

# The Genital capsule of some Aradidae (Hemiptera, Heteroptera)<sup>1</sup>

C.W. SCHAEFER

**Abstract:** The aradid genital capsule, and the eighth abdominal segment, differ in several important respects from those of other members of the heteropteran infraorder Pentatomomorpha. The eighth sternum is unusually well developed and protects the venter of the capsule; a pair of lateral projections, the eighth hypopleurites or paratergites, arising from the eighth sternum, bear the eighth spiracles, which are often nonfunctional; internal structures of other pentatomomorphans (cuplike sclerite and median projection) are fused (as they often are in other pentatomomorphans), but in aradids are often enlarged, as major supports of the aedeagus. Most significantly, the internal (anterior) opening of the genital capsule has been „displaced“ posteriorly; as a result, the two openings (internal and external) are very close to one another and, in the case of *Aneurus* (*Aneurodellus*) *brouni*, have become one. A scheme is presented to explain this displacement.

**Key words:** Aradidae, Aradimorpha, genital capsule, Heteroptera, pygophore.

## Introduction

The heteropteran infraorder Pentatomomorpha contains two groups, the Trichophora and the Aradoidea. The five superfamilies in the former Coreoidea, Idioscoloidea, Lygaeoidea, Pyrrhocoroidea, and Pentatomoidea (HENRY 1997) all have abdominal trichobothria (hence "Trichophora"), whereas the Aradoidea does not. The phylogenetic relationship of the Aradidae to the remainder of the Pentatomomorpha has been, in a sense, hesitant or tentative (see SWEET 1996).

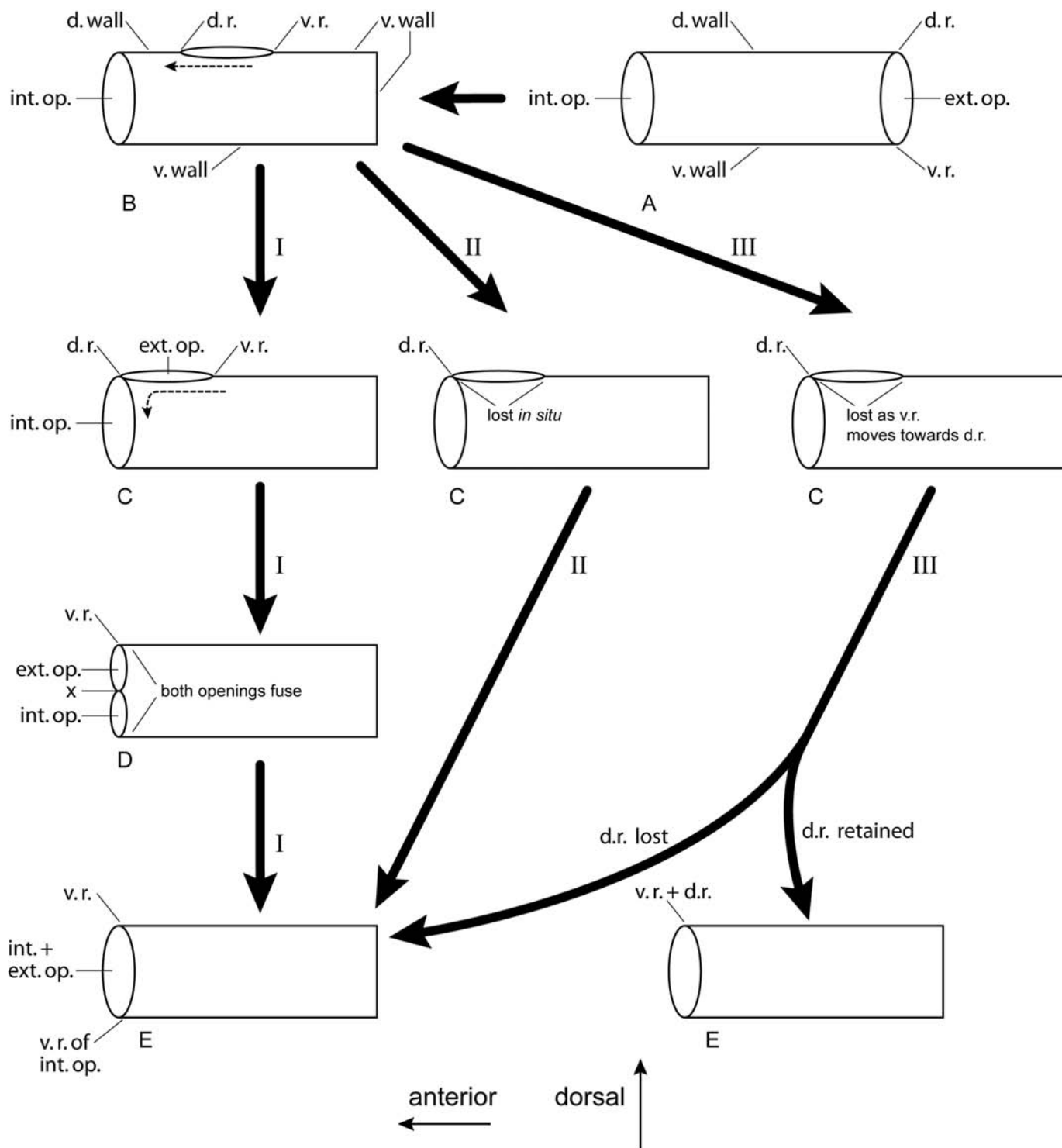
The genital capsule, or pygophore, of male heteropterans contains the parameres (claspers) and the structures for copulation (aedeagus). Because the capsule is a complex structure, and because various of its parts have evolved in different groups independently of others of its parts, the capsule provides useful characters for phylogenetic analysis and speculation.

I have studied the genital capsules (pygophores) of trichophoran males and discussed their value in family-group phylogen-

etic (SCHAEFER 1977, 1978, 1980; see also SCHAEFER 1981a, 1981b). It seems reasonable also to consider the genital capsule of the Aradidae, to see how it differs from that of the Trichophora. What follows is merely a start, a prolegomenon, to a deeper study of the aradid genital capsule and its functional and phylogenetic meanings.

In early 1989 I spent several weeks at Christ Church College (now University) in Canterbury, New Zealand. I dissected and took notes on the genital capsules of several aradid species, and followed this with a day at the B.P. Bishop Museum (Honolulu, Hawaii), taking briefer notes on a few more species; more recently, I have looked at two more species (*Aneurus inconstans* UHLER and *Dysodius lunatus* (FABRICIUS)). Here I summarize these notes as a basis for further study and suggest a highly speculative pathway for the development of the aradid genital capsule.

<sup>1</sup>With enormous pleasure, I dedicate what is good here (and only what is good) to Ernst Heiss, colleague, fellow heteropterist, and (best of all) friend.



**Fig. 1:** Schematic diagram of evolution of relationship of external and internal openings of aradid genital capsule. d. = dorsal, ext. = external, int. = internal, op. = opening, r. = rim, v. = ventral, x = dorsal rim of external opening plus dorsal edge of internal opening.

## Methods

I had representatives of all eight aradid subfamilies, although for some the sample is very small. The genital capsules of the Christ Church specimens were dissected out, softened in warm water, and studied under a dissecting microscope, as were those of the two species most recently studied. The

capsules of the Bishop Museum specimens were examined on the specimens, because of time constraints; the notes on these are perforce less detailed. Of necessity, nearly all the species are from or near New Zealand, and because of this and because of the small number of species, the conclusions are highly tentative. Unless otherwise stated, one specimen was examined of each species.

The scientific names have been checked in KORMILEV & FROESCHNER (1987).

As a necessary *point d'appui*, I point out my conviction that the entire genital capsule is the modified ninth sternum, a conviction supported by the relationships of the various connecting membranes (see SCHAEFER 1977, 1980); in my view, the dorsum (the tergum) of the ninth segment has been lost or reduced to a thin, often membranous strip, just anterior to the proctiger (the tenth segment). This ninth tergal remnant occasionally retains some degree of sclerotization or, less occasionally, attains some slight degree of secondary sclerotization subsequent to the remnant's reduction. I have found no reason to believe this is not true also of Aradidae (and it is true also of Reduviidae (SCHAEFER 1999)), despite the remarkable differences in this family. Therefore, in what follows, "dorsal" and "ventral" refer to the original state; i.e., the terms are morphological and refer to the dorsal and ventral parts of the external, originally terminal (posterior), opening of the genital capsule.

The capsule itself may be thought of (in its original state) as a short tube, one of whose openings, the anterior one, opens into the interior of the insect; the other opening is posterior and opens externally, to the outside world; it is through the latter opening that the anus deposits its materials and the aedeagus deposits its materials. Because the latter, external, morphologically posterior, opening has these responsibilities, it is in some phyletic lines modified the better to fulfill them: the edges surrounding this posterior opening are the dorsal, the lateral, and the ventral rims, and extending anteriorly from these rims are the dorsal, the lateral, and the ventral walls, these together comprising the body of the capsule itself. These rims may be modified (the ventral rim is usually modified) the better to accommodate and enhance the performance of the anus and the aedeagus – especially the aedeagus. The aedeagus lies towards the ventral rim, which is infolded upon itself; the terminus of this infolding may be turned up, as a **transverse ridge**, and from this arise two structures, the **cuplike sclerite** and the **median projection**; these originally were

separate structures, and in many bugs in which they have become united, their separate origin is sometimes discernible; separate or composite, these structures guide the aedeagus during copulation. A fuller description, with my reasons for believing my assertions, may be found in SCHAEFER (1977, 1980).

The eighth segment in male trichophorous is usually a simple ring, its dorsum membranous and the remainder lightly sclerotized. The spiracles, or spiracular remnants, lie laterally in the membranous portion. Although too membranous and poorly developed to be clearly differentiated, this region appears to be what SWEET (1996) terms a **hypopleurite**, defined in other abdominal segments as the sclerite bearing the spiracle. In Aradidae, unlike in other Pentatomomorpha, this spiracle-bearing sclerite of the male's eighth segment is well developed, and is usually termed the eighth paratergite. Sweet, however, believes this spiracle-bearing structure of the male aradid to be a hypopleurite. He reaches this conclusion after an exhaustive survey not only of Heteroptera, but of groups closely and distantly related to Heteroptera and Hemiptera. However, in Aradidae, the presence of muscle scars on these structures indicates they may not in fact be hypopleurites; SWEET (1996) suggests such scars in Aradidae are plesiomorphies. If they are not, then these spiracle-bearing structures in Aradidae may in fact be paratergites. However, because only Sweet has so far considered this question in detail, I here use his term, while recognizing that further work may prove it inaccurate. In Aradidae, the eighth sternum is also well developed.

## Results

The genital capsules of several bugs were dissected, and the descriptions of these are more detailed than the descriptions of other bugs whose capsules were merely removed from the specimens and observed. In these descriptions, 8S and 9S and 8T and 9T stand for eighth and ninth sternum and tergum, respectively. As indicated above, the posterolateral spiracle-bearing extensions (projections) of the eighth segment are termed here "hypopleurites VIII".

## Mezirinae

*Ctenoneurus myersi* KORMILEV (capsule dissected). Eighth segment: Broad, well sclerotized ventrally and laterally, with narrow nearly membranous strip dorsally; 8S exposed ventrally. Posterolateral edges of venter produced as blunt slightly divergent hypopleurites VIII, each with nonfunctional (occluded) spiracle subterminally, not visible from above. Posterior edge of venter infolded, appressed to inner surface; infolded region including projections.

Genital capsule: External opening dorsal. Most of dorsal surface of same texture as that of ventral surface, this similar region ending abruptly  $\frac{3}{4}$ 's the way anteriorly; this  $\frac{3}{4}$ 's the portion exposed to outside; remainder ( $\frac{1}{4}$ ) covered by seventh segment. Dorsal rim very narrow, dorsal wall probably represented by membrane covering anterior half of opening; anterior to membrane a pale median sclerite (9T?). Dorsal rim not infolded, restricted to a strip at anterior edge of opening; juncture with lateral rims sharp. Lateral rims prominent, infolded perpendicularly (not far); infolding slightly strengthened with small transverse ridge proceeding interiorly from infolding; lateral rims extending anteriorly to edge of internal opening. Paramere socket consisting of lateral and ventral rims; paramere base entirely filling socket. Most of ventral surface, all of posterior surface, part of dorsal surface (see above) heavily sclerotized, these regions exposed. Anterior portion of ventral surface more lightly sclerotized and of different texture, like that of dorsal surface anterior and lateral to external opening (heavier texture of ventral surface extending to posterior edge of opening). Surface just posterior to external opening broadly depressed, depression separated opening by infolded medial portion of ventral rim (see below). Where lateral and ventral rims meet, latter appearing to overlie former slightly. Ventral rim infolded only medially; cuticle of this region thinner than rest of ventral surface, and with transverse rugae. Remainder of ventral surface with small well-sclerotized knobs. Ventral rim infolding wholly fused laterally to inner surface of median region, but more free medially thus forming sharp ridge running along inner surface of this flaplike me-

dian region of ventral rim. No transverse ridge. Median region posteriorly joined to much modified cuplike sclerite and median projection. Cuplike sclerite indistinguishably fused with median projection (perhaps: see below). Composite structure broad apically, broadly joined to base of infolded portion of ventral rim, but extending beyond it laterally to join inner surface of ventral wall. Composite structure extending proximally as a broad well-sclerotized strap closely holding phallobase of aedeagus. Strap ending close to small basal plate apparatus; suspensory apodemes small, round. From point at which straps arise, well-sclerotized semicircular extension covers **dorsal**, (not ventral) surface of phallobase, closely applied to it; this covering ending in sclerotized knob. (This semitubular covering may be the median projection, at this point separate from the cuplike sclerite; the morphological relationships of its base are too complex to permit a guess.)

Note: The composite cuplike sclerite and median projection are much reduced apically, and the phallobase of the aedeagus is large, well-sclerotized, and ends in a strong dorsal knob; because the phallobase appears to be large and strong apically, there may be no need for a supporting composite structure here; the structure is better developed more proximally.

Proctiger: Embedded in dorsal-rim membrane posterior to putative 9T remnant; a complex lightly sclerotized band; sclerotized region with two small circles.

*Dysodius lunatus* (FABRICIUS) (capsule not dissected). Eighth segment: Similar to that of *Ctenoneurus myersi*. Broad, lightly sclerotized ventrally (8S) and laterally, sclerotized slightly more heavily on anterior half; reduced to narrow strip dorsally (8T), this membranous medially. Hypopleurites VIII produced posteriorly as blunt projections, each with three short blunt fingerlike extensions, these decreasing in size medially to laterally. Eighth spiracle near base of projection, occluded, nonfunctional. Posterior edge of 8S infolded, appressed to its inner surface; joined via a membrane to ventral surface of genital capsule at end of infolding; this infolding including projections, these therefore hollow.

Genital capsule: External opening dorsal, separated from internal opening by narrow strip of membrane with some secondary sclerotization. Portion of capsule covered by eighth segment and by lateral projections sclerotized; portion not covered very heavily and thickly sclerotized; latter region like a shield, rugose, with several paired “bumps” on dorsum, and with large round medial bulge on venter. Dorsal rim not infolded, pair of thin sclerotized strips on either side of midline just internal (morphologically ventral) to dorsal rim; these perhaps remnants of 9T. Lateral rims not infolded dorsally, slightly thicker ventrally; infolded ventrally to form (with ventral rim infolding) the paramere socket. Ventral rim obscured by large parameres; these not removed. Cuplike sclerite and median projection apparently fused; composite structure large, joined lateral to infolding of ventral rim; further details obscure.

Proctiger: Simple, sclerotized ventrally, mostly membranous dorsally, some light secondary sclerotization.

### Chinamyersiinae

*Tretocoris grandis* USINGER & MATSUDA (capsule dissected). Eighth segment: Dorsum reduced to narrow rodlike strip of sclerite; venter greatly expanded to cover anterior half of capsule's venter; 8S infolded as in *Ctenoneurus myersi*; Hypopleurites VIII very large, paddleshaped, somewhat resembling the parandria (see below); spiracle halfway along projection, visible from above, functional (trachea attached).

Genital capsule: External opening dorsal, occupying entire dorsal surface; anterior 1/4 of opening covered by 7T; most of opening covered by two pairs large platelike parandria (see below); opening thus entirely covered, except for a cross-shaped crease, whose horizontal component is slight space between ventral and lateral parandria, and whose vertical component is slight space between the members of the two pairs. External opening partly occluded by membrane from its edges; membrane dorsally with pale T-shaped sclerite on either side (Note: This amount of membrane unusual in bugs). Dorsal wall reduced to narrow strip of sclerite between external and internal openings;

dorsal rim infolded perpendicular to dorsal wall, semi-membranous, joined to proctiger; with large medial sclerite (9T?) lightly sclerotized except anteriorly, here dark and almost apodemelike. Dorsal rim infolding joined laterally to inner surface of lateral parandria (in the usual dorsal rim-lateral rim relationship). Lateral and ventral rims simple, their infoldings modified as parandria (hence ventral and lateral parandria); no transverse ridge. Two pairs large parandria, one from ventral one from lateral rims; ventral parandria arising from either side of ventral rim, joined to it only by narrow strip of membrane, articulated to base of cuplike sclerite (close to origin of suspensory apodemes) by small transverse process of cuplike sclerite. Lateral-rim parandria with similar relationship to lateral rims; each with stout lateral-rim apodeme extending a short way interiorly; muscle originating here apparently inserting on basal plate apparatus (Note: The four parandria are the ventral and lateral rim infoldings, semi-detached from their respective inner walls. Each is of double thickness, i.e., with a narrow space between the layers of cuticle, like the infolded rims of other bugs. It is this double-layering that reveals the parandria's origin from the ventral and lateral rims.) Cuplike sclerite and median projection fused medially, closely appressed laterally; the two structures distinct (different texture) throughout; medial projection without apodemes. Suspensory apodemes short, stout, irregular in shape.

### Carventinae

*Acaraptera myersi* USINGER & MATSUDA (capsule cleared but not dissected). Genital capsule: External opening dorsal, dorsal rim narrow, not infolded. Lateral rims infolded parallel to lateral walls, with internal apodeme at juncture with dorsal rim. Semi-circular sclerite (9T remnant?) in membrane between dorsal rim and proctiger. Cuplike sclerite and median projection separate structures, at least terminally; both structures together forming complex partial tube over aedeagus (details not seen); tube joined laterally via a midline ridge to ventral rim of infolding; this ridge running length of cuplike sclerite (=length of aedeagus), and marked externally (on ventral – anatomically poste-



**Table 1:** Features of the aradid male's eighth segment (+, spiracle visible dorsally; - not visible dorsally).

Subfamily and Species	Hypopleurites (Paratergites) VIII	Eighth sternum covering venter of genital capsule	Position of eighth spiracle
<b>Mezirinae</b> <i>Ctenoneurus myersi</i> KORMILEV <i>Dysodius lunatus</i> (FABRICIUS)	elongate, rounded elongate, digitate	yes, partly exposed yes	subterminal, nonfunctional, - ventral, near base; "nonfunctional"
<b>Isoderminae</b> <i>Isodermus planus</i> ERICHSON <i>I. tenuicornis</i> USINGER & MATSUDA <i>I. crassicornis</i> USINGER & MATSUDA <i>I. maculosus</i> PENDERGRAST	very small knob small knob small knob small knob	yes, wholly exposed yes, wholly exposed yes, wholly exposed yes, wholly exposed	lateral, + lateral, + lateral, + lateral, +
<b>Prosympiestinae</b> <i>Prosympiestus constrictus</i> USINGER & MATSUDA		yes, wholly exposed	sublaterally, +
<b>Chinamyersiinae</b> <i>Gnostocoris gressitti</i> KORMILEV  <i>Kumaessa carraiensis</i> MONTEITH <i>Tretocoris grandis</i> USINGER & MATSUDA <i>Wuessa tianmuana</i> LIU & ZHENG <sup>1</sup>	large, flattened, ending in several knobs large, flattened large, flat, paddleshaped large, clavate	yes, wholly exposed  yes yes apparently	at end of medial knob, ventral, - near base, ventrally, - at midpoint, functional, + —
<b>Calisiinae</b> <i>Calisius granuliger</i> KORMILEV <i>C. interveniens</i> BERGROTH	cylindrical short, cylindrical	yes, wholly exposed yes, wholly exposed	terminal, on tubercle, + terminal, on tubercle, +
<b>Aneurinae</b> <i>Aneurus salmoni</i> PENDERGRAST <i>A. brouni</i> WHITE <i>A. inconstans</i> UHLER	long, blunt, partly concealed long, blunt, partly concealed long, slightly digitate	partly partly partly	terminal, occluded, + terminal, occluded, + terminal, occluded
<b>Carventinae</b> <i>Acaraptera mysersi</i> USINGER & MATSUDA <i>Carventaptera spinifer</i> USINGER & MATSUDA  <i>Neocarventus angulatus</i> USINGER & MATSUDA <i>Nesiaptera zimmermani</i> USINGER & MATSUDA	small, digitate short, triangular  stubby, 2-pronged elongate, cylindrical	yes, concealed by 7S as above  as above yes	terminal, + just subterminal, +  terminal, + terminal
<b>Aradinae</b> <i>Aradus australis</i> ERICHSON	long, flattened	yes; capsule wholly concealed (except external opening), hypo- pleurites extending beyond capsule	midlaterally, +

<sup>1</sup>ZHENG & LIU (1992), Fig 2.

rior) wall by external ridge. Suspensory apodemes short, well sclerotized.

Proctiger: Bearing two small oval sclerites ventrolaterally, these probably surrounding anus.

### Aneurinae

*Aneurus brouni* WHITE (2 specimens) (capsule cleared but not dissected). Eighth segment: 8T reduced to tiny membranous remnant. 8S expanded posteromedially, to cover median part of genital capsule's venter; this median expansion lightly sclerotized; posterolateral regions not expanded, membranous; median part of 8s infolded. Hypopleurites VIII bearing remnant of non-functional spiracle at tip.

Genital capsule: Single opening, anterior, probably result of fusion or combining of external (posterior) and internal (anterior)

openings (see Discussion, below); the two openings of different shape and thus distinguishable. Dorsal wall thus lost; dorsal rim reduced to tiny median strip attached subapically to edge of capsule. Small distinct median plate (9T remnant?) lying anterior to dorsal rim, this plate between tips of parameres, the three (plate and parameres) in position to protect tip of aedeagus at rest and perhaps to support it in use. Region of capsule's venter covered by 8S pale, as is also region lateral to it (although this not covered, but concealed beneath 7S). Rest of capsule darker and cuticle heavier. Lighter region of cuticle extending laterally one-third to each side of dorsal midline, where darker cuticle extends from posterior to reach opening. Lateral rim indistinguishable from ventral, not infolded. Ventral rim of external opening (i.e., of external opening component of combined openings) not infolded; therefore

no transverse ridge, and no connection of ventral rim to cuplike sclerite and median projection. Ventral rim of internal opening (i.e., of internal opening component of combined openings) excised medially, where covered by 8S expansion. Cuplike sclerite and median projection indistinguishably fused and appearing to surround base of phallotheca, with extension along surface of phallotheca to its apex (this extension on the apparent ventral region of the phallotheca). I could not see the suspensory apodemes; and the basal plate apparatus is large.

*Aneurus inconstans* UHLER (capsule cleared but not dissected). Eighth segment: 8T lost or reduced to tiny membranous remnant. 8S expanded posteromedially, to cover median part of genital capsule's venter; posteromedial expansion very lightly, secondarily, sclerotized; posterolateral region also sclerotized; anteromedial region a narrow sclerotized strip, this infolded (indicating it is indeed 8S). Hypopleurites VIII well sclerotized, large, vaguely digitate, with spiracular remnant at apex.

Genital capsule: Two openings. Internal opening large, dorsal; external opening smaller, posterior and slightly dorsal; the two openings separated only by a membrane; this probably remnant of dorsal rim of external opening (an interpretation supported by relationship between this membrane and proctiger). Lateral rims of external opening indistinguishable from ventral rim, not infolded; ventral rim (here dorsal) not infolded; no transverse ridge, and ventral rim not joined to cuplike sclerite and median projection. Cuplike sclerite and median projection indistinguishably fused, appearing to surround base of phallotheca, with extension along phallotheca's surface to its apex (this extension lying on apparent ventral region of phallotheca). I could not see the suspensory apodemes; the basal plate apparatus appears to be large.

## Discussion

Several aspects of the aradid genital capsule and the eighth abdominal segment are unusual in Heteroptera or unique to Aradidae. Here the eighth tergum is reduced (not

unusual) but the eighth sternum is very well developed and well sclerotized. It encloses the venter of the genital capsule (Table 1), whose dorsum is covered, partly or completely, by the seventh tergum (partly in Isoderminae; *Tretocoris grandis* (Chinamyersinae)). The capsule and its delicate contents are thus protected by part of the eighth and part of the seventh segments. The degree to which the capsule is visibly concealed by the eighth sternum depends upon the extent to which the capsule is withdrawn beneath the seventh sternum. Such protection is similarly afforded to the capsule in other groups (Coreoidea, many Lygaeoidea (sensu HENRY 1997)), although in these groups much of the capsule's external opening (usually dorsal) is exposed. Protection is somewhat differently provided by the withdrawal of the capsule well within the seventh segment (Pyrrhocoridae, Rhopalinae); or much differently provided by a heavily sclerotized proctiger (higher Pentatomoidea) (Schaefer unpublished).

Perhaps as part of the great development of the eighth sternum, the eighth hypopleurites are here in male Aradidae enlarged and modified (Table 1), whereas in other heteropterans they are at best poorly developed. The hypopleurite has become closely integrated with the eighth sternum: That they are hypopleurites (SWEET 1996) is shown by their bearing the spiracles. That they are intimately joined to, and become part of, the eighth sternum, is shown by their double-walled connection to the double walls of the eighth sternum itself. These hypopleurites have perhaps become well developed to aid in the protection of the genital capsule, a function performed in other ways in many other bugs (see above). Although the hypopleurites bear the eighth spiracles, these spiracles in nearly all cases lack any tracheae and their openings are occluded; these spiracles are apparently nonfunctional in many aradids (Table 1). Eighth spiracles are also nonfunctional in the males (not the females) of nearly all Pentatomomorpha (and, I suspect, of all other heteropterans) (Schaefer unpublished). I suggest then that in some phyletic lines these projections of Aradidae did not develop for any respiratory purpose, but rather to protect the capsule. As they developed, they carried with them spiracles al-

ready functionless. This suggestion (protection) does not rule out other possible explanations for the development of the eighth sternum and the eighth hypopleurites; indeed, these structures may serve a function in the ontogenetic development of the capsule, or their increased size may be a response to that development.

The cuplike sclerite and median projection are usually fused at least medially, but often the fact that they are in fact separate structures is clear in lateral view. In some cases the composite structure is large, and almost cradles the aedeagus. This large composite structure appears to be the structure labeled “strut” in Fig. 15F of USINGER & MATSUDA (1959) (*Chinamersia cinerea* (MYERS & CHINA)). In the Trichophora, the sclerite and the projection may be separate, partly fused, or indistinguishably fused. However, they do not form a structure cradling the aedeagus, as occurs in some aradids. Of particular interest in the genital capsule of Aradidae, is how close together the internal (primitively anterior) and external (primitively posterior) openings lie. This proximity culminates in *Aneurus brouni*, where the two openings have become one (although the two are distinguishable by shape); however, in this species' congener, *A. inconstans*, the two openings are not one, but very close, separated by only a bit of membrane. It is significant in this regard that *A. brouni*, together with the other New Zealand *Aneurus*, have been placed in a separate subgenus, *Aneurodellus* HEISS (HEISS 1998). Here, and in Fig. 1, I try to explain how this juxtaposition of the two openings may have come about, and how in at least one aradid the two openings have joined to become one.

I believe that there are three possible answers – scenarios, although I think one is more likely than the other two. This discussion, like Fig. 1, is based on my earlier work with the genital capsules of other groups. Each suggested sequence in Fig. 1 begins with the “primitive” capsule (A), in which the internal (anterior) and external (posterior) openings are terminal. The internal opening is undifferentiated: Its rim is merely a membranous or slightly sclerotized strip. The rim of the external opening, on the oth-

er hand, is clearly differentiated into a ventral portion (“ventral rim” or v.r.), a dorsal portion (d.r.), and between them a less well differentiated lateral rim (not labeled in Fig. 1). The tenth segment (proctiger; not shown) is joined to the dorsal rim by a membrane, and thereby helps to establish what is the dorsal rim when modifications occur. Indeed, often the true morphological relationships of the rims and associated structures can be ascertained by the relationships and attachments of the membranes uniting them (SCHAEFER 1977, 1980).

In Fig. 1, I indicate the three possible pathways of the external opening's dorsalization as I, II, and III. All sequences begin with a posterior external opening (A) which migrates dorsally and then anteriorly (B). In most Aradidae, the two openings remain, but are close to one another; this condition is indicated by C in Fig. 1. At this point the pathways diverge, to reach the single-opening condition of a few aradids.

- I. Here the external opening “moves” (by the anteriad shifting of the ventral rim) to share the anterior position with the internal opening (I-D). The two openings fuse, by elimination of the once-dorsal dorsal rim and the dorsal edge of the anterior opening, which have hitherto separated the two openings. The result is I-E. If this sequence did indeed occur, there should be no trace of the dorsal rim.
- II. Here the external opening is simply lost, without shifting its position, and its function is taken over by the internal opening (II-C). If this had in fact occurred, considerable adjustment would have been necessary of the structures associated with the ventral rim and its infolding. Also, some trace of the external opening and of the ventral rim might be expected on the dorsal surface of the capsule – that is, some difference in texture, and some ridge-like reminiscence of the ventral rim. I have not found any of these several evidences of this pathway. This pathway seems highly unlikely, particularly because any intermediate stage seem quite nonfunctional.
- III. Rather than being lost in situ, the ventral rim here is shifted anteriorly (III-C),



much as earlier it had been shifted dorsally from its originally posterior position, to yield the dorsal external opening (A => B; also SCHAEFER 1977, Fig. 12d). In this sequence, the ventral rim may eventually “meet” the dorsal rim, perhaps obliterating it (I-E). Alternatively, some remnant may remain of the dorsal rim, closely applied to the ventral rim. The latter I think occurs in *Aneurus brouni* (III-E), where a small median sclerite is attached subterminally to the ventral rim: This sclerite, I suggest, is a remnant of the dorsal rim.

If it is a remnant of the dorsal rim, then sequence III seems best of the three pathways to explain how the external and internal openings of the genital capsule have moved so close together (and, in the case of *Aneurus brouni*) to have become a single opening. Pathway III is the most satisfying also because it invokes a process already known (or very likely) to have occurred in other bugs – that is, the encroachment of the ventral wall, led by the ventral rim, onto the dorsal wall. Pathway III is a continuation of the process by which in other bugs the once-posterior external opening became dorsal (SCHAEFER 1977).

Pathway I requires that the internal and external openings have co-existed anteriorly, however briefly. This seems to me unlikely, even if it need not have occurred and been functional in an actual adult insect, but only occurred in some pre-adult developmental stage.

Similarly, Pathway II requires a complete realignment of the genital capsule and cuplike sclerite, and of their associations with the aedeagus and basal plate apparatus. Again, it is difficult to see how this might occur, the transitional stages being certainly dysfunctional. And again, it seems highly unlikely that this transition might have occurred in a pre-adult developmental stage.

In Pathway III, as the external opening became anterior (and, in *Aneurus brouni*—and others?—united with), there need not have been a major rearrangement of the structures within the capsule. However, the aedeagus would become inverted, its morphologically ventral surface becoming dor-

sal. In *Ctenoneurus* sp. an extension of the cuplike-sclerite-plus-median-projection runs along the dorsal surface of the phallobase. In *Aneurus brouni* a similar semitubular structure is closely applied to the apparently **ventral** surface of the phallobase. I suggest the two semitubular structures are homologous, and that each reinforces the morphologically dorsal surface of the phallobase.

In heteropterans, the parameres arise from the junction of the infoldings of the ventral and the lateral rims. In Aradidae the parameres appear to arise from the dorsal rim. I take this as further evidence that the dorsal portion of the aradid genital capsule is derived from the ventral wall.

## Conclusions

It is clear that the genital capsule of the Aradidae is greatly modified from those of the rest of the Pentatomomorpha, and in fact from those of the Reduviidae (Cimicomorpha) (SCHAEFER 1999), and indeed from those of many other heteropteran families (Schaefer unpublished). However, the differences are more ones of degree than of kind: Such features as the dorsalization of the external opening and the cradling of the aedeagus by the cuplike sclerite+median projection occur in other groups, but to a lesser degree. The greater degree of these differences in Aradidae may in part warrant the erection of Aradidae (and Termitaphididae?) to a separate infraorder, Aradimorpha, as SWEET (2006) suggests; but we need further analysis of additional characters, particularly that promised and discussed by SWEET (1996, 2006).

In addition, the eighth segment of the male differs from that of most (all?) Pentatomomorpha and Reduviidae. In the Aradidae the sternum of this segment is greatly developed and, perhaps as a consequence (or cause), has come to incorporate the greatly developed eighth hypopleurites, which in turn carry the eighth abdominal spiracles. However, these spiracles appear in many Aradidae to be nonfunctional, despite being exposed; in other pentatomomorphans exposed eighth spiracles (in the male) appear to be functional, and concealed ones – the usual case – are nonfunctional.

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## Zusammenfassung

Die Genitalkapsel der Aradiden und das achte abdominale Segment unterscheiden sich in mehreren wichtigen Merkmalen von anderen Vertretern der Unterordnung Pentatomomorpha. Das achte Sternum ist ungewöhnlich gut entwickelt und schützt die Unterseite der Kapsel; ein Paar seitlicher Fortsätze, die Hypopleurite VIII oder Paratergite, die vom achten Sternum entspringen, tragen die meist funktionslosen Stigmen des achten Segmentes; interne Strukturen anderer Pentatomomorpha (schalenförmige Sklerite und mittlere Fortsätze) sind verschmolzen (so wie bei den meisten anderen Pentatomomorpha), aber bei den Aradiden sind diese als wichtige Unterstützung des Aedeagus vergrößert. Höchst bedeutsam ist, dass die interne (vordere) Öffnung der Genitalkapsel nach hinten „verschoben“ wurde; dies bedeutet, dass die beiden Öffnungen (interne und externe) nahe beieinander liegen und bei *Aneurus* (*Aneurodellus*) *browni* sogar miteinander verschmelzen. Ein Schema zur Erklärung dieser Verschiebung wird präsentiert.

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## Address of the Author:

Dr. Carl W. Schaefer  
Department of Ecology and  
Evolutionary Biology  
University of Connecticut  
Storrs CT 06269-3043  
U.S.A.  
E-Mail: [carl.schaefer@uconn.edu](mailto:carl.schaefer@uconn.edu)

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