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## THE *ISOPHYA* SPECIES OF CENTRAL AND WESTERN EUROPE (ORTHOPTERA: TETTIGONIOIDEA: PHANEROPTERIDAE)

Heller, K.-G., K. M. Orci, G. Grein & S. Ingrisch, 2004. The *Isophya* species of Central and Western Europe (Orthoptera: Tettigoniodea: Phaneropteridae). – Tijdschrift voor Entomologie 147: 237-258, figs. 1-90, 1 table. [ISSN 0040-7496]. Published 1 December 2004.

The genus *Isophya* is the largest genus of bush-crickets in Central Europe and the second largest in Europe. Its members are difficult to identify because of their morphological similarity. However, most species differ distinctly in their calling songs. Nearly half of the Central European species have been described less than fifty years ago, and no detailed revision has been published since this time. We have analysed male morphology and bioacoustics, and present figures of male pronotum and tegmina, cerci, stridulatory file and oscillograms of the calling songs of all species known to occur in the region including a identification table. According to these data, the following taxa are considered to be valid species: *Isophya pyrenaica* (Serville, 1839), *I. camptoxypha* (Fieber, 1853), *I. modesta* (Frivaldszky, 1867), *I. costata* Brunner von Wattenwyl, 1878, *I. kraussii* Brunner von Wattenwyl, 1878, *I. modestior* Brunner von Wattenwyl, 1882 *I. brevicauda* Ramme, 1931, *I. pienensis* Mařan, 1954; stat. rev., *I. stysi* Cejchan, 1958, *I. beybienkoi* Mařan, 1958 and *I. posthumoidalis* Bazyluk, 1971. *I. brevipennis* Brunner von Wattenwyl, 1878 is considered a synonym (syn. n.) of *I. camptoxypha* (Fieber, 1853).

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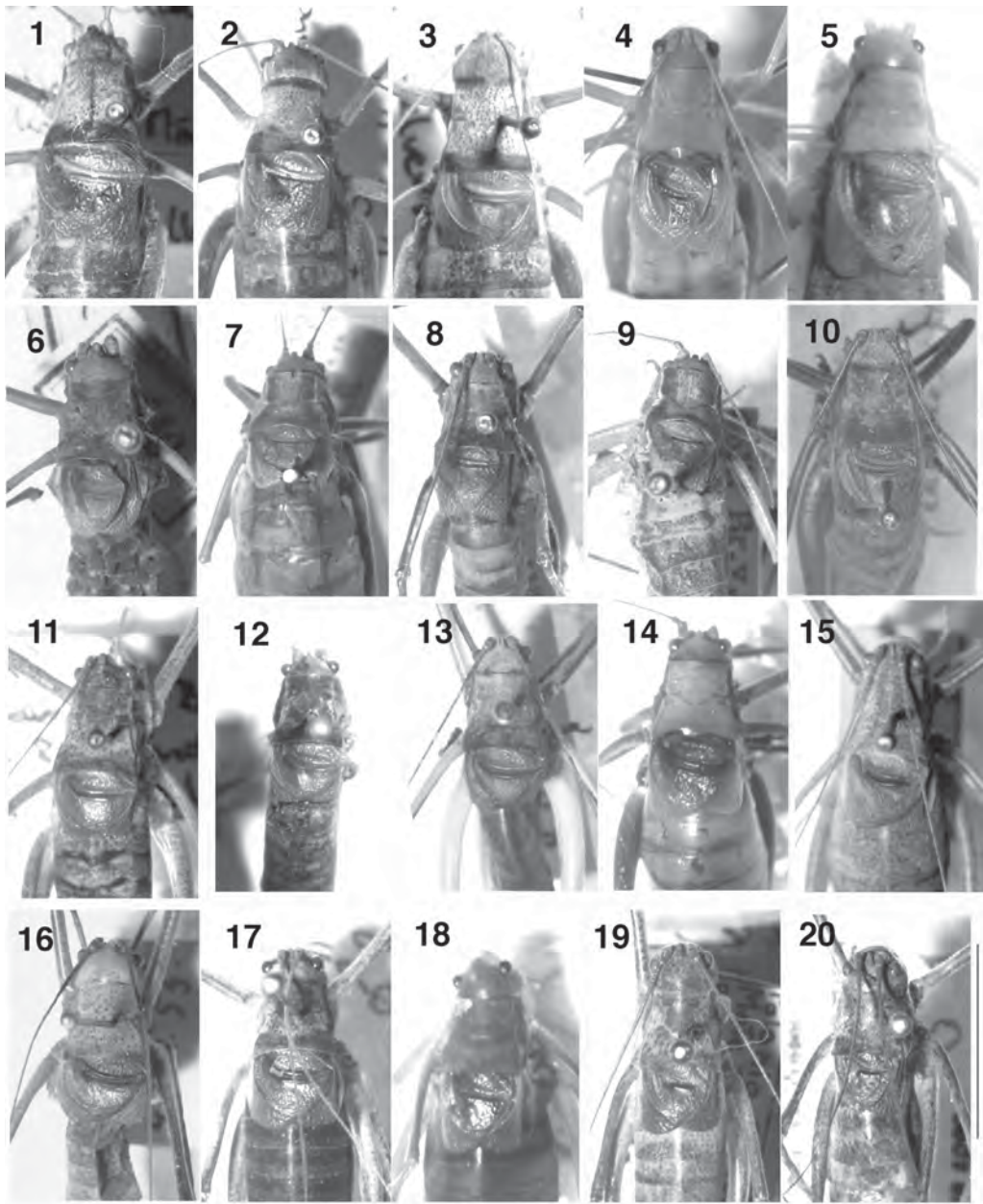
Key-words: Orthoptera; Tettigoniodea; Central Europe; *Isophya*; taxonomy; bioacoustics; morphology; key.

The genus *Isophya* has more than 45 species in Europe (Heller et al. 1998). In this region, it is second with regard to species richness after the closely related genus *Poecilimon*, but first with regard to the difficulties to identify the species. Already in naming the genus probably Brunner von Wattenwyl (1878: 59) had this characteristic feature in mind: he translated the Greek parts of the name 'isos' into Latin 'aequalis' (equal, similar) and 'phyo' into 'gigno' (to beget, to father). Both genera belong to the family Phaneropteridae and lack internal sclerotized male genital organs, which are very helpful for species identification in other bush-cricket families. The shape of the male cerci, another character often used for identification, is quite simple and does not show an elaborate shape as in some *Poecilimon* species. The identification of *Isophya*

species therefore was based mainly on subtle differences in the shape of cerci, pronotum, tegmina and ovipositor.

Thus it is not surprising, that even in Western and Central Europe nearly half of the currently recognised species have not been described before the beginning of the second half of the last century (see below). On the other hand, some of the species described during the 19<sup>th</sup> century have not been recognised as valid species until recently.

The study of the calling songs and stridulatory files as additional species-specific characters, whose significance is well known from other Orthoptera, was first applied to the genus *Isophya* by Zhantiev & Dubrovin (1977), later to the Central European forms by Heller (1988). One important finding was that what was con-



Figs. 1-20. *Isophya* species, pronotum and tegmina. – 1, *Isophya costata* (CH1916); 2, *I. modestior* (CH1915); 3, *I. modestior* (CH1913; Serbia); 4, *I. stysi* (CH6209); 5, *I. modesta* (CH5369); 6, *I. camptoxypha* (lectotype); 7, *I. camptoxypha* (lectotype *I. brevipennis*); 8, *I. camptoxypha* (nmpc); 9, *I. camptoxypha* (syntype *I. brevipennis*); 10, *I. pyrenaica* (CW; magnification different from all other photographs, no exact scale); 11, *I. kraussii* (CH1903); 12, *I. kraussii* (CH4451A); 13, *I. kraussii* (NMPC); 14, *I. kraussii* (CH2421); 15, *I. brevicauda* (holotype); 16, *I. pienensis* (NMPC, det. Mařan, paratype?); 17, *I. pienensis* (CH4905); 18, *I. beybienkoi* (CH5367); 19, *I. posthumoidalis* (ZMPA, paratype); 20, *I. posthumoidalis* (CH4909); scale bar = 10 mm.

sidered to be the most widespread form (*I. pyrenaica*) actually consists of at least two, but possibly even more species. Since insect sound libraries are still rare in public collections and the study of song patterns depends on the availability of living animals, it took a few more years until Ingrisch (1991) could clarify the status of another species (*I. brevicauda*) of this group using song recordings.

However, the systematics and taxonomic status of several Central European forms still remained unsolved. In the present paper we try to review all relevant information on the Western and Central European species (area borders as delimited in Heller et al. 1998: p. 3, region 4 and 5, but including southern Austria, Hungary and Slovenia). We present the results from the study of type material and new song recordings. As for the time being, some species can be reliably identified only by the structure of the male stridulatory file, shape of male cerci or the song, we deal with male characters only (table 1). To include also females the study of much more reliably identified material will be necessary.

#### MATERIAL AND METHODS

Examined specimens are deposited in the following museums and collections:

CH	Collection Heller
CI	Collection Ingrisch
CL	Collection Lehmann
CW	Collection Willemse
NMPC	National Museum (Natural History), Prague, Czech Republic
NMW	Naturhistorisches Museum Wien, Vienna, Austria
ZIN	Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany
ZMPA	Polish Academy of Science, Museum of the Institute of Zoology, Warszawa, Poland
ZMUM	Department of Entomology, Moscow University, Moscow, Russia

For most species additional references of taxonomically minor importance can be found in Otte (1997). They are not repeated here.

At <http://www.dorsa.de> the localities of the specimens in the Heller collection can be visualised on a map by a web-based GIS mapping tool. Digitised sound recordings are available at the taxonomic database Systax (<http://www.biologie.uni-ulm.de/systax>) under the sound file names given below.

All microphotographs (right cercus oriented horizontally) and measurements were taken using a stereo microscope Olympus SR-III.

Most Scanning Electron Microscope (SEM) pictures were made on a Hitachi S 800 SEM, a few on an Autoscanner, ETEC SEM (both Dept. of Zoology I, University Erlangen). The photograph of the stridulatory file of the lectotype of *I. camptoxypha* was made from a replica (see Ragge 1969).

For sound recording in the field an Uher tape recorder 4200 IC and a SONY WM3 tape cassette recorder (KGH, SI) as well as a SONY TCD-D7 DAT recorder (KMO) were used with microphone Uher M 645 (frequency response flat up to 20 kHz resp. 15 kHz) and Monacor ECM 920 electret condenser microphone (KMO). For sound recording in the laboratory a Racal store 4 D tape recorder with microphones Brüel & Kjaer 4133 and 4135 (frequency response flat up to 40 and 70 kHz, respectively) were used. After digitising the songs on a PC or an Apple computer, oscillograms (after filtering) and sound analysis were made using a PC and the programs Turbolab, Amadeus (Apple) and CoolEdit. Wing movements were registered by an opto-electronic device (Helversen & Elsner 1977, modified as in Heller 1988).

Song terminology: Calling song: song produced by an isolated male. Functional unit of the song: the smallest part of the song, which contains all necessary song elements in the appropriate order to elicit female response. Syllable: the sound produced by one complete up (opening) and down (closing) stroke of the forewings. Hemisyllable: the sound produced by one unidirectional movement (opening or closing) of the forewings. Impulse: a simple, undivided, transient train of sound waves (here: the highly damped sound impulse arising as the impact of one tooth of the stridulatory file; see Elsner 1974). Click: an isolated, distinct impulse. After-click: click produced with considerable delay after the main impulse group.

#### CHECKLIST

(Western and Central European Species)

Genus *Isophya* Brunner von Wattenwyl, 1878

*I. pyrenaica* (Serville, 1839)

*I. camptoxypha* (Fieber, 1853)

*I. brevipennis* Brunner von Wattenwyl, 1878 **syn. n.**

*I. modesta* (Frivaldszky, 1867)

*I. costata* Brunner von Wattenwyl, 1878

*I. kraussii* Brunner von Wattenwyl, 1878

*I. modestior* Brunner von Wattenwyl, 1882

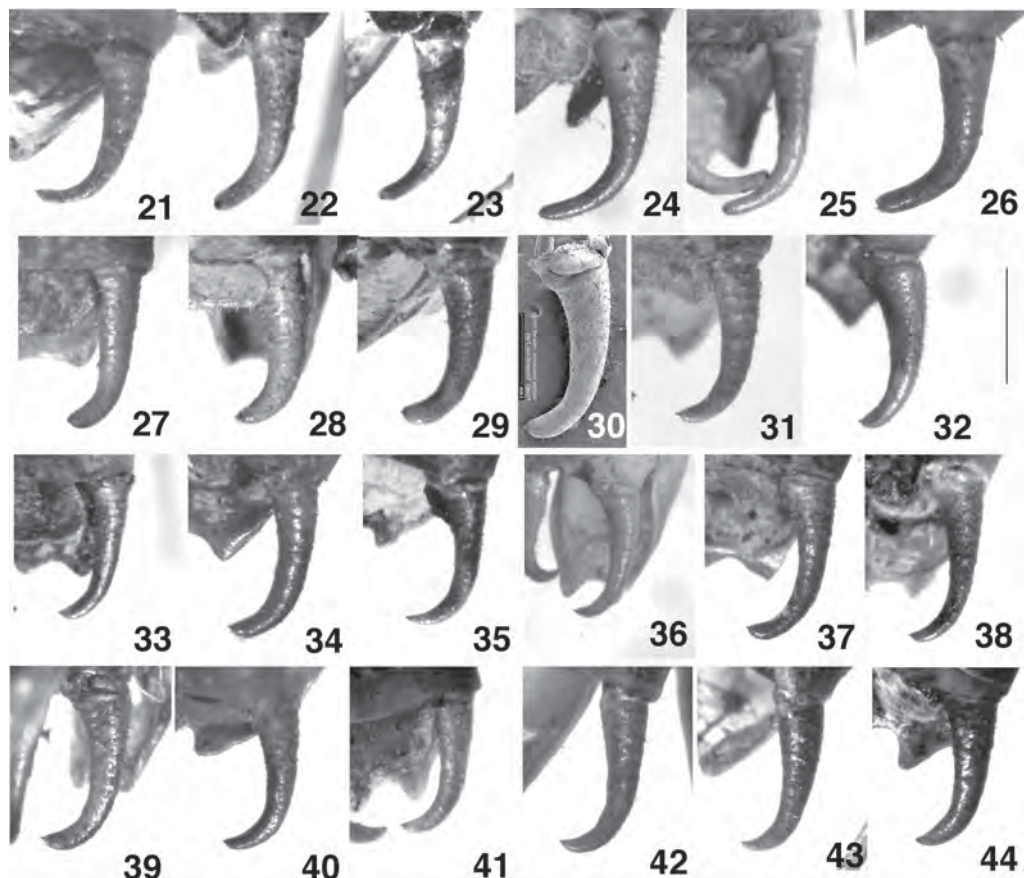
*I. brevicauda* Ramme, 1931

*I. pienensis* Mařan, 1954; **stat. rev.**

*I. stysi* Cejchan, 1958

*I. beybienkoi* Maran, 1958

*I. posthumoidalis* Bazyluk, 1971



Figs. 21-44. *Isophya* species, male, right cercus. – 21, *Isophya costata* (CH1916); 22, *I. modestior* (CH1915; Austria); 23, *I. modestior* (CH1914; Serbia); 24, *I. stysi* (NMPC); 25, *I. stysi* (zmhb); 26, *I. modesta* (NMPC); 27, *I. camptoxypha* (lectotype, left cercus, mirror image); 28, *I. camptoxypha* (lectotype *I. brevipennis*, left cercus, mirror image); 29, *I. camptoxypha* (Poland, D. Kostia); 30, *I. camptoxypha* (Poland, photo P. Naskrecki); 31, *I. camptoxypha* (syntype *I. brevipennis*); 32, *I. pyrenaea* (CH2340); 33, *I. kraussii* (CH4451A); 34, *I. kraussii* (NMPC, Mañan det.); 35, *I. kraussii* (CH2709); 36, *I. brevicauda* (zmhb, paratype); 37, *I. pienensis* (NMPC, Mañan det.); 38, *I. pienensis* (zmm, Korsunovskaya det.); 39, *I. pienensis* (CH4905); 40, *I. beybienkoi* (NMPC); 41, *I. beybienkoi* (CH5367); 42, *I. posthumoidalis* (ZMPA, paratype 2/70); 43, *I. posthumoidalis* (CH4909); 44, *I. posthumoidalis* (CH4910); scale bar = 1 mm.

## DESCRIPTIONS

### *Isophya costata* Brunner von Wattenwyl (figs. 1, 21, 45, 64, 70)

*Isophya costata* Brunner von Wattenwyl, 1878: 64. Syntypes ♂, ♀: AUSTRIA: Eichkogel near Mödling (south of Vienna) [Eichkogel bei Mödling nächst Wien (c.m. Nr. 10710), Schwabenberg bei Pest (c.m. Nr. 5540)] (NMW, Hope Entomological Collections, Oxford University Museum, Oxford) (Orte 1997) [not examined]

Material studied. – AUSTRIA: 2♂, Wien, Eichkogel bei Mödling, 4.vii.80, 48°04'N-16°17'E, K.-G. Heller (CH1916-7): stridulatory file examined in CH1916. – Sound recordings: ISCO8001-10, 12 (CH1917), ISCO80011 (CH1917 or another

animal from same population).

Morphology. – *Isophya costata* can be easily differentiated from all other species in the area by its broad fastigium (broader than or as broad as scapus). The left tegmen is very broad and protrudes at the lateral edge of the pronotum with the tip of the stridulatory vein forming an acute-angled margin (fig. 1). The cerci are relatively long and slender and incurved in a right angle (fig. 21). The stridulatory file carries about 250-280 teeth (257 teeth in a specimen collected from the Mecsek Mountains [SW Hungary; KMO], 275 teeth Heller 1988; fig. 45).

Published measurements (mm): postfemora male:

16-21 (Kis 1960, Harz 1969), 20 (Ramme 1951); ovipositor: 14-15.2 (Kis 1960), 14-15.5 (Harz 1969), 14-15 (Ramme 1951).

Song. – The description of the song follows Nagy et al. (2003): The calling song consists of isolated syllables or short sequences containing up to 10 syllables. The syllable intervals range from 2.5 to 6 s at 17°C (1.6 – 2.7 s at ca. 25°C). Each syllable consists of a series of 105-130 impulses (duration 700-850 ms at 17°C; 350-500 ms at ca. 25°C) with a nearly constant impulse rate, but increasing in amplitude at the beginning (fig. 70). After an interval of ca. 130-350 ms a series of 1-17 after-clicks follows (duration of series 300-800 ms at 17°C; 125-260 ms at ca. 25°C), which sometimes is missing (see also Heller 1988). All sounds are produced during the closing of the tegmina (fig. 64).

Distribution. – The species has been reported from Austria, Hungary and Siebenbürgen (Rumania) (see Nagy et al. 2003, Vadkerti et al. 2003).

Locations where the typical song was observed: Recordings were first available from the type locality, later the song was used to locate the species at many places in Austria (Berg et al. 1996). Now the song was also recorded from several specimens from SW Hungary and observed in some specimens from SW Rumania (between Oradea and Timisoara). No difference from the typical song were noticed (KMO).

### *Isophya modestior* Brunner von Wattenwyl (figs. 2-3, 22-23, 46, 65, 71-72, 77-79)

*Isophya modestior* Brunner von Wattenwyl, 1882: 276. Syn-types male, female: YUGOSLAVIA: Serbia: between Nish and Bela Palanka [Strasse zwischen Nisch und Ak Palanka] (NMW) [not examined]

*Isophya fusconotata* Brunner von Wattenwyl, 1882: 281. Lectotype, male (selected here) YUGOSLAVIA: Suha planina, Brunner von Wattenwyl) (NMW - ♀ 13.651) [examined]

Synonymy. – Because of the similarity of *I. stysi* and *I. modestior* it became necessary to examine the types of *I. fusconotata*. *Isophya fusconotata* may have been considered to be a synonym of *I. modestior* soon after it was described, probably by Brunner himself. He did not even mention the name *I. fusconotata* in his *Additamenta zur Monografie der Phaneropteriden* (1891) nine years after the description, but only *I. modestior*. Specimens in NMW from both type localities and collected by Brunner were identified as *I. modestior* by himself. Accordingly the distribution range of *I. modestior*, which included only the type locality in Brunner 1882, was increased to 'Montes Balcani Serbici' (Serbian mountains) in Brunner 1891. Ramme (1931) supported this opinion.

To secure nomenclatural stability we select here a lectotype for *Isophya fusconotata*. The male from Rtanj (NMW ♀ 13.609; at the time of Ramme (1931) there

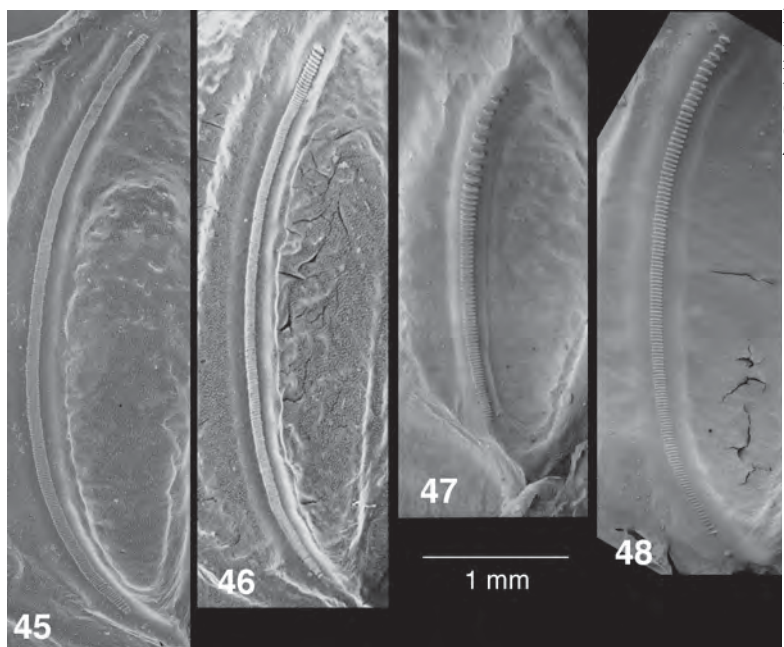
had been two males from this locality) is in very bad condition and cannot be identified with certainty. Fortunately, the male from Suha planina (at the time of Ramme (1931) there have been two males from this locality, too) is in much better condition. We (KMO) therefore select this male as lectotype. From all of its characters (except for the stridulatory file: not examined; see Orci et al. 2004) it is clear that it belongs to *I. modestior* and not to *I. stysi*. *I. fusconotata* therefore remains in the synonymy of *I. modestior*.

Material studied (see also Orci et al. 2004). – AUSTRIA: 5♂, Wien, Eichkogel bei Mödling, 16°17'E - 48°4'N, 04.vii.1980, K.-G. Heller (CH1915, CH1918); same locality, 5.vii.1999 (CH3336, CH4848-9). SLOVENIA: 1♂, Razdrto, west of Postoina (14°03'E - 45°45'N), 15.vii.1988, G. Waeber (CH2369); 1♂, either 20 km southwest of Ptuj or Kocara national park (northern Bosnia), 12.v.1989, K.-G. Heller (CH2554). YUGOSLAVIA: 4♂, Morava valley north of Grdelicka, 7.vi.1985, v. Helversen (CH1913-14), stridulatory file examined in CH1914; same locality, 19.v.1986, v. Helversen (CH0227, CH0236), erroneously assumed to be found at Mali Orasje (50 km southeast of Beograd) as mentioned in Heller 1988; 2♂, 3♀ (NMW, syntypes of *I. fusconotata*, see above). – Sound recordings: ISMO8602-3 (CH0227), ISMO8607-13 (CH0227 or CH0236), ISMO8501-14 (CH1913 or CH1914), ISCO8001 (CH1915 or CH1918, two syllables in a recording of *I. costata*), ISMO8901-06 (CH2554), ISMO9912 (CH4848), ISMO9901-11 (CH4849).

Morphology. – The straight hind margin of the pronotum seems to be an important character of this species. The left tegmen is broad, but does not protrude the right body side (figs. 2-3). The cerci are incurved in an angle of about 45 degrees (fig. 22-23; Harz 1969, but see fig. 11 in Ingrisch 1991 for a stronger incurvature). The number of teeth on the stridulatory file seems to be quite variable: Ingrisch & Pavicevic (in prep.) observed 150-250 in Serbia (about 222 in CH1914 (fig. 46); Heller 1988) and Italy (164-182 in Ingrisch 1991, 183 according to fig. 9B in Fontana 1998), while in Austria (125; CH4849) and Hungary (117-160; Orci et al. 2004) the numbers are distinctly lower. The variation in the northern part of its range (see below) would coincide with a clinal transition towards *I. stysi* (see Orci et al. 2004, see below).

Published measurements (mm): postfemora male: 17.5-21 (Harz 1969), 21-23 (Ingrisch 1991), 16-19 (Ramme 1951), 16-19.2 (Orci et al. 2004), 18 (Cejchan 1959); ovipositor: 11.5-14.5 (Harz 1969), 12-14 (Ingrisch 1991), 11.5-12 (Ramme 1951), 9.5-11.2 (Orci et al. 2004), 11.2-13 (Cejchan 1959).

Song. – According to Nagy et al. (2003) the calling song consists typically of short sequences containing (2)-3-6-(8) syllables (fig. 71-72). Sometimes long series of more than 20 syllables were observed. The syllable repetition rate within the sequence was 29-52 syllables per minute. Each syllable contained 30-60



Figs. 45-48.

*Isophya* species, stridulatory file on underside of male left tegmen. – 45, *Isophya costata* (CH1916); 46, *I. modestior* (CH1914); 47, *I. stysi* (NMPC); 48, *I. modesta* (NMPC).

impulses (duration 143-170 ms at 23-26°C [170-214 at 24°C in Ingrisch 1991 for animals from Italy]), produced at a fairly constant rate, but decreasing amplitude (fig. 77-79). After-clicks have not always been found, but were observed by several authors (e.g. Heller 1988, Ingrisch 1991, Fontana 1998, Fontana et al. 2002, Orci et al. 2004, Ingrisch & Pavicevic in prep.). All sounds were produced during the closing of the tegmina (fig. 65). Females were observed to respond acoustically to the male song (Heller 1990).

Distribution. – The species was found in two areas, which at the moment are separated by a broad gap without findings. The type locality and some additional records are situated in Serbia, Macedonia, West Bulgaria and Montenegro. Other records have been published from Slovenia, Italy, Austria and Hungary (Ingrisch 1991, Fontana 1998, Nagy & Nagy 2000, Fontana et al. 2002, Nagy et al. 2003, Vadkerti et al. 2003, Orci et al. 2004, Ingrisch & Pavicevic in prep.). Since the whole northern part of the distribution range was described only after 1991, probably the now existing gap will be closed by future research. Possibly *I. modestior* occurs also in Slovakia; Cejchan (1959) recorded specimens of this species from the south, very close to localities where *I. modestior* was later found by Orci et al. (2004). Cejchan (1959) corrected his identification into *I. pyrenaica* by an addendum after re-identification by Bey-Bienko, but his original

identification might have been correct.

Locations where the typical song was observed: Serbia: Grdelicka (Heller 1988); Italy: Aviano (Ingrisch 1991); Mt. Summano (Fontana 1998); Austria: Eichkogel (Nagy et al. 2003); Hungary: several localities (Nagy et al. 2003, Orci et al. 2004).

#### *Isophya stysi* Cejchan

(figs. 4, 24-25, 47, 73, 80)

*Isophya stysi* Cejchan, 1958a: 124. Holotype male: SLOVAKIA: Carpathian Mountains, near Ulic, 11.viii.1957 [Cejchan collection, paratypes 1 M and 1 F ZIN] - not examined.

*Isophya modestior stysi*: Harz 1969: 53; Kis & Vasiliu 1970: 210.

*Isophya stysi*: Heller 1988: 38.

Material studied. – HUNGARY: 1♂, Mályvádi erdő (Szarvas), 29.vi.2003, K. M. Orci (CH6209). RUMANIA: 1♂, Cluj (?), 29.vii.1959, leg. Kis (locality name difficult to read, at that date a large series was collected at Cluj by Kis, Kis 1960), det. Kis (ZMHB). SLOVAKIA: 1♂, labelled: Slov. cr., Rocok 796 m, 10.viii.1961, A. Cejchan (NMPC): stridulatory file examined.

Morphology. – In contrast to the opinion of Cejchan (1958a), *I. stysi* is not closely related to *I. modesta*, but to *I. modestior* (Harz 1969, Kis & Vasiliu 1970, Orci et al. 2004) regarding shape and length of fore wings, body size, and length of ovipositor. There are,

however, clear differences to this species (see Orci et al. 2004). The tegmina are longer and much narrower than in *I. modestior* (fig. 4). According to the specimens studied here and as described by Kis & Vasiliu (1970) the cerci are more slender and more incurved than in *I. modestior* (fig. 24-25). The stridulatory file carries about 70 teeth in Hungary and Slovakia (fig. 47; 54-79 Orci et al. 2004; 69 teeth in the specimen examined here), however Orci et al. (2004) found a higher number of stridulatory teeth (67-128) in the Rumanian population of this species.

Published measurements (mm): postfemora male: 17-20.7 (Kis 1960), 17-20 (Harz 1969), 17.5-19 (Cejchan 1958a), 17.5-19.8 (Orci et al. 2004); ovipositor: 9.5-11.5 (Kis 1960, Harz 1969), 10-11.2 (Cejchan 1958a), 9.5-11.1 (Orci et al. 2004).

Song. – In the description of the song we follow Orci et al. 2004, where also more details can be found: The male calling song consists of single syllables which are produced in short sequences generally composed of (2-)-4-6(-8) syllables (fig. 73). Sometimes long sequences with more than 30 syllables were observed. In the basic structure the song is quite similar to that of *I. modestior*, however in *I. stysi* syllables begin with 1-5 distinct impulses repeated relatively slowly, forming a 'slow phase' of the syllable which is followed by a 'fast phase' during which the impulse repetition rate is much higher (fig. 80). This kind of syllable structure can be seen also in an oscillogram published by Zhantiev & Dubrovin (1977) on the song of a specimen from the Ukraine (surroundings of Uzhgorod).

Distribution. – Carpathian mountains in Slovakia, Eastern Hungary, Poland, Rumania, Ukraine.

Locations where the typical song was observed: Ukraine (near Uzhgorod; Zhantiev & Dubrovin 1977); several localities in Eastern Hungary and Rumania (Orci et al. 2004).

### *Isophya modesta* (Frivaldszky) (figs. 5, 26, 48, 66, 74, 87)

*Odontura modesta* Frivaldszky, 1867: 96. Type lost: RUMANIA: southwest of Mehadia

Synonymy. – Here we consider only the nominate subspecies *I. modesta modesta*. Outside Central Europe three other related forms have been found, currently treated as subspecies: *Isophya modesta intermedia* Kis 1960 (type locality Rumania), *Isophya modesta longicaudata* Ramme 1951 (type locality Bulgaria) and *I. modesta rossica* Bey-Bienko, 1954 (type locality Kupyansk, eastern Ukraine; Orci & Heller 2004).

Material examined (see also Orci & Heller 2004). – HUNGARY: 2♂, 2♀, Baranya Megye, Remete-ret, a meadow near the city of Pecs, 18°13'E - 46°04'N, elev. 400 m, 23.vi.2000,

G. Szövényi & K.M. Orci (CH5369-72). RUMANIA: 1♂, labelled: Rom. mer., Bageesa, vii.58, P. Stys lgt. (NMPC): stridulatory file examined: 124 teeth. UKRAINE: 4♂, 2♀, Kanev, Forest Reserve, 18.-23.v.1996, K.-G. Heller (CH3333-5, 4492-94). – Sound recordings: ISRO9601-5 (CH3334 or another animal from same population), ISRO9606-7,13-16 (CH3333), ISRO9608-12 (CH4492), ISRO9617-21 (CH4493 or another animal from same population).

Morphology. – The tegmina are relatively long, in most cases longer than the pronotum (fig. 5; Harz 1969). The cerci are similar to *I. stysi*, but the straight, basal part is shorter than in that species (fig. 26; already described by Cejchan 1958a). The stridulatory file has between 95 (Ingrisch & Pavicevic, in prep.) and 124-143 teeth (11 specimens in Orci & Heller 2004; fig. 48).

Published measurements (mm): postfemora male: 19.6-21.9 (Kis 1960, Harz 1969), 19-20 (Cejchan 1958a), 16-19 (Ramme 1951); ovipositor: 16-17.5 (Kis 1960), 16-17.8 (Harz 1969), 15-17 (Cejchan 1958a), 15-17 (Ramme 1951).

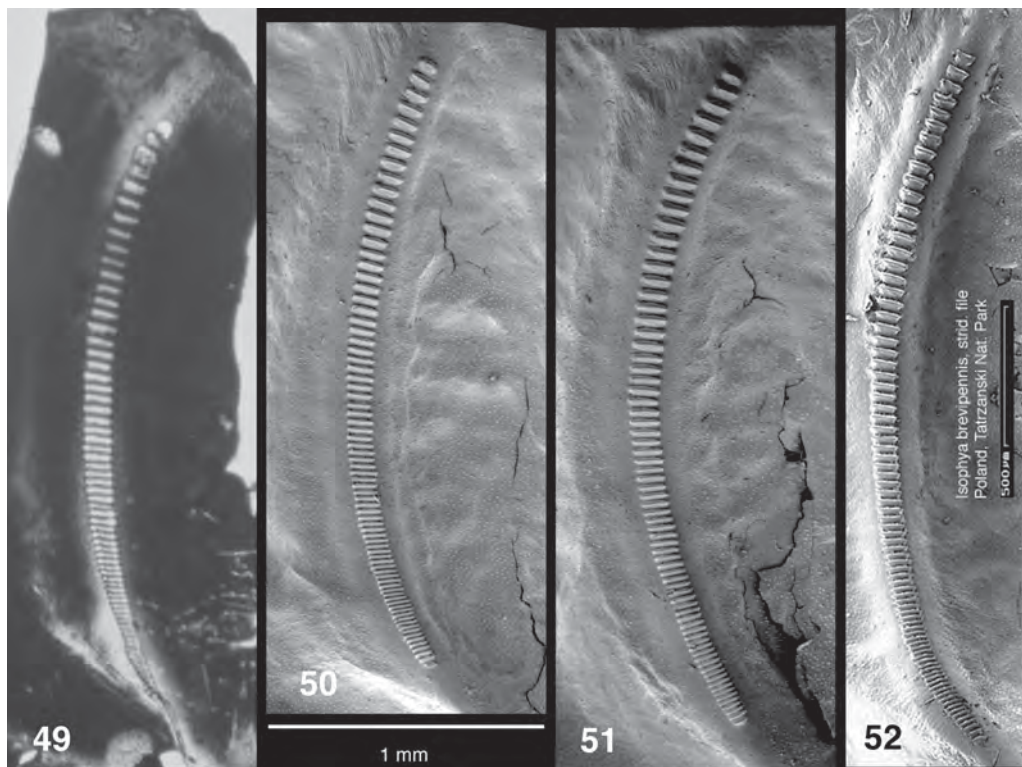
Song. – The song consists of isolated syllables each containing two temporally widely separated parts. The first part of the syllable consisting of a dense impulse sequence is followed by a second part after several seconds. Here the intervals between the impulses are distinctly larger (fig. 66, 74; see Orci & Heller 2004 for details). The complicated song pattern is accomplished by a stridulatory movement as in *I. costata*, but with the number of after-clicks increased, made more regular, and temporarily separated from the first part of the syllable (see fig. 66, 74). In some specimens a faint opening sound of the tegmina was observable before the main part of the syllable as indicated in fig. 66. The carrier frequency of the song shows a band between 10 and 20 kHz with a maximum in the upper range (fig. 87).

Distribution. – Slovakia, Hungary, Rumania, Ukraine (Gavlas & Chladek 2003, Nagy 1981, Nagy & Rácz 1996, Orci & Heller 2004). The record for Poland (Lysa Gora; Ramme 1951) is erroneous and refers to a locality in Ukraine (Bazyluk & Liana 2000, own check (KGH) in ZMHB).

Locations where the typical song was observed: several localities in Hungary, Rumania, Ukraine (Kanev) (see Orci & Heller 2004).

### *Isophya camptoxypha* (Fieber) (figs. 6-9, 27-31, 49-52, 81)

*Barbitistes camptoxypha* Fieber, 1853: 185. Lectotype, male (selected here): (♂) CZECH REPUBLIC, Bohemia [in Böhmen Vor- und Mittelgebirge auf grasigen Triften, *Corylus avellana*, in Österreich, Ungarn, der Türkei bis Klein-Asien] - probably incorrect, presumed range of lectotype locality: Slovakia, Poland, Hungary, Ukraine or Austria (NMW - type ♀ 9639).



Figs. 49-52. *Isophya* species, stridulatory file on underside of male left tegmen. – 49, *Isophya camptoxypha* (lectotype); 50, *I. camptoxypha* (NMPC); 51, *I. camptoxypha* (CH6124); 52, *I. camptoxypha* (Poland, photo P. Naskrecki).

*Isophya camptoxypha*; Brunner von Wattenwyl 1878: 64.

*Isophya camptoxypha*; Brunner von Wattenwyl 1882: 280.

*Isophya pyrenaica*; Kirby, 1906: 384.

*Isophya brevipennis* Brunner von Wattenwyl, 1878: 66. Lectotype, male (selected here; from syntypes two males, two females): RUMANIA: Siebenbürgen (NMW) [examined] Syn. n.

Synonymy. – *Isophya camptoxypha* was listed under the synonymy of *I. pyrenaica* Serville by Kirby in 1906, probably because Brunner von Wattenwyl (1882, not 1878) listed *I. pyrenaica* Serville (without year) as a synonym of *I. camptoxypha* and mentioned explicitly that both species are identical, but retained the younger name *I. camptoxypha* without comment. For a long time *I. camptoxypha* was then considered as a synonym of *I. pyrenaica* (e.g. Ramme 1951), until Bazyluk (1971) used it again for specimens from Poland. Heller (1988) found out that under the name *I. pyrenaica* several species were confounded, but despite examining the type of *I. camptoxypha* he found no clear characters to separate it from *pyrenaica*. The differences in the structure of file and cercus compared

with *pyrenaica* are not large (compare fig. 49-52 to 63 and 28-31 to 32), the song was not known at that time. Now, after examining the songs and stridulatory files of other Central European *Isophya* species, it became obvious that there are several species with similar and relatively low numbers of stridulatory teeth, but different song patterns. Searching for differential characters, we analysed the structure of the cerci. After comparing holo-, paratypes or at least topotypes of all forms synonymized under *I. pyrenaica* it surprisingly became clear that *I. brevipennis*, a well known and widespread species, has to be synonymized with *I. camptoxypha*. Since the name *I. camptoxypha* has been used a few times in recent years the name cannot be suppressed in favour of the better known *I. brevipennis* (conditions of Art. 23.9 of the ICZN not met).

There are two aspects to complicate the situation even more. First, the type locality of *I. camptoxypha* given by Fieber is probably not correct. Up to now, in Bohemia no other *Isophya* species except *I. kraussii* has been found (Kocarek et al.1999). So it is unknown



where the type of *I. camptoxypha* was collected. Despite this problem but to secure nomenclatural stability, we select the obviously only remaining male individual (Kaltenbach, 1.viii.1985, in litt.) from Fieber's series as lectotype of *I. camptoxypha*. As type locality we assume a place in Slovakia, Poland, Hungary, Ukraine or Austria. Second, the type series of *I. brevipennis* (two male and two female syntypes) shows a quite high variability in shape of male cercus (fig. 28, 31). One male concurs with 'typical' *I. brevipennis*, the other is slightly, but distinctly different. Thus the syntypes may possibly contain several different species. Again, to secure nomenclatural stability we choose the 'typical' male as lectotype despite the fact that the other male is mentioned in the type description (c.m. 7991). The option to choose this other male could result in a different meaning of the name *I. brevipennis* than up to now, if future studies of bioacoustics will show that in northern Rumania several morphologically similar species are found. In morphology alone the differences are not large enough to justify a separation. It has to be mentioned, however, that the number of teeth on the stridulatory file is quite low in both syntypes compared to specimens found more North.

Kis (1960) discussed the high morphological variability of *I. brevipennis* in Rumania. Without more data, especially about the acoustic behaviour, it is impossible to draw any conclusions as to the reasons for the variability. It would be not surprising, if in the South of the distribution range additional species could be found (see second male of type series).

Harz (1966) mentioned a phasis gregaria of *I. brevipennis* from the Tatra Mountains, which differs in several measurements from typical specimens. Since several similar species occur in this region (see below), it is difficult to estimate which species was observed by Harz. In any case, the name has no nomenclatural relevance.

Material studied. – (?) CZECH REPUBLIC: 1♂; labelled: 9639//Coll. Br.v.W. ex Coll. Fieber, *Isophya camptoxypha*//9639 *camptoxypha* Fieb.//Coll. Nat. Mus. Wien//Lectotype (NMW): stridulatory file examined by means of replica technique (Heller 1988 according to Ragge 1969): ca. 70 teeth). Here designated as lectotype of *I. camptoxypha*. POLAND: 1♂ 1♀, Tatry Mts. Pyszna Valley, N. Pysina Pot., 1.ix.1988, E. Warchalowska (CH6124-5): CH6124 stridulatory file examined: 72 teeth; 2♂, collected and identified by D. Kostia (CH6122-3): CH6122 stridulatory file examined: 70 teeth; 1♂, Tatrzański National Park (Otte & Naskrecki 1997), P. Naskrecki cerci (fig. 30) and file (fig. 52) from a specimen of this population examined by P. Naskrecki: 82 teeth. RUMANIA: 2♂: ♂1, labelled: 2-digit-number (unreadable)//Coll. Br. v. W., Siebenbürgen, Hermann//det. Br.v.W. *Isophya brevipennis* Br.//Coll. Nat. Mus. Wien//Lectotype (NMW): here designated as lectotype of *I. brevipennis*, stridulatory file examined: ca. 49 teeth; ♂2, la-

belled: Coll. Br. v. W., Siebenbürgen, Hermann//7991//det. Br.v.W. *Isophya brevipennis* Br. //Coll. Nat. Mus. Wien//paralectotype, stridulatory file examined: ca. 60 teeth). SLOVAKIA: 1♂, labelled: Slov. cr., 5.8.1961, Durkovec 1190 m, A. Cejchan lgt. (NMPC): stridulatory file examined: 72 teeth; 1♂, labelled: Slov. cr. 8.8.1961 Hrubky 1180 m, A. Cejchan lgt. (NMPC).

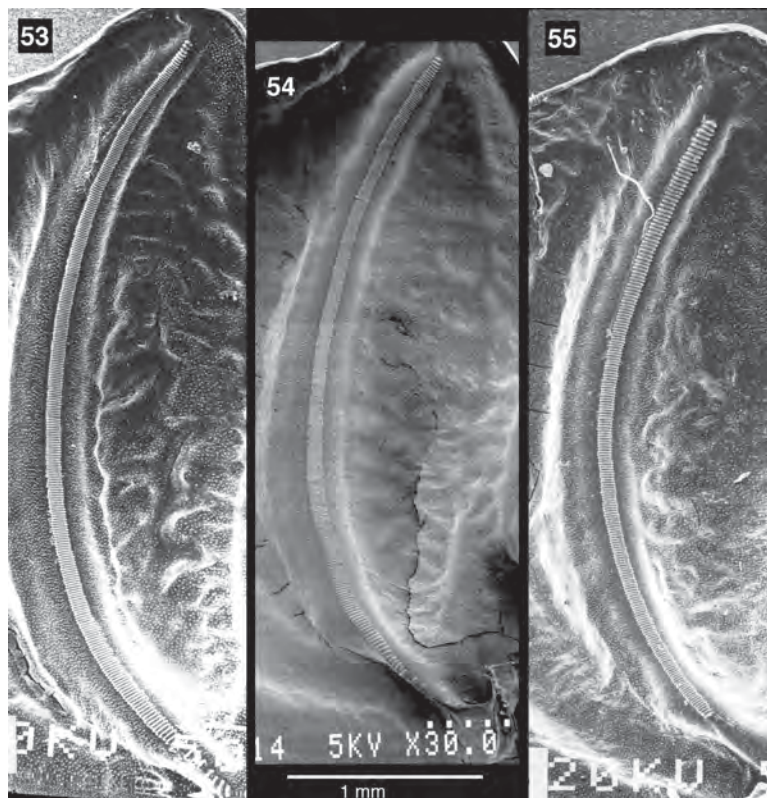
Morphology. – The left tegmen is relatively narrow and broadly rounded around the tip of the stridulatory vein (fig. 6-9). The species is characterised by the shape of the cerci. The straight, basal part is relatively thick and ends in a broad, short, incurved apex (fig. 27-31). This apex is not tapered into an apical spine, but blunt with an independent tooth at the upper edge of the apex (see SEM photograph fig. 30). The stridulatory file bears a relatively low number of teeth (ca. 50 - 80) thus differing strikingly from the otherwise similar species *I. kraussii* and *I. pienensis*, which both have more than twice as many stridulatory teeth. However, the stridulatory file is quite similar to that of *I. beybienkoi* and *I. posthumoidalis* (see fig. 59-62).

Published measurements (as *I. brevipennis*)(mm): postfemora male: 14-19.4 (Kis 1960), 14-18.5 (Harz 1969), 15-16 (Ramme 1951); ovipositor: 8-10 (Kis 1960), 7-12.5 (Harz 1969), 8.5-9 (Ramme 1951).

Song. – The calling song of *Isophya camptoxypha* consists of long sequences of syllables which can last up to several minutes (data mainly from Nagy et al. 2003 for *I. brevipennis* at 23-24°C, n = 13 animals). The syllables were repeated regularly with a repetition rate of 89-221 syllables per minute (fig. 81). Each syllable consisted of a main impulse group (composed of 11-25 impulses [mean ± SD: 18,4 ± 3,9] duration 27-46 ms [mean ± SD: 35,9 ± 6,3 ms]) and a few after-clicks. The after-clicks follow the main impulse group after a short interval of 56-151 ms (mean ± SD: 111,1 ± 29,3 ms). The animal recorded by Naskrecki from Poland (Otte & Naskrecki 1997) showed a very similar song pattern.

Distribution. – The species is characteristic for the Carpathian Mountains, found here in Slovakia (Cejchan 1958b, Nagy et al. 1998), Poland (Bazyluk 1971, Naskrecki & Otte 1997), Ukraine (Storozhenko & Gorochov 1992) and Rumania (Kis 1960). However, isolated populations occur in the mountains of western and southern Hungary and reach Austria (Nagy & Szövényi 1997, Vadkert et al. 2003, Nagy et al. 2003).

Locations where the typical song was observed: Austria: Ternitz: Gösing, (Nagy et al. 2003); Poland: Tatrzański National Park near Zakopane (Naskrecki & Otte 1997); Hungary: Günser mountains (Nagy et al. 2003), and Mecsek mountains (Orci 2002).



Figs. 53-55.  
*Isophya* species, stridulatory file on underside of male left tegmen. – 53, *Isophya kraussii* (CI, Germany, Rhön); 54, *I. kraussii* (NMPC); 55, *I. brevicauda* (CI, Austria).

***Isophya pyrenaica* (Serville)**  
(figs. 10, 32, 63, 82)

*Barbitistes Pyrenaica* Serville, 1839: 481 (p. 767: *Barbitistes pyrenaica*). Type lost (*vide* Otte 1997): FRANCE: Pyrenees: Bagnères dans les Pyrénées

Synonymy. – Under the name *I. pyrenaica* several species were combined (see above: *I. camptoxypha*, *I. kraussii*, later *I. pienensis*, *I. brevicauda*) for a long time (ca. 1906-1971/1988/1991 and until now)). From song pattern and stridulatory file (see below) it is now obvious that the individuals found in Southern France and the Spanish part of the Pyrenees differ from all other populations. So the name *I. pyrenaica* is applied only to the populations living in those regions.

The name *Isophya pyrenaica obtusata* nova forma proposed by Harz (1965, p. 447) has no taxonomic relevance because according to the Code (Art. 1.3.4) the term 'forma' published after 1960 denotes an infrasubspecific rank and is not available for taxonomic nomenclature.

Material studied. – FRANCE: 1 ♂, 1 ♀, Ardeche above Aigueze, Garigue, 44°18'N - 4°34'E, 2.-5.vi.1973, v. Hel-

versen (CH2340, CH1908): stridulatory file examined: ca. 80 teeth; 1 ♂ Luchon, Mail de Criq, 18.vii.1886: examined 1986 (see Heller 1988, p. 187-8) (CW). – Sound recordings: ISPY7301 (CH2340)

Morphology. – The edge of the left tegmen is angular at the tip of the stridulatory vein and seems to be broader than in *I. camptoxypha* (compare fig. 10 to fig. 6-9). The cerci are similar to that of *I. camptoxypha*, but the apex is more gradually incurved and not so blunt as in that species (compare fig. 32 to 28-31). The stridulatory files bears about 80 teeth (fig. 63).

Published measurements (mm): postfemora: 18-20; ovipositor: 9. These data from Chopard (1951) refer probably to *I. pyrenaica* sensu stricto.

Song. – The song is a series of syllables repeated at the rate of about 0.6 - 1.5/s. The main impulse group (ca. 35 impulses) lasts about 70-120 ms and is often followed after an interval of about 80 - 250 ms by an after-click (fig. 82; description according to Ragge & Reynolds 1998).

Distribution. – Southern France (Voisin 2003) and Spanish part of the Pyrenees (Olmo-Vidal 2002,

Pomares 2002).

Locations where the typical song was observed: France: Montagne de Lure (Bonnet 1995), Hérault (Ingrisch in Ragge & Reynolds 1998), Ardeche (Helversen in Heller 1988).

### *Isophya kraussii* Brunner von Wattenwyl

(figs. 11-14, 33-35, 53-54, 67-68, 83-84, 88)

*Isophya kraussii* Brunner von Wattenwyl, 1878: 65. Type male: GERMANY: Baden-Württemberg: near Urach [Schwäbische Alb bei Urach, auf krautigen Pflanzen in Bergwiesen] (NMW -No. 9813)

Synonymy. – The species is characterised by its song and the stridulatory file. It was synonymized with *I. pyrenaica* (as *I. camptoxipha*) by Brunner von Wattenwyl (1891) and re-established by Heller (1988). The situation in the southern part of its range is still not sufficiently understood. Male CH2907 from Croatia shows a song pattern quite similar to that of typical specimens from Germany (compare fig. 67 and 68). However, it has cerci similar to *I. brevicauda* and was collected together with a female, which undoubtedly has to be identified as *I. brevicauda* according to its short ovipositor. This may be either an example of the syntopic occurrence of these two species or another presently undescribed taxon is involved. However we have to notice that south of Austria no females with long ovipositor have been observed up to now.

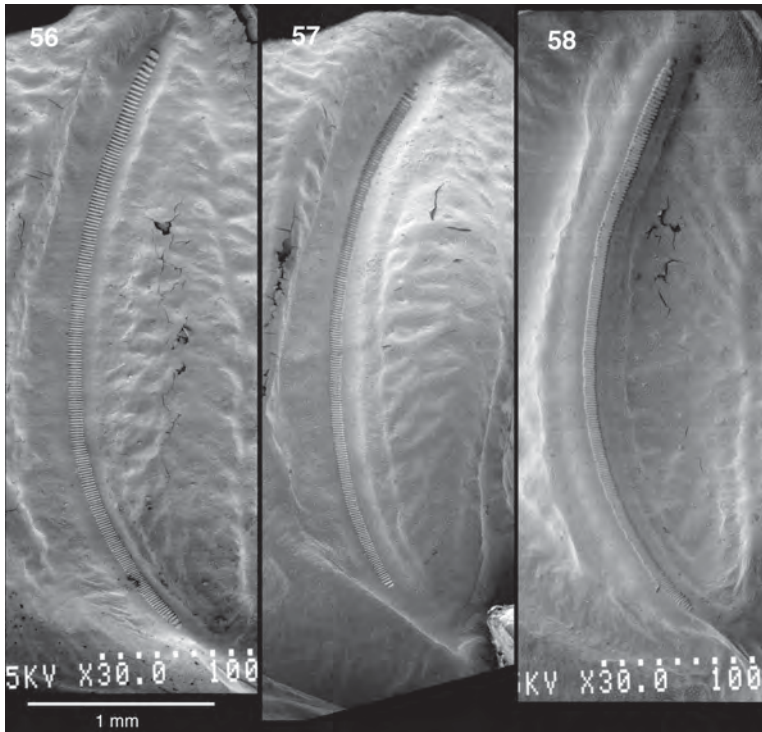
Material studied. – CROATIA: 1♂, Krapina near Ptuj, 15°52'E - 46°09'N, 4.vi.1988, O.v.Helversen (CH2907): stridulatory file examined: 302 teeth). CZECH REPUBLIC: 2♂, labelled: Pod. Milesovkou, 9.vi.1953; one specimen additional label: *Isophya pyrenaica* (Serv.) vi.1953, Dr. J. Mařan det. (NMPC): stridulatory file examined: 303 teeth. GERMANY: 1♂, holotypus (NMW): examined 1986; 2♂; Bavaria: Ailsbachtal, 11°20'E - 49°48'N, 25.vi.1981, Heller (CH1897-8); 1♂, 3♀, Bavaria, Altheim, west of Neustadt/Aisch, 10°29'E - 49°33'N, 5.v.1984, Heller (CH1904-7), CH1907: stridulatory file examined: 285 teeth; 1♂, Bavaria, surroundings of Ebermannstadt, 11°11'E - 49°47'N, v.1986, H. Kriegbaum (CH1285); many ♂; Bavaria, surroundings of Forchheim, 11°05'E - 49°44'N, 1995 and 1996, Ch. Voigt (CH4450-1, CH4508-10). 1♂, Bayern, Burg Frankenberg, 10°15'E - 49°34'N, 26.v.1985, K.-G. Heller (CH23399); 1♂, Bavaria, Kaubenheim, 10°27'E-49°32'N, 1987, K.-G. Heller (CH2414); 3♀, Bavaria, Obernesselbach, 10°28'E -49°35'N, 7.vii.1987, K.-G. Heller (CH2633-5); 1♀, Bavaria, Petersberg near Bad Windsheim 10°27'E - 49°29'N, 16.vii.1987, K.-G. Heller (CH2632); 3♂, 3♀, Bavaria, Pretzfeld, east of Forchheim. 11°10'E - 49°45'N, 12.vii.1987, K.-G. Heller (CH2415-20); 1♂, 1♀ Bavaria, Spielberg near Bad Windsheim, 10°25'E - 49°31'N, 1.vi.1983, Heller (CH0402, CH1903); 6♂, 4♀; Bavaria, surroundings of Würzburg, 9°06'E - 49°47'N, v/vi. 1981, R. Hess (CH0445-8, CH0461-2, CH1899-902), CH0445: stridulatory file examined: 271 teeth; HUNGARY: 2♂, Aggtelek karst region, surroundings of the village Josvaf, 20°37'E - 48°29'N, 6.viii.1998 and 26.vi.1999, I. A. Rácz & K. M. Orci, male calling songs

recorded and analysed (Orci 2002), stridulatory files checked: 295 and 296 teeth); 2♂, 1♀, Bükk Mount, near Miskolc, surroundings of Cserepfalu, 20°38'E - 48°04'N, 18.vi.1996, von Helversen (CH4512-3, CH5071): CH4513 stridulatory file checked: much higher tooth number than in *I. pienensis*; 1♂, Zemplén Mountains, surroundings of the village Telkibánya, 21°21'E - 48°28'N, 27.v. 2000, K. M. Orci, sound analysis in Orci 2002, stridulatory file examined: 298 teeth). POLAND: 1♂, Wotosate, Bieszczady NP, 1.vii.2002, 22°41'E - 49°04'N, J. Theuerkauf (CH6323). SLOVAKIA: 2♂, Bile Karpaty, Zalostina, 24.vi.2002, leg. & det. A. Lehmann (CL): ca. 280 teeth. SLOVENIA: 2♂, locality uncertain: either 20 km southwest of Ptuj or Kocara national park (northern Bosnia), 12.v.89, K.-G. Heller (CH2421, CH2553); both as *I. kraussii* det. S. Ingrisch, 1990). – Sound recordings: ISKR8101-6 (CH0445), ISKR8107-9, 12 (CH1900). ISKR8110-11 (CH1899), ISKR8401-8 (CH1904), ISKR8601-10 (CHX118), ISKR8611-16 (CHX116), ISKR8617-18 (CHX117), ISKR8801-19 (CH2907)

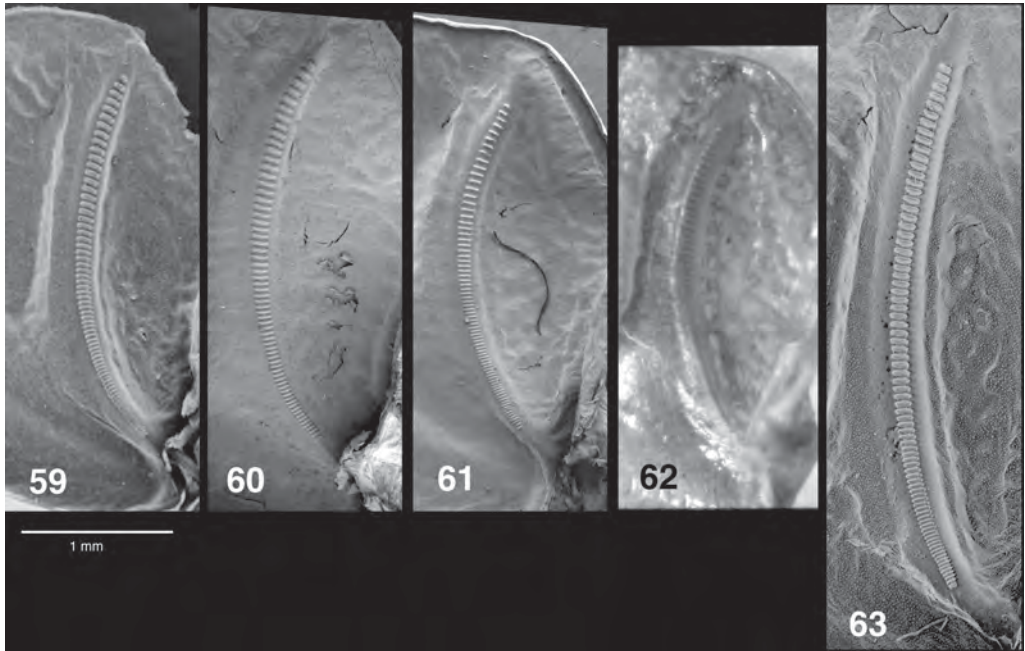
Morphology. – The left tegmen is very broad, sometimes protruding the lateral edge of the pronotum with the tip of the stridulatory vein (fig. 11-14). Its general shape is quite variable, not in all cases as acute-angled as in fig. 12-13. The cerci are gradually curved inwards in the distal third. Viewed from above, at the end they are relatively abruptly tapered towards the tip (fig. 33-34, but see 35). However, in lateral view it is obvious that the final tooth is much narrower than the previous part and is sitting at the upper edge of the cercus tip. The stridulatory file bears 260-305 teeth (fig. 53-54; Ingrisch 1991: 298 teeth; Orci 2002: 263-298 teeth (n=4)). At present all examined tegmina of this species had tooth numbers above 260, but the variability of this characteristic is insufficiently known. Heller (1988) did not consider the possibility that more than one species with high tooth number could be hidden in *I. pyrenaica*. Therefore tegmina of one or both specimens from Slovakia with tooth numbers near 200, which he mentioned as belonging to *I. kraussii*, probably belonged to *I. pienensis* (see below). The teeth become gradually less wide towards the distal end as mentioned by Ingrisch (1991), but sometimes the effect is very small.

Published measurements (mm): postfemora male: 15-17 (Ingrisch 1991); ovipositor: 9-11 (Ingrisch 1991).

Song. – The song is described by many German authors (for a review of papers see Ragge & Reynolds 1998). It consists of a long, uninterrupted, dense sequence of syllables. Each syllable starts with a long series of impulses (80-90 impulses in 250-320 ms at 23°C; results from 10 Hungarian specimens: 85-125 impulses per syllable, 256-364 ms at 20-24 °C), followed after an interval of around 80 ms by one to a few much louder impulses. The next syllable begins 115-170 ms later (fig. 83-84). All impulses are produced during the closing movements of the tegmina (fig. 67-68; Heller 1988). The relatively large interval



Figs. 56-58. *Isophya* species, stridulatory file on underside of male left tegmen. – 56, *I. pienensis* (NMPC, Mařan det.); 57, *I. pienensis* (zmum); 58, *I. pienensis* (CH4906).



Figs. 59-63. *Isophya* species, stridulatory file on underside of male left tegmen. – 59, *Isophya beybienkoi* (CH5030); 60, *I. beybienkoi* (NMPC); 61, *I. posthumoidalis* (CH4910); 62, *I. posthumoidalis* (ZMPA, paratype 1/99); 63, *I. pyrenaea* (CH2340).

after each syllable seen in the record of the male from Croatia (CH2907) is possibly the result of an acoustic interaction between two males (song of the second male visible in fig. 68). In spectral composition (fig. 88) there was no significant difference to typical specimens (compare Heller 1988, fig. 87). A female ready to mate can respond acoustically to the male song (Heller 1990), but quite often it approaches the singing male silently (unpublished observations KGH).

Distribution. – Germany (distribution map in Maas et al. 2002), Poland, Czech Republic, Slovakia (see Kocarek et al. 1999), Hungary, Austria (Ingrisch 1991).

Locations where the typical song was observed: Many places in Germany (it is the only *Isophya* species in Germany; for a list of papers see Ragge & Reynolds 1998), Poland: eastern Bieszczady (G. Grein, personal observation 1996), Hungary: Günsler mountains (Nagy et al. 2003), Aggtelek karst, Zemplen mountains (Orci 2002).

***Isophya brevicauda* Ramme**  
(figs. 15, 36, 55, 75)

*Isophya brevicauda* Ramme, 1931:168. Holotype male: CROATIA: Zagreb (paratypes Krapina) (ZMHB). Ingrisch 1991

*Isophya pyrenaica*; Harz 1969: 40

Material studied. – AUSTRIA: 2♂, 1♀, Karinthia: Kötschach, Dellacher Alpe, ca.1000m above sea level, 19.v.1990, e.l., leg S. Ingrisch (CI). CROATIA: 1♂ (holotypus; Sámobor near Zagreb, viii,1929, W. Ramme (ZMHB): stridulatory file examined: ca. 200 teeth); 1♂, paratypus, Krapina, viii,1929, W. Ramme (ZMHB); 1♀ Krapina near Ptuj, 15°52'E - 46°09'N 4.vi.1988, O.v. Helversen (CH2908).

Morphology. – The species is characterised by a much shorter ovipositor than the otherwise similar species *I. kraussii* (7.1-7.6 mm compared to 9-11 mm; Ramme 1951, Ingrisch 1991). The shape of the male tegmina is similar to that of *I. kraussii*. However, the elevated vein following immediately behind the depressed stridulatory vein is not as strong, long, and shiny as in this species (fig. 15). The cerci are often more continuously tapering into the tip than in *I. kraussii* from the northern part of its range (fig. 36), but quite similar to specimens of that species from Croatia and Slovenia (compare fig. 35 and 36). The stridulatory file carries 204-219 teeth (Ingrisch 1991; n = 2), which do not become narrower distally (fig. 55).

Published measurements (mm): postfemora male 16-17 (Ingrisch 1991), 18 (Ramme 1931), 17-18 (Ramme 1951), ovipositor 7-8 (Ingrisch 1991), 7.1-7.6 (Ramme 1951).

Song. – The calling song consists of sequences of 6-16 (typically 8-9) syllables which become increasingly longer within the sequence (fig. 75). The duration of

the syllables at the beginning was 126-180 ms at 23-26°C, at the end of a sequence 220-390 ms. The intervals between the syllables were 390-1350 ms between first and second and 390-790 (-900) ms between the following ones (all data from Ingrisch 1991). Sometimes an after-click followed the syllables. Females ready to mate responded acoustically to the male song. Female signals (a single impulse or a series of a few impulses) could be registered about 320 to 600 ms after the beginning of a male syllable (at 22.5°C).

Distribution. – From Austria and Slovenia to the south. It is not restricted to altitudes above 1000 m above sea level. According to the figures published by Ebner (1948) *I. kraussii* and *I. brevicauda* may both occur in Steiermark (Austria) (shown as *I. pyrenaica* and *I. brevicauda*).

Location, where the typical song was observed: Austria: Karinthia: Kötschach (Ingrisch 1991).

***Isophya pienensis* Mařan stat. rev.**  
(figs. 16-17, 37-39, 56-58, 69, 76, 89)

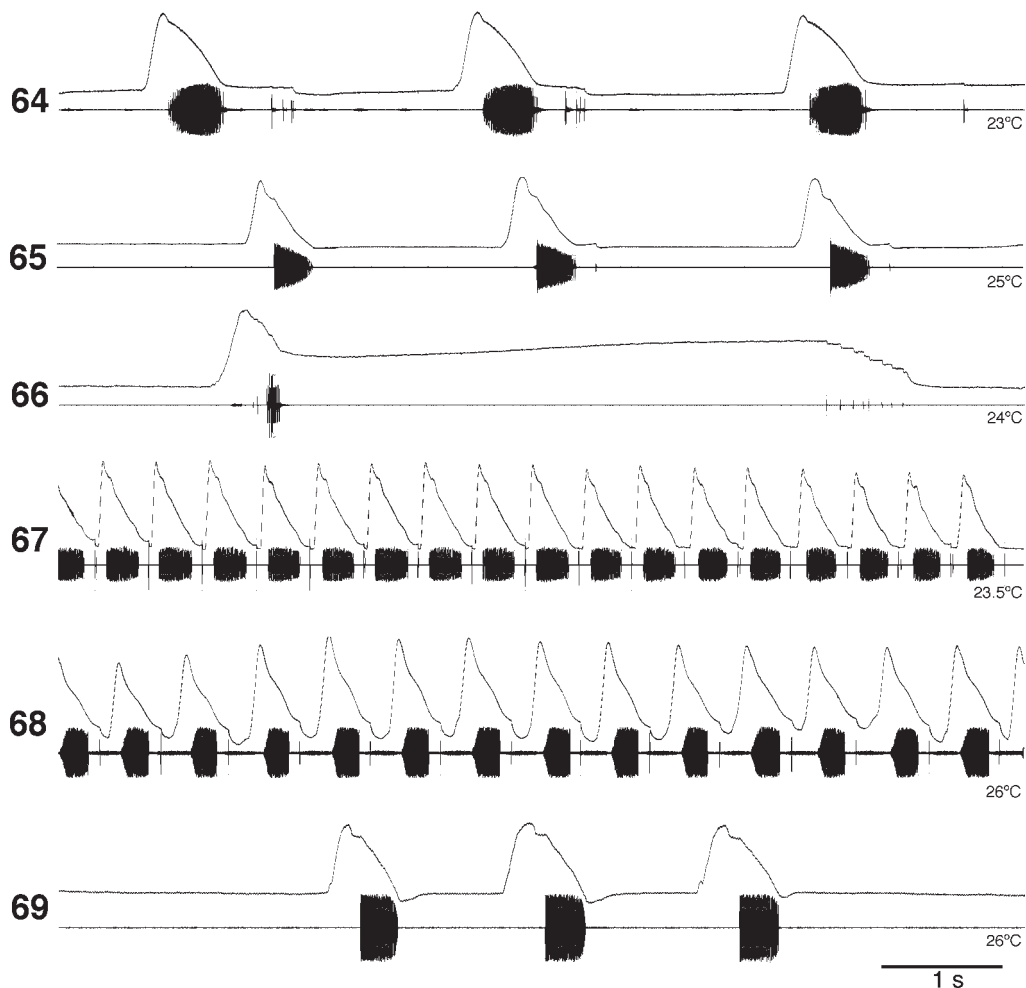
*Isophya pienensis* Mařan, 1954: 132. Holotype male: SLOVAKIA: State Nature Reserve Pieniny (4.viii.1953) (NMPC: not found during a visit on 3.vii.1998)

*Isophya pyrenaica*; Harz 1969: 40

Synonymy. – Harz (1969) synonymized the species with *I. pyrenaica*. However, from song and stridulatory file structure it is clear that it is a good species clearly separated from all other Central European *Isophya* species.

Material studied. – POLAND: 2♂, 2♀, Bieszczady, sw Weiler Muczne (so Stuposiany), 22°38'E - 49°09'N, 17.vii.1997, G. Grein (CH4905-8): stridulatory file in CH4906 examined: 198 teeth; 1 male left tegmen, unknown locality, D. Kostia (CH6126): stridulatory file examined: 192 teeth). SLOVAKIA: 1♂, labelled: Pieniny 4.viii.1953 Slov.//*Isophya pienensis* sp. nov., VIII.1953, Dr. J. Mařan det. (NMPC): paratypus?: stridulatory file examined: 188 teeth; 1♂, labelled: Pieniny, 4.viii.1953 (NMPC) paratypus?: 1 male left tegmen, Belanske Tatry, Faixova polana, 20°11'E - 49°14'N, 20.viii.1970, F. Chladek (CH5032): identified according to stridulatory file: 205 teeth). UKRAINE: 1♂, Zakarpat'e, Mukachevo, vi.1987, G. Rjazanova [kyrillic] (ZMUM): *I. pienensis* Korsunovskaya det., stridulatory file examined:184 teeth). – Sound recordings: ISPI9701-4, 11-12 (CH4905), ISPI9705-10 (CH4906).

Morphology. – The left tegmen is broad and angular at the tip of the stridulatory vein (fig. 16-17). The cerci are gradually curved inwards (fig. 37-39). The shape of the apex is intermediate between *I. campitoxypa* and *I. kraussii*, not as blunt as in the first, but not tapered towards the tip as in the second. The cercus carries an independent tooth at the upper edge of the tip. The stridulatory file bears 180-210 teeth (n = 6; fig. 56-58).

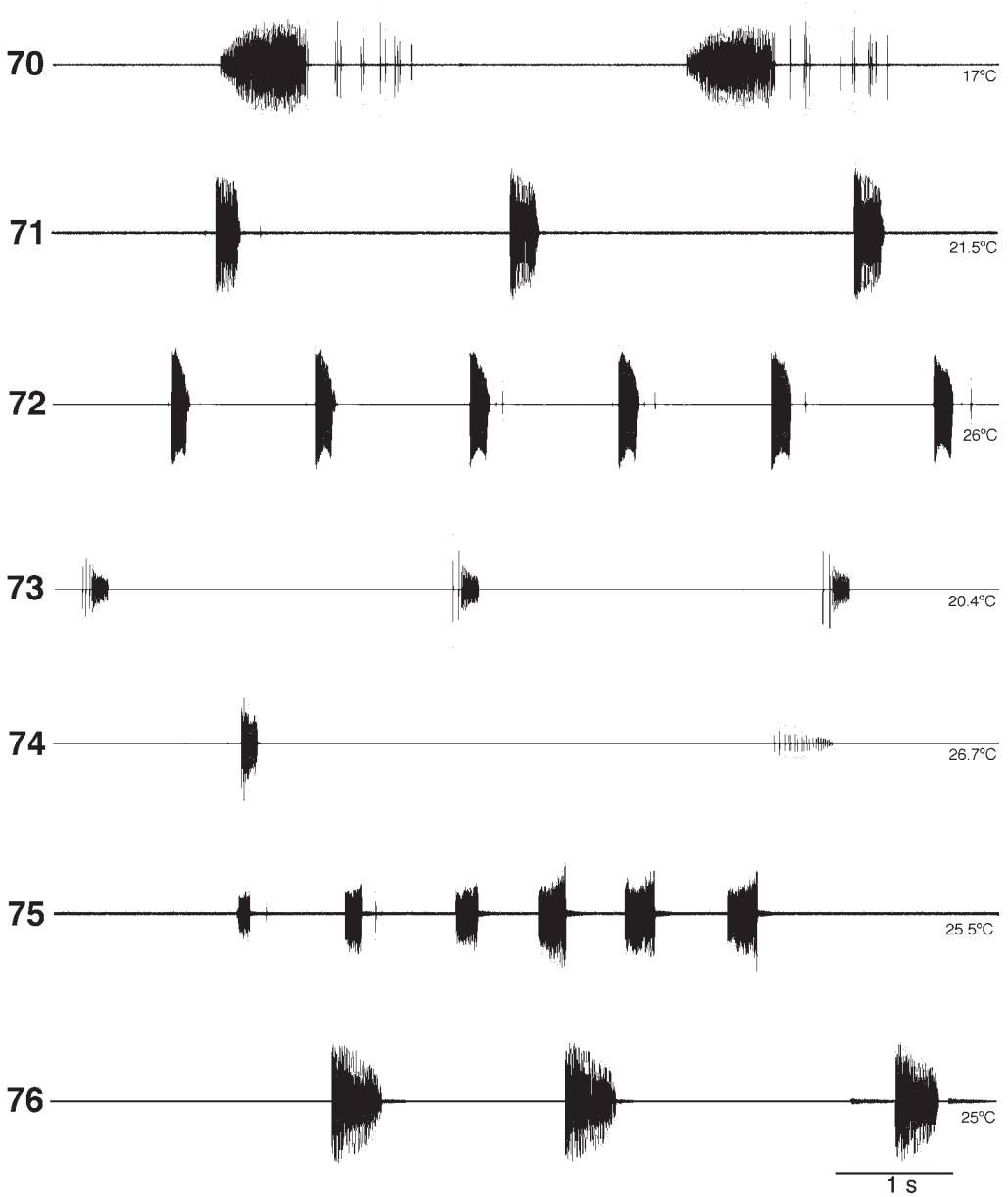


Figs. 64-69. *Isophya* species, oscillograms of stridulatory movement and male calling song, synchronous registration of left tegmen movement (upward deflection represents opening, downward closing) and sound. The body temperature of the animals may have been 1-4, degrees higher than the air temperature given below because of the intensity of the recording light (see Heller 1988). – 64, *Isophya costata* (CH1917); 65, *I. modestior* (CH0227); 66, *I. modesta* (CH4492); 67, *I. kraussii* (CH1900); 68, *I. kraussii* (CH2907); 69, *I. pienensis* (CH4905).

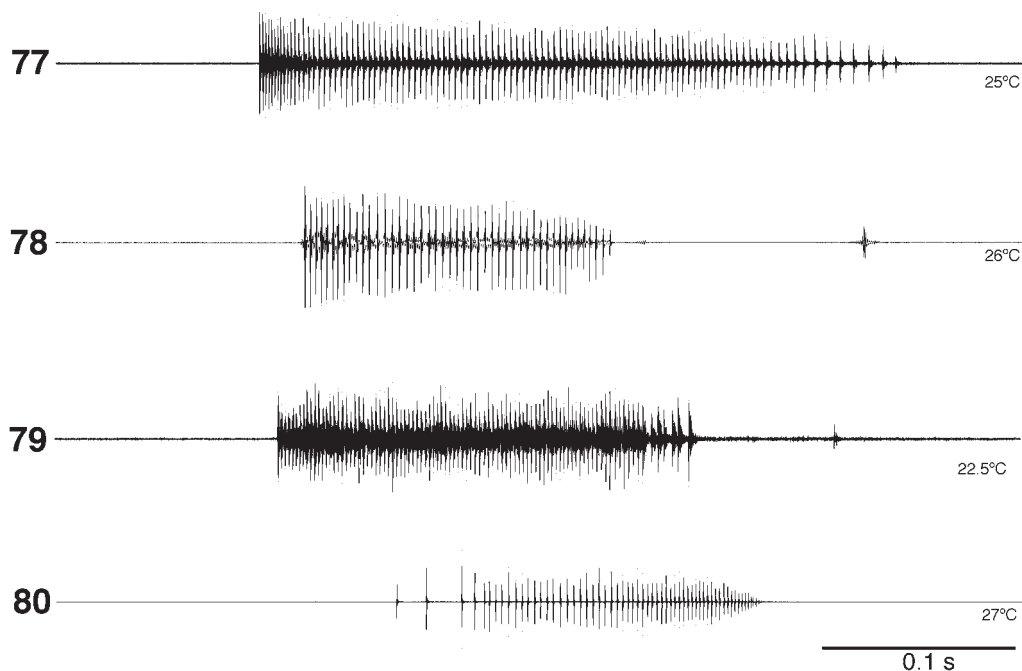
Published measurements (mm): postfemora male: 17-17.5 (Mařan 1954); ovipositor: 9.5 (Mařan 1954).

Song. – The calling song consists of single syllables (duration 300-400 ms, impulse number 76-96 at 25-26°C) which were produced at quite variable intervals. The impulses are produced during the closing movement of the tegmina (fig. 69). An isolated male may call at intervals of 1.5 s or longer, sometimes producing small groups of 2 -3 syllables, separated by inter-

vals of several seconds (fig. 76). Two interacting males produced fast syllable groups of up to 14 syllables with syllable periods (syllable + interval) of 500-700 ms. The data obtained by Korsunovskaja (unpublished) agree very well with our observations (syllable: 84 impulses, 440 ms duration, interval 2 s, 24°C). The carrier frequency of the song has its maximum in the ultrasonic range, between 20 and 30 kHz (fig. 89). A female ready to mate can respond acoustically to the male song (unpublished observation G. Grein).



Figs. 70-76, *Isophya* species, oscillograms of male calling song. – 70, *Isophya costata* (CH1917); 71, *I. modestior* (CH2554); 72, *I. modestior* (CH4848); 73, *I. stysi* Northern-Eastern Hungary (near the village Barabás); 74, *I. modesta* (Rumania, Transylvania (near Cluj)); 75, *I. brevicauda* (CI, Austria); 76, *I. pienensis* (CH4905).



Figs. 77-80, *Isophya* species, oscillograms of male calling song. – 77, *Isophya modestior* (CH0227, see fig. 65); 78, *I. modestior* (CH4848); 79, *I. modestior* (CI, Italy, Aviano/Udine); 80, *I. stysi* (Rumania, Transylvania (near Cluj)).

Distribution. – Slovakia, Poland, Rumania, Ukraine.

Locations where the typical song was observed: Slovakia: Slovensky Raj and Nizke Tatry (G.Grein, unpublished), Poland: Bieszczady (this paper), Ukraine: Mukachevo (Korsunovskaja, unpublished).

*Isophya beybienkoi* Mařan  
(figs. 18, 40-41, 59-60, 85)

*Isophya bey-bienkoi* Mařan, 1958: 514 (incorrect original spelling, corrected to *I. beybienkoi* according to Art. 32.5.2 of the ICZN). Holotype male: SLOVAKIA: Zadielska planina above Hrhov (NMPC; not found during a visit on 3.vii.1998)

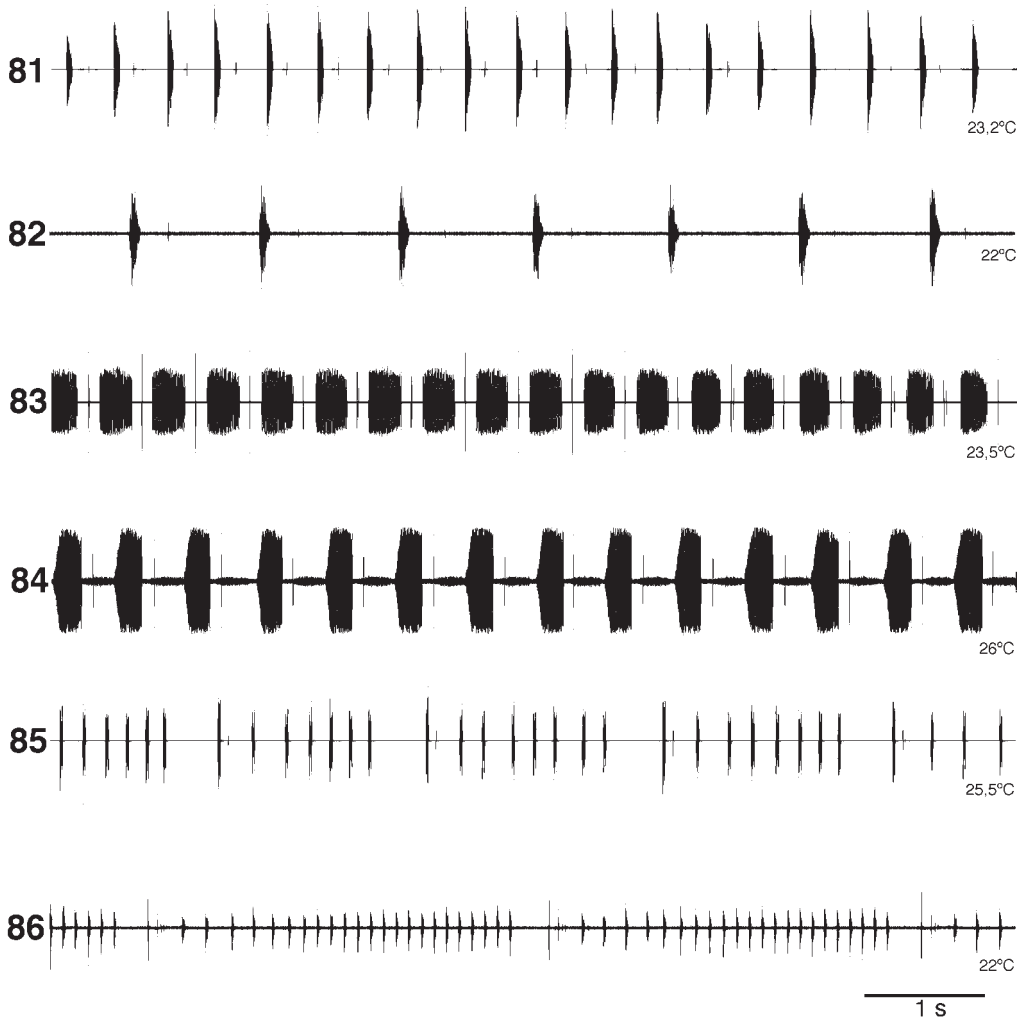
Material studied. – 1 ♂, without any labels, but in the museum collection (NMPC) placed under *I. beybienkoi*: stridulatory file examined: 65 teeth. SLOVAKIA: 1 ♂, 1 ♀, limestone rock steppe near village of Hrhov, 48°36'N - 20°45'E, 12.vi.2000, G. Szövényi & K.M. Orci (CH5367-8); 1 male left tegmen, Zadie, 8.vii.1976, F. Chladek (CH5030): stridulatory file examined: 72 teeth (Heller 1988).

Morphology. – *I. beybienkoi* has longer tegmina than *I. kraussii* and *I. camptoxypha*, the two other *Isophya* species reported from the Slovakian Karst (fig. 18). During a visit at the type locality no specimen of these two species were found together with *I. beybienkoi*, so these species are sympatric but not syntopic with *I. beybienkoi* (unpublished observation by KMO and G. Szövényi). Bazyluk (1971) compared *I. beybienkoi* with *I. posthumoidalis*, the latter being smaller with shorter ovipositor. The cerci are gradually tapering into the tip (fig. 40-41). The stridulatory file was studied by Heller (1988) in a specimen identified by Chladek (or Harz?) (72 teeth). The file agrees quite well with that of the specimen studied here (65 teeth; see fig. 59-60). In three other males we (KMO) counted 63, 66 and 66 teeth. *Isophya beybienkoi*, *I. camptoxypha* and *I. posthumoidalis* are quite similar to each other regarding this character.

Published measurements (mm): postfemora male: 16-19 (Mařan 1958, Harz 1969); ovipositor: 11.7-13.2 (Mařan 1958), 11.7-13.5 (Harz 1969).

Song. – The song pattern (fig. 85) is described by Orci et al. (2001): It is a long syllable-sequence in

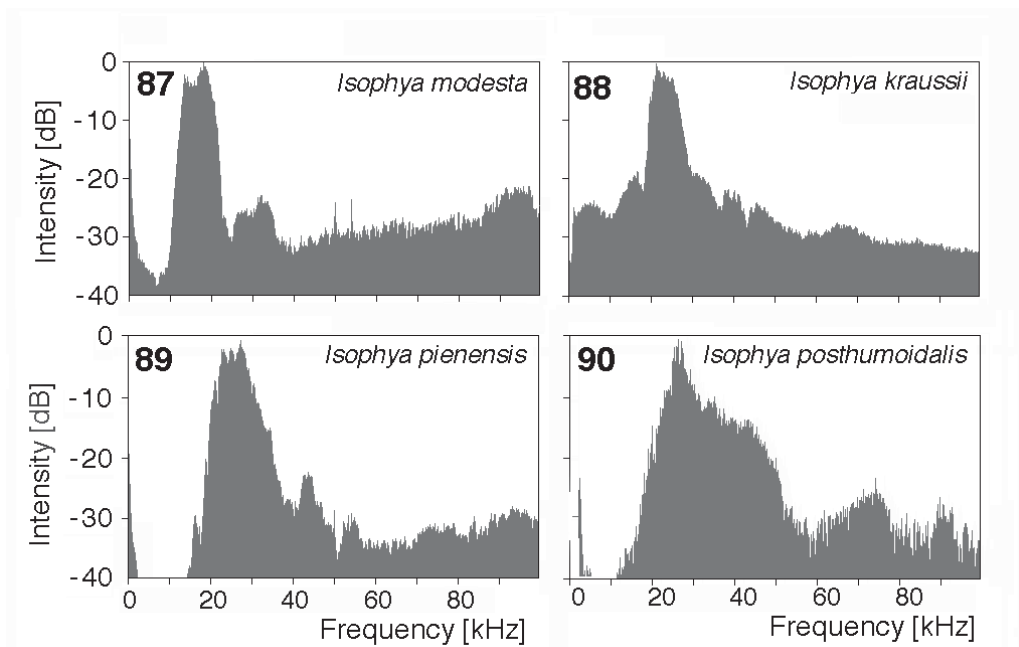




Figs. 81-86, *Isophya* species, oscillograms of male calling song. – 81, *Isophya camptoxypha* (Western Hungary (Kőszeg Mountains)); 82, *I. pyrenaea* (Ragge & Reynolds 1998); 83, *I. kraussii* (CH1900; see fig. 67); 84, *I. kraussii* (CH2907; see fig. 68); 85, *I. beybienkoi* (Orci et al. 2001); 86, *I. posthumoidalis* (CH4910).

which two types of syllable can be observed. An 'A' syllable consists of a series of 5-13 impulses. In this syllable type the terminal impulse is not longer than the preceding ones and there is not any after-click. A 'B' syllable consists of a main impulse-series and a few after-clicks. The main impulse-series is composed of 2-9 relatively short impulses (approx. 0.5 ms) and a longer terminal one (approx. 1.25 ms). The number of after-clicks varied from 1 to 3. Both types are closing hemi-

syllables. Syllables are produced in a characteristic rhythm so that the whole song can be formulated as 'AAA...A - BAAA...A - BAAA...A - BAAA...A' and so on, and it ends with ' - BAAA...A', where '...' means a variable number of 'A' syllables, and ' - ' means a distinctively longer intersyllable interval. During 'AAA...A' sequences the syllable repetition rate tends to increase so that generally the last A-A interval is the shortest. The number of 'A' syllables in 'AAA...A' se-



Figs. 87-90. *Isophya* species, frequency spectra of male calling song. – 87, *I. modesta* (CH3334); 88, *I. kraussii* (CH2907); 89, *I. pienensis* (CH4905); 90, *I. posthumoidalis* (CH4909/10).

quences varied randomly during the whole song, from 4 up to 32. At night, which is the main period of sound production in this species, undisturbed males sing continuously for several minutes and the termination of the song is apparently accidental. Therefore the whole syllable sequence has no characteristic, definite duration.

Distribution. – *Isophya beybienkoi* was described from Zadiělská planina and Plešivecká planina, Slovenskie Kras, south-east Slovakia (Mařan 1958). According to Orci et al. (2001) it has not been found anywhere outside this small area since that time, not even in the closest neighbouring mountain ranges.

***Isophya posthumoidalis* Bazyluk**  
(figs. 19-20, 42-44, 61-62, 86, 90)

*Isophya posthumoidalis* Bazyluk, 1971: 131. Holotype (male): POLAND, Bieszczady (ZMPA)

Material studied. – POLAND: 2♂, 1♀, Bieszczady, SW Weiler Muczne, SE Stuposiany, 22°38'E - 49°09'N, 17.vii.1997, G. Grein (CH4909-11): stridulatory file in CH4910 examined: 76 teeth; 1♂, labelled: Polonia: Bieszczady: Mate Jaslo - Jaslo polanki i potonina, 23.vii.1970, A. Liana leg.//Inst. Zool. P.A.N. Warszawa 32/70//Paratypus (red)//*Isophya posthumoidalis* n.sp. Paratypus, det. W. Bazyluk//1/99 (ZMPA); 1♂, 1♀, labelled: Polonia: Bieszczady: Jaslo potonina, 23.vii.1970, W. Bazyluk

leg.//Inst. Zool. P.A.N. Warszawa 2/70//Paratypus (red)//*Isophya posthumoidalis* n.sp. Paratypus, det. W. Bazyluk//2/99[M], 3/99[F] (ZMPA); stridulatory file examined: 69 teeth. – Sound recordings: ISPO9701-2, 9 (CH4909), ISPO9703-8 (CH4910).

Morphology. – The females of this species can be recognised by the short ovipositor (Bazyluk 1971) not found in other *Isophya* species in Poland and Slovakia. The tegmina of the male are relatively small compared to the other *Isophya* species studied here (fig. 19-20). The stridulatory vein is quite short and the edge around its end is broadly rounded. The cerci show a relatively short, incurved end, gradually tapering into the tip. The end spine sometimes is distinct, sometimes looking as if fused to the tip (fig. 42-44). The figures in Bazyluk's (1971) description agree quite well with the photographs shown here. The stridulatory file bears ca. 70-80 teeth (fig. 61-62).

Published measurements (mm): postfemora male: 14-16 (Bazyluk 1971); ovipositor: 6.5-7.5 (Bazyluk 1971).

Song. – The song pattern (fig. 86) is similar to that described for *I. beybienkoi*. It is a long syllable-sequence (up to 80 s recorded) in which two types of syllable can be observed. An 'A' syllable consisted of a series of 5-10 impulses (syllable duration about 12 - 15 ms). A 'B' syllable consisted of one main impulse and a few (1 - 3) after-clicks. Both types are probably clos-

ing hemisyllables. Syllables are produced in a characteristic rhythm so that the whole song can be formulated as 'AAA...A - B - AAA...A - B - AAA...A - B - AAA...A' and so on, and it ends with '- B - AAA...A', where '...' means a variable number of 'A' syllables, and '-' means a distinctively longer intersyllable interval. During 'AAA...A' sequences the syllable repetition rate increased so that generally the last A-A intervals are shorter (duration relatively constant about 100 ms) than the first (duration about 100 to 350 ms). The number of 'A' syllables in 'AAA...A' sequences varied during the whole song, from 11 up to 56 (mean  $23.8 \pm 8.4$ ;  $n = 54$ ; recording temperature 21-25°C, two males recorded). At the end of the sequence syllable-groups tend to be shorter (4-13). If the differences to *I. beybienkoi* (number of A syllables per group, structure of B syllable) are species-specific or characteristic only for different populations, has to be clarified by further studies. The carrier frequency of the song shows a relatively broad band with a maximum in the ultrasonic range, between 20 and 30 kHz (fig. 90).

Distribution. – Poland, Slovakia (Kocarek & Jezowski 1999).

Location where the typical song was observed: Poland: Bieszczady (this paper).

## DISCUSSION

The data of the reviewed literature and our new findings presented here show clearly that the most important character to identify *Isophya* species is the structure of the male calling song (fig. 70-86). The songs of the species can be separated into four groups: (A) songs constituted by a long sequence of regularly repeated syllables (*I. camptoxypha*, *I. pyrenaea*, *I. kraussii*), (B) songs containing a long sequence of regularly repeated syllable groups (*I. beybienkoi*, *I. posthumoidalis*), (C) songs composed of short sequences of simple structured syllables (*I. costata*, *I. modestior*, *I. stysi*, *I. brevicauda*, *I. pienensis*), (D) songs composed of single, two-part syllables (*I. modesta*). This grouping probably reflects the phylogenetic relationships between the species only partly. The presumption of a close relationship between the two species with song type B is supported by the certainly highly derived syllable pattern as well as by the close proximity of their distribution ranges and the similarity in cercus shape. From the similarity in genital structures and song and from the important function of the song in pre-gametic isolation these species may even be considered as geographically isolated subspecies of one species. Both forms may have evolved from a species with song type A. The combined ranges of the species with this song type cover a large part of Central Europe. However, it is not clear if they can be considered as a natural unit. First, the plesiomorphic condition of the song pattern

within *Isophya* is not known. Some arguments from other genera of Barbitistinae (Barbitistini) would favour a song type like type C as ancestral (Heller 1990). But even if a long sequence of syllables (type A) were considered as apomorphic character, the differences in the structure of the stridulatory file are unexpectedly large and would indicate another grouping (see below). If, as mentioned above, song type C represents the plesiomorphic condition, then nothing can be said about the relationships between the four species belonging to this song type. The same is true for *I. modesta*, which has no similarly singing relatives in Central Europe. Its song may be derived from a pattern similar to that of *I. costata* but with much-enlarged interval between main impulse group and after-clicks.

The structure of the stridulatory file allows another grouping of the species that does, however, not coincide with the song type grouping: (A) Stridulatory file with (50-)70-90 teeth (*I. camptoxypha*, *I. pyrenaea*, *I. beybienkoi*, *I. posthumoidalis*), (B) stridulatory file with 180-210 teeth (*I. brevicauda*, *I. pienensis*), (C) stridulatory file with more than 270 teeth (*I. costata*, *I. kraussii*), (D) number of teeth on file relatively variable (90-145 *I. modesta*, 115-250 *I. modestior*, 54-128 *I. stysi*). According to the presently available data these teeth numbers can be used for identification. Surprisingly, the variation in the number of teeth in the stridulatory file is relatively low in most species with few important exceptions. This may partly be the result of the low sample size and has certainly to be examined in further studies. On the other hand, even specimens from different species have quite similar files. The species with low numbers can be recognised from the relatively short and weakly sclerotized stridulatory vein even without examining the underside of the left tegmen. Species with high numbers typically have long and strongly sclerotized stridulatory veins and the tegmen edge at the end of this vein is often angular reaching or surpassing the right body side.

A third character extensively examined in this study, the shape of cerci, can also be used for grouping the species. (A) The cerci have a straight part (1/4-1/5 of the length of the cercus) at the distal end after the incurvation: *I. stysi*, *I. modestior*, *I. modesta* and *I. costata*, but in *I. costata* the end part of the cercus is not as straight as in the other three species. (B) There is no distinct straight part at the distal end after the incurvation, the cerci show a continuous incurvation leading to the distal end: all the other species not included in the first group. This grouping does not coincide with those based on song types or stridulatory files.

The differences in grouping the species according to either song, stridulatory file or cercus shape indicate that one, two or all three types of characters may have evolved quite fast. The evolution of the length of ovipositor, another character, which is in some cases

important for species identification, may be equally fast. The two species *I. beybienkoi* and *I. posthumoidalis*, which are closely related according to distribution and song type, differ strongly in ovipositor length. Kis (1960) already mentioned for *Isophya camptoxypha* (as *I. brevipennis*) that this character is variable and subject of ecological influences.

Thus at present the evolutionary history of this genus in Central Europe remains an unsolved puzzle and much research is needed on additional characters (e.g. DNA sequence data) to track its evolution. Additional sound data will show if there are even more morphologically cryptic species present than already known.

#### ACKNOWLEDGEMENTS

We are grateful to Prof. Dr. T. L. Wasserthal for his permission using the SEM and Dr. W. Heimler for his technical assistance (both Department of Zoology I, University Erlangen). For loan of material we are grateful to Dr. Ohl and Dr. I. Dorandt, Berlin, Prof. R. D. Zhantiev and Dr. O. Korsunovskaya, Moscow, the curator of the National Museum, Dept. Entomology, Prague, Dr. A. Kaltenbach and Dr. U. Aspöck, Vienna, and Dr. A. Liana and Dr. W. Tomaszewska, Warszawa. In addition, we thank Dr. E. Warchalowskaja-Sliwa and Dr. D. Kostia (Krakow) for specimens, Dr. P. Naskrecki, Cambridge, USA, for pictures and informations, and T. Herrmann, Langenhagen, for checking of the English. The work of KMO was supported by the Hungarian Scientific Research Fund (OTKA T029357).

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Received: 20 January 2004

Revised version accepted: 25 June 2004

Table 1. Key to species (males only):  
Range of variation of some morphological characters insufficiently known

species / character	fastigium verticis	cerci	stridulatory file	song	distribution
<i>I. costata</i>	wider or as wide as scapus	with straight apical area; fig. 21	with 250-280 teeth	groups of syllables (figs. 64, 70)	Austria, Hungary, Rumania
<i>I. modestior</i>	narrower than scapus	with straight apical area; fig. 23	with more than 150 teeth (150-250)	groups of syllables (fig. 65, 77)	Serbia, W-Bulgaria, Montenegro, Italy
<i>I. modestior</i>	narrower than scapus	with straight apical area; fig. 22	with 95-150 teeth	groups of syllables (figs. 71-72, 78-79)	Austria, Hungary, Slovenia
<i>I. styxi</i>	narrower than scapus	with straight apical area; figs. 24-25	with less than 90 teeth (50-80)	groups of syllables (fig. 73)	Slovakia, Poland, Hungary, Ukraine
<i>I. styxi</i>	narrower than scapus	with straight apical area; figs. 24-25	with 60-130 teeth	groups of syllables (fig. 80)	W Rumania
<i>I. modesta</i>	narrower than scapus	with straight apical area; fig. 26	with 95-150 teeth	single syllables (figs. 66, 74)	see text
<i>I. kraussii</i>	narrower than scapus	with gradually curved apical area; figs. 33-35	with more than 230 teeth (260-305)	homogenous syllable sequence (figs. 67-68, 83-84)	see text
<i>I. brevicauda</i>	narrower than scapus	with gradually curved apical area; fig. 36	with 210-220 teeth	groups of syllables (fig. 75)	southern Alps
<i>I. pienensis</i>	narrower than scapus	with gradually curved apical area; figs. 37-39	with 180-210 teeth	groups of syllables (fig. 69, 76)	northern Carpathians
<i>I. campoxyppha</i>	narrower than scapus	with gradually curved apical area; figs. 27-31	with 50-80 teeth	homogenous syllable sequence (fig. 81)	see text
<i>I. pyrenaea</i>	narrower than scapus	with gradually curved apical area; fig. 32	with ca. 80 teeth	homogenous syllable sequence (fig. 82)	southern France, Spain
<i>I. beybienkoi</i>	narrower than scapus	with gradually curved apical area; figs. 40-41	with 60-75 teeth	complex syllable sequence (fig. 85)	Slovakia
<i>I. posthumoidalis</i>	narrower than scapus	with gradually curved apical area; figs. 42-44	with 70-80 teeth	complex syllable sequence (fig. 86)	northern Carpathians