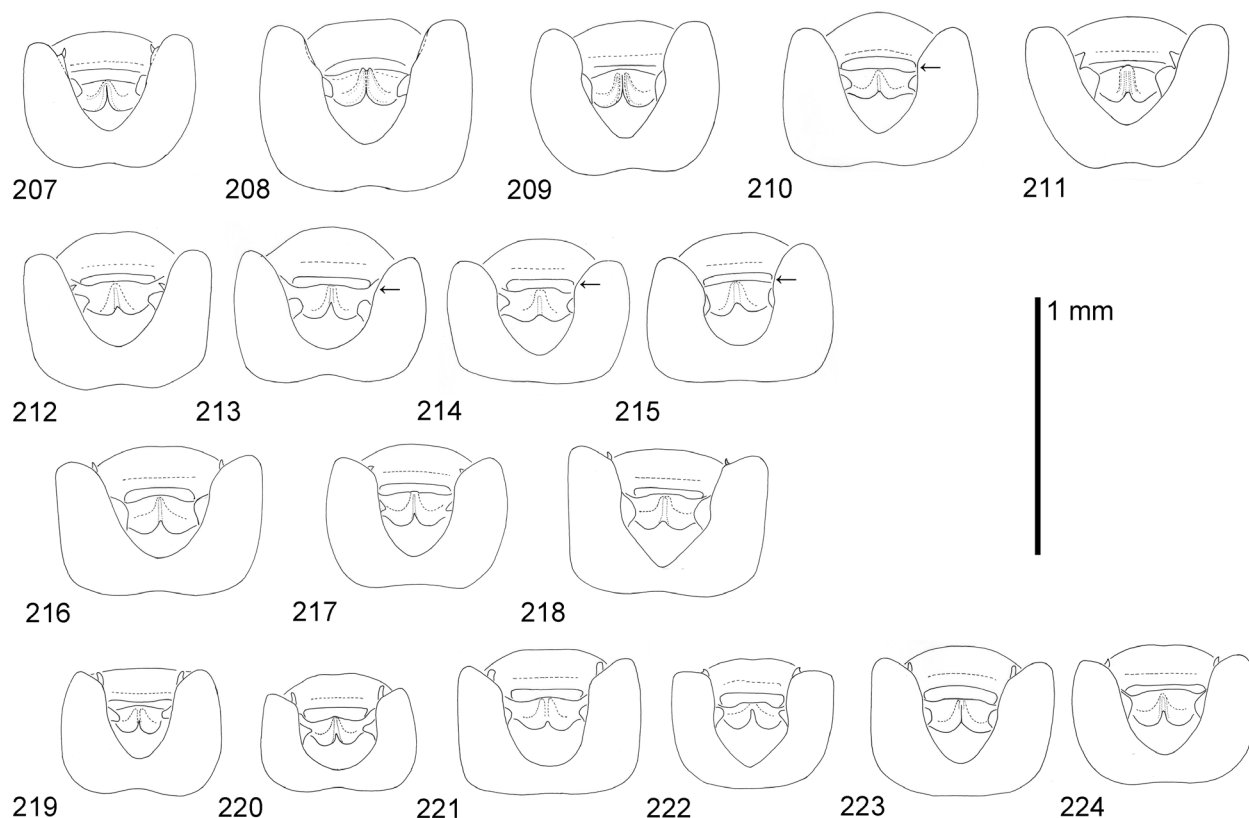
in *D. remaniaca*) are present. Both aedeagus types are not rare. The proportion, based on 40 specimens, is not far from 50:50 (the phallotreme on the left side, i. e. the “*hamata*-type”, is slightly prevailing). Two scenarios are possible: (1) the fixation of directional asymmetry is lost and the supposed hybridisation resulted in a real anti-symmetry (i.e. a not fixed direction of the (asymmetric)



Figures 189–206. *Dicranotropis hamata* group, pygofer, ventral view. **189–197:** *Dicranotropis hamata* (Boheman). **189:** France, Nantes. **190:** Finland. **191:** Switzerland, Jura. **192:** Germany, Baden-Württemberg, Kaiserstuhl. **193:** Germany, Bayern, Berchtesgaden. **194:** Austria, Niederösterreich, Himberg. **195:** Slovenia, Zgornje Jezersko. **196:** Macedonia, Strumica distr.. **197:** Russia, Krasnodar. **198–200:** Transitional forms between *D. hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?). **198:** France, Haute-Garonne, St. B at. **199:** France, Aude, Laroque de Fa. **200:** France, Haute-Garonne, Luchon. **201–206.** *Dicranotropis remaniaca* sp. n.. **201:** Switzerland, Canton Ticino. **202:** Switzerland, Canton Ticino, Monteggio. **203:** Slovenia, Vogrsko. **204:** Italy, Basilicata, Monte Sirino. **205:** Germany, Bayern, Füssen, Trauchberg. **206:** Spain, Girona, Ripoll.

aedeagus shape and consequently a 50:50 proportion of both aedeagus types); (2) each specimen has its individual aedeagus orientation not by chance, as in true antisymmetry, but due to special genetic constraints based on the combination of its genetic heritage as the result of hybridisation between populations each of which had their fixed aedeagus directionality. Thus, the hybrid populations consist of a mixture of specimens with different directionally asymmetric aedeagi. In this case, the proportion of the two aedeagus types may be different from the 50:50 proportion, moreover it may be varying between different areas of the hybrid area. This condition may be named “pseudo-antisymmetry”.

We may mention in this context a similar case in the *Zyginidia pullula* group in northwestern Italy. Mazzoglio and Arzone (1993) found hybrids including a vast spectrum of intermediate forms between *Z. pullula* (Boheman, 1845) and *Z. ribauti* Dworakowska, 1970 in Liguria, and Bocca et al. (1988) describe hybrids between *Z. pullula* and *Z. scutellaris* (Herrich-Sch affer, 1838) in the Aosta Valley. Della Giustina (1989) considers the possibility of *Zyginidia ribauti* (present in the whole Apennine Peninsula) being a hybrid between *Z. pullula* (present in north Italy and eastern Central Europe) and *Z. scutellaris* (present in Western Europe and Sardinia).



Figures 207–224. *Dicranotropis hamata* group, pygofer, caudal view. **207–215:** *Dicranotropis hamata* (Boheman). **207:** France, Nantes. **208:** Finland. **209:** Switzerland, Jura. **210:** Germany, Baden-Württemberg, Kaiserstuhl. **211:** Germany, Bayern, Berchtesgaden. **212:** Austria, Niederösterreich, Himberg. **213:** Slovenia, Zgornje Jezersko. **214:** Macedonia, Strumica distr.. **215:** Russia, Krasnodar. **216–218:** Transitional forms between *D. hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?). **216:** France, Haute-Garonne, Luchon. **217:** France, Aude, Laroque de Fa. **218:** France, Haute-Garonne, St. B at. **219–224:** *Dicranotropis remaniaca* sp. n.. **219:** Switzerland, Canton Ticino. **220:** Switzerland, Canton Ticino, Monteggio. **221:** Slovenia, Vogrsko. **222:** Italy, Basilicata, Monte Sirino. **223:** Germany, Bayern, Füssen, Trauchberg. **224:** Spain, Girona, Ripoll. (the arrows in Figures 210, 213–215 indicate the position of the preapical tooth)

Biogeographical aspects (Fig. 257)

There is little doubt that the division of *D. hamata* and *D. remaniaca* from each other happened not long ago, probably during the last glaciation. The two taxa have a nearly identical aedeagus shape (except for the opposite orientation of one taxon in respect of the other, see above), with only some barely discernible differences in the pygofer morphology and the different shape of the central and apical parts of the genital styles, i.e. differences that certainly need a relatively short time to evolve.

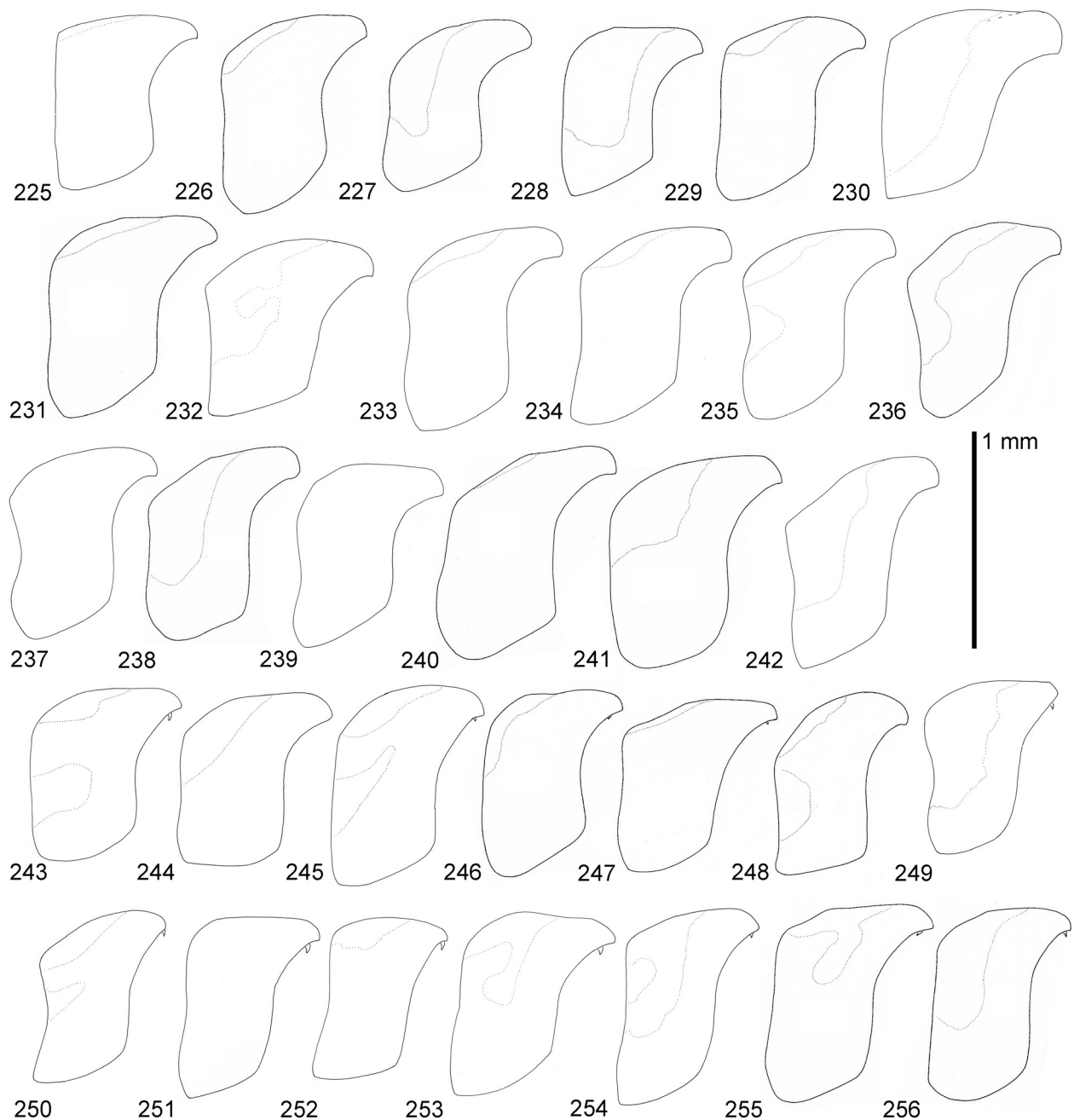
We suppose that the area of the common ancestor of both taxa was restricted during a cold climate period, and finally divided in two separate areas, which was the basal situation for a speciation process towards the presently observed two taxa. During a following warmer period both groups may have extended their areas, and developed a hybrid area where they got in contact with each other.

The present disjunct distribution of *D. remaniaca*, occurring on parts of the Iberian Peninsula on the one and continental Italy with some adjacent areas on the other hand requires further explanation.

One scenario is the colonisation of the Iberian Peninsula directly from Italian mainland or, less probably, viceversa via drifted macropterous specimens crossing the Mediterranean Sea. Generally macropterous specimens are found quite frequently within *D. hamata* and *D. remaniaca* populations, even though brachypterous ones prevail by far. Thus, this possibility cannot be completely excluded. On the other side it is noticeable that for *D. remaniaca*, in spite of the flight ability of macropterous specimens, there are no records from Sicily and Sardinia, though it is present on the entire peninsular Italy until Calabria.

In our opinion another scenario is more probable: we suppose that the taxon in former times had a continuous distribution in the Westmediterranean region (and possibly not only there) including at least southern France. A following restriction of its area due to climatic changes may have resulted in the division in two separated areas on the two Peninsulas, respectively.

Finally, *D. hamata* populations might have extended their area in southwestern direction, filled in southeastern France the gap between *D. remaniaca* populations in Italy and Spain and hybridized with *D. remaniaca* north of the Pyrenees.



Figures 225–256. *Dicranotropis hamata* group, pygofer, left lateral view. **225–242:** *Dicranotropis hamata* (Boheman). **225:** France, Nantes. **226:** France, Hérault. **227:** France, Ardèche. **228:** France, Vaucluse. **229:** France, Jura. **230:** Finland. **231:** Denmark. **232:** Switzerland, Jura. **233:** Germany, Baden-Württemberg, Kaiserstuhl. **234:** Germany, Bayern, Berchtesgaden. **235:** Austria, Niederösterreich, Himberg. **236:** Hungary, Velence. **237:** Slovenia, Zgornje Jezersko. **238:** Serbia, Džep. **239:** Macedonia, Strumica distr.. **240:** Greece, Katara region, Pindos. **241:** Greece, Katara region, Pindos (other specimen). **242:** Russia, Krasnodar. **243–248:** Transitional forms between *D. hamata* (Boheman) and *D. remaniaca* sp. n. (hybrids?). **243:** France, Haute-Garonne, St. Béat, **244:** France, Aude, Laroque de Fa. **245:** France, Haute-Garonne, Luchon. **246:** France, Ariège. **247:** France, Saone-et-Loire. **248:** France, Gard. **249–256:** *Dicranotropis remaniaca* sp. n. **249:** Switzerland, Canton Ticino. **250:** Switzerland, Canton Ticino, Monteggio. **251:** Slovenia, Vogrsko. **252:** Italy, Basilicata, Monte Sirino. **253:** Germany, Bayern, Füssen, Trauchberg. **254:** Spain, Girona, Ripoll. **255:** Spain, Lerida. **256:** Spain, Teruel.

In the central part of the Alps *D. remaniaca* apparently passed the barrier of the main Alpine chains and established itself in a small part of south Germany (probably it is present also in the western parts of Austria: Tirol and

Vorarlberg). On the other side *D. hamata* occurs in a small part of the southern Alps in northern Friuli-Venezia Giulia; north of this area in Carinthia *D. hamata* is found as well, whereas in western Slovenia *D. remaniaca* occurs.



Figure 257. Outline map of the distribution of the species of the *Dicranotropis hamata*-group. **1** = *Dicranotropis remaniaca* sp. n.; **2** = *Dicranotropis hamata* (Bohemian); **1/2** = transitional forms between *D. remaniaca* and *D. hamata* (hybrids?); **2!** = *D. hamata* specimens from northern Poland with particular style shape; **3** = *D. zenata* Logv.; **(2)** *D. hamata* specimen from northern Friuli, checked by Manfred Asche; **(2!)** *D. hamata* specimen figured by Ossiannilsson (1978).

Phylogenetic aspects

It is quite evident that *D. sagata* differs distinctly from the other taxa treated in this study. The large protruding dorsocaudal protuberances of the pygofer are less developed, the styles (Fig. 42) are small and devoid of a basal spine shaped process, the gonocoxae VIII (Fig. 49) have a distinct basal protuberance. Nevertheless it shares with the three other taxa the general morphology of the aedeagus (even though in a smaller and more simple version, Figs 40, 41), the deep caudal incision in the genital scale of females (Fig. 48) and a small thorn near the caudolateral part of the pygofer. These features might represent a synapomorphy of all four taxa.

D. hamata, *D. remaniaca* and *D. zenata* are very closely related taxa. They share with each other (1) the general shape of their pygofer (Figs 7, 23, 38) with its dorsolateral parts distinctly protruding caudad, (2) their aedeagus shape (Figs 1, 2, 17, 18, 33, 34) including the arrangement of spines and teeth on both sides, and (3) the subbasal thorn on their genital styles (Figs 5, 21, 36).

D. zenata differs from *D. remaniaca* only slightly in the more robust aedeagus (Figs 33, 17), the longer tooth on the genital style (Figs 36, 21), and in the shape of the genital scale (Figs 47, 45). Both species have as a common character an aedeagus with its phallotreme

on the right side. They share this aedeagus directionality with *D. sagata* (Fig. 40), what suggests that this is the plesiomorphic condition and the phallotreme on the left side of the aedeagus in *D. hamata* is apomorphic. Furthermore, they have generally a shorter pygofer (Figs 38, 23) than *D. hamata* (Fig. 7), but this character is quite variable. The genital styles with their distinctly bent central part and the robust preapical tooth is structurally similar in *D. zenata* and *D. remaniaca* as well (Figs 36, 21), even if this tooth is distinctly longer in *D. zenata*. Possibly this preapical tooth is a synapomorphic character of both taxa, and *D. zenata* and *D. remaniaca* are sister species, and together the sister group to *D. hamata*. Alternatively, it may represent an apomorphic character of the common ancestor of the three *hamata* group taxa, which is lost in *D. hamata*. In this case it is a plesiomorphic character of the three *hamata* group species and does not support monophyly of *D. remaniaca* + *D. zenata*.

The small preapical tooth in two *D. hamata* specimens from northern Poland (Fig. 74) can be interpreted as a residue of the preapical tooth which is generally lost in *D. hamata* but was possibly present in its ancestor populations, or it may be a result of hybridisation in the past. Presently these populations are apparently surrounded exclusively by areas with pure *D. hamata* populations.

Further research

For a better understanding of the distribution of *D. hamata* and *D. remaniaca* it would be necessary to collect more material above all from the region where the areas of both taxa are adjacent to each other, specifically in the Alpine region, Slovenia, southern Germany, western Alps and southeastern France, but also in Spain, northeastern Europe, and, of course, around the supposed hybrid area in southwestern France.

Furthermore, it would be interesting to compare morphological data, gathered in the presented paper and in future studies, with bioacoustic and molecular data, in order to get further hints on how the present disjunct area of *D. remaniaca* may be explained, and to assess the hypothesis of a hybrid area in southwestern France.

Crossing experiments between populations from the latter region, and the examination of the offspring of left side phallotreme and right side phallotreme males would as well furnish interesting results.

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Supplementary material 1

Detailed list of study materials

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Data type: Excel

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