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To the knowledge of *Sarabandus robustus* (LECONTE) (Col.: Scirtidae: Scirtinae), and on the groundplan of male marsh beetle genitalia

Peter ZWICK

A b s t r a c t : The monotypic endemic North American genus *Sarabandus* was described as a close relative of the southern hemisphere genus *Pseudomicrocara*. Other authors regard it as a member of the *Elodes* clade. The terminalia of both sexes are described, they support neither of these assumptions. *Sarabandus* is probably an isolated Pleistocene relict, the closest relative is unknown.

The probable evolution of male scirtid genitalia is re-assessed. According to NYHOLM (1972) male genitalia of extant Scirtinae belong to two fundamentally different types. I doubt this and suggest that all are descendants of a *Microcara*-like ancestor.

K e y w o r d s : *Elodes*-clade, *Microcara*-type, Pleistocene relict, presumed ancestor, homology, *Sacodes*, *Odeles*, *Elodes*.

Introduction

The brief original description of *Sarabandus robustus* (LECONTE, 1875), an endemic North American marsh beetle, placed the new species in genus *Cyphon*. Good habitus photographs of the female holotype are available:

(http://140.247.119.225/mcz/Species_record.php?id=2129). LEECH (1955) described the external morphology in detail and proposed a new genus, *Sarabandus*, which was believed to be most closely allied to the Australian genus *Pseudomicrocara* ARMSTRONG of which LEECH had studied two species. In contrast, a diagram by LAWRENCE and YOSHITOMI (2007) shows *Sarabandus* as sister group of *Elodes*¹ + *Sacodes*, a clade restricted to the northern hemisphere.

I describe the unknown terminalia (the invaginated segments 8 and 9, and the genitalia proper) of both sexes and discuss the probable relations of *Sarabandus*. This leads to questions about the ancestral groundplan and the evolution of male scirtid terminalia and especially genitalia. The model by NYHOLM (1972) is re-assessed and an alternative proposed.

¹ *Elodes* s.l., incl. *Odeles*

Material and methods

Specimens were studied with a WILD M5A dissecting microscope and a LEICA DMLS compound microscope. Abdomina were cleared in KOH, the dissected terminalia mounted in Euparal. Illustrations were prepared with a camera lucida, or from digital photographs taken with a Canon Eos mounted on the scopes and enhanced with Zerene Stacker software.

Sarabandus robustus (LECONTE): 1♂, 1♀: USA: NH: Straf. Co., Spruce Hole 3km SW Durham vi-9-1982 \ DSCHANDLER sift fern and pine litter on bog edge \ SARABANDUS ROBUSTUS (LeConte) det. D.K. Young.

Sacodes fuscipennis (GUÉRIN) and *S. pulchella* (GUÉRIN): adults reared from larvae coexisting in a phytotelma: USA: MD, Greenbelt, June 2009, P. Zwick.

Sacodes flavicollis (KIESENWETTER), numerous larvae: Slovenia, Trnovo [45°58'N,13°45'E], phytotelmes in beech trees, 2010 and 2011, P. Zwick.

Elodes minuta (L.) and *Odeles marginata* (F.): numerous adults and larvae from streams around Schlitz [50.67N, 09.56O], Germany, various dates, P. Zwick.

All specimens in my collection.

Abbreviations:

BL body length (= combined length of prothorax + elytra)

BW maximum body width

S, T..... abdominal sternites and tergites, with the ordinal number of the respective morphological segment.

Taxonomic Part

***Sarabandus robustus* (LECONTE, 1875) (Figs 1-15, 21)**

Cyphon robustus LECONTE, 1875, Trans. Amer. ent. Soc. 5.

Sarabandus robustus (LECONTE) - LEECH, 1955, Pan-Pacific Entomologist 31.

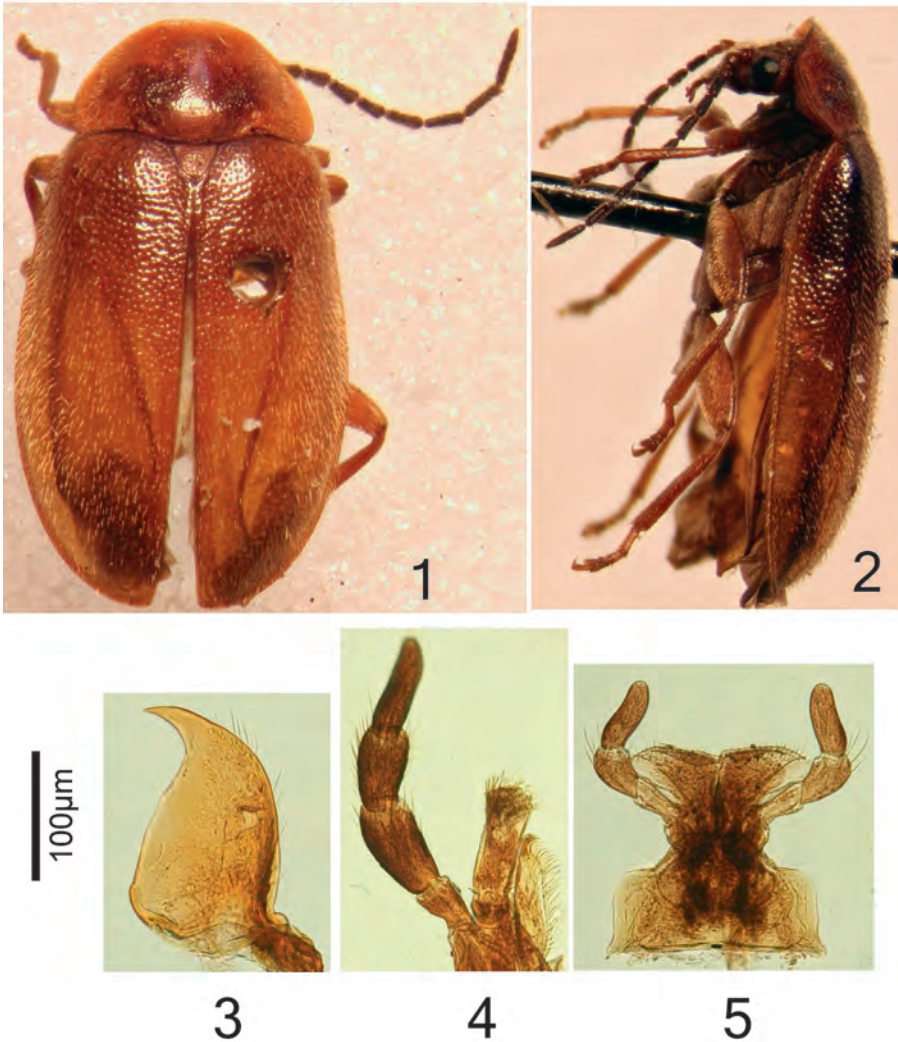
Habitus (Figs 1, 2): Elongate oval, relatively flat, BL 5.0-5.7mm, BL/BW ~1.85. Light brown, dorsal side irregularly punctate and finely pilose, elytra with 3 very shallow costae, no sutural stripe. Head orthognathous, in dorsal view concealed by pronotum. Base of pronotum wide, straight in front of equilateral scutellum, sinuous laterally, rear corners blunt. Sides curved, converging forward, front rounded, no trace of front corners. Disc uniformly convex. Elytra widening slightly backward from blunt humerus, body widest in caudal fourth. Epipleura narrow. Antenna longer than half BL, flagellar segments cylindrical, each several times longer than wide. Scapus unmodified, pedicle club-shaped, shorter, antennomere 3 still a bit shorter, more distal antennomeres long (Fig. 1). Mandibles equal, stout with short curved sharp tip, no teeth, mola smooth and hairless (Fig. 3). Maxillary palpus 4-segmented, slender, segments 2 and 3 thicker than 1 and 4 (Fig. 4). Labial palpus 3-segmented, second segment widening a little distally, edge oblique, last segment long, slender, curved gently outward (Fig. 5). Legs strong, unmodified. Fully winged.

Underside. Lower face of head flat, subgenal ridge unmodified, ending near insertion of maxilla, close to a branch from gular suture. Prosternal process not projecting between coxae, thin, blade-like, no setation. Mesoventral groove poorly defined, a flat roundly triangular area on front edge of mesoventrite. Mesoventral process a short pointed triangle not reaching metasternum, middle coxae partly contiguous. Discrimen visible over half of metaventrite. Abdominal sternites unmodified.

Male (Figs 6-11, 21): Plate of T8 sclerotized, wider than long, caudal margin rounded, distal region with scattered setae, the largest along caudal margin without forming a regular fringe (Fig. 6). Apodemes short, not connected, caudally tapering in the plate, front end sinuous. S8 a triangular membranous structure containing a weak barely visible widely U-shaped sclerite (Fig. 7), 1 or 2 minute setae caudolaterally. T9 wider than T8, apodemes short and unconnected, plate soft, bare, caudal edge not well defined (Fig. 8). S9 (Fig. 9) is a barely sclerotized oval plate, caudally bilobed, caudal half with long setae.

Base of tegmen (Fig. 10, te) shaped like a swallowtail, strongly widening caudad and supporting two large triangular parameres (pe) whose soft blunt tips lean against the penis. There is a strong supporting rod (sr) near the medial edge of each paramere, but no spines or other armature. Styles (st) unusually large, triangular, resembling the parameres in size and shape, the blunt tip is bare. Penis strongly sclerotized, the wide front of the large oval pala shallowly excised (pa). Trigonium (Figs 10, 11, tr) a slender triangle with widely divergent basal arms (ba), dorsally with a pair of triangular outward projections near half length. The slender tip in its distal half beset with distinct teeth, mainly ventrally. Parameroids (pd) resembling elongate ears, distally with dense external denticulation, their base is of complex shape: dorsal edge of parameroid basally with large medially serrate lobe (Fig. 10, sl) extending over basal arm of trigonium. Edge of sclerite surrounding pala continues caudally as ventral edge of parameroid (Fig. 11). Transparent unarmed membranes connect parameroids and trigonium. The membrane attached to the front end of tegmen is transversely wrinkled, the outer edge appears in dorsoventral view finely serrate.

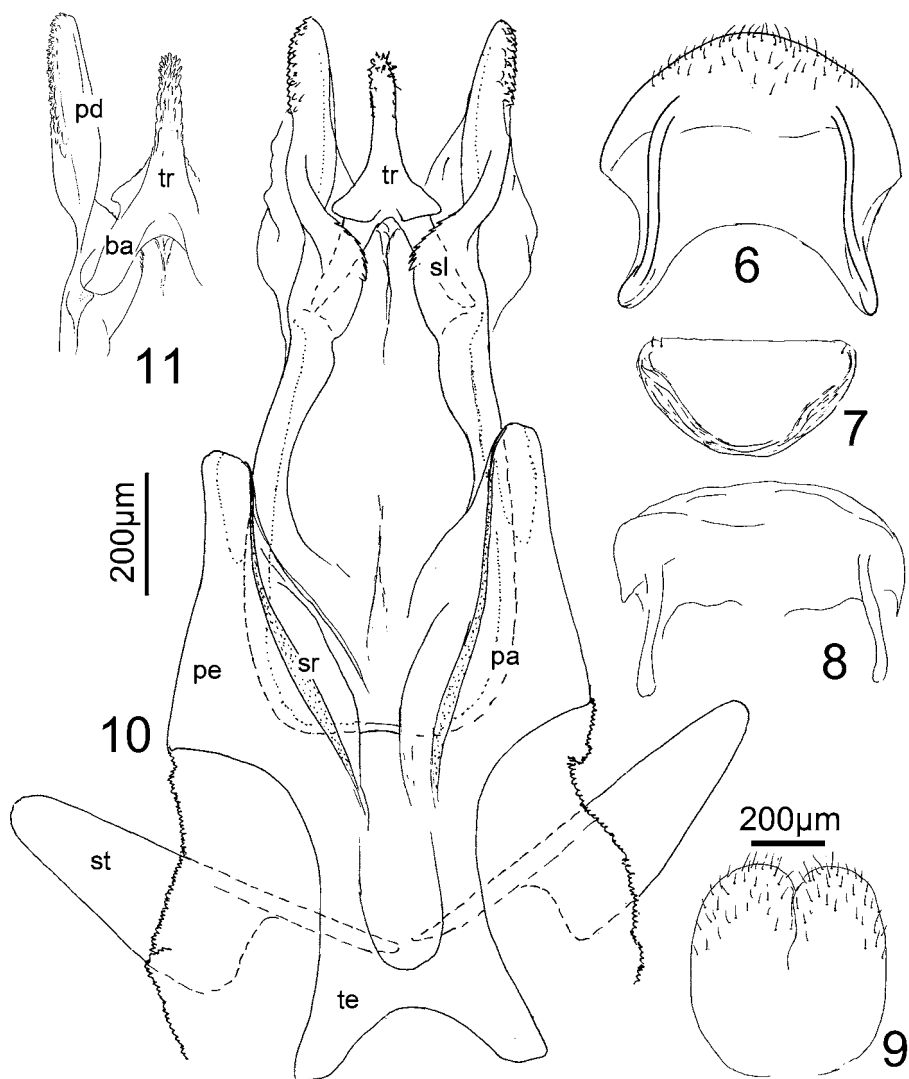
Female (Figs 12-15): Abdominal sternites unmodified. Ovipositor long and slender, unmodified. Gonocoxites (gc) slender, the gonostyles (gs) are elongate slender clubs with apical sensilla. Bacula with small recurrent branchlet. The shapes of T8 and S8 are not clearly visible in the preparation. The long apodemes of T8 (aT8) converge and taper in the front edge of T8. The sclerites of S8 (aS8) delineate a slender rhomboid. Anteriorly they converge but the fine tips remain separate. Surface of the sclerites of S8 prickly, sparsely beset with microscopic spinules. Terminal section of the bacula of ovipositor similar. No vulvar sclerite but cuticle in vulva complexly folded, details not recognized. Prehensor (pr) a widened section of the gonoduct containing caudally a pair of triangular plates, each with 3 large sharp anterolateral hooks. Between the plates is a small serrate median crest. Anterolaterally the prehensor bears a pair of band-shaped lateral sclerites and a frontal sclerite arch beneath which lies the narrow anterior opening of the prehensor. At a short distance in front of the prehensor lies the balloon-like hyaline bursa (bu). The empty bursa has a diameter of 0.7mm. Its surface bears numerous circular sclerites, most 10-15µm across. Each sclerite with a central group of ~8 curved hair-like outgrowths projecting into the lumen.



Figs 1-5: *Sarabandus robustus*, habitus and mouthparts. (1) female, dorsal; (2) male, lateral; (3) mandible; (4) maxillar palpus; (5) labium. 1 and 2 not to scale, 3-5 to the same scale.

Immature Stages: Unknown.

Relations of *Sarabandus*: In habitus *Sarabandus robustus* resembles several genera representing both the *Microcara*- and *Elodes*-types (in the sense of NYHOLM 1972) but it fits in none. The *Elodes*-clade will be discussed below. *Sarabandus* genitalia agree with the *Microcara*-type, its slender body with rounded pronotal front margin resembles, e.g., *Microcara*, some *Pseudomicrocara*, or *Heterocyphon*. However, the first has modified labial palpi, all three have a well developed prosternal process ending in a plate, and a complete mesoventral process separating the middle coxae.

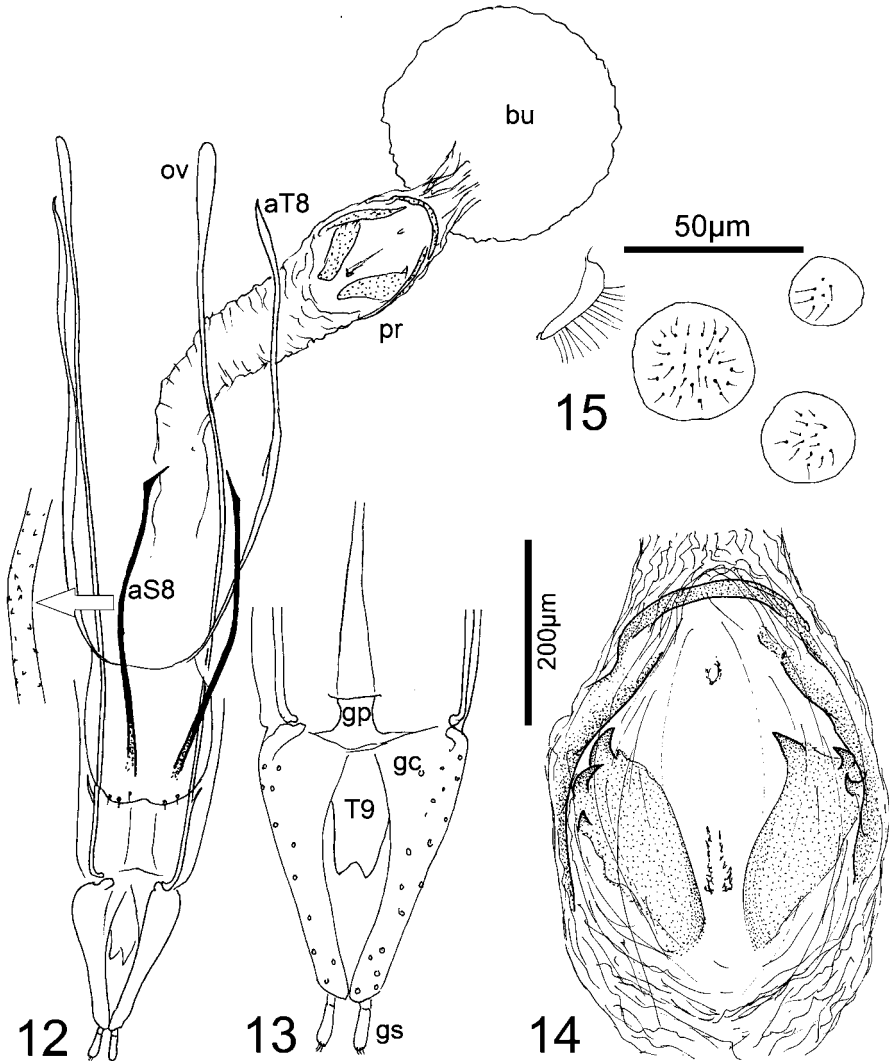


Figs 6-11: *Sarabandus robustus*, male terminalia. (6) T8; (7) S8; (8) T9; (9) S9; (10) dorsal view of protracted tegmen and penis; (11) penis tip, ventral view. 6-9 and 10-11 to the same scale, respectively.

ba, basal arm of trigonium; pa, pala; pd, parameroid; pe, paramere; sl, serrate lobe; sr, supporting rod; st, stylus; te, tegmen; tr, trigonium.

Sarabandus robustus is a member of subfamily Scirtinae (in the sense of LAWRENCE & YOSHITOMI 2007). Below I discuss that its resemblances with *Pseudomicrocara* are in plesiomorphic traits providing no evidence of close relationships between these widely disjunct taxa, and that *Sarabandus* shares also no apomorphies with the *Elodes*-clade.

The closest relative of *Sarabandus* remains unknown. The number of scirtid genera in the Holarctic region is comparatively low, only four are endemic in the huge Holarctic area. Probably, this poverty reflects Pleistocene impact. I regard *Sarabandus* as a relict, as an isolated survivor of the Pleistocene.



Figs 12-15: *Sarabandus robustus*, female genitalia. (12) overview, sclerites of S8 shown in black, plus an enlarged detail (arrow); (13) tip of ovipositor; (14) prehensor; (15) ornaments on surface of bursa. 12 not to scale, 13, 14 to the same scale.

aS8, sclerite of S8; aT8, apodeme of T8; bu, bursa; gc, gonocoxa; gp, gonopore; gs, gonostylus; ov, baculum of ovipositor; pr, prehensor.

The groundplan of male scirtid genitalia

According to NYHOLM the male genitalia of the *Microcara*-type are fundamentally different from the *Elodes*-type. His outstandingly well illustrated paper (NYHOLM 1972) shows numerous genera from all faunal regions, plus representatives of several families presumed related to Scirtidae. Findings were arranged in what NYHOLM regarded as the evolutionary sequence, from "the least specialized to the most derived forms" (my translation), starting with *Elodes*, then *Odeles*, *Sacodes* (all three as *Helodes*), thereafter the *Microcara*-type and its modifications leading to *Cyphon* and its subgroups.

The approach is typological, the ideas were summarized in a diagram (NYHOLM 1972: fig. 10). According to the text the ancestral scirtid probably had a trilobate aedeagus but in the diagram the ancestral form ("Urspungsform") of the scirtid penis is shown as a simple structureless half tube through which the ejaculatory duct passes to an apical gonopore. The *Elodes*-type would have evolved directly from such unrealistic ancestral form, while the *Microcara*-type would *quasi* have restored the trilobate aedeagus (via hypothetical steps) and developed it further.

The *Microcara*-type. The male terminalia of *Sarabandus* resemble most genera of the *Microcara*-type: Segments 8 and 9 are complete. The genitalia consist of a tegmen with parameres and large styles, a flat penis with large pala, a trigonium that can be bent down, and rigid parameroids with apical sensilla. The same set of structures is observed in, e.g., *Prionocyphon*, in primitive species of *Scirtes* (like *S. haemisphaericus* (LINNÉ) (both genera global), in *Pseudomicrocara* (Australia, New Guinea, New Caledonia, South America: LIBONATTI & RUTA 2013), *Heterocyphon*, *Macrohelodes*, *Macrodascillus* (all Australian), *Atopida* and *Cyprobius* (both New Zealand). Styles may or may not be present, *Microcara* lacks them, species of *Pseudomicrocara* vary. In the genera in question, tergites 8 and 9 have strong paired apodemes. Plates vary, T8 is normally well sclerotized and provided with socketed setae, T9 is often soft and always lacks true setae. S8 is provided with a wide rectangular or U-shaped anterior sclerite, the plate is often membranous, except the caudolateral corners where a few setae stand. S9 is often little sclerotized but bears large socketed setae caudally. I regard this character syndrome as the ancestral pattern, the groundplan, of terminalia of the *Microcara*-type.

The above set of plesiomorphic character expressions provides no evidence of the monophyly of representatives of the *Microcara*-type. Many taxa, mainly smaller ones, show modifications of the above pattern, but homology with elements of the groundplan is evident. The modifications may help to recognize groups of related genera. Some changes are reductions, e.g., the tendency for S8 to become anteriorly narrow and assume V- or Y-shape, or be entirely reduced. Modifications of the tergites occur, e.g., the special structures of T9 in *Austrocyphon*. In some other genera, e.g., *Ypsilonyphon* and *Papuacyphon*, S9 is strongly modified.

NYHOLM (1972) proposed how changes of the *Microcara*-type genitalia may have led to *Cyphon* (s.l.) and subgroups. The "Cyphon-like" endemic Australian genera are different, they do not share these changes but agree with the basic *Microcara*-type (e.g., ZWICK 2012, 2013a, b, c). *Calvarium* PIC and *Paracyphon* ZWICK are unexplained exceptions.

The *Elodes*-clade. The well supported monophyly of the *Elodes*-clade is generally accepted (e. g., LAWRENCE & YOSHITOMI 2007, KLAUSNITZER 2009). *Elodes*, *Odeles* and *Sacodes* share several apomorphic character expressions none of which occurs in

Sarabandus. I list a selection, leaving the terminalia aside:

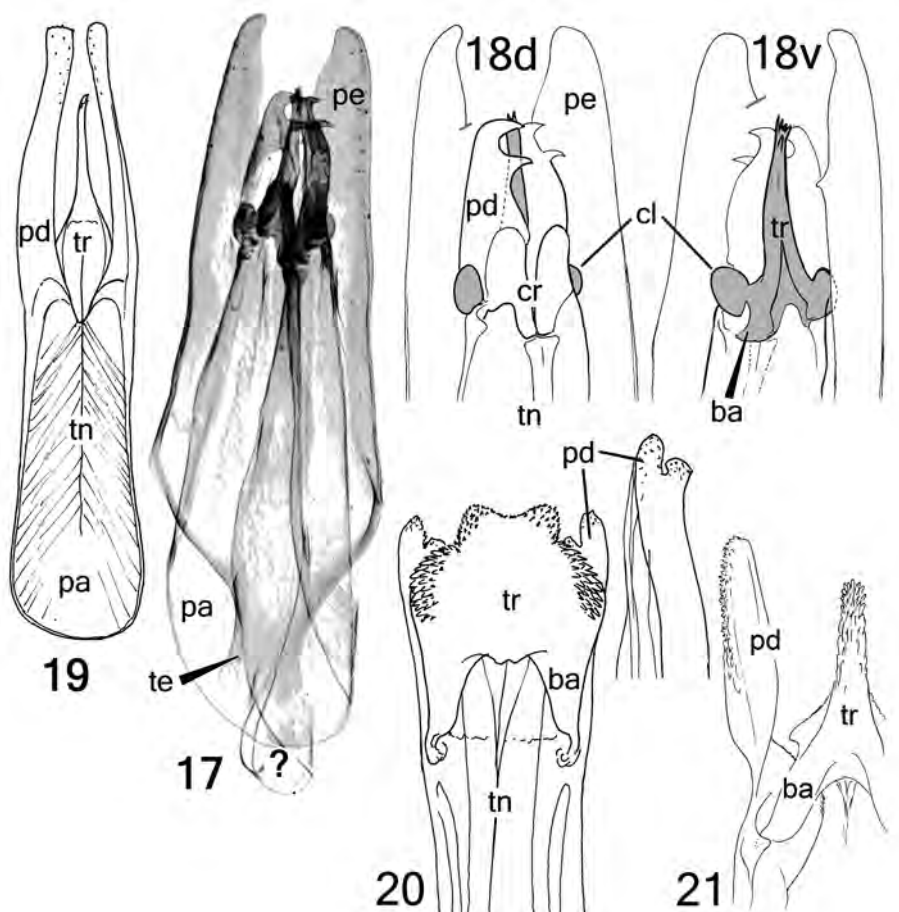
- Tibial crests continuing on the elongated 1st and 2nd segment of hind tarsus, and the spine-like medial end of segment 2.
- FRIEDRICH & BEUTEL (2006) rated several traits of the large hanging middle coxae of *Elodes* as derived among Coleoptera. However, this is not characteristic of the family Scirtidae but only of the *Elodes*-clade.
- In most Scirtidae, abdominal sternites 1 + 2 form an intercoxal process and a small concealed vertical sclerite in front of the freely visible S3. Only the *Elodes*-clade lacks an intercoxal process (LAWRENCE & YOSHITOMI 2007). Instead, sternites 1 + 2 form a flat region largely concealed by the large hind coxae which enable adults (*E. minuta* (L.)) to perform wild jumps when in a sweepnet.
- Larvae possess 6 eyes whose well defined convex corneae are directed straight forward (Fig. 16; not known for *Sarabandus*).



Fig. 16: *Elodes minuta*, frontal view of head of last instar larva; not to scale.

Last instar larvae of all three genera have long antennae but they are composed of only ~40 segments and annuli (ZWICK & ZWICK 2010). This differs from the short antennae of saproxylic scirtid larvae with still fewer annuli (WATTS 2014) but is probably primitive compared to other Scirtinae with ~ 70 to 180 annuli of the larval flagellum (ZWICK & ZWICK 2010, WATTS 2014).

Homologies between the *Elodes*-clade and representatives of the *Microcara*-type: I doubt the fundamental difference of the *Elodes*- and *Microcara*-types and propose to reverse the direction of view: starting with *Sacodes*, which is the sister group of (*Odeles* + *Elodes*) (KLAUSNITZER 2009). In *Sacodes fuscipennis* (GUÉRIN) (in the sense of NYHOLM 1972 and KLAUSNITZER 1974, 1975) there is agreement of structures with genitalia of the *Microcara*-type. In his detailed description of *S. fuscipennis* NYHOLM used neutral terms (my translations), avoiding terms established for the *Microcara*-type, e.g., *appendage* instead of *parameroid*, even though he noticed the



Figs 17-21: Suggested homologies between penes of different Scirtinae. (17) *Sacodes fuscipennis*, overview of tegmen and penis; (18) *Sacodes fuscipennis*, enlarged apex of penis in dorsal (d) and ventral (v) views; (19) *Microcara testacea*, penis, ventral; (20) *Pseudomicrocara orientalis*, caudal part of penis, ventral view, with detail of apex of parameroid in dorsal view; (21) *Sarabandus robustus*, partial ventral view of penis tip. Not to scale.

ba, basal arm of trigonium; cl, connecting lobe; cr, crura; pa, pala; pd, parameroid; pe, paramere; te, tegmen; tn, tendon; tr, trigonium.

resemblance of some parts with *Microcara*: "strikingly similar to the trigonium of a *Microcara* provided with a long centema" (NYHOLM 1972: 91).

Presumably homologous structures are labelled in diagrammatic figures (Figs 17-21) of the penes of *S. fuscipennis*, *Microcara testacea* (F.), *Sarabandus*, and *Pseudomicrocara orientalis* ARMSTRONG. Retractors bending the trigonium attach laterally to the pala, but medially to a tendon which is actually a thin lamella (Mittelblatt) in vertical position. Muscles are shown only in *Microcara*, the other specimens were cleared.

Unlike the compared genera *S. fuscipennis* has a caudally narrow, almost tubular penis

(Figs 17, 18). The basolateral arms of the trigonium (ba) are connected to the bases of the parameroids by a lobe (cl). The bases of the parameroids also possess dorsobasal shields, the crura (cr) which articulate basally with a sclerotized rod to which muscles certainly attach. The rod appears to be homologous with the tendon of other taxa. NYHOLM (1972) focused on the partial or complete horizontal division of the penis into dorsal and ventral sheets. I have difficulty seeing in my slide where the approximately tubular membranous structure projecting anteriorly from the penis attaches caudally.

Not all of the above parts are retained in other *Sacodes* species. The Nearctic *S. pulchella* (GUÉRIN) possesses a minute trigonium (NYHOLM 1972: fig. 2 J) while none is shown in figures of the European *S. flaviventris* KIESENWETTER (NYHOLM 1972: fig. 2I; KLAUSNITZER 1974: fig. 13) and several Far Eastern species (e.g., YOSHITOMI 1997, 2005, YOSHITOMI & SATÔ 1996) in which the divergent crura are prominently visible. Within the *Elodes*-clade, the genitalia of some *Sacodes*-like ancestor were secondarily modified, leading to the derived genitalia of *Elodes* and *Odeles*. Details remain to be investigated.

Conclusion: *Sacodes fuscipennis* is a member of the monophyletic *Elodes*-clade. Homology of several of its genital structures with those of representatives of the *Microcara*-type disproves the suggested (NYHOLM 1972) independent evolution of the two types of genitalia. Instead, probably both evolved from *Microcara*-like ancestors: the male genitalia of the *Microcara*-type represent the ancestral groundplan of all Scirtinae.

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