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An Exaggerated Trait in Insects: The Prothoracic Skeleton of *Stictocephala bisonia* (Homoptera: Membracidae)

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**ABSTRACT**  
The prothoracic skeleton of *Stictocephala bisonia* was investigated in adults and fifth-instar nymphs on a gross morphological (SEM, maceration) and light microscopic level. In both nymphs and adults, the prothoracic skeleton consists of the pronotum, episternum, epimeron, precoxale, sternum, trochantin, and two endoskeletal characters (furcal arms and pleural apophyses). In nymphs, the entire pronotum is a single-layered outgrowth of the integument communicating with the body cavity and filled with hemolymph and fat body cells ("spine"); the dorsal and ventral processes and the suprahumeral bud are extensions of this single-layered integument. In adults, the pronotum is composed of (1) a proximal, single-layered part, and (2) a larger, distal, double-layered part ("posterior reduplication") with two cuticular layers separated by a thin lumen. The posterior reduplication is elevated above the body and forms hollow (air-filled) extensions (e.g., suprahumeral horns). Its two cuticular layers are connected through cuticular columns that appear on the external surface as pits. The lumen between these layers communicates with the body cavity and contains nerves and tracheae. In the lumen of newly eclosed adults, intercellular space, epidermal cells with long processes, and hemocytes with nonlipid granules are present. In the lumen of sclerotized adult pronota, the intercellular space has disappeared, together with definite cell boundaries. Several structures are associated with the external cuticle: two types of innervated sensilla trichodea that articulate in the center of external pits, sensilla campaniformia, sensilla coeloconica, and cuticular canals with exterior openings. The morphogenetic implications of pronotal construction, various aspects of adult prothoracic anatomy, and the value of glands and sensilla for an adaptive interpretation of the pronotum are discussed. *J. Morphol.* 238:157–178, 1998. © 1998 Wiley-Liss, Inc.

**KEY WORDS:** *Stictocephala bisonia*; prothorax; pronotum; lobe; double-layer; morphogenesis; function

In many treehoppers (Membracidae), the dorsal sclerite of the prothorax is extraordinarily enlarged, assuming an array of bizarre shapes across the family—a fact that has attracted an equally diverse community of adaptive and nonadaptive hypotheses over the decades and still awaits satisfactory evolutionary explanations (e.g., Wood, '93). In dealing with the Membracidae, the taxonomists of the eighteenth and nineteenth centuries (e.g., Linnaeus, 1758; De Geer, 1773; Stoll, 1788; Latreille, 1802; Fabricius, 1803; Germar, 1835; Burmeister, 1839; Amyot and Serville, 1843; Fairmaire, 1846; Stål, 1859, 1866; Fowler, 1894) based their work largely on the external appearance of this sclerite (the pronotum). These investigators introduced terms describing its commonly found external characters: the lateral horn ("cornus": Linnaeus, 1758), humeral angle ("angles humeraux": Amyot and Serville, 1843), posterior process ("cornu postico": Stål, 1859), and the frontal and dorsal parts of the sclerite ("metopidium" and "dorsum," respectively; Fowler, 1894).

The first achievement toward an understanding of pronotal anatomy of the Membracidae was the recognition of the potential functional significance of these structures. This was achieved by a) the study of histological and histochemical features of the pronotum (e.g., Wood, 1993), b) the consideration of behavioral and ecological consequences of the modification of pronotal shape (e.g., Raubenhorst, 1993), and c) the analysis of the role of the pronotum in the context of the life cycle and seasonal patterns of development (e.g., Hinton, 1995).

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cidae was to recognize this sclerite in adults as the pronotum in the proper anatomical sense. Linnaeus (1758) attributed the sclerite to the dorsal part of the thorax, and De Geer (1773) correctly specified that it belonged to the prothorax or "corselet." De Geer’s interpretation was challenged by Ger- mar (1835), who thought the exaggerated sclerite was a unified dorsal thoracic plate. When Burmeister (1839) refuted Germar’s view, he was the first to explicitly acknowledge this sclerite as the notum of the prothorax ("Vorderrücken").

Buckton (03) observed that the external pronotal processes are not integumental outgrowths communicating with the body cavity, but rather are parts of one enlarged, cuticular plate ("shell": Buckton, ’03) extending over the body and so arched as to form these pronotal processes as hollow extensions ("hollow chambers," "air-chambers"; Buckton, ’03). He illustrated his findings, establishing the "septum" as an internal character of the pronotum and, for the first time, defined pronotal features that had been used by taxonomists for more than a century. Referring to external processes, he made the important observation that "there are no corresponding sutures to mark them anatomically" (Buckton, ’03). Consequently, Buckton must have realized that even his definitions were anatomically ambiguous. This conclusion may also be the background to Funkhouser’s (’17) remark that the pronotal processes "have no anatomical significance [sensu anatomical definition, U.E.S.] and are merely hollow extensions of the chitinized wall." The considerable confusion in early systematics, which relied largely on descriptions of external pronotal morphology (e.g., Wood and Pesek, ’92), is likely to have originated from this lack of sutures.

After Buckton’s (’03) pioneering work, the literature became scattered with few cross-references, and his own study on pronotal anatomy was largely forgotten. While the existence of the pronotal plate was accepted by later investigators, as can be inferred from some of their drawings (Marcus, ’50; Kopp and Yonke, ’72; Strümpel, ’72), its internal composition remained controversial. Some investigators apparently considered the pronotal plate to be a massive, cuticular structure (Kramer, ’50; Kopp and Yonke, ’72; Strümpel, ’72), while others, working specifically on pronotal histology, discovered living tissue within (Marcus, ’50; Richter, ’54; Wood, ’75b). With one exception (Riechel, ’87), even basic gross morphological aspects either were not investigated or remained obscure; e.g., the articulation of the pronotal plate with the rest of the body. Buckton (’03) depicted a "crescentic process for articulating the pronotum" on the mesonotum, while Richter (’53, ’54) assumed muscles to fix an extended part of the pronotum ("apéndice pronal") to the rest of the sclerite. Knowledge of the prothoracic anatomy of nymphs remains restricted to the rough external shape of the pronotum and its processes found in various species (e.g., Funkhouser, ’17; Yothers, ’34). Considering the numerous speculations about the adaptive significance or insignificance of the exaggerated pronotum, this scarcity of knowledge about pronotal anatomy is surprising.

Here, the prothoracic skeleton of adults and last-instar nymphs of Stictocephala bisonia, Kopp and Yonke (’77), was investigated at the gross morphological and histological level. Emphasis in both nymphs and adults was on the attachment of the pronotum to the rest of the body and on the histology and external morphology of the posterior reduplication in adults. The results are not only discussed with respect to earlier studies on S. bisonia, but to any other membracid species in order to review the current knowledge of the prothoracic anatomy in the Membracidae. Stictocephala bisonia is a univoltine species that is widely distributed and seasonally abundant in North America (e.g., Kopp and Yonke, ’73, ’77) and was introduced to Europe early in the twentieth century (e.g., Poisson, ’37; Hoffrichter and Troger, ’73; Günthart, ’80).

MATERIALS AND METHODS

A colony of Stictocephala bisonia was obtained from H. Strübing (’92) and reared on Vicia faba and Prunus amygdalus (for details, see Stegmann, ’97). The exo- and endoskeleton were investigated using specimens (six males, eight females, six fifth-instar nymphs) that were macerated for up to 1 hr in hot KOH (10%), washed, and dissected under a Wild stereomicroscope. Figures 1B–E, 2A, 48–E, and 5A–C are camera lucida drawings of specimens in glycerin. Dissections of muscles, nerves, and tracheae were performed with four females fixed in 4% formalin and half-embedded in paraffin wax (modified after Kramer, ’50), and with two males and one female, using a modified vital staining procedure (Yack, ’92) with saline (0.1 M phosphate buffer with 5.5% sucrose, pH 7.2) and 0.01% anest Green B.
Whole-mounts of the metopidium, dor- sum, and septum were prepared from two males and four females; 0.5–3 mm² frag- ments were cut in saline, fixed in 1.75% glutaraldehyde (in 0.1 M phosphate buffer, pH 7.2), washed, stained for 12–24 hr in 0.75% Orange G, washed again, and then stained for 12–24 hr in 0.5% Light Green. Fragments were then dehydrated in a graded ethanol series and mounted on microscope slides in Entellan. Only cellular components were stained, while the cuticle remained transparent (Figs. 7C,E, 8D,E,I).

Sections for light microscopy were prepared from four males, four females, and two third-instar nymphs. After dissection in saline, relevant material was fixed in a vacuum-desiccator for 1 hr and then for 24 hr at +6°C (1.75% glutaraldehyde in 0.1 M phosphate buffer, pH 7.2), and vacuum-washed in saline. Except for nymphs (Fig. 2C–E) and one female (Fig. 8A,N), tissue was postfixed for 24 hr at +6°C (2% osmium tetroxide and 5.75% sucrose in 0.1 M phosphate buffer) and washed. Following dehy- dration in a graded series of ethanol, most material was imbedded in Technovit 7100 VLC, and stained with Toluidine Blue O/Methylene Blue (Fig. 2C–E; 10 µm), Methylene Blue/Azure II (Fig. 8F,M,O; 0.7 µm), Azure II/Basic Fuchsin (Figs. 7A,F, 8B,C,G,H,L; 5 µm), or Delafield’s hematoxy- lin and eosin Y (H&E) (5 µm). One female was Bouin-fixed, embedded in Durcupan, and stained with Heidenhain’s triple chrome stain (Fig. 8A,N; 2 µm). Material for Figure 7F was imbedded in Spurr’s medium (2 µm). All staining procedures followed Romeis (‘89). Sections were cut on a Reichert microtome with glass knives and examined with an Olympus BH-2 and a Zeiss–Axiophot micro- scope. Sections with untanned or slightly tanned cuticles were from newly ecosed adults (i.e., 18–24 hr of age (Figs. 6A, 7A,F, 8B,C,G,H,L); sections with fully tanned cuticles are from adults at least 1 month old (Figs. 6B, 8A,F,M,O).

Specimens for scanning electron microscopy (SEM) were fixed in 4% formalin for 24 hr, sonicated for 10 min, treated with glycerin for 24 hr, and dehydrated in a graded series of acetone or a graded ethanol series with a final acetone treatment (30 min per 10% interval from 50% to 100% ethanol or acetone; five males, five females, four fifth-instar nymphs). After air-drying, they were mounted on aluminum stubs, gold-coated, and examined under a Zeiss DSM or ISI-100B SEM.

Body width (the distance between the outer edges of the eyes) and pronotum width (the distance between the lateral tips of the suprhumeral horns) was measured to the nearest 0.01 mm, using digital calipers. Den- sities of sensilla trichodea were measured from en face whole mounts of dried pronotum fragments under a Wild stereomicro- scope, using a grid ocular at 40× magnification. Sensilla were counted indirectly by the number of columns, as sensilla could not be discerned individually but were always associated with columns (see under Results). Outer ocular width was used as a measure for body size, width between suprhumeral as a measure for pronotum size. These and the data on sensilla density were compared using t-tests after being tested for normality (KS-tests, 0.25 < P < 0.91) and homogeneity (F-tests, 0.18 < P < 0.49).

Systematic divisions are sensu Deitz and Dietrich (‘93). General gross morphological terms follow Matsuda (‘70); those specific for membracids follow Buckton (‘03). Terminol- ogy of sensilla follows Zacharuk (‘85). Three anatomical terms were coined to accommod- ate new findings. The choanidium of adults (choan-, greek: “funnel” and -idium, greek: “diminutive for small structures”) is the area of fusion of the pronotal canal with the interseg- mental membrane. The pronotal canal of adults is a canal formed by the interior cu- ticular layer of the posterior reduplication. The bases of sensilla trichodea are connected to the lumen of the posterior redupli- cation by columnar canals. “Distal” and “proximal” refer to the anatomical (not the spatial) distance from the body’s center.

RESULTS

Fifth-instar nymphs

The prothorax consists of six sclerites: pro- notum, episternum, epimeron, precoxal bridge, sternum, and trochantin (Fig. 1). From a ventral view (Fig. 1B) the sternum is a small, nearly rectangular plate with two pits marking the base of the furca that has two furcal arms on each side. Anteriorly the sternum is continuous with a narrow precoxal bridge fused to the episternum. There is no postcoxal bridge. The trochantin lies between the coxa and the episternum. The episternum is bordered posteriorly by the pleural sulcus adjacent with the epimeron. At its dorsal end, the pleural sulcus deepens into a pit (Fig. 1B) that is the origin of the pleural apophysis (Fig. 1C,E). From a lateral perspective, the apophyseal pit is covered by the pronotal cone (Fig. 1D) lying...
on an edge formed by the pronotum. In situ, the cone is largely covered by the eyes.

The main part of the pronotum extends dorsal to this edge—a sclerite as broad as the head in frontal view but converging more dorsally in a triangular shape (Fig. 1C). From a lateral view, the pronotum appears elongated in a ventrodorsal axis and bends over...
the mesonotum, forming a tip (Figs. 1A,D, 2A). The pronotum covers the mesothorax laterally where its sclerotized part gradually becomes membranous and contains the stigma (not illustrated). Where the endoskeletal prephragma extends into the body cavity, the posterior pronotal margin joins the mesonotum (Fig. 2A). For comparison with adults, it should be emphasized that the nymphal pronotum is single-layered throughout, even though the integument folds in the lateral extensions and in the posterior tip, so that two layers come into close contact (Fig. 1E). Internally, the pronotum is filled with hemolymph and fat body cells that usually extend only into the bases of the ventral and dorsal processes (Figs. 1D,E, 2C,E; see Table 1 for synonyms). Hence, these processes are single-layered extensions of the pronotal integument as are the suprahumeral buds (Fig. 1D). The external pronotal surface is covered with sensilla trichodea, each articulated in an elongate base (Fig. 1B,C). Supraocular callosities are located on the external surface lateral to the ventral processes (Fig. 1C,D). Prothoracic leg muscles originate on their interior side (Fig. 2D).

**Adults**

**Gross morphology of the prothorax**

Female body size (ocular width) and pronotum size (suprahumeral width) are larger than in males (Table 2). In both sexes, pronotum size correlates with body size, fitting a positively allometric power function (Fig. 3). Nevertheless, the shape and components of the prothoracic skeleton, including pronotal histology, are the same in females and males.

Hence, the following observations apply to both.

Adults have the same prothoracic sclerites as nymphs: pronotum, episternum, epimeron, precoxal bridge, sternum, and trochantin (Fig. 4; see Table 3 for synonyms). Cervical sclerites were not found. The sternum is small, rectangular, and fused to the episternum by the precoxal bridge (Fig. 4C). No postcoxal bridge (postcoxale) was found. External pits in the sternum mark the origin of the endoskeletal furca, whose lateral arms merge on each side with the pleural apophyses (Fig. 4B,E). The area of fusion usually remains visible. The trochantin articulates freely with the coxa and the episternum. A marked pleural sulcus separates the pleuron into the episternum and epimeron, and its dorsal end forms a pit on the outside (Fig. 4B,D), the base of the endoskeletal pleural apophysis.

The adult pronotum, however, is more complex than its nymphal form, because it is composed of two subunits: a proximal single-layered region, and a distal double-layered region. The proximal region is a single-layered integument wall (Fig. 5C) defined through its boundaries. Ventrally it extends to the tergopleural boundary that has no physical demarcation in adults, because the propleuron fuses seamlessly with the pronotum. Nevertheless, the tergopleural boundary can be estimated to extend from the pleural pit to the ventral edge of the (pronotal) ventral lobe (Fig. 4D) (Stegmann, '97), e.g., because the dorsal termination of the pleural sulcus is a general criterion for the tergopleural boundary in the pterygote prothorax (Parsons, '67). The ventroanterior termination of the single-layered part of the pronotum consists of the anterior pronotal margin lined by the dorsal part of the cervical membrane (Figs. 5C, 7F). This membrane does not contain cervical sclerites. Dorso-posteriorly, the single-layered pronotal region terminates with the posterior margin of the pronotum that is lined by the intersegamental membrane (Figs. 5C, 7F). Mesally, the posterior margin runs in immediate proximity to, and parallel with, the anterior pronotal margin: in a median section through the proximal pronotum and adjacent areas, the posterior margin ends very close to the anterior margin, leaving only a narrow single-layered strip (Fig. 7F). Thus, the prephragma is close to the occiput (Fig. 7F). Laterally, the posterior margin bends ventrally in a curve ending near the ventral

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**TABLE 1. List of prothoracic features previously described for nymphal Stictocephala bisonia**

<table>
<thead>
<tr>
<th>Terminology used in this work</th>
<th>Terminology of previous investigators</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorsal and ventral processes</td>
<td>[Drawn in figs. 10 and 11, pl. xxiv, but not named]</td>
<td>Funkhouser ('17)</td>
</tr>
<tr>
<td>Suprahumeral bud</td>
<td>Pronotal horn bud, suprahumeral horn bud</td>
<td>Quisenberry et al. (78)</td>
</tr>
<tr>
<td>Sensilla trichodea on elongated bases</td>
<td>Chalazae, lateral soli</td>
<td>Quisenberry et al. (78)</td>
</tr>
<tr>
<td>Supraocular callosities</td>
<td>[Drawn, but not named]</td>
<td>Quisenberry et al. (78)</td>
</tr>
</tbody>
</table>
edge of the ventral lobe (Fig. 5C). Within the curve, the sclerotized pronotal canal joins the intersegmental membrane in a funnel-shaped zone (choanidium). A stigma is located within the posterior area of the intersegmental membrane (Fig. 5C). From a frontal view (Fig. 4B), the single-layered region of the pronotum contains the supraocular callosities and the mesal parts of the fossae. Muscles arise from the interior surface of the supraocular callosities (Fig. 7A), whose external surfaces are covered with low naps 5–11 µm in diameter (Fig. 7B). In situ, the eyes fit into the shallow caves of the fossae and the postgenae cover the anterior part of the episternum.

Fig. 2. Nymphs of Stictocephala bisonia. A: Diagrammatic representation of a median section through a fifth-instar nymph showing the relations between prothorax (white), head (dark pattern), and pterothorax and abdomen (light pattern). B: Sensillum trichodeum on the pronotum (fifth instar). C: Sensillum trichodeum on the dorsal process (fifth instar). D: Pronotal muscle originating at the supraocular callosity (fifth instar). E: Frontal section (third instar) with the pronotal interior filled with fat cells. D, dorsal; ba, base of sensillum trichodeum; dp, dorsal process; e, eye; f, fat body cells; mu, pronotal muscle; p, pronotum; ph, pharynx; pr, prephragma; oe, esophagus; sg, salivary gland; soc, supraocular callosity.
Distad of the posterior pronotal margin the pronotum is double-layered; i.e., it consists of two adjacent integumental walls (e.g., Fig. 6) forming a large, complexly bent plane (about 50 µm thick). Frontal (Fig. 4B) and ventral views (Fig. 4C) show that the double-layered region forms the strong suprahumeral horns. The median carina runs in the median plane across the frontal pronotum (metopidium, Fig. 4B). Posterior to the suprahumerals the dorsum is triangular in cross-section with the median carina as its dorsal edge and both the left and right lateral carinae (Fig. 4C) as its ventral edges. Seen in median sections, the double-layered region of the pronotum rises dorsally over the head (Fig. 7F; metopidium), bends posteriorly in a wide arch extending as the posterior process, reflects and continues anteriorly to end over the scutellum (Figs. 4E, 5A). The latter, reflected part (= septum sensu Buckton, ’03) is concealed by the dorsum and is seen en face only in ventral view (Fig. 4C). More anteriorly, the septum, with its lateral margins, separates from the lateral carinae in a bow and its

### Table 2. Sexual size dimorphism (mean ± sd) in *Stictocephala bisonia*¹

<table>
<thead>
<tr>
<th></th>
<th>Females</th>
<th>Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outer ocular width (mm)</td>
<td>3.39 ± 0.10² (3.56; 3.1–3.5 [sic!]₄)</td>
<td>2.98 ± 0.12²</td>
</tr>
<tr>
<td>Suprahumeral width (mm)</td>
<td>5.78 ± 0.32³ (5.99; 5.45–6.4)₄</td>
<td>4.83 ± 0.35³</td>
</tr>
<tr>
<td>n</td>
<td>51</td>
<td>61</td>
</tr>
<tr>
<td>Regression of pronotum size (y) on body size (x)</td>
<td>y = 1.0457 × x^{1.4012}</td>
<td>y = 0.8053 × x^{1.6385}</td>
</tr>
<tr>
<td>Regression coefficient</td>
<td>0.7286</td>
<td>0.8755</td>
</tr>
</tbody>
</table>

¹Outer ocular width (a measure of body size) is greater in females than in males, as is suprahumeral width (a measure of pronotum size). In both sexes, these two measures are strongly correlated, fitting an allometric power function. With an a > 1, the allometric relationship is positive in both sexes. See also Fig. 3.

²Unpaired *t*-test, *t* = 19.9, *P* < 0.0001.

³Unpaired *t*-test, *t* = 15.0, *P* < 0.0001.

⁴Kopp and Yonke (’77); n = 20.

![Graph](image_url)
anterior margin contacts the scutellum (Fig. 4E). Laterally, the anterior margin of the septum continues into the left and right pronotal canals that run along the interior of the dorsum and terminate in the choanidium (Figs. 4E, 5C). The pronotal canal is seen only from an internal (Figs. 4E, 5C) or ventral view (Fig. 4C), because only the inte-
rior integument is arched in a semicircle (Fig. 8B).

The pronotum attaches to the head and mesothorax through the cervical and intersegmental membranes, respectively. Because of the shape and large size of the pronotum, especially of its double-layered part, there are seven areas of secondary contact between pronotum and nonpronotal body parts: (1) fossae: postgenae (Fig. 4B,C); (2) metopidium: mesoscutum (Fig. 5A,B, arrowhead #1); (3) dorsum: mesoscutum (Fig. 5B, arrowhead #2); (4) dorsum: lateral projection of the scutellum (Fig. 5B, arrowhead #3); (5) septum: scutellum (Fig. 5A, arrowhead #4); (6) septum: abdomen (Fig. 5A, arrowhead #5); and (7) ventral lobe/humeral angles: mesepisternum/upper episternal hook (Fig. 7G).

Histology of the double-layered region of the pronotum

The double-layered region of the pronotum consists of two integumental walls lying adjacent and parallel to each other with their cuticles locally fused to massive columns (Fig. 6). Between the two cuticles is a lumen, an extension of the body cavity (Fig. 5F). This general composition is seen not only in cross sections (e.g., Fig. 6), but also in en face views of pronotum fragments (Fig. 7C,E), in which only the cellular components within the lumen are stained dark, while the cuticle layers remain transparent. Thus, seen along their longitudinal axis, columns, consisting of massive, transparent cuticle, appear as light circles (Figs. 7E, 8E).

In pronota of newly eclosed adults, the untanned or slightly tanned external cuticle is approximately 4–8 µm thick, the internal cuticle approximately 1 µm (internal cuticle/integument forming the posterior pronotal margin; external cuticle/integument = the cuticle/integument forming the anterior pronotal margin). When tanning is completed the external cuticle thickens to 25–40 µm, the internal cuticle to 3–8 µm, depending on where exactly measurements are taken. The columns in fully tanned individuals attain a diameter of 40–70 µm in the metopidium, and about 20 µm in the dorsum. Tanned cuticle stains light brown/green with Azure II/Basic Fuchsin and H&E, while untanned cuticle stains red or pink. Large pits cover the external surface of the external cuticle and can be seen in the SEM (Fig. 7H) or as circles under a stereomicroscope (e.g., Fig. 4B). Each pit corresponds to one column (Fig. 6). On the external surface of the internal cuticle each column produces a low cone about 12–20 µm in diameter (Figs. 6B, 7D, 7D insert).
sections stained with Methylene Blue/Azure II the most exterior layer of the external cuticle stains brownish, while the main cuticular body stains blue. Where the column is sectioned through its axis, it can be seen that the brownish cuticle extends into the cone. The surface of the internal cuticle is covered with tiny cuticular protuberances (Fig. 7D, insert).

As the cuticles thicken after molting the lumen becomes thinner (30–50 µm in newly eclosed adults; ≤20 µm or less in fully tanned individuals). The more dramatic effect of age on the lumen, however, concerns its histology. Only in newly eclosed adults can epidermal cells be distinguished from hemocytes and the (unstained) intercellular space (Fig. 6A).

Epidermal cells are characterized by their smooth cytoplasm, their oval, horizontal nuclei, their position along the internal surface of the internal and external cuticles, and their extensions that may run obliquely or straight across the entire lumen (Figs. 6A, 8G,L). Extensions of both epidermal layers seem to intertwine, implying the breakdown of the basal lamina; however, epidermal extensions do not occur in areas in which the two integumental layers are farther apart, e.g., along the median carina (Fig. 7F) or the pronotal canal (Fig. 8B).

Hemocytes are usually located in the middle of the lumen (Figs. 6A, 8L), often elongated horizontally, and situated along tracheae or nerves (if present; Fig. 8G). They usually occur as single cells, lack the extensions across the lumen, and have round nuclei (Fig. 8L). Their cytoplasm contains densely packed granules that stain in the same colors as epidermal granules, albeit
more intensively, especially in H&E and Heidenhain’s stains (Fig. 8A). These granules are found both in non-lipid-fixed (Fig. 8A) and in lipid-fixed material (e.g., Fig. 8L).

No fat cells were found within the lumen, except in the most ventroanterior part of the median carina where a few cells enter from the large fat body that fills the mid-sagittal, dorsal region of the head, pro-, and mesothorax (Fig. 7F). Fat cells can be distinguished from hemocytes by their position and type of granules. While hemocytes usually occur as single cells and occasionally in strands, fat body cells form clumps containing many, roundly shaped, large cells (Fig. 8A). Lipid-fixed fat body cells (Fig. 7A,F) show a great variety of small to large vesicles that may also differ in color. For example (Azure II/Basic Fuchsin; Spurr), within one cell, the largest vesicles stain olive green, small vesicles remain transparent, while others stain blue, purple, and pink. Presumably, only the large green vesicles contain a large portion of lipids, because in non-lipid-fixed material large areas of the fat body cells are depleted, while small, dark granules remain (Fig. 8A,N).

In fully sclerotized pronota (e.g., Fig. 6B), the lumen is filled with four components: (1) small, dark granules (Fig. 8M); (2) large, sometimes entirely transparent compartments that are only recognized by their boundaries (Fig. 8F,O); (3) nuclei (Fig. 6B); and (4) dendrites within columnar canals (Fig. 8F). Neither cell bodies nor intercellular space can be found.

The cellular components described below occur in the lumen of both teneral and old adults. Tracheae are easily recognized by their taenidia and by being unstained internally (Fig. 8C). Apparently, tracheae enter the double-layered pronotum through the pronotal canal (Fig. 8B) and other areas of the metepisternum and dorsum, but not through the median carina. No attempt was made to trace their branching patterns. Nerve bundles are recognized by horizontal fibers in cross sections (Fig. 8G). Individual nerves entering the double-layered pronotum through the pronotal canal (Fig. 8B) or through the metepisternum were traced back to the prothoracic ganglion, using serial sections and gross dissections. The prothoracic ganglion is fused to the mesothoracic ganglion but can be distinguished in microscopic sections by its neuropil. No nerve was found within the median carina. The dorsal vessel extends through the mesothorax into the prothorax, ending near the pharynx/esophagus transition (Fig. 7F), but no accessory pulsatile organs were found.
Sensilla trichodea articulate in the center of the pits on the external cuticle (Figs. 7E, H, 8E, F). A columnar canal runs through the column to the base of the seta (e.g., Fig. 8E) containing the dendrite(s) (Fig. 8F), but cell bodies could not be localized. Type A setae (Figs. 7H, 8E) are shorter and thinner (approximately 25–40 µm long, n = 24; approximately 1 µm diameter, n = 10) than type B setae (approximately 65–80 µm long, n = 29; approximately 3.5 µm diameter, n = 6) (Figs. 7H, 8F). At least the setae of B-sensilla are hollow (Fig. 8F), but no cuticular openings on the setal surface were found. The density of sensilla trichodea is greater in males than in females, irrespective of the pronotum region examined (Table 4). Both males and females have a greater density on the metopidium than on the dorsum (Table 4). Sensilla campaniformia occur in low densities on the external surface of the metopidium and dorsal external cuticle. The apical dome appears as a circle in an en face view (Fig. 8E), but can also be seen in cross sections through un坦ned (Fig. 8H) and fully tanned cuticle (Fig. 8O). A canal through the cuticle (approximately 6 µm wide) leads the dendrite(s) (Fig. 8O). Sensilla coeloconica (Fig. 8K, N) were only found in the fossae.

In metopidial and dorsal en face fragments, light circular structures of approximately 8–10 µm in diameter occur in the focal plane of the lumen with a canal terminating on the surface (Fig. 8I). These openings are the small pores (diameter approximately 3 µm) seen in the SEM (Figs. 7H, 8J). The canals through the external cuticle are distinguished from those of sensilla campaniformia in that they consist of an approximately 5 µm wide basal part, an approximately 1 µm wide apical part (Fig. 8I, M), and an approximately 4 µm wide sphere just below the external opening (Fig. 8L, M).

**DISCUSSION**

Prothoracic sclerites of last-instar nymphs and adults

Last-instar nymphs and adults of Stictocepha bisonia share the same prothoracic sclerites (pronotum, epimeron, episternum, sternum, precoxale, and trochantin) and endoskeletal features (pleural apophysis and furca). However, in adults the lateral furcal arm on each body side is fused with the pleural apophysis, while in nymphs it is not. With the exception of the epimeron, these sclerites and their endoskeletal components were already recognized in adults of S. bisonia by Kramer (‘50) and his findings were later confirmed (Hasenoehrl and Cook, ‘65; Table 3). As in those studies, no cervical sclerites and no postcoxal bridge were found in the present study.

The first report on the various prothoracic sclerites of (generalized) adult membracids was from Funkhouser (‘17), who acknowledged the pronotum, episternum, epimeron, trochantin, and sternum. He did not describe endoskeletal structures. The pronotum, episternum, sternum, precoxale, trochantin, pleural apophysis, and furca were also found in adult Oxyrachiniae (Has-
The pronotum is a "spine" in nymphs...

A basic difference between pronotal anatomy of adults and nymphs of *Stictocephala bisonia* was found in this study: the interior of pronotal substructures, e.g., suprahumeral/suprahumeral buds, communicates with the body cavity in nymphs but is air-filled in adults.

A single-layered outgrowth of the integument communicating with the body cavity is termed "Dorn" (Weber, '33) or "spine" (Snodgrass, '35). Thus, in *Stictocephala bisonia*, not only the nymphal pronotal substructures are "spines," but the entire nymphal pronotum is a large "spine." This result may well be generalized to the homologous nymphal pronotum of the Membracidae, because, in *Tricentrus albomaculatus*, Kershaw ('13) found that the tegumentary bristles of the nymph are hollow and communicate with the body cavity. Judging from his diagram (fig. 1, Kershaw, '13), he referred to the elongated bases of sensilla, but also to tergal substructures such as the dorsal processes.

Except for Kershaw's ('13) findings, the nymphal pronotum and its substructures were known only with respect to external morphology. Pronotal processes were reported from *Stictocephala bisonia* (Funkhouser, '17; Quisenberry et al., '78; see Table 1) and other membracids (e.g., Stoll, 1788; Syn.: "tuberosities": Yothers, '34). Suprhumeral buds occur in several New World genera (Quisenberry et al., '78), in many Oxyrhachininae (Capener, '62), and in many Centrotinae (Capener, '68). Published figures show setae (as "chalazae" and "scoll") on the nymphal pronotum of *S. bisonia* and other New World genera (Quisenberry et al., '78), but also on the pronotum of several Centrotinae species (Capener, '68). These setae are presumably sensilla trichodea.

Nymphal supraocular callosities were labeled as such in the Oxyrhachininae (Capener, '62) but were also depicted in figures of *S. bisonia*, of several other New World species (Quisenberry et al., '78), and of Centrotinae species (Capener, '68).

...but a "posterior reduplication of the notum" in adults

Except for the proximal single-layered region, the pronotum of adult *Stictocephala bisonia* is a plate arched in itself far beyond the body outline, covering the pterothorax and abdomen and forming extensions (e.g., suprahumeral horns) that are hollow in the sense that their interior does not communicate with the body cavity, but with the air; the pronotal plate is composed of two integumental layers connected through cuticular columns comprising a lumen that communicates with the body cavity. Therefore, what appear to be the lateral pronotal margins, i.e., the lateral carinae, are blind endings of the pronotal plate, not the true terminations of the sclerite (which are lined, per definitionem, by membranes). In short, the distal region of the adult pronotum is a double layer or lobe—an exceptionally large "posterior reduplication of the notum" sensu Snodgrass ("the posterior edge of the notum folded downward and forward upon itself, leaving a free margin overlapping succeeding parts"; Snodgrass, '09).

In *Stictocephala bisonia*, the plate aspect might be inferred from Branch's ('13) remark that the dorsum forms a "tectiform hood" and from drawings by Kramer (fig. 72,
pl. ix and fig. 106, pl. xii, Kramer, '50). On a greater taxonomic scale, the plate aspect was the first insight into pronotal anatomy of adult membracids (Buckton, '03; Branch, '13; Funkhouser, '17; Marcus, '50; Kopp and Yonke, '72; Strümpel, '72). For example, Buckton (‘03) wrote that "the remarkable spines of these insects have no bulbous origin, but are hollow tubes rising directly from the surface" and are "filled with air."

Whether this pronotal plate is single-layered (massive cuticle) or double-layered (lobe) remained controversial. A massive cuticle could be inferred from drawings of Stictocephala bisonia (fig. 72, pl. ix and fig. 106, pl. xii, Kramer, '50), Entylia bacteriana (fig. 1, Kopp and Yonke, '72), and a generalized membracid (fig. 36, Strümpel, '72). But studies focusing on the composition of the plate always revealed living tissue. Nerves and tracheae were reported from Aethalion sp., Aconophora sp., Alchisme sp. (Marcus, '50), and linear structures ("venas") associated with stigmata were described in Membracis spp., Lycoderes spp., Stegaspis sp., Oeda inflata, and Gelastogonia sp. (Richter, '54). Eventually, Wood (‘75b) found that "a matrix of cells between two cuticular layers characterize the wall of the expanded pronotum" of Umbonia crassicornis.

The location of the posterior pronotal margin, the course of the intersegmental membrane, and the presence of a proximal, single-layered pronotal area were not previously reported in the Membracidae. This led to considerable confusion as reflected, e.g., by Kramer’s ('50) misinterpretation of the posterior pronotal margin in Stictocephala bisonia as a "muscle partition formed by [the] apodermal wall of [the] pronotum" (mp—fig. 106, pl. xii). Also, it was difficult to understand why and exactly which part of the pronotum is detachable in Anchistrotus spp. and why this apparently does not harm the insect (e.g., Bouard, '83, Strümpel, '83, Rietschel, '87). It seems that if the gross morphological (pronotal plate) and histological aspects (double layer) had been considered together, the conspicuous part of the membracid pronotum would have been immediately recognized as the posterior reduplication of the pronotum.

In this study, internal and external cuticle of the lobe were found to be fused to columns with each column associated with an external pit. Both also occur in beetle elytra that represent another type of lobe (e.g., Weber, '33; Reuter, '36; Krzelj, '69). External pits were reported by earlier workers in Stictocephala bisonia ("punctured," Branch, '13; "punctate," Funkhouser, '17; "impunctations" Kramer, '50) and other membracids (Fabricius, 1803; Kirby, 1829; Buckton, '03). Columns were never explicitly described in the Membracidae; however, a close look at some studies suggests their presence in many species. Buckton's (‘03) "shallow depressions or punctures" appeared as "bright dots when suitably placed" and could easily be interpreted as columns, because this is the way they appear in en face views (of S. bisonia).

For the same reason Marcus’ ('50) "cercos redondos" in the pronota of Aethalion sp., Aconophora sp., and Alchisme sp. could be interpreted as columns, especially because they correspond to external pits ("hoylelos"), at least in the proximal area of the pronotum. A SEM study showed pronotal pits in 100 species from six membracid subfamilies (Wood and Morris, '74). If pronotal pits are indeed associated with columns, columns are common to the Membracidae and Aetalionidae.

From spine to lobe: morphogenetic implications

When Latreille (1802) noted that "La larve du membrane du genêt diffère peu de l’insecte parfait" he was the first to indicate strong similarities between nymphs and adults in respect to the externally visible substructures of the pronotum. Prominent examples are the dorsal spine in Umbonia crassicornis (Pelaez, '40, '41) and the dorsal bulb in Anchistrotus amitteraglobus (Boulard, '83).

Such pronotal substructures were generally interpreted as adult primordia, e.g., Funkhouser’s (‘17) "vestigial lateral horns" (=suprahumeral buds) in the Ceresini. Consequently, postembryonic pronotal development was regarded as a progressive, molt-to-molt enlargement (e.g., Funkhouser, '17; Strümpel, '72), suggesting shifts in body proportions but minor morphological change. But occasionally, even the external pronotal development seemed to exceed paurometabolism (Müller, '84).

If pronotal substructures of membracid nymphs are indeed "spines," e.g., suprahumeral buds, then they are anatomically distinguished from adult features of similar appearance, e.g., suprahumeral horns, that are parts of the pronotal "reduplication." Therefore, nymphal substructures are not early (small) stages of adult substructures.
Rather, they may be regarded as sheaths inside of which the adult substructures develop, necessarily taking the approximate shape of adult processes. I hypothesize that the primordium of the adult pronotum develops only within last-instar nymphs, i.e., between apolysis and adult ecdisis, because otherwise an imaginal disc (non-cuticle-producing epidermis) must be assumed, which is known only from Holometabola.

Occasional reports of postecdysial expansion of the pronotum (Richter, '54; Suchantke, '76; personal observation in laboratory colonies of Stictocephala bisonia) provide circumstantial evidence for (1) the existence of a unique adult primordium within the pronotum of last-instar nymphs and for (2) the hypothesis that due to limited space within the nymphal sheath the adult primordia unfold completely only after ecdisis. Membracid last-instar nymphs fasten themselves to the underside of a leaf or twig before ecdisis (e.g., Funkhouser, '17; personal observation in S. bisonia). Hanging upside down, adults may help to expand the pronotal lobe as they do with their wings.

Another line of evidence for a separate adult primordium in Stictocephala bisonia and its expansion after adult ecdisis comes from histological parallels between postecdysial development (1) of insect wings and (2) of the pronotal lobe of S. bisonia. These parallels concern the occurrence of epidermal feet and hemocytes, the presumed lack of a basement membrane, the dissolution of cell membranes, and the disappearance of intercellular space with age.

Pronotal lobes of newly eclosed Stictocephala bisonia exhibit epidermal feet connecting the two integumental layers, thereby leaving ample space in between for hemolymph. Epidermal feet (Locke and Huie, '81) seem to intertwine in S. bisonia, because extensions of both epidermal layers may form a single strand on a light microscopical level. Such epidermal feet are known from the development of other lobes, such as wings (e.g., Rehberg, 1866; Weber, '33; Chapman, '82; Nardi and Magee-Adams, '86) and antennal primordia (e.g., Kl and Steiner, '90). Intertwining of epidermal feet without the occurrence of a membranous middle layer implies breakdown of the basement membrane, which was observed in the development of wings (e.g., Weber, '33; Chapman, '82; Nardi and Magee-Adams, '86), and antennae (e.g., Steiner and Keil, '93).

Hemocytes are regularly found in double layers like wings (e.g., Reuter, '36; Zeller, '38; Nardi and Magee-Adams, '86) and antennal primordia (Keil and Steiner, '90; Steiner and Keil, '93), where they are involved in the formation (Nardi and Miklasz, '89) and breakdown of the basement membrane (Nardi and Miklasz, '89; Steiner and Keil, '93). "Hemocyte" is used here in the widest sense, meaning "the loose cells in the body cavity of insects" (Wigglesworth, '65). This definition incorporates the fact that often there is no sharp distinction between free-floating fat cells and hemocytes sensu stricto (Wigglesworth, '65; Chapman, '82). A similar situation is suggested for Stictocephala bisonia, because (1) the dominance of nonlipid granules clearly separates the hemocytes in the pronotal lobe from fat body cells, but (2) the hemocytes are linked to the fat body, and (3) are unusually large. Whatever the genesis of these hemocytes in S. bisonia, the parallels to the loose cells in wings are obvious: the granules, the position in the middle of the lumen and between the epidermal feet, and the presumed mechanism of entering into the lumen by blood pressure during inflation.

In the fully sclerotized pronotal lobe of Stictocephala bisonia, the intercellular space occurring in teneral adults has disappeared. Whether cell membranes dissolve or still exist in the sclerotized lobe, albeit not visible on a light microscopic level, remains an open question. In postecdysial insect wings, the intercellular space disappears (e.g., Weber, '33; Zeller, '38), cells fuse after dissolution of the basement membrane and the lumen either becomes a syncytium or is completely reduced (e.g., Weber, '33).

Gross morphological features of the adult pronotum

The general, external shape of the adult pronotum of Stictocephala bisonia was often portrayed illustrating features such as the metopidium, the dorsum, the suprahumeral horns, the humeral angles, and the posterior process (Marlatt, 1894; Buckton, '03; Branch, '13; Funkhouser, '17; Yothers, '34; Poisson, '37; Kramer, '50; Kopp and Yonke, '77; for the following, see Table 3). The fossae were not previously described or illustrated for S. bisonia but were reported from several other species (Branch, '13; Funkhouser, '17; drawn in: Richter, '54; Wood, '75b; Ahmad and Khan, '79). Supraocular callosities in adults were noticed early in S. bisonia (Funkhouser, '17;
Poisson, '37; Kopp and Yonke, '77) and many other genera (e.g., Fowler, 1894; Buckton, '03; Funkhouser, '17; Capener, '62; Capener, '68). Capener ('62) remarked that "their function is unknown," but in Anchistrotus spp. Boulard ('83) noted that muscles of the forelegs originate at the callosities, as was also found in S. bisonia. Kramer ('50) described the musculature of S. bisonia but neither mentioned nor depicted the callosities. At this point it is uncertain whether muscle origins are confined to the callosities.

The septum was never described in Stictocephala bisonia, but its external traces can be found in figures of S. bisonia (Kopp and Yonke, '77) and of S. diceros (as Ceresa diceros) (Branch, '13). It was first recognized by Buckton ('03) in Hemiptycha punctata, and a similar structure was located in Anchistrotus sp. ("Unterseite des Pronotums"; Rietschel, '87). Possibly, the septum occurs in many treehopper species but was overlooked as in S. bisonia. Other internal substructures are the prothoracic canals containing nerves and tracheae. Similar features, two pairs of internal ridges containing tracheae, were mentioned in Umbonia crassicornis (Wood, '75b). Although some type of accessory pulsatile organs (e.g., Krenn and Pass, '94) may be expected in the membracid pronotum, no membranous canals or layers were found within the prothoracic canal and the median carina of S. bisonia. Nevertheless, a more detailed future investigation may reveal them, possibly in the lateral areas.

As described for Stictocephala bisonia (Kramer, '50) and a generalized membracid (Funkhouser, '17) the prothoracic stigma is located in the intersegmental membrane just anterior to the mesepisternum, a common position in insects (Weber, '33; Snodgrass, '35). Connections from the stigma to the meso- and prothoracic tracheae were found in S. bisonia, but not in Umbonia crassicornis, where an "external opening" in or near the lateral part of the fossa was interpreted as the opening of prothoracic tracheae (Wood, '75b). In S. bisonia, a similar pit represents the external base of the pleural apophysis. Richter ('53) mentioned proximolateral stigmata in several genera. However, their exact position remains obscure, despite later drawings (Richter, '54).

Richter ('53) interpreted the distal pronotum as being transformed prothoracic wings fused along their costal margins to form the median carina. He described "venas" and pronotal areas (e.g., "parte dorsal," "membrana basal") that supposedly correspond to wing veins and wing areas, respectively, but cannot be located despite later figures (e.g., figs. 7–10; Richter, '54). He further assumed that the distal pronotal plate was fixed to the proximate pronotum by muscles, but it seems to have confused the mesonotum with the pronotum (Boulard, '73), because he depicted propleural characters ("ondulaciones y dilataciones pleurales") on the lateral part of the mesonotum (fig. 7, Richter, '54). Boulard's (73) arguments against Richter's hypothesis still hold: median carinae occur in many insects, the only muscles found are those inserting on the occiput and anterior legs, and in nymphs there are no indications for paired buds.

Cuticular canals and sensilla of the pronotal lobe

Because of their abundance and wide distribution, cuticular canals in the external cuticle of the metopidium and dorsum of Stictocephala bisonia are most easily interpreted as ductules of exocrine glands, specifically of class 3 gland cells (Noirot and Quennedey, '74). Apart from the light circles in en face views, no indications for corresponding cell bodies were identified, though. In the pronotum of Umbonia crassicornis, two of three cell types ("large cuboidal cells" and "squamous epithelial cells with elongate nuclei") were regarded as "probable secretory and/or neurosecretory cells" on the basis of similarities in staining properties to neurosecretory cells in a brain (Wood, '75b). This interpretation is questionable, though, because neither the brain nor the similarities were detailed, and an unspecific stain (H&E) was used to demonstrate similarities. These difficulties also weaken the hypothesis that, because pronotal pits are surrounded by those cells "the pits function as chemoreceptors or perhaps as dispersal sites for pheromones" (Wood, '75b). In S. bisonia, pronotal pits are not chemoreceptors and there are no indications that pheromones diffuse through the cuticle of pits whose bases are massive, cuticular columns. As suggested by circumstantial evidence (see above), other species are likely to share these features of S. bisonia.

Setae were noticed early in Stictocephala bisonia (Funkhouser, '17) and many other membracids (e.g., Fairmaire, 1846; Fowler, 1894; Buckton, '03; Branch, '13; Funkhouser, '17; Capener, '62; '68). Marcus ('50) first real-
ized their morphology to be that of sensilla trichodea ("cerda táctil") and documented their innervation in three genera. Pronotal sensilla trichodea in Umbonia crassicornis are innervated, as well (Wood, '75b). Sen-silla campaniformia were not previously described in the Membracidae and sensilla coe-loconica were only found on abdominal tergites (Dietrich, '89).

Males of Stictocephala bisonia have greater sensilla trichodea densities than females. However, in absolute terms males have fewer sensilla than females, because comparing the factor of density increase ("D") with the squared factor of pronotal size decrease (i.e., the correction term, "P") gives $D < P^2$ both for the metopidium $[1.223 < (1.197)^2]$ and for the dorsum $[1.295 < (1.197)^2]$ (data from Table 4); if absolute sensilla numbers were equal between the sexes, the expected relation was $D = P^2$. It cannot be decided at this point whether the observed differences represent sex-specific functions or males achieve the same functions as females with increased sensilla density, tolerating fewer sensilla in absolute terms.

Biological functions of the pronotal lobe

From the various adaptive (e.g., Kirby, 1829; Poulton, '03; Wood, '93) and nonadaptive explanations for pronotal enlargements (e.g., Funkhouser, 21; Strümpel, '72; Boulard, '73), only the mechanical defence and aposematic coloration hypotheses were tested. In captivity studies, mature Umbonia crassicornis were protected from being swallowed by a natural predator (Anolis) mainly due to their acute dorsal horns (Wood, '75a, '77). However, pronota of eight other species were not mechanically protective (Wood, '75a). The conspicuously colored, ten-neral adults of U. crassicornis and Platycotis vittata are unpalatable to Anolis and Anolis learns to avoid this prey, suggesting an aposematic role of the pronotum (Wood, '75a). However, at least in U. crassicornis pronotal coloration did not promote learning to avoid adults (Wood, '77). Possibly, Anolis instead recognizes pronotal shape (Wood, '77). It is likely, but has not been tested, that the pronotum itself contributes to unpalatibility.

A group of adaptive hypotheses refers to pronotal physiology and a critical evaluation of facts and arguments is appropriate. Ac-cordingly, pronotal enlargement is due to selection on the pronotum for increasing surface area, because this would either (i) increase "the amount of directional sensory input" (Wood and Morris, '74; Wood, '93) or (ii) "facilitate dispersal of volatiles" (Wood, '93). Various sensory functions were proposed (Marcus, '50; Wood, '75b, '93), e.g., "the detection of odor, air currents, or airborne sound" (Wood and Morris, '74). These functions could mediate intraspecific communication (Wood, '75b), e.g., when males touch the female's pronotum during precopulatory behavior (Wood, '93).

In a narrow sense, these hypotheses potentially could explain pronotal size, but not shape (Strümpel, '83), because the same surface area may be achieved by many shapes. However, additional hypotheses on how shape affects perception or pheromone dispersal could be proposed. Although it is true that the pronotal lobe is a living tissue and most probably its components have special functions, it is not self-evident to postulate any of these functions as one or the main adaptive reasons for past or current evolution of the lobe. Reversing the argument is just as plausible. Sensilla may occur, because sensory input from an already large and exposed pronotum is no less vital than it is from other sclerites. Similarly, pheromonal glands may occur in the pronotum simply because it is more exposed than many other sclerites. Thus, physiological functions, by themselves, neither exclude (other) adaptive hypotheses of pronotal evolution nor non-adaptive explanations such as correlated re-sponse to increasing body size (e.g., Strümpel, '72; Boulard, '73).

While sensilla occur in many species, so far there is no evidence for pheromone glands within the pronotal lobe, a prerequisite for the pheromone dispersal hypothesis. Cells found in the pronotum of Umbonia crassicornis (Wood, '75b) are not necessarily gland cells (see above), and if they are, they might not produce pheromones. As dermal glands they may well be involved in cuticle formation (Chapman, '82). Moreover, there is no evidence for pheromones as a regular means of communication between living individuals or as a means of defense. Sex phero-mones are not known in membracids (Wood, '93) and alarm pheromones were released only after deadly ruptures of the body wall (Nault et al., '74; Wood, '76). Finally, intra-specific communication, a central target of surface hypotheses, was shown to be mediated by vibrational signals (Strübing, '92;
Hunt, '93; Cocroft, '96). It is likely, but unknown, whether other sensory modes are involved (e.g., Hunt, '93).

In summary, while the mechanical defence hypothesis was supported in one species, the aposematic coloration hypothesis was not and whether the physiological functions of the pronotal lobe are (part of) its adaptive causes is just as likely. Conclusions at the highest explanatory level, i.e., adaptive versus nonadaptive hypotheses, could be drawn from tests of nonadaptive hypotheses, for example, by deriving and testing central predictions such as genetic correlations.

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