

Parameres – Similarities and Differences in Chrysomelidae and Cerambycidae (Coleoptera)¹

Lasse HUBWEBER & Michael SCHMITT

Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany

Abstract. Parameres, or lateral lobes, of the male copulatory organ are present in many insect groups, while in others they are reduced or completely lacking. Nearly all long-horned beetles have parameres, while only the leaf beetle sub-taxa Megalopodinae, Zeugophorinae, Orsodacninae, Bruchidae, Sagrinae, Donaciinae and the genus *Timarcha* possess them. In these taxa, parameres can consist of one or two lobes, can be very long or quite short, and the number and density of their setae can vary. Based on this wide morphological variability, we draw conclusions on the phylogeny of Chrysomeloidea and then formulate a hypothesis accounting for the probably diverse functions parameres might have in both the long-horns and in the leaf beetles. One recent discovery is the existence of minute openings in the surface of the parameres, which may indicate the presence of glands. These structures are illustrated and their possible functions discussed.

Key words. aedeagus, male genitalia, morphology, phylogenetics

1. INTRODUCTION

1.1. General

Surprisingly there are only few papers on parameres, or lateral lobes, of the male aedeagus found in many beetles. Although parameres are quite complex and species-specific, their functional role is largely unknown, even though these structures have at least one known function. Hubweber (unpubl. data) used genital characters, including those of the aedeagal parameres in an analysis of the phylogenetic relationships among the subfamilies of the Cerambycidae. Because some Chrysomelidae groups also possess parameres, we expanded this initial survey to include both the Cerambycidae and Chrysomelidae. We then compared character states of parameres between the two groups. In addition, we briefly examined the function of the parameres and then went on to discuss the discovery and possible significance of minute holes indicative of glandular openings on the surface of the parameres.

1.2. Terminology

Over the decades many genitalic structures in beetles have been described, mostly for taxonomic purposes. But not all entomologists have followed the same terms in the description of these different structures. The term “aedeagus” for example, is often used synonymically with “median lobe”, but we use it to describe the median lobe and the tegmen together. In our opinion the latter structure, the tegmen, consists of the parameres

(or lateral lobes) and the basal piece or tegminal struts, connected by the tegminal ring.

1.3. Literature Review

VERMA (1996) and CHEN (1985) illustrate the loss of the parameres within the Chrysomelidae. While Megalopodinae, Zeugophorinae, Orsodacninae, Bruchidae, Sagrinae, Donaciinae and *Timarcha* show a typical tegmen, the tegminal ring and therefore also the parameres, are reduced in all other subfamilies. *Stenomalus* is the single cerambycid genus known lacking parameres (WU & JIANG 1993). Another question concerning the homology of genitalia in chrysomelids is the single genus within Chrysomelinae, *Timarcha*, showing a complete tegminal ring with parameres.

HARNISCH (1915) examined the male genital system of some chrysomelids including *Plateumaris sericea*. Harnisch observed that in this species the tegmen remains outside the female genitalia during copulation, acting as a grasping organ and lever. This case is quite similar to Bruchidae as DÜNGELHOEF & SCHMITT (2006) show, but they observed slight movements in *Acanthoscelides-obtectus*-parameres during copulation. Similar movements of the parameres have been observed in the carabid beetle *Pasimachus punctulatus* (ALEXANDER 1959) and in the coccinellid beetle *Cycloneda sanguinea* (EBERHARD 1985). These movements could serve as a kind of stimulation, supporting the “cryptic-female-choice”-hypothesis (EBERHARD 1985, 1996).

KINGSOLVER (1970) observed that in *Mimosestes sallaei* (Bruchidae) the parameres are known to enter the female vaginal tract during copulation. In all other

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bruchids investigated, the parameres obviously “serve as guides to position the median lobe opposite the vaginal opening.”

EBERHARD (1993) examined the functional role of parameres in the scarabaeid species, *Macroductylus costulatus*. He described a “foot-in-door-sac” that is inflated right beneath the apex of the parameres and thus occupies the entrance to the female genitalia and can trigger the vulva to open.

2. MATERIALS AND METHODS

We examined dry museum specimens (from the ZFMK collection) and some field-collected fresh specimens. These latter specimens were collected mostly in summer 2002 near Dahlem and Blankenheim in the Eifel mountain region (about 70 km SW of Cologne).

The structures of the aedeagi of 1-5 specimens of the following species have been studied:

Cerambycidae

Cerambycinae: *Stenopterus rufus* (Linnaeus, 1767), *Obrium brunneum* (Fabricius, 1792), *Pyrrhidium sanguineum* (Linnaeus, 1758), *Plagionotus detritus* (Linnaeus, 1758)

Lamiinae: *Dorcadion pedestre* (Poda, 1761), *Acanthocinus aedilis* (Linnaeus, 1758), *Agapanthia villosoviridescens* (Degeer, 1775)

Lepturinae: *Dinoptera collaris* (Linnaeus, 1758), *Carilia virginea* (Linnaeus, 1758), *Grammoptera ruficornis* (Fabricius, 1781), *Alosterna tabacicolor* (Degeer, 1775), *Anastrangalia dubia* (Scopoli, 1763), *Stictoleptura scutellata* (Fabricius, 1781), *Stictoleptura maculicornis* (Degeer, 1775), *Stictoleptura rubra* (Linnaeus, 1758), *Rutpela maculata* (Poda, 1761), *Leptura quadrifasciata* Linnaeus, 1758, *Stenurella melanura* (Linnaeus, 1758)

Prioninae: *Prionus coriarius* (Linnaeus, 1758)

Spondylidinae + Aseminae: *Spondylis buprestoides* (Linnaeus, 1758), *Asemum striatum* (Linnaeus, 1758), *Arhopalus rusticus* (Linnaeus, 1758), *Tetropium castaneum* (Linnaeus, 1758)

Chrysomelidae

Chrysomelinae: *Timarcha tenebricosa* (Fabricius, 1775)

Donaciinae: *Donacia vulgaris* Zschach, 1788

Orsodacninae: *Orsodacne cerasi* (Linnaeus, 1758)

In addition, many drawings from the literature were examined in order to reach a wider basis for comparison. Illustrations of male genitalia of the following taxa were included in our analysis:

Cerambycidae

Anoplodermatinae – 5 taxa (DIAS 1984, 1986, 1987)

Cerambycinae – 27 taxa (BAHILLO DE LA PUEBLA & ITURRONDOBEITIA 1996; FRAGOSO 1985a; FRANCESCINI 2002; IUGA & ROSCA 1961; KUMAR & VERMA 1980; MONNÉ & NAPP 2000; MOURA & GALILEO 1992; NIISATO 1987; SHARP & MUIR 1912; WANG 1995; WU & JIANG 1993; ZIA 1936)

Lamiinae – 53 taxa (BAHILLO DE LA PUEBLA & ITURRONDOBEITIA 1996; BENSE 1995; BREUNING & TECOCHI 1977; IUGA & ROSCA 1961; JULIO 1999; MARTINS & GALILEO 1998; SAMA 1988; SHARP & MUIR 1912; TSHERNYSHEV & DUBATOLOV 2000; TYSON 1973; VERDUGO PAEZ 1994; WU & JIANG 1989; ZIA 1936)

Lepturinae – 22 taxa (BAHILLO DE LA PUEBLA & ITURRONDOBEITIA 1996; BENSE 1995; DEVESA REGUEIRO & BAHILLO DE LA PUEBLA 2003; IUGA & ROSCA 1961; KINNEL 1931; OHBAYASHI 1970; VILLIERS 1982)

Oxypeltinae – 2 taxa (FRAGOSO 1985b)

Parandrinae – 1 taxon (GILBERT 1952)

Philinae – 6 taxa (WU & JIANG 2000)

Prioninae – 73 taxa (IUGA & ROSCA 1961; QUENTIN & SIMONETTA 1992; QUENTIN & VILLIERS 1977, 1978, 1981, 1983; ZIA 1936)

Spondylidinae + Aseminae – 2 taxa (BAHILLO DE LA PUEBLA 1991)

Vesperinae – 2 taxa (BENSE 1995)

Chrysomelidae

Aulacoscelidinae – 4 taxa (JOLIVET 1957; SUZUKI 1994)

Bruchidae – 10 taxa (KINGSOLVER 1970; SCHMITT 1985a; TERAN & MURUA DE L'ARGENTIER 1981; ZIA 1936)

Chrysomelinae (*Timarcha*) – 4 taxa (IABLOKOFF-KHNZORIAN 1966; JOLIVET 1957; POWELL 1941; SHARP & MUIR 1912)

Donaciinae – 8 taxa (HARNISCH 1915; IABLOKOFF-KHNZORIAN 1966; POWELL 1941; SCHMITT 1985a, 1985b; SHARP & MUIR 1912; ZIA 1936)

Megalopodinae – 3 taxa (JOLIVET 1957; ZIA 1936)

Orsodacninae – 1 taxon (POWELL 1941)

Palophaginae – 2 taxa (KUSCHEL & MAY 1990)

Sagrinae – 18 taxa (JOLIVET 1957; MANN & CROWSON 1991; SCHMITT 1985b; ZIA 1936)

Zeugophorinae – 2 taxa (CHUJO 1952; IABLOKOFF-KHNZORIAN 1966)

In total the parameres of 216 taxa of Cerambycidae and 55 taxa of Chrysomelidae have been compared.

Genitalia were dissected using forceps and insect pins under a WILD M3 Z stereoscope. The genitalia were placed in 80% ethanol for 20 min and then in 100% ethanol until dissection. Finally, they were treated with ultrasound to complete the cleaning process.

In preparation for scanning electron microscopy, the air-dried genitalia were coated with gold in an ANATECH HUMMER VII and examined with an HITACHI S-2460 N (SEM).

3. RESULTS

3.1. Characters of the parameres

The first character we examined was the degree of sclerotization of the aedeagus, including the tegmen which varies from extreme, with nearly black pigmentation in lepturine beetles of the genera *Leptura*, *Stictoleptura*, *Rutpela* and *Stenurella* and in *Agapanthia* (Lamiinae) to weak with light yellow in other lepturine genera (*Alosterna*, *Carilia*, *Dinoptera*, *Grammoptera*). Most of the long-horned species studied have reddish-brown aedeagi, representing a medium sclerotized state. In chrysomelids, the species studied have poor to medium degrees of sclerotization of their aedeagi with light yellow to brown colours.

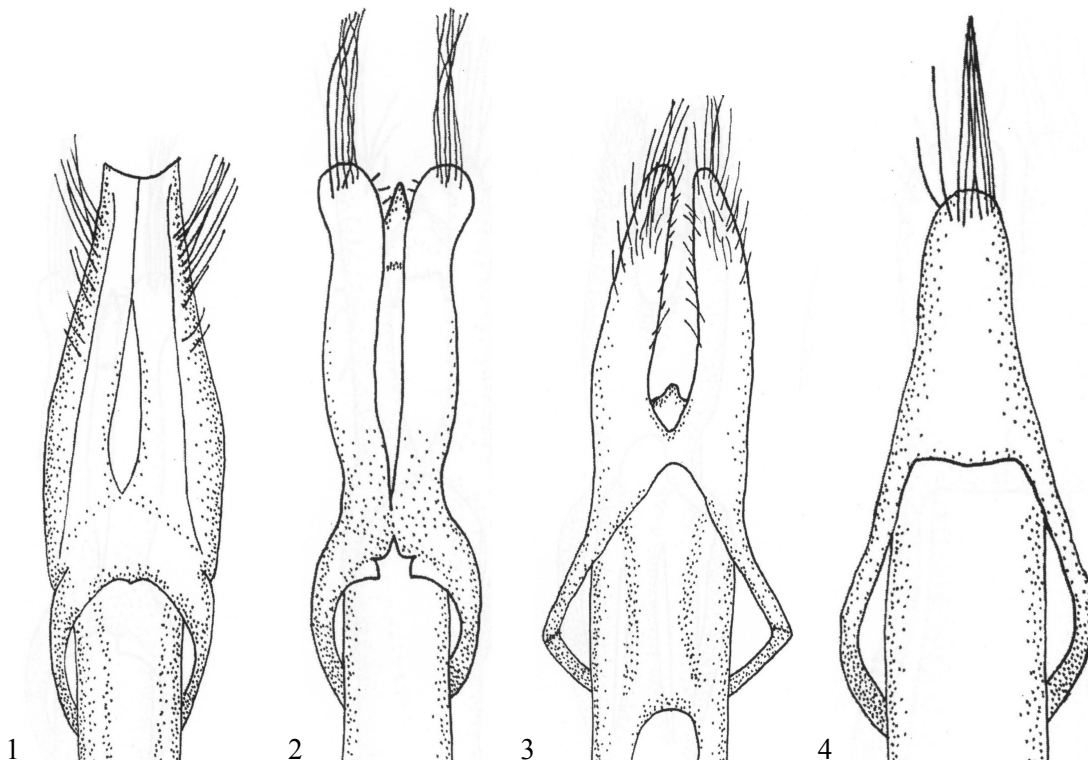


Fig. 1-4. Parameres of *Rutpela maculata* (1), *Leptura quadrifasciata* (2), *Spondylis buprestoides* (3), and *Obrium brunneum* (4).

The second character we measured was the relative paramere length, which is herein referred to only as the non-fused portion of each paramere or lobe. The paramere width was measured at the mid point of the non-fused portion to its lateral extension and then was related to the overall length of the lobes. Sometimes there is no division of the parameres if they are fused together (Fig. 4). In other cases the parameres are divided, very long and slender (Fig. 2). Within some subfamilies of Cerambycidae, it is possible to separate some genera from others with the help of this character. There is only one known genus in the Cerambycidae (*Stenhomalus*) without parameres (WU & JIANG 1993). Within the taxa

of this family studied, only some genera of Cerambycinae (*Callimellum*, *Hybodera*, *Obrium*, *Skeletodes* and *Stenopterus*) and the Oxypeltinae – altogether only 5 % of the cerambycid taxa studied so far – show totally fused parameres. Within Chrysomelidae, the parameres in Donaciinae, *Timarcha*, Zeugophorinae and some Bruchidae are fused, but in the other groups, like Orsodacninae, Sagrinae and most Bruchidae, they are divided. Parameres are fused in 34 % of the paramere-possessing chrysomelid taxa we studied. However, even in the chrysomelid groups with non-fused parameres, these structures are comparatively short. The mean relative length of all taxa with non-fused parameres is 3.2 in

Cerambycidae (standard deviation = 1.4; $n=194$) and 1.6 in Chrysomelidae (standard deviation = 0.9; $n=34$). Only two of the chrysomelids (both from Aulacoscelidinae) have parameres with a relative length of 4, all other taxa 1 to 3. In both families, Cerambycidae and Chrysomelidae, there are taxa with exceptionally long and slender parameres, which were not considered in calculating the mean values, because they would have disturbed the other data: The Madagascan Lepturinae of the genus *Mastododera* and related genera (VILLIERS 1982) with a relative length of 13 (other cerambycids not higher as 7) and an undetermined *Bruchus* (ZIA 1936) with a relative length of 32 (other chrysomelids not higher as 4).

The third character we considered was the orientation of the lobes, or the direction of the apex. They can be shaped like an arrow (Fig. 3), V-shaped (Fig. 2) or cling tightly next to each other (Fig. 1). Most cerambycids have converging lateral lobes, but most subfamilies show two or three conditions. Among chrysomelids with non-fused parameres, only most Sagrinae and some Bruchidae have divergent parameres. Only one species of Sagrinae has parameres which stretch out parallel. All Megalopodinae, Palophaginae, Aulacoscelidinae and Orsodacninae studied have converging parameres.

Additionally, the apex of the parameric lobes can look ragged or cut (Fig. 1), pointed (Fig. 3) or broadly rounded (Fig. 2). Most cerambycid parameres are pointed, but at least in Lepturinae, there are also some species with ragged and broadly rounded lateral lobes. Chrysomelid beetles show in addition to pointed apices of lateral lobes, protracted parameres (in Orsodacninae).

Hubweber (unpubl. data) divided the number and density of setae on the parameres into three different characters, according to their position (apical, ventral and dorsa-lateral). Probably the best character of these is the number and density of dorsa-lateral setae. All studied

species of Lepturinae (Cerambycidae) lack setae at this region (Fig. 2), except one species with a few sparse setae (Fig. 1), while all species of the other long-horn subfamilies studied possess setae dorsalaterally (Fig. 3). On the other hand, ventral setae are widely variable, even between very closely related groups. The leaf beetle species examined possess long setae at the apex of the parameres, but only a few taxa are known with dorsalateral or ventral setae.

The tegminal ring can either be narrow (Fig. 2) or wide (Fig. 3). "Wide" means that the lateral gap between the ring and median lobe is at least as wide as the ring itself. In cerambycid beetles, most lepturine species have a narrow tegminal ring, while most (but not all) species of the other subfamilies have a broad ring. In Cerambycids, 39 % of the taxa studied ($n=37$) have a wide tegminal ring, while only 19 % of chrysomelid taxa studied ($n=26$) show this condition.

Additionally, the connection of between the parameres and the basal piece is either angular (Fig. 3) or rounded (Fig. 2). It is not easy to distinguish between "angled" or "rounded", consequently if there is a sudden bend we call it "angled". In the longicorn beetles studied ($n=68$), 44 % show the angled condition, while only 7 % or two species, *Amblycerus robiniae* (KINGSOLVER 1970) and *Orsodacne cerasi* (own observation), of the leaf beetles studied ($n=26$) show this condition.

3.2. Presumed glandular openings

A recent discovery is tiny holes near the apex of the parameres of *Donacia* (Fig. 5). We suggest that these are most probably not sensilla, because they do not contain traces of setae. Similar, but not so many holes are found on the parameres of *Prionus* (Fig. 6), *Stenopterus* and *Zeugophora*. In *Alosterna* none such holes are found on the parameres.

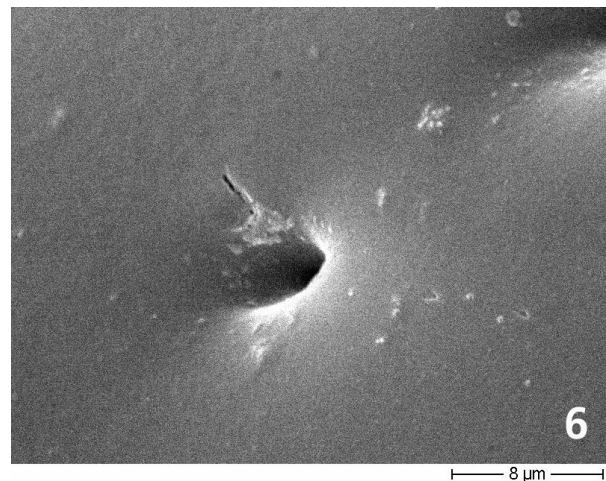
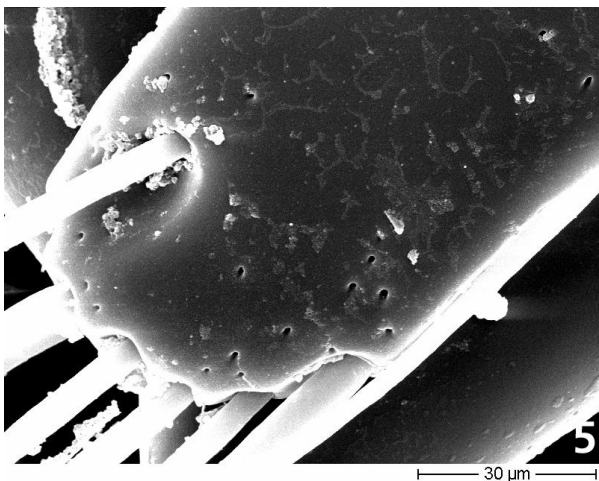


Fig. 5–6. (5) Apex of the paramere of *Donacia vulgaris* with tiny holes, (6) Tiny hole on paramere of *Prionus coriarius*.

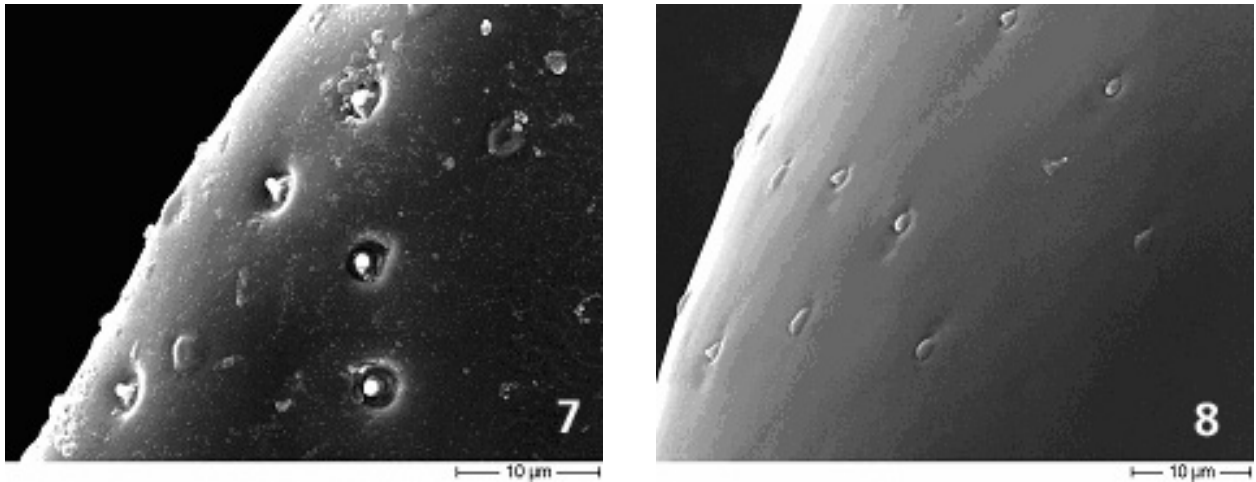


Fig. 7–8. (7) Sensilla on the median lobe of *Donacia vulgaris*, (8) Sensilla on the apex of the median lobe of *Orsodacne cerasi*.

HAMMOND (1972) described true, peg-like setae of unknown function on the parameres of Staphylinidae. In contrast to the holes on the parameres, sensilla with a minute seta can be found along the inner margin of the median lobe in *Donacia* and *Orsodacne* (Figs. 7 and 8). These campaniform sensilla look similar as those observed on the median lobe of Platypodidae (EPILATARA & TRIPLEHORN 1990).

4. DISCUSSION

We suggest that the sclerotization in Cerambycidae is thicker than in Chrysomelidae generally, because of thicker sclerotization of the female vaginal tract. Many species of long-horned beetles lay their eggs just beneath the bark of trees and presumably a more stout or heavily sclerotized ovipositor is required and – possibly – a more thickly sclerotized aedeagus, too.

The mean value of the relative length of the lateral lobes through 194 cerambycid species is 3.2. We know only a few chrysomelid species from our own investigations or from drawings in the literature with a relative length greater than 3. Of course, there is one subfamily among Chrysomelidae with long and narrow parameres, the Donaciinae, but these parameres are fused. We can also summarise that the parameres of Cerambycidae are generally more deeply divided than those of Chrysomelidae.

Obviously, the parameres of Chrysomelidae bear less dorsolateral and ventral setae than Cerambycidae. We have no proper explanation for this observation. However, if KINGSOLVER'S (1970) hypothesis holds true – that parameres outside the female genital tract are used to position the male genitalia – then it may be that the setae on the parameres perform a sensorial function. For example they could sense the position of the median lobe inside the female or press on the sternites of the

female to facilitate the release of sperm to the proper regions inside the female.

What is the function of the tiny holes on the parameres? One possibility is that they serve as glandular openings, but what could they secrete? Striking is the fact that they are more numerous on the parameres of *Donacia*, a beetle with a semi-aquatic mode of life. Therefore it may be they secrete a hydrophobic substance.

One question remains: Why are parameres divided in most of the groups studied, but undivided or totally reduced in some chrysomelids and in some Cerambycinae like *Obrium* and *Stenhomalus*? Possibly the function of these two states is quite different, for example the undivided condition serves like a lever in Donaciinae, as described by HARNISCH (1915) and in divided parameres they are sensory, as suggested by DÜNGELHOEF & SCHMITT (2006), or stimulatory, as assumed by EBERHARD (1985), and others. CROWSON & CROWSON (1996) suggested that the parameres have been reduced in some groups because of the problems of copulation on an unstable leaf surface. However, nearly all cerambycid beetles have parameres and many of them copulate on an unstable flower or leaf surface.

Future studies should include a comprehensive comparison of paramere morphology in more closely related cerambycids and chrysomelids. Because the taxa studied may not be representative, or taxa with especially noticeable parameres could have been overlooked in this study, we recommend selecting paired groups of sister taxon. In addition, live beetles in copula should be observed to solve the riddle of the parameres' function. In particular, the function of the tegmen in the closely related genera of *Obrium* and *Stenhomalus* could prove very interesting because of the obvious reduction and loss of parameres in these groups. The Madagascan species of Lepturinae and the bruchid species also have in-

teresting morphologies with very long and narrow parameres. Histological and TEM-studies should clarify the structure of the tiny holes found on the apex of the parameres.

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REFERENCES

- ALEXANDER, R. D. 1959. The courtship and copulation of *Pasimachus punctulatus* Haldeman (Coleoptera: Carabidae). *Annals of the Entomological Society of America* **52**: 485.
- BAHILLO DE LA PUEBLA, P. 1991. La armadura genital masculina en la diagnosis específica de los *Arhopalus* Ibericos (Coleoptera, Cerambycidae). *Estudios del Museo de Ciencias Naturales de Alava* **6**: 115-119.
- BAHILLO DE LA PUEBLA, P. & ITURRONDOBEITIA, J.C. 1996. Cerambycidos (Coleoptera, Cerambycidae) del País Vasco. *Cuadernos de Investigacion Biologica (Bilbao)* **19**: 1-244.
- BENSE, U. 1995. Bockkäfer: illustrierter Schlüssel zu den Cerambyciden und Vesperiden Europas. Margraf, Weikersheim.
- BREUNING, S. & TEOCCHI, P. 1977. Création de la tribu des Aderpasini, nov. Révision et bionomie des espèces des genres *Aderpas* Thoms. et *Ancylonotopsis* Br. (Coleoptera Cerambycidae Lamiinae). *Bulletin de l'Institut Fondamental d'Afrique Noire, Série A* **39**: 142-168.
- CHEN, S. 1985. Phylogeny and classification of the Chrysomeloidea. *Entomography* **3**: 465-475.
- CROWSON, R. A. & CROWSON, E. A. 1996. The phylogenetic relations of Galerucinae – Alticinae. Pp. 97-118 in: JOLIVET, P. H. A. & COX, M. L. (eds.) *Chrysomelidae Biology, Vol. 1: The Classification, Phylogeny and Genetics*. SPB Academic Publishing, Amsterdam.
- DEVESA REGUEIRO, S. & BAHILLO DE LA PUEBLA, P. 2003. Primer registro de *Paracorymbia maculicornis* (Degeer, 1775) en Galicia (N.W. de la Peninsula Ibérica) con datos sobre su armadura genital (Coleoptera, Cerambycidae). *Boletín de la SEA* **32**: 83-86.
- DIAS, M. M. 1984. Revisão da subfamília Anoplodermatinae. Parte I. Tribo Anoplodermatini. Género *Migdolus* Westwood, 1863 (Coleoptera, Cerambycidae). *Revista Brasileira de Entomologia* **28**: 507-535.
- DIAS, M. M. 1986. Revisão da subfamília Anoplodermatinae. Parte II. Tribo Anoplodermatini. Gêneros: *Acanthomigdolus* Bruch, 1941, *Paramigdolus*, gen. n., *Anoploderma* Guérin-Méneville, 1840, *Sypilus* Guérin-Méneville, 1840 (Coleoptera, Cerambycidae). *Revista Brasileira de Entomologia* **30**: 115-139.
- DIAS, M. M. 1987. Revisão da subfamília Anoplodermatinae. Parte III. Tribo Anoplodermatini. Gêneros: *Cherrocarius* Berg, 1898, *Hypocephalus* Desmarest, 1832 (Coleoptera, Cerambycidae). *Revista Brasileira de Entomologia* **31**: 101-112.
- DÜNGELHOEF, S. & SCHMITT, M. 2006. Functional morphology of copulation in Chrysomelidae – Criocerinae and Bruchidae (Insecta: Coleoptera). *Bonner zoologische Beiträge* **54**: 201-208.
- EBERHARD, W. G. 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge Massachusetts & London.
- EBERHARD, W. G. 1993. Copulatory courtship and genital mechanics of three species of *Macroductylus* (Coleoptera Scarabaeidae Melolonthinae). *Ethology, Ecology and Evolution* **5**: 19-63.
- EBERHARD, W. G. 1996. *Female control: Sexual selection by cryptic female choice*. Princeton University Press, Princeton.
- EPILA-OTARA, J. S. & TRIPLEHORN, C. A. 1990. Mechano-receptors on the male genitalia of Platypodidae (Coleoptera): a pregamou isolation mechanism? *Journal of African Zoology* **104**: 345-350.
- FRAGOSO, S. A. 1985a. The terminalia as a basis for the classification of Cerambycidae (Coleoptera) subfamilies. Part I. Terminology and genital morphology of *Cerambyx cerdo* L. *Revista Brasileira de Entomologia* **29**: 125-134.
- FRAGOSO, S. A. 1985b. The terminalia as a basis for the classification of Cerambycidae (Coleoptera) subfamilies. Part II, Oxypeltinae. *Revista Brasileira de Entomologia* **29**: 165-168.
- FRANCESCHINI, A. F. 2002. Revisão do gênero *Appula* (Coleoptera, Cerambycidae, Cerambycinae, Elaphidiini). *Iheringia, Série Zoologia* **92**: 5-40.
- GILBERT, E. E. 1952. The homologies of the male genitalia of Rhynchophora and allied Coleoptera. *Annals of the Entomological Society of America* **45**: 633-637.
- HAMMOND, P. M. 1972. The Micro-Structure, Distribution and Possible Function of Peg-Like Setae in Male Coleoptera. *Entomologica Scandinavica* **3**: 40-54.
- HARNISCH, W. 1915. Über den männlichen Begattungsapparat einiger Chrysomeliden. Ein Beitrag zur Phylogenie des Copulationsapparates der Käfer. *Zeitschrift für wissenschaftliche Zoologie* **114**: 1-94.
- IABLOKOFF-KHNZORIAN, S. M. 1966. Considérations sur l'édéage des Chrysomelidae et son importance phylogénique. *L'Entomologiste* **22**: 115-137.
- IUGA, V. G. & ROSCA, A. 1961. La morfologia de l'apex abdominal chez les Cerambycidae (Col.), comparé à celui des Hyménoptères. *Travaux du Museum d'histoire naturelle «Grigore Antipa»* **3**: 101-156.
- JOLIVET, P. 1957. Recherches sur l'aile des Chrysomeloidea (Coleoptera). *Mémoires Institut Royal des Sciences Naturelles de Belgique, 2. Série* **57**: 1-180.
- JULIO, C. E. de A. 1999. Revisão do gênero *Scleronotus* White, 1855 (Coleoptera, Cerambycidae, Lamiinae, Acanthoderini). *Boletim do Museu Nacional do Rio de Janeiro, N.S., Zoologia* **406**: 1-35.
- KINEL, J. 1931. *Leptura inexpectata* Janss. & Sjöb. na ziemiach polskich oraz pozycja systematyczna tej formy. *Bulletin entomologique de Pologne* **10**: 189-196.
- KINGSOLVER, J. M. 1970. A study of the male genitalia in Bruchidae (Coleoptera). *Proceedings of the Entomological Society of Washington* **72**: 370-386.
- KUMAR, D. & VERMA, K. K. 1980. Aedeagal musculature in Phytophaga (Coleoptera). *Journal of Natural History* **14**: 237-270.

- KUSCHEL, G. & MAY, B. M. 1990: Palophaginae, a New Subfamily for Leaf-Beetles, Feeding as Adult and Larva on Araucarian Pollen in Australia (Coleoptera: Megalopodidae). *Invertebrate Taxonomy* **3**: 697-719.
- MANN, J. S. & CROWSON, R. A. 1991. Some observations on the genitalia of Sagrinae (Coleoptera: Chrysomelidae). Pp. 35-60 in: ZUNINO, M., BELLÉS, X. & BLAS, M. (eds.) *Advances in Coleopterology*. AEC, Barcelona.
- MARTINS, U. R. & GALILEO, M. H. M. 1998. Revisão da tribo Aerenicini Lacordaire, 1872 (Coleoptera, Cerambycidae, Lamiinae). *Arquivos de Zoologia* **35**: 1-133.
- MONNÉ, M. L. & NAPP, D. S. 2000. Revisão do gênero *Ceralocyna* (Coleoptera, Cerambycidae, Cerambycinae, Trachyderini, Ancylocerina). *Iheringia, Série Zoologia* **88**: 103-137.
- MOURA, L. de A. & GALILEO, M. H. M. 1992. Genitália masculina e feminina de *Dorcacerus barbatus* (Olivier, 1790) (Coleoptera, Cerambycidae, Cerambycinae, Trachyderini). *Iheringia, Série Zoologia* **72**: 135-139.
- NIISATO, T. 1987. A new *Cyrtoclytus* (Coleoptera: Cerambycidae) from Northern Thailand. *Coleopterists' Bulletin* **41**: 297-301.
- OHBAYASHI, N. 1970. On some cerambycid-beetles from the Ryukyu Islands. *Bulletin of the Japan Entomological Academy* **5**: 1-4.
- POWELL, E. F. 1941. Relationships within the Family Chrysomelidae (Coleoptera) as Indicated by the Male Genitalia of Certain Species. *American Midland Naturalist* **25**: 148-195.
- QUENTIN, R. M. & SIMONETTA, J. 1992. Révision du genre *Cantharocnemis* Serville (Coleoptera: Cerambycidae). Les sous-genres *Cantharocnemis* sensu stricto et *Cantharofœdes* Gilmour. *Annales de la Société Entomologique de France N.S.* **28**: 83-100.
- QUENTIN, R. M. & VILLIERS, A. 1977. Genera et catalogue raisonné des Prioninae africains. I. Ergatini (Col. Cerambycidae). *Annales de la Société Entomologique de France N.S.* **13**: 509-523.
- QUENTIN, R. M. & VILLIERS, A. 1978. Genera et catalogue raisonné des Prioninae africains. II. Macrotomini (Col. Cerambycidae). *Annales de la Société Entomologique de France N.S.* **14**: 207-274.
- QUENTIN, R. M. & VILLIERS, A. 1981. Les Macrotomini de l'ancien monde (région Éthiopienne exclue). *Genera et catalogue raisonné* (Col. Cerambycidae Prioninae). *Annales de la Société Entomologique de France N.S.* **17**: 359-393.
- QUENTIN, R. M. & VILLIERS, A. 1983. Genera et catalogue raisonné des Prioninae africains. III. Acanthophorini (Col. Cerambycidae). *Annales de la Société Entomologique de France N.S.* **19**: 79-100.
- SAMA, G. 1988. *Phytoecia flavipes* (Fabricius, 1801) a valid species, not a synonym of *P. rufipes* (Olivier, 1795) (Insecta, Coleoptera, Cerambycidae). *Stenstrupia* **14**: 121-125.
- SCHMITT, M. 1985a. Versuch einer phylogenetisch-systematischen Analyse der Criocerinae (Coleoptera, Chrysomelidae). *Zoologische Beiträge N.F.* **29**: 35-85.
- SCHMITT, M. 1985b. On the Phylogeny of the Criocerinae (Coleoptera, Chrysomelidae). *Entomography* **3**: 393-401.
- SHARP, D. & MUIR, F. 1912. The comparative anatomy of the male genital tube in Coleoptera. *Transactions of the Royal Entomological Society of London* **60**: 477-642.
- SUZUKI, K. 1994. The systematic Position of the Subfamily Aulacoscelinae (Coleoptera: Chrysomelidae). Pp. 45-59 in: FURTH, D.G. (eds.) *Proceedings of the Third International Symposium on the Chrysomelidae*, Beijing, 1992. Backhuys, Leiden.
- TERAN, A. L. & MURUAGA D'ARGENTIER, S. 1981. Observaciones sobre Bruchidae (Coleoptera) del noroeste Argentino. IV. Estudios morfológicos y biológicos de *Amblycerus hoffmannseggi* (Gyll.), *Acanthoscelides comptus* Kingsolver y *Merobruchus bicoloripes* (Pic). *Acta Zoologica Lilloana* **36/2**: 61-84.
- TSHERNYSHEV, S. E. & DUBATOLOV, V. V. 2000. A new species of longhorn-beetle from East Siberia (Insecta: Coleoptera: Cerambycidae). *Reichenbachia* **33**: 385-389.
- TYSON, W. H. 1973. The *Spalacopsis* of the West Indies and America north of Mexico (Coleoptera: Cerambycidae). *Coleopterists' Bulletin* **27**: 117-137.
- VERDUGO PAEZ, A. 1994. *Los Iberodorcadion* (Breuning, 1943) des suroeste ibérico. Anatomía des las fases inmaduras, ciclo vital, ecología y distribución (Coleoptera: Cerambycidae). *Zapateri* **4**: 87-103.
- VERMA, K. K. 1996. Inter-subfamily relations among Chrysomelidae (Coleoptera) as suggested by organization of the male genital system. Pp. 317-351 in: JOLIVET, P. H. A. & COX, M.L. (eds.) *Chrysomelidae Biology, Vol. 1: The Classification, Phylogeny and Genetics*. SPB Academic Publishing, Amsterdam.
- VILLIERS, A. 1982. Démembrement du genre *Mastodera* Thomson (Coleoptera, Cerambycidae, Lepturinae). *Annales de la Société Entomologique de France N.S.* **18**: 129-162.
- WANG, Q. 1995. The Australian longicorn beetle genus *Skeletodes* Newman (Coleoptera: Cerambycidae). *Coleopterists' Bulletin* **49**: 109-118.
- WU, W.-W. & JIANG, S.-N. 1989. A taxonomic study of the male genitalia of the genus *Anoplophora* Hope (Col. Cerambycidae). *Acta Entomologica Sinica* **32**: 211-220.
- WU, W.-W. & JIANG, S.-N. 1993. On the male genitalia of the genus *Stenhomalus* (Coleoptera: Cerambycidae). *Acta Entomologica Sinica* **36**: 81-84.
- WU, W.-W. & JIANG, S.-N. 2000. A taxonomic study of the male genitalia of some philid beetles with one new species in China (Coleoptera: Cerambycoidea). *Acta Entomologica Sinica* **43**: 78-87.
- ZIA, Y. 1936. Comparative studies of the male genital tube in Coleoptera Phytophaga. *Sinensia* **7**: 319-352.

Authors' address: Lasse HUBWEBER (corresponding author), Michael SCHMITT, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany. E-mail: l.hubweber.zfmk@uni-bonn.de, m.schmitt@uni-bonn.de