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On the taxonomy and natural history of *Oxypoda brachyptera* and *O. tarda*

(Coleoptera: Staphylinidae: Aleocharinae)

With 28 figures and 2 tables

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Summary

Based on a revision of types and additional material, *Oxypoda brachyptera* (STEPHENS, 1832) and *O. tarda* SHARP, 1871, two species with a controversial and confusing taxonomic history, are regarded as distinct species, redescribed, and illustrated. A lectotype is designated for *Oxypoda tarda*. Numerous field studies conducted in northwestern Germany during the period from 1981 through 2001 yielded approximately 8,500 adult specimens of *O. brachyptera* and *O. tarda*. Based on these data, as well as on anatomical studies, the life histories of both species, including their seasonal activity, seasonal density, reproduction periods, duration of pre-imaginal development, and pupal emergence, are investigated. Both species are epigeically active from spring through autumn, develop without diapause, and hibernate in the adult stage. In contrast to *Oxypoda tarda*, which has only one generation per year, *O. brachyptera* is apparently bivoltine. Both species are generally found in open, unshaded biotopes. Nevertheless, regarding their respective habitats, they are distinctly segregated. While *O. brachyptera* was recorded from drier and wamer habitats on sandy or calcareous soils, *O. tarda* usually occurs in moist localities on heavier soils. Rarely, they were found to occur syntopically. Both species are wing-dimorphic, the macropterous morph being distinctly rarer than the micropterous morph; the dimorphism is not sex-related.

Key words

Coleoptera, Staphylinidae, Aleocharinae, Oxypodini, *Oxypoda*, West Palaearctic, taxonomy, ecology, lectotype designations, natural history, seasonal activity, seasonal density, oviposition, flight muscles, wing dimorphism

Zusammenfassung

Die Identität von Oxypoda brachyptera (STEPHENS, 1832) und O. tarda SHARP, 1871 war in der Vergangenheit immer wieder Gegenstand kontroverser Sichtweisen; beide Arten wurden oft konfundiert. Eine Untersuchung der Typen und weiteren Materials ergab, dass es sich zweifelsfrei um verschiedene Arten handelt; sie werden redeskribiert und abgebildet. Für Oxypoda tarda wird ein Lectotypus designiert. Zahlreiche Freilanduntersuchungen, die in verschiedenen Biotopen Nordwestdeutschlands in der Zeit von 1981 bis 2001 durchgeführt wurden, ergaben eine Datenbasis von insgesamt annähernd 8500 Imagines von O. brachyptera und O. tarda. Auf dieser Grundlage sowie anhand anatomischer Untersuchungen wird die Phänologie beider Arten, einschließlich der saisonalen Aktivität, der saisonalen Dichte, Reproduktionsphasen, Dauer der Präimaginalentwicklung und Emergenz, geklärt. Beide Arten sind vom Frühjahr bis in den Spätherbst epigäisch aktiv, entwickeln sich ohne Diapause und überwintern im Adultstadium. Anders als Oxypoda tarda, für die nur eine Generation pro Jahr nachgewiesen wurde, ist O. brachyptera offenbar bivoltin. Beide Arten kommen in der Regel in unbewaldeten

Biotopen vor. Trotzdem sind sie hinsichtlich ihrer Habitate deutlich gesondert. Während *O. brachyptera* trockenere und wärmere Lebensräume auf Sand- oder Kalkböden besiedelt, war *O. tarda* gewöhnlich in feuchteren Biotopen auf schwereren Böden vertreten. Selten wurden beide Arten syntop nachgewiesen. Sowohl *O. brachyptera* als auch *O. tarda* sind flügeldimorph; bei beiden ist die macroptere Morphe fast immer deutlich seltener als die brachyptere Morphe. Hinsichtlich dieses Dimorphismus wurden keine Unterschiede zwischen den Geschlechtern beobachtet.

Introduction

Oxypoda brachyptera (STEPHENS, 1832) and O. tarda SHARP, 1871 have had a long history of taxonomic confusion. The original description of the former is based on specimens from two localities in England. SHARP (1871) described O. tarda from Scotland, stating that the species was distinguished from O. brachyptera by darker coloration, larger size, longer elytra, and shorter and finer antennae. However, O. tarda was regarded as either a synonym or a variety by most subsequent authors (e.g., GANGLBAUER 1895, BERNHAUER 1902, BERNHAUER & SCHEERPELTZ 1926, Joy 1932, HORION 1967, POPE 1977). In an article on some Central European Oxypoda species, LOHSE (1970) stated that what had been recorded as O. difficilis ROUBAL, 1931 from Germany in fact referred to O. tarda, but had not studied the types of the latter. According to a key he published a few years later (LOHSE 1974), O. tarda and O. difficilis are distinguished from O. brachyptera by the denser punctation of the abdomen (particularly abdominal tergite VIII), the longer elytra, the weaker punctation of the pronotum, and the longer and more slender antennae. Apparently based on a personal communication by ZERCHE, LOHSE (1989) synonymised O. difficilis with O. brachyptera. In a contribution specifically dealing with the identities of O. brachyptera and O. tarda, WHITEHEAD (1996) discussed the taxonomic status of both names without studying type material and without arriving at plausible conclusions. It can be inferred from his diagnoses and illustrations that he attributed macropterous specimens to O. tarda and micropterous individuals to O. brachyptera. The rough sketches of the genitalia provided in the article suggest that most specimens he had identified as O. tarda in fact refer to O. brachyptera.

The drawings of the primary sexual characters in LOHSE (1974) indicate that the aedeagus of *O. tarda* is larger than that of *O. brachyptera*, but additional distinguishing characters are difficult to appreciate. Recently, KLIMASZEWSKI et al. (2006) published photographs of the habitus, as well as the primary and secondary sexual characters of *O. brachyptera*.

The ecology of *O. brachyptera* and *O. tarda* has been the subject of controversy. According to LOHSE (1974), both species are found in the same localities, with *O. tarda* being the rarer of the two. Based on pitfall trap studies in northern Germany, ASSING (1988) suggested that *O. brachyptera* is found in drier and warmer habitats on sandy soils, whereas *O. tarda* occurs in moist habitats on heavier soils. The observations pointed out by WHITEHEAD (1996) are not conclusive. The life histories of both species have never been studied in detail.

The present study was mainly initiated by repeated requests from colleagues regarding the identities, separation, and ecological characteristics of *O. brachyptera* and *O. tarda*. In order to verify if both species had been interpreted correctly, an examination of the type respective material was required. Also, since abundant material of both species had been accumulated in the course of numerous field studies during a period of more than two decades, a taxonomic study *O. brachyptera* and *O. tarda* provided an opportunity to clarify their natural history.

Material and methods

The material treated in this study is deposited in the following public institutions and private collections:

BMNH	The Natural History Museum, London (R. G. Booth)
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg (L. Zerche)
cAss	author's private collection
cSch	private collection Michael Schülke, Berlin

Morphology and anatomy:

The morphological studies were conducted using a Stemi SV 11 microscope (Zeiss Germany) and a Jenalab compound microscope (Carl Zeiss Jena). For the photographs a digital camera (Nikon Coolpix 995) was used.

Elytral length was measured at the suture from the apex of the scutellum to the posterior margin of the elytra. The length of the median lobe of the aedeagus was measured from the apex of the ventral process to the base of the capsule.

The parameral side of the median lobe of the aedeagus (i.e., the side where the sperm duct enters) is referred to as the ventral, the opposite side as the dorsal aspect.

The abdomen of several thousand females was dissected to examine the condition of the ovaries. The presence of mature eggs was interpreted as evidence of oviposition activity. In all the studied specimens the length of the hind wings was recorded. In order to assess the presence or absence of flight muscles, the thorax of more than a hundred macropterous specimens was dissected by removing the dorsal portion of the thoracal ectoscleleton.

Ecology:

During a period of more than two decades (1981-2001), field studies were conducted on the staphylinid fauna of a variety of habitats, particularly *Calluna* heathlands on sandy soils, in Niedersachsen, northern Germany. These studies yielded more than 100,000 adult Staphylinidae and more than 15,000 larvae. The localities where either *Oxypoda brachyptera* or *O. tarda* were recorded are listed in Tab. 1. For more details on these sites see Assing (1988, 1992, 1993, 1994), HOFMEISTER et al. (2001) and MELBER et al. (1996).

In all the study sites pitfall traps were used to assess the species inventory and seasonal activity. The number of pitfall traps varied between three and 52 per year and site. For details regarding the type, construction, and maintenance of the pitfall traps see MELBER (1987). The traps remained installed throughout the year (i.e., also in winter) and were emptied at half-monthly intervals, in some sites at monthly intervals. The data shown in Figs 26-27 are exclusively based on those full-year studies with pitfall traps that were emptied at half-monthly intervals. In all, more than 700 one-year pitfall traps were installed and maintained.

In addition to pitfall trapping, soil extractions after KEMPSON et al. (1963) were conducted in several heathlands to assess the densities of Staphylinidae. The samples were taken at halfmonthly intervals throughout the year. For more information on the field methods used see ASSING (1993).

site	habitat	study period	methods
Helstorfer Reiterheide near Neustadt/	Calluna heathland in succession	1981-91	pitfall traps,
Rbg.	to pine forest		soil extractions
Lüneburger Heide, Niederhaverbeck	dry <i>Calluna</i> heathland	1983-86	pitfall traps,
			soil extractions
Lüneburger Heide, Niederhaverbeck	sandy grassland	1986	pitfall traps,
			soil extractions
Lüneburger Heide, Schneverdingen	<i>Calluna</i> heathland, grassy dunes with sparse vegetation cover	1992-2001	pitfall traps
Lüneburger Heide, Haverbeck	<i>Calluna</i> heathland	1993-99	pitfall traps
Glider airfield Scheuen near Celle	<i>Calluna</i> heathland	1984	pitfall traps, soil extractions
NSG "Heiliger Hain" near Gifhorn	dry <i>Calluna</i> heathland	1983-87	pitfall traps, soil extractions
NSG "Heiliger Hain" near Gifhorn	sandy grassland	1986	pitfall traps, soil extractions
NSG "Heiliger Hain" near Gifhorn	sandy pine forest	1987	pitfall traps
Bokeler Heide SE Bokel	grassy <i>Calluna</i> heathland	1985-86	pitfall traps
Garlstedter Heide N Bremen	sandy heathland with old <i>Calluna</i>	1985	pitfall traps
NSG "Rössenbergheide-Külsenmoor" S Oerrel	transsect from <i>Calluna</i> heat- land to moist Erica heathland	1986-1987	pitfall traps
Wurster Heide near Cuxhaven	<i>Calluna</i> heathland with <i>Empetrum</i>	1987	pitfall traps
Hannover	floodplain meadows	1986/87	pitfall traps
Hannover	moist fallows/meadows	1986/87	pitfall traps
Hannover	sandy grassland	1986/87	pitfall traps
Hannover	urban lawns	1986-87, 1989	pitfall traps
Hannover	cultivated gardens	1986/87	pitfall traps
Hannover	garden hedges/bushes	1986-87, 1989	pitfall traps
Bad Nenndorf	garden	1987/88	pitfall traps
Öselberg near Wolfenbüttel	calcareous grassland	1999	pitfall traps
Wernershöhe near Hildesheim	calcareous field margin	1998	pitfall traps
Ortsberg near Alfeld/Leine	xerothermous calcareous gras- land with shrubs	1985-87	pitfall traps
Steinberg near Hildesheim	xerothermous slopes (grassland, shrubs, forests)	1996/97	pitfall traps
Düt near Hameln	xerothermous sandy Arrhena- theretum	1990	pitfall traps
	ulciclum		

Tab. 1: Study plots where either Oxypoda brachyptera or O. tarda were recorded. All sites are located in Niedersachsen, northern Germany.

Results

In the course of the studies, nearly 8,000 adult specimens of *O. brachyptera* and approximately 450 specimens of *O. tarda* were examined (Tab. 2 and additional material examined). The bulk of this material was collected with pitfall traps. In order to ensure that the previous (and present) interpretation of both species is correct, the type material was studied.

Tab. 2: Number of adult specimens recorded in the study sites. The number of macropterous individuals is given in parentheses.

site	habitat	brachyptera	tarda
Helstorfer Reiterheide	<i>Calluna</i> heathland	158 (1)	
Lüneburger Heide, Niederhaverbeck	dry <i>Calluna</i> heathland	714	
Lüneburger Heide, Niederhaverbeck	sandy grassland	33	
Lüneburger Heide, Schneverdingen	dry, sparsely vegetated, grassy <i>Calluna</i> heathland	2892 (105)	
Lüneburger Heide, Haverbeck	<i>Calluna</i> heathland	154 (7)	
Scheuen	<i>Calluna</i> heathland	21	
Heiliger Hain	dry <i>Calluna</i> heathland	2433 (2)	
Heiliger Hain	sandy grassland	33	
Heiliger Hain	sandy pine forest	5	
Bokeler Heide	grassy <i>Calluna</i> heathland	1	
Garlstedter Heide	heathland with old Calluna	14	
Rössenbergheide	Calluna/Erica heathland	281	
Wurster Heide	<i>Calluna</i> heathland	1	
Hannover	floodplain meadows		417 (4)
Hannover	moist fallows/grassland		22
Hannover	sandy grassland	136 (20)	
Hannover	urban lawns	258 (35)	
Hannover	cultivated gardens	13	
Hannover	garden hedges/bushes	13	
Bad Nenndorf	garden	1	
Öselberg	calcareous grassland	7	
Wernershöhe	calcareous field margin	124 (1)	
Ortsberg	xerothermous calcareous grass- land with shrubs	21	
Steinberg	xerothermous slopes	195 (15)	
Düt	xerothermous slopes	6	
Immensen	sandy arable land	2 (1)	
total		7826 (187)	439 (4)

Oxypoda brachyptera (STEPHENS, 1832) (Figs 1-7, 15-18, 24-27)

Aleochara brachyptera STEPHENS, 1832: 128. Oxypoda forticornis FAIRMAIRE & BRISOUT DE BARNEVILLE, 1859: 37 f. Bessopora subrugosa SAHLBERG, 1876: 111 f. Oxypoda difficilis ROUBAL, 1931: 70 f. Oxypoda maritima DONISTHORPE, 1932a: 3. Oxypoda salictaria DONISTHORPE, 1932b: 4. Oxypoda brachyptera f. obscura KORGE, 1959: 61. Oxypoda brachyptera f. wagneri KORGE, 1959: 59 ff.

Type material examined:

Syntype \mathfrak{P} : "h3 5/1 / 9 [6?] / Kirby / brachyptera / Syntype / Syntype Aleochara brachyptera Stephens from Kirby colln., det. R. G. Booth 2011 / Oxypoda brachyptera (Stephens) det. V. Assing 2011" (BMNH).

Comment:

The original description of *Aleochara brachyptera* is based on an unspecified number of syntypes from "Norfolk" and "Barham" (STEPHENS 1832). From the punctuation code (HAMMOND 1972) used by STEPHENS (1829) and the fact that the species was attributed to "Kirby MSS" by STEPHENS (1829, 1832), it can be inferred that the syntypes are not deposited in the Stephens collection, but in other collections. One female syntype was located in the Kirby collection. This syntype is conspecific with the previous interpretation of *Oxypoda brachyptera*.

Additional material examined:

Apart from the material listed in Tab. 2, the following material was studied:

Germany: Niedersachsen: 1 σ [macropterous], Hannover, Osterfelddamm, pitfall, VIII-IX.1991, leg. Sprick (cAss); 1 σ , 2 φ φ [micropterous], Hannover-Herrenhausen, garden, pitfall, IV.1986 (cAss); 1 σ [micropterous], same data, but VI.1985 (cAss); 2 σ σ , Hannover-Langenhagen, sandy grassland, pitfall, V.1991, leg. Sprick (cAss); 4 σ σ , 2 φ φ [micropterous], S Hannover Ronnenberg, potash mine, salt habitat, pitfall, VII.1995, leg. Schmidt (cAss); 1 σ [macropterous], Neustadt/Rbg., Himmelreich, window trap, VII.1991, leg. Assing (cAss); 1 σ [micropterous], Hameln env., Großenwieden, field margin, pitfall, IV.1986, leg. Sprick (cAss); 2 σ σ [micropterous], Süntel, Rannenberg, calcareous arable land, pitfall, V.1988, leg. Sprick (cAss); 1 φ [micropterous], Göttingen env., Fredelsloh, calcareous grassland, pitfall, VI.1984, leg. Joger (cAss); 1 φ [macropterous], same data, VI.1986 (cAss); 1 φ [micropterous], Bückeburg env., Ahnsen, arable land, pitfall, V.1986, leg. Sprick (cAss); 1 φ [macropterous], wilhelmshaven, Neuenburger Urwald, window trap, VIII.1996, leg. Menke (cAss). Schleswig-Holstein: 124 exs. [11 macropterous], Husum env., Beltringharder Koog [54°33'N, 8°55'E], salt marsh, meadow, pitfall, VI-X.1991 (cAss): 1 σ [macropterous], Leipzig, uncultivated arable land, pitfall, V.1995, leg. Sprick (cAss); 1 σ .

Austria: Kärnten: 1 ^Q [micropterous], Gurktaler Alpen, Innerkrems, Gaipahöhe, 2100-2150 m, N-slope, 17.VII.1986, leg. Assing (cAss).

Redescription:

Small species; body length 2.2-2.6 mm. Coloration variable; usual coloration: head reddishbrown to blackish-brown; pronotum and elytra reddish-yellow to reddish; abdomen reddish, with segment VI and anterior portion of segment VII infuscate; legs yellowish to reddish-yellow; antennae dark-yellowish to brown. Occasionally, especially in macropterous specimens, the coloration is significantly darker, with the head almost blackish, the pronotum and elytra dark-brown, and the abdomen more extensively infuscate. Beitr. Ent. 62 (2012) 1

Head transverse; eyes moderately large, approximately as long as postocular portion in lateral view, not larger in macropterous than in micropterous specimens. Antenna relatively long and massive, moderately and gradually incrassate apically; preapical antennomeres approximately 1.5 times as wide as long; antennomere XI with weakly pronounced sexual dimorphism, on average slightly longer in males than in females. Maxillary palpus not conspicuously elongated; preapical palpomere approximately 3 times as long as wide.

Pronotum approximately 1.35 times as broad as long, widest approximately in the middle; hind margin broadly convex, not distinctly bisinuate; punctation dense and shallow; interstices with microsculpture (Fig. 1).

Elytra dimorphic, in micropterous morph 0.7-0.8 times, in macropterous morph 0.90-0.95 times as long as pronotum; posterior margin distinctly sinuate near postero-lateral angles; punctation dense, usually somewhat coarser than that of pronotum (Fig. 2). Hind wings dimorphic, either fully developed (macropterous morph) or reduced to short stubs (micropterous morph); exceptionally (only one specimen seen) submacropterous. Metatarsomere I almost as long as combined length of metatarsomeres II-IV.

Abdomen with segments III-VI of subequal width; segments VII-X tapering. Punctation fine, dense on tergites III-VI, somewhat sparser on posterior tergites (Fig. 3); posterior margin of tergite VII with palisade fringe in both morphs; posterior margin of tergite VIII weakly convex.

♂: sternite VIII produced posteriorly (Fig. 4); aedeagus with median lobe 0.30-0.35 mm long (Fig. 15-17); ventral process apically incised in ventral view (Fig. 18); paramere with long apical lobe.

^{φ}: sternite VIII with broadly convex posterior margin, with row of modified, stouter marginal setae (Fig. 5); spermatheca as in Figs 6-7.

Systematic position:

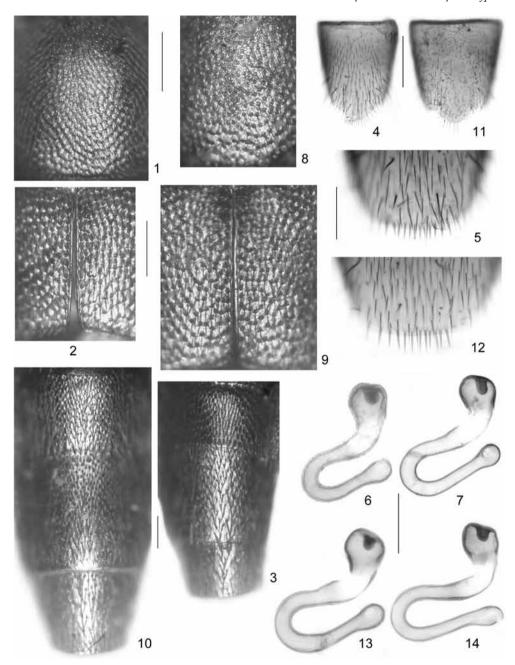
Oxypoda brachyptera is currently placed in the subgenus *Bessopora* THOMSON, 1859 (type species: *Oxyopda testacea* ERICHSON, 1837).

Comparative notes:

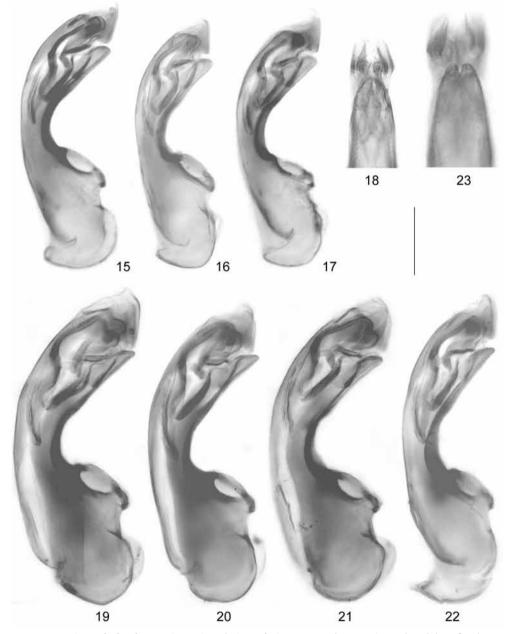
In Central Europe, the only species of similarly small size, similar coloration, body shape, punctation, a pronounced pterodimorphism, and similar sexual characters is *O. tarda*. For notes on the separation of *O. brachyptera* from this species see the following section. In external morphology, the macropterous morph of *O. brachyptera* also somewhat resembles *O. ferruginea* ERICHSON, 1839, with which it has had a history of confusion (HORION 1967). For illustrations of the sexual characters of this species see ASSING (2011). From similar Mediterranean representatives of the *O. brachyptera* group and of other species groups, such as *O. caespita* ASSING, 2003, *O. lesbia* ASSING, 2005, *O. ahirica* ASSING, 2006, *O. afimbriata* ASSING, 2006, *O. praecisa* ASSING, 2006, and *O. cingulum* BERNHAUER, 1902, *O. brachyptera* is separated by the combination of larger eyes, relatively longer elytra (even in the micropterous morph), the presence of a pterodimorphism, as well as by the sexual characters. For illustrations of the compared species see ASSING (2003, 2005, 2006a, 2006b). For more images of the habitus, as well as of the primary and secondary sexual characters of *O. brachyptera* see KLIMASZEWSKI et al. (2006).

Distribution:

According to HORION (1967) and SMETANA (2004), *O. brachyptera* is distributed in the North Palaearctic from Italy, France, and the British Isles across Central Europe eastwards to East Siberia and the Russian Far East. However, in view of frequent previous confusion with other similar



Figs 1-14: *Oxypoda brachyptera* (1-7; 6: syntype) and *O. tarda* (8-14; 11: lectotype; 13: paralectotype): median portion of pronotum (1, 8); median portion of elytra (2, 9); abdominal tergites VI-VIII (3, 10); male sternite VIII (4, 11); posterior portion of female sternite VIII (5, 12); spermatheca (6-7, 13-14). Scale bars: 4, 11: 0.2 mm; 1-3, 5-10, 12-14: 0.1 mm.



Figs 15-23: Oxypoda brachyptera (15-18) and O. tarda (19-23; 22: lectotype): median lobe of aedeagus in lateral view (15-17, 19-22); apical portion of median lobe in ventral view (18, 23). Scale bar: 0.1 mm.

Oxypoda species, the distribution requires revision. So far, I have seen true O. brachyptera only from Central Europe and Great Britain. KLIMASZEWSKI et al. (2006) report the species from Canada, where it is probably adventive.

Natural history:

Habitat. In northern Germany, *O. brachyptera* occurs in more or less unshaded lowland habitats on well-drained, sandy or calcareous soils (Tab. 2). It is particularly abundant in dry, xerothermous *Calluna* heathlands and in grasslands with either sparse or low vegetation cover (early succession stages of sandy habitats, lawns). The species was not recorded in dense forests, in moist grass- or heathland, and on heavy soils. In the pitfall transsect in the study site Rössenbergheide-Külsenmoor, it was recorded in greater numbers in the drier *Calluna* slopes, whereas it was absent from the lower *Erica* heathland (Fig. 24). One specimen was collected in a subalpine habitat in the Alp, at an altitude of 2100-2150 (see additional material examined). In view of the frequent confusion with other species, particularly *O. tarda* and *O. ferruginea*, possibly also the similarly coloured and similarly small *O. exoleta* ERICHSON, 1839, literature data on the ecology of *O. brachyptera* are mostly unreliable. HORION (1967), for instance, reports the species from both moist soils, shores, and banks, and from dry sandy soils.

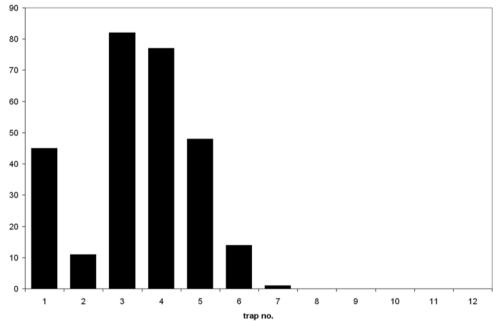


Fig. 24: Pitfall trap catches of *O. brachyptera* in a transsect in the study site Rössenbergheide-Külsenmoor. Traps 1-6 were situated on a dry *Calluna* slope, 8-12 in an adjacent *Erica* heathland, and 7 at the border between both habitats.

Phenology:

Adult *O. brachyptera* were recorded with pitfall traps from the beginning of March to the beginning of December. However, epigeic activity is low to very low in March and from September through the first half of December and probably only occurs when the weather conditions are favourable. The core activity period lasts from April through August, with a conspicuous peak in the second half of April and two less evident maxima in the second half of June and in the second half of August (Fig. 25).

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In some study sites, especially Heiliger Hain and Schneverdingen, *O. brachyptera* was among the most abundant staphylinid species in the pitfall traps, despite its small body size. As can be seen in Fig. 26, the pooled seasonal densities are relatively low. They are highest in spring and range between less than one to approximately 4.5 individuals per square meter. Thus, it can be concluded that, in comparison to other staphylinids of similar and even larger body size, the epigeic activity of *O. brachyptera* from April through August is enormous. The sex ratio (males:females) in the soil samples was 0.62, whereas in the pitfall traps it was 1.24, suggesting that the epigeic activity of males is distinctly greater than that of females. This particularly applies to the period from the second half of April through the first half of August, during which time the proportions of males in the pitfall traps ranged between 55.5 and 61.6 %.

As can be inferred from the data shown in Fig. 27, *O. brachyptera* apparently has two generations per year. Oviposition takes place from the second half of March to the second half of September. However, there are two maxima, one from mid-April to mid-May and one from Mid-June to mid-August. Emergence from the pupa occurs from the beginning of May to the first half of December, again with two maxima. The first one is from the beginning of June to mid-July and the second one in the second half of August. A comparison of the two curves in Fig. 27 suggests that pre-imaginal development from oviposition to emergence from the pupa lasts approximately 1.5-2 months and that hibernation occurs in the adult stage. There appears to be no aestivation period or diapause.

On one occasion (Hannover, August), one dissected female was found to be infested with nematodes.

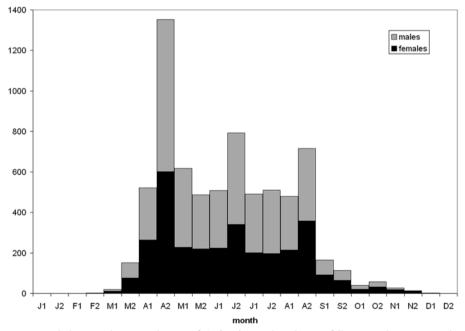


Fig. 25: Pooled seasonal activity density of *O. brachyptera* based on pitfall trap studies in 20 study plots in Niedersachsen during the period from 1981 to 2001 (total: 7110 specimens). The months are given in half-monthly intervals (F1 = first half of February, F2 = second half of February, etc.).

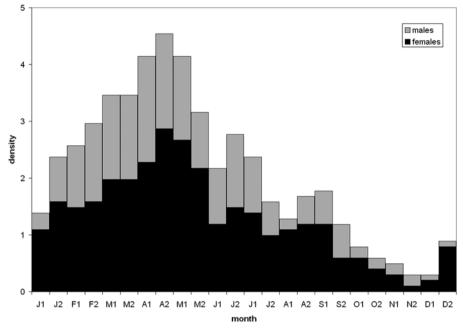


Fig. 26: Pooled seasonal densities (individuals/m²; floating arithmetic means) of *O. brachyptera* based on full-year soil extractions in 6 heathland study plots in Niedersachsen during the period from 1981 to 1986 (total: 165 specimens). For additional explanations see Fig. 25.

Pterodimorphism and dispersal:

The wing dimorphism in *O. brachyptera* is not sex-related; the proportions of both morphs were similar for both sexes. In all the study plots, the vast majority of specimens was micropterous. The macropterous morph made up only some 2.4 % of the grand total. The proportion of macropterous specimens was highest in sandy habitats in early succession stages, in urban habitats (lawns, sandy grassland) (Tab. 2), on arable land, and in a coastal meadow. Approximately 85 % of the dissected macropterous specimens had fully developed flight muscles. It is uncertain if the absence of flight muscles in the remaining 15 % is a result of post-mortem decay, genetic disposition, or metabolic reduction. In any case, the data suggest that at least the vast majority of macropterous individuals is capable of flight. On three occasions, flying specimens were recorded with window traps in July and August.

Oxypoda tarda SHARP, 1871 (Figs 8-14, 19-23, 28)

Oxypoda tarda SHARP, 1871: 192.

Type material examined:

Lectotype &, present designation: "1066 [written on reverse side of mounting label] / brachyptera Steph., ferruginea Er., forticornis Fairm. / tarda / Syntype / D. Sharp Coll. B. M. 1932-116 / Lectotypus & Oxypoda tarda Sharp, desig. V. Assing 2011 / Oxypoda tarda Sharp, det. V. Assing 2011" (BMNH). Paralectotypes: 1 &: "1066 [written on reverse side of mounting label] / tarda Sharp. / Syntype / D. Sharp Coll. B. M. 1932-116" (BMNH); 3 & : "1066 [written on reverse

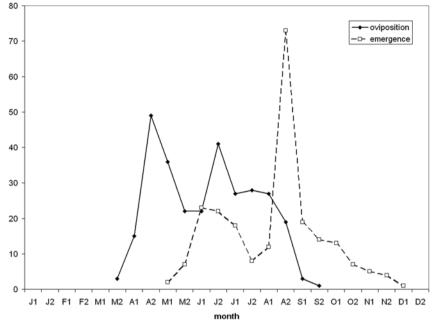


Fig. 27: Oviposition activity and emergence of adults from the pupa in *O. brachyptera*. Oviposition activity is given as the number of females with mature eggs in ovaries, emergence as the presence (not number) of teneral adults per trap series (study plot) and year.

side of mounting label] / Syntype / D. Sharp Coll. B. M. 1932-116" (BMNH); 1 9: "1066 [written on reverse side of mounting label] / tarda / Syntype / D. Sharp Coll. B. M. 1932-116" (BMNH); 1 9: "1066 [written on reverse side of mounting label] / O. tarda Sharp / brachyptera Steph., forma major, obscura / Syntype / D. Sharp Coll. B. M. 1932-116" (BMNH); 1 9: "1066 [written on reverse side of mounting label] / O. tarda type. D. S. / Syntype / D. Sharp Coll. B. M. 1932-116" (BMNH).

Comment:

The original description is based on several syntypes ("all the specimens I have seen") from "the salt marshes near Dumfries" (SHARP 1871). Eight syntypes were located in the Sharp collection at the BMNH. One of the two males is designated as the lectotype. According to BOOTH (e-mail 3 Oct., 2011), Sharp's catalogue number 1066 refers to Caelaverock on the coast just south of Dumfries, 25 May 1867. According to the description, *O. tarda* is distinguished from *O. brachyptera* by larger body size, darker coloration, the uniformly dark coloration of the abdomen, relatively somewhat shorter and more slender antennae, and slightly longer elytra.

Additional material examined:

Apart from the material listed in Tab. 2, the following material was studied:

Germany: Niedersachsen: 1 σ [macropterous], Hannover, Osterfelddamm, pitfall, VIII-IX.1991, leg. Sprick (cAss); 1 \circ [micropterous], W Hannover, Haste, arable land, VI.1987 (cAss); 1 σ [micropterous], Süntel, Rannenberg, calcareous arable land, pitfall, VI.1987, leg. Sprick (cAss); 1 σ [micropterous], same data, but V.1988 (cAss); 2 \circ [micropterous], Bückeburg env., Ahnsen, shrubs, pitfall, VI.1986, leg. Sprick (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], same data, but meadow, XII.1985 (cAss); 1 \circ [micropterous], micropterous], micropterous], micropter

data, but arable land, VII.1986 (cAss); 1 & 2 exs. [micropterous], Stadthagen, moist forest clearing, pitfall, VIII-IX.1991, leg. Sprick (cAss); 1 & [micropterous], Harz, St. Andreasberg, 700 m, pitfall, VIII-IX.1991 (cAss); 1 & [macropterous], Herzberg, 200 m, Oder floodplain, VII.1992 (cAss); 3 & d, 1 & [macropterous], Braunschweig env., Hötzum, arable land, VI.1988 (cAss); 1 & [macropterous], Braunschweig, arable land, VI.1988 (cAss). Schleswig-Holstein: 1 & [micropterous], Neustadt in Holstein env., Brodau, 30.IV.1989 (cAss); 33 exs. [16 macropterous], Husum env., Beltringharder Koog [54°33'N, 8°55'E], salt marsh, meadow, pitfall, V-X.1991 (cAss). Hessen: 2 & d [micropterous], Hanau env., Schlüchtern, pitfall, VII.1993, leg. Sprick (cAss). Nordrhein-Westfalen: 1 & [micropterous], Höxter env., Beverungen, pitfall, 17.V.1990 (cAss).

Diagnosis:

Body length 2.5-3.0 mm. Coloration similar to that of *O. brachyptera* and similarly variable, but specimens of darker coloration are more common than in *O. brachyptera*. Body shape on average slightly broader than in *O. brachyptera*.

Elytra dimorphic, in micropterous morph 0.75-0.90 times, in macropterous morph 0.90-0.95 times as long as pronotum. Hind wings either fully developed (macropterous morph) or reduced to short stubs (micropterous morph), these rudiments slightly longer than elytra.

Abdomen punctation of tergite VII practically as dense as that of anterior tergites (Fig. 10); posterior margin of tergite VII with palisade fringe in both morphs.

Other external characters (punctation, microsculpture, etc.) as in O. brachyptera (Figs 8-9).

 σ : sternite VIII of similar shape as that of *O. brachyptera* (Fig. 11); median lobe of aedeagus 0.38-0.40 mm long, of similar morphology (including internal structures) as that of *O. brachyptera*, but apex of ventral process more acute in lateral view and internal structures longer (Figs 19-23).

^{φ}: sternite VIII of similar shape and chaetotaxy as that of *O. brachyptera* (Fig. 12); spermatheca of similar shape as that of *O. brachyptera*, but apical cuticular intrusion slightly less deep (Figs 13-14).

Comparative notes:

Oxypoda tarda is most reliably distinguished from the extremely similar *O. brachyptera* by the larger median lobe of the aedeagus (no overlap) and the more acute apex of the ventral process of the aedeagus in lateral view (see Figs 15-17 and Figs 19-22). Additional, but less reliable characters are the on average longer elytra (in both morphs), the on average darker coloration, the on average larger and broader body, and the more densely punctate abdominal tergite VII (see Figs 3, 10).

Distribution:

According to SMETANA (2004), the distribution of *O. tarda* is confined to Denmark, Sweden, and Germany. Remarkably, Great Britain is not listed in the catalogue, although the species was described from Scotland. For additional records from Germany, Denmark, and Sweden see BARANOWSKI (1979), BRENNER (1993), FELDMANN & LÜCKMANN (1998), HANSEN et al. (1995), HENNICKE & MÜLLER-MOTZFELD (1998), KLAUSNITZER et al. (1980), KÖHLER (1997), KORGE (1990), KUNZE & KACHE (1998), LUNDBERG (1978a-b), RENNER (2001), ROSE (2000), VOGEL (1978, 1980), and VOGEL & DUNGER (1980); references with obviously doubtful records from habitats that are generally inhabited by *O. brachyptera* are not included. It appears likely that *O. tarda* is much more widespread, but owing to its similarity to, and the previous confusion with *O. brachyptera*, it is unknown which of the literature records of *O. brachyptera* in fact refer to *O. tarda*.

Natural history:

Habitat. In northern Germany, *O. tarda* is not particularly rare. The examined material was found in various unforested, generally in more or less moist habitats on heavier, often more or less loamy, or on calcareous soils, particularly in moist meadows, floodplains, arable land, fallows, and in coastal meadows. The species appears to be absent from dry habitats on sandy soils.

According to LOHSE (1974), *O. tarda* occurs in the same localities as *O. brachyptera*. However, the present data do not confirm this observation. In the vast majority of the studied sites, only either of the two species was present. Both species were recorded as syntopic only in a coastal meadow, in arable land, and in a fallow. In most cases of syntopic occurrence, at least one of the two species was represented exclusively by the macropterous morph. In localities where either of the two species was very abundant, the other species was always absent (Tab. 2). Thus, regarding their respective habitats, *O. tarda* and *O. brachyptera* appear to be clearly segregated.

Phenology:

The epigeic activity period measured with pitfall traps in 1986/1987 lasted from May to the first half of November. The highest activity was observed from the second half of May through June and in September (Fig. 28). The sex ratio (males:females) was similar to that of *O. brachyptera* (1.27). Mature eggs were found in the ovaries of dissected females from the second half of June through the first half of August. Teneral adults were observed from the second half of August through September, with a maximum in the second half of September. These data suggest that *O. tarda* has only one generation per year, that the duration of pre-imaginal development is similar to that of *O. brachyptera* (1.5-2 months, without diapause), and that hibernation occurs in the adult stage.

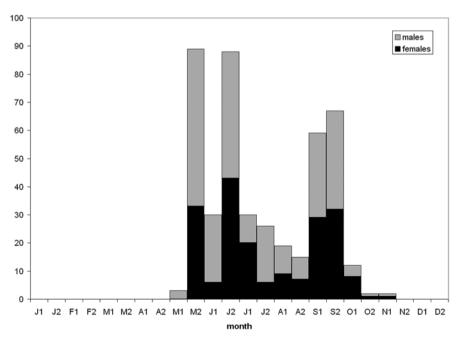


Fig. 28: Pooled seasonal activity density of *O. tarda* based on pitfall trap studies in Hannover in 1986/1987 (total: 442 specimens). For additional explanations see Fig. 25.

Pterodimorphism:

As in *O. brachyptera*, the micropterous morph of *O. tarda* is much more common than the macropterous morph (Tab. 2). At least this is true of the study sites where the species was abundant. Higher proportions of the macropterous morph were observed only on arable land and in a salt meadow. The flight muscles were not studied, and flying specimens have not been recorded.

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