The European ant hunters Tracheliodes curvitasus and T. varus (Hymenoptera: Crabronidae): taxonomy, species discrimination, distribution, and biology

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Abstract

Crabro varus PANZER, 1799 has been originally described from Austria. After the type material has been destroyed, species identity was controversial. Most recently (Bitsch & Leclercq 1993, Leclercq 1993), the taxon has been interpreted as a species of the ant hunters, genus Tracheliodes, based on a single female collected in Corse, France. New records of Tracheliodes varus from Lower Austria confirm this interpretation; in order to stabilize the species identity, we designated a neotype from the type area, Austria. Tracheliodes varus is most similar to T. curvitasus (Herrich-Schaeffer, 1841). We present diagnoses and illustrations, describe the variation of colour patterns and give new information on the discrimination of the females of these two sibling species. New records from Austria are reported for Tracheliodes curvitasus after more than 100 years, and for T. varus after more than 200 years. Tracheliodes curvitasus is recorded for the first time from Bulgaria and the Czech Republic, T. varus for the first time from the Czech Republic, Slovakia, and Bulgaria. In Laxenburg, Lower Austria, females of T. curvitasus and T. varus have been found syntopic, both of them hunting workers of the dolichoderine ant Liometopum microcephalum (Panzier, 1798). Based on film sequences, we present first observations on the hunting behaviour of T. varus.

Key words: crabronid wasp, sibling species, behaviour, faunistics, neotype designation, Austria, Bulgaria, Czech Republic, Slovakia, Liometopum microcephalum

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Introduction

Tracheliodes A. Morawitz, 1866 is a small genus of the Crabronini and comprises seven species from the Palaearctic Region (Nemkov 1988, Bitsch & Leclercq 1993, Li 1999, Li & He 1999), three species from the western United States (Bohart & Menke 1976), three species from the Neotropical Region (Leclercq 1981, Cooper 1988, Leclercq & Cambra 2003), and three fossil species from Colorado shale and Baltic amber (Bohart & Menke 1976). Morphologically, species of Tracheliodes differ from related genera by a comparatively large distance between antennal socket and corresponding inner eye orbit, resulting from anteriorly less converging inner eye orbits (Fig. 1). As far as their biology is known, all species are specialized on hunting ant workers of the subfamily Dolichoderinae.
Only three species are known from Europe: the circum-Mediterranean* T. quinquenotatus* (JURINE, 1807) provides its larvae with ants of the genus *Tapinoma* A. FÖRSTER (e.g., EMERY 1893, GRANDI 1961), while *T. curvitarsus* (HERRICH-SCHAEFFER, 1841) from southeastern and central Europe takes only *Liometopum microcephalum* (PANZER, 1798) (EMERY 1893, KOHL 1915, BITSCH & LECLERQ 1993). The third species, *T. varus* (PANZER, 1799), was only recently recognized as a representative of the ant hunters. Because the type specimens from Austria are destroyed, all knowledge was based on a single specimen from Corse (BITSCH & LECLERQ 1993). In this paper we report *T. varus* also from the Czech Republic, Slovakia, and Bulgaria.

In the summer of 2003, we discovered female specimens of two species, *T. curvitarsus* and *T. varus*, in Lower Austria. These are the first Austrian records of *T. curvitarsus* since the original description of its synonym, *Crabro megerlei*, by DAHLBOM (1845) and another undated specimen from Vienna published by KOHL (1893), and of *T. varus* since PANZER’s (1799) original description. We provide first notes on the biology of *T. varus*, which has been observed in hunting ant workers of *Liometopum microcephalum*. As our material of *T. varus* only partly agrees with the diagnosis based on the Corse female (BITSCH & LECLERQ 1993), we add descriptive notes and illustrations for *T. varus* and *T. curvitarsus*, which facilitate a safe identification of these sibling species. PANZER’S (1799) original description and illustration (Fig. 11) supports the interpretation as *varus* in the present sense. However, because of the strong colour variation of both species, similarly small, dark specimens of *T. curvitarsus* may occur. Therefore, we meet the necessity for a fixation of the taxon *Crabro varus* PANZER, 1799 by neotype designation.

**Material and methods**

**Material**: All specimens examined are dry-mounted, pinned or glued on card labels. Nineteen specimens of *T. curvitarsus* and fourteen specimens of *T. varus* deposited in the following collections have been available for this study.

Acronyms of repositories of specimens:

- CGW Coll. G. Grabenweger, Vienna, Austria
- CLS Coll. T. Ljubomirov, Sofia, Bulgaria
- CZW Coll. H. & S.V. Zettel, Vienna, Austria
- MGB Faculté des Sciences Agronomiques de l’Etat, Gembloux, Belgium
- NHMW Natural History Museum, Vienna, Austria
- OÖLM Oberösterreichisches Landesmuseum, Biologizezentrum, Linz, Austria

**Morphology**: External structures were examined and measured with a LEICA Wild M10 stereo-microscope (max. 108 × magnification); Figures 1 - 6 were made by using a camera lucida. Photographs (Figs. 7 - 10) were taken with the digital camera Nikon Coolpix 990 attached to a Nikon SMZ1500 high resolution dissecting microscope with a 1.6 plan-apochromatic front lens, at magnification up to 320 ×.

**Acronyms of morphometric characteristics:**

- **OOD** oculo-ocellar distance: minimum distance between eye and posterior ocellus
- **POD** postocellar distance: minimum distance between posterior ocelli

**Behaviour**: Film sequences have been made on 5 August 2003 in Laxenburg, Lower Austria, with a Sony Camcorder DSR-PDX10P in format PAL, 25 frames per second (50 fields displayed and interlaced per second, making for a 25 frames per second system).

**Results**

**Tracheliodes curvitarsus** (HERRICH-SCHAEFFER, 1841) (Figs. 4, 6, 8, 10)

**Material examined**: Austria: Vienna, undated [before 1846], leg. Kollar, 1 ♀, 1 ♀ [NHMW; syntypes of *Crabro (Brachymerus) megerlei*]; Lower Austria: Bezirk Mödling, Laxenburg, Schlosspark, 175 m, 16° 21' E 48° 04' N, 15.VII.2003, leg. G. Grabenweger & F.M. Steiner, 2 ♀♂ (CGW), 5.VIII.2003, from stem of oak tree, leg. H. Zettel, 1 ♀ (CZW); Czech Republic: Moravia, Čejě, VI. 1973(?), 4 ♀♂, 1 ♀ (OÖLM); Moravia, Ladna, VII.1986, leg. M. Kocourek, 1 ♀ (OÖLM); Italy: Sicily, 1858, leg. Mann (NHMW); Bologna, VII. 1890, 1 ♀ (with worker specimen of *Liometopum microcephalum* on pin) (NHMW); Bulgaria: Struma valley, Kressna, 200 m, 23°10′E 41°47′N, 1.V. 2003, leg. T. Ljubomirov, 1 ♀ (CLS); Black Sea coast, Nessebur, 27° 42′ E 42° 39′ N, 28.VI.1982, leg. M. Kocourek, 3 ♀♂ (OÖLM); Plovdiv, Proslav suburb, 24° 40′ E 42° 07′ N, 10.VII.1997, leg. A. Zaykov, 1 ♀ (OÖLM); Greece: Phthiotis, S Timfristos, 38° 55′ N, 21° 51′ E, 750 m, 22.VII. 1990, leg. H. Rausch, 1 ♀ (OÖLM).

**General distribution**: previously recorded from Germany (Nassau; doubtful record, because *Liometopum microcephalum* is absent from Germany), Austria, Italy (including Sicily), Hungary, Romania, and Greece (BITSCH & LECLERQ 1993). First records from Czech Republic and Bulgaria.

Notes on previous records from Austria: Formerly this species was only known from Vienna. The syntype specimens of *Crabro (Brachymerus) megerlei* are from Vienna, without further locality information. KOHL (1893) mentioned another specimen (female) from the Türkenschranz in Vienna (today: Türkenschanzpark, 18th district), at that time deposited in NHMW, but now lost. DÖLFUSS (1983, 1991) refers only to KOHL’s (1893) specimen, ZETTEL & al. (2001) misinterpreted KOHL (1893) and erroneously combined the data of the two records.
Diagnosis: Female: body length 8.6 - 11.4 mm (smallest specimen from Bulgaria, largest from Moravia); head width 2.20 - 2.92 mm (mean = 2.56 mm; n = 17); OOD : POD = 1.4 - 1.8 (mean = 1.6; n = 17); lateral teeth on clypeus distinct, bilobate, separated from eye margin by deep incision (Fig. 4: arrow); vertex and mesonotum (Fig. 8) dull, with dense microsculpture, with fine punctures of same size as those scattered punctures on mesopleuron; mesopleuron completely and densely striate (Fig. 10); occipital carina directed to mouthparts, therefore without edge in lateral view of head (Fig. 6: arrow); midfemur posterovertrally and hindfemur antevertrally each with large, shallow excavation set with long setae; hindtibia markedly incrassate; midbasitarsus slightly, hindbasitarsus conspicuously curved; gastral sternum I completely black; hindtibia completely yellow or apically infuscated with brown. – Male: body length 8.3 and 8.7 mm; head width 2.11 and 2.26 mm; OOD : POD = 1.5 and 1.6; clypeus similar as in female, but teeth less distinct due to dense pilosity; sculpture of vertex and mesonotum similar as in female; sculpture of mesopleuron either similar as in female or striation slightly reduced (in male from Czech Republic); gastral sternum I black; hindtibia apically more infuscated than in female; illustration of genitalia: see Bitsch & Leclercq (1993).

Variation of yellow colour pattern (females only): Along dorsal inner eye margin with yellow stripes, usually broad, rarely narrow, rarely reaching clypeus; clypeus with yellow central spot (frequently) to mainly yellow with black margins only; at lower gena rarely completely black, usually with yellow patch which often extended dorsal far along outer eye margin (Fig. 6); mandible yellow to variable extension; scape either completely yellow or with black stripe medially; pronotal dorsum with yellow fascia
(either entire or medially interrupted); pronotal lobe yellow, rarely black; tegula yellow to light brown; mesonotum in one specimen with very small, paired, yellow spots anterolaterally; mesopleuron anteriorly varying from all black to all yellow; mesoscutellum varying from all black to nearly all yellow, mostly yellow anteriorly and black posteriorly; gastral tergum I yellow laterally, with transverse band posteriorly, terga II - V variably coloured, bands on terga II and III often continuous, sometimes also on terga IV and V, but in some specimens widely interrupted, in one female yellow colour on tergum IV reduced to small paired lateral dots; gastral sternum I black; sterna II - V variably coloured, from nearly all black with small dot on sternum II to mainly yellow with black marks at base; hindcoxa with yellow marks in some specimens; fore- and midrthrochanters variably coloured (from black to yellow); hindrthrochanter yellow; on fore- and midlegs tibiae, tarsi and apices of femora yellow; on hindleg tibia and apex of femur yellow, rarely tibia apically brownish and femur completely black.

Biology: The biology of most species of Tracheliodes is not or little known (NEMKOV 1988). As far as known, all species are specialized on hunting ants of the subfamily Dolichoderinae as food for the larva (NEMKOV 1988 and references therein) and have developed an advanced hunting behaviour (PATE 1942). In contrast to most other crabronids, which capture soft-bodied insects, females of Tracheliodes spp. have to overcome hard-bodied and fit-to-fight ants. The thickened head and the rather ventrally oriented face is interpreted as a morphological adaptation to this prey (PATE 1942). Females catch their prey by hovering above or nearby the foraging worker ants to wait for a suitable situation, suddenly accelerate, grasp a worker with the mandibles and fly off (PATE 1942). In some distance they land, paralyzed their prey, transport it to their nest and lay eggs on it; after some weeks of feeding on the ant, the Tracheliodes larvae spin a cocoon (PATE 1942, NEMKOV 1988). Tracheliodes curvitarsus hunts L. microcephalum (EMERY 1893, NEMKOV 1988; own observations). The nest of T. curvitarsus is located in the abandoned holes of wood-boring beetles (EMERY 1893, PATE 1942), but T. quinquenotatus excavates cells in the soil (FERTON 1912, GRANDI 1928, 1935, 1961, BERNARD 1934).

Tracheliodes varus (PANZER, 1799) (Figs. 1 - 3, 5, 7, 9, 11, 12)

Material examined: Austria: Lower Austria: Bezirk Gänserndorf, Marchegg, Storchenwiese near Schloss Marchegg, 16° 54'E, 48° 17'N, 14.VIII.2003, from stem of oak tree, leg. H. Zettel, 1 ♀, neotype by present designation (NHMW); Bezirk Mödling, Lan-
the presence of *T. varus* within the present borders of Austria.

Diagnosis: Female: body length 5.6 - 8.6 mm (smallest specimen from Corse, largest from Slovakia); head width 1.80 - 2.17 mm (mean = 2.01 mm; n = 14); OOD : POD = 1.1 - 1.5 (mean = 1.3); lateral teeth on clypeus reduced, slightly projecting from outline, separated from eye margin by shallow indentation only (Figs. 2, 3: arrows); occipital carina strongly curved and directed to foramen, therefore with sharp edge in lateral view of head (Fig. 5: arrow); vertex and mesonotum (Fig. 7) appearing glabrous, with microsculpture evanescent, mesonotum with large, deep punctures much larger than those on mesopleuron; mesopleuron appearing glabrous (Fig. 9), only with very short striae close to mesometapleural suture; modifications of mid- and hindlegs as in *T. curvitarsus*; gastral sternum I anteriorly with yellow marks; hindtibia basally yellow, distally black. – Male unknown.

Variation of yellow colour pattern (females only): colouration on average darker than in *T. curvitarsus*; integument completely black along dorsal inner eye margin, with small yellow dots or narrow stripes (most frequently; Fig. 1), or with long yellow stripes reaching clypeus in one specimen; clypeus all black or with small central yellow (or brownish) spot; lower gena all black, or with small to medium sized yellow patch (Fig. 5); base of mandible yellow to variable extension; stripe on scape yellow; pronotal dorsum yellow (either entire or variably widely interrupted); pronotal lobe black, rarely yellow; tegula yellow to brownish; mesopleuron anteriorly varying from all black to all yellow; mesoscutellum from nearly all black with two small yellow spots anteriorly to nearly all yellow with small black patch posteromedially; gastral tergum I laterally yellow, posteriorly with transverse band, usually terga II - V posteriorly with paired patches; tergum II rarely with continuous band; patches on terga III and IV narrowly separated in some specimens; gastral sternum I anteriorly yellow (rarely indistinctly so), sterna II - V with yellow bands posteriorly or spots medially; trochanters usually black, rarely yellow; on fore- and midlegs apex of femora, most of tibiae (except black stripe) and base of tarsi or all tarsi yellow; on hindleg base of tibia yellow to variably extension, but distally always black.

**PANZER**’s (1799) original illustration (Fig. 11) shows a specimen which fits quite well this variable pattern, except that the apex of the hindfemur appears narrowly yellow in the same way as the apices of the fore- and midfemora. This may be an incorrectness by the illustrator, although such a variation might exist. The clearly bicoloured hindtibia on the illustration supports the interpretation of *varus* in the present sense versus a synonym of *T. curvitarsus*.  

Neotype designation: This study follows the most recent interpretation of *Crabro varus PANZER, 1799* by BITSCH & LECLERCQ (1993), who have transferred this taxon in *Tracheliodes* and rejected earlier suggestions or interpretations that *C. varus* might be a species of *Crossocerus* LEPELETIER & BRULLÉ, 1835, or a senior synonym of *T. curvitarsus* (LEPELETIER & BRULLÉ 1835, KOHL 1915, LECLERCQ 1979, RICHARDS 1980). BITSCH & LECLERCQ (1993) refer to a single specimen from Corse (MGB) which agrees with PANZER’s (1799) original illustration. New records from Lower Austria testify that the same species indeed occurs in the type area of *T. varus*.

The type of *Crabro varus* is lost (PANZER 1806). Referring to Art. 74c of the International Code of Zoological Nomenclature (3rd edition, 1985), BITSCH & LECLERCQ (1993) suggested to designate PANZER’s (1799) original illustration as the lectotype of *Crabro varus* for taxonomic stability, but did not perform the action. In the case of *Crabro varus*, the lectotype designation by Art. 74c (Art. 74.4 in the 4th Edition, 1999) would be meaningless, because this article treats the designation of the lectotype by means of an illustration, but the depicted type specimen is being the lectotype (I. Kerzhner, pers. comm.). In the past, there have been various interpretations of the taxon *Crabro varus*, and the fact that we have found a very dark specimen of *T. curvitarsus* (from Bulgaria) favours one of KOHL’s (1915) proposals that *curvitarsus* and *varus* could be synonyms. To prevent further instability, we designate a neotype, which well corresponds with PANZER’s (1799) description and illustration, except a few minor details in colour which are regarded as individual varia-
tions or incorrectness. The current interpretation and its fixation by a neotype is best to obtain stability for the taxa *T. curvitarsus*, *T. varus*, *Crossocerus varus* LEPELETIER & BRULLÉ, 1835, and possibly junior synonyms in *Crossocerus*.

Description of neotype: body length 7.5 mm; head width: 2.02 mm; OOD : POD = 1.3; yellow colour: narrow stripes along dorsal inner eye margin (Fig. 1); small patch at lower gena (Fig. 5); base of mandible; stripe on scape laterally; pronotal dorsum (medially interrupted); mesopleuron anteriorly; anterior half of mesoscutellum; gastral tergum I ventrolaterally, and posteriorly with transverse band; terga II - V posteriorly with paired patches (nearly confluent on tergum II); bands on gastral sternum I anteriorly, and on sterna II - IV posteriorly; on fore- and midlegs apex of femora, most of tibiae (except black stripe) and base of tarsi; on hindleg base of tibia; tergum VI orange, medially black.

Biological: Hitherto nothing has been known on the biology of *T. varus*. Like in the other species of *Tracheliodes*, females of *T. varus* hover in the air in a distance of a few centimetres from a *L. microcephalum* trail on a tree stem (Fig. 12). Although the ants are abundant, it is difficult for the female to catch one of the defending worker ants, which are sitting in crevices of the bark and threaten the attacking wasp with open mandibles. The wasp tries to tease and startle the ants by flying mock attacks. Only if one ant moves out of its hiding place and runs over the bark's flat surface, the *Tracheliodes* female starts a real attack. Attacks are often suddenly interrupted, obviously when the position of the ant does not allow an accurate grab, for which the ant runs straight or obliquely downwards. It may take up to several minutes until the *T. varus* female accelerates to grab a worker of *L. microcephalum*. In some attacks, the female is taking speed against the running direction of the ant. Repeatedly, wasps were observed flying side to side in movements parallel to the surface on which the prey ants were hiding. This is interpreted as motion parallax behaviour, i.e. movements enabling the hunter to estimate the exact distance to prey: side to side motion moves the visual array such that objects will move across the visual field with different velocities depending on their distance from the surface of the compound eye (HORRIDGE 1986).

The following takes 2 - 5 frames on the film sequences (Fig. 13), i.e. about 0.1 - 0.2 sec. Because of the fast movements of the wasp, pictures are fuzzy and difficult to interpret. The attack starts by a fast turn of the hindlegs forwards, which suggests that the wasp uses them for catching and holding the ant. However, mid- and hindlegs of the females of *T. varus* (and *T. curvitarsus*) appear modified (see above), probably a morphological adaptation for holding the ant prey: the concavities on the ventral surfaces of the femora and the curved basitarsi have the right size and shape for embracing the gaster of workers of *Liometopum microcephalum*. The wasp now flies a narrow, horizontal or more upward curve against the running direction of the prey. One video sequence supports the assumption that it grasps the gaster of the prey, so that the ant's head is positioned under the wasp's gaster. Such a position of the dangerous prey – the thorax and head of the ant hanging below the wasp's gaster – is probably the safest for the predator.

Although in the Nearctic *T. hicksi* SANDHOUSE, 1936 the hunting strategy in most details is the same as it has been observed in *T. varus*, the former wasp grasps its prey with the head in front (HICKS 1936) in contrast to *T. varus*.

In all sequences, grabbing seems to have been successful, because the attacked ant has been removed from the bark. The wasp rapidly sinks towards the ground, but without landing, and subsequently flies off. We could not make observations on following behaviour.

Some specimens of *T. varus* and *T. curvitarsus* miss terminal parts of the tarsi and, more often, of the antennae; the raptures on tarsi are partly blackish, which we interpret as melanisation in the course of wound closing (DETTNER & PETERS 1999). Most of these injuries are apparently old and may result from bites by *Liometopum microcephalum*.

There are still many open questions regarding the biology of *T. varus*. The nesting site remains unknown. Probably wood holes are used like in *T. curvitarsus* (EMERY 1893, PATE 1942). *Liometopum microcephalum*, and subsequently *Tracheliodes curvitarsus* and *T. varus*, depend on big old trees, which are generally infested by wood-boring beetles. Although we have swept with a net large fields with flowering Apiaceae close to the hunting grounds of *Tracheliodes* spp., we could not observe feeding specimens there. Further investigations should clarify whether *T. varus* preys exclusively on *L. microcephalum* in Central Europe or whether other ant species are taken as well. At least in Corse, *T. varus* probably hunts another ant species, as *L. microcephalum* has not been recorded on that island (CASEVITZ-WEULERSE 1996; J. Casevitz-Weulersse, pers. comm.).

Notes on the prey ant

The dolichoderine ant *Liometopum microcephalum* is a Pontomediterranean species (MARTINEZ & TINAUT 2001). In Central Europe, *L. microcephalum* has its westernmost populations in Moravia (Czech Republic) and Lower Austria (BEZDEČKA 1995, SCHLICKSTEINER & al. 2003). The species builds carton nests in big old trees, mainly in oaks (Quercus spp.), but also in trees such as horse chestnuts (Aesculus hippocastani) and maples (Acer spp.) (EMERY 1891, WIEST...
It obviously depends on a portion of rotten wood inside the living tree. The general decrease of this resource is probably one of the reasons for the ant becoming endangered (SCHLICK-STEINER & al. 2003). Big colonies can comprise hundreds of thousands individuals and dominate a territory of up to 600 m² (WIEST 1967), and the trails of single colonies are reported to cover distances of up to 80 m (EMERY 1891). Although trophobiotic relationships have been observed (WIEST 1967), L. microcephalum is mainly zoophagous. The ant is very aggressive and, besides feeding on various arthropod and annelid carrion, actively hunting (EMERY 1891, WIEST 1967; own observations). LUDESCHER (1979) reports that the species tries to enter breeding holes of birds with nestlings inside. EMERY (1891) suggest that the ants are even able to capture flying insects with their sharp mandibles. The striking behaviour of lifting the forelegs from the ground and swaying to and fro with opened mandibles might be an ethological adaptation to active hunting (cf. EMERY 1891).

### Syntopic occurrence of T. curvitarsus and T. varus

We found the two species T. curvitarsus and T. varus at the same locality, synchronously hunting the same ant species, partly from the same colony. This observation is interesting with regard to competition. It contradicts the hypothesis of PATE (1942) that every species of *Tracheliodes* has its specific ant prey, and agrees with NEMKOV (1988). A possible explanation is the superabundance of L. microcephalum workers. Furthermore, the body size of the two ant hunting wasps might cause prey partitioning, with T. varus preying on smaller workers of L. microcephalum workers than T. curvitarsus. This is likewise supposed for the syntopically occurring species *T. ghilovari* NEMKOV, 1988 and *T. alinae* NEMKOV, 1988, both hunting L. microcephalum (NEMKOV 1988). Our observations suggest that T. varus hunts exclusively on vertical stems, while T. curvitarsus hunts also on horizontal roots and on the ground.

Local segregation of the wasp species could be due to the different head width (maximum body width) of the females and a correspondingly different diameter of the nest entry. Finally, collection data indicate a slight phenological difference: *Tracheliodes curvitarsus* seems to appear earlier than T. varus.

Considering the specialized life habits of the two *Tracheliodes* and their dependence on an endangered ant, further investigations are desirable also for reason of conservation.

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