Justification for the Aradimorpha as an infraorder of the suborder Heteroptera (Hemiptera, Prosorrhyncha) with Special Reference to the Pregenital Abdominal Structure[1]

M.H. SWEET

Abstract: Aradomorpha SWEET 1996 is replaced with Aradimorpha because of homonymy with *Aradomorpha* CHAMPION 1899, a genus of Reduviidae. The Aradimorpha differ from the Pentatomomorpha *s.s.* and the Leptopodomorpha in having a plesiomorphic connexivum of dorsal epipleurites and ventral hypopleurites rather than having the connexivum turned over so that the hypopleurites are dorsalized and the epipleurites folded into the abdomen. In most Aradimorpha, in both males and females, sterna 3 to 7 are free with intersegmental conjunctiva; terga 1-2 and 3 to 6 are united, but all epipleurites are free. In the Pentatomomorpha at least abdominal sterna 2 to 4 in females and sterna 2 to 5 in males are united or fused without conjunctiva. In some aradids the hypopleurites are united or fused with the sterna, but hypopleurite 2 is usually free. Sternum 2 is sometimes united to fused with sternum 1 and the metasternum. The abdominal spiracles in the Aradimorpha are ventral on the hypopleurites, although sometimes very lateral in position on the hypopleurites, with the exception of the Chinamyersiini in which spiracles 4, 5 and 6 are dorsal on the epipleurites in *Chinamyersia*, and 5 and 6 dorsal in *Gnostocoris*, while in the Tretocorini (*Tretocoris* and *Kumaressa*) spiracle 2 seems dorsal but is actually very lateral on the hypopleurite. In the Termitaphididae, epipleurites and hypopleurites are distinct, forming mobile lateral abdominal lobes. In the Aradidae the metapleuron abuts the abdominal margin, that is hypopleurite 2, leaving segment 2 and spiracle 2 completely exposed laterally, as compared to the Pentatomomorpha and Leptopodomorpha where a large metapleural flange laterally covers the base of abdominal segment 2 and nearly always covers spiracle 2. Sternum 1 is present between the metacoxae, sometimes free as in Aradinae, sometimes united to the metasternum. Synapomorphies defining the infraorder Aradimorpha include: The stylets are very elongate and coiled in the tylus (clypeus), and are used for feeding on fungi. The body is extremely flattened for living under bark or being concealed on surfaces or in leaf litter. Muscle scar apodemes (glabrous areas) are present on the epipleurites and hypopleurites as well as on the terga and sterna. This strong musculature is probably related to the need for these insects to greatly flatten themselves to fit into crevices. With the exception of the Isoderminae, the cuticle has peculiar inflorescent incrustations not known in other Heteroptera, which probably relates to concealment in these slow moving insects. With few exceptions, the unguitractor plate in the Aradidae is arrowhead-shaped or pentagular, a form unique to the Heteroptera. In the male, spiracle 8 is exposed on the apex of, or basal to a projecting tubercle of segment 8, and sternum 8 forms a cup that is exposed and is not cylindrical, nor withdrawn into segment 7 at rest, as in the Pentatomomorpha. The cuplike sternum 8 cradles and protects the genital capsule. The mating behavior of the Aradidae in which the male is ventral to the female is considered to be plesiomorphic as compared to the side-by-side position of the Leptopodomorpha and the Cimicomorpha or to the end-to-end rotated position of the Pentatomomorpha. The cuplike sternum 8 is a special synapomorphy to support this type of mating. The two-segmented tarsus is an apomorphy within the Aradidae because the plesiomorphic three-segmented tarsomere condition occurs in the Tretocorini (*Tretocoris* and *Kumaressa*). The ocelli are lost, in all Aradoidea except *Kumaressa*, which has small ocelli present, so the loss of ocelli is an apomorphy within the Aradidae. Other plesiomorphies of the Aradidae with respect to the Pentatomomorpha are: The bulbus ejaculatorius is simple, consisting partly of only two layers as compared to the three-layered condition of the bulbus ejaculatorius of the

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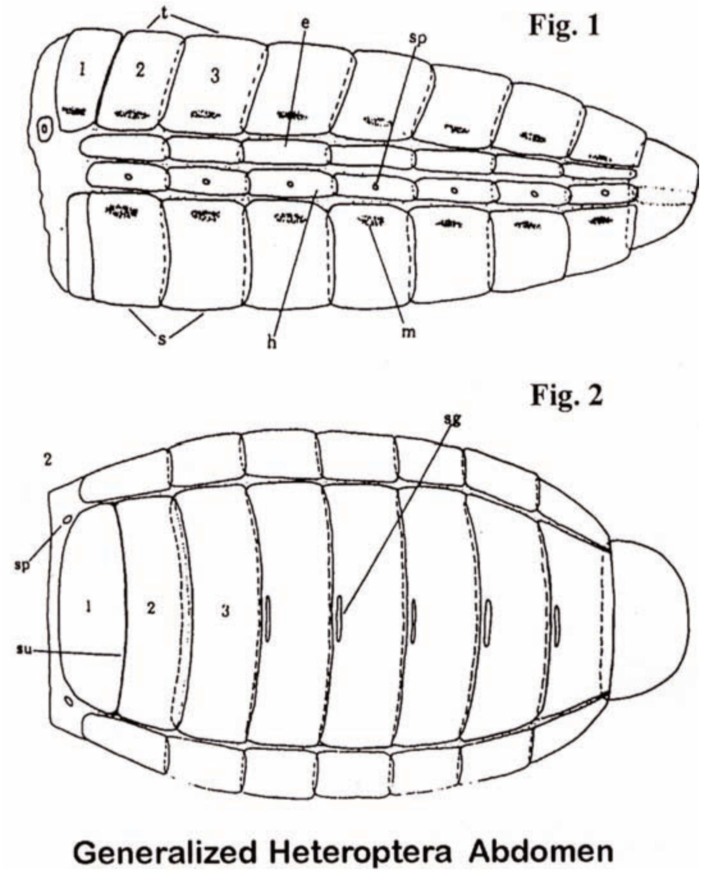
[1] It gives me great pleasure to dedicate this paper to my good friend and colleague Ernst Heiss in honor of his outstanding contributions to the taxonomy of the Heteroptera, especially the Aradoidea.

Pentatomomorpha and the Cimicomorpha. The three-parted midgut lacks the gastric caeca found in most Pentatomomorpha, and a true ileum is present (except in the Aradinae), which organ is lacking in the Pentatomomorpha. The labrum of the Aradinae is plesiomorphic in being free, and has a protruding epipharyngeal process. The pretarsus has pulvillae, which are lost in the Aradinae. In the hemelytra of the macropterous Aradidae the clavi over lap and do not meet form a commissure, and the clavi contribute to the membrane, which is considered plesiomorphic. In the Pentatomomorpha, as in most Heteroptera the clavi normally meet to form a commissure, and if the commissure is absent it is due to an expansion of the scutellum or reduction of the clavi and the clavi do not contribute to the membrane. In the Chinamyersiini and the Aradinae, there are several sc-r, r-m, and m-cu cross veins in the corium, which are considered plesiomorphic, as are the cross-veins forming cells in the membrane among the 6 veins entering in to the membrane, the Sc, R, M, Cu, Pcu, and A. There appears to be either no m-fracture in the corium, or a short fracture runs anteriorad of R, not posteriorad, as in all Heteroptera, except the Enicocephalomorpha. The R and M veins begin basally separate, and run separately or together from the base of the corium to the distal corial margin, which is bent basad by a long m-cu cross vein that sets off the distal corial margin. The presence of gonoplacs in the female genitalia is shown by their clear presence in the Tretocorini, whereas in the Pentatomomorpha the gonoplacs are either absent or more likely, fused with valvifer 9. The simple egg without an operculum and with aeromicropyles and an embryonic egg burster, is considered symplesiomorphic, not synapomorphic with the pentatomomorphan egg, as compared to the apomorphic operculate egg of the Cimicomorpha. This morphological evidence, together with the ecological evidence, the fossil evidence and the biogeographical evidence support the thesis that the Aradimorpha is an ancient terrestrial infraorder that diverged early in the phylogeny of the Prosorrhyncha or Heteroptera before the Leptopodomorpha, the Cimicomorpha and the Pentatomomorpha.

Key words: Aradimorpha, Aradoidea, abdominal morphology, biogeography, forewing venation, fossils, fungus feeding, mating position, mouthparts, thoracic morphology.

Introduction

I gave evidence (SWEET 1996) that in insects the abdominal pleural region is not a membranous area bearing spiracles as SNODGRASS (1931, 1935, 1963) and other morphologists had envisioned, but is characterized by the primitive possession of dorsal epipleurites and ventral hypopleurites, which latter bear the spiracles. Both pleurites are primitively derived from limb bases, the epipleurites associated with wings or winglets, the hypopleurites with spiracles in the interpretations of KUKALOVA-PECK (1983, 1987) of the pleural region. In the Heteroptera I argued that these two sets of sclerites form the connexivum of the abdomen with the lateral edge being the flexible connexive between the pleurites (Figs 1-2) (SWEET 1996). While the tergum itself may be divided into tergites (mediotergites and laterotergites), the dorsal lateral sclerites called the connexivum are thus pleural, and therefore are epipleurites, not laterotergites. In the Pentatomomorpha s.s., and also in the Leptopodomorpha, there are longitudinal series of dorsal sclerites that fold into the abdominal conjunctiva. These had been called internal laterotergites (DUPUIS 1949, 1953), or inner or mesal laterotergites (SWEET 1967, 1981). I proposed (SWEET 1981, 1996) (Fig. 5) that the connexivum had been turned or rolled over so that the so-called inner laterotergites are actually the former epipleurites of the connexivum, and the hypopleurites have become the dorsal connexivum. I proposed that this allowed for dorsal-ventral expansion under the hemelytra, and promoted the union or fusion of sterna and terga to achieve a strong, tanklike structure. This turning over of the connexivum helps to explain the common presence of dorsal spiracles in the Pentatomomorpha and the Leptopodomorpha, and the absence of dorsal spiracles in other infraorders, the Cimicomorpha, the Gerromorpha, the Nepomorpha, the Dipsocoromorpha and the Enicocephalomorpha, for in these infraorders the connexivum is not turned over, and the dorsal connexivum is the epipleurites, and ventral connexivum, the hypopleurites, which bear the spiracles. The Reduviidae, which have the plesiomorphic dorsal epipleurite and ventral hypopleurite connexival sclerites (DAVIS 1957; SWEET 1981), show an analogous infolding



Figs 1-2: Morphology of generalized male hemipteran pregenital abdomen. (**1**) lateral view (**2**) dorsal view. e – epipleurite; h – hypopleurite; m – muscle scar; s – sternum; sg – scent gland; sp – spiracle; su – suture; t – tergum: numerals, abdominal segments. (After Sweet 1996).

in the Triatominae, in that the hypopleurites fold into the abdomen under the epipleurites, to enhance the inflation of the abdomen during blood feeding and shrinkage afterwards (Lent & Wygodzinsky 1979). The position of the spiracles on the lateral side of the abdomen probably benefits breathing respiration, providing the selection pressure for the spiracles to migrate from dorsal on the hypopleurite to lateral on the sternal margin, which gives rise to the diversity of spiracle positions in the Pentatomomorpha (Sweet 1981, 1996) so important in the phylogeny of the Lygaeoidea (Henry 1997). The dorsal position of spiracles thus becomes a plesiomorphy, whose retention dorsad may possibly reflect selection for moisture conservation. Indeed, spiracles may readily remigrate dorsad to the hypopleurites, as this is the original position of spiracles. Note that in the other infraorders without the turned-over connexivum the spiracles remain ventral so dorsal spiracles on the epipleurites are unknown in the Enicocephalomorpha, the Dipsocoromorpha, the Nepomorpha, the Gerromorpha, and the Cimicomorpha. I consider this turning-over of the connexivum to be a major character transformation, a strong synapomorphy not to be lightly disregarded. In the context of this analysis of the structure of the abdomen in the Hemiptera, and insects in general, I illustrated the plesiomorphous structure of the abdomen in the Aradidae (Figs 3-4) with dorsal epipleurites and ventral hypopleurites as comprising the connexivum as a pleural structure (Sweet 1996). This is in contrast, as noted above, with the abdominal structure of the Pentatomomorpha s.s., the Trichophora of Tullgren (1918), in which the connexivum is turned over so that the hypopleurites are dorsalized and the epipleurites are infolded into the abdomen (Sweet 1981, 1996) (Fig. 5). This is clearly an adaptation that promotes dorsal-ventral expansion, while allowing the terga and sterna to unite and fuse with each other, promoting a well-sclerotized tanklike structure, as is commonly seen in pentatomomorphans (Sweet 1981, 1996). Because the Leptopodomorpha similarly show a turned-over connexivum with infolded epipleurites, I proposed a sister-group relationship between the Leptopodomorpha and the Pentatomomorpha s.s. based on this synapomorphy (Sweet 1996). I therefore regard the dorsal abdominal spiracles of the Leptopodidae to be plesiomorphous, not apomorphic. The alternative would be for this unusual large morphological feature to have evolved independently in the ancestors of the Leptopodomorpha and the Pentatomomorpha. I reasoned that this seems unlikely, given the absence of such infolded epipleurites in the Cimicomorpha, the Nepomorpha, the Gerromorpha, the Dipsocoromorpha, the Enicocephalomorpha, and the Coleorrhyncha (=Peloridiomorpha). My proposal has not been widely accepted (Aukema & Rieger 2001), so the purpose of the present paper is to give additional evidence on the validity of recognizing the Aradimorpha as an infraorder of the Heteroptera, or Prosorrhyncha (Campbell et al. 1995; Sorensen et al. 1995). First, let us examine the abdomen in the Aradidae and the Termitaphididae in the context of the subfamily classification, and then discuss the Aradimorpha in the context of the infraordinal classification of the suborder Heteroptera or Prosorrhyncha.

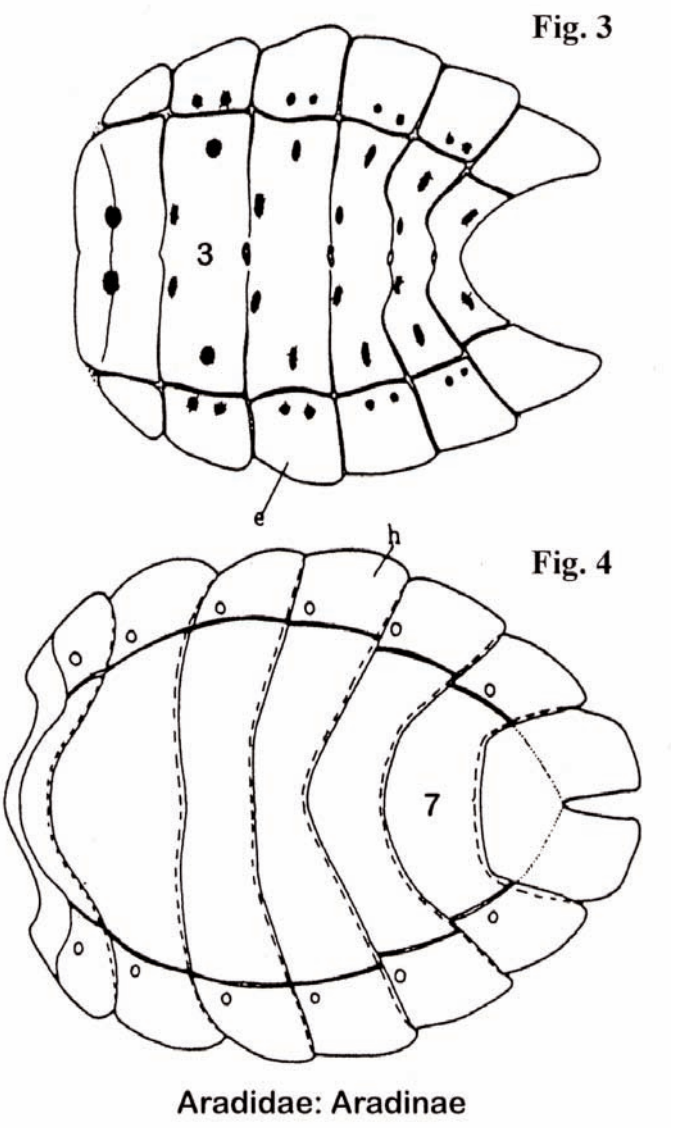
The Abdomen of the Aradimorpha

Methodology. – The abdomen was studied by heating the abdomen or the whole insect in KOH solution until the protein was cleared, allowing the visualization of the cuticular structures. Studies were made using a Wild Dissecting Stereomicroscope, and as needed, with Olympus compound microscopes. The illustrations were prepared using a grid micrometer.

Specimens examined. – ARADIDAE: Aneurinae: *Aneurus* spp. [USA, Europe, South Africa]; Aradinae: *Aradus acutus* SAY, *A. cinnamomeus* PANZER, *A. funestus* BERGROTH, *A. lugubris* FALLÉN, *A. inornatus* SAY, *A. quadrilineatus* SAY, *A. robustus* UHLER, *Quilnus niger* (STÅL); Calisiinae: *Calisius* spp. [South Africa, Australia]; Carventinae: *Glyptocoris verus* DRAKE; Chinamyersiinae: Chinamyersiini: *Chinamyersia cinerea* (MYERS & CHINA), *Gnostocoris gressiti* KORMILEV; Tretocorini: *Kumaressa storeyi* MONTEITH, *Tretocoris* sp. [Australia]; Isoderminae: *Isodermus gayi* (SPINOLA); Mezirinae: *Bergrothiessa intermediaria* (KORMILEV), *Dysodius lunatus* (FABRICIUS), *Helenus hirsutus* CHAMPION, *Hesus cordatus* (FABRICIUS), *H. flaviventris* (BURMEISTER), *H. subarmatus* STÅL, *Mezira emarginatus* (SAY), *M. pacifica* USINGER, *Neuroctenus spiniplex* (UHLER); Prosympiestinae: *Adenocoris brachypterus* USINGER & MATSUDA, *Neadenocoris acutus* USINGER & MATSUDA; TERMITAPHIDIDAE (slides): *Termitaradus australinensis* MJÖBERG, *T. guianae* (MORRISON).

The superfamily Aradoidea, here considered as being the infraorder Aradimorpha, includes the well-known flatbugs of the family Aradidae and the peculiar Termitaphididae, minute tropical symbionts in termite nests. The Aradidae are divided into eight subfamilies: Aneurinae, Aradinae, Calisiinae, Carventinae, Chinamyersiinae, Isoderminae, Mezirinae, and Prosympiestinae (USINGER & MATSUDA 1959). The subfamilies of the Aradidae are keyed out in CHINA & MILLER (1959), USINGER & MATSUDA (1959) and SCHUH & SLATER (1995). The cladistic relationships among the subfamilies were analyzed by VÁSÁRHELYI (1986) and GROZEVA & KERZHNER (1992). On particular organ systems of Aradidae, ŠTYS (1969) studied the labrum; LEE & PENDERGRAST (1976, 1983) the stylets and the spermathecae; KUMAR (1967) the reproductive and alimentary systems; and VÁSÁRHELYI (1986) the pretarsus. Important phylogenetic discussions are in MYERS (1924, 1932), and USINGER (1942) on the Termitaphididae; MONTEITH (1969, 1980, 1982) on the Chinamyersiinae; PENDERGRAST (1965) on the Isoderminae; ŠTYS (1974) and HEISS (1998) on the Aneurinae and on the Aradidae in general by USINGER & MATSUDA (1959), KORMILEV & FROESCHNER (1987); and JACOBS (1980). An excellent summary of the subfamilies is given by SCHUH & SLATER (1995). I must stress that my sampling of the Aradoidea for this study of their abdomen structure is but minimal, and a much more extensive study of abdominal external and internal structure is needed. Nevertheless, among the Heteroptera, the abdomen of the Aradoidea is better known and used much more in taxonomy than most other families, which assisted the present study considerably. For each of the subfamilies I will discuss the abdomen in the context of other characters defining the subfamilies.

Aradinae BRULLÉ 1836 – CHINA & MILLER (1959) and FROESCHNER (1988) consider the Aradinae as being established by AMYOT & SERVILLE (1843), but HEISS (2001) accepts BRULLÉ (1836) as the author. In this section I discuss the Aradidae in general as well as the subfamily Aradinae, and differences from this subfamily are noted under the specific subfamilies, to avoid undue repetition. The abdomens of the aradid subfamily Aradinae (SWEET 1996) and the Chinamyersiini show the most plesiomorphic condition among the Aradidae in that there are clearly defined free dorsal epipleurites and free ventral hypopleurites with the spiracles borne by the hypopleurites. STÅL (1873) used this character of a ventral connexival suture to distinguish the subfamily Aradinae (-a) from the Isoderminae (-a) and the Brachyrhynchinae (-a), the three subfamilies he recognized. Terga 1 and 2 and terga 4 to 6 are united, while terga 2-3, terga 6-7 and 7-8 are free with intersegmental conjunctivae (Figs 3-4). The conjunctiva between terga 2 and 3 raises the question: is there a functional tymbal (OSSIANNILSSON 1949; CLARIDGE 1985; GOGALA 1984; HARRIS et al. 1982) in the Aradidae as proposed by SWEET (1996) for both Auchenorrhyncha and Heteroptera based on this structure of tergum 1+2? Certainly hearing is present in the Aradidae as shown by the presence of stridulatory organs (USINGER 1954; LESTON 1957). Scent gland scars are present between terga 3-4, 4-5, 5-6, and also a scar seems present between terga 6-7, although the nymphs show only three scent glands. The abdominal scent glands appear to be functional in the adults, based on the scent gland pores and sacs. Sterna 2 and 3 are united, and the remainder of the sterna are free, with well-developed intersegmental conjunctivae, which contrasts with the union to fusion of at least sterna 2 to 4 in females, 2-5 in males in the Pentatomomorpha. The terga are not impressed to receive the hemelytra. Unique to Aradinae is a longitudinal flexible suture along the midline of the sterna, and I agree with USINGER & MATSUDA (1959) that this is probably an autapomorphy of the Aradinae, given its evident absence in other Hemiptera. Abdominal sternum 2 is free of sternum 1, and a distinct sternum 1 is present that is free of the metasternum and articulates with hypopleurite 2 (Fig. 4). An interesting field of small trichobothrial-like hairs cover the meson venter of segment 3. The prothorax and head both have flexible intersegmental conjunctivae. JACOBS (1980) considered the Aradinae to be the most plesiomorphic among the Aradidae in other characters: the genae do not surpass the tylus (clypeus) and the posterior two scent glands are not reduced in size as in the Aneurinae, Carventinae, and Mezirinae.



Figs 3-4: Morphology of Aradinae pregenital abdomen: *Aradus robustus* UHLER, male. (**3**) dorsal view (**4**) ventral view. e – epipleurite; h – hypopleurite. (After SWEET 1996).

Chinamyersiinae USINGER & MATSUDA 1959. – In the other subfamilies of Aradidae, the ventral sutures delimiting the hypopleurites are often present, but there is a tendency for the union and fusion of the hypopleurites with the sterna, which is understandable as a consequence of the extremely flattened shape of these insects in adaptation to their cryptic subcortical habitats, because there is little room for dorsoventral expansion in crevices. The muscles scars run just dorsad and ventrad to the suture delimiting the hypopleurites, which readily indicate the lines of fusion or union of the hypopleurites with the sterna. This divergence is seen in the subfamily Chinamyersiinae. The tribe Chinamyersiini shows the plesiomorphic condition similar to that of the Aradinae. There are distinct ventral sutures demarcating the hypopleurites, and have a distinct flexible suture setting off ventral hypopleurite 2 from the metapleuron and hypopleurite 3 much as in the Aradinae, while abdominal sternum 2 is free of the metasternum, as a free sternum 1 is present behind the coxae that extends to hypopleurite 2. This is not well illustrated in USINGER & MATSUDA (1959). In the other tribe, the Tretocorini, the hypopleurites are fused with the abdominal sterna and hypopleurite 2 is united with hypopleurite 3, and sternum 1 is united with the metasternum and with sternum 2. The apterous genera *Tretocoris* and *Kumaressa* are unusual in being unusually thickened for an aradid and deeply concave dorsally, with spiracle 2 and 3 distinctly lateral on the hypopleurites. In all aradids examined, only Chinamyersiini has any spiracles dorsal on the epipleurites. In the Chinamyersiini, in *Chinamyersia* spiracles are distinctly dorsal on epipleurites 4 and 5, and 6, and in *Gnostocoris* the spiracles are dorsal on epipleurites 5 and 6, while in the Tretocorini (*Tretocoris* and *Kumaressa*) the spiracles of segment 2 appear dorsal but are actually just ventral of the connexive on the hypopleurites. It is very probable that these dorsal spiracles represent autapomorphies in the Chinamyersiini, and represent the only know examples of Heteroptera with the epipleurites having spiracles. In representatives of all the other subfamilies, the abdominal spiracles, despite having sometimes an extremely lateral position, are on the hypopleurites.

In their cladistic analysis of the subfamilies of the Aradidae, both VÁSÁRHELYI (1986), and GROZEVA & KERZHNER (1992) placed heavy weight on the Chinamyersiinae in their cladistic analyses of the subfamilies of the Aradidae because in the Chinamyersiini the coiled stylets show a figure 8 configuration while the other subfamilies had either a clockwise coiling, or a counterclockwise coiling of the stylets (LEE & PENDERGRAST 1983). VÁSÁRHELYI (1986) made the Chinamyersiinae a basal plesiomorphic branch, but as GROZEVA & KERZHNER (1992) emphasized, this meant a polyphyly of the clockwise coiling. They therefore argued that the clockwise and counterclockwise coiling had each evolved uniquely from the figure 8 configuration. This meant that the Chinamyersiinae gave rise via the tribe Chinamyersiini to the anticlockwise coiling shown in the subfamilies Prosympiestinae, Isoderminae, Aneurinae, Carventinae and Mezirinae, and via the Tretocorini, with clockwise coiling to the subfamilies Aradinae and Calisiinae. In terms of abdominal structure, as noted, the Chinamyersiini have a plesiomorphic structure similar to the Aradinae, whereas the Tretocorini show the apomorphic condition of fusion between the hypopleurites and the sterna. The metapleural scent gland openings are enlarged in the Chinamyersiinae, but this could well be plesiomorphic or homoplastic, not synapomorphic. Furthermore I discovered to my surprise that the Tretocorini, in *Kumaressa*, show the presence of small but distinct ocelli, unique in the Aradidae, but which are visible only on clearing the specimen because the crustose cuticle concealed the ocelli. Recall also that the Tretocorini have species with three, not two-segmented tarsi. Furthermore, there appears to be distinct gonoplacs present on the valvifers of the 9th segment. In addition, the spiracles of segment 8 are at the base, not the apex of the projection in Tretocorini (*Tretocoris* and *Kumaressa*). As this basal position of the spiracles on 8 resembles the position of the other abdominal spiracles, and is similar to the spiracle condition in the Idiostolidae, I hypothesize that this is the plesiomorphic spiracle condition of segment 8 and the apical spiracle position is apomorphic. It is difficult to thoroughly assess the phylogenetic position of the Tretocorini because these bugs show extreme aptery, so that the wing venation cannot be studied, which is important as the Chinamyersiini are macropterous, and show a wing venation as evidently plesiomorphic as the Aradinae. Nevertheless, so great are the differences between the Chinamyersiini and the Tretocorini, and so important are these taxa in the basal cladogenesis of the Aradidae as emphasized by VÁSÁRHELYI (1987) and GROZEVA & KERZHNER (1992), that I propose that these tribes should be raised to subfamily rank as Chinamyersiinae and Tretocorinae. A large difference is the long length of the labium, reaching the metasternum in the Tretocorini as compared to the Chinamyersiini where the labium is short as in most Aradidae (MONTEITH 1969, 1980). Future research using the genitalia, internal anatomy and molecular studies should throw further light on this interesting phylogenetic question.

Aneurinae DOUGLAS & SCOTT 1865. – The Aneurinae were sometimes distinguished as a family because there appears to be no ovipositor and sternum 7 is entire and not cleft, and there is no true spermatheca (PENDERGRAST 1957), although CARAYON (1955) and KUMAR (1967) demonstrated that a small diverticulum on the dorsal surface of the vagina functions to hold sperm. Next, the phallus is not differentiated into a phallotheca, conjunctiva and vesica as is general in the Pentatomomorpha (LESTON et al. 1954; KUMAR 1967; LEE & PENDERGRAST 1983; JACOBS 1980). However, while the spermatheca is absent, the ovipositor is present in *Aneurus*, although reduced in size, and it functions to hold the phallus during copulation (KUMAR 1967) as well as undoubtedly being used in oviposition. The reduced ovipositor results in sternum 7 being undivided by the ovipositor. These would be autapomorphic reductions in the Aneurinae. The often lateral spiracle positions are useful in species discriminations in the Aneurinae (PICCHI 1977; HEISS 1998). Such lateral spiracles may assist breathing in the tight subcortical spaces inhabited by these tiny aradids. The dorsum and venter of abdomen are not encrusted. The species I examined have no sutures visible on the sternum separating the hypopleurites, except for hypopleurite 2. Sternum 1 is distinct and united with the metasternum. Distinctive in the Aneurinae is the triangular sclerite, lateral to and at the junction of terga 2 and 3, which is called the contergite (HEISS 1998). Other species, as the ones illustrated by PICCHI (1977) and HEISS (1998), show distinct hypopleurites. The Aneurinae are also unusual in having a very short corium and elongated membrane with weak venation. For all these reasons, the Aneurinae had been elevated to family rank in the past (DOUGLAS & SCOTT 1865; LESTON et al. 1954). As mentioned earlier, it would not surprise me if the Aneurinae and some other subfamilies were raised in rank as MIYAMOTO (1961) and ŠTYS (1969) had suggested.

Calisiinae STÅL 1873. – The scutellum is very enlarged in the Calisiinae and the epipleurites have conspicuous thickened mesal margins, and the terga are depressed to accommodate the hind wings and the hemelytra, which are concealed under the scutellum, much as in some Pentatomoidea, and only the outer visible margin of the corium is sclerotized. This creates a division of the terga into true mediotergites and narrow laterotergites. The epipleurites, terga, sterna and hypopleurites show otherwise a similar structure of the Aradidae except that the hypopleurites are united to the sterna, including hypopleurite 2. The sternum 2 is free of a narrow sternum 1, that is firmly united with the metasternum. The relationship of the Calisiinae with the Aradinae lies basically in the coiling of the stylets in clockwise manner, which also links this clade with the Tretocorini (LEE & PENDERGRAST 1976; MONTEITH1980; GROZEVA & KERZHNER 1992).

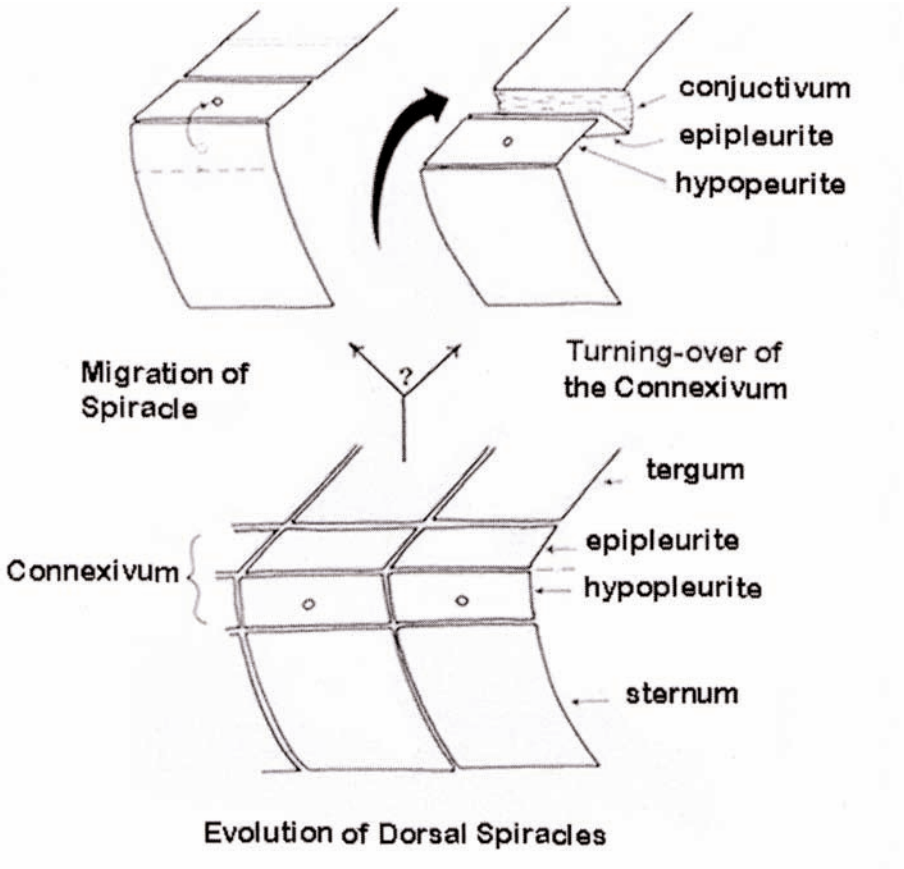


Fig. 5: Proposed evolution of the turned-over connexivum. (After SWEET 1981).

Isoderminae STÅL 1873. – The abdomen is generalized, with the exception of the fusion of the hypopleurites, including segment 2, with the abdominal sterna in both males and females. In contrast with most Aradidae, the junction between sternum 2 and sternum 1 + metasternum is flexible with a conjunctiva, not united. Sternum 1 is a narrow sclerite united with the metasternum as illustrated by WYGODZINSKY (1946). The terga of segments 3 to 6 are flexible, not united, as in most Aradidae. The anterior scent gland scar is a little wider than the posterior two, and there appears to be a small scent gland scar between terga 6 and 7. The segments bearing the scent glands are straight, and not bent posteriorally at the level of the glands. The spiracles of the eight segment are large, and in the male the eight segment is not extended into a projecting side lobe, and the spiracles are on the side of the segment, resembling other abdominal spiracles in position. The general cuticle is without any crustose granulosity visible, indeed looking polished, giving the insect the habitus of some flattened Blissidae. It is interesting that behind the 7th spiracle is a depressed area with five setae that may prove, on further study to be trichobothria, perhaps homologous with trichobothria of the Pentatomomorpha s.s.

The Isoderminae show an interesting mix of plesiomorphic and apomorphic characters. The labium arises from the apex of the clypeus, which is plesiomorphic, but is apomorphic in having semideciduous wings (LEE & PENDERGRAST 1976), in which the corium is short and commonly the membrane breaks off. The venation of the hind wing and fore wing is highly reduced and little venation is visible, aside from a reticulation of the membrane. The cuticle appears to lack any granulosity, thus the name of the taxon. Given the presence of the peculiar cuticular granulosity in the two basic clades of the Aradidae in the cladograms of VÁSÁRHELYI (1987) and GROZEVA & KERZHNER (1992), and Vásárhelyi's reasonable presumption that the normal cuticle without granulosities was plesiomorphic, then it follows that the granulose cuticle must have originated at least twice, once in the common ancestor of the Isoderminae and the clade leading to the Mezirinae, and the other in the common ancestor of the clade leading to the Aradinae. The alternative is either that the Isoderminae lost the crustose granulosity, and its normal cuticle is secondary or the Isoderminae are indeed plesiomorphic in its cuticle, in which case the Isoderminae are ancient off shoot of the Aradidae before the evolution of the crustose cuticle. This would also mean the evolution independently of the counter-clockwise coiled stylets. The flexible connection between the abdominal sternum 2 and metasternum + sternum 1 also supports the pleisiomorphy of the Isoderminae, as originally suggested by USINGER & MATSUDA (1959).

Prosympiestinae USINGER & MATSUDA 1959. – The abdomen is similar to the Isoderminae, but differs in that the metasternum is firmly united with sterna 1 and 2. Epipleurites 2 and 3 are fused together, but otherwise the epipleurites are free of the terga and sterna. While in *Adenocoris* the hypopleurites are firmly united with the sterna, with a clear suture present, in *Neadenocoris* the hypopleurites are nearly fused with an indistinct junction with the sterna. The abdominal spiracles are lateral on the hypopleurites, none dorsal of the connexive. In *Prosympiestus* the spiracles are more ventral on the hypopleurites (USINGER & MATSUDA 1959). The scent glands of the Prosympiestinae are similar to those of the Isoderminae, and the wing venation is similarly reduced to but a vein in the hind wing. Similar to the Isoderminae, segment 8 is small with non-protruding spiracles. Moreover, while the cuticle is roughed, the encrusting granulosity appears to be absent, allying the Prosympiestinae further with the Isoderminae.

Mezirinae OSHANIN 1908. – I wish to first address the name of this subfamily. The original name was Brachyrhynquides AMYOT & SERVILLE 1843, which name STÅL (1870) emended to Brachyrhynchina with *Brachyrhynchus* LAPORTE 1833, as the type genus. On the belief that *Brachyrhynchus* was a junior primary homonym of a genus of Coleoptera, OSHANIN (1908) renamed the subfamily the Mezirina, with *Mezira* AMYOT & SERVILLE 1843 as the type genus. However, KORMILEV & FROESCHNER (1987) discovered that the senior homonym for a coleopteran had only been used in synonymy so it was not an available name (RIDE et al. 1985), thus releasing the aradid *Brachyrhynchus* from homonymy and restoring the generic name. This being so, why is not Brachyrhynchinae the correct subfamily name? Moreover *Mezira granulata* AMYOT & SERVILLE 1843 is preoccupied, and the next available name is *Brachyrhynchus abdominalis* STÅL 1873 (FROESCHNER 1988).

This is the largest subfamily of the Aradidae, with a rich representation in tropical areas. It would be remiss not to emphasize the wealth of morphological variation in overall external structure among the Aradidae, especially in the Mezirinae, as shown by the illustrations in USINGER & MATSUDA's (1959) masterly monograph on the Aradidae. The small number of genera that I could examine showed some of this diversity. While *Mezira*, *Neuroctenus*, *Helenius* and *Dysodius* have the hypopleurites fused with the sterna, in *Hesus* and *Bergrothiessa* the ventral sutures delimiting the hypopleurites are very clear. It is probable then that the loss of the ventral sutures in the Mezirinae is an infrasubfamily event. In *Dysodius lunatus* (FABRICIUS) (which genus was once the basis for a family name), the wings are sunk into a depression on the abdomen, and a clear suture runs along the margin of the depression, setting off distinct true mediotergites and laterotergites on terga 3 to 6. The impressed tergites under the wings are desclerotized. In *Neuroctenus*, there is a similar depression to hold the wings, but it is not desclerotized. In *Dysodius* the mesosternum, metasternum, sternum 1, and the second abdominal sternum are completely fused, although the second sternum and the third sternum are united with a distinct suture present. Other than the fusion of the hypopleurites with the sterna, the pattern of free epipleurites, abdominal terga and sterna are the same as in Aradinae, including the free hypopleurite 2. The great diversity in the subfamily needs careful study as the subfamily is close to the Carventinae USINGER, so much so I did not study adequately the Carventinae, especially as I had only nymphoid apterous adults available.

Termitaphididae MYERS 1924. – These are very modified bizarre insects that resemble scale insects. They are known only from termite nests and the two genera examined, *Termitaphis* WASMANN with four species from the Neotropics and *Termitaradus* MYERS with eight species, five from the Neotropics, one Australian, one African, one Indian (MYERS 1924; MORRISON 1923; USINGER 1942). As MJÖBERG (1914) noted, the circumtropical distribution of such a wingless insect genus suggests, as in *Peripatus*, a taxon of considerable antiquity. These insects have no eyes, no scent glands or wings, and like nearly all Aradidae, no ocelli. The labium and the geniculate antennae are short and four-segmented. MYERS (1924) and USINGER (1942) in their discussions of these insects, place them close to the Aradidae, based on their flattened shape and coiled mouthparts in the head region. Unique as compared to the Aradidae is the long whip-like vesica on the phallus, the vesica being short in known Aradidae, and the lack of a buccal groove and bucculae on the underside of the head (MYERS 1924). They also have distinct pulvillae on the pretarsus, a plesiomorphic trait.

Although highly modified, and lacking any traces of scent glands in the nymphs, the abdomen of the Termitaphididae, while rather unsclerotized, has distinct dorsal epipleurites and ventral hypopleurites on segments 2 to 8. Similar lobes are present on the thorax and head (MORRISON 1923; MYERS 1924). MYERS (1932) described in *Termitaradus jamaicensis* MYERS that the flexible lateral lobes (clearly the connexiva of the abdomen) moved in a wave-like motion as the animal ran, and were compressed to the ground when the insect was disturbed by the host termites. This great flexibility of the connexivum is evidently unique in the Hemiptera.

POINAR & DOYEN (1992) discovered a species of *Termitaradus* from Mexican amber dated at 25 million years, and suggested that the dead shriveled termites next to the bug indicated that it may be predaceous. However, I agree with SCHUH & SLATER (1995) that all species of the Aradoidea will prove to be mycetophagous as are Aradidae whose feeding habits are known, with the single known exception of *Aradus cinnamomeus*, which feeds on live pine trees as discussed earlier.

Infraordinal Status of the Aradimorpha

Actually the first formal recognition of the Aradoidea as comprising a separate suprafamilial taxon was by VERHOEFF (1893) who recognized the suborder Aradina, and by REUTER (1912) who recognized them as the series Phloeobiotica. As Verhoeff's name is based on a genus, the higher group name Aradimorpha should be attributed to him, the -morpha just being an indicator of infraordinal rank. I was initially reluctant to add to the forest of higher taxon names, which COBBEN (1968) had deplored, because as ŠTYS & KERZHNER (1975) acidly noted, there are 96 names of subordinal (above superfamily) rank for 73 families. However, after reviewing the data, I now believe the recognition of this infraorder to be well-warranted. Originally in my discussion of the abdominal structure, I coined the name Aradomorpha (SWEET 1996) as a higher group name parallel with the other infraordinal names in the Heteroptera, but the name Aradomorpha is unfortunately already a generic name for a genus of Reduviidae, *Aradomorpha* CHAMPION (1899), so I here amend the infraordinal name to Aradimorpha to receive the superfamily Aradoidea. Let us now examine additional evidence for the placement of the Aradoidea by first examining the Pentatomomorpha.

The Pentatomomorpha was first discriminated as a higher taxon by LESTON et al. (1954) when they separated the Geocorisae into the Cimicomorpha and the Pentatomomorpha. The Pentatomomorpha were distinguished from the Cimicomorpha on the basis of: 1) a spermatheca is present that has a basal duct, an apical sperm storage bulb and a muscular pump (PENDERGRAST 1957); 2) the ovipositor lacks gonoplacs (third valvulae) (SCUDDER 1959); 3) the aedeagus is divided into a phallobase, conjunctiva and vesica with a gonoporal process (SINGH-PRUTHI 1925); 4) a bulbus ejaculatorius is differentiated in the vas deferens (PENDERGRAST 1957); 5) the basal plates of the aedeagus are rod-like and not fused (SINGH-PRUTHI 1925); 6) the eggs have micropylar processes for sperm passage, each micropyle surrounded by a spongy or porous chorionic area for gas exchange (COBBEN 1965, 1968); 7) the eggs are without an operculum surrounded by separate micropyles and aeropyles and are rarely embedded in plant tissue (SOUTHWOOD 1956; HINTON 1981); 8) a median egg burster is on the vertex of the embryonic cuticle (SOUTHWOOD 1956; COBBEN 1968); 9) hindwings have the radius and medius veins not fused distally (DRAKE & DAVIS 1958), except for the Microphysidae (ŠTYS 1962); 10) fore wings are without a costal fracture (TANAKA 1926; ŠTYS 1996); 11) pulvilli are present (<u>not</u> pseudoarolia as noted by GOEL & SCHAEFER (1970), GOEL (1972) and SCHUH (1976); 12) the accessory salivary gland is tubular not vesicular (BAPTIST 1941; SOUTHWOOD 1955; BUGNION & POPOFF 1968). SCHUH & ŠTYS (1991) in their cladistic analysis of the Cimicomorpha, diagnosed the infraorder on two synapomorphies: 1) the ectodermal median spermatheca is nonfunctional as a sperm storage organ, is either absent, vestigial, or modified into a vermiform gland, or entirely absent (CARAYON 1954, 1955); 2) the eggs have micropyles that are distinct from aeropyles ("pseudomicropyles") and both are arranged in a ring outside of the operculum, although there are some exceptions (COBBEN 1968). This initial reorganization of the Geocorisae of Dufour, led later to the recognition of the infraorders Nepomorpha (basically Dufour's Hydrocorisae), Gerromorpha (basically Dufour's Amphibiocorisae), Leptopodomorpha, Dipsocoromorpha, and Enicocephalomorpha (ŠTYS & KERZHNER 1975; SCHAEFER 1993, 1996; WHEELER et al. 1993). HENRY (1997) in his phylogenetic analysis of the Pentatomomorpha discussed well the nomenclatural history of the infraorder. He acknowledged the isolation of the Aradoidea from the Pentatomomorpha s.s., the trichophorous Pentatomomorpha, as did WHEELER et al. (1993), based on molecular data from 18s rDNA data. However, of the characters Henry listed to separate the Aradoidea in his cladogram, only the coiled mouthparts in the tylus appear to be synapomorphic for the superfamily. As discussed earlier, the 2-segmented tarsi, the loss of ocelli, are characters evolved within the Aradidae. The antennal characters of an enlarged basal segment and thickened segment 4 are homoplastic, being evolved in other taxa within the Pentatomomorpha and the Heteroptera.

It is important to note that compared with the Cimicomorpha, most of the characters of LESTON et al. (1954) are plesiomorphic for the Pentatomomorpha, so the Aradoidea must be compared with the other heteropterous infraorders and with the Coleorrhyncha (=Peloridiomorpha) and the Fulgoromorpha, the probable sister group to the Prosorrhyncha (CAMPBELL et al. 1995; SORENSON et al. 1995). Possible synapomorphic characters with the Pentatomomorpha may be the tubular accessory salivary glands and division of the phallic endosoma into a conjunctiva and vesica. However, the tubular accessory salivary gland is the condition in Peloridiidae (PENDERGRAST 1962) and the two-parted endosoma is found also in the Fulgoroidea (SINGH-PRUTHI 1925; FENNAH 1945a) so these characters may well be plesiomorphies not synapomorphies. While SCUDDER (1959) emphasized the loss of the gonoplacs (third valvulae) in the Pentatomomorpha, in other Heteroptera that have gonoplacs, the gonoplacs often serve as a sheath or part of the sheath that the first and second valvulae (gonopophyses) fold into. Valvifer (gonocoxa) 2 in pentatomomorphans is very elongated and serves as a sheath much as do the gonoplacs in other hemipterans. I propose that the gonoplacs are not actually lost in the Pentatomomorpha but are instead fused with the valvifer to strengthen the sheathing structure. Moreover, in the aradid Tretocorini, of the Chinamyersiinae, *Kumaressa* and *Tretocoris* apparently have projections on the valvifer 2 that closely resemble gonoplacs as illustrated by SCUDDER (1959), so the Aradoidea may primitively possess gonoplacs that are lost within the Aradidae as are other structures normally used to define the Aradidae.

I agree with GOEL & SCHAEFER (1970) that tarsal pulvilli should be included in the ground plan of the Heteroptera and not be treated as an apomorphy as suggested by SCHUH (1981). SCHUH (1976) notes that in the Cimicomorpha, while pulvilli are generally absent, they are present in the thaumastocorid subfamily Xylastodorinae, and in the anthocorid tribe Oriini, one species of Plokiophilidae, and in some Miridae (Phylinae). He reasons from this that pulvilli are apomorphic structures. He therefore extends this argument of apomorphy to the Pentatomomorpha where they are almost universally present. I believe this reasoning is inadmissible. On one hand, in the Cimicomorpha, pulvilli are seen as sporadically evolved and of little significance, while on the other hand pulvilli are a major importance in the cladistic separation of the Pentatomomorpha from the Cimicomorpha. Much more likely, pulvilli are part of the ground-plan of Hemiptera (and insects, generally) and have been frequently lost in some lineages. In the Auchenorrhyncha, pulvilli are found in all the families except the Cicadidae (MYERS 1928; FENNAH 1945b) and especially in the Fulgoromorpha (DOERING 1956) which gives additional outgroup evidence of their plesiomorphy. If not completely lost, being simple pads, pulvilli can be readily reduced or expanded with adaptive pressures, which is what MYERS & CHINA (1928) stressed in assessing the importance (and homoplasy) of the pretarsus in classification. However it seems probable, following Dollo's law, that once lost, the pulvillae would not re-evolve in the same form. In the Aradidae, the pulvillae are retained in all subfamilies, but absent from the Aradinae, which loss would then be an apomorphy within the family. DASHMAN'S observation (1953a, 1953b) that the Aradidae characteristically have an unusual arrowhead-shaped or pentagonal unguitractor plate is supported by the exhaustive study by VÁSÁRHELY (1986) of the pretarsus. One genus, *Clochocoris*, of the Mezirinae is unusual in lacking the parempodia, as was noted by GOEL & SCHAEFER (1970) and GOEL (1972).

The two-segmented tarsi characteristic of the Aradidae, both adults and nymphs, is shown to be an apomorphy within the family as the primitive tribe Tretocorini of the Chinamyersiinae have three-segmented tarsi (MONTEITH 1980). The reduction of the tarsal segmentation to two segments is a common, very probably paedogenetic character, as the nymphs are universally 2-segmented in the Hemiptera with the third segment appearing in the moult to the adult stage in both the Auchenorrhyncha and the Heteroptera. However, recall that COBBEN (1968, 1978) believed that the 2-segmented condition as in the Hebridae was plesiomorphic tarsal condition of the Heteroptera, but I think he was mistaken, given the universal 3-segmented tarsal condition in the Auchenorrhyncha and, especially the Fulgoromorpha (DOERING 1956) as molecular evidence and some morphological evidence indicate that the Fulgoromorpha are the sister group to the Prosorrhyncha (Peloridiomorpha + Heteroptera) (CAMPBELL et. al. 1995; SORENSON et al. 1995).

As the Aradidae are universally described as being without ocelli, which would be an autapomorphy of the superfamily (USINGER & MATSUDA 1959), I was very surprised to see in *Kumaressa* the presence of small, but distinct ocelli mesad and behind the eyes, which means the loss of ocelli in the Aradimorpha would be an autapomorphy within the Aradimorpha. Such a loss is not unusual in the Heteroptera, as the Pyrrhocoroidea, for example, similarly lack ocelli, and the Miridae were once distinguished from the Isometopidae on this basis (SCHUH & ŠTYS 1991).

While cladists often appear to discount plesiomorphic conditions, in searching for synapomorphies, pleisiomorphies are important in establishing the ancestral ground plan of a taxon. Some plesiomorphic differences of the Aradidae from the Pentatomomorpha are as follows. The Aradidae have in the male a simple bulbus ejaculatorius without a complete third layer, contrasting with the Pentatomomorpha and also the Cimicomorpha, which both have a complete three-layered bulbus ejaculatorius (PENDERGRAST 1957; KUMAR 1961, 1967). The accessory gland of the salivary gland has no distinct duct (MIYAMOTO 1961), which is similar to the condition in the Peloridiidae (PENDERGRAST 1962). The labrum in the Pentatomomorpha has a relatively similar structure with an elongated labrum with a more sclerotized basilabrum and a less sclerotized distilabrum (SPOONER 1938). ŠTYS (1969) remarked on the comparative diversity of labral structure in the Aradoidea, and noted that the Aradinae appear to have the most primitive labral structure with a free epipharyngeal projection, much as in the nepomorphan families Ochteridae and Gelastocoridae, the Gerromorpha, and Dipsocoromorpha. Moreover, he notes that the diversity of labral structure may indicate that the lumping of the aradid subfamilies in the one family Aradidae (USINGER & MATSUDA 1959) may conceal the true diversity of the Aradidae. In any case, the Aradidae show the much more plesiomorphic abdominal condition as compared with the Pentatomomorpha s.s. Indeed, if it can be shown that the highly derivative Termitaphididae are derived from some subfamily of the Aradidae, then the Aradidae would need to divided into monophyletic families to avoid paraphyly (SCHUH 1986), which given the great morphological diversity, especially of the wings, would seem warranted.

There are several characters that indicate the synapomorphic isolation of the Aradoidea from the Pentatomomorpha. Outstanding are the remarkable stylets, which are coiled within the clypeus, are undoubtedly an adaptation for the mycetophagous feeding habits of aradids (CHINA 1931; SPOONER 1920, 1938; USINGER & MATSUDA 1959). The primitive aradid stylet condition appears to be the figure 8 condition found in *Chinamyersia* (LEE & PENDERGRAST 1976; MONTEITH 1980). The other subfamilies show either a clockwise or anticlockwise coiling of the stylets (LEE & PENDERGRAST 1976). ŠTYS (1969) noted the great diversity in labral structure in the Aradidae, that both broad and narrow labra exist in contrast to the similar narrow shape among the Pentatomomorpha (s.s.).

The metapleuron in Aradidae abuts at an oblique angle to abdominal segment 2, and there is no subcoxal flange of the metapleuron (the metepisternum) overlapping the abdomen as in the Pentatomomorpha s.s. (LARSÉN 1945) and in the Saldidae (Leptopodomorpha) (PARSONS 1963). TAYLOR (1918) called this flange the metepimeron, but as BRINDLEY (1934) showed, it is actually an extension of episternum, as the metapleural suture runs along the hind margin of the metathorax next to the abdomen and the true epimeron is actually very reduced. As Brindley noted this reduction is part of the general reduction of the metathorax in the Heteroptera, as the wings are powered by the mesothoracic muscles, in contrast with other orders where the metathoracic wings are important (MATSUDA 1960). I suggested (SWEET 1996) that the reduction in the metathoracic wing musculature was related to the evolution of metathoracic-abdominal tergal tymbals. In the Fulgoromorpha the metepimeron is more visible, but is small (KRAMER 1950; EVANS 1939). In the female of the Aradidae, hypopleurite (=paratergite) 8, which bears spiracle 8, resembles in form the other abdominal hypopleurites. In the males of Aradidae, segment 8 is not telescoped into segment 7, but is exposed and forms an external cup into which the 9th segment, the genital capsule, sits. The spiracles of segment 8 are well-developed and are presented posteriorly on projecting tubercles in the Aradinae. In the Pentatomomorpha, only the Idiostolidae has the 8th spiracle exposed at rest although the 8th segment is cylindrical and withdrawn into the 7th segment as in other Pentatomomorpha (SCHAEFER 1966).

Another feature of the Aradidae is the presence of muscle scars, or apodemal impressions, not only on the terga, but on the connexivum as well. These muscle scars are extensively used in the higher taxonomy of the Aradidae (USINGER & MATSUDA 1959; VÁSÁRHELYI 1987; GROZEVA & KERZHNER 1992). As far as I know, no such connexival muscle scars occur on the connexivum in the Pentatomomorpha but are restricted to the true terga and sterna. The tergal muscle scars are often confused with delimiting a ventral connexivum, which as I argue, has turned over, so that the hypopleurites have become dorsalized to form the connexivum distinguished by students of the Pentatomomorpha. That this may be a deep plesiomorphy is shown by the presence of muscle scars or apodemal impressions on the connexivum of nepomorphan family Naucoridae (Sweet unpublished). Another feature of the Aradinae, and of the subfamilies Calisiinae, Chinamyersiinae, Mezirinae and Carventinae, is the lack of preflagelloids in the antennae, which are interpreted by ZRZAVY (1990) as a loss. However such sclerites are absent in the non-Heteroptera, and I would like to suggest that this is a plesiomorphy.

The hemelytra are unusual, in that they overlap without the clavi forming a commissure and in species with large hemelytra, the clavus clearly loosely overlaps the other clavus and the apex of the clavus contributes to the membrane with one vein leaving the clavus and entering into the membrane. This overlapping of the forewings in the Aradidae resembles the overlapping of the wings in the Enicocephalomorpha and the Gerromorpha. Moreover, in the Aradidae, especially the Aradinae and the Chinamyersiini there are an unusual number of cross veins in the corium that differ considerably from the conditions in the Leptopodomorpha, Pentatomomorpha and the Cimicomorpha, and which should be studied carefully in the light of the isolated phylogenetic position of the Aradidae as discerned here. Such cross veins are seen in many fulgoroids and the Peloridiidae. Six veins and their trachea enter separately from the hemelytron into the membrane, which veins I interpret to be the Sc, R, M, Cu and Pcu from the corium and A from the clavus, and two or three series of cells are formed by cross veins in the membrane among these veins. I have earlier thought a simple set of 5-6 veins with no cross veins was plesiomorphic because this is essentially the condition in the Saldidae, but I may be mistaken, as the fulgoroid wings commonly show such cells, and often a series of cross veins separating a basal part of the tegmen from the apical part (FENNAH 1944; SHCHERBAKOV 1981). Next, the Aradidae characteristically have an enlarged basal arched anterior corial margin that resembles the same area in the Peloridiidae, and which also may be a plesiomorphic feature. It seems to be part of the clasping structure which is restricted to the thorax, and I see no knob to anchor the hemelytra as seen in other Heteroptera. The wing venation in the hemelytron is entirely different from the Pentatomomorpha: the medial fracture is either absent, or in Chinamyersiini and Aradinae very short and runs anterior (preradially) of the R vein, not posterior postradial to it as in all the Pentatomomorpha that I have studied. ŠTYS (1996) in discussing the uniqueness of the enicocephomorphan wings notes this same phenomenon of a preradial m-fracture, and he considers this to be plesiomorphic to the Heteroptera, which would again indicate the uniqueness of the Aradoidea. Another unique feature of the forewing hemelytral venation in the Aradinae and the Chinamyersiini is the wide separation at the base of the wing of two veins that I interpret to be the R and the M (USINGER & MATSUDA 1959). This seems to resemble the condition in some Fulgoroidea (FENNAH 1944). When turning the fore wings over to see the veins better because of the encrustations on the veins from above, the two veins, R and M can be seen not to join to form a single vein, but to run as veins side-by-side, and separating distally to enter into the membrane. This is quite different in most other Heteroptera where a single vein called the R+M leaves the base of the forewing with the medial fracture posterior to it (TANAKA 1926; DAVIS 1961). ŠTYS (1996) believes the costal fracture in the hemelytron is plesiomorphic, but I am persuaded by the arguments of WOOTTON (1982) and WOOTTON & BETTS (1986) that on aerodynamic grounds such a flexure point is a useful apomorphy in bending the wing, and its loss would be unlikely, so the lack of such a lateral fracture in the Aradidae is more likely the plesiomorphic condition. The Fulgoromorpha differ from the Cicadomorpha in that the veins attain the margins of the forewings, rather than forming apical cells, the cells being internal cells formed by crossveins (FENNAH 1944; SHCHERBAKOV 1981, 1996). As this is the condition basically in the primitive Aradidae hemelytron of the Aradinae and the Chinamyersiini, this would be the plesiomorphic membrane vein condition, as compared to the apical cells in the Leptopodomorpha.

Finally it is noteworthy that the encrusted heavy veins in the Chinamyersiini and some Aradinae set off the hemelytral corium, but the corial tissue between the veins is tegminous, and not heavily sclerotized, much as in the Enicocephalomorpha, and in contrast with most other Heteroptera in which the corium and clavus are strongly sclerotized.

Similarly the distinct presence of sternum 1, free of the metasternum in Aradinae, must be very plesiomorphic and is very different from all the Pentatomomorpha I have dissected, which show no trace of sternum 1 that I could observe. ŠTYS (1996) emphasizes the presence of sternum 1 in the Enicocephalomorpha as unusual to the Acercaria, the hemipteroid insects. If so, this similarly would indicate also the archaic position of the Aradoidea.

The gut of the Aradidae differs considerably from that of the Pentatomomorpha and Cimicomorpha. The midgut in the Aradidae is characteristically three parted, not four parted, and there are no gastric caecae as in most of the Pentatomomorpha (GLASGOW 1914; MIYAMOTO 1961; KUMAR 1967). The hind gut in the Aradoidea except the Aradinae has a true ileum and a rectum much as in the Nepomorpha and the Leptopodomorpha (Saldidae). MIYAMOTO (1961) considers the sac that receives the malpighian tubules to be a pylorus, the ileum a division of the hindgut, unlike GOODCHILD (1963, 1966) who considers the ileum to be the former, unlike other morphologists (SNODGRASS 1935, 1963). I believe Miyamoto is correct as the sac receiving the malpighian tubules has no cuticular layer characteristic of the hind gut. In the Aradinae the ileum is absent (MIYAMOTO 1961; KUMAR 1967), and I agree with Miyamoto that it is likely this absence is a loss apomorphy of the Aradinae, and its retention is plesiomorphic for the Aradoidea.

Similarly the absence of a pulvillus in the pretarsus of the Aradinae is likely also a loss apomorphy, not a plesiomorphy (USINGER & MATSUDA 1959; VÁSÁRHELYI 1986). The absence of m-chromosomes is distinctive to the Aradidae as compared with m-chromosomes in the Pentatomomorpha (LESTON 1958; JACOBS 1986). It was thought that the Pentatomoidea also lacked m-chromosomes (UESHIMA 1979), but the discovery by JACOBS (1989) that the primitive pentatomoid family Thaumastellidae has m-chromosomes suggests that the Pentatomoidea had lost them in the beginning of their radiation. I hypothesize that the lack of m-chromosomes in the Aradidae is instead plesiomorphic to the Heteroptera ,as LESTON (1958) suggested in noting the distant relationship of the Aradidae to the trichophorous Pentatomomorpha.

The Aradinae are distinctive in containing the only Aradidae known to feed on vascular plants and one species (*Aradus cinnamomeus* PANZER) is a well-known pest on pines in the West Palearctic. HELIÖVAARA (2000) summarizes the extensive economic literature. Is this plesiomorphic? Is it possible that the Aradidae use their long stylets to feed on phloem tissues as well? Nevertheless the consensus of literature (SCHUH & SLATER 1995) is that the flatbugs are primitively mycetophagous, and phloem feeding by *Aradus cinnamomeus* would represent an evolutionary advancement into a new adaptive zone by the Aradidae. Moreover, HEISS (2001) states "Several species of Aneurinae, Aradinae and Calisiinae feed on sap of dying or living trees.“ Clearly more work needs to be done on the feeding habits of the Aradidae. For example, do aradids secrete the sheath fluid to line their feeding paths as do the Pentatomomorpha *s.s.*, just as do the "homopterous“ hemipterans, both Sternorrhyncha and Auchenorrhyncha (MILES 1972), unlike the carnivorous heteropterous lineages, with the interesting exception of the carnivorous Pentatomomorpha (SWEET 1979)?

Copulation in the Aradidae is especially unusual and very likely primitive because the male positions himself under the female, and the genital capsule does not turn over 180 degrees as in the trichophorous Pentatomomorpha (WEBER 1930; BONHAG & WICK 1953; USINGER & MATSUDA 1959; JORDAN 1972). This latter posture is difficult to relate to the subcortical habitat of most Aradidae for this posture requires a larger (thicker) crevice size than the side-by-side position as in Thaumastocoridae, some of which insects are flattened and also live in tight crevices (BARANOWSKI 1958). It is important to note that the female superior position is found in many relatively primitive insects, the Ephemeroptera, Blattaria, and some Orthoptera. This mating posture is probably primitive to the Insecta (ALEXANDER 1964; DODSON et al. 1983), derived initially through female apterygote insects picking up spermatophore deposited on the substrate (PARKER 1970; SCHALLER 1971). Outgroup evidence from other Acercaria substantiate this mating posture as plesiomophic. NEW (1987) summarizes the mating behavior of psocids (Corrodentia). The male moves about agitatedly courting the female, and positions himself in front of the female facing the same direction. The male either walks backward under the female or, in the more primitive psocids as *Archipsocus*, the female mounts the male and the male effects copulation from under the female. In thrips of the family Aeolothripidae, the male, although he seizes the female from the side facing the same direction, twists his abdomen under the female, so his genitalia essentially lock on to the ovipositor in a ventral position (STANNARD 1952, 1968; LEWIS 1973). While no information is available on the Peloridiidae (Coleorrhyncha) mating behavior, the structure of the male pygophore is highly instructive for it is cup-like, very much as in the Aradidae, with symmetrical claspers (CHINA 1962). The shape and structure of the pygophore suggests that it is not inverted as in the Pentatomomorpha s.s. in copulation. I predict that in the Peloridiidae the male takes a position under the female much as in psocids. In the Sternorrhyncha, among psyllids and aleyrodids the genital capsule is also cup-like (OSSIANNILSSON et al. 1956), suggesting that this shape may be plesiomorphic to the Hemiptera as a whole, and the more ring-like pygophore in the Auchenorrhyncha, with the claspers in a posterior position is a more apomorphic position to allow mating with each individual clinging to vegetation. In the Cicadidae, the male's abdomen is clearly ventral in position while mating (KATO 1961).

This mating posture helps explain the evolution of other mating postures and reproductive external morphology in the Heteroptera. The marked asymmetry in the genitalia in many heteropterans would be a consequence of a side-to-side position in which the male genitalia are twisted to one side to effect copulation, from which the asymmetry naturally follows in adaptation to this copulation posture. In the Pentatomomorpha s.s., unique among the Heteroptera, the male genital capsule is inverted 180°. This is logically derived from the male inferior position in which the capsule would fit on the ovipositor as in the Aradidae. Rotate the male through 180° on the ovipositor both horizontally and vertically reverses the male position so he faces away end to end, allowing these heteropterans to run together while mating, and allowing prolonged mating so characteristic of the Pentatomomorpha. The rotation of the genital capsule from the side position on to the ovipositor makes more efficient the maneuver to end to end position. Logically, such prolonged mating would enhance female choice and the elaboration of complex genitalia (LLOYD 1979; EBERHARD 1986, 1990). This complex maneuver is clearly more derivative than that of the Aradidae in which the genital capsule is extruded and placed directly on the ovipositor. I therefore hypothesize that the Aradimorpha show the most plesiomorphic mating position known in the Heteroptera. It is unlikely to be result of the flattened abdominal shape because similarly flattened Blissidae and Thaumastocoridae have mating positions similar respectively of the Pentatomomorpha and the Cimicomorpha (SCUDDER 1959).

In possible relation to their mating behavior position, the genital capsule (segment 9) of many Aradidae bears not only the normal claspers homologous with those of other hemipterans but bears accessory articulated clasper-like organs called parandria but which are quite different from the immobile structures called parandria in other Heteroptera as the Lygaeidae (SLATER & SWEET 1977). In USINGER & MATSUDA (1959) these structures are illustrated and called styli. TAMANINI (1950) believed that these structures represented harpagones, the inner claspers, parameres. LESTON (1955) disagreed vigorously with Tamanini and considered the clasper-like organs to be secondary outgrowths or "parandria" of the genital capsule such as often occurs along the inner surface of the dorsum of genital capsule and which may guide the phallus in copulation. He considered the more mesal mobile claspers to be harpagones of paramere origin and therefore properly called parameres as is the present nearly universal practice among heteropterists. However BONHAG & WICK (1953) demonstrated by the pattern of the clasper musculature that in Lygaeidae the claspers are true harpagones derived from the 9th coxal styli and the true parameres are lobes fused to the phallotheca of the aedeagus or phallus. Nevertheless these clasper-like organs resemble very much and appear to be homologous with the clasper-like structures in the dipsocoromorphan genital capsule (WYGODZINSKY 1947), which were called the laterotergites of tergum 9 by ŠTYS (1970). I propose that the dipsocoromorphan clasper-like structures are hypopleurites homologous with the subgenital plates of the Cicadelloidea (SINGH-PRUTHI 1925) and the fulgoroid Tettigometridae (MUIR 1923, 1930) and perhaps are the origin of the aradid genital capsule structures that USINGER & MATSUDA (1959) carefully labeled styli. Additional evidence supporting these dual organs is the genital capsule of the Psocida, which clearly shows both structures (NEW 1987). If so, this would be an important character indicating the plesiomorphous nature of the Aradoidea and supporting its being recognized as a separate infraorder from the other heteropterous infraorders. SCHAEFER (2006) finds the aradid genital capsule unusual as compared to the capsule of the trichophorous genital capsule (SCHAEFER 1966) and in need of careful study to understand its evolutionary trends in the Aradidae. Also important in understanding the genital capsule and the phallus is the ovipositor, which is under ecological selection for oviposition as well as selection for successful copulation (FLETCHER 1979; ZEH et al. 1989). The Aradidae have short ensiform or bladelike ovipositors for placing the eggs in crevices, in contrast with ovipositors adapted for cutting into plant tissues as in many cimicomorphans or platelike for laying on surfaces as in pentatomoids and coreoids in general do (LESTON et al. 1954; ŠTYS 1961), which, of course, would greatly effect the shape of the eggs as ZEH et al. (1989) stressed but also the copulatory apparatus would be affected (LUDWIG 1926). It is not surprising then, that the Aneurinae have evolved reduced ovipositors and lost the cleft of sternum 7 in the female, probably to enhance oviposition in tight spaces under bark. Field and laboratory studies would be useful to address this question.

The only apparent synapomorphy evident possibly linking the Aradidae with the trichophorous Pentatomomorpha is the three-parted division of the aedeagus or phallus into phallotheca, conjunctiva and vesica. However SINGH-PRUTHI (1925) observed this three-parted division in the Leptopodomorpha as well as in the Fulgoroidea, which incidentally substantiates the sister group relationship of the Fulgoroidea to the Heteroptera + Coleorrhyncha discerned in molecular studies (CAMPBELL et al. 1995; SORENSON et al. 1995); KUMAR (1967) was not able to ascertain whether a similar sperm reservoir exists in the Aradidae, but internal sclerites were illustrated, which I have observed as well in the phallus of Aradidae. I would like to suggest here that this three-parted division of the phallus may be the plesiomorphic condition and the absence of this structure in the Cimicomorpha is linked to the absence of a true spermatheca in the Cimicomorpha. Given that the spermatheca is similarly lost or modified for another purpose in the Cimicomorpha, and the phallus lacks the three-parted structure, it seems entirely possible that the two are related as the function of the complex phallus is to place the sperm in the spermathecal bulb, which often requires penetrating a long spermathecal duct, the loss of the spermatheca and its pumping structure to move the sperm from the spermatheca to the vagina to fertilize the eggs requires other methods to deposit the sperm safely, that does not require the complex three-parted phallus. In the Idiostolidae, there is similarly a lack of the spermatheca, and the phallus similarly lacks the three-parted structure (SCHAEFER 1966; SCHAEFER & WILCOX 1969; WOODWARD 1968). I consider this to be a convergence, not evidence of relationship to the Cimicomorpha as the Idiostolidae show the turned-over connexivum characteristic of the Pentatomomorpha together with abdominal trichobothria.

Another possible synapomorphy is the tubular, not vesicular accessory gland as in the Cimicomorpha (MIYAMOTO 1961). However, the tubular accessory gland may be symplesiomorphic because the Peloridiidae also have a tubular accessory gland (PENDERGRAST 1962). The available characters thus are either plesiomorphies or autapomorphies of each infraorder and do not indicate the synapomorphic relationship of the Aradoidea to the other infraorders.

Given this weak relationship with the Pentatomomorpha and the wealth of autapomorphies distinguishing both the Aradidae and the trichophorous Pentatomomorpha *s.s.*, I therefore believe that the Aradoidea should be recognized as the infraorder Aradimorpha, coordinate with the other infraorders of the Heteroptera. It would appear then, that ELSON (1937) was correct in emphasizing the uniqueness of the Aradidae, both morphologically and biologically as feeders on fungi. In reviewing the literature I am impressed how much remains to be done, especially on the internal anatomy and I hope this paper will stimulate such research as SCHAEFER (1996) exhorted.

Another line of evidence that supports the infraordinal status of the Aradimorpha is the fossil record. The Aradidae are known from amber of the Cretaceous of Northeast Siberia (KORMILEV & POPOV 1986), which specimen, *Aradus cretaceus* was considered as belonging to the living Aradus "lugubris-group". This would be a remarkable example of bradytelic evolution. Similarly an Aradidae specimen was illustrated in GRIMALDI et al. (2002) from the Turonian-Cenomanian age of the Cretaceous, which has been described as *Archearadus burmensis* by HEISS & GRIMALDI (2001, 2002). USINGER (1942) remarked on this bradytelic evolution in describing from Baltic amber of the Oligocene *Calisius* and *Mezira* species remarking on the close resemblance of the fossil species to living species, the fossil *Mezira succinica* USINGER resembling closely *Mezira tremulae* (GERMAR), which occurs now along the shores of the Baltic Sea. How far back in time does the aradimorphan lineage extend? I would suggest that fossils such as those described by POPOV & WOOTTON (1977) from the Lias should be carefully re-examined for evidence of such ancestral stocks.

Finally, the famous biogeography of the Aradidae supports its great antiquity. All of the recognized subfamilies occur in New Zealand and in Australia suggesting a Gondwanaland origin for the Aradoidea. The Isoderminae have a classic Antarctic distribution in Chile, New Zealand, and Tasmania-Australia. The Aradinae, Calisiinae, Mezirinae, Carventinae, and Aneurinae have cosmopolitan distributions with richest species concentrations in tropical forested areas (USINGER & MATSUDA 1959; MONTEITH 1982), with the Aradinae especially rich in the Holarctic region. Only the Chinamyersiinae (including the Tretocorini) and the Prosympiestinae are restricted to New Zealand and Australia (USINGER & MATSUDA 1959; MONTEITH 1980; LARIVIERE & LAROCHELLE 2006).

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Zusammenfassung

Aradomorpha SWEET 1996 wird wegen Homonomy mit *Aradomorpha* CHAMPION 1899, einer Reduviiden-Gattung, durch Aradimorpha ersetzt. Aradimorpha unterscheiden sich von Pentatomomorpha s.s. und Leptopodomorpha durch das plesiomorphe Connexivum aus dorsalen Epipleuriten und ventralen Hypopleuriten, im Unterschied zu einem dorsal umgeklappten Connexivum bei dem die Hypopleurite oben und die Epipleurite in einer Falte zum Abdomen liegen. Männchen und Weibchen der Aradimorpha haben durch Intersegmentalmembranen verbundene, freibewegliche Sterna 3-7; Terga 1-2 und 3 bis 6 sind verschmolzen, aber alle Epipleurite sind ebenfalls frei. Weibchen der Pentatomomorpha besitzen zumindest verschmolzene Sterna 2 bis 4 und deren Männchen verbundene oder verschmolzene Sterna 2 bis 5 ohne Intersegmentalmembranen. Bei manchen Aradiden sind die Hypopleurite verbunden oder mit den Sterna verschmolzen, aber Hypopleurit 2 ist meist frei. Sternum 2 ist manchmal verbunden bis verschmolzen mit Sternum 1 und dem Metasternum. Die abdominalen Stigmen der Aradimorpha liegen ventral auf den Hypopleuriten, obwohl sie manchmal auch lateral angeordnet sind, mit Ausnahme der Chinamyersiini, bei denen die Stigmen 4, 5 und 6 dorsal auf den Epipleuriten (*Chinamyersia*) bzw. 5 und 6 dorsal (*Gnostocoris*) liegen, während bei den Tretocorini (*Tretocoris* und *Kumaressa*) Stigma 2 dorsal zu liegen scheint, jedoch lateral auf den Hypopleuriten liegt. Termitaphididae besitzen deutliche Epipleurite und Hypopleurite, aber abdominale Stigmen wurden nicht festgestellt. Bei den Aradidae grenzt das Metapleuron an den Rand des Abdomen, gebildet durch Hypopleurite 2, sodass Segment und Stigma 2 lateral exponiert sind, im Unterschied zu den Pentatomomorpha und Leptopodomorpha, bei denen ein großer metapleuraler Lappen seitlich die Basis von Abdominalsegment 2 (und meist das Stigma 2) bedeckt. Sternum 1 ist zwischen den Metacoxae vorhanden, manchmal freiliegend wie bei den Aradinae, manchmal mit dem Metasternum verwachsen. Synapomorphien der Unterordnung Aradimorpha sind: Die Stechborsten sind stark verlängert und im Tylus (Clypeus) spiralig aufgerollt und dienen der Nahrungsaufnahme an Pilzhyphen. Der Körper ist extrem abgeflacht, entsprechend der Lebensweise unter Rinde, versteckt auf Oberflächen oder in der Laubstreu. Apodeme (Muskelansatzstellen) befinden sich an den Epipleuriten und Hypopleuriten sowie an den Terga und Sterna. Die starke Muskulatur is vermutlich notwendig um sich in engen Spalten zu bewegen. Mit Ausnahme der Isoderminae weist die Kutikula besondere Inkrustationen auf, die von keiner anderen Wanzengruppe bekannt sind, und die vermutlich mit der versteckten Lebensweise dieser sich langsam bewegenden Insekten zu tun hat. Einzigartig innerhalb der Heteroptera ist die Klauenbasis der Aradidae, welche mit wenigen Ausnahmen pfeilartig geformt oder fünfeckig ist. Bei Männchen ist Stigma 8 frei an der Spitze oder basal an einem hervorstehenden Tuberkel von Segment 8; Sternum 8 ist schüsselförmig und exponiert und ist nicht zylindrisch und in Ruhelage ins Segment 7 zurückgezogen, wie bei den Pentatomomorpha. Das schüsselförmige Sternum 8 umhüllt und schützt die Genitalkapsel. Das Paarungsverhalten der Aradidae, bei dem das Männchen bei der Kopula unterhalb des Weibchens sitzt, wird als plesiomorph im Vergleich zur seitlichen Kopulationsstellung der Leptopodomorpha und Cimicomorpha oder der antagonistischen Kopulationsstellung der Pentatomomorpha gewertet. Dieses schüsselörmige Sternum 8 ist eine spezielle Synapomorphie zur Unterstützung dieser Paarungshaltung. Der zwei-gliedrige Tarsus ist eine Apomorphie innerhalb der Aradidae, weil der plesiomorphe drei-gliedrige Tarsus bei den Tretocorini (*Tretocoris* und *Kumaressa*) vorkommt. Mit Ausnahme von kleinen Ocellen bei *Kumaressa* fehlen Ocellen bei allen Aradoidea. Die Reduktion der Ocellen ist somit eine Apomorphie innerhalb der Aradidae. Weitere Plesiomorphien der Aradidae gegenüber den Pentatomomorpha sind: Der bulbus ejaculatorius ist einfach und besteht teilweise nur aus zwei Gewebslagen im Vergleich zur drei-lagigen Ausbildung bei den Pentatomomorpha und

den Cimicomorpha. Der Verdauuungstrakt besitzt keine blind endenden Darmdivertikel und ein echtes Ileum ist bei Mezirinae und Aneurinae ausgebildet. Letzteres fehlt bei allen Pentatomomorpha. Das freie Labrum der Aradinae ist plesiomorph und besitzt einen nach vorne gerichteten epipharyngealen Fortsatz. Der Praetarsus besitzt Pulvillae, die den Aradinae fehlen. Die Clavi der Hemielytren makropterer Aradidae überlappen sich und bilden keine Kommissur; die Clavi sind Teil der Membran, was als plesiomorph gilt. Bei den Pentatomomorpha wie bei den meisten Heteropteren stoßen die Clavi mittig hinter dem Scutellum zusammen und bilden dort eine Kommissur; diese kann fehlen, wenn das Scutellum vergrößert ist oder die Clavi reduziert und kein Teil der Membran sind. Bei den Chinamyersiini und Aradinae sind mehrere sc-r, r-m und m-cu Queradern im Corium, ein plesiomorpher Zustand, wie auch die Zellen bildenden Queradern zwischen den sechs Adern der Membran, welche Sc, R, M, Cu, Pcu und A entsprechen. Es scheint, daß entweder keine oder nur eine kurze m-Fraktur ausgebildet wird, welche aber vor und nicht hinter der R-Ader verläuft, wie bei allen anderen Heteropteren (ausgenommen Enicocephalomorpha). R- und M-Adern verlaufen getrennt oder vereinigt von der Coriumbasis bis zum distalen Rand des Coriums, der basal von einer langen gebogenen m-cu Ader gebildet wird und den distalen Rand des Coriums begrenzt. Sogenannte Gonoplacs sind bei Tretocorini-Weibchen ausgebildet, bei den Pentatomomorpha fehlen sie oder sind mit Valvifer 9 verschmolzen. Das einfache Ei ohne Operculum, mit Aeromikropylen und einem embryonalen Eissprenger ist symplesiomorph und nicht synapomorph innerhalb der Pentatomomorpha, verglichen mit dem apomorphen Ei mit Operculum der Cimicomorpha. Diese morphologischen Merkmale, zusammen mit den ökologischen, fossilen und biogeographischen Daten unterstützen die Hypothese, dass die Aradimorpha eine sehr alte, terrestrische Unterordnung darstellen, die sich schon früh in der Phylogenie der Prosorrhyncha oder der Heteroptera, noch vor den Leptopodomorpha, Cimicomorpha und Pentatomomorpha, abgespalten hat.

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Address of the Author:

Prof. Emeritus Merrill H. SWEET
Department of Biology
Texas A&M University
College Station
Texas 77843-3225
U.S.A.
E-Mail: msweet@bio.tamu.edu

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