

The male genitalia of *Oxyartes lamellatus* – phasmatodeans do have complex phallic organs (Insecta: Phasmatodea)

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Abstract

A detailed study of the exoskeleton and musculature of the phallic organ of *Oxyartes lamellatus* (Kirby, 1904) (Phasmatodea: Necrosiinae) is here presented – the first study of this kind for Phasmatodea. The asymmetrical phallic organ shows a highly complicated morphology, with several sclerites and many formative structural elements, of which a sclerotised bulb in the ejaculatory duct wall and a long flagellum arising from near it are among the most conspicuous. Four extrinsic and 20 intrinsic phallic muscles were found; many of these are quite compact bundles or sheets, while a few others are diffuse groups of fibres. Phallic morphology in *Oxyartes* is compared with the literature data on male genitalia in other Phasmatodea, but this is limited by the superficial treatment of phallic organs in the few relevant previous contributions. Yet, phallic organs appear as a useful new character system for phylogenetic reconstruction and species distinction in Phasmatodea. Comparison with phallic organs in other ‘orthopteroid’ insects shows that these organs are too different among orders as to allow for sound homologisation of phallic substructures. Consideration of development of phallic organs does not help in this aspect. There is no evidence of phasmatodean phallic organs being pedomorphic.

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1. Introduction

Phasmatodea (stick insects) includes more than 3000 accepted species (Bradler, 2009) and is diverse mainly in tropical and subtropical regions. The group is classified into the relictual Timematodea (only genus *Timema* Scudder, 1895 in western North America) and the Euphasmatodea (sensu Bradler, 1999, 2009; remaining taxa), which likely are sister

taxa (Whiting et al., 2003; Terry and Whiting, 2005; Bradler, 2009). The monophyly of Phasmatodea – including *Timema* – is well supported in some molecular analyses (Whiting et al., 2003; Terry and Whiting, 2005). However, this is not the case in Kjer et al. (2006), where the relationships between Euphasmatodea, *Timema*, and Embioptera are differently resolved in different analyses, and in Kōmoto et al. (2011), where *Locusta* Linnaeus, 1758 appears to be more closely related to Euphasmatodea than *Timema*. Phasmatodean monophyly is well documented by morphological characters (extensively discussed in Bradler, 2009: pp. 16–18); examples are the prothoracic defensive glands (e.g. Tilgner, 2002; Bradler, 2003), pyriform appendages of the midgut (Kristensen, 1975), the

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numerous isolated dorsoventral muscle fibres in the midabdominal segments (Klug and Bradler, 2006; Klug and Klass, 2007), and perhaps the male vomer (Bradler, 1999, 2003; Bradler et al., 2003; Tilgner et al., 1999).

In many groups of Pterygota the true male genitalia (phallic organs of abdominal segment IX) are highly complicated structures, bearing a number of sclerites, muscles, and formative elements (such as processes, pouches, or apodemes). In the same taxa the phallic organs represent a very useful character system both for taxonomic work and phylogeny reconstruction (Song and Bucheli, 2010). Taxa with especially complicated male genitalia are the Dictyoptera (Klass, 1995, 1997; Klass and Meier, 2006), Mantophasmatodea (Klass et al., 2003), Notoptera (=Grylloblattodea; Walker, 1922, 1943), and Orthoptera (Snodgrass, 1937). In some other pterygotan subgroups, however, the phallic organs are quite reduced and offer little complexity and few useful characters. In many of these taxa other parts of the male abdomen show male-specific differentiations. One example is the Odonata (e.g. Walker, 1922: Fig. 21 for phallic organs), which have a complicated secondary male copulatory organ on abdominal venters II and III (e.g. Pfau, 1971); the Embioptera have asymmetrical differentiations on coxosternum IX, terga X and XI, and cerci (Ross, 2000); and the Plecoptera show highly differentiated Xth- and XIth-segmental structures (Zwick, 1973, 1980).

In Phasmatodea the postabdomen has distinct male-specific differentiations in several elements surrounding the male genitalia. This concerns most usually venter X, which bears a sclerotised process (the abovementioned vomer), often the subgenital plate (coxosternum IX), and sometimes also the cerci, which can serve as clasping organs during copulation. The diversity of these elements is surveyed, illustrated, and analysed phylogenetically in Bradler (2009). However, very little is known about the true phallic organs of Phasmatodea. Up to the present, their existence is only evidenced by sporadic, mostly superficial or cursorial reports in the literature. Chopard (1920) provides crude drawings for 28 euphasmatodean species, all in ventral view. In his illustrations the phallic organ is asymmetrical and consists of several discrete lobes in some species but of lobes more strongly fused in others. He also describes a variable extent of sclerotisation and equipment with sclerites. For *Phasma gigas* (Linnaeus, 1758), Chopard (1920) studies the nymphal development of the male genitalia and finds them to originate from four ‘valves’ (phallic lobes). He considers phasmatodean phallic organs as somewhat reduced structures that can be compared to nymphal phallic lobes in other lower neopteran insects. Walker (1922: p. 37, Figs. 6e and 72–75) provides simple drawings of male genitalia of *Anisomorpha buprestoides* (Stoll, 1813) and *Diapheromera femorata* (Say, 1824) (dorsal and ventral views). He characterises them as an “irregular, asymmetrical mass”, being divided into terminal lobes to a varied extent, and bearing a sclerite, a process, and (probably) a tendon. He labels the various lobes and the sclerite. Snodgrass (1937: p. 26, Fig. 8) briefly describes and

crudely illustrates phallic organs of the same two species and an additional unidentified one; the only element specifically labelled is a dorsal sclerite (“e” therein), whose left posterior part terminates into a process. Günther (1956) and Matsuda (1976) only summarise previous knowledge in a few sentences, and in Beier (1968) the phallic organs are only mentioned without any detail. Tilgner et al. (1999), in their morphological study of *Timema cristinae* Vickery, 1993, outline a longitudinal section of the male postabdomen in this species and *A. buprestoides*; a phallic organ is clearly present in both species, but no details are considered. Crude dorsal and ventral views of the organ in *Timema* are also given, but only two terminal lobes are labelled. Huber et al. (2007) only briefly review data from previous publications, and Bradler (2009) does not consider the phallic organs. This all gives the impression that phasmatodean phallic organs do not show much structural differentiation. On the other hand, Chopard’s (1920) treatment indicates considerable morphological variation throughout the order, but this has not yet been explored in any detail.

During a molecular-focused phylogenetic study of the genera *Oxyartes* Stål, 1875 and *Phaenopharos* Kirby, 1904 (C. Helm, D. Bernhard, and K.-D. Klass, unpublished), which are closely related (Buckley et al., 2009; Diapheromeridae–Necrosiinae according to the classification of Bradley and Galil, 1977), we also investigated the male postabdomen of our sampled specimens. We found that the phallic organs in these taxa show a rich structural differentiation, much richer than evident from any of the previous illustrations or descriptions in the literature. We thus decided to study these organs in detail for an exemplary species, *Oxyartes lamellatus* (Kirby, 1904). This resulted in the first in-depth description of the exoskeletal and muscular components of the phallic organ in a phasmatodean, which is here presented. As male genitalia may have a complicated structure in many other phasmatodeans as well – judging from the crude illustrations in previous publications – we hope our study will motivate inclusion of male genitalic morphology in taxonomic and phylogenetic studies on Phasmatodea.

2. Material and methods

2.1. Specimens

For our study we used eight males of *O. lamellatus* of the phasmatodean subfamily Necrosiinae. These originated from different breeding cultures, and had either been stored in 80–96% ethanol prior to examination, or were freshly killed.

2.2. Morphological studies

For the study of the exoskeleton, the posterior part of the abdomen was cut off and macerated using ca. 10% KOH solution (usually boiled for a few minutes). The macerated

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