SOUND PRODUCTION BY AQUATIC INSECTS

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(Received 12 April 1984, accepted 8 November 1984)

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I. INTRODUCTION

Air-borne sounds emanating from every nook and cranny of ponds and lakes on summer evenings are familiar to almost everyone. Birds, amphibians and insects all contribute to this cacaphony. The existence of similar acoustic activity below the water’s surface, however, is less appreciated and sound producing capability in aquatic insects comes as a surprise to even experienced biologists. Because their habitat is relatively
inaccessible to direct observation and because few entomologists possess the requisite recording equipment, the singing of aquatic insects has remained relatively unexplored.

In this review, I include those aquatic insects that produce sound while submerged. Consequently, surface dwelling insects (Gyrinidae, Gerridae, Veliidae) are excluded, even though gerrids communicate by surface waves (Wilcox, 1972, 1979) and veliids stridulate (Andersen, 1982; Distant, 1910; Hungerford, 1929; Poisson, 1951). This distinction divides the insects by both habitat and type of wave produced. Surface dwelling animals generate transverse waves, whose particle motion is perpendicular to the direction of propagation. Such waves cannot propagate within most liquids or any gas (Tucker & Gazey, 1966) but are important in substrate signalling (Bell, 1980). Submerged animals produce longitudinal waves, whose particle motion is parallel to the direction of propagation.

Dumortier (1963) lists five general methods of sound production by invertebrates: (1) friction of differentiated parts, (2) expulsion of a fluid (gas or liquid), (3) vibration of membranes, (4) shocks to the substrate and (5) vibration of appendages.

Sound production by aquatic insects is by either of the first two methods but overwhelmingly by friction of differentiated parts or stridulation. Stridulation is the physical interaction of any two hard parts of the body that results in propagation of a longitudinal wave and is always accomplished by rubbing of a plectrum (or scraper) across a differentiated region of the body – the pars stridens (or file). As Dumortier points out, these distinctions can be artificial or impossible to make. In instances where the two parts of the apparatus are similar or identical or both parts move equally, the distinction becomes arbitrary.

Sound production in aquatic insects is confined to four orders – Trichoptera, Odonata (Anisozygoptera), Coleoptera and Heteroptera – but, especially in the bugs and beetles, occurs widely. In this paper, I will review, by order, documented methods of sound production and contexts in which they are known to occur. I will then discuss the evolutionary pressures that have affected the form of signals and the structures and contexts in which acoustic signals are used by aquatic insects.*

II. SOUND PRODUCTION BY IMMATURE AQUATIC INSECTS

(1) Trichoptera

Sound production by larval hydropsychids is receiving increasing attention. Ross (1944) described a 'stridulator' at the base of the forelegs in two species (Hydropsyche cheilonis Ross and Smicridea fascicella McLachlan) (Fig. 1). Johnstone (1964), demonstrating that Ross’ stridulator is not positioned to function as a scraper (plectrum), showed that the actual mechanism involves a scraper on the prothoracic femur and a file on the underside of the head (Fig. 1).

The scraper consists of a prominent, dorsally oriented ridge with a smaller ridge anterior to it and up to six small ridges posterior (Jansson & Vuoristo, 1979; Johnstone, 1964; Silver, 1980). All ridges are oriented at 45° to the longitudinal axis of the foreleg (Jansson & Vuoristo, 1979). The scraper is present in third instars but is used in stridulation only by fifth instar larvae (Silver, 1980). The files are a paired series of

* Literature search for this review was completed in December, 1983.
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60–75 parallel striations on the underside of the head and differ little among species (Jansson & Vuoristo, 1979).

Hydropsychid larvae construct funnel-shaped nets for food capture. Stridulation occurs when a larva is in its net with its forelegs anchored in the strands. Such support is apparently necessary for stridulation (Jansson, 1979d). Johnstone (1964) claimed that freely moving larvae would stridulate but Jansson & Vuoristo (1979) were unable to substantiate this. Larvae stridulate by drawing the head back, placing the scrapers on the file and then thrusting the head forward (Jansson & Vuoristo, 1979). Both files are involved in a single, stridulatory movement and consequently the sound has no recognizable pulse structure (Jansson, 1979d).

Each stridulatory movement produces a burst of sound and, occasionally, secondary bursts of sound are caused by the file contacting the plectrum as the head is drawn backward (Jansson & Vuoristo, 1979). Each burst of sound lasts about 0.1 s and a bout of stridulation consists of from 1 to 6 bursts of sound (Jansson & Vuoristo, 1979; Silver, 1980).

There is considerable disparity in reported frequencies of hydropsychid sounds. Jansson & Vuoristo (1979) found frequencies extending to 10 kHz with principal frequencies between 0 and 4 kHz while Silver (1980) showed frequencies extending well into the ultrasonic range (up to 110 kHz) in the same species. Silver's results are remarkable for they constitute the first record of ultrasound production by any aquatic insect. Differences in recording technique between the two studies, while leading to Silver's discovery, make it difficult to comment on this disparity of recorded frequencies. Silver's use of a 6.4 kHz filter is unfortunate for it attenuated the very frequencies Jansson & Vuoristo (1979) found to predominate.

Silver attributed ultrasonic frequencies to size of the insect (smaller insects producing higher frequencies) and nature of the stridulatory apparatus. Both explanations are
dubious. Wiggins (1977) cited sizes of hydropsychid larvae ranging from 9.5 to 30 cm, which is larger than many aquatic insect adults, none of which have frequency spectra extending into the ultrasonic even though several (Aiken, 1982a, Jansson, 1973a, 1976; Jansson & Vuoristo, 1979) were recorded and analysed with equipment that would have detected such frequencies.

Stridulation is part of an agonistic interaction between larvae (Jansson & Vuoristo, 1979). Hydropsychid larvae build nets facing upstream that act as passive food filters. Larvae without nets (for whatever reason) crawl over the substrate, attempting to displace resident net-holders. Residents probably detect intruders by substrate vibrations transmitted through the net. The resident lunges and attempts to grapple with, bite and shake the intruder. If this does not repel the intruder, the resident retreats into the net and stridulates. Stridulation was observed at 41% of 1485 staged encounters and, in most (86.7%), only the resident stridulated. Intruders only stridulated when in the net and stridulation is thus a behavioural component of defense and not intrusion (Jansson & Vuoristo, 1979). Jansson & Vuoristo (1979) were able to show that defenders that did stridulate were significantly more successful as defenders.

Three questions arise from this study. First, why do animals fight before stridulating? In other studies of insect aggression and stridulation (e.g. Morris, 1967, 1971), stridulation preceded fighting and appeared to be a mechanism for potential combatants to assess each other’s fighting ability and thus avoid the costs inherent in fighting. Secondly, is it water-borne sound waves or substrate transmitted vibrations in the net that are important? Silver (1980) speculated that near-field displacements (see below) are important but did not consider substrate signals. Finally, what is the direct function of stridulation as a part of aggressive behaviour? Although Johnstone (1964) and Hawkins & Johnstone (1978) have speculated that it could repel predators, a role in aggressive behaviour seems more realistic. The proximate cause is repulsion of an intruder but what, ultimately, are the animals fighting over? Authors have suggested a role in density regulation (Johnstone, 1964; Mackay & Wiggins, 1979) or territorially (Johnstone, 1964; Silver, 1980).

If sound were to advertise territorial limits, then it should, like other territorial displays, either be given at regular intervals without any obvious external stimulation or at least be given at the beginning of an interaction rather than part way through it as Jansson & Vuoristo (1979) observed.

Aggressive behaviour having effects in density regulation (Mackay & Wiggins, 1979) is more reasonable. It would seem though that such aggressive interactions are a result of high density rather than a regulator of it. The number of sites available for net construction would depend more on surface area and topography of available substrate. Once nets are placed in all available sites, aggressive interactions would simply decide which animal occupies a site. Obviously more data are needed on incidences of aggression and stridulation as related to density. Even Jansson & Vuoristo (1979) admitted that their study shows little about any direct effect of stridulation in density regulation.

Sound production is obviously more widespread in the Hydropsychidae than presently documented. Members of all twelve North American genera possess both components of the stridulatory mechanism which those of no other family of Trichoptera appear to possess (Wiggins, 1977).
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Fig. 2. Dorso-lateral view of stridulatory file on tergites of abdominal segments 3 through 6 (ps3-ps6) of nymphs of *Epiophlebia superstes* Selys (Odonata). (After Asahina, 1954.)

(2) Coleoptera

Mukerji (1929) reported that a *Cybister confusus* Sharp (Dytiscidae) larva produced a "squeaking sound" accompanied by "muscular jerks" when removed from water or otherwise disturbed. The sound, described as being of short duration and intense, is produced by expulsion of air from the mesothoracic spiracles. This sound would seem to function in dissuading predators of which dytiscid larvae have a number (Balduf, 1935).

Allen (1956) reported that, upon disturbance, a *Hydrolinus piceus* L. larva (Hydrophilidae) arches its body, throws its head back over its thorax and produces a sharp hiss. Allen surmised that the hiss is incidental to body motion.

(3) Odonata

Asahina (1938, 1939, 1954) described sound production in larval odonates. A series of elevated dorso-ventrally oriented ridges are present on abdominal segments 3–7 in larval *Epiophlebia superstes* Selys (Anisostygoptera) (Fig. 2). These ridges are first evident in the sixth instar before eclosion and are fully developed in the penultimate instar. The metafemur has minute serrations that are adpressed to the abdomen and held stationary. The abdomen is then twisted or telescoped about the longitudinal axis of the body. In laboratory experiments, sound was produced in response to any mechanical disturbance of the animal. Asahina (1950) noted that stridulation was part of a behaviour sequence involving death feigning and may represent the nymph's last line of defence against a predator.
II. SOUND PRODUCTION BY AQUATIC INSECT ADULTS

(a) Nepidae

Stridulation has been documented only in members of the genus Ranatra. Kirkaldy (1906) claimed that both adults and nymphs stridulate but this has not been confirmed. Swinton (1877, 1880) described a supposed pronotum–mesonotum stridulatory device (see Naucoridae) for Nepa cinerea L. that was discounted by Handlirsch (1900a). Lauck (1959), Torre-Bueno (1903, 1905) and Hungerford (1919, 1922) described a roughened patch at the base of each fore coxa that is rubbed over a file on the femur of the corresponding prothoracic leg (Figs. 3 A, B). The forelegs are held directly in front of the body and at a slight angle to its longitudinal axis (Torre-Bueno, 1903). In this position, the legs contact the coxae. Torre-Bueno (1905) speculated that the coxae act as sounding boards and described the sound as a “raspy creaking chirp”.

When an animal appears to be stridulating the sound is not always audible but vibrations can be felt through its body (Torre-Bueno, 1903). Hungerford (1919) noted that the animal had to be held up to the ear in order that the sound be heard.
Wesenburg-Lund (1943) reported that stridulatory structures were absent in European Ranattra species.

(b) Pleidae

In the only account of stridulation in Pleidae, Wefelscheid (1912) noted a noise resembling “a slight rubbing over a fine file” in Plea minutissima F. and discovered, in both sexes, a striated area on the mesothorax between the sternite and subcoxal plate that was met by a projection from the prothorax (Fig. 4). The prothoracic projection rubbed on the striated area as a result of a nodding motion of the head (cf. Hydraenidae).

Wefelscheid (1912) could ascribe no function to pleid stridulation. Since sound was heard only when a number of animals were confined together, he speculated that it could function in joining isolated adults with groups of conspecifics. Although his speculation is interesting, a clear distinction must be made between cause and effect. While it may be true that, as in some Corixidae (Aiken, 1980, 1982b), groups of singing Plea attract conspecifics, interactions within the group may be responsible for sound production.

(c) Naucoridae

Naucoris cimicoides L. was the first aquatic insect for which sound production was described. Frisch (1740) noted that “males can produce a violin sound with the nape of the neck...” and Swinton (1877, 1880) described a series of mesonotal striations (‘limae’) in N. cimicoides rubbed by the overlapping pronotum. Such an interaction produced a sound like ‘the scratching of a needle-point’. Handlirsch (1900a) reviewed Swinton’s work and, unable to find any limae, denounced it as “outpourings of inflamed fantasy” and dubbed the device a “Swintonophone”.

Handlirsch supposed that the hind edges of the fifth and sixth abdominal tergites would be rubbed over grooved areas on the fore edges of the sixth and seventh tergites
A. R. Aiken

Fig. 6, A. Left foreleg of Buenoa margaritacea Bueno showing three pairs of proposed stridulatory structures. (1) ps1, tibial comb; (2) ps2, femoral file and pl2, coxal peg and (3) ps3, femoral setae rubbed on a rostral flange. (After Bare, 1925.) B. Detail of rostral prong (pl1) contacted by the tibia comb (Fig. 6 A, ps1). (After Bare, 1928.)

respectively (Fig. 5A). This structure appears only in males. Hofeneder (1937) raised doubts that the device described by Handlirsch is stridulatory. He found even more pronounced ridges on the second abdominal tergite that could be rubbed by the hind margin of the first (Fig. 5B). Hofeneder cast some doubt on even this structure, stating that it is too variable in males (he studied two) to be a reliable stridulatory structure. Since Hofeneder (1937) there appears to have been no more original work done on sound production by naucorids.

(d) Belostomatidae

Harvey (1906, 1907), noting a "soft chirping" when an Abedus (= Pedinocoris) bug came to the surface, stated that sound was produced by expulsion of air through the ventral spiracles that contracted and relaxed coincident with each burst of sound. A "wheezing noise" accompanied by a "fishy odor" was described by Hungerford (1925) for adults of Benacus griseus Say.

Smith (in litt.) has discovered a buzzing sound produced by male Abedus herberti Hidalgo during 'display pumping' (see Smith, 1979). This buzzing sound was always produced during courtship and females responded, on occasion, with a less intense buzz. Smith did not hear the sound from isolated animals. Unfortunately, he was unable to discover a stridulatory mechanism.

(e) Notonectidae

Among Notonectidae, only members of the genera Buenoa (New World) and Anisops (Old World) in the subfamily Anisopinae can stridulate (Hungerford, 1933). None of the other known genera possess stridulatory apparatus.
The first record of stridulatory apparatus in notonectids is that of Swinton (1880) in which the ubiquitous 'limae' were invoked as the stridulatory apparatus in *Notonecta glauca* L. Handlirsch's (1900a) objections have been outlined (see Naucoridae). Swinton never heard *N. glauca* stridulate but produced sound by forcing a projection of the prothorax over the mesonotum.

Stridulatory apparatus of *Buenoa* is complex. Hungerford (1924) described the stridulatory structures on the inner surfaces of the fore femora and tibiae and at the base of the beak. Sound was correlated with simultaneous movements of the femora and tibiae over the beak. Three separate pairs of stridulating structures appear in *Buenoa* (Figs 6A, B) (Bare, 1925, 1926, 1928; Goertz, 1963; Hungerford, 1917, 1919; Lauck, 1959; Truxal, 1953; Wilcox, 1969, 1975).

1. The first is an elevated comb that rests on a thickened area at the base of the fore tibia (Fig. 6A, ps1). This comb is drawn over a striated projection of the third segment of the rostrum (rostal prong) (Fig. 6B, p/1).

2. The second is a series of parallel ridges on the inner face of the fore femur (Fig. 6A, ps2) that are struck by a peg on the lateral surface of the corresponding coxa (Fig. 6A, pl2).

3. The third apparatus is a thickened area at the distal end of the fore femur lined with heavy setae (Fig. 6A, pl3). These are thought to be rubbed over a flange at the base of the rostrum.

The simultaneous existence of more than one stridulatory structure in one animal is unique although the work of Wilcox (1975) suggests that all structures listed above may not be used in stridulation. In a series of experiments, Wilcox was able to inhibit the production of all types of calls by ablating only the tibial comb/rostral prong (no. 1) and femur/coxal peg (no. 2) mechanisms (Fig. 7). Hence, there is no evidence that the femoral setae/rostal flange mechanism (no. 3) is used in stridulation. Each set of structures appears to be used in the production of different calls (Poisson, 1951; Wilcox, 1969, 1975). Wilcox (1975) experiments showed that the tibial comb-rostral prong mechanism was involved in producing trills, chirps and dart-chirps and the femur-coxal peg in producing grasping-chirps and cleaning chirps (see below for descriptions of call types).

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*Redfern's (1859) reference to notonectid stridulation refers to a corixid (cf. Larsen (1938)).*
Stridulatory structures of *Anisops* are simpler than those of *Buenoa*. Hale (1923a) described only the tibial comb-rostral prong mechanism for males (Fig. 8) and specifically stated that there are no femoral mechanisms. Males of most *Anisops* species examined appear to possess well-developed tibial combs (Brooks, 1951; Hutchinson, 1929, 1930; Lundblad, 1934). Poisson (1926) accurately described the tibial combs but erred in assuming that the plectrum was a pair of club-shaped spines on the contralateral femur.

Calls produced by *Buenoa* males have been described on numerous occasions. Hungerford (1924) described the sound as resembling a ticking watch. Goertz (1963) presented the first audiospectrographic analysis and coined the terms chirp, twirr, and buzz for the various calls of *Buenoa macrotibialis* Hungerford. The chirp is a single pulse of sound repeated three times, ranging in frequency from 3 to 7 kHz and lasting about 0.033 s. The twirr lasts 1.7 s and has a frequency range of 2.5–3.5 kHz. The buzz has a range of 0.85–4.0 kHz and lasts 0.81 s.

Goertz' (1963) records of frequency are inaccurate. To record, she suspended a microphone above the water surface, introducing a filtering bias at the air–water interface. Frequency spectra in Wilcox's (1969) analysis of calls of nine species of *Buenoa* are more reliable. He recorded with a hydrophone, thereby escaping Goertz's methodological problems.

Wilcox (1969) recognized seven calls in *Buenoa macrotibialis*. His designations may be superfluous in terms of call types in that he recognized four additional types of chirp (grasp, disturbance, cleaning and capture) based on context. His audiospectrographic analyses of capture-chirp, disturbance-chirp and grasping-chirp indicate that the three are, in effect, the same call used in different contexts.
Songs of Buenoa are used in courtship and mating. Several authors (Goertz, 1963; Hungerford, 1924; Wilcox, 1969) have described the courtship of Buenoa and, while differences between species exist (see Wilcox, 1969), the general courtship pattern is as follows. Terms are those of Wilcox (1969).

Males trill (= twirr (Goertz, 1963)) and chirp spontaneously while swimming. Upon encountering a female, a male continues to maintain a fixed orientation to her. The male then dives rapidly in an arc either above or below the female, giving a third signal—the dart-chirp (= buzz dive (Goertz, 1963)). This dive usually places the male below the female. From this position, the male then flutters the swimming legs and swims forward up to the female and grasps her, giving a fourth signal—the grasping chirp (Wilcox, 1969). Goertz (1963) describes this sequence as a feather dive.

Goertz divided the courtship of B. macrotibialis into four phases. Wilcox (1969) adopts Goertz’ phase terms but added three more phases that take into account the sequence of events occurring when a male fails to maintain proper orientation to the female or is unsuccessful in a mating attempt.

When females are grasped by males they may swim violently in tight circles (pinwheeling (Wilcox, 1969)) and shake the abdomen to dislodge the male, pinwheel without shaking the abdomen or remain quiescent. The latter two responses result in copulation.

Acoustic behaviour of Anisops has not received as much attention as that of Buenoa but has been consistently associated with mating (Hale, 1923a, b; Leong, 1962). Hale (1923a, b) described the stridulations of A. hyperion Kirkaldy as resembling the sound of a “distant grindstone”. While stridulating, males hold the forelegs close to the body and rapidly move the tibiae over the rostral prong. Hale (1923a) described the sound as beginning with “a rapid series of squeaky notes” that increased in intensity until they become a “shrill and loud chirrup”. Leong (1962) described the song as “high-pitched with short intervals of silence”, audible up to 5 m away.

During courtship, males stay below and behind females, constantly stridulating and make mounting attempts from below. The courtship pattern appears to be similar to that of Buenoa males and, in a general way, to that of non-singing notonectids (Clark, 1928).

In males of both Buenoa (Goertz, 1963) and Anisops species (Hale, 1923a), chirping occurs during the mating season with or without the presence of other animals (Goertz, 1963). Although this observation, together with the assertion of Wilcox (1969) that chirps function in a calling context, suggests a rhetoric signalling role (Morris, 1980), such is not likely since these calls travel only short distances (Aiken, 1982c). The effect of chirping on females seems to be to increase swimming activity (Goertz, 1963; Wilcox, 1969) that would serve to increase chances of encountering a male. This corresponds with Schaller's (1951a) assertion for the Corixidae.

(f) Corixidae

Among aquatic insects, acoustic behaviour of corixids is best documented. Of the six subfamilies (Cymatiinae, Stenocorixinae, Heterocorixinae, Diaprepocorinae, Micronectinae and Corixinae (Hungerford, 1948), stridulation has been confirmed in only the Micronectinae and Corixinae (Hungerford, 1948), and presumed to occur in the Diaprepocorinae and Cymatiinae.
Fig. 9. A, Dorsal view of abdomen of *Diaprepocoris zealandiae* Hale showing position of stridulatory device (str) on sixth abdominal segment. B, Detail of stridulatory device of *D. zealandiae*. File (ps) and scraper (pl) having been arbitrarily assigned. (After Jaczewski, 1939.)

(i) *Diaprepocorinae*. Several authors (Hale, 1922; Jaczewski, 1939; Knowles, 1974; Young, 1962) have shown a paired structure on the dorsal surface of the sixth abdominal segment (Fig. 9A) resembling a pair of tongs of which only one part is moveable. Opposing patches of minute pegs presumably meet (Fig. 9B) as the moveable element passes the stationary one in a scissor-like fashion. Only Hale (1922) and Young (1962) have specifically stated that this is a stridulatory structure, although I can find no record of *Diaprepocoris* bugs actually generating sound.

(ii) *Cymatiinae*. Hutchinson (cited in Butler, 1923 (p. 601)) described the singing of *Cymatia coleoptrata* F. as a “short, sharp scrape” and he and Poisson (1935) describe the stridulatory apparatus as being the pala and opposite femur. Butler (1923) observed that each femur of this bug has a number of minute pegs on its inner face. Poisson (1935) commented that males of *C. coleoptrata* strike palar pegs on the opposite femur, a difficult feat considering that these bugs have long bristles instead of palar pegs.

Any role for sound production in *Cymatia* is unknown. Walton (1943), in a discussion of mating in *C. bonsdorfi* Sahlb., does not mention stridulation.

(iii) *Micronectinae*. The stridulatory apparatus of male micronectines has also been a puzzle. Handlirsch (1900a), the first worker to carefully analyse the group, surmised that the strigil, a rigid projection on the tergum of the sixth abdominal segment, rubbed across the edges of the hemelytra. Mitis (1936), too, thought that the strigil was involved and speculated that the other half of the apparatus might be the aedeagus or right paramere. Walton (1938) also favoured the strigil as the pars stridens, noting that it was amply supplied with muscles and could be rubbed against an overlapping lobe of the fifth tergite. In addition, however, he noted that the “spiny aedeagus” could be rubbed on “irregularities” of the eighth segment. This notion has been repeated by other authors (Haskell, 1961; Leston & Pringle, 1963). King (1976) maintained that the strigil is rubbed over the posterior edge of the fifth abdominal segment in male *Micronecta batilla* Hale.

The strigil has not met with universal acceptance as the stridulatory apparatus of
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micronectines. Walton (1938) stated that either the strigil or eighth segment and paramere could be involved, while Jansson (pers. comm.) and Wroblewski (in litt.) believe that striations on the right paramere are rubbed over a ribbed area on the margin of the eighth segment. Striations on the paramere have been found in several African (Hutchinson, 1932) and Australian and Asian (Chen, 1965; Wroblewski, 1970, 1972, 1977) species.

Recently, Bailey (1983), following Walton’s (1938) suggestions, has contributed the most plausible explanation of the mechanics of micronectine stridulation. As in all male corixids, the eighth abdominal tergite is divided. Bailey (1983) described a concavity in the right tergite as fitting into a convexity in the left. The left tergite bears a plectrum—a ‘thickened lip’ on the median edge. The pars stridens is a series of rows of small pegs lining the inner face of the right tergite. The teeth are sloped so they will slide smoothly past the plectrum on the return stroke. Sound is produced as the insect shakes the abdomen laterally, the medial-to-lateral stroke producing the sound.

Bruyant (1894) mentioned a single “monotonous, non-metallic sound” from *M. minutissima* L. that was extremely loud. Both he and King (1976) were able to locate animals in a pond by listening from the shore and Jansson (1976b) used male signals to locate individuals in low density populations. Mitis (1936) also described the sound as a loud chirp.

King (1976) described three types of calls by males of *M. batilla*—chirp, click and chatter. All have the same frequency range (5–10 kHz) with a peak at about 8 kHz. The calls differ in intensity and temporal patterning. His sonograph for *M. australiensis* Chen is remarkable because it shows these bugs can frequency modulate, i.e. change the frequency within a call element. He described the call as “bird-like”. Bailey (1983) recorded a peak frequency in male *M. batilla* of 15 kHz. Jansson (1977a) recorded male signals of three *Micronecta* species (*griseola* Horvath, *minutissima* and *poweri* Douglas & Scott) and found all calls to be species specific with differences in temporal patterning of rapidly repeated pulses that were detectible with the human ear. Dominant frequencies were between 10 and 11 kHz.

The role of sound production in micronectines has not been directly established but circumstantial evidence argues strongly for one in courtship and mating. Fernando & Leong (1964) noted that male *M. quadristrigata* Bredd. stridulated at any time of day and that the stridulation was associated with mating. When the peak of mating passed, the incidence of stridulation decreased (Leong, 1961). Wroblewski (1958) observed that *Micronecta* adults exhibited a tendency to aggregate but Jansson (1977b) did not think that acoustic signals need be invoked since nymphs also aggregate. The role of signalling in aggregation of corixids is discussed more fully below (see Corixinae).

(iv) Corixinae—Corixini. Acoustic capabilities of corixines have received more attention than those of any other group of aquatic insects. For several years after Ball’s (1845, 1846) first description (see Hutchinson, 1982) of the sound of a singing corixid as a “loud and powerful sound somewhat like that of a cricket. audible in an adjoining room through a closed door”, there was considerable controversy over the method of stridulation.

At the root of this controversy is the structure of the corixine head and fore limb. In singing bugs, Ball (1845) noted movement of the forelegs over the rostral area. In this area of the body, four structures are potentially stridulatory; rostral striations, edge
of the head (plectrum), palar pegs and a peg field on the fore femur. Suggested mechanisms have included three combinations of these four elements: (1) palar pegs across rostral striations (Ball, 1845, 1846; Carpenter, 1894; Hagemann, 1910, 1916; Handlirsch, 1900a, b; Jordan, 1925; Landois, 1874; Nichols, 1895; Poisson, 1927, 1935; Prochnow, 1907; Schmidt Schwedt, 1891), (2) palar pegs on the opposite femoral peg field (Hale, 1922); Kirkaldy, 1901a, b) and (3) palar pegs across the edge of the head (Robertson, 1895). Involvement of rostral striations has been dismissed by Hsü (1937) on the grounds that the rostrum was too highly innervated and delicate to withstand interaction with the palar pegs. Furth et al. (1978), Larsen (1938), Popham (1961a) and Reichenbach-Klinke (1949) have shown that palar pegs are used to grasp the hemelytra of the female during copulation. Indeed, their size and shape could function as a reproductive isolating mechanism (Furth et al., 1978).

Mitis (1936) was the first to correctly elucidate the mechanism of sound production in corixines. A peg field on the fore femur (Fig. 10) is pushed anteriorly across a slightly thickened flange on the maxillary plate. Jansson (1972), in the most complete study of sound production mechanisms in Corixidae, substantiated the findings of Mitis (1936).

Scanning electron micrographs of adults of several species (Aiken, 1980, 1982a; Jansson, 1972, 1979b, c) show individual pegs to be broad at the base and to taper distally and the pegs of males to be sturdier than those of females. The tapered end of the peg strikes the plectrum first. Aiken (1982a) argued that as individual pegs in the femoral field move past the plectrum they catch and are bent backwards (i.e. proximally) storing kinetic energy in both the plectrum and peg. At some point, the energy stored in the peg is greater than the resistance between the peg and plectrum and the peg slips past the plectrum, driving the head into oscillation.

Finke (1968) claimed that the legs were moved synchronously or in alternation depending on the song type but Theiss, Prager & Streng (1983) and Jansson (1979c) have since disputed this claim. Theiss (1981) maintained that certain song elements can be produced by the legs moving alternately or by use of one leg only.

Working primarily with Corixa dentipes Thms., Theiss et al. (1983) have added important details to the mechanism of corixid stridulation. They report that the legs are moved asynchronously at different rates during the production of even the most simple songs. There is no predictability as to which leg would move fastest during a particular singing bout. For other songs, the legs move alternately. In all instances, one downward (or forward) stroke produces a single train of pulses (cf. Aiken, 1982a).
Jansson (1972) was not sure whether the pegs or maxillary plate radiate sound. Since male and female calls had similar frequencies produced with substantially different sized pegs, Aiken (1982a) proposed that the head was involved in sound radiation. This proposal has recently been substantiated (Theiss et al., 1983). Schulze (1977) and Theiss (1982) have shown that the head and ventral air store of corixines are coupled to produce a sound radiating system. The resonant frequency of an air bubble of the same volume as that carried by a corixid is similar to the carrier frequency of corixid songs. Furthermore, Theiss showed an increase in frequency as the air store was depleted and as the volume of the bubble decreased.

In addition to the above, other mechanisms, not involving the head or fore limbs have been proposed. Ball (1845) observed a rapid shaking of the abdomen in Corixia striata L. when the second of two sounds he heard in that species was produced. Following this observation, Handlirsch (1900b) proposed that the strigil, a striated plate attached to the sixth tergite was rubbed across the edge of the hemelytra as the abdomen was moved laterally. Other authors have disputed this claim (Hagemann, 1910) since corixids without strigils can still sing. Moore (1961) noted a "shuffling noise" in Hesperocorixa atopodonta Hungerford and Sigara grosselineata Sahlb. males that was correlated with a rubbing of the metathoracic tibiae and tarsi above the hemelytra. These movements, however, are grooming activity and the associated sound incidental. Prochnow (1907) reported a "buzzing" sound from male Corixa geoffroyi Leach that he imagined to result from the elytral tips striking each other. From his description, it appears that this sound is incidental to preparation for flight.

Characterization of corixid songs, like that of other aquatic insects, went through a protracted stage of phonetics and analogy. Songs have been described as sounding like a comb passed over a thin plate (Bruyant, 1894), "distant crickets" (Hungerford, 1919), the striking of a knife on the edge of a pot (Hagemann, 1910; Poisson, 1935) and the "imperfect pronunciation of the letters 'chew' three times in succession" (Redfern, 1859). Several authors have identified more than one call from various species. Ball (1845, 1846) noted that the sounds resemble the "grinding of a knife" and a "brisk little chirp" and Thompson (1894) described the sounds as being "acute and shrill" and "like the twittering of a bird". Mitis (1936), Schaller (1951a, b) and Finke (1968) have described a grinding sound and a chirp.

In spite of the lack of technical sophistication in such characterizations, they did contain valuable clues as to the important communicative parameters. Leston's (1955) phonetic description of calls of several species most clearly indicates that major interspecific differences appeared in temporal patterning and amplitude modulation. The supplanting of phonetic description of corixid calls with more sophisticated electronic recording and analysis techniques has verified this. Finke (1968), Jansson (1973a, 1974b, 1976a, 1979a), Aiken (1980, 1982a) and Theiss et al (1983) have all reported that interspecific variation in calls is in temporal patterning and amplitude modulation and Jansson (1976a) has detected such differences in conspecifics from different populations. Theiss et al. (1983) have discovered that such differences are produced by different rates and patterning of leg motions and by changing the angle of attack of the pars stridens against the plectrum.

Corixid sound production follows both daily and annual cycles. A singing peak seems to occur in early evening (Ball, 1845; Carpenter, 1894; Jordan, 1925; Leston, 1955,
Mitis, 1936; Schaller, 1951a, b; Schmidt Schwedt, 1891; Thompson, 1894). Jansson (1968) reported the strongest component determining diel periodicity of singing to be light level. In a subsequent study (Jansson, 1973b), he found that different species in the genus Cenocorixa had different peak singing periods.

Observations that corixids sing mainly in spring and summer months (Ball, 1845; Fernando & Leong, 1964; Jansson, 1974a; Mitis, 1936, Schaller, 1951a, b) led to the supposition that calls were related to courtship and mating (Hagemann, 1910; Larsen, 1938; Mitis, 1936; Schaller, 1951a). This idea is further supported by close correlation between onset of male sexual maturity and stridulation (Jansson, 1974a).

Sound production is a component of the reproductive behaviour of corixines but its importance and precise role are not clear. Difficulties arise from a lack of data about context of calls and phonetic descriptions of calls that makes comparison between calls described in different studies difficult. Nine functions have been proposed for corixid calls: territory maintenance (Leston & Pringle, 1963; Jansson, 1979a), long distance attraction of females (Jansson, 1979b, c), aggression (Aiken, 1982a; Jansson, 1973a; Leston & Pringle, 1963), female agreement to mate (Aiken, 1980, 1982a; Jansson, 1973a), courtship (Aiken, 1982a; Jansson, 1973a), mounting (Aiken, 1982a; Jansson, 1975) and copulatory (Aiken, 1982a). Some functions, however, can be eliminated.

Several workers (Leston & Pringle, 1963; Jansson, 1979a, c) have claimed that songs could be used in maintaining territories. Aiken (1980, 1982a), however, found no evidence of territoriality in male Palmacorixa nana Walley even if territory is defined broadly as occurring when animals are "dispersed more than would be expected from a random occupation of suitable habitats" (Davies, 1978). Aiken (1982b) found that males tended to be underdispersed in suitable habitat.

Although apparently not territorial, males used stridulation agonistically (Leston & Pringle, 1963; Jansson, 1973a, 1979a). Jansson (1973a) showed that stridulation partially replaced physical contact in Cenocorixa males and suggested that it served to maintain some individual distance between males. The synchronized singing reported for some European species (Mitis, 1936; Schaller, 1951a; Finke, 1968) and convincingly demonstrated by Finke & Prager (1980) for Sigara striata may be the same type of male-male interaction.

Apparently acoustic signals do not act as long range (several metres) attractants and, experimentally, prove to be poor phonotactic models. Aiken (1982c) has demonstrated that in shallow water, the songs of these animals are transmitted less than 1 m. Neither Finke (1968) nor Schaller (1951a) could elicit phonotaxis by females to male song. Although Jansson (1979b, c) has maintained that songs could attract females over long distances, there has not been a published study in which corixid females exhibited phonotactic behaviour. Behavioural measures of female responsiveness other than phonotaxis to signals of males have been used. Finke (1968) and Schaller (1951a) noted increased rates of and changes in modes of swimming and Jansson (1973a, 1976a, 1979a, b, c) the production of a female answer signal. Aiken (1980, 1982b) measured changes in rate of swimming of females (phonokinesis).

Most research into the biological significance of corixid sounds has centred on their role in reproductive isolation and effects on females. Jansson (1973a) studied the role of acoustic signals as a premating isolating mechanism in members of the genus Cenocorixa. As with other corixines, calls of different Cenocorixa species are differentiated by the temporal patterning and amplitude modulation of various call elements. Sexually
receptive *Cenocorixa* females respond to male courtship signals with an answering call. Jansson reported that females most frequently answered courtship calls that most closely resembled those of their own species' males. In another study, Jansson (1979b) found that *Arctocorisa carinata* Sahlb. males could be duped into mounting *A. germari* Fieber females if the *germari* answer signal were played. Recently, Theiss (1983) found that an exchange of signals between the sexes is necessary for mating in *Corixa dentipes*.

Other workers, however, have found that such responses from females are not necessary for mating. Mitis (1936) could see no reaction of females to male song. Finke (1968) maintained that song was not necessary for mating and Schaller (1951a) and Crisp (1962) indicated that males mount moving animals. Schaller (1951a) and Leston & Pringle (1963) thought that the effect of male song was to make females swim in a jerky circular fashion thereby attracting the attention of males who would attempt to mate with any moving object of the right size. Finke (1968) agreed with Schaller and suggested that the song also functioned to aid in the synchrony of mating behaviour and to stimulate females.

Jansson (1973a) has cast some doubt on the validity of these studies. He maintained that Shaller's (1951a) observations of jerky swimming in females were a result of confused females responding to reflections of sound waves from aquarium walls and that the females used by Finke (1968) were sexually immature. Jansson's criticisms, especially with reference to Schaller's work, must be taken cautiously. Aiken (1982a) has quantified changes in swimming behaviour of females when male song was broadcast that correspond to Schaller's (1951a) description of jerky swimming by females in an experimental situation where reflection and reverberation were substantially reduced.

Jansson (1976a) found that singing corixids seem to fall into two categories. There are those with functionally distinct calls (e.g. *Cenocorixa* spp. (Jansson 1973a), *Palmacorixa* (Aiken, 1980, 1982b)) used in several different contexts and those with one call used in several different contexts (e.g. *Arctocorisa carinata* (Jansson, 1979)). For purposes of simplification, I shall label these two types of communication systems complex and simple respectively.

Presently, it is difficult to identify in which category many species belong. Finke & Prager (1981) have highlighted an aspect of complex communication systems that seems to be generally applicable. Males use the shorter, simpler calls agonistically and then assemble several of these short calls to form sexual signals. This trend is seen in several genera (e.g. *Palmacorixa* (Aiken, 1982a; Jansson, 1976a) and *Cenocorixa* (Jansson, 1973a)). Presumably, if more detailed information on the structure and behavioural contexts of different calls of those species already recognized as having distinct calls (Ball, 1845, 1846; Finke, 1968; Mitis, 1936, Schaller, 1951a, b; Thompson, 1894) were available, it would fit this pattern.

An important qualification must be made, however. Aiken (1982a) has shown that while a species may have a large repertoire of signals, they need not all be used all the time. Consequently, it is most useful to consider complex communication systems as being very plastic, elements of which can be used as suits the needs of the animal. Jansson (1973a) has already noted that Finke's (1968) failure to evoke phonotaxis may be due to the sexual immaturity of his females. I think, however, that this is not solely an experimental artifact. Aiken (1982b) has suggested that the extent to which a signal system is invoked may be a function of the sexual state of the animals in question. In *Palmacorixa nana*, recently captured animals show little courtship behaviour (Aiken,
unpublished observations). This lack of courtship behaviour and, indeed, of sexual discrimination is underscored by the high incidence of homosexual mounting between males of this species (Aiken, 1981, 1982a, b). The only signals heard from such recently captured animals were aggressive signals exchanged between males. However, animals that have been isolated for some period of time exhibit the entire signal repertoire. This laboratory isolation may well correspond to a natural sexual isolation that would occur if animals were either in assemblages of large numbers of species or in very low population densities. The sexual state of the animal may then be a result of the ecological situation in which it finds itself. Consequently, one may dispute Jansson's (1979b) assertion that random mounting is not important in the field and may result from females being too easily detected in laboratory experiments. Rather, random mounting may be an alternate mating strategy for corixids in dense aggregations.

Corixids can occur in very dense aggregations during the mating season (Aiken, 1982b; Ekblom, 1928, Kirkaldy, 1898, Savage, 1971a, b). Aiken (1982b) explored this phenomenon and found that isolated males would not sing (cf. Finke, 1968) and that the incidence of agonistic (= spontaneous) call production increased exponentially with density. In addition, females showed a significant phonokinetic preference for call rates representative of the densest groups of males. In fewer than 20% of male-female encounters was a courtship call given. Aiken (1982b) speculated that this disuse of the acoustic component of courtship was a result of the high density, single species populations in which *P. nana* was found. In such situations, the greatest mating success accrued to males who relied on a rape type of mating strategy and dispensed with time-consuming courtship behaviour.

Signals that do seem indispensable in species in which they occur are those identified as mounting (Aiken, 1980, 1982a; Jansson, 1975) and copulatory (Aiken, 1980, 1982a). In three species of *Sigara*, Jansson (1975) found that males produce a signal as they mount females by stretching each mesothoracic femur backward and rubbing it on the corresponding metathoracic femur. These signals were produced throughout a copulation and given by species that were otherwise mute. Aiken (1980, 1982a) found similar signals in *Palmacorixa nana*. In *P. nana*, however, the signals were produced by the male rubbing a row of pegs on the mesothoracic femora along the edges of the female's hemelytra. This is one of the rare instances in which the plectrum and pars stridens are on different animals. Aiken (1982a) differentiated between mounting signals (those given when males first mount) and copulatory signals (those given throughout a copulation) by differences in temporal patterning and amplitude modulation. The function of these signals seems to be to sedate females during copulation.

(v) *Corixinae – other tribes.* Information on stridulation in other tribes of *Corixinae* (Graptocorixini, Agraptocorixini and Glaenocorisini) is scanty. From Hungerford's (1948) discussion, species in only one genus in the Glaenocorisini (*Dasycorixa*) are stridulatory. Kirkaldy (1906) mentioned a stridulator in *Glaenocoris*. Hungerford's (1948) list of stridulating corixids included no graptocorixines. Jaczewski (1931a, b) incorrectly assumed that the palar pegs of *Graptocorixa melanogaster* Kirkaldy to be stridulatory but described (1939) an area of thickened hairs (= spines?) on the fore femur of *Pseudoglaenocorixa hugoscotti* Hutchinson that may bear investigation. Hutchinson (1939) mentioned a row of comb-like spines on the fore femur of *Agraptocorixa sacra* Huchinson (Agraptocorixini).
Sound production by aquatic insects

Fig. 11. Ventral view of right elytron of *Hygrobia tarda* showing file (ps) that is rubbed by the tip of the abdomen. (After Balfour-Browne, 1922.)

Determining presence or absence of acoustic capability by the degree of development stridulatory structures, however, is risky. Jansson (1972, 1976a) has shown that several species of Corixini that, according to Hungerford (1948) did not have well developed stridular areas, could indeed sing.

(2) Coleoptera—Adephaga

(a) Hygrobiidae

In the late nineteenth century, many British children were undoubtedly amused by the antics of 'squeakers' sold in London's Covent Garden Market. Squeakers were beetles of the genus *Hygrobia* (Sharp, 1901).

*Hygrobia* (= *Pelobius*), the only genus in the family known to stridulate (Dudich, 1922), is the first aquatic beetle in which sound production was described (Kirby & Spence, 1828). Its stridulation has variously been described as a "shrill, silibant or creaking sound" (Kirby & Spence, 1828), "a shrill grating" (Laker, 1878), a "squeaking, piping and comparatively loud sound" (Schmidt, 1840) and a "strong rattling sound" (Zaitsev, 1953).

In both sexes, the file is a band of teeth running down the posterior third of the elytra near the sutural margin (Fig. 11) and the scraper is a sharp ridge on the tip of the abdomen (Balfour-Browne, 1922; Britton, 1970; Darwin 1880; Erichson, 1837; Gahan, 1900; Kletke, 1889; Schmidt, 1840; Zaitsev, 1953). The tip of the abdomen is flexed upwards and rubbed against the underside of the elytra (Burmeister, 1832; Kirby & Spence, 1828). Kirby & Spence (1828) noted that if a pin were inserted between the elytra and abdomen, the sound ceased. Sharp (1882, p. 830) hypothesized that sound radiation was made more effective by a locking of the elytra to the sides of the body. When the abdomen was flexed, tension was transmitted to the elytra as sound was produced. Thus, body position necessary for stridulation would automatically 'tune' the elytra.

The biological function of stridulation in *Hygrobia* is inadequately understood. Several authors (Balfour-Browne, 1922; Erichson, 1837; Kirby & Spence. 1828; Schmidt, 1840; Westwood, 1839) noted that sound is produced when the animal is held in the hand and described it as a sound of excitement or distress. Laker (1878) noted that the sound was heard after an animal was attacked by a *Ranatra*. Balfour-Browne
Table 1. *Stridulatory structures proposed for various genera within the Dytiscidae*

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Sound production by aquatic insects

Table 1. (cont.)

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<td>Hind coxa/hind femur</td>
<td>Dudich (1922)</td>
</tr>
<tr>
<td><em>Laccophilus</em></td>
<td>Costal vein/elytra</td>
<td>Reeker (1891)</td>
</tr>
<tr>
<td></td>
<td>Wing patch/elytra</td>
<td>Marcu (1936)</td>
</tr>
<tr>
<td></td>
<td>Wing patch/abdomen</td>
<td>Arrow (1924)</td>
</tr>
<tr>
<td></td>
<td>Hind coxa/hind femur</td>
<td>Balfour-Browne (1940)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Crotch (1873)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sharp (1882)</td>
</tr>
<tr>
<td><em>Noterus†</em></td>
<td>Costal vein/elytra</td>
<td>Marcu (1936)</td>
</tr>
<tr>
<td><em>Platambus</em></td>
<td>Wing patch/elytra</td>
<td>Marcu (1936)</td>
</tr>
<tr>
<td><em>Rhantus</em></td>
<td>Costal vein/elytra</td>
<td>Reeker (1891)</td>
</tr>
<tr>
<td></td>
<td>Axillary sclerites</td>
<td>Smith (1973)</td>
</tr>
</tbody>
</table>

* Includes Cymatopterus; † Now Noteridae.

(1922) and Douglas (1872) described sound production by two beetles fighting over food and Morley (1902) noted that *Hygrobia* stridulated when removed from water and that one was inclined to drop the animal. Such anecdotal observations suggest some defensive function for the sound but no conclusions can be drawn until further evidence is gathered. As yet, no role in courtship or mating has been described.

(b) *Dytiscidae*

Marcu (1936) complained that complete uncertainty prevailed concerning the stridulatory organs of dytiscids. At this writing little has changed. Much confusion results from workers finding a series of teeth, grooves, ridges etc. and assuming them to have a stridulatory function. For some unaccountable reason, little behavioural work has been done on the family. Arguments about mechanisms of stridulation closely parallel those for the Hygrobiidae since the two were once in the same family. Supposed stridulatory mechanisms are found on every part of the body (Table 1) and show a great tendency to be author specific. In discussing these mechanisms, I cite what little behavioural and experimental evidence that exists to discount some proposed mechanisms (Table 1).

Landois (1874) noted that in both sexes of several dytiscid species, the costal vein, noticeably heavier than other wing veins, is extended down the side of the dorsum and is curved medially (i.e. it is J-shaped) when the wings are folded at rest. This vein has prominent transverse grooves down its entire length. Landois (1874) imagined that this vein was rubbed by a downward projection of the elytra and that an expanded wing cell ('tambourine') intensified the sound. Reeker (1891)*, Hirsch (1904) and Prochnow (1907) concurred with Landois.

Blunck (1913) and Dudich (1921) have dismissed this stridulatory structure. Their objections are essentially the same and can be summarized as follows:

* Reeker’s analysis is inaccurate in that he included *Hygrobia* (=*Pelobius*, Hygrobiidae) and *Haliplus* (Haliplidae) in the Dytiscidae.
(1) The elytral ridge is too far anterior to the costal vein and hence could not contact it.

(2) Many species sing with closed elytra which would necessitate the elytral ridge moving at right angles and not parallel to the grooves.

(2) The folded wing would lie between the costal vein and ridge.

(4) The mechanism is found in species which do not stridulate and in those which stridulate by other means.

(5) The wings and elytra open and close too slowly for stridulation.

Marcu (1936) reviewed the entire question of dytiscid sound production and provided the only experimental evidence of its origin. He agreed that closing and opening of the wings would be too slow to result in stridulation. However, when the abdomen is moved sideways, ridges and grooves move in proper orientation and sound results. He then removed the outer edge of each elytron and still elicited sound refuting Reeker's (1981) idea of a wing vein-elytral mechanism. In spite of this, the costal vein-elytral mechanism is still invoked to explain stridulation in other beetles (e.g. Freitag & Lee, 1972).

Coxa-femur and coxa-tibia mechanisms proposed for Cybister (Crotch, 1873; Dudich, 1921; Hirsch, 1904; Larson & Pritchard, 1974) are dubious. Clainpanain (1917) observed that stridulating Cybister aegypticus were immobile except for a slight trembling of the elytra. He stated that the elytra vibrated as a result of being struck by the underwings.

Marcu (1936) proposed that the mechanism consisted of two opposed patches of minute chitinous teeth - one on the underwing (Fig. 12 A) and the other on the elytron (Fig. 12 B). Interaction of such patches to produce sound has proved an attractive idea in study across many insect orders (see Common, 1969; Riek, 1967). Balfour-Browne (1944) agreed that such patches could be stridulatory and speculated that they could have arisen as a result of "the rubbing of that portion of the wing on the underside of the elytron".

Such wing patches, however, are probably not involved in stridulation. Hammond (1979) has demonstrated that all such opposing patches of minute teeth are wing-binding
Sound production by aquatic insects

mechanisms, serving to secure the wings under the elytra. Such patches can produce a ripping sound when pulled apart (Common, 1969) but the biological significance of such sounds is debatable.

The stridulatory function of the remaining structures cited in Table 1 are best considered speculative until experimental evidence is offered. While it may be possible that a single species possesses more than one stridulatory structure, such is not generally so in insects.

The function of sound in dytiscids is inadequately understood. Several authors (Arrow, 1942; Balfour-Browne, 1922; Clainpanain, 1917; Kraft, 1907; Lacordaire, 1854; Morley, 1902) noted sound production by beetles under stress, indicating some defensive function. 'Humming' sounds produced by Acilius (Brischke, 1875; Laker, 1879; Schenkling, 1897; Westwood, 1839) are in this category. Arrow (1942) speculated that vibrations produced by a stridulating animal would be unpleasant in the mouth of a predator. Brocher (1927), Clainpanain (1917), Gardner (1887), Griffini (1896), Isenschmid (1876), Laker (1879), Leston, Pringle & White (1965), have indicated that sound is heard preparatory to flight. This would seem to be an incidental sound and to have no communicative function. Individuals of Rhantus gutticolis Say and R. binotatus Harris (Smith, 1973) and Acilius sulcatus L. (Leston et al., 1965) emit a clicking sound coincident with a longitudinal movement of the hindwings under the slightly elevated elytra. Leston et al. (1965) thought this sound is produced by a click mechanism involving the axillary sclerites. This sound, however, was produced out of water and, again, seems to be incidental to preflight activity. Isenschmid (1876) speculated that the sound resulted from a rapid exchange of air through the spiracles and Schiøtte (1841) noted a series of transversely striated plates on the edges of the second tergite that could, he speculated, be set into motion by passage of air from the spiracles. Sopp (1901) described a loud, shrill sound and a less intense buzz from Dytiscus marginalis L. and D. punctulatus F. Sopp believed the sounds to be related to flying but gave no reason why there should be two.

Smith (1973) has done the most detailed study of the biological role of stridulation in any dytiscid. Both sexes of two species of Rhantus produced buzzing sounds of variable duration and temporal patterning. Conditions that would indicate a degrading aquatic habit (e.g. increasing temperature, crowding) all stimulated acoustic behaviour and such acoustic behaviour was followed by emigration. Smith argued that the sounds serve to co-ordinate dispersal from such degrading habits. Such co-ordination would allow any individual to disperse to a habitat with a large number of its kind, ensuring chances for reproduction and reducing the risk of being taken by a terrestrial predator. The beetles could also undertake their pre-flight warm up while submerged, avoiding risk of detection by a terrestrial predator.

Sound production has been associated with mating in several dytiscids (Blunck, 1912; Haupt, 1907; Miall, 1895; Régimbart, 1877; Schiøtte, 1841; Wesenburg-Lund, 1943). Parfitt (1862) described a “faintly gryllous noise” from Agabus bipunctatus L. that he thought was given in a sexual context because the animals appeared to answer one another. Blunck (1912) described mating in Dytiscus marginalis as a virtual rape by the male during which he vigorously strokes the edges of the female's abdomen. During this stroking, a “knocking” sound that resemble the “slow winding of a watch” (Blunck, 1912) was produced in conjunction with the flexing of the mesothoracic legs.
Haupt (1907) thought the sound resulted from the male's episternum striking the female's elytra—an observation that Wesenburg-Lund (1943) was unable to confirm.

Blunck (1912), noting that this knocking sound accompanied each power stroke of the swimming legs, investigated the femur-coxa joint as a sound producing structure. He speculated that sound resulted from movement of the proximal end of the femur over a sharp edge of the trochanter and was able to produce the knocking sound by manually moving the leg of a living beetle. Wesenburg-Lund (1912, 1943) indicated that the signal was produced by the mounted male rubbing tibial spines over the grooved elytra of the female.

Function of the sound is not clear. Haupt (1907) noted aedeagal extrusion after each stridulation. Schiéte (1841) and Blunck (1912) saw the sound as an acoustic attractant functioning as 'an invitation to the female to undertake the sex act' (Blunck, 1912), thus serving the same function as mounting (Aiken, 1982a; Jansson, 1975) and copulatory (Aiken, 1982a) signals in corixids. If this so, it is probably inaccurate to consider these sounds acoustic attractants or mating invitations. The mating behaviour of dytiscids seems to be such that the signal would serve more as a sedative. Smith (1973) studied the mating behaviour of three species of *Rhamius* and found no role for sound production.

(c) Haliplidae

Literature on sound production in the Haliplidae is scanty. *Haliplus* figured in the anatomical debates of Reeker (1891) and Dudich (1921) reviewed above.

For *Haliplus wehnckei* Gehr., Beier (1929) assumed that a field of sclerotized teeth on the underside of the elytra that extends from the articulation point of the elytra and coxae to the elytral tips was the pars stridens. The plectrum is a toothed area in the pleural fold of the second, third and fourth abdominal tergites. Teeth of these two structures point in opposite directions. Both structures are present in both sexes but well developed only in the male. Beier (1929) speculated that the structures could have evolved through thickening and sclerotization of the mat of waterproofing hairs that cover the body.

During stridulation, the abdomen is telescoped anteriorly and then extended posteriorly and down. Sound is produced on the down stroke and the opposite orientation of teeth allows the return stroke to be relatively free of resistance. The sound produced resembles that of a 'fingernail on a comb' and lasts from 0.2 to 0.25 s. Mechanisms in which both the plectrum and pars stridens are both toothed areas must be treated cautiously, however, in view of Hammond's (1979) finding that such structures in dytiscids are wing binding patches.

Stridulation would not seem to be critical in haliplid mating. Seeger (1970) observed mating in several species of *Haliplus* and noted few instances of sound production.

(d) Amphizoidae

The one speculative reference to stridulation in *Amphizoa* involves well developed wing patch/elytra structures similar to those in many Dytiscidae (Arrow, 1924). Hammond (1979), however, has cast serious doubts that such mechanisms are stridulatory.
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Fig. 13. Cross section through the third abdominal segment of Hydrophilus piceus (A) and Hydrochus elongatus (B) at the level of the stridulatory apparatus. (After Maillard, 1969.)

(3) Coleoptera—Polyphaga

(a) Hydrophilidae

More is known about the biological meaning of stridulation in Hydrophilidae than in any other family of aquatic beetles. Study of this family has benefitted from early, precise determination of stridulatory apparatus which forestalled function-from-structure arguments found in studies of Dytiscidae.

Kolbe (1877) described a series of grooves on the underwing that rubbed on the sharp, lateral margin of the abdomen as the abdomen pressed upwards. These structures, however, appear to be similar to the costal vein/elytral mechanisms described for several dytiscids (Table 1) that have been shown not to be involved in stridulation. Buhk (1910) described a finger-shaped grooved area on the dorsal edge of the first abdominal segment of Spercheus emarginatus Schall.* that could be rubbed on a field of fine teeth on the underside of the elytra. Ablation of the field on the elytra rendered the animal silent. Similar experiments confirmed similar stridulatory structures in Hydrophilus (Procher, 1912) and Tropisternus (Ryker, 1972). This type of elytral-abdominal mechanism has been detected in species of Anacaena (Maillard, 1969), Berosus (Maillard, 1969; Maillard & Sellier, 1970; Procher, 1912; van Tassel, 1965), Cymbiodyta (Maillard, 1969), Derallus (van Tassel, 1965), Enochrus (Maillard, 1969), Helophorus (Maillard, 1969), Hemiosus (van Tassel, 1965), Hydrobius (Maillard, 1969; Marcu, 1932), Hydrochara (Maillard, 1969), Hydrochus (Maillard, 1969), Hydrophilus (Maillard, 1969);

* Since Spercheus was figured in the Hydrophilidae at the time sound production mechanisms were elucidated, I am keeping it there although some authors (Britton, 1970; Crowson, 1955) place it in a separate family—Spercheidae.
Fig. 14. Hypothesized structural progression in the development of the pars stridens in the Hydrophilidae from a common starting point of spiniform hairs. Pathway A is followed by *Laccobius minutus* and pathway B by the genera *Limnoxenus*, *Enochrus*, *Hydrophilus*, and *Berosus*. (After Maillard & Sellier, 1970.)

Fig. 15. A, Ventral view of right elytron of *Tropisternus mixtus* showing pars stridens (*psR*). B, Dorsal view of abdomen of *Tropisternus mixtus* showing right (*plR*) and left (*plL*) plectra. (After Ryker, 1972.)

Maillard & Sellier, 1970; Marcu, 1932; Procher, 1912), *Laccobius* (Hammond, 1979; Maillard, 1969; Maillard & Sellier, 1970; Scheloske, 1974; van Tassel, 1965), *Limnoxenus* (Maillard & Sellier, 1970; Marcu, 1933), *Paracycymus* (Maillard & Sellier, 1970) and *Spercheus* (Frankenburg, 1937, 1940). In most genera, the structures occur in both sexes. Maillard (1969) found that the structures of *Hydrochus* differed in form and location from those of other hydrophilids. In all other hydrophilids, the plectrum and pars
stridens are on planar surfaces that contact each other (Fig. 13A). The plectrum in *Hydrochus* is produced dorsally forming a sharp carina that fits into a fold in the edge of each elytron (Fig. 13B).

Maillard & Sellier (1970) found the topography of the pars stridens to vary from hooked teeth (*Hydrophilus* and *Enochrus*) through irregular lamellae (*Limnoxenus*) to a very regular series of lamellae (*Berosus* and *Laccobius*) (Fig. 14). They hypothesized that these types formed an evolutionary series from the basic hair-like ornamentation of the pleuron through to the regular lamellae by two possible evolutionary pathways. Either the normal spines shortened and flared basally to eventually coalesce into irregular plates or they became hooked teeth which eventually coalesce into plates. Structural progression is visible around the edges of the pars stridens in several species.

Ryker (1972) and Van Tassel (1966) described the mechanics of sound generation for several species of *Tropisternus* and *Berosus*. The file, situated on the dorsal edge of the first visible laterosternite, is brought up and forward, coming into contact with the plectrum – a roughened area on the ventrolateral face of each elytron (Figs 15, 16). Sound is produced as the file moves anteriorly (Ryker, 1972; Scheloske, 1974) at an angle of 45° to the body axis (Rush, 1974). Rush (1974) argued that, at least in *T. lateralis limbalis* Say, only a triangular area on the anterobasal portion of the laterosternite is used in sound generation. The width of the pars stridens was roughly equal to the length of the plectrum allowing efficient use of the entire toothed area (Rush, 1974).

Frequency spectra of hydrophilid sound show wide band signals with dominant frequencies between 3 and 10 kHz for *Berosus* (Van Tassel, 1965), 1 and 7 kHz for *Tropisternus* (Rush, 1974; Ryker, 1972, 1976a, b) and 3 and 5 kHz for *Laccobius* (Scheloske, 1974). Rush (1974) recorded a lowering of the carrier frequency of disturbance sounds from about 7.5 to 3.5 kHz (*T. ellipticus* Le Conte) and 11 to 2 kHz (*T. lateralis limbalis*) as beetles were immersed into the water. These frequency shifts result from the damping effect of a more viscous medium. Rush (1974) found that from 12 to 40 °C there was no change in frequency of *Tropisternus* signals but a decrease in such temporal measures as call duration and inter-call intervals.

Sounds produced by hydrophilids are grouped into two categories – defensive/aggressive and reproductive. Frankenburg (1937, 1940) described a 'fright sound' ("Schreckton") from both sexes of *Spercheus emarginatus* that consisted of two
alternating sounds, one more intense, produced at a rate of 4 calls/s. He induced the beetles to stridulate by disturbing them with forceps. White (1936) described the sound of *Limnoxenus semicylindricus* as a “protesting squeak”, audible up to 1 m away. Van Tassel (1965, 1966) found that *Berosus* emitted a ‘stress’ chirp spontaneously while feeding, when held with forceps or when encountering another beetle. She could ascribe no function to the calls. Rush (1974) observed *T. ellipticus* and *T. l. limbalis* to give disturbance chirps when attacked by *Ambrusus* bugs (Heteroptera: Naucoridae). Britton (1970) maintained that members of the genera *Berosus*, *Hydrobius* and *Sternolophus* emitted alarm stridulations. Masters (1979) showed that *Tropisternus* that stridulated while being attacked (albeit by an unlikely predator) reduced the duration of attack. His sample sizes were too small to indicate a significant reduction in mortality.

Most early writing on the role of sound production in hydrophilid beetles has linked it to pair formation, courtship and copulation. Buhk (1910) reported that males of *Spercheus emarginatus* produced sound during copulation and spontaneously during the mating season. Balfour-Browne (1909) heard *Hydrobius fuscipes* males sing during both courtship and copulation. Male *Hydrophilus piceus* have been reported to stridulate nearly continuously prior to (Heider, 1889) and during (Donisthorpe, 1900; Procher, 1912) copulation. In addition to the fright sound, Frankenburg (1937, 1940) suggested that male *Spercheus emarginatus* had an ‘accompanying sound’ (“Begleitton”) in which calls were produced at the rate of 1/s and were less intense, given apparently in response to external stimulation. Frankenburg (1937, 1940) attracted female *Spercheus* by mimicking the “Begleitton”. In *Berosus*, premating sounds (“tremolos”), a series of regularly repeated pulses of increasing intensity, are known only from females (Van Tassel, 1965). Tremolos vary most strikingly in temporal patterning especially between sympatric species. No sounds were detected during copulation. Adams & Miller (1980) reported sound production associated with reproductive behaviour in *Enochrus*. Meyer-Rochow (1971) established that the Australian species *Limnoxenus mastersi* and *Hydrophilus latipalpus* stridulate but gave no ideas about function.

Sound and mating behaviour have been best documented in *Tropisternus* (Rush, 1974; Ryker, 1972, 1975a, b, 1976a). Ryker (1972) listed five situations in which sound was produced:

1. Spontaneously by isolated or grouped animals of either sex.
2. By sexually responsive males.
3. By non-copulating but mounted males.
4. By either sex when handled or disturbed.
5. By a mated female when a male sings near her.

He designated these situations functionally as calling (1), courtship (2 and 3) and disturbance (4 and 5).

Mating in *Tropisternus* takes place several times per season (about once every 3 weeks for females (Ryker, 1975a)). During foraging and feeding, both males and females chirp intermittently. As a prelude to mating, males begin to either chirp more regularly (*T. mixtus* LeConte, *natator* D’Orchymont, *ellipticus*, *columbianus* Brown, *lateralis limbalis*), buzz (*glaber*) or tick (*natator*). Both males and females emit calling chirps and such chirps can be given spontaneously or in response to sight or sound of another beetle (Ryker, 1976a). Males orient visually to females within a few centimeters and mount with no preliminary courtship behaviour.
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Most courtship takes place while the male is mounted on the female’s dorsum. Males have two courtship positions—a forward position during which the male strokes the female’s palpi and a probing posture during which coupling is attempted. There appears to be no obligatory connection between courtship and stridulation, although males of most species either buzzed or trilled during this phase of mating. In the forward position, males sweep the elytra of the female (Ryker, 1976a) with the hind legs in a motion similar to that described for males of Palmacorixa (Aiken, 1982a), Dytiscus (Blunck, 1912; Wesenburg-Lund, 1943) and Hydrophilus species (Donisthorpe, 1900). Receptive females sit quietly and mate while non-receptive females vigorously shake the abdomen from side-to-side and stridulate, rejecting the advances of the male (Ryker, 1976a).

Rush (1974) detected some differences in the mating behaviour of western (Arizona) populations of Tropisternus ellipticus and T. l. limbalis. Rush’s beetles produced post-copulatory sounds not reported by Ryker but found no sounds that could be described as calling chirps. Contrary to Ryker’s (1972) assertion of no obligatory role for sound in courtship, Rush (1974) stated that it is only during courtship contact that the sounds are functional. He proposed that since mating sounds are produced only when the animals are in contact, it is vibrations transmitted through the body that function in information transfer. Their effect is to subdue females.

Ryker (1975a, b) offered, to my knowledge, the first experimental evidence of signal discrimination by aquatic beetles. Males of both T. natator and T. lateralis nimbatus species responded with significantly more calling chirps to calls of conspecific females than to other signs and males also tended to walk more freely and feed less. Since Ryker found that males move to females for mating, Rush’s (1974) statements of no calling chirps in Tropisternus may be premature.

(b) Hydraenidae

There are two proposed stridulatory mechanisms in hydraenids. Hammond (1979) mentioned a baso-lateral plectrum on the elytron and a file on the basal abdominal pleuron of Hydraena testacea Curtis. Perkins (1980) reported that in males of a number of species of New World Hydraena, the occipital portion of the head bears a number (depending on species) of transverse ridges that could be rubbed by the anterior portion of the pronotum (the ‘scintilla’). No sounds have been detected from hydraenids, but the sexually dimorphic nature of the ridges suggests a role in courtship and mating. Perkins (1980) suggested that differences in structure and number of grooves “result in a different pitch for each species”. If hydraenids resemble most other aquatic insects, however, frequency (= pitch) differences are not biologically significant.

IV. EVOLUTION OF ACOUSTIC SIGNALLING SYSTEMS IN AQUATIC INSECTS

Few who have worked on acoustic communication in aquatic insects have tried to speculate on the evolution of such systems. I undertake this discussion with the reminder that much of it is speculative and the ideas subject to change. I hope this discussion will have the ancillary effect of indicating those areas in which research is most needed.

Otte (1974), in a review of the evolution of signalling systems, has outlined the major selective forces that can bear upon such systems. These forces are (re-ordered from Otte (1974)); historical and environmental constraints, compromise and allocation,
identification and discrimination, predation, sex-specific selection, intrasexual competition, mate choice. For ease of discussion, I am including Otte's historical and environmental constraints, and compromise and allocation categories under one category – environmental constraints – and his categories on sex – specific selection, intrasexual selection and mate choice under sexual selection and mating systems. Otte included an eighth category – social complexity – but since the insects discussed below show few complex social interactions, I am omitting this category. I will discuss each category and show how each may apply to aquatic insects.

(1) Environmental constraints

Transmission of sound in water presents different problems to a signaller than those experienced by its terrestrial counterpart. To simplify, I consider an insect signalling in an open field and one in a weedy pond. To further simplify, I will only consider sound travelling vertically and horizontally. The hypothetical field insect has little concern with sound travelling vertically from itself since few recipients are above it. Horizontally, the path of sound is obstructed by grass, shrubbery and the like. All of these can, to varying degrees, reflect and absorb a sound wave. Some work has been done on which frequencies best penetrate such uncertain environments (Marten & Marler, 1977; Marten, Quine & Marler, 1977; Michelson, 1977; Morton, 1975).

Aquatic insects face environmentally imposed uncertainty from a different source. For an animal signalling in a weedy pond there is little horizontal interference because aquatic plants, being mostly water, present little substantial change in medium to a sound wave. They are, in effect, acoustically transparent.

The situation in the vertical plane is radically different. Especially in very shallow water (<1 m), the air–water interface represents an almost impenetrable barrier to sound and the bottom an unpredictable source of reflection and absorption. The ratio of impedances between air and water is $150000:43$ (or nearly $3500:1$) and a boundary of this nature reflects sound better than most mirrors reflect light (Parvulescu, 1964). Frequency spectra of signals can be altered radically by interference of waves reflecting from the air–water interface. Officer (1958, pp. 115) has shown that a simple monotonic frequency spectrum can take on several distinct peaks as a result of reflection of waves from this boundary. (Fig. 17).

Lack of predictability in frequency components in a transmitted signal eliminates such components as parameters for encoding important information. If, for example, two species depended on frequency peaks being a few kHz apart for interspecific recognition, such differences would be masked by the interference patterns described by Officer (1958). By default, temporal patterning and amplitude modulation are left as sources for species discrimination. That temporal patterning and amplitude modulation differentiate species signals has been shown repeatedly for congeners in several different families (Aiken, 1982a; Jansson, 1973a, 1976a, 1977a; Theiss et al., 1983; Ryker, 1972). In view of this, Silver and Halls' (1980) findings that distortion in laboratory recordings primarily affects frequency components may be of little functional importance. Experiments by Theiss et al. (1983) have demonstrated that temperature dependent frequency differences in corixid calls elicit similar responses by the animals.

Any source of sound has around it a sound field that has a characteristic shape depending on the way in which the source itself is oscillating. Although sound fields
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Fig. 17. Schematic representation of the fate of a monotonic frequency spectrum (A) being broken into several distinct frequency peaks (B) after reflection from the water surface. (After Officer, 1958.)

Fig. 18. Motions of spheres and resulting pressure fields for each of monopole, dipole and quadrupole sound sources. (After Harris, 1964.)

can be extremely complex, those associated with natural sources can be represented by three spherical models—a monopole, dipole and quadrupole. A monopole source is a pulsating sphere (Harris, 1964) whose circumference begins at a certain point, increases symmetrically, decreases symmetrically and returns to the starting point for each wave (Fig. 18). A dipole source can be represented by either two aphasic monopoles oscillating near each other or by a vibrating sphere (Harris, 1964) whose volume does not change as it moves along one axis (Fig. 18). The quadrupole is the most complex. It can be described as either two aphasic dipoles oscillating near each other or as a deforming sphere (Harris, 1964). The sphere first stretches along one axis, say the vertical, returns to its original position and then stretches along the horizontal axis at 90° to the original deformation (Fig. 18). For studies of sound production by aquatic organisms, a dipole source is taken as the most representative (Harris & van Bergeijk, 1962; Popper & Fay, 1973).
Table 2. Distance of the near/far field boundary from the source for monopole, dipole and quadrupole sources for frequencies typical of aquatic insect sounds (speed of sound = 1480 m/s).

<table>
<thead>
<tr>
<th>Type of source</th>
<th>Formula</th>
<th>For 2 kHz (cm)</th>
<th>For 10 kHz (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Monopole</td>
<td>Wavelength/π</td>
<td>11.78</td>
<td>2.35</td>
</tr>
<tr>
<td>Dipole</td>
<td>2 wavelength/2π</td>
<td>23.56</td>
<td>4.70</td>
</tr>
<tr>
<td>Quadrupole</td>
<td>3 wavelength/2π</td>
<td>35.34</td>
<td>7.05</td>
</tr>
</tbody>
</table>

Frings & Frings (1966) have pointed out that sound fields experienced by aquatic invertebrates are very different from those experienced by terrestrial forms. The main reason is that the extent of the so-called 'near field' is far greater in water than in air and hence could have a greater role in communication. Discussions of the relative importance of the near and far fields have been underway in studies of fish hearing for some time (see Popper & Fay, 1973) but have rarely been adequately applied to discussions of sound production in aquatic insects.

Any source of sound in water is producing two types of waves—pressure and displacement. If water could not be compressed, the only type of wave coming from a vibrating sphere would be a displacement wave (van Bergeijk, 1964). Water, however, can be compressed (albeit only slightly) and a pressure wave, resulting from the elasticity in the medium, is propagated simultaneously. The amplitude of the displacement wave is high near the source and attenuates rapidly. The pressure wave, on the other hand, begins relatively lower but attenuates much less rapidly. At some finite distance from the source the amplitudes are equal and it is at this distance that the boundary of near and far fields is delimited. Three caveats, however, must be kept in mind. The first is that as the limits of the near field change with the type of sound source so do the shapes of those fields. Harris (1964) illustrated what the near field boundaries look like for the three different types of sources (Fig. 18).

Siler (1969) also pointed out an unfortunate conceptual oversimplification. The near/far field boundary should not be thought of as an abrupt change from a zone of displacement waves to a zone of pressure waves but rather a point where the two types of waves are of equal amplitude.

Finally, near and far field equations are based on the assumption that the medium is both unbounded and infinite. Both these are violated in conditions under which insect sounds are recorded. No pond, lake, river or aquarium is either infinite or without some boundary. Because of reflection from walls and surface, the sound field in small tanks cannot be defined mathematically (Parvulescu, 1964). Hence, conclusions drawn about any animal's reaction to sound fields made in such situations are speculative at best.

Near and far field phenomena could have potentially significant influences on the way we treat the role of sound in the lives of aquatic insects. For a monopole, dipole and quadrupole source the near/far field boundary is set at wavelength/2π, 2 wavelength/2π, 3 wavelength/2π respectively (Siler, 1969). Table 2 lists the boundary distances involved. Since the wavelength of sound at any frequency is four times longer in water than in air, the near field extends four times the distance from the source. The sounds of most aquatic insects are between 2 and 10 kHz. For these two frequencies, the near
field extends to 23.5 and 47 cm respectively (for a dipole source). This is well within the distances to which acoustic communication is restricted in aquatic insects (Aiken, 1982c). Hence, displacement waves in the medium could have significant effects that have not been investigated.

That such displacement waves could be important can be inferred from the structure of aquatic insect ears. The ear of corixids, for example, consists of an innervated club-shaped structure (Garner, 1864) resting atop a tympanal membrane (Hagemann, 1910; Popham, 1961b; Prager, 1973, 1976). This ear is structurally analogous to the neuromast cells in the lateral lines of fish (Dijkgraaf, 1962). These types of structures are better suited for detecting displacements in the medium.

As with the type of signals produced, I believe the influence of a dense medium (i.e. water) has been considerable in shaping the structures used in stridulation. Several general properties of aquatic insect sounds and sound producing structures appear to result from the physical constraints imposed by the medium in which these insects exchange signals.

Aquatic insects stridulate in a medium that, because of its great inertial mass, requires a relatively great input of energy to be set into motion. Since aquatic insects need to overcome a greater inertia in the medium than their terrestrial counterparts, it follows that structures forming the stridulatory apparatus should be relatively stronger and more massive. This expectation is realized. All vibrating structures noted above – elytra, heads, abdomens – are heavy enough to withstand the resistance of water. No aquatic insect yet described possesses the membrane type of sound producing apparatus found in the acoustic Ensifera (see Dumortier, 1963 for a review). Such a radiating apparatus would be too easily ruptured by resistance from the water.

Sound radiating structures have been described for only a few aquatic insects. Aiken (1982a) has inferred that the head radiates sound in corixines and it seems likely that those beetles with some elytral mechanism radiate sound from the elytra. Beyond these, however, the situation is more complex. Wilcox (1975) tried unsuccessfully to determine the radiating mechanism of Buenoa (Notonectidae) experimentally and Silver (1980) was unable to determine the radiating mechanism for caddisfly larvae. Ablation experiments such as those conducted by Ryker (1976a) and Marcu (1936) do not conclusively prove the identity of the sound radiator but only of those structures which interact to set the radiator into motion. Studies on the use of air stores that many aquatic insects carry as resonators illustrate this (Mitis, 1936; Schulze, 1977; Theiss, 1982). Theiss (1982) has convincingly demonstrated that the air stores of corixids are coupled to the head and serve to radiate sound. Hence, the corixid head and forelimb are only part of the system.

Identification and discrimination

Otte (1974) listed in this category those signals which 'may identify organisms either as individuals or as members of more inclusive groups'. We can presently recognize that several groups of aquatic insects can discriminate both species and sex specific signals. Species specific signals are well documented. By monitoring the presence or absence of answer signals of females, Jansson (1973a) has shown conclusively that Cenocorixa (Corixidae) males deliver species specific signals that females can discriminate. Van Tassel (1965) documented differences in premating tremolos in Berosus (Hydro-
philidae) but did not show how such differences may be used in species discrimination. Ryker (1975a, b) showed that males of Tropisternus (Hydrophilidae) discriminated calling chirps of conspecific females from those of other females. For reasons stated above, aquatic insects are restricted to using differences in amplitude and temporal patterning of song elements for species differentiation of signals. In all groups for which data are available, this is so.

Information about variation in acoustic signals over the geographic range of most aquatic insects is lacking. The most complete (and to my knowledge, only) study of geographic variation in the signals of any aquatic insect is Jansson’s (1979a) work on Arctocorisa carinata (Corixidae). He found significant differences in the songs of geographically isolated populations of A. carinata, especially in the number of louder song elements produced and speculated that this insertion of loud song elements permitted individuals living in marginal areas or uncertain habitats to more easily find mates. Jansson later (1980) reiterated this idea that signals reflect adaptations to local conditions but stated further that they show little about the relatedness of populations.

Other examples offer tantalizing possibilities for investigation. Comparison of descriptions of mating behaviour of Tropisternus ellipticus and T. l. limbalis (Hydrophilidae) (see Rush, 1974; Ryker, 1972) indicates differences in use of post-mating sounds between eastern (Michigan) and western (Arizona) populations. Whether these differences are sufficient to effect reproductive isolation is not known.

Presently, there is no information about differences in signals in areas of sympatry and allopatry of closely related species. It is in areas of sympathy that one would expect to find the most severe selection for divergence of song types.

(3) Defence against predators

Sounds produced by larvae of Odonata (Asahina, 1939, 1954) and Coleoptera (Allen, 1956; Balfour-Browne, 1958; Mukerji, 1929) are part of behavioural sequences functioning to dissuade predators. Among adult aquatic insects, a function for sound production in predator defence has been described for three beetle families – Dytiscidae, Hydrophilidae and Hygrobiidae. Direct observation of predators being dissuaded by disturbance sounds has been documented for certain hydrophilids (Masters, 1979; Rush, 1974).

The extent to which predators influence the evolution of acoustic systems has not been examined in aquatic insects. Physical constraints imposed by water on signals eliminate some predator avoidance mechanisms present in terrestrial insects. For example, several orthopterans change from production of high intensity signals to a less conspicuous signal (either lower intensity song or substrate signalling) (Gwynne, 1977; Morris, 1980; Otte, 1972) when females are nearby. Such signals are thought to reduce chances of predation or of mating interference. Similar changes in signals have not been noted in aquatic insects principally because there are no long range signals (see Aiken, 1982c) for predators to detect. I know of no examples of predators of aquatic insects using sound to locate prey although such is known for terrestrial insects (Bell, 1979). Members of groups which do not use stridulation for predator avoidance resort to other mechanisms (repugnatorial glands (Betten, 1943; Brindley, 1929; Pinder & Staddon, 1965a, b) or crypsis (Popham, 1942, 1943)).

Mechanistically, it is uncertain how sound may operate as a predator avoidance
mechanism. The sound could serve to startle the predator, affording the victim a few seconds to escape. It could also act as a substrate signal that, transmitted through the body of the prey, could create a vibrating sensation in the mouth of the predator causing prey release.

(4) Sexual selection and mating systems

In spite of Hewitt's (1906) assertion that sexual selection does not operate in aquatic Heteroptera, several aspects of acoustic communication are interpretable in light of the predictions of sexual selection theory. I have already considered, in some detail, mating in several groups and will here deal only with a few general points. As with other categories examined, theoretical consideration of the evolution of sound production and mating in aquatic insects is lacking.

The most obvious indication of the influence of sexual selection is the sexually dimorphic nature of the structures and signals. In members of most groups, stridulatory apparatus is either absent in females or structurally distinct. Among heteropterans, signals and structures differ in corixids (Aiken, 1982a; Jansson, 1973a) and notonectids (Wilcox, 1975) and these differences are associated with differences in behaviour during courtship. Most beetles, however, seem to have similar structures in both sexes. This may be due to the use of sound in predator avoidance as well as in courtship. Disturbance sounds noted for almost all aquatic beetles in which sound production has been confirmed are similar in both sexes. Since the structures (and sounds) have evolved in both sexes of the same species for the same function, such is hardly surprising. Indeed, it may be that in these beetles, defensive sounds were the first use of stridulation and sound in mating is a more recent elaboration.

Aiken (1980, 1982a, b) has done the only experimental work investigating the role of sound as applied to sexual selection in aquatic insects with Palmacorixa nana (Corixidae). Data from these experiments indicated that males sang at greater rates in denser groups. Females, in turn, exhibited a phonotactic preference for higher call rates, thus exerting a selective pressure on males to be in such groups. When males were in denser groups (and attracting more females) their frequency of copulation increased, indicating a higher reproductive success.

Mating behaviour of several aquatic groups is often attempted with little observable courtship (Aiken, 1982a; Blunck, 1912; Wesenburg-Lund, 1943) and the first approach by a male is to force a copulation upon a female. In such groups, signals of males seemed aimed at calming an attacked female rather than enticing a coy one. Lack of field study of several groups in which courtship has been observed in the laboratory (e.g. Notonectidae, Hydrophilidae) makes further generalization about the prevalence of this type of behaviour impossible. Clearly, much more work is required on the contexts in which acoustic signals are used in all aquatic taxa.

(5) Phylogenetic considerations

To a reconstructed phylogeny of the orders of extant pterygote insects (Boudreaux, 1979), I have added information on which orders have aquatic representatives and which have stridulatory representatives (Fig. 19). Since there are no orders with a common last branching point that have both stridulatory and aquatic representatives, it is certain that stridulation evolved after differentiation at the ordinal level. It is also likely that
the ancestors of these present day forms (except for Coleoptera) that invaded the water were probably silent.

In the Heteroptera, Trichoptera and Odonata, I can find no evidence that the terrestrial relatives of any singing aquatic form possess similar stridulatory mechanisms. Leston (1957) presents a table indicating distribution of stridulatory organs among terrestrial heteropterans, none of which would serve as precursors of any organs found in aquatic forms. This is true even though many of the structures outlined by Leston incorporated non-membranous elements and could be used, with little modification, under water. The isolated occurrences of stridulatory organs in hydropsychid caddisflies (Trichoptera) and epiphelebiid dragonflies (Odonata) speak for themselves.

Among beetles (Coleoptera), however, there is a strong parallelism between some terrestrial and aquatic groups not found among Heteroptera. For example, the abdominal/elytral mechanism found in Hygrobota tarda has counterparts in the Trogidae (Sharp, 1897) and some weevils (Curculionidae) (Dumortier, 1963). The abdominal/elytral mechanism described for hydrophilids is present in members of the Chrysomelidae, Tenebrionidae, Carabidae, Curculionidae, Silphidae and, especially, Scarabaeidae (Dumortier, 1963). It may be that such mechanisms were present in the various terrestrial ancestors of aquatic Coleoptera and were fortuitously useful in signalling under water. Mechanisms involving elytra would support this hypothesis. The use of elytra as a part of the stridulatory mechanism works well in an aquatic medium because of the rigidity in the structure necessary for signalling underwater (see above).

At lower taxonomic levels, the appearance of stridulatory organs is more difficult to interpret largely because of the lack of comparative data. Resh & Solem (1978) presented
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Fig. 20. Reconstructed phylogeny of the orders of aquatic and semi-aquatic Heteroptera with indication of stridulatory forms. (after Resh & Solem, 1978). *Indicates families with stridulatory species; (?) Stridulatory organs unknown (after China, 1955 and Andersen, 1982).

a reconstructed phylogeny of the aquatic and semi-aquatic Heteroptera. I have added to their figure an indication of those families that have representatives known to stridulate (Fig. 20). This type of analysis shows that stridulation is an important phenomenon in members of several distinct family-level taxa and illustrates its utility as a communicative tool. It does not demonstrate, however, that stridulation arose once in ancestral heteropterans. If this were so, the mechanisms used should be the same and plainly they are not.

Leston (1957) asserted that stridulation arose independently about twelve times in the aquatic Heteroptera but gave no empirical evidence for this. I find it hard to reconcile Leston's claim with the available data and can infer only nine independent appearances of stridulatory structures in aquatic Heteroptera: (1) Nepidae, (2) Naucoridae, (3) Pleidae, (4) Micronectinae (Corixidae), (5) Diaprepocorinae (Corixidae), (6) Cymatiinae (Corixidae), (7) Corixinae (Corixidae), (8) Anisops (Notonectidae) and (9) Buenoa (Notonectidae – addition of the femur/coxal peg mechanism). If this is so, the family or subfamily level seems to be a common historical point of elaboration of stridulatory organs.

The few phylogenetic schemata for aquatic groups that are available suggest this is so. Hungerford (1933) showed an early branching of the Notonectidae into the Anisopinae and Notonectinae. It is at this point too that the family can be divided into singing and silent forms. The presence of different types of mechanisms among the subfamilies of Corixidae and the existence of a unique stridulatory family within the Trichoptera also support this hypothesis.

Once stridulation is present within an aquatic insect family or subfamily, it seems to be a general feature of the group. Dunn (1979) presented cladograms for species of Hesperocorixa (Corixidae) and for other genera closely related to it. If a list of species
that should be able to stridulate (Hungerford, 1948) is superimposed upon this cladogram it seems that at both the genus and species level, the most parsimonious explanation for spotty distribution of stridulatory structures is early elaboration and secondary loss.

How intimately stridulatory structures are associated with the emergence of new taxa is unknown. It may depend on the function of the signal. Disturbance or alarm calls show little species specificity. The only way such calls would influence the appearance of new species would be if individuals that produced such sounds became more prevalent in the population because they were less susceptible to predation. Acoustic signals used in mating, however, could be far more directly effective in the development of new species, both when stridulation arose de novo and when extant acoustic signals were modified. Genetically related males that, at some time in the past, produced even the most rudimentary sounds could be more attractive to females. This group of sound producers and responders would then presumably form a unit that preferentially mated within itself or males in this group would attract a disproportionate share of matings.

Before such hypotheses can be seriously pursued, however, it is necessary to examine the mechanisms of stridulation for clues as to their origin and subsequent elaboration. Two evolutionary pathways are possible. First, Dumortier (1963) has proposed that some stridulatory structures were originally non-stridulatory body parts that came into contact for some other function. Secondly, I propose that, in a few instances, the evolution of these structures was accelerated because they made more effective the behaviour patterns in which they are presently used.

The great diversity of stridulatory structures (see Dumortier, 1963) among arthropods suggests that for any animal with an exoskeleton such structures are not difficult to evolve. Any insect has many sites in which parts of the exoskeleton are juxtaposed and at least one is moveable. It may be reasonable to assume, therefore, that several different stridulatory structures could have arisen independently in any group. There is, however, a remarkable (although not absolute) consistency in the parts used by several groups in stridulation that suggests some strong and consistent selective pressure along either of the evolutionary pathways noted above.

Examination of structures in some groups will verify this. First, let us consider those stridulatory structures derived from structures devoted to some other function. Hammond (1979) noted a correlation between taxa of beetles possessing abdomen/elytra stridulatory mechanisms and beetles that use their abdomens to assist in wing folding. He also noted that this led to confusion concerning organs of stridulation in such groups. If one assumes that stridulation has secondarily evolved, then its origins in the wing-folding movements of these beetles is not difficult to envision. Dumortier (1963), too, has cited mechanisms that function in 'immobilising at rest mobile appendages' as precursors of stridulatory mechanisms. In some families of aquatic beetles, especially Dytiscidae, failure to accurately identify the structures interacting to produce sound has retarded progress in the development of logical scenarios for the evolution of such structures.

Among other beetles, however, the situation is different. Maillard & Sellier (1970) show the only published evolutionary sequence for the elaboration of a stridulatory structure (Fig. 14). By examining the occurrence of different types of structures that compose the pars stridens in several species and by noting the change in structure of
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elements in the pars stridens as the stridulatory surface becomes the common hairs of
the pleuron, they proposed two possible pathways for the elaboration of the pars stridens
from existing ornamentation on the pleura of hydrophilid beetles (Fig. 14 – see
Hydrophilidae above).

Among aquatic heteropterans, there is a striking (although not absolute) consistency
in the use of the fore limbs as the moveable part of the stridulatory mechanism. If groups
for which stridulatory mechanisms have not been well documented or rigourously
confirmed (Naucoridae, Pleidae, Belostomatidae, Diaprepocorinae and Cymatiinae) are
ignored, structures in most remaining groups involve the forelegs and their evolution
can be reasonably traced from feeding motions. Feeding movements of the fore limbs
are very similar to and could have acted as precursors for stridulation in corixines
(Corixidae). Jansson (1975) observed that, during courtship, males of silent corixids
exhibit motions of the forelegs similar to those involved in stridulation. Elaboration of
existing femoral hairs into stridulatory pegs in corixines is not difficult to envision.
Indeed, in several corixines, a reduction of the femoral pegs to common femoral hairs
similar to that observed in hydrophilids can be seen (Aiken, 1982a; Jansson, 1972).

In nepids and notonectids, stridulatory structures are on the limbs used for prey capture.
Due to a lack of comparative data on structures and calls across several of these groups,
however, we are limited to generating reasonable first hypotheses for the origin of
stridulatory structures from structures that originally served non-stridulatory
functions.

The elaboration of structures which evolve in the context in which they are presently
used are more easily envisioned and appear to be confined to those mechanisms involved
in predator avoidance or aggressive interactions. From the descriptions of the aggressive
behaviour of hydropsychid caddisfly larvae in repelling intruders (Jansson & Vuoristo,
1979) an important act seems to be to anchor the forelegs in the net and lunge at the
intruder. This motion is so similar to that involved in sound production that its role
as a precursor for stridulatory movements is inescapable. Similarly, the escape
behaviour of most dragonfly nymphs would seem to be easily modified into the
stridulatory behaviour of Epiophlebia superstes (Anisozygoptera) nymphs. The legs are
adpressed to the side of the abdomen (the position for stridulation) and the abdomen
pumped for locomotion (similar to the telescoping or twisting of the abdomen in
stridulation). Why stridulation has not evolved in the dragonflies (Anisoptera) whose
nymphs use the same escape behaviour is unknown.

Aside from the lack of a wide base of comparative information across several taxa,
examination of phylogenetic aspects of stridulation suffers from the lack of information
in the fossil record. Stridulatory structures, usually being well sclerotized, should be
evident fossils and allow tracing the development of these structures. I know of no study
of fossil aquatic insects that deals with stridulatory structures.

V. SUMMARY

1. Sound production by aquatic insects is found in four orders – Trichoptera,
   Odonata, Heteroptera and Coleoptera.

2. Immature aquatic insects that produce sound are rare, stridulation being present
   in one family of Trichoptera (Hydropsychidae) and one genus and species in a relic
suborder of Odonata (Anisozygoptera) – *Epiophlebia superstes*. Hydropsychid larvae produce sound with a head/fore femur mechanism and use sound as part of aggressive behaviour for defence of feeding nets. Larval *E. superstes* use a hind femur/abdominal mechanism to dissuade predators.

3. Sound production has been documented in adults of all families of aquatic Heteroptera except Helotrephidae. In corixids and notonectids, acoustic signals play a role in mating. Members of the genus *Buenoa* (Notonectidae) are unique in having two stridulatory mechanisms in the same individual. Sound production has been most intensively studied in the Corixidae. Although sounds are used in mating by all singing corixids, their use seems to be facultative in some species and obligatory in others. Recent experiments by Theiss (1982) have shown that the air stores carried by corixids are used for both sound radiation and reception.

4. The adephagan beetle families Hygrobiidae, Dytiscidae and Haliplidae have all been shown to produce sound. Mechanisms of sound production have been established for haliplids and hygrobiids but have yet to be for most dytiscids. Sound production is used by beetles as part of sequences of aggressive/defensive and reproductive behaviour.

5. Sound production is especially well documented in the Hydrophilidae (Polyphaga). Hydrophilids use an abdominal/elytral mechanism and sound appears to be used in the same contexts as in adephagans.

6. Insects that produce sound under water must contend with the physical problems of sound transmission in a relatively dense, viscous medium with sharp boundaries. Because of potential distortion of the frequency components in a signal by reflection from the air/water interface in very shallow water, frequency is unreliable for encoding information. Aquatic insects use instead amplitude modulation and temporal patterning of signals.

7. For aquatic invertebrates, sound fields are different than those in air because the extent of the near field is approximately four times greater in water. This near field, a region in which displacement waves are predominant over pressure waves, extends to a greater distance than most aquatic insects communicate over. Such displacement waves could have important but as yet unconsidered effects.

8. The mass and viscosity of the water dictates that sound producing structures of aquatic insects should be heavier and more massive than those of terrestrial insects. A survey of stridulatory organs of aquatic insects reveals this to be true and reveals that the relatively fragile, membranous stridulatory organs of some terrestrial insects (especially Orthoptera) are absent.

9. The elaboration of sound producing structures in aquatic insects probably occurred at the family or subfamily level and for Heteroptera, Trichoptera and Odonata evolved after the invasion of the water. Acoustic signals used reproductively would probably be more closely associated with the emergence of new taxa.

10. Stridulatory structures have been derived from either structures devoted to some other function or from structures involved in the behaviour currently enhanced by sound production.
This paper would not have been possible without the assistance of many. I thank Drs Darryl Gwynne, J. Fullard, A. Jansson, A. Popper and, especially, Glenn K. Morris for stimulating discussions, ideas and letters. David Gwynne, Darryl Gwynne, P. Bell, J. Ciborowski, R. Rutowski and S. Sakaluk kindly sent solicited references. R. E. Roughley drew my attention to several papers on aquatic beetles. Mrs J. Keller and Mrs M. Byrne of the Erindale College (University of Toronto) Library deciphered and obtained my sometimes bizarre and usually incomplete bibliographic requests. Ms R. Sharrett of the Biosystematics Research Institute Library (Agriculture Canada) was of great help during my visits there. The manuscript was improved as a result of criticism by Drs G. E. Ball, D. A. Craig, B. S. Heming and G. K. Morris. I especially thank J. Scott, Department of Entomology, University of Alberta for re-drafting all figures.

I began this review while supported by NSERC (Canada) Operating Grant 4946 to G. K. Morris. The final stages of manuscript preparation were funded by the Department of Entomology, University of Alberta and NSERC (Canada) Operating Grant 1399 to G. E. Ball and an NSERC Postdoctoral Fellowship and University of Alberta Central Research Fund Operating Grant to RBA.

All non-English papers were translated by the author and English quotes from such papers are based on those translations.

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* This is certainly a journal error. The author should be Brocher.


