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Beitr. Ent.	Berlin	ISSN 0005 – 805X
49 (1999) 2	S. 295 – 342	13.09.1999

A revision of *Ilyobates* KRAATZ, 1856

(Coleoptera: Staphylinidae, Aleocharinae, Oxypodini)

With 15 figure plates (from it 8 diagrams), and 1 table

VOLKER ASSING

Summary

The types and additional material of the species of *Ilyobates* KRAATZ are revised. Six valid species are recognized: *I. nigricollis* (PAYKULL), *I. bennetti* DONISTHORPE, *I. propinquus* (AUBÉ), *I. mech* (BAUDI), *I. merkli* EPPELSHEIM, and *I. mirabilis* **sp. n.** The following synonymies are established or confirmed, respectively: *I. nigricollis* (PAYKULL) = *I. haroldi* IHSSEN, = *I. nigricollis deubeli* BERNHAUER, **syn. n.**, = *I. hoelzeli* SCHEERPELTZ, **syn. n.**; *I. bennetti* DONISTHORPE = *I. subopacus* PALM; *I. propinquus* (AUBÉ) = *I. rufus* KRAATZ; *I. mech* (BAUDI) = *I. hustachei* MÉQUIGNON, **syn. n.**, = *I. pseudomech* LOHSE, **syn. n.**, = *Calodera sulcicollis* AUBÉ; *Pyroglossa* BERNHAUER = *Gennadota* CASEY, **syn. n.** Lectotypes are designated for *I. haroldi* IHSSEN, *I. nigricollis deubeli* BERNHAUER, *I. subopacus* PALM, *Calodera sulcicollis* AUBÉ, and *I. rufus* KRAATZ. *Callicerus puberulus* CASEY and *Gennadota canadensis* CASEY, two North American species previously attributed to *Ilyobates*, are transferred to *Pyroglossa* BERNHAUER. The taxonomic history of *Ilyobates* is outlined. The diagnoses of the genus and of the species are complemented by a key and by figures of the mouthparts, primary and secondary sexual characters, and further distinguishing characters. The biogeographical data available suggest that all the species of *Ilyobates* are Pontomediterranean faunal elements. Based on measurements of various body parts, intraspecific morphological variation is assessed and found to be enormous. As can be concluded from field studies and collection data, species of *Ilyobates* are monovoltine, with reproduction taking place in spring and summer. The adult beetles overwinter in a cryptic habitat. The life histories and possible explanations for the pronounced intraspecific variation of the species of *Ilyobates* are discussed.

Key words

Coleoptera - Staphylinidae - Aleocharinae - Oxypodini - *Ilyobates* - *Pyroglossa* - *Gennadota* - Palaearctic region - Europe - taxonomy - biogeography - ecology - intraspecific variation - life history - new species - new synonymy - new combination - lectotype designation

Zusammenfassung

Nach Revision der Typen und weiteren Materials der Arten der Gattung *Ilyobates* KRAATZ werden sechs valide Arten erkannt: *I. nigricollis* (PAYKULL), *I. bennetti* DONISTHORPE, *I. propinquus* (AUBÉ), *I. mech* (BAUDI), *I. merkli* EPPELSHEIM und *I. mirabilis* **sp. n.** Die folgenden Taxa werden neu synonymisiert bzw. als Synonyme bestätigt: *I. nigricollis* (PAYKULL) = *I. haroldi* IHSSEN, = *I. nigricollis deubeli* BERNHAUER, **syn. n.**, = *I. hoelzeli* SCHEERPELTZ, **syn. n.**; *I. bennetti* DONISTHORPE = *I. subo-*

DOI: 10.21248/contrib.entomol.49.2.295-342

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pacus PALM; *I. propinquus* (AUBÉ) = *I. rufus* KRAATZ; *I. mech* (BAUDI) = *I. hustachei* MÉQUIGNON, **syn. n.**, = *I. pseudomech* LOHSE, **syn. n.** , = *Calodera sulcicollis* AUBÉ; *Pyroglossa* BERNHAUER = *Gennadota* CASEY, **syn. n.** Für *I. haroldi* IHSSEN, *I. nigricollis deubeli* BERNHAUER, *I. subopacus* PALM, *Calodera sulcicollis* AUBÉ und *I. rufus* KRAATZ werden Lectotypen designiert. *Callicerus puberulus* CASEY and *Gennadota canadensis* CASEY, zwei bisher der Gattung *Ilyobates* zugeordnete Arten aus Nordamerika, werden in die Gattung *Pyroglossa* BERNHAUER transferiert. Die Gattungs- und Artdiagnosen werden durch eine Bestimmungstabelle sowie durch Abbildungen der Mundteile, der primären und sekundären Geschlechtsmerkmale und weiterer Differentialmerkmale ergänzt. Nach den vorliegenden biogeographischen Daten sind alle *Ilyobates*-Arten pontomediterrane Faunenelemente. Die intraspezifische morphologische Variabilität der Arten ist, wie eine morphometrische Auswertung ergab, enorm. Freilanduntersuchungen sowie Sammlungsdaten zeigen, daß die *Ilyobates*-Arten monovoltin sind und sich im Frühjahr und Sommer fortpflanzen; die Imagines überwintern offenbar in einem unterirdischen, nicht näher bekannten Habitat. Die Bionomie sowie mögliche Erklärungen für die erhebliche intraspezifische Variabilität werden diskutiert.

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1. Introduction and taxonomic history

Ilyobates was described by KRAATZ (1856) to include four species, *Ilyobates nigricollis* (PAYKULL), *I. mech* (BAUDI), previously attributed to *Calodera* MANNERHEIM, the new species *I. rufus* KRAATZ, which the author already suspected to be a synonym of *Calodera propinqua* AUBÉ, and *I. forticornis* (BOISDUVAL & LACORDAIRE), which was later transferred to *Amarochara* THOMSON. KRAATZ (1856) placed the new genus near *Calodera*, emphasizing as distinguishing characters the morphology of the mouthparts (maxilla, labium), the massive and long antennae, the coarse punctation, and the different coloration. In 1859, *I. nigricollis* (PAYKULL) was designated as the type species of the genus by THOMSON (BLACKWELDER, 1952). In the second half of the last century, three further species of *Ilyobates* were described: *I. crassicornis* by QUEDENFELDT (1882) and *I. baicalicus* by EPPELSHEIM (1883), which were

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later transferred to *Amarochara* THOMSON and *Parocalea* BERNHAUER, respectively (BERNHAUER, 1902a), and *I. merkli* by EPPELSHEIM (1883). GANGLBAUER (1895) presented a diagnosis of the genus and a key to the four Central European species known at that time: *I. nigricollis*, *I. mech*, *I. merkli*, and *I. propinquus* (AUBÉ) with the junior synonym *I. rufus* KRAATZ. In a synopsis published a few years later, BERNHAUER (1902a) described *Ilyobates nigricollis deubeli* from the southern Carpathians. Two further species had been described up to 1902: *I. brevicornis* by WASMANN (1902), which was synonymized with *Silusa rubra* ERICHSON by *Bernhauer* (1902b), and *I. bergi* from Argentina by FAUVEL (1901), which was recently transferred to *Spanioda* BLACKWELDER by PACE (1988). Apart from the inclusion of *I. bennetti* DONISTHORPE as species dubia, which was described from Great Britain (DONISTHORPE, 1914), the catalogue by BERNHAUER & SCHEERPELTZ (1926) indicates no taxonomic or systematic changes. Since then, five species of *Ilyobates* have been described: *I. hustachei* from the Western Alps by MÉQUIGNON (1933), *I. haroldi* by IHSSEN (1934), *I. subopacus* by PALM (1935), *I. hoelzeli* from the Eastern Alps by SCHEERPELTZ (1947), and *I. pseudomech* (also from the Eastern Alps) by LOHSE (1994). IHSSEN (1934) was the first to realize that what had previously been treated as *I. nigricollis* (PAYKULL) in fact comprised two distinct species, the larger of which he described as *I. haroldi*. PALM (1935), however, after examination of a type specimen from the Paykull collection, found that the larger species was identical with *I. nigricollis* and named the smaller species *I. subopacus*. Consequently, *I. haroldi* had to be considered a junior synonym of *I. nigricollis*, a fact that was largely ignored by several later authors, who regarded *I. subopacus* as a junior synonym of *I. haroldi* (e. g. IHSSEN, 1935, 1937; SCHEERPELTZ, 1947).

In his revision of North American Aleocharinae, SEEVERS (1978) synonymized *Gennadota* CASEY with *Ilyobates*, without explicitly stating the reasons, and placed the genus in the *Ocalea* group together with *Ocalea* ERICHSON and *Longipeltina* BERNHAUER. Two North American species had been attributed to *Gennadota*: the type species *G. puberula* (CASEY, 1893) (originally described as *Callicerus*) and *G. canadensis* CASEY, 1906.

Thus, before the present revision, eleven species and subspecies of *Ilyobates* were recognized, nine of them from the Western Palaearctic region (*I. nigricollis nigricollis* (PAYKULL), *I. nigricollis deubeli* BERNHAUER, *I. subopacus* PALM, *I. propinquus* (AUBÉ), *I. mech* (BAUDI), *I. merkli* EPPELSHEIM, *I. bennetti* DONISTHORPE, *I. hoelzeli* SCHEERPELTZ, *I. pseudomech* LOHSE), and two from the Nearctic region (*I. puberulus* (CASEY), *I. canadensis* (CASEY)).

2. Material, measurements and abbreviations

Types and additional material from the following institutions and private collections were examined:

BMNH	The Natural History Museum, London (M. BRENDELL)
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Ottawa (A. SMETANA)
DEI	Deutsches Entomologisches Institut, Eberswalde (L. ZERCHE)
FMNH	Field Museum of Natural History, Chicago (A.F. NEWTON JR., P.P. PARRILLO)
HNHM	Hungarian Natural History Museum, Budapest (O. MERKL)
MHNG	Muséum d'Histoire Naturelle, Genève (I. LÖBL)
MNHNP	Muséum National d'Histoire Naturelle, Paris (N. BERTI)
MNHUB	Museum für Naturkunde der Humboldt-Universität, Berlin (M. UHLIG)
MRSNT	Museo Regionale di Scienze Naturali Torino (M. DACCORDI)
NHMB	Naturhistorisches Museum Basel, coll. Frey (E. SPRECHER)
NHMW	Naturhistorisches Museum Wien (H. SCHILLHAMMER)

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NHRM	Naturhistoriska Riksmuseet Stockholm (B. VIKLUND)
SMNS	Staatliches Museum für Naturkunde in Stuttgart (W. SCHAWALLER)
SMTD	Staatliches Museum für Tierkunde, Dresden (O. JÄGER)
TLMFI	Tiroler Landesmuseum Ferdinandeum, Innsbruck (M. KAHLEN)
USNM	U. S. National Museum of Natural History, Washington (via S. ASHE, Kansas)
ZIN	Zoological Insitute, St.-Petersburg (A. SOLODOVNIKOV)
ZML	Zoological Museum Lund (R. DANIELSSON)
cAss	author's private collection
cKap	Private collection A. KAPP, Rankweil
cKöh	Private collection F. KÖHLER, Bornheim
cRen	Private collection K. RENNER, Bielefeld
cRos	Private collection A. ROSE, Oldenburg
cSch	Private collection M. SCHÜLKE, Berlin
cSol	Private collection A. SOLODOVNIKOV, St. Petersburg
cStu	Private collection T. STUMPF, Rösrath
cVog	Private collection J. VOGEL, Görlitz
cWit	Private collection, A. WITTWER, Couvet
cWun	Private collection P. WUNDERLE, Mönchengladbach
cZan	Private collection A. ZANETTI, Verona

In order to assess intraspecific variation in the species, approximately 750 specimens were measured. The measurements are given in mm and abbreviated as follows:

AL:	length of antenna
HW:	head width across (and including) eyes
PW:	maximal width of pronotum
PL:	length of pronotum along median line
EL:	length of elytra from apex of scutellum to elytral hind margin
HTiL:	length of metatibia (external face)
HTaL:	length of metatarsus (claws not included)
HT1L:	length of first metatarsomere (dorsal view)
HT2L:	combined length of second to fourth metatarsomere (dorsal view)
ML:	length of median lobe of aedeagus (from base to apex of ventral process)
TL:	body length from apex of mandibles to hind margin of abdominal segment VIII.

The internal structures of the aedeagus were examined after dissecting the median lobe: After macerating the aedeagus in KOH, the dorsal membrane of the median lobe was removed with fine needles, the internal structures were then separated from the median lobe and mounted for examination under a compound microscope.

3. The genus *Ilyobates* KRAATZ

3.1. Diagnosis

Species of medium to rather large size; size and proportions in all species subject to considerable intraspecific variation; colour of of body reddish to dark brown, sometimes ± bicoloured; whole body, especially forebody, with distinct, often remarkably coarse and dense punctation.

Head relatively small, distinctly narrower than pronotum, usually widest across eyes, not distinctly transverse; postgenae behind eyes tapering in dorsal view; posteriorly without distinct neck; eyes well developed and with micropubescence; genae and hind margin distinctly carinate; pubescence directed ± anteriorly.

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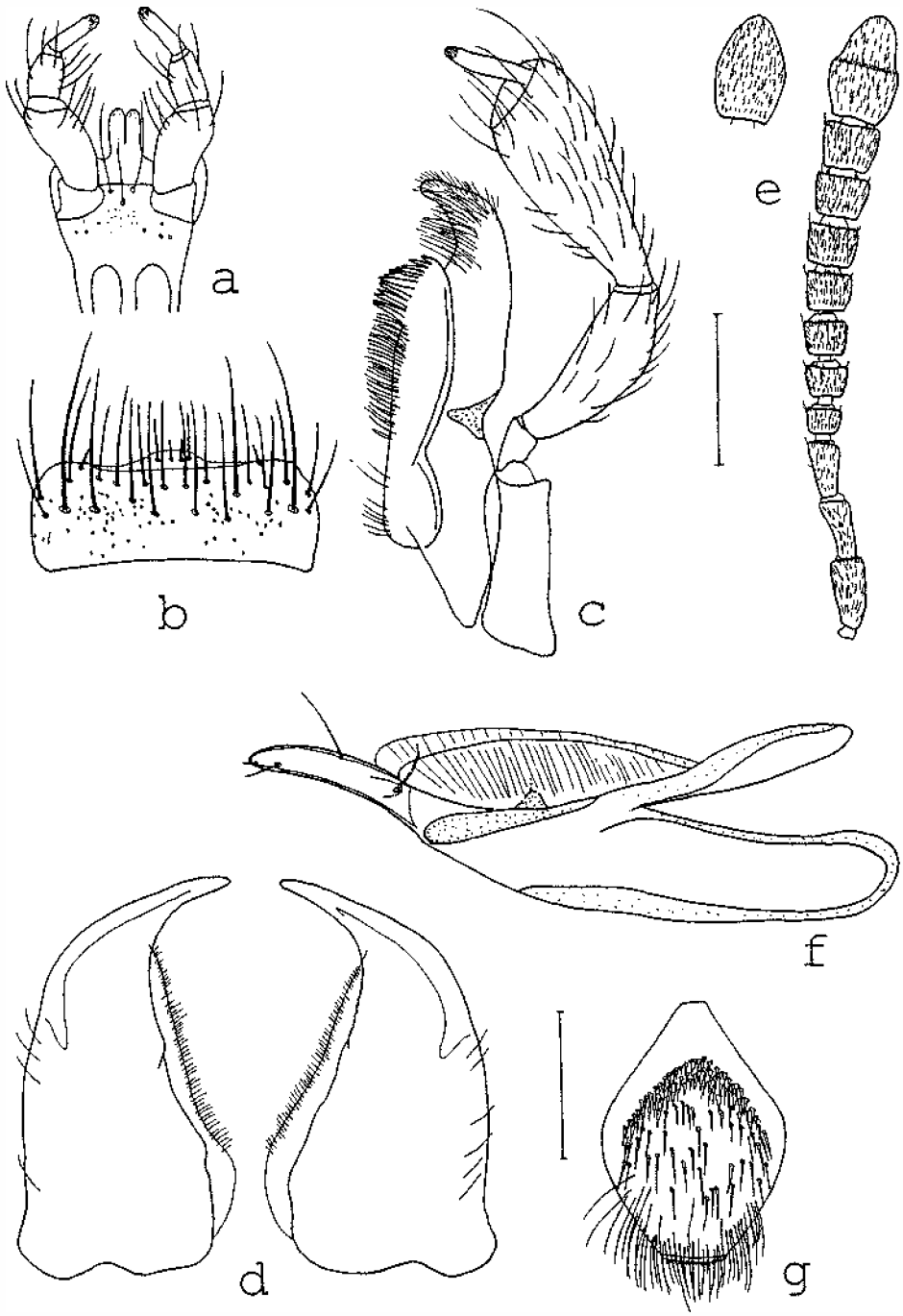


Fig. 1: *Ilyobates bennetti* DONISTHORPE. Labium (**a**); labrum (**b**); maxilla (**c**); mandibles (**d**); ♂ antenna and ♀ antennomere XI (**e**); paramere (**f**); ♂ tergum X (**g**). Scales: a - d: 0.1 mm; e - g: 0.2 mm.

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Antennae massive and long, antennomeres I - III distinctly oblong, IV - X gradually increasing in width and often also in length apically, penultimate joints at most moderately transverse, XI approximately as long as combined length of IX and X; relative length of antennomeres subject to considerable intraspecific variation; ♂ antennomere XI in apical half ± distinctly, usually asymmetrically narrowed or constricted (as in some species of *Oxypoda* MANNERHEIM), ♀ antennomere XI either without or with very indistinct apical constriction, or shaped like ♂ antennomere XI; whole antenna with dense, fine and short pubescence (Fig. 1e). Maxillary and labial palpi 4- and 3-jointed respectively (Figs 1a, c); ligula deeply bifid (Fig. 1a); mandibles apically acute, right mandible without distinct tooth (Fig. 1d); shape and chaetotaxy of labrum as in Fig. 1b.

Pronotum weakly or moderately transverse, maximal width in anterior half; pubescence ± semi-erect, directed caudad in median line, ± diagonally latero-caudad or laterad in lateral areas and ± transversely laterad near hind margin; hypomera in lateral view distinctly visible; prosternum with pronounced median carina.

Elytra well-developed, distinctly wider than pronotum; pubescence ± semi-erect, directed ± caudad; scutellum visible, coarsely punctate and sculptured, mat; hind wings fully developed or submacropterous; mesosternum with median carina at least in anterior half, mesosternal process long, reaching about halfway between mesocoxae; mesocoxal cavities posteriorly delimited from metasternum by weak carina; metasternum without median carina; metepisterna large and distinctly visible in lateral view.

Legs long and slender, tibiae without spines on external faces; first metatarsomere distinctly longer than second, approximately as long as the combined length of the two following metatarsomeres, but relative length of tarsi and tarsomeres subject to considerable intraspecific variation.

Abdomen subparallel; terga III - VI with pronounced, tergum VII with very shallow transverse impression anteriorly, these impressions in some species without, in most species with median carina of variable length; sterna III - VI anteriorly constricted; punctation much sparser than on forebody. Tergum VIII posteriorly ± convex, near hind margin with row of sparse thin setae; tergum X without distinct sexual dimorphism, anteriorly with dense and short stout setae, in central posterior area with longer, sparser and more slender setae (Fig. 1g); sternum VIII with sexual dimorphism: in ♂ ± pointed or strongly convex posteriorly, hind margin with row of thin and relatively long setae; in ♀ posteriorly ± convex, hind margin with row of very dense, short and stout setae.

♂: aedeagus with ventral process apically incised; internal structures of characteristic arrangement and especially the apical structures of characteristic shape; apical lobe of paramere moderately long (shorter than in *Oxypoda*) and with 4 setae, the apical seta very short.

♀: spermatheca with ± bulbous capsule and relatively short and wide duct.

3.2. Intraspecific variation

Intraspecific variation in the genus is enormous and has resulted in the description of several synonymous species. It particularly affects the absolute size of the whole body and all body parts, remarkably also of the aedeagus, and the proportions especially of the elytra, the antennae and the legs. The shape and relative length of the antennomeres, the tarsi, and of the first metatarsomere - characters often referred to as distinguishing characters in Aleocharinae - are extremely variable and therefore of very little significance for the separation of *Ilyobates* species (Table 1).

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Tab. 1: Maximum/minimum ratios for size measurements and proportions. For an explanation of abbreviations see section 2.

	n	AL	HW	PW	PL	EL	HTiL	HTaL	HT1L	HT2L	ML
I. nigricollis	220	1.71	1.57	1.72	1.76	1.91	1.88	1.98	2.42	2	1.60
I. bennetti	263	1.56	1.54	1.69	1.76	1.96	1.85	1.81	2.25	1.81	1.63
I. propinquus	78	1.39	1.36	1.45	1.47	1.56	1.61	1.41	1.71	1.42	1.28
I. mech	152	1.58	1.61	1.85	1.89	2.00	2.00	2.03	2.50	2.25	1.33
I. merkli	19	1.22	1.25	1.23	1.33	1.35	1.21	1.24	1.44	1.18	1.11
I. mirabilis	3	1.23	1.10	1.16	1.13	1.08	1.16	1.10	1.24	1.11	1.19

	TL	PW/ HW	PW/ PL	EL/ PL	HTaL/HTiL	HT1L/HT2L
I. nigricollis	2.11	1.21	1.17	1.36	1.19	1.47
I. bennetti	2.23	1.25	1.16	1.34	1.46	1.77
I. propinquus	1.90	1.21	1.12	1.25	1.12	1.36
I. mech	2.27	1.24	1.14	1.36	1.35	1.72
I. merkli	1.47	1.10	1.13	1.23	1.15	1.37
I. mirabilis	1.09	1.12	1.03	1.04	1.06	1.20

In addition, the coloration and the punctation, which have been emphasized as distinguishing characters in the keys available, may vary considerably. The shapes and arrangement of the internal structures of the aedeagus, however, and to some extent also the shapes of the median lobe and of the spermatheca were found to be highly characteristic and the most reliable characters for the identification of the species. For more details regarding the extent of intraspecific variation see section 3.3 and the species sections.

3.3. Distribution and bionomics

The distribution of genus is apparently originally confined to the Western Palaearctic region, with one species recently introduced into North America; based on the biogeographical evidence available, all the species can be classified as Pontomediterranean faunal elements (see species sections).

Little is known regarding the ecology of the genus. Species of *Ilyobates* are inhabitants of both woodland and open biotopes; some of them have often been observed in areas strongly influenced by human activity (urban and agricultural biotopes). All of them are apparently univoltine with the reproduction period in spring and early summer, and with overwintering adults (see comments especially below *I. bennetti*). However, there are only few records of *Ilyobates* taken during the winter months; whenever details regarding the circumstances of collection were available, they usually indicated habitats such as ant nests or nests of small mammals, especially moles, or debris near inundations. These observations and the near absence of confirmed winter records by sifting or extracting litter suggest cryptic hibernation habitats. Using methods like sifting or manual sampling, species of *Ilyobates* are usually collected only in small numbers even during spring and summer. It is probably for this reason that practically all the species of the genus are considered more or less rare. On the other hand, larger numbers of specimens have been taken near river banks, especially during periods of inundation, and by using pitfall traps. Thus, the evidence available suggests both high epigeic (searching?) activity and, at the same time, an unknown cryptic habitat.

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As indicated above and demonstrated in more detail in the species sections, species of *Ilyobates* display remarkable intraspecific variation especially in body size. The measurements of HW, PW and PL in *I. bennetti*, *I. nigricollis* and *I. mech*, of which most material was available for analysis, yielded ratios of maximum/minimum from 1.5 up to 1.9 (one dimension) (Table 1). The difference in three-dimensional body size between specimens of the upper and those of the lower end of the size range can thus be estimated to amount to a factor between 4 and 7. Among Aleocharinae, such extreme intraspecific variation is also known for species of *Aleochara* GRAVENHORST, whose larvae are parasitoids of dipteran puparia. In view of the ecological and morphological evidence available, a similar life history may be true for species of *Ilyobates*, an assumption supported also by my observation that the ovaries of females during the egg-laying period usually contain 4 - 6 more or less equally developed and relatively small eggs, and by the fact that the larvae are still unknown. According to WELCH (1993) the ovary of one examined specimen of *I. nigricollis* had 7 ovarioles. No data are available regarding the feeding habits and the function of the massive antennae.

4. The species of *Ilyobates*

4.1. *Ilyobates nigricollis* (PAYKULL, 1800)

Figs 2 - 5, Table 1

Staphylinus nigricollis PAYKULL, 1800: 400
Calodera nigricollis (PAYKULL): ERICHSON (1837, 1839)
Ilyobates nigricollis (PAYKULL): KRAATZ (1856)
Ilyobates haroldi IHSSEN, 1934: 217ff.; synonymy confirmed
Ilyobates haroldi: IHSSEN (1935, 1937); SCHEERPELTZ (1947)
Ilyobates nigricollis deubeli BERNHAUER, 1902a: 273, **syn. n.**
Ilyobates hölzeli SCHEERPELTZ, 1947: 339ff., **syn. n.**

Types examined

Ilyobates nigricollis (PAYKULL) [remounted, aedeagus examined]: Lectotype ♂: Naturhistoriska Riksmuseet Stockholm, Loan no 835/98/ Lectotypus Staphylinus nigricollis Paykull, desig. T. Palm 1935, rev. V. Assing 1998 (NHRM).

PAYKULL (1800) did not specify the number of specimens which the original description was based on. In stating that he saw "das im schwedischen Reichsmuseum befindliche Typusexemplar", PALM (1935) designated a lectotype, the single specimen in the Paykull collection here examined. Therefore, IHSSEN´s (1937) argument that what he considered to be *nigricollis* (i. e. *I. bennetti* DONISHORPE) was in better agreement with PAYKULL´s original description and that *I. subopacus* was consequently a junior synonym of *I. nigricollis* is invalid, since it is not in accordance with the ICZN.

Ilyobates haroldi IHSSEN: Lectotype ♂, present designation: Wettersteingbg, 18.VI.34/ Coll Dr. Ihssen/ Type/ Haroldi Ihssen/ Lectotypus ♂ Ilyobates haroldi Ihssen, desig. V. Assing 1998 (MNHUB). Paralectotypes, here designated and labelled accordingly: 1♂, same data as lectotype; 1♀, Wettersteingbg., 26.7.33 (MNHUB); 1♂ [with worker of *Formica rufa* attached to the same pin], Wettersteingbg. 4.8.33 (MNHUB); 1♂, 1♀, Ilidze, Hochwasser der Bosna/ Ug. Sarajevo, leg. Apfelbeck (MNHUB, NHMB); 1♀, Apfelb. 02, Ilidže/ Hochwasser/ Cotype/ Ilyobates haroldi Ihssen det. Ihssen (NHMB); 1♀, Seeshaupt, Frachensee, 26.8.30, Stöcklein/ Cotype (NHMB); 1♀, Oberbayern, Königsee, 13.8.19, Stöcklein/ Bartholomae Eiskapelle/

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Cotype (NHMB); 1♂, Niederbaiern, Dreitannenriegel, Bayr. Wald, 18.6.19, Stöcklein (MNHUB); 1♀, Gilgenburg, Ostpreussen, leg. Seidlitz (MNHUB); 1♀, Niederbaiern, Rachel, Bayr. Wald, 22.6.19, Stöcklein/ Cotype (NHMB); 1♂, Bayr. Wald, Rache., 22.6.19, Stöcklein/ Cotype (NHMB).

The types of *I. haroldi* IHSSEN are conspecific with *I. nigricollis* (PAYKULL); the previously established synonymy is here confirmed. The original description is based on numerous syntypes from various collections (IHSSEN, 1934). Therefore, and in view of the frequent confusion of *I. nigricollis* and *I. bennetti* and their respective synonyms, a lectotype designation was deemed necessary.

Ilyobates nigricollis deubeli BERNHAUER: Lectotype ♀, present designation: Fogarascher Gbg. Deubel/ nigricollis Payk. Siebenbürgen/ Deubeli Bernh., det. Bernhauer/ Chicago NHMus, M. Bernhauer Collection/ Lectotypus ♀ Ilyobates nigricollis deubeli Bernhauer, desig. V. Assing 1998 (FMNH). Paralectotypus ♀, here designated and labelled accordingly: Rosenhauer Gbg. Deubel/ Paratypus [sic] Ilyobates nigricornis [sic] v. Deubeli Bernhauer 1902/ Deubeli Brh., det. Bernhauer (HNHM).

The original description is based on two syntypes from the surroundings of Braşov, Romania, one of them deposited in the FMNH and one in the HNHM. The syntype in the Bernhauer collection is here designated as lectotype. A lectotype designation was necessary in the interest of stability of nomenclature, as the similar *Ilyobates bennetti*, too, occurs in the Carpathians, and there is some uncertainty regarding the identity of the syntype here chosen as paralectotype. The types are small specimens at the very low end of the size range of *I. nigricollis*. The relative length of the elytra, which according to BERNHAUER (1902a) is the only distinguishing character of *I. nigricollis deubeli*, was found to be well within the range of *I. nigricollis* (EL/PL in LT, PLT: 0.87, 0.89). An examination of additional material from the Carpathians showed that the relative length of the elytra is variable and yielded no differences in the sexual characters (both sexes). Therefore, in the absence of further evidence supporting the presence of a distinct subspecies in the Carpathians, *I. nigricollis deubeli* BERNHAUER is here synonymized with *I. nigricollis* (PAYKULL).

Ilyobates hoelzeli SCHEERPELTZ: Holotype ♂: ♂/ Carinthia, Koschuta, Hölzel leg./ Typus Ilyobates Hölzeli O. Scheerpeltz/ ex coll. Scheerpeltz (NHMW).

The holotype of *I. hoelzeli* is a relatively small specimen with distinctly sparser punctation on the pronotum than in average *I. nigricollis*. The examination of the aedeagus, however, showed that it is doubtlessly conspecific with that species, so that *I. hoelzeli* SCHEERPELTZ must be considered a junior synonym of *I. nigricollis* (PAYKULL).

Additional material examined

Latvia: 1♂, Dundaga [Dondangen], 19.VI.1989 (MNHUB).

Sweden: 4♂♂, 3♀♀, S Göteborg, Mölndal, leg. Ericson (NHMW, cAss).

Germany: Niedersachsen: 1♀, Harz, grassland near Herzberg, pitfall trap, 16.VI.1992 (cAss); 1♂, Solling, IV.1976, leg. Hartmann (MHNG); 1♂, 1♀, Solling, 1977, leg. Hartmann (MHNG); 7♂♂, 5♀♀, E Hannover, N Lehrte, pitfall trap, V.-VIII.1989 (cAss); 1♀, NE-Hannover, grassland, pitfall trap, 17.VII.1989, leg. Assing (cAss); 1♂, W Hannover, field near Stadthagen, V.-VI.1991, pitfall trap (cAss); 3♂♂, 1♀, Stadthagen, 28.VII.1991, leg. Assing (cWun); 4♂♂, 1♀, Düt near Hameln, pitfall trap, V.-VII.1988, leg. Sprick (cAss); 1♂, 2♀♀, Süntel, Rannenberg, field, pitfall trap, VI.-VII.1987, leg. Sprick (cAss); 1♂, Hildesheim, Wohldenberg, 28.VIII.1944, leg. Dorn (MNHUB); 2♀♀, Lüchow-Dannenberg, 23.IV.1983, leg. Renner (cRen); 1♀, Oldenburg, Wildeshausen-Pestrup, 25.V.1973, leg. Papperitz (SMNS); 1♂, Oldenburg, Wildenloh, pitfall, 27.V.-1.VII.1992 (cRos); 1♂, same locality, 2.-30.

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VI.1995 (cRos); 1♂, Oldenburg, Mardersee, pitfall, 9.V.-6.VI.1996 (cRos); 1♂, Neuenburger Urwald near Wilhelmshaven, beech trunk eclector, 17.VII.1995, leg. Menke (cAss); 3♂♂, 3♀♀, Wurster Heide near Cuxhaven, V.-VII.1987 (cAss); 1♂, Wangerooge, heathland, 27.VII.1982, leg. Assing (cAss); 1♂, Norderney, pitfall, 28.VII.-28.VIII.1990 (cRos); 1♀[with eggs in ovaries], Norderney, pitfall, 23.VII.1991 (cRos); 1♀, same data, 20.VIII.1991 (cRos); 1♀, Memmert, pitfall, 25.VI.-10.VII.1995 (cRos). **Nordrhein-Westfalen:** 1♂, 1♀, Porta Westfalica near Minden, Wittekindsberg, 4.VII.1992, leg. Borcherding (cAss); 1♂, Höxter, dry grassland, 29.VI.1989 (cAss); 2♂♂, 1♀, Detmold, 6.VIII.1980, leg. Renner (cRen); 1♂, Overath, 1985, leg. Stumpf (cStu); 1♀, same data, but 14.VI.1987 (cStu); 1♀, W Uhlenbruch, 23.VI.1994, leg. Stumpf (cStu); 1♂, 1♀, Wahner Heide near Köln, Hirzenbachweiher, 18.VI.1996, leg. Stumpf (cStu); 1♂, same data, but 31.VII.1996 (cStu); 1♂, Kölner Bucht, Chorbusch, 19.VII.1985, leg. Köhler (cKöh); 1♀, Düsseldorf, Eller Forst, 18.V.1974, leg. Brenner (cAss); 1♂, Altenahr, pitfall trap, 17.X.1988, leg. Büchs (cWun); 1♂, Nottuln, 2.VI.1982, leg. Terlutter (cTer); 1♂, Münster, VI.1960 (SMNS); 1♂, 1♀, NSG Amtsvenn, 29.VIII.1982, leg. Terlutter (cTer); 1♀, Nachrodt near Lüdenscheid, 27.VI.1994, leg. Terlutter (cTer); 1♂, 1♀, Ostwig near Lüdenscheid, V.1983, leg. Erbeling (cTer); 1♀, Bornheim, Rösberg, Tietmaar, 13.V.1992, leg. Köhler (cKöh); 1♂, Aachen, Schmithof, 16.V.1987, leg. Köhler (cKöh); 1♂, Eifel, Kermeter, Lohrbachskopf, VI.1992, leg. Köhler (cKöh); 1♀, Kermeter, NWZ Wiegelkammer, 29.V.1993, leg. Köhler (cKöh). **Rheinland-Pfalz:** 1♀, Kappel, LSG Taubergießen, 6.VI.1968, leg. Schmid (SMNS); 1♂, Hunsrück, Steeg, 9.VII.1967, leg. Schawaller (SMNS); 1♀, Dielkirchen, pitfall trap, 31.V.1989 (cAss). **Baden-Württemberg:** 1♂, Kreis Reutlingen, St. Johann, VIII.1983, leg. Handke (cTer); 1♀, Kaiserstuhl, Durbach, Rheinauen, 14.VII. 1971, leg. Lohse (MHNG); 1♂, Emmendingen-Windenreute, 28.-29.VIII.1954 (MNHUB); 1♀, Walddorf/Tübingen, 16.V.1964, leg. Köstlin (SMNS); 1♂, Schwarzwald, 2.VIII.1949, leg. Zastler (MNHUB). **Bayern:** 1♂, 1♀ [♂ teneral; the ♀ with worker of *Myrmica ruginodis* attached to the pin], Wettersteingebiet, 18.VII.1955, leg. Ihssen (MNHUB); 1♀, same locality, 12.VII.1935, leg. Ihssen (MNHUB); 2♂♂, Zugspitze, Riffelriss, 17.VI./ 22.VII.1937, leg. Ihssen (MNHUB); 1♀, München, 26.IV.1884 (NHMW); 1♂, Schrobenhausen, 25.VI.1972, leg. Papperitz (SMNS); 1♀, Fichtelgebirge, Berneck, Wischnitztal, 17.VI.1967, leg. Papperitz (SMNS). **Hessen:** 1♂, Wiesbaden, grassland, pitfall trap, V.-VI.1986, leg. Steinwarz (cWun); 1♀, Schlitz, Heidberg, garden, VII.1981, leg. Puthz (MHNG). **Mecklenburg-Vorpommern:** 1♂, Rostock Land, Graal-Müritz, 20.V.1980, leg. Schülke (DEI); 1♀, Rostock, beech trunk, 21.V.1936, leg. Derksen (MNHUB); 1♀, SE Greifswald, Hanshagen, 6.V.1992, leg. Wrase (cSch); 1♀, Greifswald, 8.V.1966, leg. Zerche (DEI); 1♂, Grevesmühlen, beech forest, 12.VII.1983, leg. Dieckmann (DEI); 1♂, 3♀♀, Waren, Müritzhof, NSG "Ostufer der Müritz", V.-VI.1975, leg. Martin (MNHUB); 1♀ Waren, Bruchwald Tiefwarensee, 18.VI.1988, leg. Uhlig (MNHUB); 1♂, Rügen, Binz, VI.1913 (MNHUB); 1♀, Rügen, 1912 (MNHUB). **Berlin/Brandenburg:** 1♀[teneral], Berlin, Grunewald, 15.IX.1986, leg. Winkelmann-Klöck (cSch); 1♂, Berlin Hahneberg, 12.V.1985, leg. Winkelmann-Klöck (cSch); 1♀, Berlin, Neukölln, Sportplatz, 16.IV.-22.V.1994, leg. Uhlig (MNHUB); 1♀, Berlin [locality illegible] (DEI); 1♂, 1♀, Berlin, locality not specified (MNHUB, SMTD); 6♂♂, Strausberg, 16.V.1909 (MNHUB); 2♀♀, Strausberg (MNHUB); 1♂, Hennigsdorf, 1909 (MNHUB); 2♂♂, Finkenkrug, 13.V.1928 (MHNG); 1♂, Finkenkrug, 11.VII.1924 (MHNG); 1♂, Finkenkrug, leg. Frankenberger (SMTD); 1♂, Finkenkrug, 6.V.1904 (MNHUB); 2♀♀, Finkenkrug (MNHUB); 2♂♂, 1♀, Brieselang (DEI); 2♂♂, 2♀♀, Brieselang, leg. Müller (MNHUB); 2♂♂, 2♀♀, Brieselang, 2.V.1920, 18.V.1924, 19.IV.& 4.V.1919, leg. Müller (MNHUB); 1♂, Nauen, VI.1910, leg. Ude (MNHUB); 2♂♂, 1♀, Nauen, Stadtforst, leg. Müller (MNHUB); 1♂, Erkner, 16.IV.1949 (MNHUB); 1♀, Glambeck, Angermünde (MNHUB); 2♀♀, Chorin (DEI); 1♂, Chorin, leg. Müller (cAss); 2♂♂, 1♀, Chorin, 15.V.1920, 1.V.1940, leg. Müller (MNHUB, cAss); 1♂, 2♀♀, Eberswalde (DEI); 1♀, Eberswalde, Klobbicke, 4.V.1990, leg. Müller (DEI); 1♂, Eberswalde, N Golzow, 25.VIII.1993, leg. Sommer (DEI); 1♂, Grünheide, Alt Buchhorst, 7.VI.1990, leg. Heinig (MNHUB); 1♀, Lossow, leg. Schukatschek (MNHUB); 1♀, Beeskow, Dammer Moor, Torfstiche, VI.1978, leg. Knöfel (MNHUB); 1♀, Buckow, leg. Lebus (SMTD); 1♀, Buckow (MNHUB). **Sachsen-Anhalt:** 3♂♂, Schlüchtern near Hanau, pitfall trap, 14.-17.VI.1993, leg. Sprick (cAss); 1♂, 1♀, Dübener Heide, Wöllnau, 2.VI.1967, 23.IV.1972, leg. Linke (SMTD); 1♂, 1♀, Dübener Heide, Winkelmühle, 26.V.

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1973, leg. Uhlig (MNHUB, cAss). **Thüringen:** 1♂, Ronneburg, 22.VIII.1927 (DEI); 1♀, Ronneburg, 22.VIII.1927, leg. Scheffler (MNHUB); 1♀ [with worker of *Myrmica rubra* attached to pin], Ronneburg, leg. Scheffler (MNHUB); 1♀, Oldisleben, 11.VII.1915, leg. Petry (MNHUB); 1♀, Kyffhäuser, Bad Frankenhausen, 21.IV.1957, leg. Ermisch (SMTD); 1♀, Naumburg, Mordtal, 23.VIII.1919, leg. Maertens (MNHUB). **Sachsen:** 1♂, Zittauer Gebirge, Jonsdorf, 17.V.1990, leg. Sorge (DEI); 1♀, Wechselburg, 8.VII.1982, leg. Zerche (DEI); 1♂, Erzgebirge, Gornau, 15.VII. 1971, leg. Zerche (DEI); 1♂, Erzgebirge, Stollberg, Stegewiesen, nest of *Talpa*, leg. Uhmann (DEI); 1♀, Erzgebirge, Fichtelberg, 4.VI.1913, leg. Linke (SMTD); 1♀, Leipzig, Sellerh., 20.VI.1911, leg. Linke (SMTD); 1♀, Leipzig, Grim., 13.VI.1909, leg. Linke (SMTD); 1♂, 1♀, Leipzig, S. Garten, 15.V.1912, leg. Linke (SMTD, cAss); 1♂, Leipzig, Garten, 2.V.1913, leg. Linke (NHMW); 1♀, Leipzig, Tobersch. [?], 20.V.1917, leg. Linke (SMTD); 1♂, Leipzig, Wurzen, 23.V.1920, leg. Linke (cAss); 1♀, Großenhain, Kmehlen, 6.VIII.1959, leg. Reßler (MNHUB); 1♀, Sächsische Schweiz, Papstdorf, VII.1953 (MNHUB).
Spain: 1♀, Gerona, Playa de Aro, 14.V.1977, leg. Ulbrich (SMNS); 1♀, E Burgos, Sierra de la Demanda, S El Rio, 2.VIII.1971, leg. Lohse (MHNG); 1♂, Asturias (DEI); 1♀, Barcelona, Caldetas, leg. Heine (MNHUB).
France: 2♂♂, Pyrenées or., Col de Jau, 1500m, 22.VI.1979, leg. Löbl (MHNG, cAss); 1♀, Hautes Pyrenées, leg. Pandellé (NHMW); 1♂, Lot-et-Garonne, Sos, leg. Bauduer (NHMW); 1♂, 1♀, Bretagne, Morlaix, leg. Hervé (HNHM, NHMW); 1♀, Gironde, Royan, 20.IX.1899 (MHNG); 1♀, Gironde, Facture, 6.VII.1929, leg. Tempère (MHNG); 1♂, Gironde, Gajac, 24.VII.1904 (MHNG); 1♂ [teneral], Cuz [?] aux lac, 7.IX.1927, leg. Tempère (MHNG); 1♀, Poitou, Angoulims (MHNG); 1♂ [with two workers of *Myrmica rubra* attached to the pin], Clermont-Ferrand, Puy-de-Dôme, 14.VII.1949, leg. Bureau (SMNS); 1♂, Pas-de-Calais, Norrent, VI.1922 (MNHUB); 1♀, Saclas near Paris, 30.V.1946 (SMNS); 1♀, NW Paris, Meulan, bois de Verneuil, 26.VI.1955, leg. Bureau (SMNS); 1♀, Longueville-Uscie, bois du Héron, 13.VIII.1951, leg. Bureau (SMNS); 1♂, Landes, Pomarez, 18.V.1963, leg. Tempère (MHNG); 2♀♀, Camargue, 'avec fourmis', 24.III.1926, leg. Puel (NHMB); 1♀, Gard, Colognac, 2.VI.1916 (NHMB); 3♂♂, Avignon, leg. Nicolas (NHMB); 1♀, Ain, Crête [?] du Merle, 1400m, 19.V.1980, leg. Löbl (MHNG); 1♀, Ain, La London, 7.V.1965, leg. Comellini (MHNG); 1♂, Ain, Chèzery, 20.VI.1976, leg. Vit (MHNG); 1♂, Ain, Lent [?], VI.1952, leg. Audras (MHNG); 1♀, Haute Savoie, Annemasse, 11.VI.1960, leg. Besuchet (MHNG); 1♂, Alpes maritimes, Mogneville, IX.1942, leg. Méquignon (MHNG); 1♀, Doubs, Lomont (MHNG); 1♀, 'Gallia', leg. Croissandeau (NHMW). **Locality not identified:** 1♂, Boutaut, 7.X.1891 (MHNG).
Switzerland: Basel: 1♀, Basel, VII.-VIII.1944 (MHNG). **Obwalden:** 1♀, ob. Lungern, moss in mixed forest, 31.VII.1979, leg. Puthz (MHNG). **Solothurn:** 1♂, Hasenmatt, 1450m, 5.VI.1979, leg. Kiener (MHNG). **Fribourg:** 1♂, Estavayer, 1.IV.1959 (MHNG). **Vaud:** 1♂, Lausanne, V.1958 (MHNG); 3♂♂, 2♀♀, Prévondavaux, 2.V.1976, leg. Comellini (MHNG, cAss); 1♂, Buchillon, in dead leaves, 13.V.1954, leg. Besuchet (MHNG); 1♂, St. Sulpice, date illegible, leg. Comellini (MHNG); 1♀, Solalex, 1600m, 16.VIII.1959, leg. Besuchet (MHNG); 1♂, Bavois, V.1973, leg. Toumayeff (cAss). **Genève:** 1♂, Les Bailiets, compost, 29.VII.1988, leg. Besuchet (MHNG); 1♀, Chancy, La Laire, 12.IV.1962 (MHNG); 1♀, Chancy, La Laire, 20.IV.1966, leg. Besuchet (MHNG); 1♀, Aïre: Le Lignon, 26.VII.1963, leg. Besuchet (MHNG); 1♀, Petite-Grave, 11.VII.1988, leg. Besuchet; 1♀, Moulin de Vert, VIII.1984, leg. Toumayeff (MHNG); 1♂, Aliondon, Russin, 15.VI.1958 (MHNG); 1♀, Peney, leg. Tournier (MHNG). **Bern:** 1♀, Court, meadow, pitfall trap, 11.VII.1991 (cWit); 1♂, Bienne, pitfall trap, 22.V.1993 (cWit); 1♂, Bienne, 12.V. (MHNG); 1♂, Aarwangen, V.1968 (MHNG); 1♀, Stockhorn, 1700m, in moss, 26.VII.1979, leg. Besuchet (MHNG); 1♂, Bödeli, Beatenberg, 1250m, 15.VII.1979, leg. Puthz (MHNG). **Valais:** 1♀, Dents du Midi, 1800m, 17.VI.1990, leg. Zerche (DEI); 1♂, Vernayaz, 450m, 12.V.1983, leg. Feller (MNHUB); 1♂, Safanie, 27.VI.1964, leg. Besuchet (MHNG); 1♀, Glacier-Trient, 1400m, 16.V.1974, leg. Besuchet (MHNG); 1♀, Valsorey, 1750m, 26.V.1965, leg. Comellini (MHNG); 1♂, Erde, 11.VII.1979, leg. Besuchet (MHNG); 2♂♂, Les Evouettes, 22.V.1979, leg. Besuchet (MHNG, cAss); 1♂, 2♀♀, Saxon, Le Daillay, 27.V./ 14.VI./ 13.VII.1980, leg. Delarze (MHNG); 1♂, Vionnaz, 11.IV.1989, leg. Besuchet (MHNG); 1♀, Grammont, 2000m, in moss, 30.VI.1989, leg. Besuchet (MHNG); 1♀, Gondo, 900m, VII.1966, leg. Besuchet (MHNG); 1♂, Col de la Forclaz

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(MHNG); 2♂♂, Martigny, 14.IV. & 5.V.1891 (MHNG). **Schwyz:** 1♀ Urmiberg near Seewen (MHNG). **Appenzell:** 1♀, Seealpsee, 26.VII.1967 (MHNG). **Graubünden:** 1♂, Val Poschiavo, Selva, 1500m, in dead leaves, 28.VIII.1983, leg. Besuchet (MHNG); 1♀, Le Prese, 26.VIII.1955, leg. Besuchet (MHNG). **Glarus:** 1♂, 1♀ [the ♀ teneral], Klöntal, Riedern, 700m, in old tree trunk, 30.VIII.1980, leg. Besuchet (MHNG, cAss); 2♂♂, Ennenda, 1.VI.1992, leg. Besuchet (MHNG, cAss). **Ticino:** 1♂, Medeglia, pitfall trap, 9.VII.1992 (cWit); 1♂, Spruga, 1000m, in moss, 22.VII.1983, leg. Besuchet (MHNG); 1♀, Vergeletto, 1000m, in dead leaves, 22.VII.1983, leg. Besuchet (MHNG).

Austria: Vorarlberg: 1♀, Götzis, Klauser Wald, 450m, near stream on meadow, 1.V.1991, leg. Kapp (cKap). **Tirol:** 1♀, Innsbruck, Ahrnwald, in *Alnus* litter, 20.VII.1971, leg. Zschàstak (TLMFI); 1♀, Kitzbühel, leg. Skalitzky (NHMW); 1♂, Blaser, 1200-2000m, 24.VI.1988 (SMNS); 1♂, Nauders, 22.VI.1959 (MHNG). **Osttirol:** 1♀, Matrei, Schöfnerberg, leg. Zschàstak (TLMFI). **Salzburg:** 1♀, Radstädter Tauern, locality illegible (NHMW). **Niederösterreich:** 2♂♂, Rekawinkel, leg. Scheerpeltz (NHMW, cAss); 1♂, 1♀, surroundings of Wien, leg. Hille (NHMW); 1♀, Schneeberg, leg. Hoffmann (NHMW). **Steiermark:** 2♂♂, 2♀♀, Rottenmanner Tauern, leg. Winkler (NHMW); 1♀, Turnau, 1948, leg. Winkler (TLMFI); 1♀, Turnau (NHMW); 1♀, Hochschwab, 1700m, 10.VIII.1918 (NHMB); 1♂, Ameringkogel, leg. Lang (NHMW); 1♀, Eisenerzer Alpen, 4.-8.VI.1922, leg. Käufel (NHMW). **Kärnten:** 1♀, Gurktaler Alpen, St. Lorenzen, bog, 1500m, 19.VII.1986, leg. Wunderle (cWun); 1♂, Gailtaler Alpen, leg. Klimsch (NHMW); 1♀, Karawanken, Petzen, 1891, leg. Ganglbauer (NHMW); 1♀, Karawanken, Koschuta Haus, 1500m, 10.VIII.1985, leg. Wolf (DEI). **Steiermark or Kärnten:** 1♂, Koralpe, 1890, leg. Ganglbauer (NHMW). **Burgenland:** 1♂, Eisenstadt, Leithagebirge, 16.V.1970, leg. Lohse (MHNG); 1♂, Leitha-Gebirge, 8.V.1992, leg. Renner (cRen). **Locality not specified:** 1♀, `Alp. Aust.´, leg. Hoffmann (NHMW).

Italy: Lombardia: 1♂, Iseo (BS), nest of *Talpa*, 26.XI.1973, leg. Osella & Zanetti (cZan); 1♂, 1♀, Passo di Croce Domini, 1800m, litter of *Alnus viridis* and *Rhododendron*, 25.VI.1993, leg. Assing (cAss); 1♂, Brescia, Esine, Valle del Cul, 1700m, in litter of *Alnus viridis*, 11.VII.1980, leg. Kahlen (TLMFI); 1♀, Passo di Vivione, 1800m, litter of *Larix* and *Rhododendron*, 27.VI.1993, leg. Assing (cAss); 3♂♂, 1♀, Oltre il Colle (NHMW); 1♂, Mt. Gigna, leg. Moczarski (NHMW). **Alto Adige/ Trentino:** 1♂, Bressanone, Lago di Varna, 24.VI.1955, leg. Peez (TLMFI); 1♀, Bressanone, garden, 4.V.1959, leg. Peez (TLMFI); 1♀, Passo di Monte Giovo [Jauffenpass], 18.VI.1928, leg. Linke (SMTD); 1♂, Val Pusteria, Tures [Taufers], 9.VII.1976, leg. Freude (SMNS); 1♀, Val d'Ultimo [Ultental], 29.V.1967 (cTer); 1♀, Val di Non (TN), Castelfondo, 1230m, 2.VIII.1982, leg. Zanetti (cZan); 1♂, W Trento, M. Bondone, Cima Palon, NW-slope, 9.V.1978, leg. Kahlen (TLMFI); 3♂♂, Levico (TN), moist woodland, 16.-30.VI./ 16.VII.-2.VIII./ 2.-17.VIII.1989, leg. Perini (cZan, cAss); 1♀, S. Cristoforo (TN), 16.VII.-2.VIII.1989, leg. Perini (cZan); 4♂♂, 2♀♀, Loppio (TN), 5.VI.-6.VII.1990, leg. Perini (cZan); 1♀, P. Lavaze (TN), `Picet. subalp.´, 1.IX.1992 (cZan); 1♂, Riva/Garda, Lago di Loppio, 22.VI.1989, leg. Wunderle (cWun); 1♀, summit of Cima Pari, 1950-1990m, in litter of *Alnus viridis*, 6.VII.1986, leg. Kahlen (TLMFI); 1♂, 1♀, Monte Pari, leg. Feige, Strupi (NHMW, SMTD); 1♀, Monte Pari, 1903, leg. Ganglbauer (NHMW); 1♂, Monte Pari (MNHUB); 1♀, Pieve di Ledro, 10.VII.1908 (DEI). **Emilia - Romagna:** 1♂, Piandelagotti (MO), 29.VII.1915, leg. Fiori (MNHUB). **Toscana:** 1♀, locality illegible, 14.VI.1900 (leg. Fiori (MNHUB). **Locality ambiguous:** 1♂, Mt. Alto (MNHUB).

Italian or Slovenian territory: 1♂, Gorizia, leg. Ludy (NHMW).

Poland: 1♀, Cedynia-Bielinek [Bellinchen], 22.V.1939, leg. Papperitz (SMNS); 1♀, Szczytno [Ortelsburg], 23.V.1937, leg. Folwaczny (SMNS); 1♀, Kołobrzeg [Kolberg], leg. Lass (MNHUB); 1♀, Międzyzdroje [Misdroy], VIII.1911 (MNHUB); 1♂, Międzyzdroje (MNHUB); 1♂, Gdańsk [Danzig], `Haubude´ (MNHUB); 1♂, 1♀, Zalew Wiślany [Frische Nehrung] (MNHUB); 1♂, Baroszyce [Bartenstein] (MNHUB); 1♀, Legnica (SMTD); 1♂, Radom, VII.1895 (ZIN).

Czech Republic: 1♀, Praděd [Altvater], leg. Letzner (DEI); 1♂, Praha, leg. Skalitzky (NHMW); 1♂, Bohemia, Mladá Boleslav [Jungbunzlau], leg. Skalitzky (NHMW); 1♂, Riesengebirge, Johannisbad, leg. Skalitzky (NHMW); 1♀, Moravia, `Paskau´, leg. Reitter (HNHM). **Polish or Czech territory:** 1♀, `Riesengebirge´ (DEI).

Polish or Slovakian territory: 2♂♂, 1♀, Beskidy Zachodnie (DEI, NHMW).

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Slovakia: 1♀, Bratislava (NHMW); 1♂, Trenčin, leg. Steidl (MHNG); 1♂, Hrhov, 7.V.1967, leg. Lohse (MHNG); 1♂, Mala Fatra, Vratna Dolina, 650m, 5.-7.VIII.1980, leg. Uhlig (MNHUB); 1♂, Rožňava [Rosenau], leg. Moczarski (NHMW); 1♂, locality not specified (HNHM).
Hungary: 1♂, 1♀, Budapest, Nagyteteny [?], 25.IV.1982 (HNHM); 1♂, Budapest, 7.VII.1915 (HNHM); 1♀, Budapest, Visegrad (HNHM); 1♂, Budapest surroundings (HNHM); 1♀, Zirc, leg. Lichtneckert (HNHM); 1♂, 2♀♀, Siófok, leg. Lichtneckert (HNHM); 1♂, Pest m., Szigetbecse, 100m, 29.IV.1990, leg. Merkl (HNHM); 1♂, 1♀, Kiskunsági National Park, Dabas, Sári, 17.IV.-12.VI.1979, leg. Ádám & Hámori (HNHM); 1♂, Heves m., Mátraszentimre, Vándor-forrás, 11.V.1980, leg. Ádam & Migály (HNHM); 1♀, Sátoraljaúhely, 10.IX.1880 (HNHM); 1♂, Bükki National Park, Szilvásvárad, Tar-kő, 950m, Aconito-Fagetum, 24.VIII.1981, leg. Ádám (HNHM); 1♀, Bükki N. P., Cserépfalu, Hór-völgy, 250m, Querco petraeae-Carpinetum, 14.III.-11.V.1984, leg. Merkl (HNHM); 1♂, 1♀, 1 ex., Bükki N. P., Miskolc, Lyukas-gerinc, 850m, Aconito-Fagetum, 4.VII.1981, leg. Migály (HNHM, cAss); 1♀, Bükki N. P., Miskolc, Forrás-vögły, 250m, Melittio-Fagetum, 25.VII.1981, leg. Ádám & Hámori (HNHM); 1♀, Bükki N. P., Miskolc, Szentléleki-völgy, 650m, Chaerophylletum aromatici, 7.V.1981, leg. Ádám & Migály (HNHM); 2♂♂, 1♀, Bükki N. P., Nagyvisnyó, Ablakos-kő-völgy, 650m, Phyllitidi-Aceretum, 13.VII.1983, leg. Ádám (HNHM, cAss); 2♂♂, Bükki N. P., Szilvásvárad, Köves-gerinc, 850m, Festuco ovinae-Nardetum, 28.V.1981, 2.VII.1981, leg. Ádám & Hámori (HNHM); 2♂♂, same locality, but Tar-kő, 950m, Aconito-Fagetum, 24.VIII.1981, leg. Ádám (HNHM); 1 ex., Bükki N. P., Varbó, Dobrica, 300m, Querco petraeae-Carpinetum, 1.VII.1981, leg. Ádám & Hámori (HNHM); 2♂♂, Bükki N. P., Bélapátfalva, Ravaszlyuk, 300m, Carici acutiformis-Alnetum, 4.VII.1981, leg. Ádám (HNHM, cAss); 1♂, same locality, 350m, Querco petraeae-Carpinetum, 25.V.1981, leg. Ádám & Migály (HNHM); 1♀, Bükki N. P., Bükkzsérc, Aegopodio-Alnetum, 14.IV.-14.V.1985, leg. Merkl (HNHM); 2♂♂, Bükki N. P. Cserépfalu, Hór-völgy, 250m,k Querco petraeae-Carpinetum, 11.V.-13.VI.1984, leg. Merkl (HNHM); 1♀, Bükki N. P., Felsötárkány, Tar-kő, Seslerio-Fagetum, 13.VII. 1983, leg. Ádám (HNHM); 1♀, Bükki N. P., Felsötárkány, Bánua-hegyeröse, 850m, Atropetum belladonnae, 30.VII.1984, leg. Ádám (HNHM); 1♀, Debrecen, 2.V.1943 (HNHM); 1♀, Aggteleki National Park, Szögliget, Derenk, Cirsio-Festucetum pratensis, 4.V.1988, leg. Merkl (HNHM); 1♀, Aggteleki N. P., Szögliget, Ménes-völgy, Melittidi-Fagetum, 11.V.1987, leg. Merkl (HNHM); 1♀, Aggteleki N. P., Szögliget, Patkós-völgy, Aegopodio-Alnetum subcarpaticum, V.-VIII.1987, leg. Ádám (HNHM); 1♂, 1♀, Aggteleki N. P., Szögliget, Ménes-völgy, Aegopodio-Alnetum subcarpaticum, 9.V.1987, leg. Podlussány (cAss); 2♀♀, Kalocsa, leg. Eppelsheim, Speiser, (HNHM); 1♀, Szeged, leg. Stiller (HNHM); 1♂, Pécs, V.1905, leg. Kaufmann (HNHM); 1♀, Maros, Klárafalva, 22.IV.1964, leg. Endrödy-Younga (HNHM); 1♂, 1♀, Baranya, Mohács, 1902, 1908, leg. Kaufmann (HNHM); 1♀, Mohács (HNHM); 1♀, locality illegible, 12.IV.1936, leg. Kaszab (HNHM).
Slovenia: 3♀♀, Ljubljana, 26.IV./ 1.V./ 2.VI.1917, leg. Staudacher (DEI, TLMFI); 1♂, 1♀, Ljubljana, 1930, leg. Prettner (NHMW).
Croatia: 1♀, Rab Island (NHMW); 2♂♂, Zagreb, leg. Stiller (HNHM, cAss); 1♀, Slavonia, Jurici, 9.-20.VI.1915, leg. Fodor (HNHM); 1♀, 'Croatia', leg. Reitter (HNHM).
Bosnia-Herzegovina: 1♂, Zavidovići (HNHM); 1♀, Sanski Most, 'Achmedbeg' (NHMB); 1♀, locality not specified, 1902, leg. Leonhard (DEI); 1♀, locality not specified, 1901 (MNHUB).
Yugoslavia: 1♀, Montenegro, Ivangrad, 800-1400m, 24.VIII.1978, leg. Chernini (cZan); 1♀, Serbia, Paraćin, 1918, leg. Maertens (MNHUB); 1♂, Serbia, 1879, leg. Merkl (NHMW); 1♀, Serbia, Ruma (NHMB).
Romania: 1♂, SE Botoşani, Baia de Arama, leg. Winkler (MHNG); 1♂, Băile Herculane [Herkulesbad], 15.V.1931 (MNHUB); 1♂, 1♀, Retyezát, Riumare (NHMW); 1♂, W Braşov, Teleki (NHMW); 1♀, Munţii Bucegi [Bucsecs], leg. Diener (HNHM); 2♂♂, 2♀♀, Munţii Parîngu [Hunyad m., Paring], 5.-11.VII.1925, leg. Fodor (HNHM, cAss); 1♂, Borsabánya, Csiszla-v., 21.-27.VII.1941, leg. Kaszab (HNHM); 1♂, Mehadia (HNHM).
Bulgaria: 1♂, Stara planina, Shipka, Usanna-Hütte, 1400-1800m, summer 1935, leg. Schubert (NHMW); 1♀, Pirin planina, Popina Laka, 1200m, 2.VI.1983, leg. Behne (MNHUB); 1♀, 20km E Tolbuchin, Senokos, 4.V.-19.VI.1987, leg. Penev (DEI); 3♂♂, SE Sofiya, Samokov, 1911, leg. Hilf

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(DEI, cAss); 1♂, 1♀, Kalofer VIII, 1912, leg. Hilf (NHMW, cAss); 1♂, Rodopi planina, Pamporovo, 25.VI.1966, leg. Ermisch (cAss); 1♂, Varna, Gündusa-erdö, 17.VI.1956, leg. Balogh (HNHM).
Albania: 1♀, Mali e Tomorit [Tomor-Geb.], leg. Winkler (NHMW).

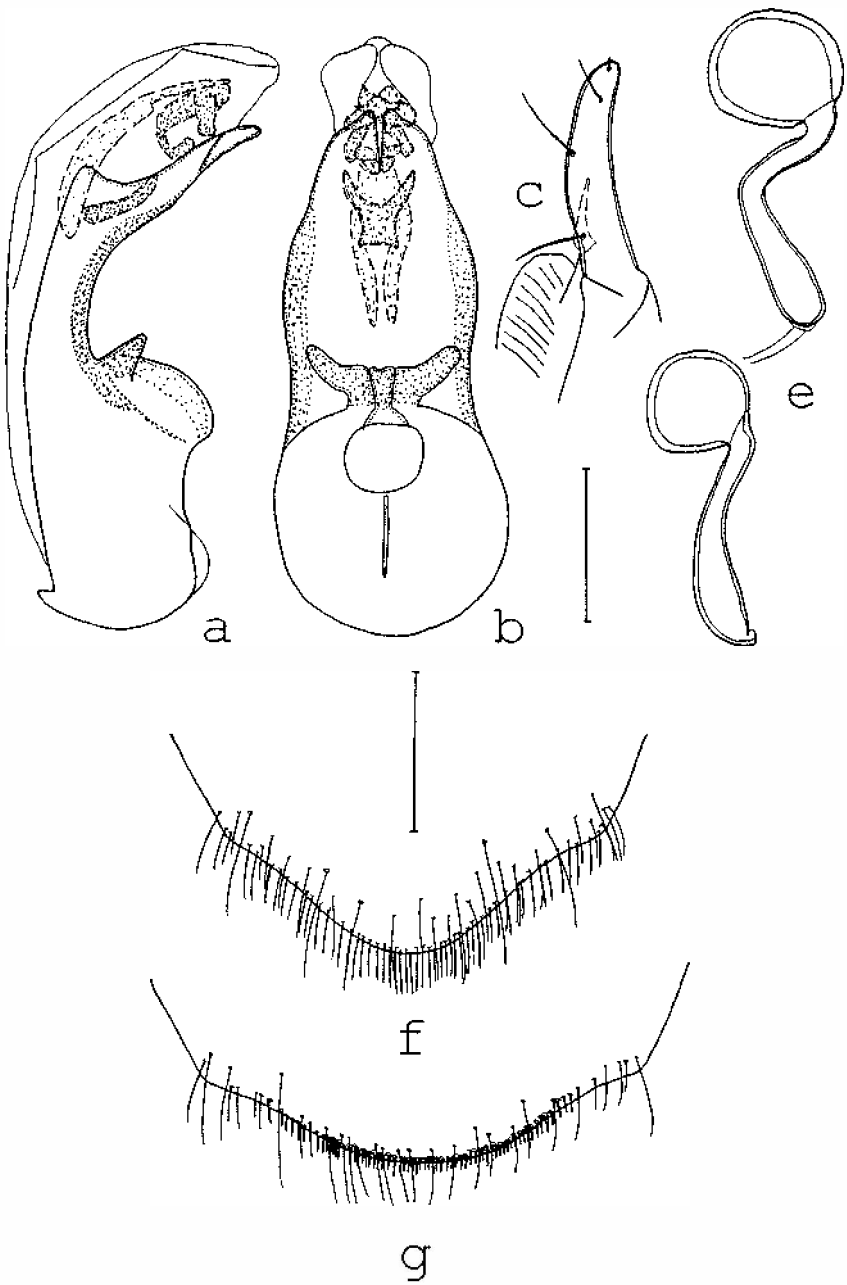
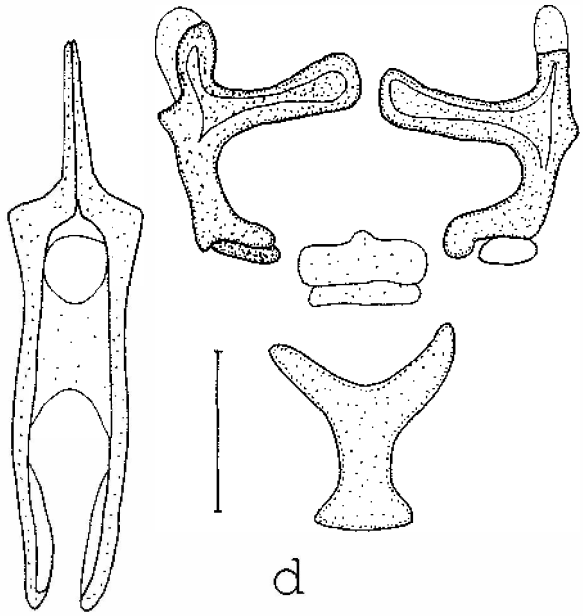


Fig. 2: *Ilyobates nigricollis* (PAYKULL). Median lobe of aedeagus in lateral (**a**) and in ventral view (**b**); apical lobe of paramere (**c**); internal structures of median lobe in ventral view (**d**); spermathecae of 2 ♀♀ (**e**); hind margin of ♂ sternum VIII (**f**); hind margin of ♀ sternum VIII (**g**). Scales: a - c, e - g: 0.2 mm; d: 0.1 mm.

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Russian Federation: 1♂, surroundings of St. Petersburg [? locality not explicitly indicated, but inferred] (ZIN).
Locality not identified, illegible, ambiguous or not indicated: 1♀, leg. P. de Borre (MHNG); 1♀, Zariel[?] (Zaviel?), 6.V.1967, leg. Lohse (MHNG); 2♀♀, Czorba, leg. Leonhard (DEI); 1♀, 'Hungaria', leg. Merkl (HNHM); 1♀, 'Bisch. Lim' (NHMB).



Diagnosis

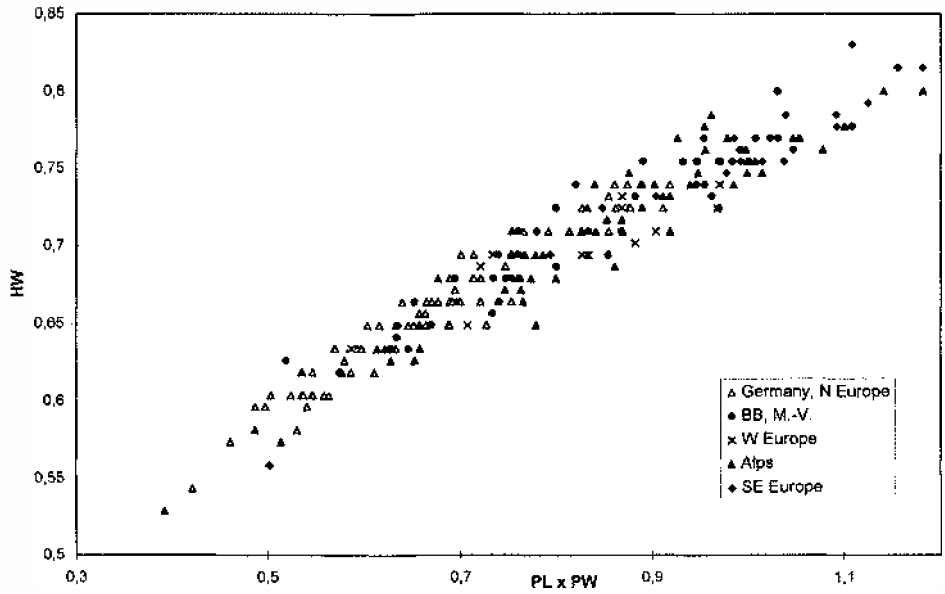
Measurements and ratios (range, arithmetic mean; n = 220): AL: 1.60 - 2.74, 2.25; HW: 0.53 - 0.83, 0.69; PW: 0.65 - 1.12, 0.91; PL: 0.60 - 1.06, 0.85; EL: 0.51 - 0.98, 0.77; HTiL: 0.79 - 1.48, 1.14; HTaL: 0.62 - 1.22, 0.89; HT1L: 0.18 - 0.44, 0.28; HT2L: 0.24 - 0.48, 0.36; ML: 0.60 - 0.97, 0.73; TL: 3.6 - 7.6, 5.6; PW/HW: 1.18 - 1.43, 1.30; PW/PL: 1.01 - 1.18, 1.07; EL/PL: 0.74 - 1.01, 0.90; HTaL/HTiL: 0.71 - 0.85, 0.79; HT1L/HT2L: 0.64 - 0.94, 0.78.
Colour of body very variable, usual coloration: head and pronotum dark brown to black, elytra reddish, abdomen darkened to various degrees with at least the tergal and sternal hind margins and segments VIII - X reddish to brown; mouthparts and antennae ± rufous, legs yellowish to reddish brown; occasionally whole body ± unicoloured reddish.
Head, pronotum and elytra usually with dense and coarse punctation, interstices very narrow, but shining and without microsculpture; occasionally punctation of pronotum less coarse and less dense than on head. Pubescence of pronotum in latero-median areas ± diagonal, but usually directed more caudad than laterad. Eyes moderately convex, in dorsal view slightly shorter than temples. Antennae long and massive, antennomeres IV and V transverse to weakly oblong, VI - X not or only weakly transverse; antennomere XI with usually distinct sexual dimorphism, in ♂ apically constricted, in ♀ without or with very weak apical constriction. Hind wings fully developed.
Abdomen without microsculpture and shining; punctation in transverse tergal impressions coarse and dense, on remainder of tergal surface fine and sparse; pubescence fine, long, and semi-erect; transverse impressions of terga III - IV anteriorly with ± short, those of terga V - VI with longer, but not very pronounced median carina.
♂: sternum VIII posteriorly obtusely pointed (Fig. 2f); aedeagus of very variable size, ventral process laterally dilated in ventral view, internal structures characteristic, pair of apical structures with long processes (Figs 2 a - d).
♀: sternum VIII posteriorly ± distinctly convex (Fig. 2g); spermatheca of somewhat variable shape, with large bulbous capsule and rather long and thin, ± curved duct (Fig. 2e).

Intraspecific variation

All measured size parameters are subject to enormous intraspecific variation. Particularly large specimens were observed in material from eastern Germany, the Alps, the southeast of central Europe, and from southeastern Europe, whereas beetles from western and northern Europe, and from the west of Central Europe were on average smaller (Fig. 3).

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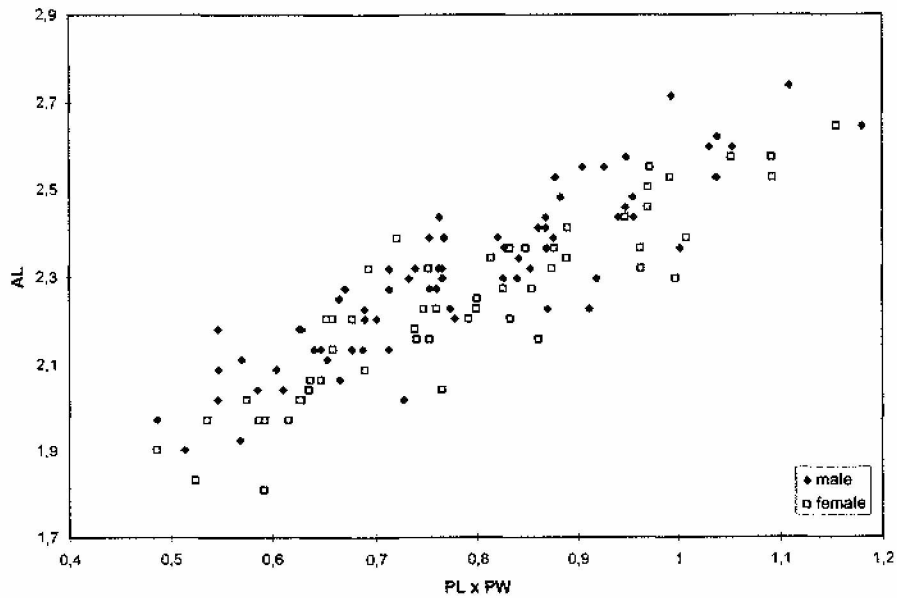


Fig. 3: *Ilyobates nigricollis* (PAYKULL). Variation of head width in relation to pronotum size in material from Northern Europe, Germany (exclusive of Berlin/Brandenburg and Mecklenburg-Vorpommern), Berlin/Brandenburg and Mecklenburg-Vorpommern (BB, M.-V.), Western Europe, the alpine and adjacent regions of Switzerland, northern Italy, Austria, and Slovenia (Alps), and from the southeast of Europe.

Fig. 4: *Ilyobates nigricollis* (PAYKULL). Variation of length of antennae in relation to pronotum size in males and females.

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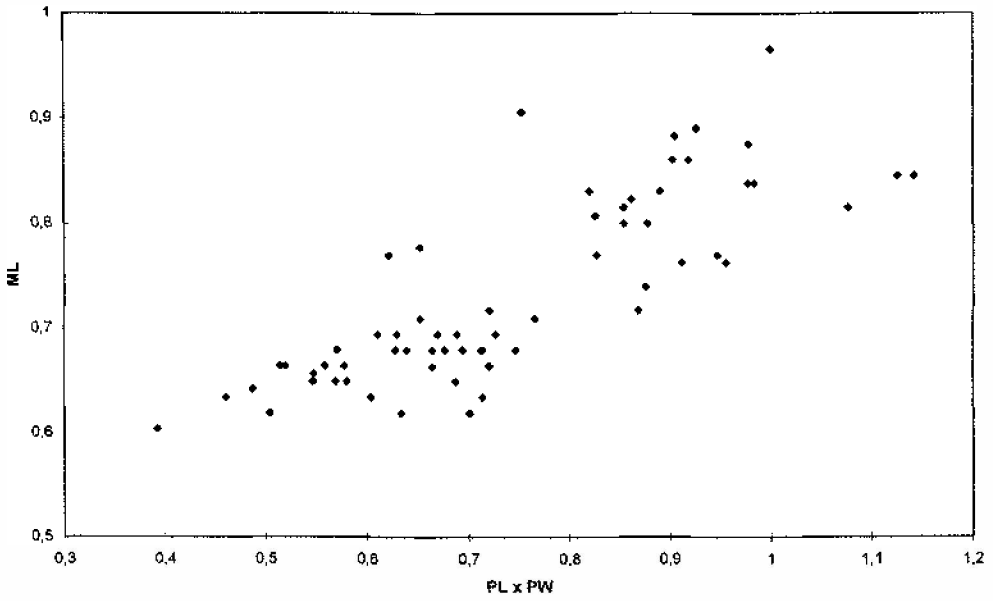


Fig. 5: *Ilyobates nigricollis* (PAYKULL). Variation of the length of the median lobe of the aedeagus in relation to pronotum size.

Except for the Carpathians, size variation was lower and body size almost constantly large in material from the southeast of the area of distribution (Hungary, Croatia, Bosnia-Herzegovina, Bulgaria etc.). On average, specimens from the Carpathians tend to have shorter elytra and a wider pronotum. The highest variation in size and proportions were observed for the absolute and relative lengths of the elytra, metatibia, metatarsi, and the metatarsomeres (Table 1). The antennae tend to be slightly longer in ♂♂ than in ♀♀ (Fig. 4). Size variation of the median lobe of the aedeagus is considerable (Fig. 5, Table 1).

Distribution and bionomics

Since it was only discovered in 1934 that what had been treated as *I. nigricollis* in fact represented two distinct species, literature data on the distribution and ecology of *I. nigricollis* published before that time are here neglected, as they may refer to either of the two species. *I. nigricollis* is widespread in Europe; judging from the known distribution it can be classified as an expansive Pontomediterranean faunal element. In the north and northeast, where it is apparently much rarer than *I. bennetti*, it has been recorded from southern Norway, Sweden north to Jämtland and Medelpad, southern Finland, Karel'skaya Respublika, the surroundings of St. Petersburg, Latvia, Lithuania, and Denmark (HANSEN, 1996; HORION, 1967; PALM, 1935, 1972; SILFVERBERG, 1992; TELNOV et al., 1997; material examined). In the British Isles it is known only from England and Wales and also rarer than *I. bennetti* (HODGE & JONES, 1995; JOHNSON, 1968). In the west and southwest, *I. nigricollis* has been recorded from various localities in France and is here reported for the first time from northern Spain (HORION, 1967; material examined). It is known from all regions in Germany, from most areas in Switzerland, from all of Austria, the Czech Republic, Slovakia, and from Poland (HORION, 1967; JANÁK, 1992; KIENER, 1986; KÖHLER & KLAUSNITZER, 1997; PUTHZ, 1981;

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SMETANA, 1954, 1964b; SMOLEŃSKI, 1996; ŠUSTEK, 1995; WÖRNDLE, 1950; material examined). In Italy, it occurs in most of the north (Lombardia to Friuli - Venezia Giulia) and ranges south to Emilia-Romagna and Toscana; there are no confirmed records from southern Italy (HORION, 1967; LUIGIONI, 1929; OSELLA & ZANETTI, 1974; PEEZ & KAHLEN, 1977; ZANETTI, 1995; material examined). In the southeast and east, the species has been recorded from Slovenia, Hungary, Romania, Croatia, Bosnia-Herzegovina, Yugoslavia, Bulgaria, and Albania (HORION, 1967; IHSSEN, 1935; material examined). HORION (1967) and SMOLEŃSKI (1996) report *I. nigricollis* from the Ukraine (L'vov, Krym), but these records require confirmation; I have seen only *I. bennetti* from there.

I. nigricollis has been collected in a great variety of biotopes and habitats, often together with other congeners (*I. bennetti*, *I. propinquus*, *I. mech*): often in forests (mixed forests, beech, birch, pine etc.), but also in agricultural biotopes (usually in pitfall traps), in various urban biotopes, swamps, bogs, flood-plains, meadows, dry grasslands, heathlands, in leaf litter, moss, *Sphagnum*, under cut grass, in compost and rotting debris, on old fungus, in old tree trunks, and in the Alps up to an altitude of 2000m in litter of *Larix*, *Rhododendron*, *Alnus viridis*, and *Pinus mugo* (ASSING, 1989, 1994; HARTMANN, 1979; IHSSEN, 1934; KACHE & ZUCCHI, 1993; KÖHLER, 1996; KORGE, 1991; LOHSE, 1967; PALM, 1935, 1972; PEEZ & KAHLEN, 1977; PUTHZ, 1981; RENKONEN, 1938; SCHATZ, et al. 1990; SMETANA, 1964b; UHLIG & VOGEL, 1981; WÖRNDLE, 1950; material examined). On several occasions *I. nigricollis* was taken together with ants (*Lasius* spp., *Myrmica* spp., *Formica* spp.) (HORION, 1967; KOCH, 1968; material examined); there is, however, no further evidence of obligatory myrmecophily, and the observed association with ants is apparently accidental. In view of the variety of biotopes and habitats, the relevant ecological factors explaining the occurrence and distribution of *I. nigricollis* remain a mystery.

Adult beetles have been found from April through November (most records from May through August); teneral specimens were observed during the period from July through September. Oviposition takes place in summer; the ovaries of dissected females contained eggs from June through August (ASSING, unpubl.). Although it seems certain that adults overwinter, records from the winter months are almost absent; the single record from November was from a *Talpa* nest (OSELLA & ZANETTI, 1974), which suggests that the adult beetles hibernate in cryptic, subterranean habitats. In a systematic study of the burrows and nests of voles, however, BAUMANN & IRMLER (1979) found two specimens in summer, but none during the winter.

4.2. *Ilyobates bennetti* DONISTHORPE, 1914

Figs 6 - 9, Table 1

Ilyobates bennetti DONISHORPE, 1914: 137.
Ilyobates subopacus PALM, 1935: 43ff.; HAMMOND (in prep.)
Ilyobates nigricollis: IHSSEN (1934, 1935, 1937); SCHEERPELTZ (1947)

Types examined

Ilyobates bennetti DONISHORPE: Holotype ♂ [dissected prior to present study, aedeagus missing]: Ilyobates bennetti [handwritten behind specimen]/ Holotype [curator label]/ H. Donisthorpe B.M. 1934-4. (BMNH).

In the original description, which is explicitly based on a single specimen collected together with *Lasius fuliginosus*, DONISTHORPE (1914) compares the holotype with "*I. nigricollis*" stating that the new species is distinguished by a shorter antennomere XI, different pubescence and punctation, the different shape of the pronotum and elytra, and especially by shorter and stouter maxillary and labial palpi. An examination of the holotype showed,

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however, that regarding all these characters, it is well within the range of intraspecific variation of what has so far been treated as *I. subopacus* (see also measurements and remarks on intraspecific variation below). Unfortunately, the aedeagus is lost, but the external morphology of the holotype of *I. bennetti* leaves no doubt that *I. bennetti* and *I. subopacus* are conspecific. According to a manuscript kindly made available to me, HAMMOND (in prep.) arrives at the same conclusion.

Ilyobates subopacus PALM: Lectotype ♂, present designation: ♂/ Bhl. Orust, 12/7 28, T. Palm/ Typus/ subopacus Palm/ Naturhistoriska Riksmuseet Stockholm, Loan no 838/98/ Lectotypus Ilyobates subopacus Palm, desig. V. Assing 1998 (NHRM). Paralectotypes, here designated and labelled accordingly: 1♀, same data as LT, but labelled 'Allotypus' (NHRM); 1♀: Orust, Bhl./ Paratypus (ZML); 1♂, Bhl. Nösund/ Paratypus (ZML); 1♂: Hlm. [according to original description: Uppland]/ Ths. (NHRM); 1♂: Sc [according to original description: Skåne], Stehag. (NHRM); 1♀: Sc/ Bhm. (NHRM); 2♂♂, 1♀: Sc. Skg. V.85 (ZML); 1♂, 2♀♀: Sc. Skg. IV.85 (ZML); 1♀: Scania, Stehag, IV.85 (ZML); 1♂: Scania, Stehag, V.85 (ZML); 2♂♂, 1♀: without locality labels (ZML); 2♂♂: Vg. Mösseberg, 26/5 25, Lohm. (ZML); 1♂: Öl. Ottenby, 20/5 1924 (ZML); 1♀: Kullaberg, 23/5 (ZML); 1♂: Sk. Söderåsen, 8/6, Lohmander (ZML); 1♂, 1♀, 1 ex.: Skåne (ZML).
The original description is based on numerous syntypes from various collections (PALM, 1935). In view of frequent misidentifications and previous confusion of *I. bennetti* and *I. nigricollis* and their synonyms, a lectotype designation was deemed appropriate. A male in good condition and collected by PALM himself was selected as lectotype.

Additional material examined

Sweden: 5♂♂, 2♀♀, S Göteborg, Mölndal, leg. Ericson (NHMW); 2♂♂, Värmland, 29.VI.-14.VIII.1979 (MHNG); 2♂♂, 3♀♀, 'südl. Schweden', leg. Münster (NHMW, cAss); 3♂♂, locality not specified (DEI, NHMW).
Finland: 2♀♀, Vammeljoki, 15.&17.VI.1923, leg. Krogerus (MNHUB).
Latvia: 2♀♀, Liepāja [Liebau] (SMTD).
Denmark: 1♀, Sjælland, 29.VII.1987 (MHNG); 1♂, Sjælland, 3.VIII.1909 (NMHW).
Germany: Schleswig-Holstein: 1♂, Niendorf, 7.V.1964 (TLMFI); 1♂, Kiel, leg. Tischler (MHNG); 1♂, 1♀, Geesthacht, 17.IV.1880 & 12.VI.1897 (DEI). **Hamburg:** 1♂, 1♀, Wilhelmsburg, 19.IV.1867 (DEI); 1♀, Bergedorf, 23.V.1895 (DEI). **Niedersachsen:** approximately 500 ex. (cAss, if not indicated otherwise) from the following localities: Hannover (various urban localities), Langenhagen (NW Hannover), Ortsberg (near Alfeld/Leine), Wernershöhe (near Alfeld/L.), Ahnsen (near Bückeburg), Bad Eilsen (near Bückeburg), Stadthagen (W Hannover), Großenwieden (near Hameln), Düt (near Hameln), Öselberg (near Wolfenbüttel), Wendhausen (near Braunschweig); Solling (MHNG); Göttingen (MHNG); Oldenburg, Schwanenteich (cRos). **Nordrhein-Westfalen:** 1♂, 1♀, Elsdorf, 1985, leg. Siede (cWun); 1♂, 2♀♀, N Hamm, Drensteinfurt, 16.-20.VI.1986 (cTer); 1♀ [teneral], Münster Wolbeck, Tiergarten, 14.IX.1991, leg. Köhler (cKöh); 2♂♂, 2♀♀, Münster, Gittrup/Ems, 12.V.1990, leg. Terlutter (cTer); 1♀, Ostwestfalen-Lippe, Herford, Langenberg, 50-100m, 10.V.1969, leg. Rothe (cRen); 1♀, Godelheim, Weser bank, 25.V.1991, leg. Terlutter (cTer); 1♂, NW Köln, Worringer Bruch, 20.VI.1986, leg. Wunderle (cWun); 1♀, Worringer Bruch, 16.VIII., leg. Köhler (cKöh); 2♀♀ [1♀ teneral], same data, but 2.IX.1989 (cKöh); 1♀, Bornheim, Hemmerich, garden, 20.VII.1994, leg. Köhler (cKöh); 1♂ [teneral], Mönchengladbach, Depot Hehn, 21.VIII.1989, leg. Fritz (cKöh). 1♀, S Köln, Weilerswist, 11.VI.1982, leg. Boneß (cRen); 1♂, W Bonn, Zülpich, 9.V.1979, leg. Boneß (cRen); 1♂, Düsseldorf, Meererbusch, leg. Ermisch (SMTD); 1♀, Düsseldorf, Schwarzbachgraben, VIII.1987, leg. Terlutter (cTer); 1♀ [teneral], Eifel, Euskirchen, Kirchheim, leg. Fritz, 13.VIII.1988, leg. Fritz (cKöh); 2♂♂, 1♀, same data, but 8.VI., 26.VI. & 24.VII.1988 (cKöh). **Rheinland-Pfalz:** 1♂, Südeifel, Cochem, Alfbach near Bengel, 21.V.1994, leg. Köhler (cKöh); 1♂, Nahetal, Staudernheim, Naheauen, 19.V.

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1986, leg. Wunderle (cWun); 1♂, Nahe, Heinzenberg, Kellenbachtal, 9.V.1988, leg. Wunderle (cWun); 1♂, Winningen, V.1937 (SMTD); 4♂♂, 6♀♀ [1♀ with worker of *Lasius platythorax* attached to the pin], Ludwigshafen, 15.V.1917, leg. Ihssen (MNHUB); 2♂♂, Dürkheim, Saline (NHMW); 1♂, 3♀♀, Grünstadt, Neuleiningen, field, 1993, leg Köhler & Fritz (cKöh); 1♂ [teneral], Andernach, Kruft, Korretsberg, 4.VI.1994 (cKöh); 1♂, Speyer, XI.1882, leg. Hammon (NHMW); 1♂, 1♀, Ingelheim, Neumühle, field, 1993, leg. Köhler & Fritz (cKöh); 1♀, Rockenhausen (NHMW); 1♀, Rheinhessen, Essenheim, 25.IV.1977, leg. Schawaller (SMNS). **Baden-Württemberg:** 1♀, Überlingen/Bodensee, 14.VI.1963, leg. Horion (MHNG); 1♀, Schwäbische Alb, Schmiechen, 22.IX.1968, leg. Schrepfer (SMNS); 1♂, Tiengen near Freiburg, 200m, 7.V.1972, leg. Pankow (SMNS); 1♂, Oedheim near Heilbronn, pitfall trap on arable land, 21.V.-18.VI.1986 (SMNS); 1♂, 4♀♀, Mannheim, 15.V.1917 (NHMB, SMNS). **Bayern:** 1♀, München, Isartal, inundation, 8.VI.1936, leg. Frey (NHMB); 2♂♂, Eschenlohe, Murnau, 3.VIII.1937, 22.VI.1965, leg. Ihssen (MNHUB); 1♀, Pfarrkirchen, 'Anspülicht', leg. Stöcklein (NHMB); 2♂♂, 2♀♀, Vilshofen, 26.VI.1920, 31.V. & 13.VI.1921, 4.IV.1924, leg. Stöcklein (NHMB); 1♀, Plattling, 15.VII.1918, leg. Stöcklein (NHMB); 1♂, locality and date illegible, leg. Stöcklein (NHMB). **Hessen:** 1♀, Hofgeismar, 20.IV.1931 (SMNS); 4♂♂, 2♀♀, Wiesbaden, grassland, pitfall trap, V.1985, leg. Steinarz (cWun); 1♂, Bad Nauheim (DEI); 2♂♂, 1♀, Frankfurt, coll. Heyden, Kraatz (DEI). **Mecklenburg-Vorpommern:** 1♂, Plau, Pötzenhöhe, near pond, 5.VIII.1977, leg. Uhlig (MNHUB); 1♂, Neubrandenburg, Tollensee, Wustrow, 2.VI.1983, leg. Bringmann (MNHUB). **Berlin/Brandenburg:** 1♂, Berlin, Karow, Wotanstr., VI.1992, leg. Schwartz (cSch); 1♀ [teneral], Berlin, Pankow, Zingerwiesen, 20.VIII.-3.IX.1996 (cSch); 1♂, 1♀, Berlin, Schildow-Siedlung, 4.VI.1972, leg. Hieke (MNHUB); 2♀♀, Berlin, locality not specified (DEI, MNHUB); 1♀, Potsdam, Großbeeren, 14.VI.1986, leg. Arnold (MNHUB); 3♀♀, Finkenkrug, 4.VI.1912 (MNHUB); 1♀, Finkenkrug, 2.V.1920, leg John (MNHUB); 2♀♀, Brieselang (DEI, MNHUB); 1♂, Bernau (DEI); 1♂, 1♀, Wildpark Golm (DEI); 1♀, Berlin, Friedrichshagen (MNHUB); 1♀, Berlin, Müggelsee (MNHUB); 1♀, Hönow (DEI); 2♂♂, Landkreis Havelland, N Linum, *Alnus-Betula* woodland, 1.V.1998, leg. Schülke (cSch); 1♂, Storkow, NSG Salzstelle bei Philadelphia, straw and nest of *Talpa*, 24.III.1984, leg. Schülke (MNHUB); 7♂♂, 4♀♀, Deetz, 22km WNWW Potsdam, reed, grassland, pitfall, 28.V.-16.VI.1992 [5♂♂, 3♀♀], 26.VI.-23.VII. [2♂♂], 27.VIII.-22.IX. [1♀], leg. Plötner & Uhlig (MNHUB); 1♂, 1♀, Cottbus, Leipe near Lübbenau, Erlenbruchwald, 17.V.1985, leg. Uhlig (MNHUB); 1♀, Buckow (NHMB). **Sachsen-Anhalt:** 1♂, 1♀, S Halle, Dörstewitz, field, 30.V.1996, leg. Sprick (cAss); 2♂♂, 1♀, Schönhauser Damm, Trübenbruch, pitfall trap, V.1998, leg. Sprick (cAss); 1♀, Dübener Heide, Doberschütz, 1.V.1950, leg. Linke (SMTD); 1♀, Merseburg, Wallendorf, leg. Ermisch (SMTD); 2♀♀, Thale/Harz, 18.VI. & 9.VII.1935, leg. Fehse (DEI); 1♂, Thale, 28.V.1933, leg. Fehse (MNHUB); 1♂, Thale/Harz, leg. Heidenreich (SMTD); 2♂♂, 1♀, Thale, 5.VI.1932, leg. Fehse (SMTD); 1♀, Thale, Waldkaterfenster, 16.VII.1955, leg. Dorn (MNHUB); 1♀, Thale, 30.VI.1942 (MNHUB); 1♀, Gohrau (SMTD); 1♂, 2♀♀, Naumburg, 16.V.1934, leg. Maertens (MNHUB); 1♀, Naumburg, garden, 23.VI.1922, leg. Maertens (MNHUB); 1♀, Naumburg, Rödel, 17.V.1928, leg. Maertens (MNHUB); 1♂, Naumburg, Laasen, 2.V.1925, leg. Maertens (MNHUB); 1♂, Naumburg, Schellsitzer Teiche, 11.VI. 1928, leg. Maertens (MNHUB); 1♀, Naumburg, leg. Maertens (NHMW). **Thüringen:** 1♂, Erfurt, Kelbra, 4.VI.1983, leg. Schnitter (DEI); 1♀, Buchholz, 27.V.1908, leg. Petry (MNHUB); 2♀♀, Wormsleben near Mansfeld, 3.V.&4.VI.1918, leg. Feige (SMTD); 1♀, Jena, leg. Seymer (MNHUB). **Sachsen:** 1♂, Leipzig, field, 17.V.-8.VII.1995, leg. Sprick (cAss); 1♂, Leipzig, 25.VII.1981, leg. Strzelczyk (DEI); 5♂♂, 4♀♀, Leipzig, leg. Linke (HNHM, NHMB, NHMW, SNMS); 9♂♂, 12♀♀, Leipzig, K. F., 30.V.1909, leg. Linke (DEI, MHNG, SMTD); 2♂♂, 4♀♀, Leipzig, Schkeuditz, 17.V.1903, 14.V.1935, 4.VII.1942, 16.&26.V.1948, leg. Linke (SMTD); 1♀, Leipzig, Dölzig, 12.III.1911, leg. Linke (SMTD); 1♀, Leipzig, Stötteritz, 12.VIII.1956, leg. Linke (SMTD); 1♀, Leipzig, Wallendorf, 2.V.1937, leg. Linke (SMTD); 2♀♀, Leipzig, Großteinberg, 26.V.1922 & 26.V.1940, leg. Linke (SMTD); 1♀, Leipzig, Grim., 13.VI.1909, leg. Linke (SMTD); 1♂, Leipzig, locality illegible, 22.VI.1914, leg. Linke (SMTD); 3♂♂, 3♀♀, Leipzig, Wah., 2.VI.1907, leg. Linke (SMTD); 1♀, Leipzig, Zeitig, 19.V.1902, leg. Linke (SMTD); 1♀, Leipzig, Kämm. Forst, 29.V.1924, leg. Linke (SMTD); 1♂, 2♀♀, Leipzig, S. Garten, 15.V.1912, leg. Linke (SMTD); 1♀, Leipzig, Gasch. 18.III.1906,

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leg. Linke (SMTD); 1♂, Leipzig, Dobersch., 5.V.1918, leg. Linke (SMTD); 7♀♀, Leipzig, Eilenburg, 16.VIII.1908, 8.X.1922, 20.VI.1926, 24.VII.1957, 6.&9.VII.1958, leg. Linke (SMTD); 14♂♂, 28♀♀, Leipzig, Probstheida, 1944, 1955-56, leg. Dorn [1944: 1♀, 21.VI. - 1955: 1♂, 26.V.; 1♂, 30.V.; 2♂♂, 1♀, 10.VI.; 1♀, 20.VI.; 1♀, 20.VII.; 1♀, 12.VIII.; 1♀, 24.VIII.; 1♂ [teneral], 3.IX.; 1♀, 13.IX. - 1956: 1♂, 1♀, 20.V.; 2♂♂, 2♀♀, 25.V.19; 1♂, 1♀, 4.VI.; 2♀♀, 13.VI.; 1♀, 24.VII.; 1♂, 29.VII.; 1♀, 3.VIII.; 1♂, 2♀♀, 8.VIII.; 1♀, 17.VIII.; 1♀, 27.VIII.; 1♀, 7.IX.; 2♀♀, 12.IX.; 1♀, 17.IX.; 3♂♂, 5♀♀, 27.IX.] (MNHUB); 1♀, Leipzig, Elsterflutbett, 11.VII.1954, leg. Dorn (MNHUB); 1♀, Leipzig, Connewitzer Holz, 16.V.1953, leg. Dorn (MNHUB); 1♀, Leipzig, coll. Kraatz (DEI); 1♀, Wechselburg, 12.V.1974, leg. Zerche (DEI); 1♂, Oberlausitz, Teichgebiet Daubitz, haycock, 23.IV.1994, leg. Schülke (cSch); 1♀, Erzgebirge, Grünstadt, 18.V.1967, leg. Uhlig (MNHUB); 1♀, Vogtland, Plotertal, with ants (SMTD); 1♂, `Sachsen', leg. Märkel (NHMW). **Locality ambiguous, not specified, or not identified:** 1♀, `Germania' (SMTD); 1♀, Siegmünden, 23.VI.1935 (SMTD); 1♀, `Rhenania' (ZIN); 1♂, `Germ' (ZIN).
France: 1♀, Nièvre, Brassy, VII.1903, leg. Méquignon (MHNG); 1♂, E Paris, Sucy en Brie, leg. Méquignon (MHNG); 1♂, Alsace, Fouchy, `avec fourmis', 26.VI.1879 (MHNG). Locality not identified: 1♂, Livzy [Sivzy?], VII.1917 (MHNG); 1♂, F. de Carnelle, 14.V.1901, leg. Seto (MHNG).
Switzerland: Aargau: 4♂♂, Kepers, barley field, 1.V.1987 (cWit). **Schwyz:** 1♂, Ibach, VIII.1959 (MHNG). **Vaud:** 1♂, Boussens, V.1952, leg. Besuchet (MHNG).
Austria: Vorarlberg: 1♂, Rankweil, Weitried, Frutz-Au, 430m, debris near inundation, 18.VI.1991, leg. Kapp (cKap). **Tirol:** 1♂, Hall, Absam, under rotten pumpkin, 20.IX.1964, leg. Kahlen (TLMFI); 2♀♀, Schwaz, 17.VI.1951, leg. Kofler (TLMFI). **Oberösterreich:** 1♀, Lunz, leg. Ganglbauer (NHMW); 1♂, Linz, leg. Priesner (NHMW). **Niederösterreich:** 1♂, Purgstall, 10.VII.1968, leg. Ressl (MHNG); 1♀, Purgstall, garden, 29.VII.1970, leg. Ressl (MHNG); 3♂♂, 2♀♀, Donauauen, leg. Breit (NHMW, cAss); 1♀, Wien, Donauauen (NHMW); 1♀, Wien, Donau inundation (NHMW); 1♀, Klosterneu, leg. Scheerpeltz (NHMW); 1♀, Stockerau, Donauauen, leg. Bernhauer (NHMW); 1♀, Moosbrunn (NHMW); 1♀, Pressbaum (NHMW); 2♂♂, 3♀♀, Greifenstein, leg. Curti (MHNG, NHMW); 1♀, Sollenau, 6.I.1955, leg. Malicky (MHNG); 1♂, Wien (NHMW); 2♂♂, 6♀♀, surroundings of Wien, leg. Haberditz, Moczarski (NHMW). **Steiermark:** 1♀, Ehrenhausen, leg. Haberditz (NHMW); 1♀, Gams, leg. Scheerpeltz (NHMW). **Kärnten:** 2♂♂, 1♀, Kleblach, leg. Meschnigg (NHMW); 1♀, Koralpe, leg. Klimsch (NHMW). **Locality not specified:** 1♂, 1♀, `Austria' (ZIN).
Italy: Trentino: 1♂, Pinzolo (TN) (NHMW).
Poland: 1♂, Bytom Odrzański [Beuthen], 30.V.1927 (SMNS); 1♀, Kraków, 29.V.1908 (NHMB).
Polish or Czech territory: 1♀, `Riesengebirge' (MNHUB).
Czech Republic: 1♀, Bohemia, Neratovice, leg. Hanzlig (cKap); 4♀♀, Moravia (DEI, MHNG); 1♀, Moravia, Prostějov [Prossnitz], leg. Zoufal (NHMW); 1♂, Praděd [Altvater], leg. Letzner (DEI); 1♂, Okoll Prahy (MNHUB); 1♂, 1♀, S Ostrava, `Paskau', leg. Graf (MNHUB); 2♂♂, 3♀♀, `Paskau', leg. Reitter (HNHM, SMNS); 1♀, `Moravia', leg. Reitter (HNHM).
Hungary: 1♂, Neusiedlersee (NHMW); 1♂, 2♀♀, Budapest, Budai hegys (HNHM, cAss); 1♂, 1 ex., Kiskunsági National Park, Tabdi, VII.-IX.1978, leg. Hámori (HNHM); 1♀, Tabdi, 4.IV.-11.V.1977, leg. Ádám & Hámori (HNHM); 4♂♂, same data, but 11.V.-3.VIII.1977 (HNHM); 2♂♂, 2♀♀, same data, but 3.VIII.-5.IX.1977 (HNHM); 2♂♂, 1♀, same data, but 5.IX.-25.X.1977 (HNHM); 3♂♂, 2♀♀, Tabdi, 9.V.-30.VI.1977, leg. Ádám (HNHM); 1♂, 2♀♀, Tabdi, 27.V.1950, leg. Kaszab (HNHM); 1♀, S Budapest, Ócsa, Nagyerdö, 18.VI.1953, leg. Zsirkó (HNHM); 2♀♀, S Budapest, Kiskunsági National Park, Ócsa, Madencia-erdö, V.-IX.1978, leg. Hámori (HNHM); 1♂, 3♀♀, same locality, 3.IV.-9.V.1977, leg. Ádám & Hámori (HNHM); 2♂♂, 1♀, same data, but 9.V.-1.VIII.1977 (HNHM); 1♂, Kiskunsági N. P., Dabas, Sári, 9.V.-1.VIII.1977, leg. Hámori (HNHM); 5♂♂, same data, but 18.III.-12.V.1978 (HNHM, cAss); 4♂♂, same locality, 17.IV.-12.VI.1979, leg. Ádám & Hámori (HNHM); 1♂, 1♀, Kiskunsági N. P., Kiskörös, 11.VII.-7.VIII.1978, leg. Tóth (HNHM); 8♂♂, 4♀♀, same data, but 26.IV.-1.VI.1978 (HNHM); 12♂♂, 1♀, same data, but 1.VI.-10.VII.1978 (HNHM); 1♂, 5♀♀, same data, but 11.VII.-7.VIII.1978 (HNHM); 5♂♂, 4♀♀, 1 ex., same data, but 7.VIII.-5.X.1978 (HNHM); 1♀, Siófok, leg. Lichtneckert (HNHM); 1♂, Hegyalja, 9.VII.1955, leg. Erdös (cAss); 2♀♀, Baranya, Pécs [Fünfkirchen] (NHMW); 1♀, Baranya, Harkány, leg. Stiller (HNHM); 1♂, Hortobágy National Park, Püspö-

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kladány, 12.VII.1976, leg. Hámori (HNHM); 2♀♀ [1 teneral], same data, but 26.VIII.1976 (HNHM); 1♂, Hortobágy N. P., Hortobágy-Máta, 26.VIII.1976, leg. Hámori (HNHM); 1♀, Hortobágy N. P., Nagylván, 9.V.-11.VI.1974, leg. Kaszab (HNHM); 1♂, 1♀, Hortobágy N. P., Újszentmargita, 16.VII. 1974, leg. Kaszab (HNHM); 2♂♂, 2♀♀, same data, but 9.V.-11.VI.1974 (HNHM); 1♂, same data, but 11.VI.1974 (HNHM); 1♂, 1♀, same data, but 18.-19.VI.1976 (HNHM); 2♂♂, same locality, 9.V.-11.VI.1974, leg. Hámori (HNHM, cAss); 1♂, Nyírség, Batorliget, 8.-15.VI.1949 (HNHM); 1♂, 1♀, Békés m., Sarkad, 90m, Festuco pseudovinae-Quercetum, 13.XI.1982, leg. Ádám (HNHM); 1♂, same data, but 25.VI.1983 (HNHM); 1♂, 1♀, Békés m., Gerla, 90m, Festuco pseudovinae-Quercetum, 25.VI.1983, leg. Ádám (HNHM).

Romania: 1♂, Munţii Bihor, Petroasa, Varasoaea, VI.1922, leg. Jeannel & Winkler (NHMW); 1♂, Munţii Bihor, 14.III.1926, leg. Stöcklein (cAss); 1♂, Turnu Roşu Pass [`Roter Turm-Pass'], 26.V.1910, leg. Pinker (DEI); 1♂, mountains near Braşov [`Kronstädter Gebirge'], leg. Deubel (MNHUB); 1♀, SW Braşov, `Rosenauer Gebirge', leg. Deubel (NHMW); 1♂, Mehadia (NHMW); 1♀, S Bucuresti, Comana vlasca, leg. Gassner (NHMW).

Bosnia-Herzegovina: 2♀♀, Sarajevo, leg. Apfelbeck (NHMNB); 2♀♀, Ilidža, 1902, leg. Apfelbeck (NHMB).

Yugoslavia: 1♀, Fruška gora, 1933 (NHMB).

Bulgaria: 1♂, Kalofer VIII, 1912, leg. Hilf (DEI); 1♂, Nesebâr, Sl. Brjag, 7.V.1985, leg. Jaeger (MNHUB); 1♀, Stara planina, Kodscha, 1879, leg. Merkl (NHMW); 1♀, Stara planina, 8 km N Kalofer, 800m, 22.VI.1989, leg. Zerche & Behne (DEI).

Turkey: Thrace: 2♂♂, 6♀♀ [3 ex. teneral], Kirklareli, Demirköy, 31.VII.1969, leg. Besuchet (MHNG, cAss).

Caucasus region: 1♂, Krasnodar prov., Krasnyi, Les, 10 km S of vill. Oktabrskyi, forest litter, 6.V.1995, leg. Solodovnikov (cSol); 2♂♂, Cherkesskaya, Teberda, `*nigricollis* ssp. *caucasicus* IHSSEN' (MNHUB); 1♂, `Circassien', leg. Rost (cAss); 1♀, locality not specified, leg. Schneider (SMTD); 1♂, Ardon station near Vladikavkaz, 18.-19.V.1900, leg. Demokidov (ZIN); 1♀, surroundings of Vladikavkaz, 5.IV.1886, leg. Ananov (ZIN).

Russian Federation: 1♂, St. Petersburg area, Peterghoff, 25.VI.1935, leg. Kirschenblatt (ZIN); 1♀, Moscow prov., Pushino-na-Oke, bank of forest pool, 27.VI.1996, leg. Sodovnikov (cSol); 1♀, Moscow, township, botanical garden, 8.VIII.1990, leg. Fritz (cKöh).

Ukraine: 3♂♂, 3♀♀, Bukovina, Chernovtsy (NHMW, cAss); 1♂, 4♀♀, Krym, Iaila mts., leg. Moczarski, Winkler (NHMW, SMNS, cAss).

Canada: 1♀, Quebec, Ste. Clothilde, 2.VI.1981, leg. Boivin (CNC); 1♀, Frai, Frelighsburg, 11.VI.1984, leg. Bostanian (CNC).

Locality not specified or illegible: 4 ex., `Scan' (MNHUB); 1♂, Rurna[?], leg. Hensch (NHMB); 1♀ (NHMB).

Diagnosis

Measurements and ratios (range, arithmetic mean; n = 263): AL: 1.36 - 2.12, 1.79; HW: 0.46 - 0.71, 0.57; PW: 0.54 - 0.92, 0.70; PL: 0.50 - 0.88, 0.67; EL: 0.41 - 0.80, 0.59; HTiL: 0.62 - 1.15, 0.87; HTaL: 0.47 - 0.85, 0.64; HT1L: 0.12 - 0. 27, 0.19; HT2L: 0.20 - 0.35, 0.26; ML: 0.45 - 0.74, 0.56; TL: 3.0 - 6.8, 4.4; PW/HW: 1.11 - 1.39, 1.22; PW/PL: 0.99 - 1.15, 1.05; EL/PL: 0.79 - 1.06, 0.89; HTaL/HTiL: 0.66 - 0.96, 0.76; HT1L/HT2L: 0.50 - 0.88, 0.72.

In external morphology highly similar to *I. nigricollis*. Colour of body similar to *I. nigricollis*, also very variable. Body on average smaller, but size subject to considerable intraspecific variation; antennae (Fig. 1e) of variable length, but usually somewhat shorter than in *I. nigricollis* (cf. measurements); sexual dimorphism of antennomere XI as in *I. nigricollis*.

Head, pronotum and elytra with on average denser and coarser punctation, and therefore with less shine; pronotum on average relatively narrower (cf. ratios PW/HW); hind wings fully developed.

Abdomen with punctation, pubescence and carinae as in *I. nigricollis*.

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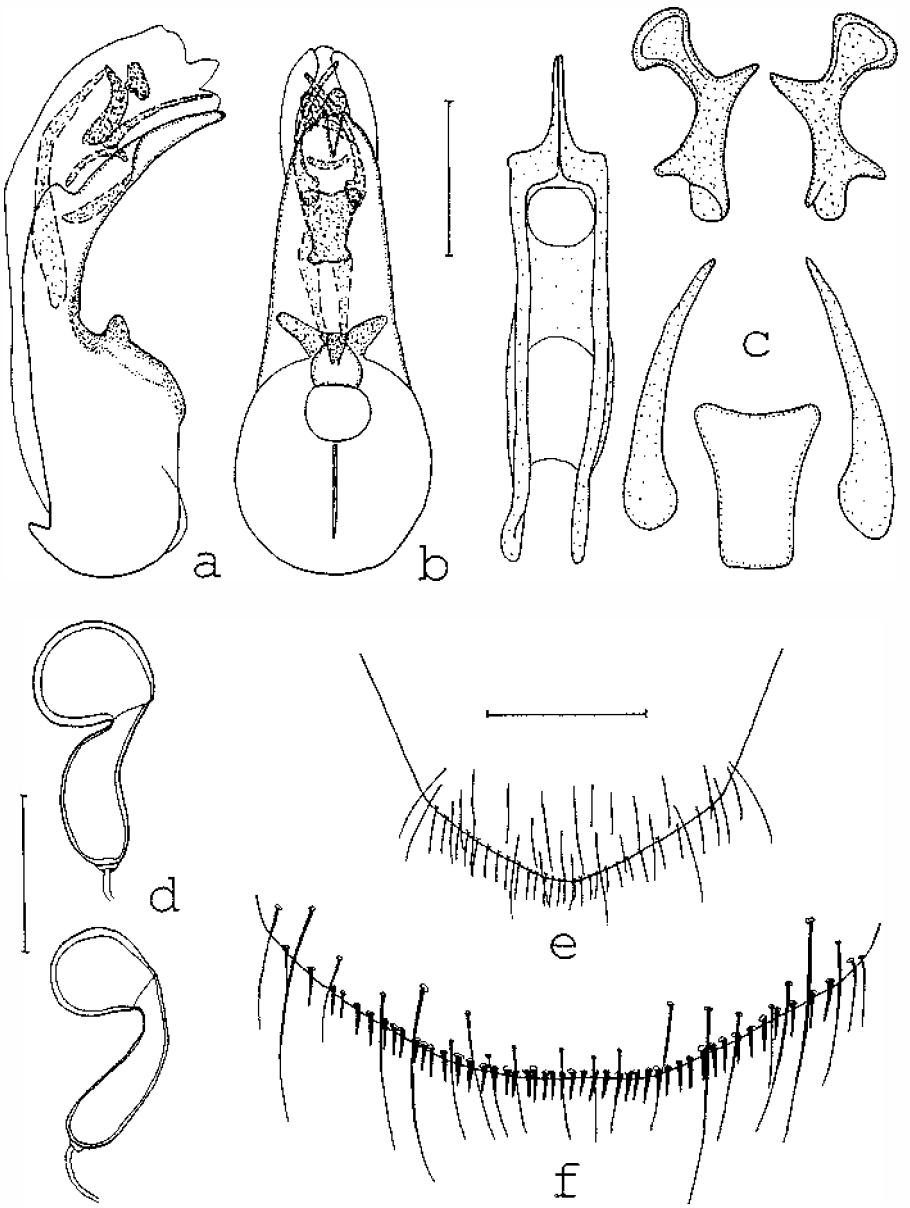


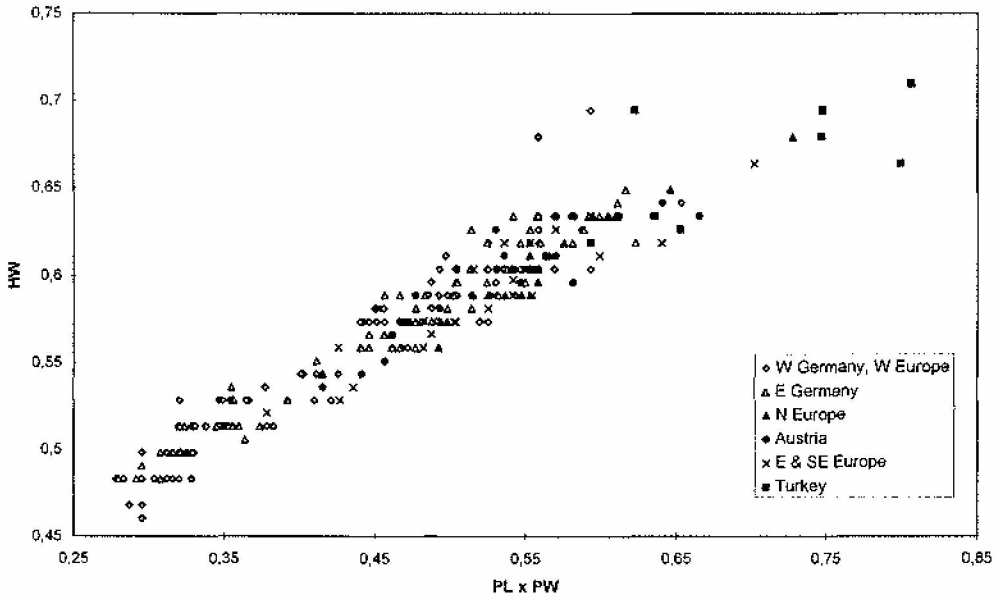
Fig. 6: *Ilyobates bennetti* DONISTHORPE. Median lobe of aedeagus in lateral (**a**) and in ventral view (**b**); internal structures of median lobe in ventral view (**c**); spermathecae of 2 ♀♀ (**d**); ♂ sternum VIII (**e**); hind margin of ♀ sternum VIII (**f**). Scales: a, b, d, e: 0.2 mm; c, f: 0.1 mm.

♂: sternum VIII posteriorly obtusely pointed (Fig. 6e); size of aedeagus subject to considerable, mostly allometric variation, ventral process distinctly more slender in ventral view than in *I. nigricollis*; internal structures of characteristic shape and arrangement, pair of apical structures with much shorter and apically distinctly dilated processes (Figs 6a - c).

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♀: sternum VIII posteriorly evenly convex (Fig. 6f); spermatheca of variable shape, as in *I. nigricollis* with large bulbous capsule, but with shorter and (near capsule) wider duct (Fig. 6d).



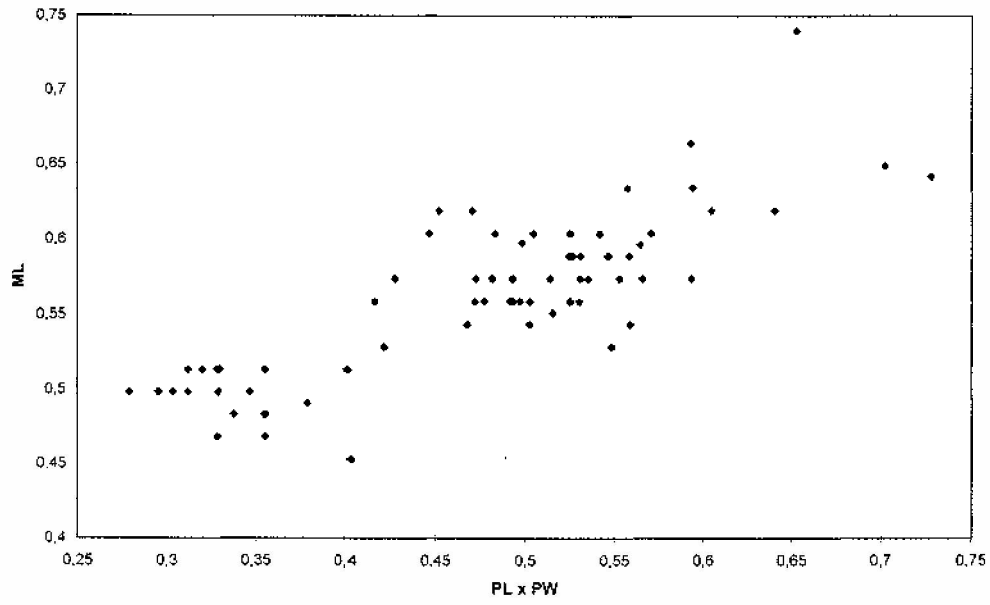


Fig. 7: *Ilyobates bennetti* DONISTHORPE. Variation of head width in relation to pronotum size in material from Western Europe and the west of Germany, from the east of Germany, Northern Europe, Austria, Europe east and southeast of Austria (E & SE Europe), and from Turkey. - **Fig. 8:** *Ilyobates bennetti* DONISTHORPE. Variation of the length of the median lobe of the aedeagus in relation to pronotum size.

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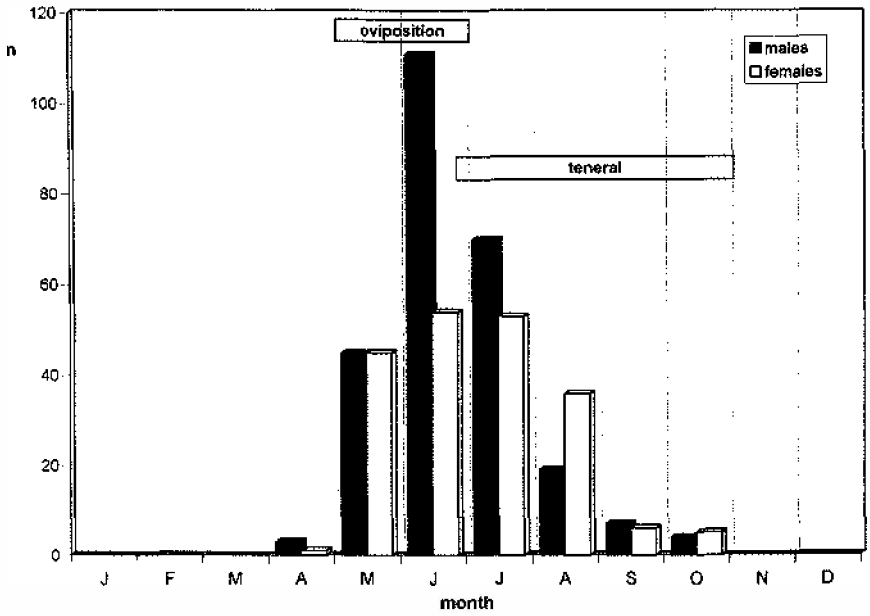


Fig. 9: *Ilyobates bennetti* DONISTHORPE. Seasonal epigeic activity of male and female beetles as measured by pitfall trapping on several study sites near Hannover, Germany (total number of beetles captured: 459). The horizontal bars (oviposition, teneral) indicate the periods during which mature eggs were found in the ovaries of the females and during which tenerals were observed in the traps, respectively.

Intraspecific variation

As in *I. nigricollis*, all measured size parameters are subject to enormous intraspecific variation. The largest specimens were observed in material from the east and southeast (especially Turkey) of the area of distribution, from the north of Europe and from Austria; beetles from western Europe and Germany were on average smaller (Fig. 7). The highest variation in size and proportions was observed for the absolute and relative lengths of the elytra, metatibia, metatarsi, and the metatarsomeres (Table 1). There is apparently no difference in the length of the antennae between ♂♂ and ♀♀. As in *I. nigricollis*, the median lobe of the aedeagus is subject to considerable, mostly allometric variation in size (Fig. 8, table 1).

Distribution and bionomics

Like *I. nigricollis*, *I. bennetti* represents an expansive Pontomediterranean faunal element. In the north and northeast, where it is less rare than *I. nigricollis*, the species has been recorded from Denmark (all regions), southern Norway, southern and central Sweden, southern Finland, Karel'skaya Respublika, Estonia, Latvia (first record), Lithuania, and from the surroundings of St. Petersburg and Moscow (ANDERSEN, 1982; ANDERSEN, et al. 1992; HABERMAN, 1983; HANSEN, 1996; HORION, 1967; PALM, 1935, 1972; SILFVERBERG, 1992; material examined). In the British Isles, where it is also more common than *I. nigricollis*, it is known from Great Britain north to southern Scotland and from Ireland (HORION, 1967; JOHNSON, 1968; JOY, 1932 [as *I. nigricollis*]). In the west, it has been recorded from several localities in France, but is apparently absent from southwestern France and Spain (material examined).

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In Germany, it has been reported from all regions and is, in many regions, distinctly more common than *I. nigricollis*. In the Alps, however, the opposite seems to be the case. It is known from relatively few localities in Switzerland (Aargau, Schwyz, Luzern, Vaud) and Austria (Tirol, Oberösterreich, Niederösterreich, Steiermark, Kärnten) (HEISS, 1971; HERGER & UHLIG, 1983; HORION, 1967; UHLIG et al., 1992; WÖRNDLE, 1950; material examined). Safe records from Italy had previously been unknown (HORION, 1967; LUIGIONI, 1929; ZANETTI, 1995); the species is here reported from Trentino (first record, see material examined). In the southeast and east, *I. bennetti* is known from the Czech Republic, from Slovakia, Poland, Slovenia, Bosnia-Herzegovina, Yugoslavia, Hungary, Romania, Bulgaria, Turkey (Thrace), the Caucasus region, and Ukraine (Krym, Bukovina, L´vov) (ÁDÁM, 1987; HORION, 1967; KOCIAN, 1993; SMOLEŃSKI, 1996; STANIEC, 1994; TÓTH, 1983; material examined). *I. bennetti* is here also reported from North America (Canada), where it seems to have been introduced in more recent times.

Like *I. nigricollis*, *I. bennetti* inhabits a great variety of biotopes and habitats, also often together with other congeners (*I. nigricollis*, *I. propinquus*), though less frequently in woodland, but mostly in open biotopes, particularly those greatly influenced by human activity: often in agricultural biotopes (usually in pitfall traps), frequently also in various urban biotopes (urban meadows, lawns, fallow areas, gardens, pioneer vegetation; often in pitfall traps), in recultivated surface mines, swamps, bogs, flood-plains, river banks, near inundations, meadows, dry grasslands, in leaf litter, moss, *Sphagnum*, grass debris, in compost and rotting debris, under reed, and under ferns (ANDERSEN, 1982; ASSING, 1988, 1992, 1994, unpubl.; FRANZEN, 1992; HARTMANN, 1979; KACHE & ZUCCHI, 1993; KOCH, 1968; KÖHLER, 1997; KORGE, 1963, 1991; LOHSE, 1967; PALM, 1972; RENKONEN, 1938; TÓTH, 1983; VOGEL & DUNGER, 1991; WAGNER, 1997; material examined). In the Alps, the species is apparently absent from higher altitudes. On a few occasions the species was observed in the vicinity of ants (*Lasius* spp.) (DONISTHORPE, 1914; KOCH, 1968), but an obligatory association with ants appears very unlikely. As in *I. nigricollis*, the variety of biotopes and habitats, where *I. bennetti* occurs, is enormous, and the relevant ecological factors are unknown.

As can be concluded from pitfall trap studies on several study sites in and near Hannover (Germany), epigeic activity of adult beetles begins in April and ends in October, the highest activity was observed during the period from May through August (Fig. 9). In June, epigeic activity was distinctly higher in males than in females, an observation suggesting that the latter may be more active subterraneously in search of suitable habitats for oviposition. Dissection of the ovaries showed that oviposition takes place from May through June, with a maximum in June. Teneral beetles were usually observed from July through October (maximum in July and August); one teneral male was collected in the beginning of June. No epigeic activity was recorded from November to March. *I. bennetti* seems to be always macropterous, but in more than 20 specimens examined, no flight muscles were found (ASSING, unpubl.). On the other hand, HORION (1967) reports that on one occasion numerous specimens were observed flying. Thus, it can be assumed that at least part of the adult population hibernates at or near the place of reproduction, and that overwintering takes place in a subterraneous habitat. In many biotopes inhabited by the species, e. g. arable land, a suitable habitat for hibernation such as a litter layer is absent. The few records from the period from November to March available are mostly from subterraneous habitats, usually *Talpa* nests (HORION, 1967; LOHSE, 1967; WÖRNDLE, 1950; material examined). One specimen was observed in mole burrows also in summer (ISRAELSON, 1971).

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4.3. *Ilyobates propinquus* (AUBÉ, 1850)
Fig. 10, Table 1

Calodera propinqua AUBÉ, 1850: 302
Ilyobates propinquus (AUBÉ): KRAATZ (1856)
Ilyobates rufus KRAATZ, 1856: 135f.; synonymy confirmed

Types examined
Calodera propinqua AUBÉ: Holotype ♀ [specimen in extremely poor condition; abdomen, dorsum of thorax, and most of left antenna missing]: Narbonne [written overleaf]/ Muséum Paris, 1869, Coll. Ch. Aubé/ Type (MNHNP).
The original description is based on a single specimen (type locality not specified), which was found in association with "*Formica rufa*". Although most of the holotype has apparently been eaten by *Anthrenus* sp., its remains, especially the punctation of the head, leave little doubt that it is conspecific with the present interpretation of the species.

Ilyobates rufus KRAATZ: Lectotype ♀, present designation: v. Bruck/ Syntypus/ rufus mihi, Germ./ propinquus Aubé/ coll. DEI Eberswalde/ Ilyobates rufus Kr./ Lectotypus Ilyobates rufus Kraatz, desig. Assing 1998 (DEI).
In his original description, KRAATZ (1856) neither designated a holotype nor did he specify the number of specimens before him. For this reason, in view of the frequent misidentifications in the genus, and in order to stabilize the synonymy, the single syntype in the collections of the DEI with KRAATZ's original labels is here designated as lectotype.
In the original description of *I. rufus*, KRAATZ (1856) already suspected that this taxon could be a synonym of *Calodera propinqua* AUBÉ. *I. rufus* was considered a synonym of *I. propinquus* by all later authors; the synonymy is here confirmed.

Additional material examined
Germany: Niedersachsen: 3♀♀, W Hannover, Süntel, Rannenberg, pitfall trap, VII.1987, leg. Sprick (cAss); 1♂ [teneral], same data, but IX.1987 (cAss); 1♀, Solling, IV.1976, leg. Hartmann (MHNG). **Nordrhein-Westfalen:** 1♂, Körbecke, 24.VI.-25.VIII.1979, leg. Kroker (cRen); 1♂ [teneral], Warburg, 4.IX.1981, leg. Renner (cRen); 1♂, Düsseldorf, Benrath, 25.VII.1936, leg. Ermisch (SMTD); 1♂, 1♀, Düsseldorf, Urdenbacher Kämpe, 1992, leg. Goese (cKöh, cAss). **Hessen:** 2♂♂, 4♀♀, Wiesbaden, grassland, pitfall trap, VIII-IX.1985, VII.1986, leg. Steinwarz (cKöh, cWun); 1♀, Oberlais (DEI); 1♀, Soden (DEI). **Rheinland-Pfalz:** 1♀, Eifel, Ulmen, Mosbruch, Zumried, 7.VI.1992, leg. Köhler (cKöh); 1♂ [teneral], Dielkirchen, 25.X.1988, leg. Niehuis (cAss); 1♂, Dielkirchen, 23.VIII.1989, leg. Niehuis (cAss); 1♀, Ludwigshafen, 15.V.1917, leg. Ihssen (MNHUB); 1♀, Nassau a. L., leg. Buddeberg (NHMW). **Bayern:** 1♀, München, Isartal, inundation, 8.VI.1936, leg. Frey (NHMB); 1♂, Pfarrkirchen, leg. Stöcklein (NHMB); 1♀, Garmisch (MNHUB). **Sachsen:** 1♂, Leipzig, Eilenburg, 2.III.1908, leg. Linke (SMTD); 1♂, 1♀, `Saxon.´, coll. Kraatz (DEI). **Locality not specified:** 1♂, `Rhenania´ (DEI).
France: 1♂, Gironde, Gajac, 15.VIII.1905 (MHNG); 1♂, SW Tours, St.-Epain, IX.1903 (MHNG); 1♀, Vienne, Les Bourielles, 1887, leg. Mesmin (NHMW); 1♂, Vienne, St. Barbant, 2.VI.1991, leg. Mesmin (NHMW); 1♂, Brie, Sucy, leg. Méquignon (MHNG); 1♀, Aude, Carcassonne, leg. Gavay (NHMW); 1♀, W Lyon, Vaugneray, 6.VII.1913, leg. Méquignon (MHNG); 1♀, Savoie, Viaison, 10.VII. (MHNG). **Locality not identified:** 1♀, Malorigues [?], VI.1917 (MHNG).
Switzerland: Aargau: 1♂, Sisseln, 5.VII.1990 (cWit); 3♂♂, 1♀, same date and locality, wheat field (cWit, cAss); 1♂, same locality, grassland, 7.VI.1990 (cWit); 1♀, same locality, dry grassland, 16.VIII.1990 (cWit). **Vaud:** 1♀ [with worker of *Lasius flavus* attached to the pin], Bussigny, 30.XI.1949, leg. Besuchet (MHNG). **Genève:** 1♂, Pregny, V.1953 (MHNG).
Austria: Tirol: 1♂, Hall, garden, 22.VII.1967, leg. Kahlen (TLMFI); 1♀, Oberinntal, Terfner Au, inundated grassland, 11.VIII.1970, leg. Kahlen (TLMFI); 1♀, Schwaz, compost, 9.VII.1950, leg. Kofler

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(TLMFI). **Niederösterreich:** 15♂♂, 10♀♀, Donauauen, leg. Breit, Smolik (DEI, MNHUB, NHMB, NHMW, SMNS, SMTD, cAss); 2♀♀, Stockerau, 21.V.1900, leg. Luze (MNHUB, NHMW); 3♂♂, 11♀♀, Stockerau, leg. Bernhauer, Luze, Skalitzky (NHMW); 1♂, 2♀♀, Wien, Donau inundation (MNHUB, NHMW); 1♀, surroundings of Wien, leg. Moczarsky (NHMW); 1♀, Wien, leg. Graf (DEI). **Steiermark:** 1♂, Hochschwabgebiet, Tragöß Pfarrerlacke, 880m, leaf litter in moist *Alnus* woodland, 24.VII.1995, leg. Kapp (cKap); 1♀, Hochschwab (NHMB); 2♂♂, 2♀♀, Turnau (NHMW, cAss). **Steiermark or Burgenland:** 1♀, Rosaliengebirge, VI.1922, leg. Natterer (NHMB). **Kärnten:** 1♀, Karawanken, Eisenkappel, VII.-VIII.1926, leg. Scheerpeltz (NHMW). **Burgenland:** 1♂, 1♀, Zurndorf, leg. Franz (MNHUB).

Poland: 1♀, Legnica (DEI).

Czech Republic: 1♂, Bohemia, Poříčany, 2.IX.1906, leg. Rambousek (MHNG); 1♀, Praha, leg. Skalitzky (NHMW); 1♀, Bohemia, Brandýs nad Labern [Brandeis a/E.], leg. Skalitzky (NHMW); 1♀, Cheb [Eger] (ZIN); 1♀, Silesia, Kimkovice [Königsberg], VII.1903, leg. Wagner (DEI).

Slovenia: 1♀, Škofja Loka [Bischoflack], VII.1986, leg. Ludy (NHMW).

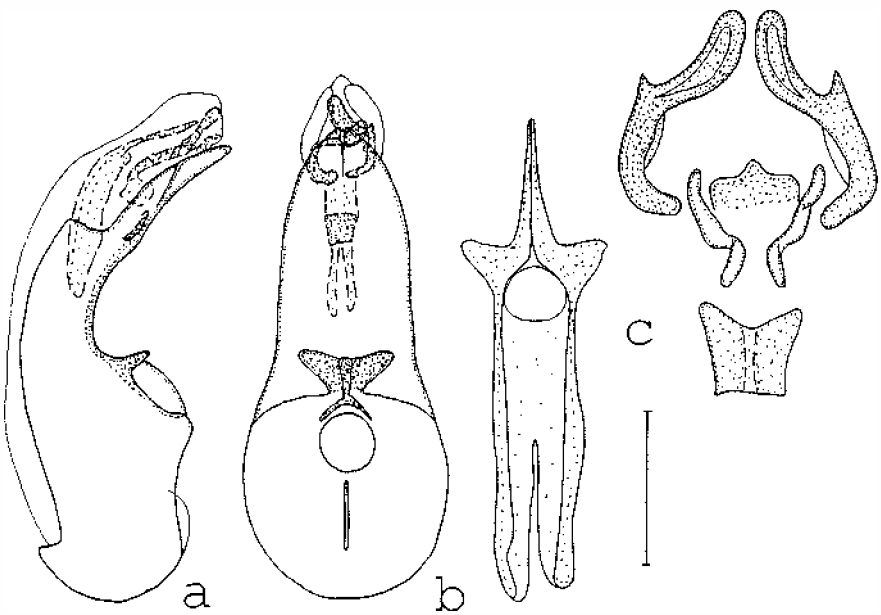
Hungary: 3♀♀, Budapest, Havos, V.-VIII.1992, leg. Loksa (cAss, cWun); 1♀, Kiskunsági National Park, Lakitelek, 1.VII.-19.IX.1978, leg. Hámori (HNHM); 1♂, same data, but 16.III.-10.V.1978 (HNHM); 1♀, Hortobágy National Park, Újszentmargita, 9.V.-11.VI.1974, leg. Kaszab (HNHM); 1♀, Szikra (HNHM).

Locality ambiguous: 1♂, 'Hungar. mer.', leg. Merkl (NHMW).

Diagnosis

Measurements and ratios (range, arithmetic mean; n = 78): AL: 1.59 - 2.20, 1.99; HW: 0.50 - 0.68, 0.60; PW: 0.60 - 0.88, 0.76; PL: 0.57 - 0.85, 0.72; EL: 0.48 - 0.76, 0.65; HTiL: 0.69 - 1.12, 0.95; HTaL: 0.59 - 0.83, 0.72; HT1L: 0.16 - 0. 27, 0.22; HT2L: 0.23 - 0.33, 0.28; ML: 0.48 - 0.62, 0.55; TL: 3.1 - 5.9, 4.2; PW/HW: 1.11 - 1.35, 1.26; PW/PL: 1.01 - 1.13, 1.05; EL/PL: 0.81 - 1.01, 0.90; HTaL/HTiL: 0.71 - 0.80, 0.76; HT1L/HT2L: 0.65 - 0.88, 0.77.

Of similar colour and size as *I. bennetti*.



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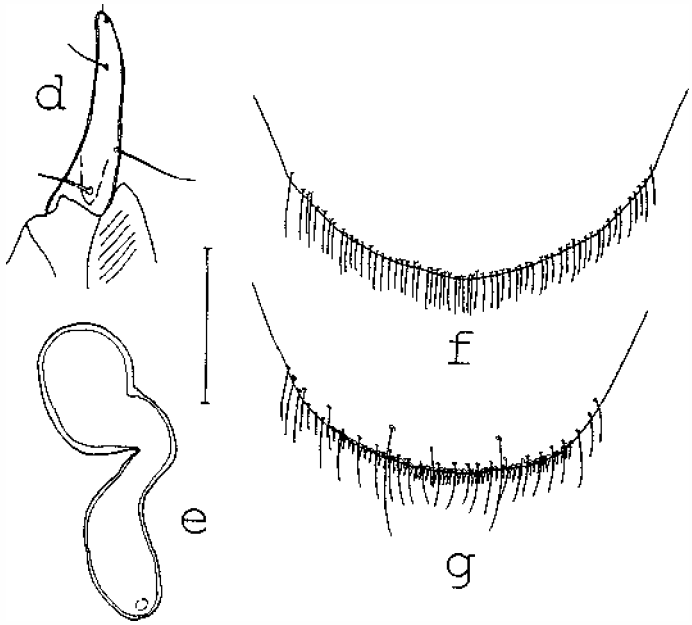


Fig. 10: *Ilyobates propinquus* (AUBÉ). Median lobe of aedeagus in lateral (**a**) and in ventral view (**b**); internal structures of median lobe in ventral view (**c**); apical lobe of paramere (**d**); spermatheca (**e**); hind margin of ♂ sternum VIII (**f**); hind margin of ♀ sternum VIII (**g**). Scales: a, b, d - g: 0.2 mm; c: 0.1 mm.

Punctation of head slightly, that of pronotum distinctly finer than in *I. bennetti* and *I. nigricollis*; forebody therefore with more shine; punctation of elytra also dense, but somewhat granulose and ± serrate. Pubescence of pronotum in latero-median areas directed more laterad than in *I. nigricollis* and *I. bennetti*. Hind wings fully developed.
Abdomen with punctation, pubescence and carinae as in *I. nigricollis* and *I. bennetti*.
♂: sternum VIII posteriorly not pointed, but strongly convex (Fig. 10f); aedeagus of similar size and outline as in *I. bennetti*, but internal structures of different shape and arrangement; pair of apical structures with longer and apically only weakly dilated processes (Figs 10a - c).
♀: sternum VIII posteriorly usually weakly convex (Fig. 10g); size and duct of spermatheca similar to *I. bennetti*, but capsule less bulbous and of different shape (Fig. 10e).

Intraspecific variation
All measured size parameters and proportions are subject to considerable variation, but less so than in *I. nigricollis* and *I. bennetti* (Table 1; see also measurements), possibly because less material was available and/or because the area of distribution is much more restricted than in those species.

Distribution and bionomics
Like the preceding species, *I. propinquus* represents a Pontomediterranean faunal element; its area of distribution, however, is much more restricted, especially in the north, and it is on the whole distinctly rarer. It is absent from all of Fennoscandia and Denmark (SILFVERBERG, 1992; HANSEN, 1996). According to HORION (1967) and JOY (1932) it occurs in southern England. HORION (1967) reports it from the Netherlands and from Belgium. In the west, it reaches France, where it is known from various localities (HORION, 1967; material examined); records from Spain are unknown. In Germany, the species has been recorded from the southern regions and, in the north, reaches the south of Nordrhein-Westfalen, the south of

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Niedersachsen, Sachsen-Anhalt and Sachsen; there are no records from the north of Niedersachsen, Hamburg, Schleswig-Holstein, Mecklenburg-Vorpommern and Berlin/Brandenburg (HORION, 1967; KÖHLER & KLAUSNITZER, 1997; material examined); the record for the Weser-Ems region in KÖHLER & KLAUSNITZER (1997) refers to *I. nigricollis* (ROSE, pers. comm.). *I. propinquus* is known from Switzerland (Neuchâtel, Aargau, Zürich, Genève, Vaud), northern Italy (surroundings of Bolzano), from Austria (numerous localities), from the Czech Republic, Slovakia, and from Poland (HEISS, 1971; HORION, 1967; PEEZ & KAHLEN, 1977; ŠUSTEK, 1995; VIT, 1983; WÖRNDLE, 1950; ZANETTI, 1995; material examined). In the southeast, it has been recorded from Slovenia, Hungary, and Bosnia-Herzegovina (ÁDÁM, 1987; HORION, 1967; TÓTH, 1983; material examined).

Like the two preceding congeners, *I. propinquus* inhabits a wide range of both woodland and open biotopes, and habitats. It has been collected in various types of woodland, rather often on arable land (usually with pitfall traps), on banks of rivers and streams, near inundations, in meadows, dry grassland, in sand pits, in leaf litter, under bark, in decaying trees, under stones, several times together with ants (*Formica* spp., *Lasius* spp.), and on some occasions together with *I. nigricollis* and *I. bennetti* (ASSING, 1989; BERNHAUER, 1902a; BRENNER, 1993; HARTMANN, 1979; HEISS, 1971; HORION, 1967; GANGLBAUER, 1895; KOCH, 1968; KÖHLER, 1997; TÓTH, 1983; VIT, 1983; material examined). Almost all records are from lower elevations, but according to HORION (1967) one specimen was collected at an altitude of 1700m in Austria (Steiermark).

Adult beetles have been collected mostly from March through October, with most records in the period from May through August; one teneral specimen was taken in October. Like the two preceding species, records during the period from November to March are very scarce: one specimen was sieved from woodland litter in November (HORION, 1967), one collected in a mole nest in February (VIT, 1983), and one was taken in March (no ecological details available; material examined). Teneral beetles were observed in September and October. Thus, it can be concluded that, as in *I. nigricollis* and *I. bennetti*, hibernation occurs in the adult stage and in a subterranean habitat. HORION (1967) reports several instances in which *I. propinquus* was collected with a net, which suggests that the species is capable of flight.

4.4. *Ilyobates mech* (BAUDI, 1848)

Figs 11 - 13, Table 1

Calodera mech BAUDI, 1848: 115.
Ilyobates mech (BAUDI): KRAATZ (1856)
Calodera sulcicollis AUBÉ, 1850: 302; synonymy suspected by KRAATZ (1856) and here confirmed.
Ilyobates hustachei MÉQUIGNON, 1933a: 283f., **syn. n.**
Ilyobates pseudomech LOHSE, 1994: 2f., **syn. n.**

Types examined

Calodera mech BAUDI: Holotype ♂: 13 43/ Holotypus, rev. Assing 1998 (coll. Baudi, MRSNT).

The original description is explicitly based on a single specimen ("Unicum exemplar in Pedontio, ...") (BAUDI, 1848). There are no type or locality labels attached to the four specimens in the BAUDI collection, but, according to the curator in charge, the first specimens (from left to right) are considered to be the types (DACCORDI, in litt.). Therefore, the first specimen is here considered the holotype and labelled accordingly.

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Calodera sulcicollis AUBÉ: Lectotype ♂, present designation [aedeagus dissected prior to present study]: Alpes du Piemont/ 6116/ I. Mech Baudi/ Muséum Paris, 1869, Coll. Ch. Aubé/ Type/ Lectotypus Calodera sulcicollis Aubé, desig. V. Assing 1998 (MNHNP).
Since the original description does not specify the number of type specimens, the single syntype in the AUBÉ collection is here designated as lectotype. The synonymy of *Calodera sulcicollis* AUBÉ with *C. mech* BAUDI, which was suspected by KRAATZ (1856) and accepted by later authors, is here confirmed.

Ilyobates hustachei MÉQUIGNON: Holotype ♂ [aedeagus dissected prior to present to study]: S. Martin Ves., VII.30/ Type/ Ilyobates Hustachei Méquignon/ Type/ coll. A. Méquignon (MHNG).
In the original description MÉQUIGNON (1933a) compares *I. hustachei* with "*I. Maerkeli* EPPELSH." [sic!]. Only in a later note does the same author refer to *I. mech* (BAUDI) emphasizing the darker colour, the coarser punctation and the more oblong antennomeres IV - XI as characters distinguishing *I. hustachei* from that species (MÉQUIGNON, 1933b). The punctation of the holotype of *I. hustachei* is indeed coarser than in average *I. mech*, especially on the pronotum, which is rugosely punctured on practically its whole surface. The colour is rather dark, and the antennomeres are more oblong (antennomeres VII - X not distinctly transverse) than is usually the case in *I. mech*, but the examination of the somewhat damaged aedeagus, especially of the internal structures, leaves no doubt that the specimen is conspecific with *I. mech*. Consequently, *I. hustachei* MÉQUIGNON must be regarded as a junior synonym of *I. mech* (BAUDI).

Ilyobates pseudomech LOHSE: Holotype ♂ [aedeagus dissected prior to present study]: Waidisch, Kärnten, 26.VII.1967/ Austria (overleaf)/ pseudomech/ mech (overleaf)/ Holotypus/ Ilyobates pseudomech Lohse n. sp. (overleaf)/ Coll. G. A. Lohse, MHNG-1994 (MHNG). Paratype ♀ [teneral]: same data as holotype, but `Allotypus' (MHNG).
According to LOHSE (1994), *I. pseudomech* is distinguished from *I. mech* especially by smaller size, the different shape of the pronotum and the different morphology of the aedeagus. The two type specimens are indeed remarkably small (similar to an average *I. bennetti*), but size is extremely variable not only in this species, but in the genus as a whole; I have seen even smaller ♂♂ from other localities. The shape of the pronotum is within the range of *I. mech*. As is shown below, the size of the aedeagus is subject to considerable - mostly allometric - intraspecific variation, which explains the small size of the aedeagus of the holotype. The general morphology and expecially the characteristic internal structures of the aedeagus, however, are the same as in *I. mech*, so that *I. pseudomech* LOHSE is here considered a junior synonym.

Additional material examined

France: Alpes Maritimes: 1♂, 1♀, St. Martin Vésubie, leg. Buchet (MHNG); 1♀, Inundat. Vésubie, 10.IV.1939 (MHNG); 1♂, Nice, Canal de la Vésubie, leg. Buchet (MHNG); 1♂, N Telle, 19.V.1961 (MHNG); 2♂♂, Valberg, VI.1952/ VI.1956 (MHNG, cAss); 1♀, Valberg, Semant, 12.VI.1979, leg. Curti (MHNG); 1♀, SE St.-Martin-Vésubie, Col de Turini, V.1949 (MHNG); 1♀, Col de Turini, 21.VII.1952 (MHNG); 1♀, Moulinet, VII.1950 (MHNG); 1♂, Lubiane-Vence, 28.III.1943 (MHNG); 1♂, Le Baz, 21.IV.1921 (MHNG); 1♂, Launes, 10.V.1955 (MHNG); 1♂, IN. [=inundation?] Launes, IV.1952 (MHNG); 1♂, V. Cairos, 20.VI.1953, (MHNG); 1♀, Col Tende, 20.VI.1951 (MHNG); 1♂, 1♀, Berthemont, 15.IV.1951 (MHNG); 1♂, 1♀, IN. Loup, 10.VI.1953 (MHNG); 1♂, IN. Loup, II.1951 (MHNG); 1♂, IN. Loup, III.1951 (MHNG); 1♂, IN. Loup, 10.VI.1953 (MHNG); 1♀, St. Augustin, IV.1953 (MHNG); 1♂, St. Auban, 6.VI.1980, leg. Curti (MHNG); 1♀, Aven Marcel, Caille,

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28.VIII.1980 (MHNG); 1♂, 1♀ [♂ teneral], Aven Marcel, Andon, 29.IX.1979, leg. Curti (MHNG); 1♂ 'Col c.'es chamhs [?]', VII.1965 (MHNG); 1♂, Eze, 20.III.1968 (cAss); 1 ex., locality not specified (HNHM). **Var:** 1♂ [teneral], Séranon, VIII.1952 (MHNG); ; 1♀, SW Grasse, Tanneron, pitfall trap, VI.1988, leg. Wunderle (cWun); 3♂♂, 4♀♀, Bagnols en Forêt, 10.VII.1975, leg. Löbl (MHNG, cAss); 1♂, IN. La Molle, IV.1963 (MHNG); 1♂, La Molle, XI.1963 (MHNG); 1♂, Monts des Maures, Lac de l'Aille (MHNG); 1♂, IN. Argens, III.1956 (cAss); Mons, Rochtailée, 20.IV.1979, leg. Curti (MHNG). **Isère:** 1♂, E Châtillon, Gorges des Gas, 650m, 26.VII.1982, leg. Schawaller (SMNS). **Hautes Alpes en Provence:** 1♂, 2♀♀, Le Villard d'Abos, 1550m, 5.VI.1974, leg. Löbl (MHNG, cAss); 1♀, Pont la Dame, Buech valley, 800m, 27.VII.1982, leg. Schawaller (SMNS). **Alpes-de-Haute-Provence:** 1♂, 1♀, St. Jacques near Barrême, 7.VII.1975, leg. Löbl (MHNG, cAss). **Basses Alpes:** 1♂, Entreveaux, leaf litter, 16.VI.1976, leg. Vit (MHNG); 1♀, Mt. Blayeul, IX.1971 (MHNG); 1♂, Col du Fa, 5.V.1973, leg. Curti (MHNG); 1♂, Verdache, 29.V.1967 (MHNG). **Vaucluse:** 1♂, Mont Ventoux, 1300m, beech litter, 21.VII.1996, leg. Brandstetter (cKap).

Italy: Liguria: 1♂, Imperia, Piággia, 1200m, 29.VI.1972, leg. Löbl (MHNG); 1♂, Imperia, Mt. Ceppo, 1500m, 26.VI.1972, leg. Löbl (cAss); 1♂ [teneral], Busalla, 24.VII.1895, leg. Fiori (MNHUB); 1♂, Ligurie, 17.V.1973, leg. Curti (MHNG). **Piemonte:** 1♂, Monte Rosa, Corno Piglimó, leg. Breit (NHMW); 1♂, Varallo (VC) (cAss); 1♂, Vercelli, Val Sesia, Cervatto, 1000m, beech litter, 21.VI.1984, leg. Kahlen (TLMFI); 1♂, Vercelli, Val Sessera, Mt. Barone, 1600m, under stone, 20.VI.1984, leg. Kahlen (TLMFI); 1♀, Vercelli, Val Sessera (MHNG); 4♂♂, 2♀♀, Valle Stura (CN), SW Vinadio, 1400m, beech wood in northern exposition, 7.V.1997, leg. Assing (cAss); 1♂, 2♀♀, Valdieri (CN) (NHMW); 1♀, Crissolo (CN), 1850m, 13.-26.VI.1927, leg. Meyer (NHMW); 1♂, 1♀, Crissolo, 24.VI.1973, leg. Curti (MHNG); 1♂, Colle di Tenda, 16.VII.1973, leg. Curti (MHNG); 2♂♂, 1♀, Baldissero Canavese, Monti Pelati, 500m, 12.III.1989, leg. Giachino (DEI); 1♂, Val Soana (TO), Piamprato, 1300m, 11.VI./27.VII.1987, leg. Giachino (DEI); 1♂, Varallo (MNHUB); 1♂, 'Pedomontio, var. minor' (coll. Baudi MRSNT); 1♀, locality illegible, leg. Fiori (MNHUB); 1♂, 1♀, 1 ex., locality not specified (DEI). **Lombardia:** 1♂, E Sondrio, Tresivio, 2.VIII.1970 (cZan); 1♂, Passo Croce Domini, 1500m, in moss near stream, 28.VI.1993, leg. Assing (cAss); 1♂, Brescia, E Brozzo, 500m, leaf litter, 31.V.1977, leg. Kahlen (TLMFI); 1♀, Mt. Grigna, leg. Strupi (NHMW); 1♀, Brescia, Mt. Guglielmo, Dosso Pedata, northeastern slope, 1850m, under *Salix*, 12.VII.1980, leg. Kahlen (TLMFI); 1♂, 1♀, Mt. Guglielmo, leg. Breit (NHMW); 1♀, Bergamo, Oltre il Colle, Val Finzel, 1050m, soil below roots, 3.VI.1980, leg. Kahlen (TLMFI); 1♀, Val Camonica, leg. Krüger (NHMW); 3♀♀, Oltre il Colle (MHNG, SMTD); 1♂, Oltre il Colle, 20.VI.1976, leg. Curti (MHNG). - **Alto Adige/ Trentino:** 1♀, Val Pusteria, Tures [Taufers], 16.VII.1880, leg. Ludy (NHMW); 1♀, Passo di Roilo, 26.VII.1909, leg. Stöcklein (NHMB); 1♂, W Trento, M. Bondone, pitfall trap, 3.VII.1992 (cZan); 1♂, Inghimie (TN), 18.VI. (cZan); 1♂, Selva di Grigno, leaf litter, 6.VIII.1978, leg. Kahlen (TLMFI); 1♂, Cima Pari, 1950-1990m, under stone, 15.VI.1979, leg. Kahlen (TLMFI); 1♂, Monte Pari, leg. Feige, Strupi (NHMW, SMTD); 1♂, Monte Pari, 1903, leg. Ganglbauer (NHMW). **Veneto:** 1♂, Giazza (VR), 18.VI.1989, leg. Zanetti (cZan); 1♀, Parco Lessinia, Ponte di Veja, 13.IV.1991, leg. Zanetti (cZan); 1♀, S. Martino B. A. (VR), Musella, Ferrazzette, nest of *Talpa*, 28.XI.1991, leg. Zanetti (cZan); Montecchio (VR), 24.V.1979, leg. Curti (MHNG); 1♂, Treviso, Montello, 27.III.1960, leg. Meggiolaro (TLMFI); 1♂, Treviso, Pradera dela Zei [?] Pollino, leg. Paoletti (NHMW); 1♂, Veneto, Cadore, leg. Breit (NHMW); 2♂♂, Padova, Colli Euganei, Mt. Ventrolone, western slope, in leaf litter, 18.III.1979, leg. Kahlen (TLMFI, cAss). **Friuli-Venezia Giulia:** 1♂, 1♀, Trieste, Opicina, leg. Schatzmayr (MNHUB, cAss); 1♂, 3♀♀, Mte. Maggiore, 2.-8.VI.1931, leg. Stöcklein (NHMB). **Sardegna:** 2♂♂, Mte. Tónneri, Seui, Mte. Arquerí, III.1979, leg. Curti (MHNG). **Locality not identified:** 1♂, 2♀♀, Passo Moncodeno, 29.VI.1907, leg. Winkler (DEI); 1♀, Passo Moncodeno, 1.VII.1909, leg. Pinker (NHMW).

Italian or Austrian territory: 1♂, 'Tyrol' (NHMW).

Italian or Slovenian territory: 1♂, Gorizia (MNHUB).

Switzerland: Valais: 1♂, Gondo, 900m, VII.1966, leg. Besuchet (MHNG). **Ticino:** 1♀, Capolago, leg. Breit (NHMW); 1♂, Sonogno, in moss, 30.VII.1954, leg. Besuchet (MHNG); 1♂, Indemini, 950m, VI.1968, leg. Toumayeff (MHNG); 1♂, Rancate, 22.IV.1976, leg. Besuchet (MHNG); 1♂, Bella Vista,

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1150m, 26.V.1982, leg. Besuchet (cAss); 2♂♂, Bella Vista, 1100m, in dead leaves, 2.VI.1981, leg. Besuchet (MHNG, cAss); 1♀, Morbio sup., 25.IV.1985, leg. Besuchet & Löbl (MHNG); 1♂, V. Vergeletto, Piano delle Cascine, 1200m, 21.VII.1990, leg. Besuchet (MHNG); 1♂, Val Colla, Colla, 950m, 1.VIII.1979, leg. Vit (MHNG); 1♂, Mondrigo, bog, pitfall, 20.-23.VI.1982 (MHNG).

Austria: Oberösterreich: 1♀, Schoberstein, leg. Petz (NHMW). **Steiermark:** 1♀, Rottenmanner Tauern, V.1919, leg. Moosbrugger (NHMW); 1♂, 1♀, Turnau (NHMW); 1♀, surroundings of Graz, leg. Penecke (NHMW); 2♀♀, Gösting near Graz (NHMW). **Kärnten:** 1♂, Ossiach, leg. Sturany (NHMW); 1♀, Klagenfurt, leg. Klimsch (NHMW); 2♀♀, Ettendorf, leg. Klimsch (NHMB); 1♂, Navernig (cAss); 1♂, Waidisch ob Ferlach, 14.VII.1975, leg. Folwaczny (SMNS); 1♂, S Ferlach, Tscheppaschlucht, 600m, beech forest, 12.VII.1991, leg. Zerche (cAss); 1♀, Karawanken, Petzen, Traventa, 1250m (SMNS); 2♂♂, 1♀, Karawanken, Ledenitzen, 9.-20.VI.1942, leg. Liebmann (DEI); 1♀, Karawanken, Eisenkappel, Ebriachklamm, 16.-17.VIII.1955, leg. Scheerpeltz (NHMW); 1♂, Eisenkappel, 25.VI. 1982, leg. Ulbrich (SMNS); 1♀, Eisenkappel, 22.VI.1963, leg. Ulbrich (SMNS); 1♂, Eisenkappel (NHMB); 1♂, Eisenkappel, Jovanberg, 1400m, northern slope, 20.VII.1938, leg. Scheerpeltz (NHMW); 1♂, Jovanberg, 1600m, 19.VI.1978, leg. Ulbrich (SMNS); 1♂, Eisenkappel, Vellachtal, Waschnigg, 7.VII.1942, leg. Scheerpeltz (NHMW).

Slovakia: 1♀, 'Kl. Beskiden', Habura, 16.VI.1990, leg. Behne (DEI); 1♀, Ubla, beech forest, 15.VI.1981, leg. Dieckmann (DEI); 1♂, Košice, 1927, leg. Machulka (MNHUB); 1♀, Koš. Hámry, leg. Roubal (MNHUB).

Slovenia: 1♂, Trnovo, Predmeja, 28.VI.1981, leg. Lohse (MHNG); 1♀, Kamniške Alpe [Steiner Alpen], Logarska valley, 750m, 25.VI.1988, leg. Dieckmann (DEI); 1♀, Ledenice Dol, Predmeja, 28.VI.1981, leg. Puthz (cAss); 1♂, Kočevje [Gottschee], 6.VI.1939, leg. Köller (SMTD); 1♀, Škofja Loka [Bischoflack], VIII.1986, leg. Ludy (NHMW); 1♀, Postojna [Adelsberg] (NHMW); 1♀, Kamniške Alpe, Grintouc (NHMW); 1♀, Žiče, Sotensko, 23.IV.1998, leg. Drovenik (cAss); 1♂, 2♀♀, Lipica Ergela (E Trieste) (NHMW); 1♂, 'Tabor', 14.V.1917 (MNHUB); 1♀, 'Carniol.' (NHMW).

Hungary: 1♀, Pécs [Fünfkirchen] (MNHUB); 1♀, Siófok, leg. Lichtneckert (HNHM).

Romania: 1♀, 'Carpathen', leg. Reitter (NHMW); 1♂, 'Siebenbürgen' (NHMW); 1♂, Munţii Bihor, Petroasa, Padis, VI.1922, leg. Jeannel & Winkler (NHMW); 1♂, Mármaros m., Gyertyánliget, 6.-16.VIII.1940, leg. Fodor (HNHM); 1♂, Borzás (DEI).

Croatia: 1♀, Istria, Učka [te. Maggior], 2.-8.VI.1931, leg. Stöcklein (MNHUB). 1♂, 'Ocura', leg. Viertl (NHMW); 1♂, Plitvice, Poljanak, 500m, pitfall trap, 9.V.1990, leg. Wunderle (cWun); 1♀, Plitvice (NHMW); 1♂, Capela, leg. Heyden (DEI); 1♂, 'Capella', leg. Ganglbauer (NHMW); 1♀, Zagreb, leg. Stüller (HNHM); 1♂, 'Lokve', leg. Stüller (cAss); 1♂, Toma [?], Bokor (HNHM); 1♂, locality not specified (DEI); 1♀, locality not specified, leg. Hampe (NHMW); 1♀, Poljana, 1910, leg. Apfelbeck (SMTD).

Bosnia-Herzegovina: 1♀, Bjelašnica planina, leg. Leonhard (DEI); 1♂, 1♀, Bjelašnica planina (SMTD, cAss); 1♂, 1♀, Majevica planina (NHMW, cAss); 1♀, Vran planina, 1902, leg. Leonhard (NHMW); 1♀, 'Bosnien', leg. Reitter & Leder (HNHM); 1♀, 'Herzegowina', leg. Reitter (HNHM); 1♀, locality illegible, 1902, leg. Leonhard (DEI).

Caucasus: 1♂, locality not specified, leg. Leder (NHMW).

Locality ambiguous or not identified: 1♂, Vertatscha, leg. Holdhaus (NHMW); 1♂, 2♀♀, locality not indicated (coll. Baudi, MRSNT).

Diagnosis

Measurements and ratios (range, arithmetic mean; n = 152): AL: 1.37 - 2.16, 1.84; HW: 0.47 - 0.76, 0.66; PW: 0.60 - 1.12, 0.92; PL: 0.57 - 1.09, 0.89; EL: 0.48 - 0.97, 0.79; HTiL: 0.68 - 1.36, 1.13; HTaL: 0.47 - 0.95, 0.79; HT1L: 0.12 - 0.30, 0.23; HT2L: 0.18 - 0.41, 0.32; ML: 0.68 - 0.91, 0.79; TL: 3.3 - 7.5, 5.7; PW/HW: 1.24 - 1.54, 1.38; PW/PL: 0.97 - 1.10, 1.03; EL/PL: 0.77 - 1.05, 0.88; HTaL/HTiL: 0.64 - 0.86, 0.71; HT1L/HT2L: 0.56 - 0.97, 0.73.

Size and proportions extremely variable (see measurements and ratios). Usually of more uniform coloration than *I. nigricollis*, mostly rather dark, ± brown to blackish, with the hind margins of the abdominal terga and often the elytra somewhat lighter; antennae brown; legs reddish to dark brown.

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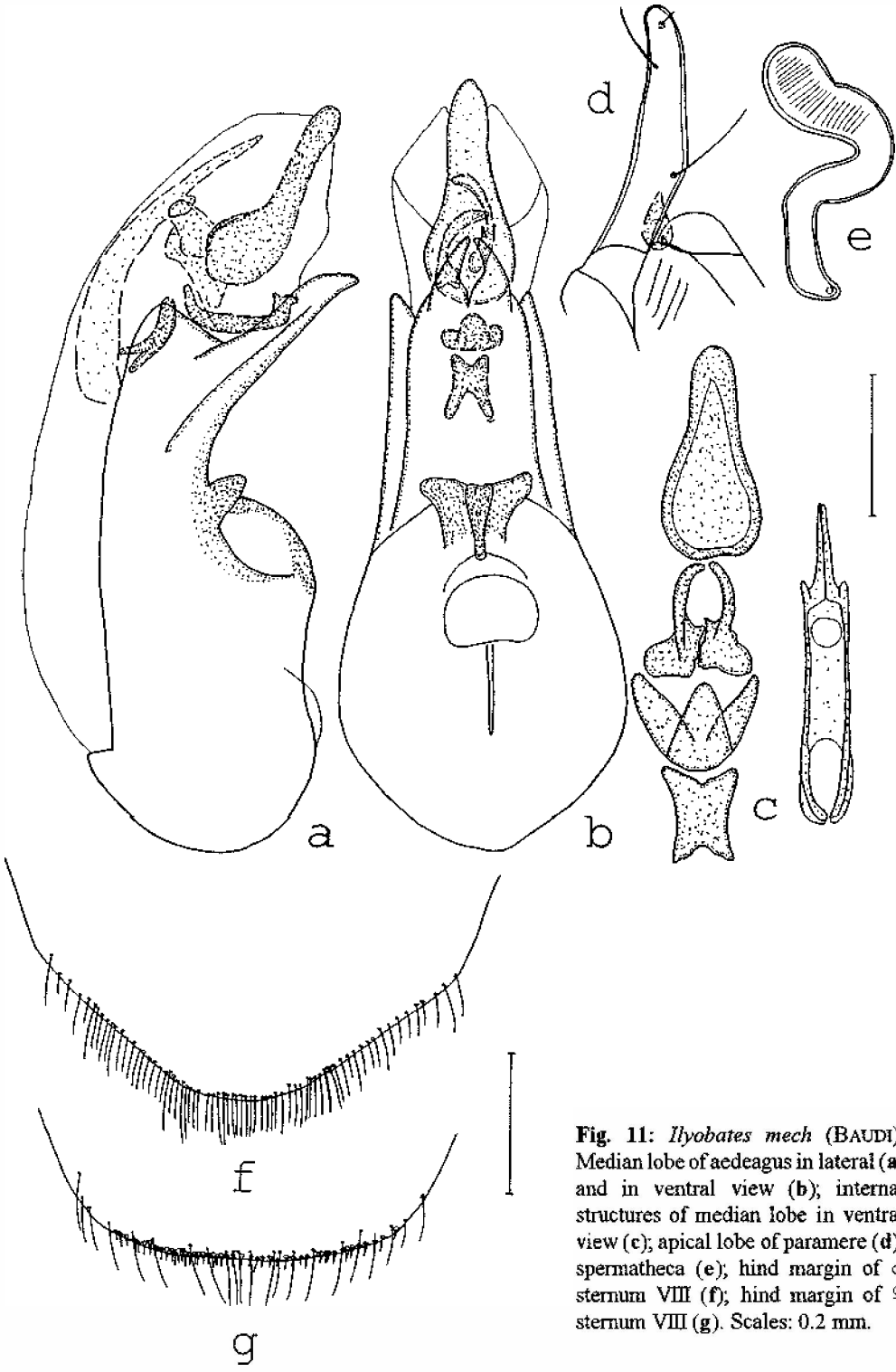


Fig. 11: *Ilyobates mech* (BAUDI). Median lobe of aedeagus in lateral (**a**) and in ventral view (**b**); internal structures of median lobe in ventral view (**c**); apical lobe of paramere (**d**); spermatheca (**e**); hind margin of ♂ sternum VIII (**f**); hind margin of ♀ sternum VIII (**g**). Scales: 0.2 mm.

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Punctation on head and elytra very close (more so than in *I. nigricollis*), on pronotum even denser and especially in the central area rugose and confluent, sometimes punctation of whole dorsal surface of pronotum rugose and confluent; integument of head and elytra with very little, that of pronotum practically without shine. Pubescence of pronotum in latero-median areas directed almost completely laterad.

Eyes smaller and more bulging than in *I. nigricollis*, in dorsal view little more than half the length of temples; antennae usually shorter than in *I. nigricollis*, antennomeres VI - X in most (!) specimens examined transverse; antennomere XI with weak sexual dimorphism, apically ± constricted in both sexes. Pronotum on average slightly more slender than in *I. nigricollis* (cf. ratio PW/PL). Hind wings (always?) of somewhat reduced length, ± submacropterous.

Abdomen with pronounced median carina in anterior transverse impressions of terga III - VI; otherwise similar to *I. nigricollis*.

♂: sternum VIII posteriorly obtusely pointed (Fig. 11f); aedeagus very large (in relation to body size), ventral process more distinctly delimited from lateral parts than in *I. nigricollis*; shape and arrangement of internal structures characteristic, with massive apical piece (Figs 11a - c); apical lobe of paramere slightly longer and more slender than in *I. nigricollis* (Fig. 11d).

♀: sternum VIII posteriorly ± truncate (Fig. 11g); spermatheca with roughly S-shaped duct, relatively smaller and with less bulbous capsule than in *I. nigricollis* (Fig. 11e).

Intraspecific variation

In most of the size parameters and proportions, *I. mech* is even more variable than *I. nigricollis* and *I. bennetti* (Fig. 12). The highest variation in size and proportions were observed for the absolute and relative lengths of the elytra, metatibia, metatarsi, and the metatarsomeres (Table 1). Variation in body size also involves the size of the aedeagus, but apparently less so than in *I. nigricollis* and *I. bennetti* (Fig. 13).

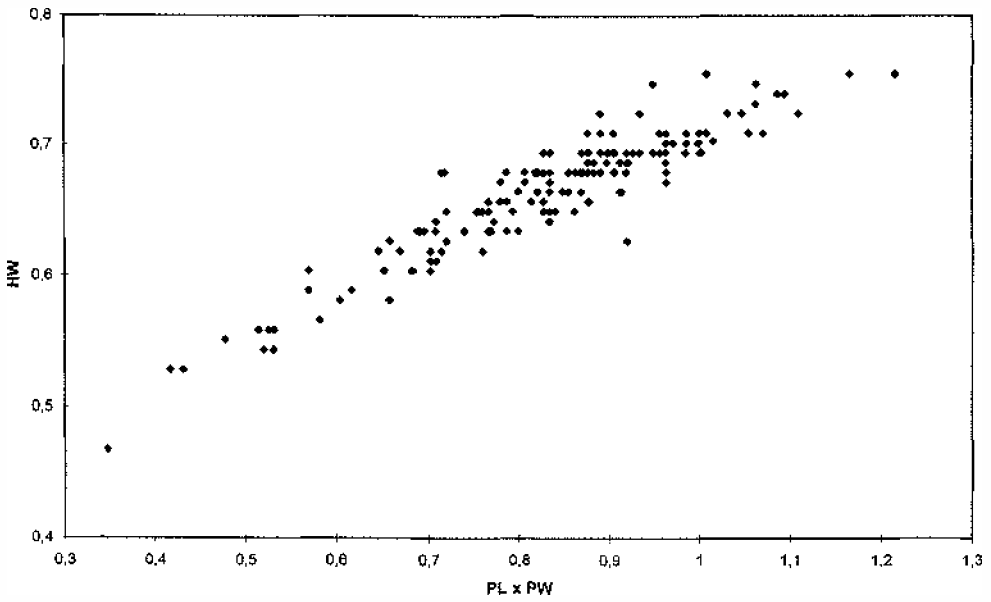


Fig. 12: *Ilyobates mech* (BAUDI). Variation of head width in relation to pronotum size.

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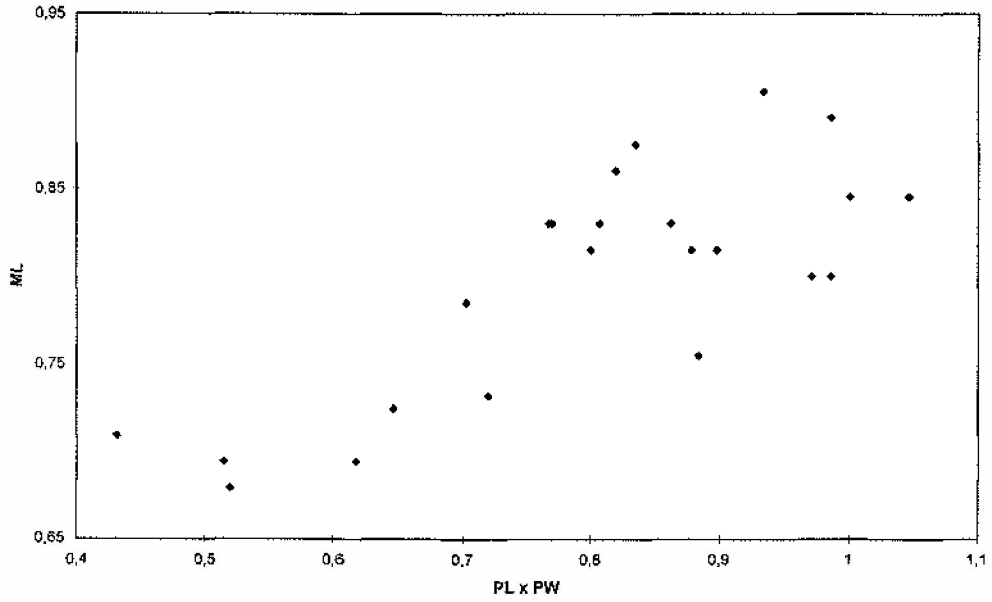


Fig. 13: *Ilyobates mech* (BAUDI). Variation of the length of the median lobe of the aedeagus in relation to pronotum size.

Distribution and bionomics

Like its congeners, *I. mech* is a Pontomediterranean faunal element, but its area of distribution extends far less north than those of the preceding species. The northwestern limit of its range is in southeastern France, where it has been recorded from numerous localities in the Grand Chartreuse, Hautes-Alpes-en-Provence, Alpes-de-Haute-Provence, Basses-Alpes, Vaucluse, Var, and the Alpes Maritimes (HORION, 1967; MÉQUIGNON, 1933a, 1933b, 1945; material examined). It occurs in practically all of the Italian Alps from Liguria (Imperia) to the surroundings of Trieste, in Emilia, and in both Corsica and Sardinia (HORION, 1967; LUIGIONI, 1929; OSELLA & ZANETTI, 1974; PEEZ & KAHLEN, 1977; PORTA, 1926; SAINTE-CLAIRE DEVILLE, 1914; material examined). In Switzerland, it has only been collected in the south (Ticino, Valais; see material examined). In Austria, it is present in Oberösterreich, Steiermark and Kärnten (material examined). HORION (1967) also reports it from Osttirol, Niederösterreich and Burgenland, but these records require verification, as I have seen no corresponding specimens, although HORION (1967) states that at least those from Niederösterreich and Burgenland should be in the SCHEERPELTZ collection. Further to the east, *I. mech* has been recorded from various localities in Slovenia and Slovakia, from Hungary, Croatia, Bosnia-Herzegovina, and from Romania (HORION, 1967; JÁSZAY & BOHÁČ, 1994; SMETANA, 1954, 1964a; material examined). HORION (1967) indicates one record from Bukovina ("Tetina"). One of the specimens examined was labelled "Caucasus, Leder". However, in the absence of further confirming evidence, this record should be considered doubtful, particularly since Caucasian and Carpathian material collected by Leder and Reitter is known to have been mislabelled occasionally (ASSING & SOLODOVNIKOV, 1998).

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Unlike the preceding species, *I. mech* seems to be absent from biotopes which are strongly influenced by human activity. It has been collected at intermediate to higher altitudes; the labels attached to the material examined indicated elevations between 500 and 2000m, and FRANZ (1932) states that he collected the species on Mt. Sernio (Alpi Carniche) in the high-alpine region. The species has been found in moist beech woodland (most records), under *Salix*, *Acer* and *Corylus*, in moist moss near streams, on river banks and near inundations, in soil between roots, under stones, in pitfall traps, and on one occasion in a nest of *Lasius fuliginosus* (BERNHAUER, 1902a; FOCARILE, 1986; GANGLBAUER, 1895; HORION, 1967; ZANETTI, 1992; material examined).
Adult beetles have been collected from February through September, with most records during the period from May through August and a maximum in June. Teneral adults have been collected in July, August and September. Altogether three specimens were found in mole nests in November, February, and March (OSELLA & ZANETTI, 1974; material examined). Most of the beetles taken in February and March were found near river inundations and probably washed out of the hibernation habitats. Thus, the evidence available suggests that regarding both its life history and the hibernation habitat *I. mech* is very similar to *I. nigricollis*, *I. bennetti*, and *I. propinquus*.

4.5. *Ilyobates merkli* EPPELSHEIM, 1883

Fig. 14, Table 1

Ilyobates merkli EPPELSHEIM, 1883: 254f.

Type material

The holotype, which according to the original description should be labelled "Südungarn" and was given to EPPELSHEIM by the collector MERKL, is apparently lost. It was looked for, but not found in the collections of the NHMW. There are, however, two further specimens in the NHMW which according to the labels attached to them were identified by EPPELSHEIM as *I. merkli* and which are in agreement with both the original description and the present interpretation of the species.

Additional material examined

Austria: Steiermark: 1♂, Bezirk Weiz, Busental near Weiz, 18.V.1990, leg. Holzer (cSch); 1♀, Nassau (NHMW). **Kärnten:** 1♂, Karawanken, Hochobir, 1000m, near snow, 11.V.1990, leg. Wunderle (cWun); 1♀, Karawanken, Jovanberg, 25.V.1983, leg. Terlutter (cAss); 1♂, Karawanken, Bärental, 18.VII.1930, leg. Scheerpeltz (cAss); 1♂, Karawanken, Koschuta, Ribnicagraben, 10.VI.1970, leg. Papperitz (SMNS); 1♂, Karawanken, Eisenkappel, Vellacher Kocna, 14.VII.1965, leg. Ulbrich (SMNS); 1♀ [teneral], Eisenkappel, 6.VII.1971, leg. Schrepfer (SMNS); 2♂♂, Navernig (NHMB, cAss); 1♀, 'Alp. Carinth', leg. Schaschl (NHMW).
Slovenia: 1♀, Kočevski rog, Rdeči Kamen/ Luža, 800m, beech litter between rocks, 6.VI.1995, leg. Kahlen (TLMFI).
Hungary: 1♀, Pécs, V.1955, leg. Lenci (HNHM).
Croatia: 1♀, Zagreb ['Agram'], 'Zeravica', leg. Apfelbeck, 'Merkli mihi', coll. Eppelsheim (NHMW); 1♂, Ozalj (NHMW).
Bosnia-Hergovina: 2♀♀, Jablanica, 14.&16.VI.1901, leg. Leonhard (DEI); 1♂, Jablanica (NHMB); 1♂, 'Central-Bosnien', leg. Reitter (HNHM).

Diagnosis

Measurements and ratios (range, arithmetic mean; n = 19): AL: 2.72 - 3.32, 3.03; HW: 0.75 - 0.94, 0.88; PW: 1.06 - 1.30, 1.20 PL: 0.94 - 1.25, 1.13; EL: 0.86 - 1.16, 1.05; HTiL: 1.50 -

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1.81, 1.68; HTaL: 1.13 - 1.40, 1.30; HT1L: 0.33 - 0.47, 0.41; HT2L: 0.49 - 0.58, 0.53; ML: 0.85 - 0.94, 0.88; TL: 6.0 - 8.9, 7.4; PW/HW: 1.30 - 1.43, 1.37; PW/PL: 1.03 - 1.16, 1.06; EL/PL: 0.81 - 1.00, 0.93; HTaL/HTiL: 0.74 - 0.85, 0.77; HT1L/HT2L: 0.64 - 0.88, 0.77. Largest species of the genus (see measurements). Coloration on the whole similar to *I. nigricollis* and also variable, but head and pronotum usually black, elytra ± castaneous, and abdominal terga VI and VII darker than the anterior terga.

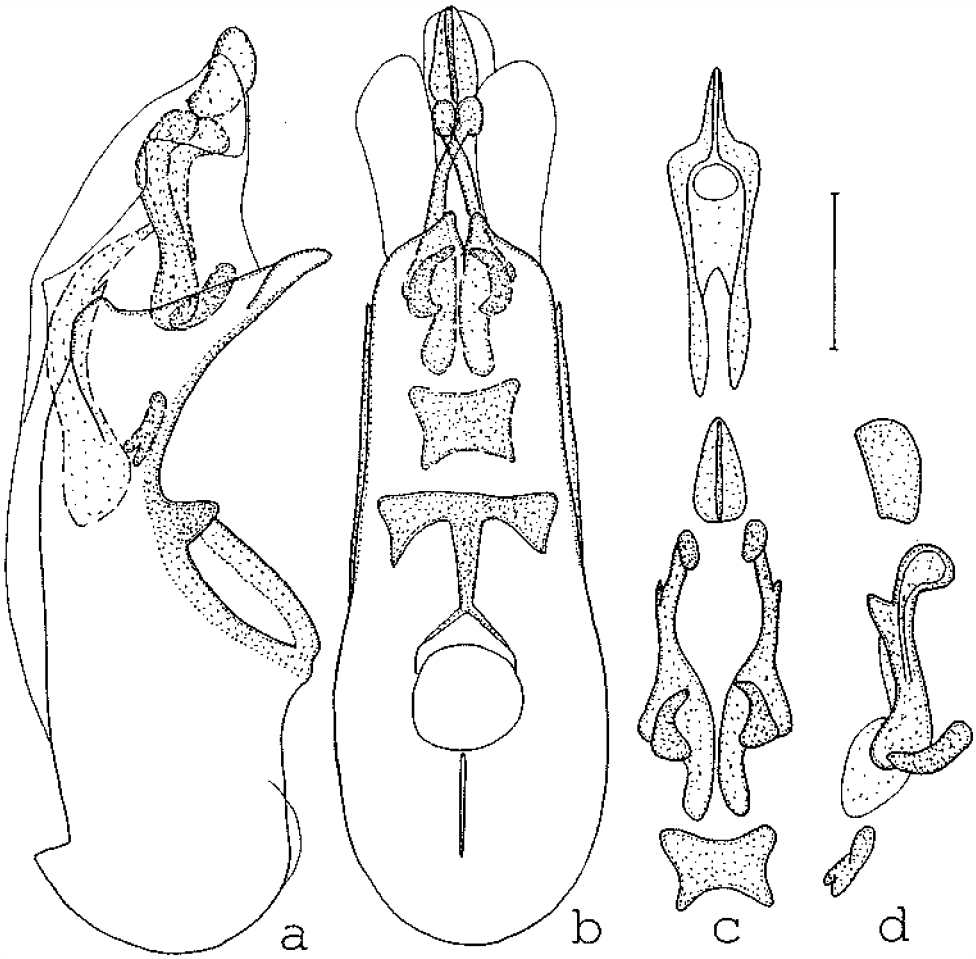


Fig. 14: *Ilyobates merkli* EPPELSHEIM. Median lobe of aedeagus in lateral (**a**) and in ventral view (**b**); internal structures of median lobe in ventral (**c**) and in lateral view (**d**). Scales: 0.2 mm.

Punctation of head less dense than in average *I. nigricollis*, punctation of pronotum distinctly finer and sparser than in *I. nigricollis* and than that of elytra; forebody therefore with more shine. Pronotal pubescence directed diagonally latero-caudad. Eyes of similar relative size and shape as in *I. nigricollis*; antennae very long (see measurements), antennomeres IV and V distinctly oblong, and X not transverse; antennomere XI without sexual dimorphism, in both sexes apically constricted. Legs very long and slender (see measurements); hind wings apparently fully developed.

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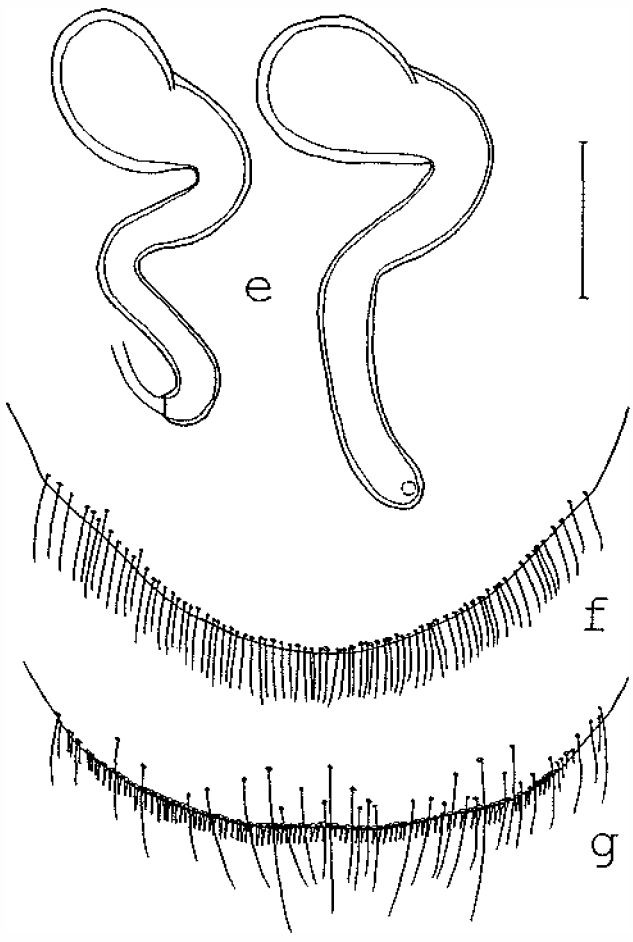


Fig. 14: *Ilyobates merkli* EPPELSHEIM. Spermathecae of 2 ♀♀ (**e**); hind margin of ♂ sternum VIII (**f**); hind margin of ♀ sternum VIII (**g**). Scales: 0.2 mm.

Abdomen with punctation and pubescence similar to *I. nigricollis*; transverse impressions without trace of median carina; tergum X very wide.

♂: sternum VIII posteriorly distinctly convex (Fig. 14f); aedeagus very large, ventral process broad, internal structures of characteristic shape and arrangement (Figs 14a - d).

♀: hind margin of sternum VIII weakly convex or ± truncate, sometimes with weak central concavity (Fig. 14g); duct of spermatheca relatively long, capsule less bulbous than in *I. nigricollis* (Fig. 14e).

Distribution and bionomics

Judging from the few known records, *I. merkli* is restricted to the southeast of Europe with the northwestern limit of distribution in southeastern Austria, where the species has been recorded only from Kärnten and Steiermark (HORION, 1967; material examined). In addition, I have seen specimens from Slovenia, Hungary, Croatia, and from Bosnia-Herzegovina (see material examined). BERNHAUER (1902a) also indicates the species for Turkey, but I have seen no material confirming this record.

Adult beetles have been collected in leaf litter, on one occasion also on a sandy bank of the Drau (Kärnten) among workers of *Myrmica* sp., in May and June (HORION 1967; material examined); one teneral specimen was taken in the beginning of July.

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4.6. *Ilyobates mirabilis* sp. n.

Fig. 15, Table 1

Holotype ♂: Ganglb. 93, Wochein (NHMW).

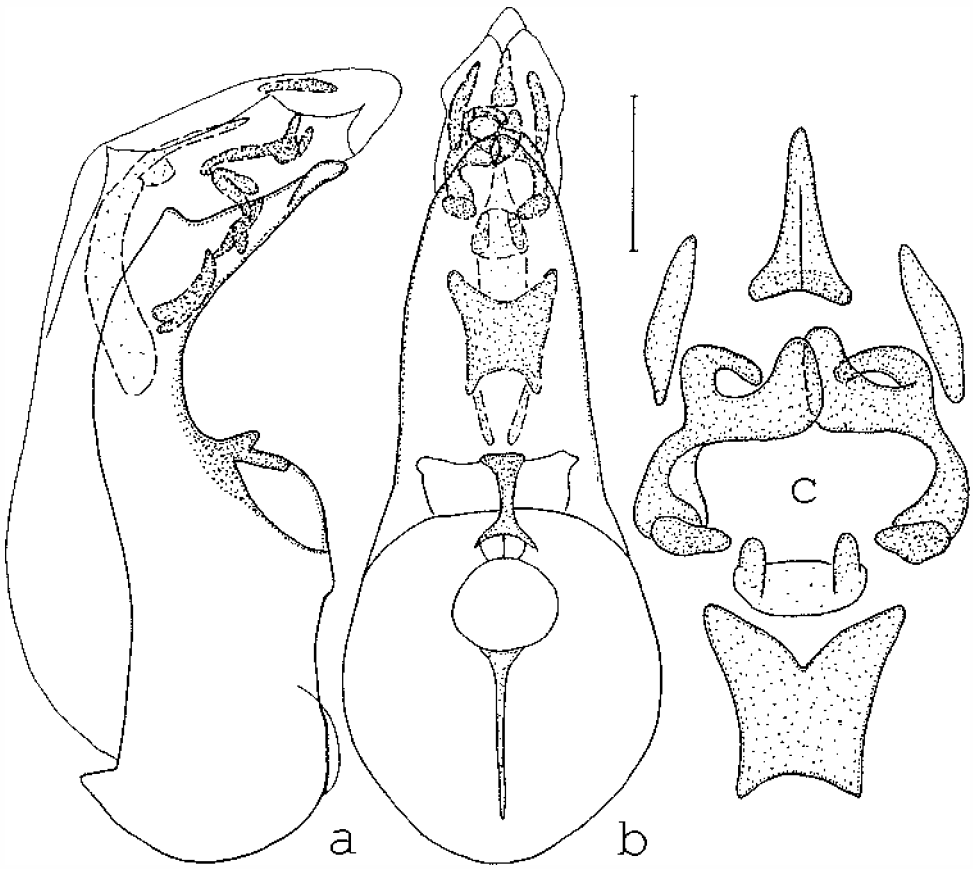
Paratypes: 1♂: ♂/ Cerna prst, Carn., Winkler/ spec. ? nov. ?/ ex coll. Scheerpeltz (NHMW); 1♂: Tarnowanerwald, 1000m, Lokay/ spec. ? nov. ?/ ex coll. Scheerpeltz (cAss).

Diagnosis

Measurements and ratios (range; n = 3): AL: 2.28 - 2.80; HW: 0.79 - 0.86; PW: 1.04 - 1.21; PL: 1.00 - 1.13; EL: 0.91 - 0.98; HTiL: 1.32 - 1.52; HTaL: 0.99 - 1.09; HT1L: 0.30 - 0.37; HT2L: 0.39 - 0.43; ML: 0.80 - 0.95; TL: 7.4 - 8.1; PW/HW: 1.33 - 1.48; PW/PL: 1.04 - 1.07; EL/PL: 0.87 - 0.90; HTaL/HTiL: 0.72 - 0.76; HT1L/HT2L: 0.74 - 0.89.

Large species, only slightly smaller than average *I. merkli* (see measurements). In general appearance somewhat resembling an oversized *I. nigricollis*. Coloration similar to average *I. nigricollis*, head and pronotum dark brown to blackish, elytra dark reddish, and abdomen, except for the lighter hind margins of the segments brown to dark brown.

Punctation of head denser and coarser than in *I. nigricollis*, interstices reduced to very narrow ridges. Eyes smaller than in *I. nigricollis*, but - like *I. mech* - more bulging than in that species. Antennae relatively longer and more massive than in *I. nigricollis*, but shorter than in *I. merkli*; apical constriction of antennomere XI very distinct (at least in ♂).



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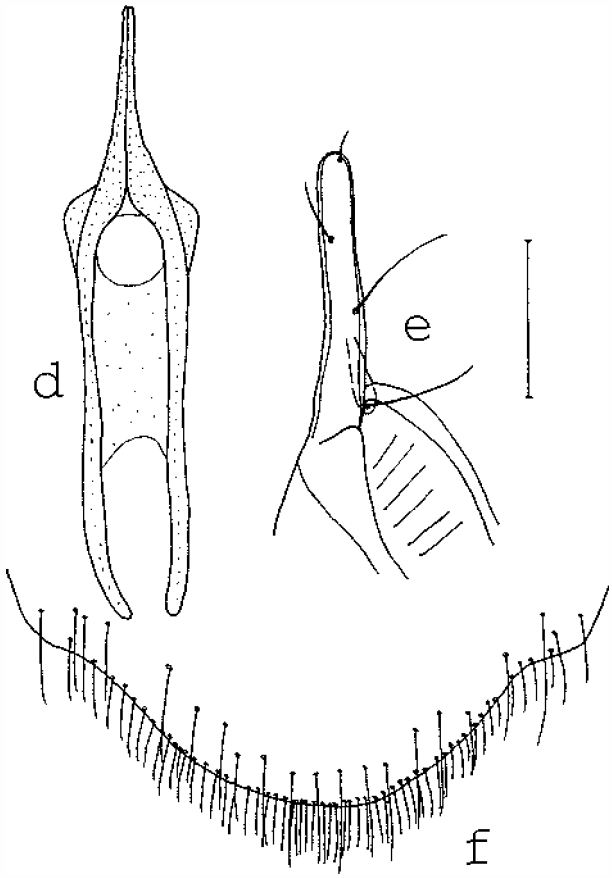


Fig. 15: *Ilyobates mirabilis* sp. n. Median lobe of aedeagus in lateral (**a**) and in ventral view (**b**); internal structures of median lobe in ventral view (**c, d**); apical lobe of paramere (**e**); hind margin of ♂ sternum VIII (**f**). Scales: a, b, e, f: 0.2 mm; c, d: 0.1 mm.

Pronotum with shallow median furrow of variable width in posterior half; punctation denser and coarser than in *I. nigricollis*, especially in central area, but not largely confluent as in *I. mech*; pubescence in lateral areas directed ± laterad (similar to *I. mech*). Elytra with punctation and pubescence similar to *I. nigricollis*; hind wings apparently developed.
Abdomen with punctation and pubescence similar to *I. nigricollis*; transverse impressions without trace of median carina.
♂: sternum VIII posteriorly distinctly convex (Fig. 15f); aedeagus large, but size very variable (see measurements); ventral process more slender than in *I. merkli*, internal structures of characteristic shape and arrangement (Figs 15a - c).
♀: unknown.

Derivatio nominis: The name (lat.: wonderful, amazing) refers to both the remarkable size and appearance of the species and the unexpected fact that the revision of *Ilyobates* material should not only yield synonyms, but also a new species.

Distribution and bionomics
The species is presently known only from three localities in northwestern and western Slovenia. The labels attached to the type specimens do not indicate any ecological details, except for the altitude (1000m) in one of the paratypes.

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5. Key to the species of *Ilyobates*

Due to the enormous intraspecific variation and consequently considerable character overlap, a safe identification often requires the examination of the primary sexual characters. For instructions regarding the dissection and examination of the internal structures of the aedeagus and for explanations of abbreviations and measurements, section 2 is referred to.

1. Punctation of pronotum at least in central area ± longitudinally confluent and rugose; surface in median area usually completely mat. Anterior transverse impressions of abdominal terga III - VI with long and very distinct median carina. Eyes bulging and much shorter than postgenae in dorsal view. Pronotal pubescence directed ± laterad in lateral area.
♂: ventral process of aedeagus more distinctly delimited from lateral parts of median lobe, in lateral view strongly bent; internal sac with very large sclerotized apical structure and further structures of characteristic shape (Figs 11a - c).
♀: spermatheca ± S-shaped (Fig. 11e).
Alps, Corse, Sardinia, Carpathians, SE Europe, Caucasus?. . . . . ***I. mech*** (BAUDI)

\- Punctation of pronotum often very dense, but not confluent, delimited at least by narrow ridges. Anterior transverse impression of terga III - IV at most with short and less distinct median carina. Eyes often larger and less bulging, pronotal pubescence in most species directed more diagonally postero-laterad. Sexual characters different. 2

2. Anterior transverse impressions of abdominal terga V - VI with longer, those of terga III - IV with very short median carina. On average smaller species (HW: <0.84; PW: <1.12; PL: <1.07). More widespread species. 3

\- Anterior transverse impressions of abdominal terga III - VI without trace of median carina. On average larger species (HW: >0.74; PW: >1.04; PL: >0.93).
Distribution confined to the southeast of Central Europe and to southeastern Europe. 5

3. Punctation of pronotum fine, distinctly finer than that of head and elytra. Pubescence of pronotum in latero-median areas directed more laterad.
♂: aedeagus and internal structures as in Figs 10a - c.
♀: spermatheca as in Fig. 10e.
Western, central and southeastern Europe, absent from northern Europe and northern Central Europe. . . . . ***I. propinquus*** (AUBÉ)

\- Punctation of pronotum coarse, not distinctly finer than that of head. Pubescence of pronotum in latero-median area directed diagonally postero-laterad. Sexual characters different. 4

4. On average larger species. Punctation of head and pronotum on average less dense, surface therefore usually with some shine. (Due to considerable character overlap, the sexual characters should always be examined.)
♂: aedeagus in ventral view distinctly broader and with wider ventral process; internal structures of characteristic shape (Figs 2a, b, d).
♀: spermatheca with longer and near capsule thinner duct (Fig. 2e).
Widespread in Europe, from the north of the Iberian Peninsula, the south of Great Britain and northern Europe to the northwest of the Russian Federation and the Balkans. . . . . ***I. nigricollis*** (PAYKULL)

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- On average smaller species (HW: <0.72; PW: <0.93; PL: <0.88). Punctation of head and pronotum on average denser, surface therefore usually ± mat.
  ♂: aedeagus in ventral view slender and with narrower ventral process; internal structures of characteristic shape (Figs 6a - c).
  ♀: spermatheca with shorter and near capsule wider duct (Fig. 6d).
  Widespread in Europe, from France (except for the southwest), the British Isles and northern Europe to the west of the Russian Federation, Ukraine, the Caucasus region, and the Balkans; introduced in North America. ..... ***I. bennetti*** DONISHORPE

5. Pronotum with coarse and dense punctation, surface ± mat; pronotal pubescence in lateral area ± transverse. Eyes smaller and more bulging.
  ♂: aedeagus in ventral view with more slender ventral process and with internal structures of characteristic shape and arrangement (Figs 15a - d).
  ♀: unknown.
  Slovenia. ..... ***I. mirabilis*** sp. n.
- Punctation of pronotum fine and relatively sparse, distinctly finer than that of elytra, surface of pronotum with more shine; pronotal pubescence in lateral area directed ± diagonally postero-laterad. Eyes larger and moderately convex.
  ♂: aedeagus in ventral view with broad ventral process; internal structures different (Figs 14a - d).
  ♀: spermatheca as in Fig. 14e.
  Southeast of Central Europe, southeastern Europe. ..... ***I. merkli*** EPPELSHEIM

6. Species excluded from *Ilyobates*

6. 1. *Pyroglossa puberula* (CASEY, 1893), comb. n.

Callicerus puberulus CASEY, 1893: 310f.
Gennadota puberula (CASEY): CASEY (1906)
Ilyobates puberulus (CASEY): SEEVERS (1978)
Ilyobates puberulus (CASEY): KLIMASZEWSKI & PECK (1986), designation of lectotype

Types examined
Lectotype ♂ [head, pronotum and terminal segments of abdomen missing): N. Y./ Gennadota puberula Cay./ Type USNM 39732/ Casey bequest 1925/ Callicerus puberulus (USNM). Paralectotype ♀: Enola Pa., IX. 3.08/ Casey determ., puberulus-2 (USNM).

Diagnosis
see KLIMASZEWSKI & PECK (1986)

For comments see below the following species.

6. 2. *Pyroglossa canadensis* (CASEY, 1906), comb. n.

Gennadota canadensis CASEY, 1906: 309
Ilyobates canadensis (CASEY): SEEVERS (1978)
Ilyobates canadensis (CASEY): KLIMASZEWSKI & PECK (1986), designation of lectotype

Type examined
Lectotype ♀: Can./ Type USNM 39733/ canadensis Cay./ Casey bequest 1925 (USNM).

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Diagnosis

see KLIMASZEWSKI & PECK (1986)

Comments

After realizing that the type species of *Callicerus* GRAVENHORST, *C. obscurus* GRAVENHORST, had 4-jointed protarsi and was a member of the Myrmedoniini (today Athetini), CASEY (1906) described the genus *Gennadota* to accommodate the designated type species *G. puberula* (CASEY) (transferred from *Callicerus*) and the new species *G. canadensis* CASEY. SEEVERS (1978) synonymized *Gennadota* CASEY with *Ilyobates*, referring to his key to North American Aleocharinae for generic characters. According to this key, *Ilyobates* is characterized within the Oxypodini by a broad neck, the presence of basal impressions without median carinae on the abdominal terga III - VI, the absence of a frontal suture and of a median carina on the mesosternum, a slender pronotum, and distinctly visible hypomera in lateral view. KLIMASZEWKI & PECK (1986), too, attribute the two North American species to *Ilyobates* and present a more detailed diagnosis of the genus.

Callicerus puberulus CASEY and *Gennadota canadensis* CASEY are here excluded from *Ilyobates* for the following reasons. They do not possess several synapomorphies present in species of *Ilyobates*, such as the massive antennae, the coarse punctation of the forebody, the apically incised median lobe of the aedeagus, the arrangement and morphology of the internal structures of the aedeagus, the short stout duct of the spermatheca, and the distinctly modified marginal setae of the ♀ sternum VIII (cf. Figs 1-14, 62 - 64, 96, 107 in KLIMASZEWSKI & PECK, 1986). In addition, they are distinguished from *Ilyobates* by the different shape of the head, the morphology of the ligula and the chaetotaxy of the labrum (see Figs 9 and 13 in KLIMASZEWSKI & PECK, 1986), and by the pubescence pattern of the pronotum (in the two North American species directed cephalad in anterior half of midline). The final argument is based on the biogeographical evidence: as has been shown above, all the species of *Ilyobates* are strictly Western Palaearctic.

On the other hand, *C. puberulus* and *G. canadensis* share many significant characters with the species of *Pyroglossa* BERNHAUER, which have been described from Eastern Palaearctic region (for a discussion see ASSING & WUNDERLE, 1997). There is remarkable agreement in external morphology, the mouthparts and the primary and secondary sexual characters - above all, the morphology of the deeply bifid ligula with stout apical appendices, and the spermatheca (cf. Figs 9 a - f, k in ASSING & WUNDERLE, 1997 and Figs 9 - 13, 64, 107 in KLIMASZEWSKI & PECK, 1986). In the North American species the pubescence of the pronotal midline is directed cephalad in the anterior half and caudad in the posterior half, whereas in the examined Eastern Palaearctic respresentatives of *Pyroglossa* it is directed cephalad also in the posterior half, but differences in the pronotal pubescence pattern are known to occur in various aleocharine genera, e. g. *Atheta* THOMSON and *Aleochara* GRAVENHORST.

In view of the evidence outlined above, *C. puberulus* and *G. canadensis* are here transferred to *Pyroglossa*, and the following synonymy is established:

Pyroglossa BERNHAUER, 1901 = *Gennadota* CASEY, 1906, **syn. n.**

Acknowledgements

I am much indebted to all the colleagues indicated section 2, who contributed to the present study by arranging loans of types and additional material. Dr. LOTHAR ZERCHE, Eberswalde, kindly reviewed the manuscript.

DOI: 10.21248/contrib.entomol.49.2.295-342

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DOI: 10.21248/contrib.entomol.49.2.295-342

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: Beiträge zur Entomologie = Contributions to Entomology

Jahr/Year: 1999

Band/Volume: 49

Autor(en)/Author(s): Assing Volker

Artikel/Article: A revision of Ilyobates Kraatz, 1856 (Coleoptera: Staphylinidae, Aleocharinae, Oxypodini) 295-342