John Brittain

THE DRUMMING OF NORWEGIAN STONEFLIES (PLECOPTERA)

Cand. Scient. Thesis in Zoology

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Abstract

Fourteen species of Norwegian stoneflies from all families represented in the Norwegian fauna were studied in an attempt to record drumming signals. Of these nine species drummed, and the drumming of these species is presented and discussed with respect to behavior, geographic variation, evolution and phylogeny. First descriptions are given of the drumming of *Isoperla obscura*, *Protonemura meyeri*, and *Capnia atra*. A grouped bi-beat signal is described for the first time in the group Euholognatha (Capniidae; *Capnia atra*). A dialect is described for a Norwegian population of *Isoperla grammatica*.

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Preface

I am greatly indebted to several people for help and advice during all stages of the work on this thesis. My advisors have been Albert Lillehammer and Jan Emil Raastad. Albert Lillehammer also assisted in the identification of species. Karsten Sund assisted me on some of the field work. Much of the field work was done at the Zoological Museum's research station in Øvre Heimdalen. I was fortunate enough to accompany John Brittain on several of his many trips there. In addition to transportation he provided me with valuable discussions and good advice. He also commented on the penultimate draft of the manuscript. My father, Harry Cleven, typed the final draft.

A special thanks is due to Torfinn Ørmen who taught me how to record stonefly drumming and who allowed me to use his tapes of the drumming of Leuctra hippopus for further study. The long discussions we had helped to develop and clarify my thinking on the topics in this thesis. He also read through the manuscript.

To everyone: Thank you!

Finally, thanks to Kristin and Sissel, who amazingly enough, still thought it was fun to collect stoneflies in the mountains even though it rained horizontally!

Erik Cleven

I. Introduction

Stoneflies or Plecoptera comprise a small group of freshwater insects with nearly 2000 species worldwide (Zwick 1974). They are divided into two suborders, the Arctoperlaria found in both the northern and southern hemispheres, and the Antarctoperlaria found only in the southern hemisphere (Zwick 1973). The former is divided further into two groups, the Systellognatha and the Euholognatha. The Systellognatha are characterized by predatory or omnivorous nymphs and reduced imaginal mandibles. The Euholognatha are characterized by herbivorous or detrivorous nymphs and well developed imaginal mandibles. Many types of life cycle occur, but in Norway a one year life cycle is the most common (Lillehammer et al. 1989). Several species have a two year life cycle, the eggs undergoing a period of diapause or quiescence (Lillehammer 1987, Lillehammer et al. 1989). Some species have been shown to have a flexible life cycle, e.g. _Nemurella pictetii_ changing from a one year to a two year life cycle under adverse conditions (Brittain 1978). _Dinocras cephalotes_ is the only Norwegian species to have a normal life cycle of more than two years (Ulfstrand 1968, Huru 1987).

Stoneflies lay their eggs in water where they either directly undergo a period of incubation, or go into diapause or quiescence. The only exception to this in the Norwegian fauna is _Capnia bifrons_ which is ovoviviparous, the eggs hatching shortly after they are laid. Upon hatching stonefly nymphs enter a period of growth culminating in emergence as adults onto land. The adult stage is short. For the Systellognatha, having reduced imaginal mandibles and therefore not feeding, the adult stage of the life cycle serves the sole purpose of finding a mate or mates, reproducing and laying eggs. The same is basically true of the Euholognatha, this group however also feeding during the adult stage.

The newly emerged adults immediately seek the cover of large stones or vegetation. They remain there during the period of pre-mating, mating, and egg maturation, at the end of which the females seek back to the stream or lake to lay their eggs (Lillehammer 1988). During the period prior to mating stoneflies utilize complex vibrational signals in order to locate mates of the same species and the opposite sex. These signals are highly species specific, though geographic variation and dialects do occur. Because of this stonefly drumming has become increasingly important in phylogenetic studies of the Plecoptera. Maketon and Stewart (1988) have formulated a hypothesis of stonefly drumming evolution on the basis of the known drumming signals of 104 world Arctoperlaria species. The majority of these signals belong to Systellognathan species, the drumming of relatively few Eugolognathan species having been described. Ørmen (1991) gave a qualitative description of the drumming of *Leuctra hippopus* from five different localities in Norway, but to date no quantitative descriptions of Norwegian stonefly drumming have been published.

The aim of the present thesis is therefore to give a quantitative description of the drumming signals of as many Norwegian stonefly species as possible with an emphasis on Euholognathan species. Furthermore, to analyze the signals for species specificity, dialects and/or geographic variation, and to discuss the results in the light of Maketon and Stewart's hypothesis of stonefly drumming evolution. Though many species have been investigated, it is impossible that one thesis alone could significantly alter the status of Maketon and Stewart's hypothesis. The present work, however, does fill some gaps in our knowledge of stonefly drumming, and seen together with other similar work it may help resolve phylogenetic relationships within the Plecoptera.

II. Stonefly Drumming and Pre-mating Behavior

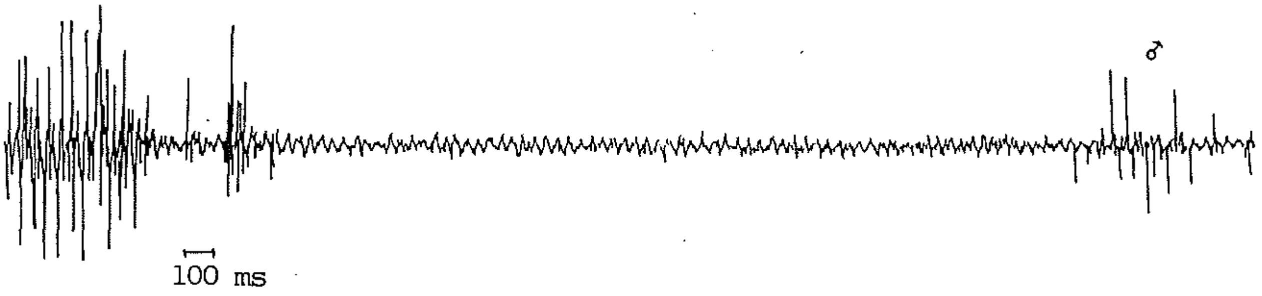
Stoneflies drum by tapping on or rubbing the substratum on which they are standing with their abdomen. In one genus, *Siphonoperla*, a signal is produced without the abdomen actually being in contact with the substratum. This is called tremulation (Rupprecht 1981). In this way stoneflies produce complex, species specific signals.

In spite of their well developed eyes, stoneflies seem to see poorly. They do not react to quick movements of the hands, and only show signs of escape when touched or when the substratum or branch etc., they are on, is touched. Males can pass females at a distance of no more than 0.5 cm and appear completely unaware of their presence (Rupprecht 1968, Andersson 1986). Though Stewart, Atmar, and Solon (1969) list visual detection as the possible stimulation of males to pursuit of females, they go on to say that "in only a few instances did the male or female seem 'aware' of the presence of the opposite sex until some movement or contact." Andersson (1986) describes a laboratory experiment to determine whether pheromones from virgin females play a role in mate localization. He showed that given a choice between two air currents, one coming from a virgin female and the other without a female, males of Isoperla grammatica showed no preference. Assuming this to be the general case with stoneflies, this leaves random contact, sound, or vibration as the only possibilities for mate localization. Random contact may certainly play a role, but it seems clear from the fact that stoneflies drum, and the detailed studies made of this behavior, that this is by far the most important method of mate location.

The earliest report of stonefly drumming stems from Newport (1851). MacNamara (1926) gave a qualitative description of stoneflies drumming in his cabin. Brinck (1949) put stonely drumming into the context of the insects' mating habits, but the first thorough, systematic and quantitative study of stonefly drumming was made by Rupprecht (1968).

He showed that both males and females drum, the females in answer to the male signals. Most commonly, the male drums and uses the female's answer to locate her. He runs in the direction of the female, often stopping to reorient himself. The female remains still during this process except to answer the male calls. For Isoperla grammatica, however, he showed that both the males and the females search.

Rupprecht (1968) found the subgenual organ on the basal portion of the tibial leg segment to be the receptor of drumming signals. He also showed that the transfer of drumming signals takes place through the vibration of the substratum and not through the air. Stewart and Zeigler (1984) later showed that drumming signals could be transferred through the air, but only across short distances and when both sexes are on a substratum capable of "sound-substratum vibration interconversion." That is, the signal can be transferred from the substratum to the air and back to the other substratum. In their natural environment this might be realistic on dried tree bark or leaves (Stewart and Zeigler 1984). However, even in this case the signal is dependent on the vibration of a substratum for transfer, and most importantly for perception by the insects. As mentioned earlier, two species of Siphonoperla produce signals by tremulation, in which the abdomen vibrates without touching the substratum. In this case as well, the signals are transferred through the substratum, the vibrations of the insect's body being transferred to the ground (Rupprecht 1981). Romoser (1981) states that insects showing the greatest sensitivity to vibrations have been found to possess subgenual organs. Rupprecht (1968) found the subgenual organs of stoneflies to be sensitive, a played back tape recording of drumming being enough to cause females to react. Ørmen (1991) simplified this further and found that verbal imitations of drumming signals on the part of the investigator was enough to stimulate males of Leuctra hippopus to drum. Drumming obtained in this way he termed "hitch drumming." I was able to get females to respond to my verbal imitations of male signals. An illustration of hitch drumming in Leuctra hippopus and an example of a verbal immitation can be seen in figs. 1 and 2. Figs. 3 and 4 show a female of Dinocras cephalotes answering my verbal imitations.



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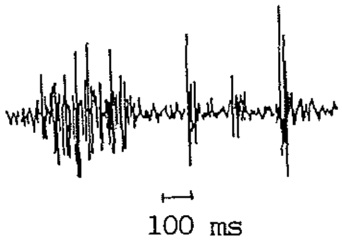

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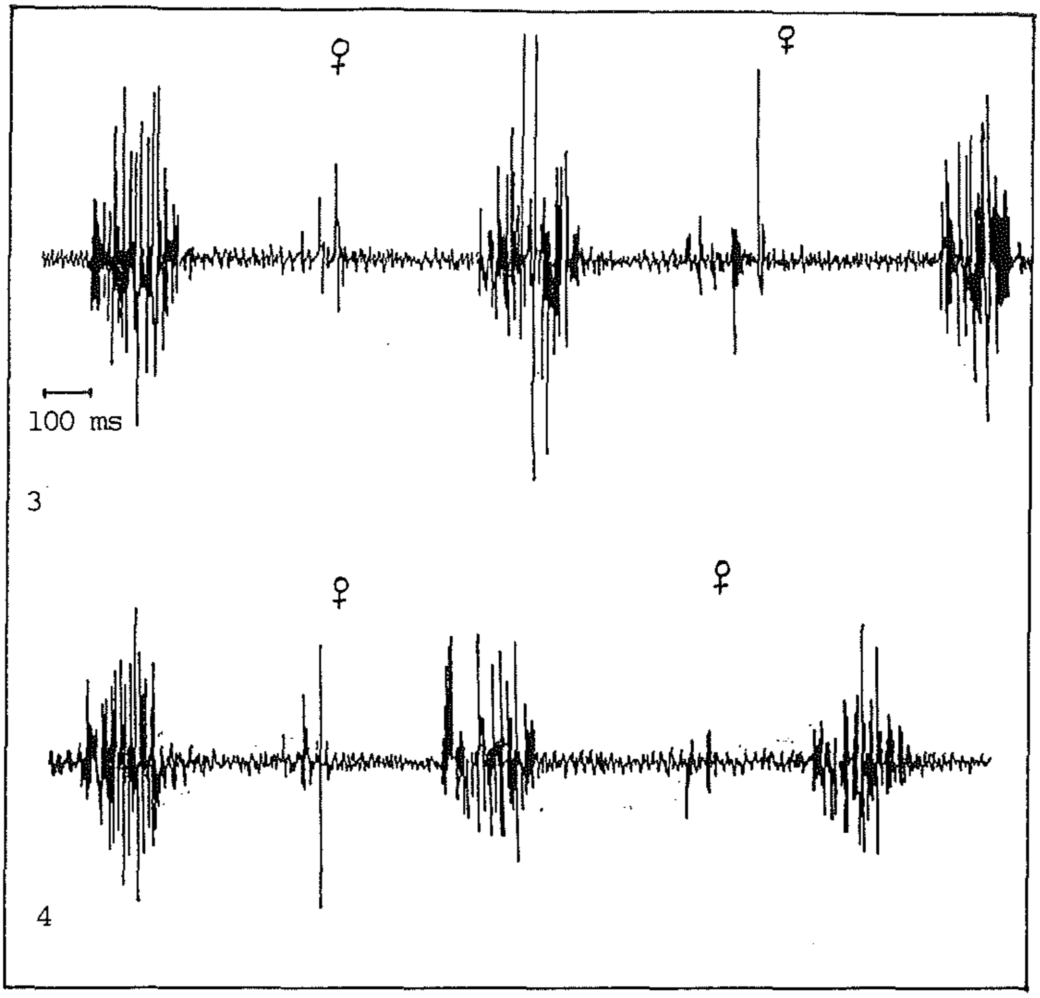
Fig. 1. A verbal imitation of the drumming of Leuctra hippopus followed by an example of male "hitch drumming".
Fig. 2. A verbal imitation of the drumming of Leuctra hippopus.

Stewart and Zeigler (1984) have studied the transmitability of drumming signals through various media. They found that drumming signals could be transferred a distance of eight meters through a wooden



Figs. 3 and 4. Two exchanges showing a female of Dinocras cephalotes responding to verbal imitations of the male calls. Each sequence begins with a verbal imitation.

rod, 5-9 mm in diameter. At a distance of two meters females answered 100% of the male calls, and at eight meters nearly 87% of the male calls were answered. They also tested the transmitability of drumming signals through a branched dried aspen limb, collected at the same stream at which the stoneflies tested were collected. They found that in all cases females answered males and stopped moving when the male called provided the substratum was continuous (Stewart and Zeigler 1984).

Males and females were also placed in separate enclosures but on the same rock, weighing 4.2 kg. At a distance of 16-24 cm not one male call was answered by a female (Stewart and Zeigler 1984). These experiments, and the one described earlier by the same authors to test the transmitability of signals through air, and the observations of the sensitivity of stoneflies to vibrations, can be summed up as follows: drumming appears to be an extremely effective method of mate localization for stoneflies in their natural habitat, where they are often found as adults on shrubs or trees, or under dried leaves or bark. Though Brinck (1949) reports observing stoneflies drumming on rocks, this cannot be an effective way of localizing a mate, and might instead indicate the inability of stoneflies to differentiate the substratum they are on, at least for drumming purposes.

III. Structures Used for Drumming.

Many studies have been made on the morphology of stoneflies where structures connected to drumming behavior have been described and discussed. Only recently, however, have studies been made on these structures in the context of stonefly drumming (Gnatzy and Rupprecht 1972, Rupprecht and Gnatzy 1974, Rupprecht 1976, and Stewart and Maketon 1991). Based on the work of Rupprecht (1976), stoneflies may be divided into four groups according to the structures used in drumming. I) Drumming without any special structure. Included in this group are Siphonoperla torrentium and S. montana shown to tremulate (Rupprecht 1981), and a number of other species producing simple tapping signals, mostly monophasic (Stewart and Maketon 1991). (The term monophasic and a number of other related terms, will be defined below). This group also includes Capnia atra whose drumming will be described in section VIII. II) Drumming with brushes. Rupprecht (1976) writes: "A dense arrangement of hair stretching away from the body and usually taking the place of the vesicle or hammer is called a brush." Included in this group are Utaperla orientalis, Paraperla frontalis, and Miniperla japonica of the Chloroperlidae, and Styloperla spinicercia of the Peltoperlidae. Also included is Etrocorema nigrogeniculata of the Perlidae (Rupprecht 1976). Rupprecht writes that the brush may be analogous to the vesicle. III) Drumming with hammers. According to Rupprecht (1976) the hammer is a ". . . median protrusion or extension of an abdominal sternum. It is firmly connected with its surroundings and overtopped by hair which crowns its edge and stretches in various directions." The hammer is found either on segment 9 of the abdomen or on one or more of the segments from 6 to 8. The part of the surface in contact with the substratum during drumming is without hair, though the dorsal side may have hair near the edge. The hammer is firmly attached and immovable relative to the sternum, except in the Peltoperlidae (see p. 8 below), where the hammer is passively movable (Rupprecht 1976). IV) Drumming with vesicles (German: bauchblase). The vesicle " . . . is a movable, median protrusion on the first half of the 9th abdominal sternite" (Rupprecht 1976). With the exception of Taeniopteryx only the ventral side and edges have hairs and there is no hair on the dorsal side. The dorsal side is connected to the overlying subgenital plate by a membrane. With the exception of the Scopuridae, which are without a ventral appendage, vesicles can be found in all families of the Euholognatha (Rupprecht 1976).

Detailed studies of the sensory hairs associated with the vesicle (Gnatzy and Rupprecht 1972, Rupprecht and Gnatzy 1974, and Rupprecht 1976), have shown them to be mechano-receptive hairs, the vesicle or hammer probably functioning to help in positioning the body during drumming, and to maintain the right frequency where the substratum is uneven or difficult.

Rupprecht (1976) went on to show that the hammer and vesicle are definitely used for drumming. In a series of experiments involving Capnia bifrons, Nemurella pictetii, and Isoperla grammatica, some or all of the mechano-receptive sensory hairs on or around the vesicle or hammer were covered with wax to render them functionless. In the case of Capnia bifrons and Nemurella pictetii the vesicle was totally removed. Drumming was recorded from insects where such modifications had been made. When compared to drumming from individuals with sensory hairs, vesicles or hammers intact any one of the following results were observed: fewer signals were produced, fewer female answers obtained probably due to shortening of all or part of the signal, leaving out parts of a signal, missing beats, cutting the signal off unfinished, fewer beats per signal, lower intensity of the signal, or a change in body position. These results clearly show that the vesicle and hammer, and the sensory hairs associated with them, are used for drumming and are crucial to the drumming of the species with these structures (Rupprecht 1976).

Stewart and Maketon (1991) have done the most recent work on the structures used for drumming. They divide stoneflies into five different groups according to these structures. I) Drumming without any special structure. II) Drumming with vesicles, agreeing with the definition given by Rupprecht (1976). III) Drumming with hammers. "Hammers represent raised discs that are variable in shape, devoid of long hairs over most of their surface and have papillar, ridged or pitted surfaces" (Stewart and Maketon 1991). The hammer as defined by these authors is not entirely identical with that defined by Rupprecht (1976) because only the ventral appendages of the Perlidae are termed hammers. Two additional terms are introduced to describe the ventral appendages of the Perlodidae and the Peltoperlidae. IV) Lobes. This term is used by Stewart and Maketon (1991) to denote the ventral appendage of some Perlodidae, and that of Kathroperla perdita (Chloroperlidae). They hypothesize that lobes have become modified from vesicles, possibly with serial homology. Rupprecht (1976) writes that the ventral appendage of Kathroperla perdita looks like a vesicle at low magnification (10x), but that at high magnification (on the order of 100x) it bears all the characteristics of a hammer. V) Drumming with knobs. This term is used for the ventral appendages of the Peltoperlidae which Stewart and Maketon (1991) state "appear to represent independent forms of drumming structures." Though Rupprecht calls these structures hammers, he states that they form an exception being "passively movable, presumably as the result of reduction," as opposed to the immovable hammers of the other Systellognathan families. Research done after Rupprecht's work supports the use of the term knob in the Peltoperlidae, as six species have developed a derived form of drumming called rubbing (Stewart and Maketon 1991). No mention is made by Stewart and Maketon (1991) of brushes, and the one species they list which Rupprecht (1976) describes as having a brush, is described as having no ventral lobe, vesicle or hammer. Table 1 summarizes the terminology reviewed here.

Table 1. Terminology of structures used for drumming

Group	Family	Rupprecht (1976)	Stewart and Maketon (1991)
Euholognatha	Leuctridae	vesicle	vesicle
	Capniidae	"	"
	Nemouridae	"	"
	Notonemouridae	"	"
	Taeniopterygidae	"	"
	Scopuridae	no special structure	no special structure
Systellognatha	Chloroperlidae	brush or no special structure	lobe or no special structure
	Perlidae	hammer	hammer
	Perlodidae	hammer	lobe
	Peltoperlidae	hammer	knob
	Pteronarcyidae	no special structure	no special structure

IV. Species Specificity and Dialects

The success of stonefly drumming as a method of mate location is dependent on the species specificity of the drumming signals. The value of stonefly drumming in systematics is also dependent on this. Rupprecht (1968) mentioned that the investigated species drummed with a frequency and duration specific to that species. Later, he investigated this further finding that the drumming of three *Perla* species and four *Isoperla* species were mutually distinguishable (Rupprecht 1969). He also placed males of one species with females of another species within the same genus, and found that males only receive answers from females of the same species.

Stewart, Szczytko and Maketon (1988), in a study of the drumming of members of the genera *Isoperla*, *Pteronarcys*, and *Taeniopteryx*, found all signals to be species specific. Discussing drumming in these three genera and the drumming of other stonefly groups reported in the literature Stewart, et al., (1988) conclude that statistical overlap between species is usually limited to one parameter. Where the drumming of both sexes of a species is known, overlap is usually limited to one sex. They correctly point out that statistical overlap in one parameter need not have any biological significance. To test this, they propose testing the response of live stoneflies to computer-simulated drumming signals where parameters can be varied through a range of values (Stewart et al., 1988). This is important to determine if drumming is to be used as a method of species delineation, especially where cryptic or sibling species are involved. This method can also help determine which parameters contain important recognitional information and which are less important (Stewart and Zeigler 1984). This has been tested for only a few species (Zeigler and Stewart 1986, Hassage, Stewart, and Zeigler 1988, and Stewart and Maketon 1990). Female responses to modified computer-simulated signals tend to be consistent with the natural variation present in drumming parameters in male signals (Stewart and Maketon 1990, Hassage et al. 1988). Females appear to respond to signals containing a minimum threshold of beat number or rub number, and more importantly, responding to specific windows of beat intervals (Stewart and Maketon 1990). It is well known that temperature affects drumming signals and it has been suggested that male call variations may serve to compensate "mechanical error and environmental temperature variation yet retain species integrity" (Hassage et al. 1988). Cooler temperatures result in slower movements (Hassage et al. 1988). Other descriptive studies of stonefly drumming all show strong species specificity in important drumming parameters (Rupprecht 1968, 1982, 1977, Zeigler and Stewart 1977, Snellen and Stewart 1979, Szczytko and Stewart 1979, Stewart, Szczytko, and Stark 1982, Stewart, Szczytko, Stark and Zeigler 1982, Maketon and Stewart 1984a, Stewart and Zeigler 1984, Zeigler and Stewart 1985).

Another question raised by Stewart, Szczytko, and Maketon (1988) is how well do statistics of important signal variables typify a species throughout its range. This raises the question of dialects which have been found for several species. The first evidence of dialects was found by Rupprecht (1972). He found significant differences in the frequency of male signals of Diura bicaudata between German populations and a population in Swedish Lapland. Stewart, Szczytko, and Stark (1982) reported dialects in Colorado and Alaska populations of Pteronarcella badia, both males and females having fewer drumbeats and shorter beat intervals in the Alaska population. This despite recording temperatures of 3^{o} C lower than for the Colorado population. Zeigler (1989) found intraspecific divergence in drumming signals of geographically separate populations of Tallaperla maria and Pteronarcys biloba. The most marked difference in drumming between two geographically separated populations of the same species is that reported by Rupprecht (1982) for Danish and German populations of Capnia bifrons (see p.42). These studies demonstrate the importance of continued investigations of the drumming signals of species even if drumming from them has been described earlier. Drumming signals from new localities may yield important information on intraspecific variation and/or dialects.

V. Stonefly Phylogeny and Classification

The stoneflies are a very old order of insects dating as far back as the Permian (Illies 1965). Several attempts have been made to determine the interfamilial relationships within the order (Tillyard 1921, Frison 1935, Ricker 1950, 1952). A general view of stonefly phylogeny did not appear, however, until the work of Illies (1960, 1961, 1965, 1966). Illies (1960) introduced a new suborder of Plecoptera, the

Archiperlaria, defining it as the most plesiomorphic state, the members of the two already existing suborders, the Setipalpia and the Filipalpia representing more apomorphic forms. On the basis of the existing information on extant and fossil forms of Plecoptera, the latter having been greatly increased by then recent finds in the Paleozoic layers of the Kusnetzk basin in Siberia, Illies (1965) proposed a family tree to show interfamilial relationships within the order (see fig. 5). Zwick (1974) pointed out that by reviewing the literature one finds that there has never been any controversy concerning the classification of stoneflies at the family level. The difficulties have always lain in determining the interfamilial relationships. The reason for this, according to Zwick, was due to the difficulty in delimiting the suborders Setipalpia and Filipalpia, both of which stemmed from pre-Darwinistic classification. Nonetheless, both had been treated as phylogenetic units. Zwick (1969, 1973) greatly simplified this work by defining two entirely new suborders, the Arctoperlaria and the Antarctoperlaria. Using the method of Hennig (1966), Zwick (1973) constructed a new phylogenetic tree on the basis of a general study of stonefly morphology (Fig. 6). The old suborder Setipalpia he considered a superfamily of the Arctoperlaria, and the Filipalpia a "polyphyletic assemblage" (Zwick 1974). He later revised this system somewhat (Zwick 1980). This view of stonefly phylogeny is now widely accepted (Zwick 1981). Brodskiy (1982) describes a third

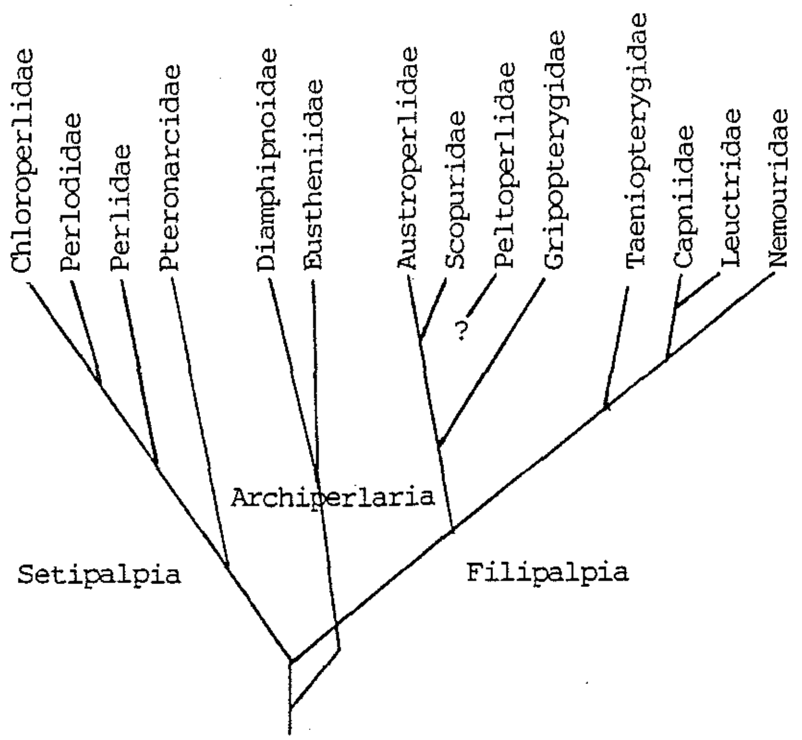


Figure 5. Stonefly phylogeny according to Illies (1965).

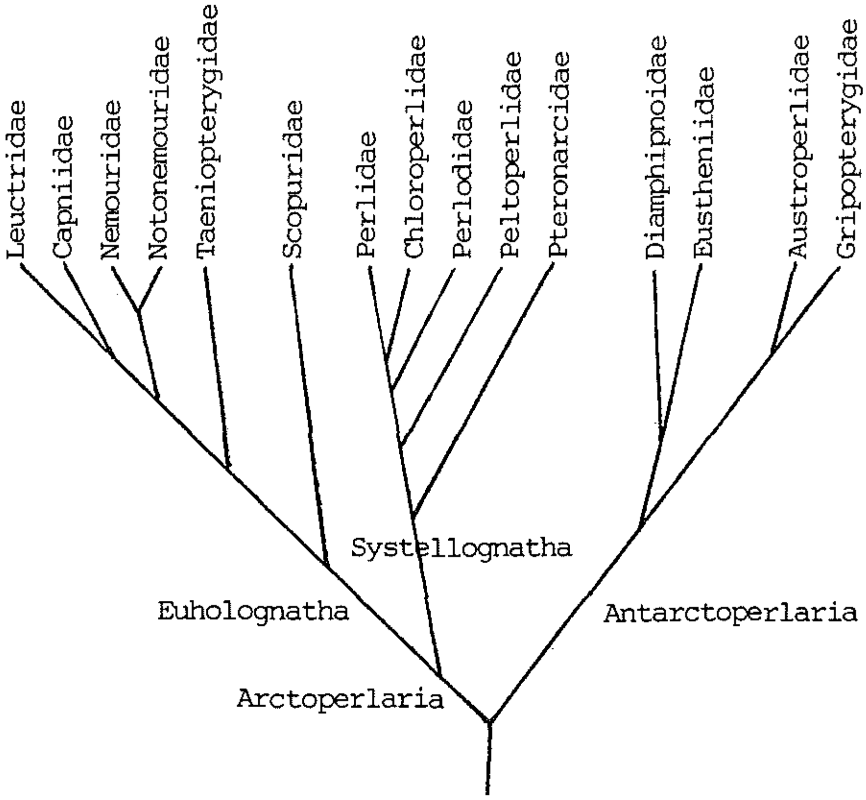


Figure 6. Stonefly phylogeny according to Zwick (1973).

view, dividing the order into two different groups, on the one hand the Eusthenioidea and the Systellognatha, and on the other the Gripopterygoidea and the Euholognatha. Nelson (1984) made a reassessment of the phylogenetic relationships of the stoneflies using a mathematical cladistic approach with the help of a computer. Using the character data and assessment of polarity used by Zwick (1980), with slight modifications, and the Wagner Parsimony Method he attempted to find the most parsimonious phylogenetic tree for the given data. He found six phylogenetic trees which were equally parsimonious, and comparing these to the work done by Ricker (1952), Illies (1965), Zwick (1980), and Brodskiy (1982), found the closest agreement with the work of Zwick and Brodskiy. He concluded that resolution of incongruities among the various phylogenetic trees must be resolved through the acquisition of additional characters (Nelson 1984).

Zwick (1974) has noted that the number of stonefly species recognized rose by 15% between 1966 and 1972 and that one may assume it will steadily increase for a long time yet. This may lead to the discovery of additional characters, however a much more immediate source of additional characters is already at hand in the existing and ever increasing data on stonefly drumming.

VI. The Use of Drumming in Stonefly Systematics and Evolution

Stewart and Zeigler (1984) have pointed out that drumming "is a fixed action behavior among groups like Pteronarcyidae and Perlidae . . . and that it represents homologous behavioral traits." In light of the discussion of drumming above there seems little doubt that this is also true of other groups of stoneflies who drum. This would be a necessary precondition for the use of drumming information in phylogenetic analysis. More difficult is the problem of defining true pair forming characters which are useful in such an analysis. Preliminary attempts at assigning characters and character states (determining plesiomorphy or apomorphy of characters) have been made in studies which are generally of a more descriptive nature (Maketon and Stewart 1984b, Stewart and Zeigler 1984). This was largely due to the relatively few drumming signals that had been described. As late as 1987 drumming had only been described for ca. 5% of the world's stonefly species (Zeigler and Stewart 1987). Nonetheless, more recent work has attempted to formulate general relationships on the basis of all the existing data (Zeigler and Stewart 1987, Maketon and Stewart 1988), and a hypothesis of stonefly drumming evolution has been proposed by Maketon and Stewart 1988).

In formulating their hypothesis of stonefly drumming evolution, Maketon and Stewart (1988) utilize the out-group comparison method of character analysis (Watrous and Wheeler 1981). Maketon and Stewart (1988) propose seven pair forming characters based on a survey of the drumming of 104 species. Since drumming is unknown in other orthopteroid neopterous groups, Maketon and Stewart (1988) believe that non-drumming is the ancestral state in Plecoptera. A difficulty arises in assigning the character "non-drummer" to a species. A species need not be a non-drummer simply because it has never been observed to drum in the lab. No member of the suborder Antarctoperlaria has yet been observed to drum though several attempts have been made. It is generally believed that members of this suborder are non-drummers (Maketon and Stewart 1988). Apart from drumming vs. non-drumming the characters are based on the following attributes: 1) method of signal production (tapping, rubbing, tremulation), 2) character of the male call (stroke phasing, stroke grouping), 3) male-female exchange pattern (sequenced or interspersed), and 4) character of the female answer (small or large number of taps) (Maketon and Stewart 1988).

Defining the Arctoperlaria group the Euholognatha as the Taxonomic Out Group and the Systellognatha as the Taxonomic In Group they show that rubbing, tremulating, beat grouping, beat phasing, interspersed exchange and prolonged female answers are strong derived characters found mainly in the Systellognathan families. Maketon and Stewart show that the Pteronarcyidae show no derived characters in their drumming behavior and are therefore more closely similar to the Euholognatha than to the other families of the Systellognatha.

Additional characters and additional descriptions of stonefly drumming should furter elucidate interfamilial relationships within the Plecoptera. Whereas the drumming signals of as many as 30 to 40 species of the Perlodidae and the Perlidae form the basis of Maketon and Stewart's study, drumming signals of less than 10 species are used in the Taxonomic Out Group the Euholognatha. It may well be that as we learn more about Euholognathan stonefly drumming the hypothesis of Maketon and Stewart (1988) may need revision.

VII. Materials and Methods

Stoneflies were collected in the field mostly as adults. In the case of Capnia bifrons, nymphs were collected and reared to adulthood in the lab to give virgin females. This was not necessary for Capnia atra. The adults found in the field of this species were only lightly sclerotized, indicating that they were newly emerged and had not yet mated. This was confirmed in the lab when drumming was recorded for several females. For other species females collected as adults either drummed or it was not possible to rear nymphs in the lab. Table 2 shows a list of localities where stoneflies used in this study were collected. In Table 3 the species collected, dates and number of individuals collected, the number of individuals that drummed and the number of signals analyzed are listed. Figure 7 shows a map of southern Norway with the localities where stoneflies were collected.

The stoneflies were kept alive in small vials with a drop of water under the lid, and a piece of a dead leaf inside for them to grasp and eat (in those groups that eat as adults). In the lab the stoneflies were kept in a refrigerator at around 10-11° C. At Øvre Heimdalen the

Table 2. Localities where stoneflies were collected

Locality	County	S=Stream L=Lake	m above sea level	Vegetation zones, regions, and belts	Dominant vegetation along streams and lakes
1	Vestfold	S. Prestegårdsbekken, Tjøme	5-10	Boreo-nemoral zone	Alnus, Fraxinus, Salix
2	Rogaland	S. Suldalslågen	60	N.-Atl. Pine-Birch Woodl. and Heath region	Alnus, Salix
3	Oslo	S. Lutdalsbekken, at Nøklevann	150	Boreo-nemoral zone	"
4	"	S. Sognsvannsbekken	183	"	"
5	Akershus	S. Lomma near Oslo	160	"	"
6	Hedmark	S. Glomma at Grindalen	180	Sub-Arctic and Boreo-mont. subzone	"
7	"	S. at Lake Istern	645	"	"
8	Oppland	S. Neselven at Osen	380	"	"
9	"	S. Leirelven near Leirinn	700	"	"
10	"	S. Main inflow Lake ØH*	1090	Sub-Alpine belt	Salix
11	"	L. ØH*	1090	"	"
12	"	S. Outflow L. ØH*	1090	"	"
13	"	S. at L. ØH*	1090	"	"
14	"	S. at Valdresflya	1400	Low-Alpine belt	mainly grass

* ØH= Øvre Heimdalsvann

Table 3. List of stonefly material used in this thesis

Species	Locality*	Date collected	No. of ind. collected and tested		No. of ind. that drummed		No. of signals analyzed	
			♂	♀	♂	♀	♂	♀
Diura bicaudata (Linnaeus, 1758)	12	11-VI-91	3	1	2	–	5	–
"	14	13-VII-91	6	–	6	–	17	–
Isoperla grammatica (Poda, 1761)	9	8-VII-91	2	3	2	–	52 (4 series)	–
"	12	12-VII-91	4	9	3	3	15 (3 series)	8 (2 series)
Isoperla obscura (Zetterstedt, 1840)	12	19-VII-91	5	–	2	–	8	–
Dinocras cephalotes (Curtis, 1827)	8	11-VII-91	7	3	6	1	29	7
Siphonoperla burmeisteri (Pictet, 1841)	9	8-VII-91	10	6	–	–	–	–
Taeniopteryx nebulosa (Linnaeus, 1758)	5	2-IV-91	1	–	1	–	15	–
Nemoura avicularis Morton, 1894	11	9-VI-91	10	4	–	–	–	–
Nemurella pictetii Klapálek, 1900	11	20-VII-91	3	2	2	–	–	–
Protonemura meyeri (Pictet, 1841)	10	20-VII-91	2	4	1	–	–	–
Capnia atra Morton, 1896	6	6-IV-91	7	8	4	3	12	11

*See Table 2.

Table 3. (cont.)

Species	Locality	Date collected	No. of ind. collected and tested		No. of ind. that drummed		No. of signals analyzed	
			♂	♀	♂	♀	♂	♀
Capnia atra Morton, 1896	11	10-VI-91	8	8	4	5	12	6
Capnia bifrons (Newman, 1839)	1	27-II-90 and 27-III-90	24	23	11	6	18	6
"	13	25-V-90	16	6	14	4	12	5
Leuctra fusca (Linnaeus, 1758)	4	24-VIII-91	8	8	-	-	-	-
Leuctra hippopus Kempny, 1899	7	3-IV-90			5	-	11	-
"	2	30-III-90	31		11	-	19	-
"	3	6-IV-90	30	10	11	-	17	-
Leuctra nigra (Olivier, 1811)	10	18-VII-91	8	1	-	-	-	-

vials were stored outdoors to maintain a natural temperature.

The equipment and procedures for recording stonefly drumming used in this study were similar to those used by Ørmen (1991). The signals were recorded on cassette tapes using a Sony TC-D5M Cassette Recorder. A Sony ECM-30 electret condenser microphone was mounted into the bottom of a plastic box with a lid. The box was partially sound proofed using foam rubber. The sensor of a small digital thermometer was placed next to the microphone in the box. Stonefly drumming has been shown to be temperature dependent (Zeigler and Stewart 1977). The temperature in

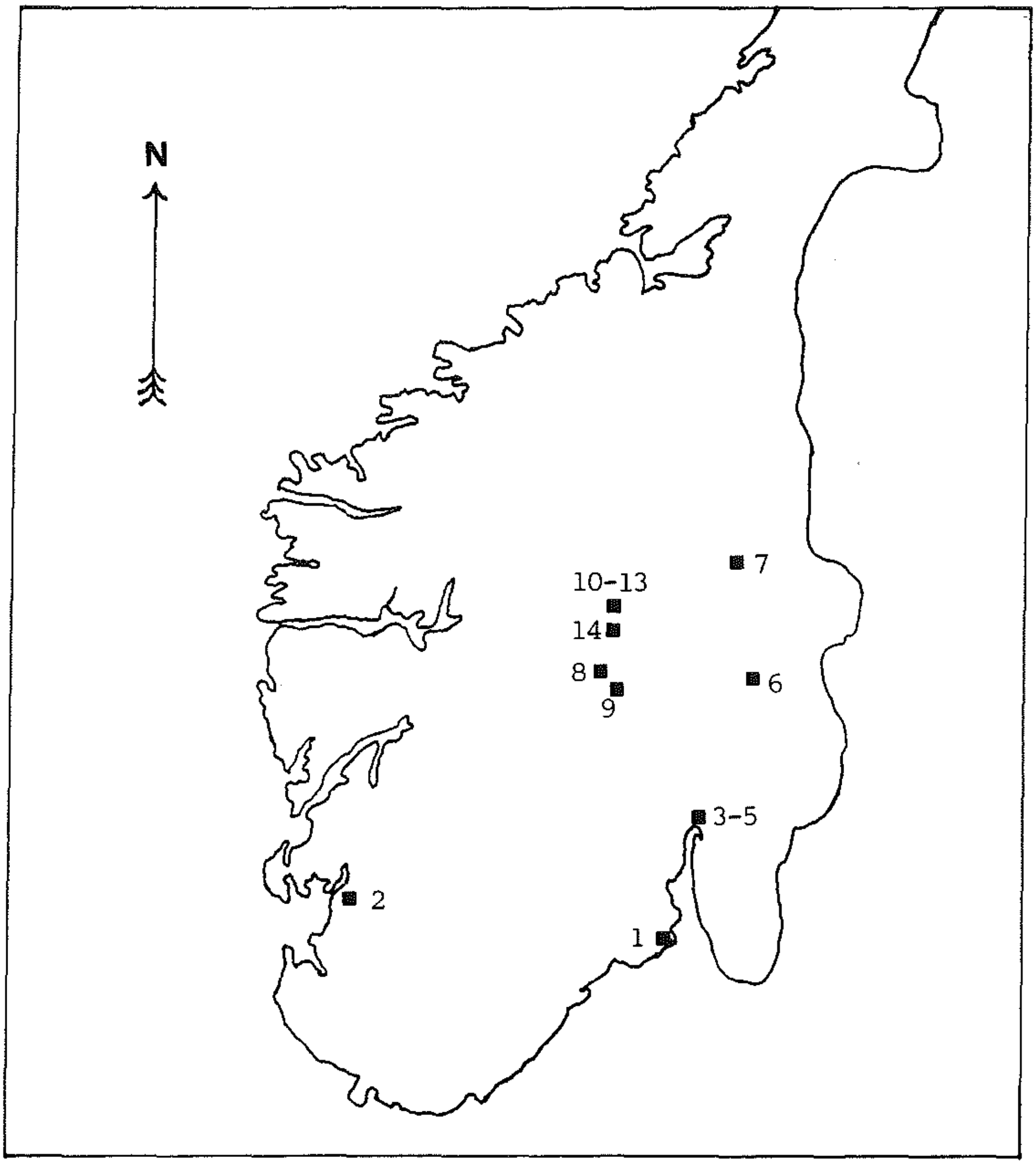


Figure 7. Map of southern Norway showing localities where stoneflies were collected. Numbers refer to locality numbers in Table 2.

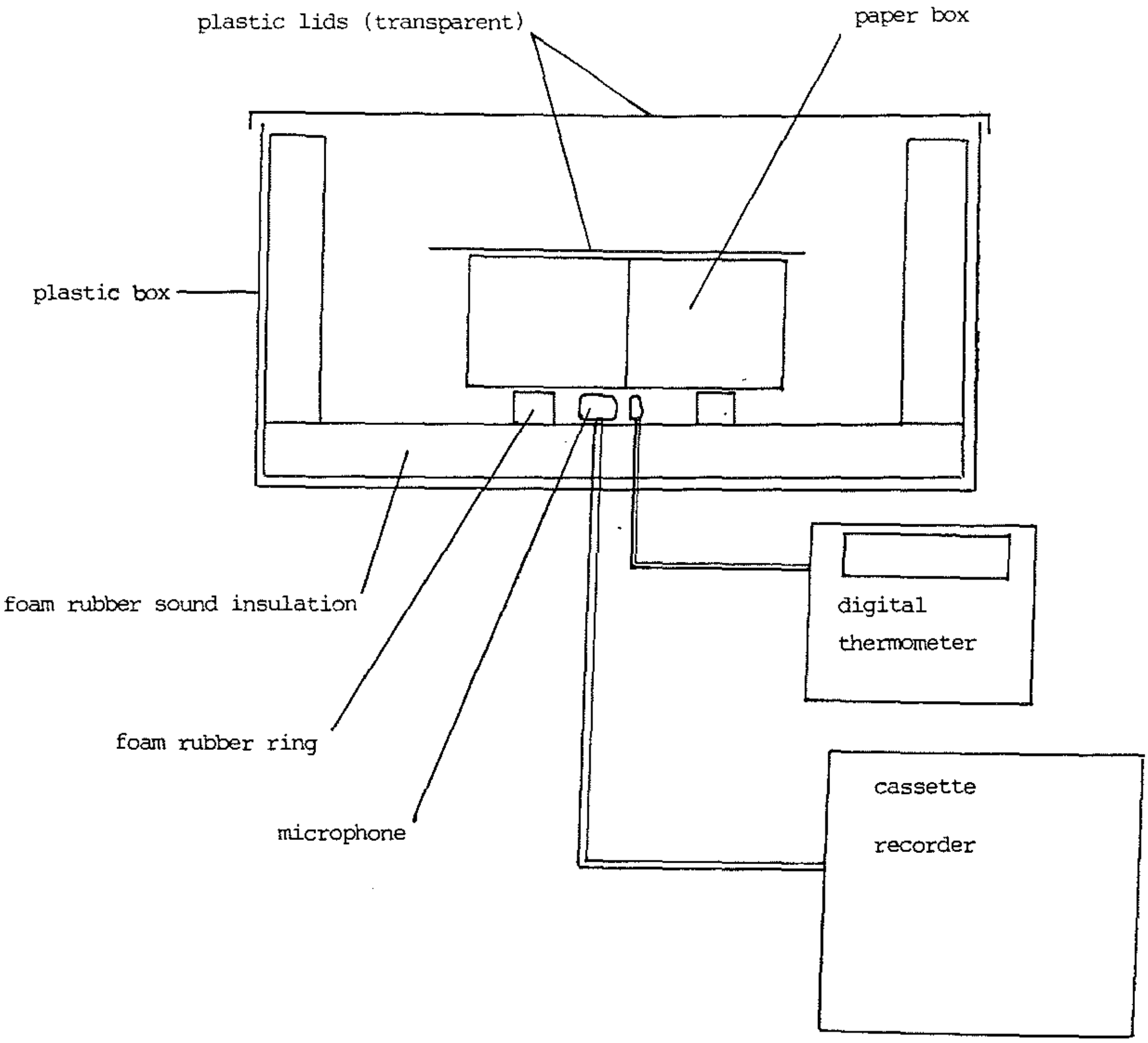


Figure 8. The apparatus used for recording drumming signals.

the recording chamber was therefore noted during each recording session. A ring of thin foam rubber was placed around the microphone/thermometer such that a small paper box rested directly above the microphone without coming into contact with it. The paper box was constructed using a regular piece of typing paper and glue. The box contained two separate compartments such that drumming from pairs of males and females could be recorded simultaneously. A thin piece of transparent plastic served as a cover for the paper box and prevented the insects from escaping, while allowing them to be observed. This paper box was used for all species with the exception of Dinocras cephalotes. A similar box specially constructed to be big enough for this species had to be made. The lid of the plastic box was also transparent. Figure 8 shows a drawing of the apparatus used.

The recorded signals were analyzed using a Nicolet 3091 Digital Storage Oscilloscope. The cassette recorder was connected directly to the oscilloscope, the signals being stored on the screen and measurement of beat intervals, frequency etc., made possible. Hard copies of some of the signals were obtained using an Hioki 8811 Memory Hi-corder, with the exception of the signals of Capnia bifrons, made with the oscillograph belonging to Dr. Rainer Rupprecht, Universität Mainz. Some aliasing distortion is present in some of the print-outs made with the Hioki 8811. This is due to the fact that the digital printer samples the signals at a higher frequency than that of the signals themselves. This results in the amplitudes of the drumming signals forming sine curves, especially those signals of low frequency. This is, however, only an artifact of the printer, not the signals themselves. Important drumming parameters such as beat interval, duration etc., are still fully readable from the graphs. An example to illustrate aliasing distortion in an extreme case is shown for Capnia atra in Figure 22.

The live stoneflies were taken out of the refrigerator for recording. Two individuals at a time were placed in the box in separate compartments and the cassette recorder turned on, ideally with one male and one female in each compartment of the paper box. Where identification of the sex of live animals was difficult or impossible, the insects were placed in the box without regard to sex. Individuals that drummed spontaneously were then assumed to be males and left in the recording chamber in the hope that they would stimulate other individuals, male or female, to drum. Pairs were usually exchanged with others if drumming was not obtained after about an hour. Where possible, individuals were tested for drumming more than once, and over a span of a few days. In some species, adults have been known to wait up to one week after emergence before beginning mating behavior. This has been reported both for a Norwegian and a German population of Leuctra hippopus (Ørmen 1991), and for Euleuctra geniculata (Elliott 1987). Ørmen (1991) found significant electrophoretical differences between premature and mature adults of Leuctra hippopus from Nøklevann, Oslo. An attempt was also made to vary the time of day when recordings were made. However, the number of species involved, often at the same time, and the separation of different localities, made it impossible to carry this through systematically and thoroughly.

The most avid drummers drummed shortly after being placed in the box. In the case of Dinocras cephalotes drumming was observed and heard with the "naked ear" even in the containers they were stored in. For other species, however, the individuals were stimulated to drum either by a verbal imitation of drumming signals or an artificial signal produced using a tweezers. Verbal drumming imitations were made the way the species drums at other localities or the way other species of the same genera drum, under the assumption that closely related species drum more similarly than distantly related ones. This did not always give results, even for species which later drummed spontaneously.

All species collected were later stored in 70% alcohol and definite species and sex identifications were made later in the lab.

Definitions of drumming terminology associated with the method of signal production and type of call have been given by Stewart and Maketon (1991). The definitions of some of these terms are presented here. The first group of terms is associated with the type of call.

Monophasic - a single phased male call followed by a female answer.

Simple diphasic - a call with two groups of unequally spaced beat intervals , the second group consisting of fewer than four beats.

Diphasic - a call with two groups of unequally spaced beat intervals.

Bi-grouped - a call with two groups of equally spaced beat intervals.

Grouped - a call of several groups of two or more single beats.

Grouped bi-beats - a highly specialized call of several groups of 1 - 2 bi-beats.

The second group of terms is associated with the method of signal production.

Tapping - the abdomen is used to strike the substratum.

Rubbing - the abdomen is rubbed across the substratum, the papillar or ridged surface of the hammer or knob producing a stridular signal.

Tremulating - the body and abdomen are jerked vertically without touching the substratum.

As mentioned earlier, tremulation has only been observed in the genus Siphonoperla. Rubbing has been observed in the Peltoperlidae and the Perlidae possessing knobs or hammers. Tapping has been observed in all groups with or without specialized drumming structures, and is by far the most common method of signal production.

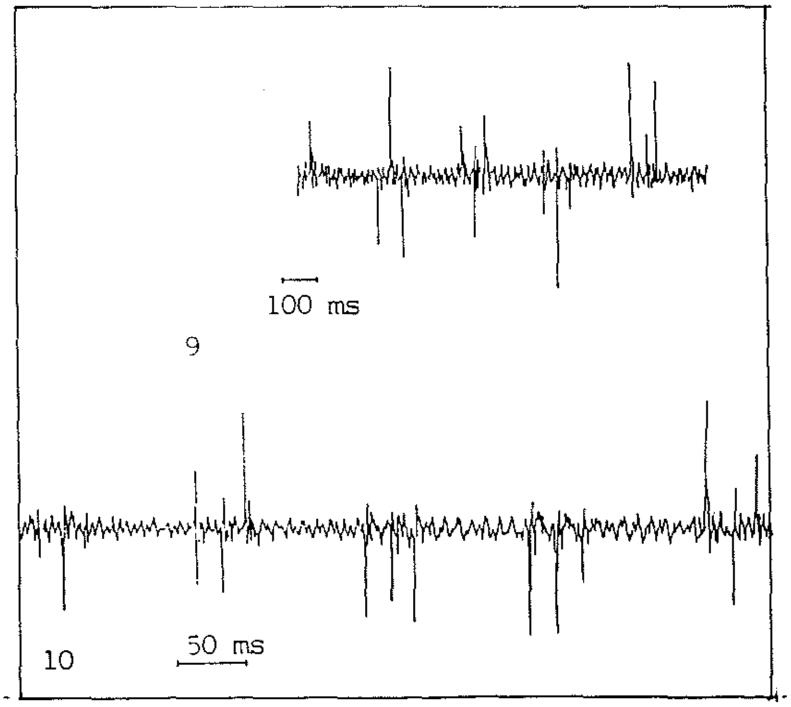
VIII. Results

All the species investigated in this study were found to be tappers. Table 3 shows how many individuals of each species were collected, how many that drummed and the number of signals analyzed. In some cases the number of individuals and signals is small, but as Maketon and Stewart (1988) have noted, even a small number of signals is sufficient to reveal the basic character of the signals of a given population, though they do not allow a description of the behavioral variation of the population or species. In some cases, e.g. *Isoperla grammatica* a relatively small number of sequences have been analyzed due to the complex structure of the signals and the time consuming nature of the analysis. A detailed analysis of a few sequences was preferred to a superficial description of many. All numbers in this section are means ± standard deviation (SD).

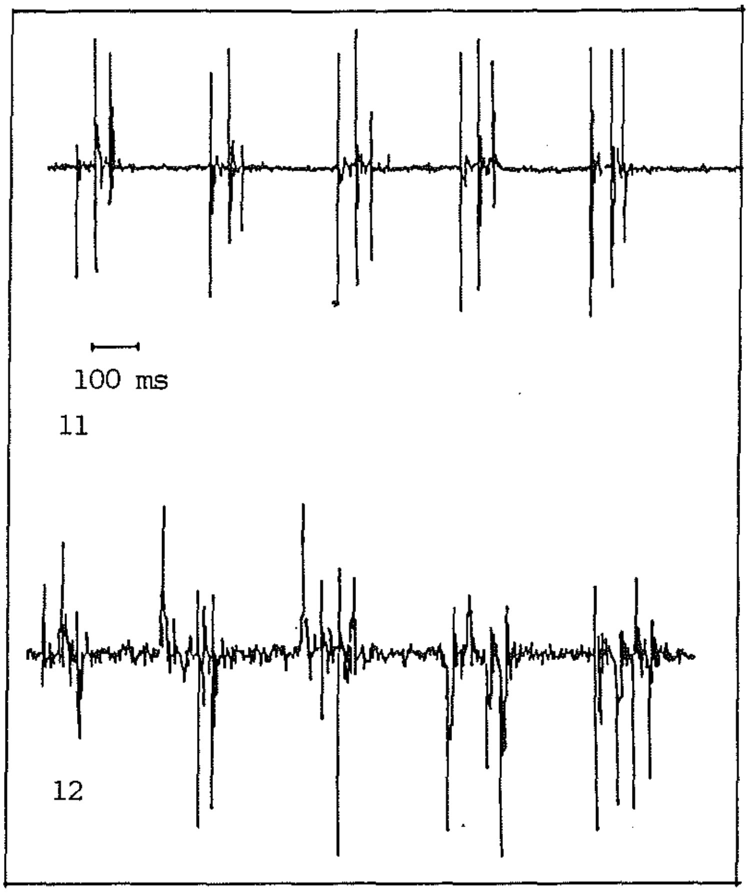
Group Systellognatha

Family Perlodidae

1. *Diura bicaudata*. The signals of *Diura bicaudata* normally consist of five groups of 2 - 4 beats. The signals from the population at Øvre Heimdalen (loc. no. 12) consisted of on average 5.2 ± 0.5 groups



Figs. 9 and 10. Two examples of the male signals of *Diura bicaudata* from Heimdalen.



Figs. 11 and 12. Two examples of the male signals of *Diura bicaudata* from Valdresflya.

of 2.65 ± 0.63 beats. Each group had an average frequency of 39.7 ± 4.3 beats/sec. The total signal duration was 1.11 ± 0.24 sec. Four beats in a group did not occur.

The signals from the population at Valdresflya (loc. no. 14) consisted of an average of 5.7 ± 1.5 groups of 3.02 ± 0.71 beats. The groups had an average frequency of 38.2 ± 6.9 beats/sec. The total signal duration was 1.56 ± 0.60 sec. Recording temperatures ranged from 16 - 21° C. Details of the drumming signals of both populations can be seen in Table 4. Some typical drumming signals are shown in Figures 9 - 12.

2. *Isoperla grammatica*. The male call consists of a sequence or series of diphasic signals. The male signals of the Leirelven population (loc. no. 9) consisted of a slow first part of 2 - 5 beats (only one male included 5 beats and only once), and a second much more rapid part consisting of an average of 5.8 ± 1.5 beats with a frequency of 62.2 ± 16.8 beats/sec. The four series analyzed contained an average of 13.0 ± 4.8 signals/series each lasting 0.34 ± 0.10 sec. The interval between signals in a series was 0.27 ± 0.04 sec. Signals were recorded at 19° C.

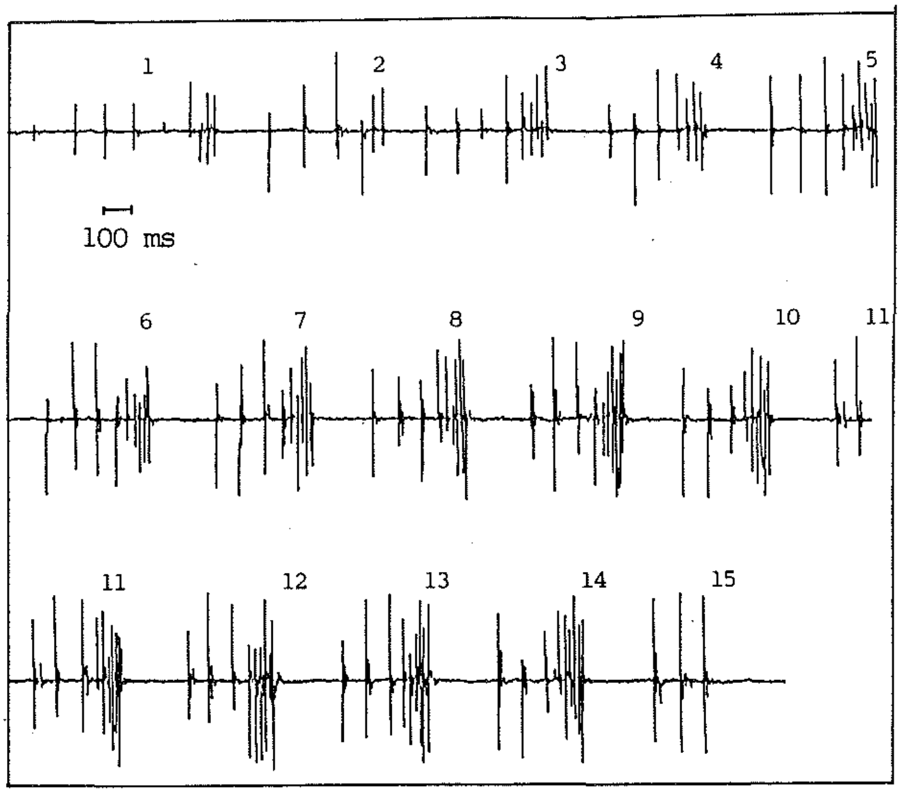


Fig. 13. A sequence of 15 drumming signals of a male of Isoperla grammatica from Leirelven. The signals are numbered in sequence.

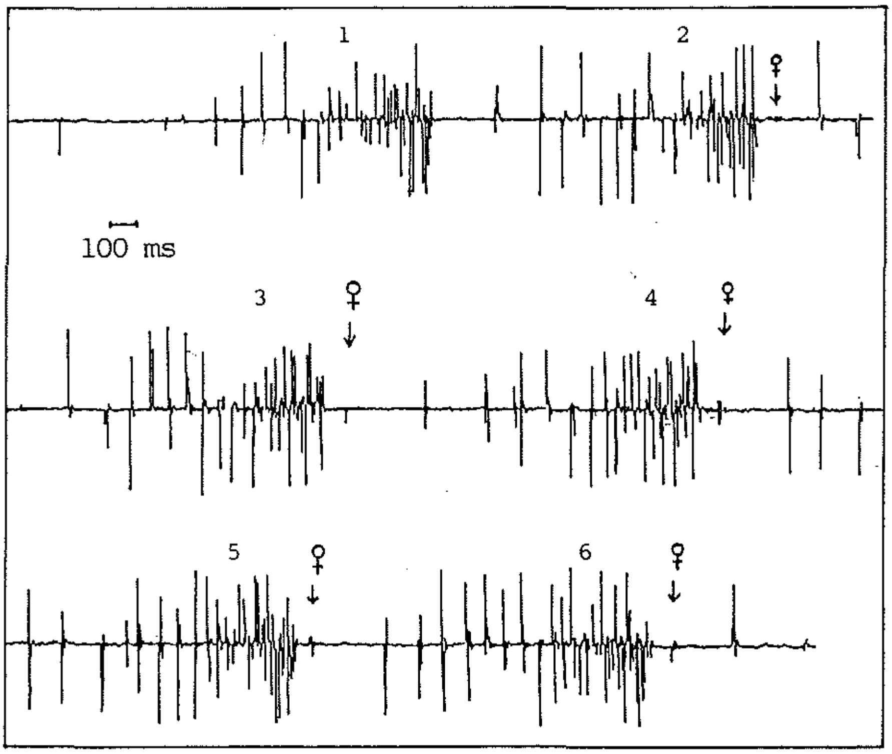
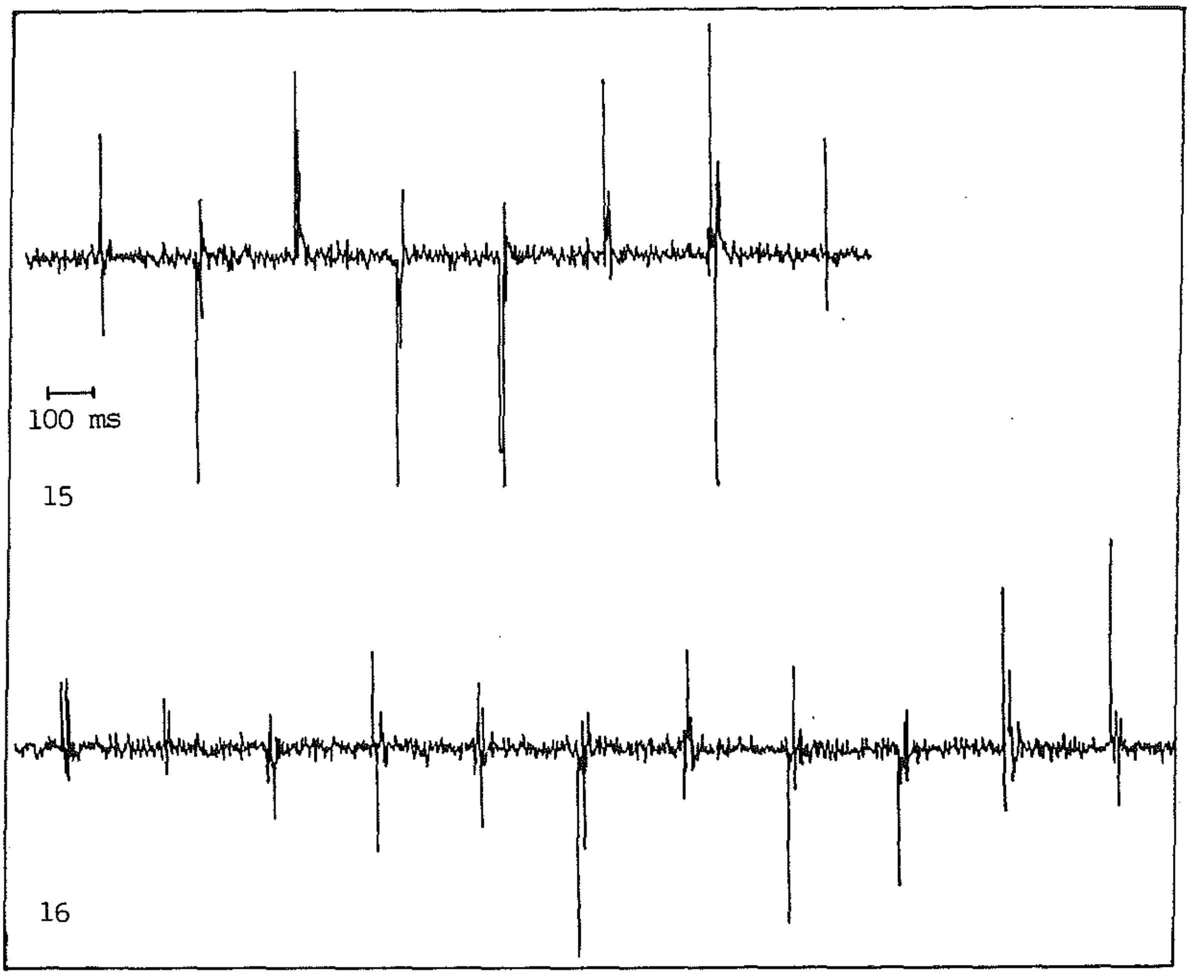


Fig. 14. A sequence of 6 drumming signals of a male of Isoperla grammatica from Heimdalen. The one beat response of the female can be seen after each male signal. The male signals are numbered in sequence.



Figs. 15 and 16. Two examples of the male signals of Isoperla obscura from Heimdalen.

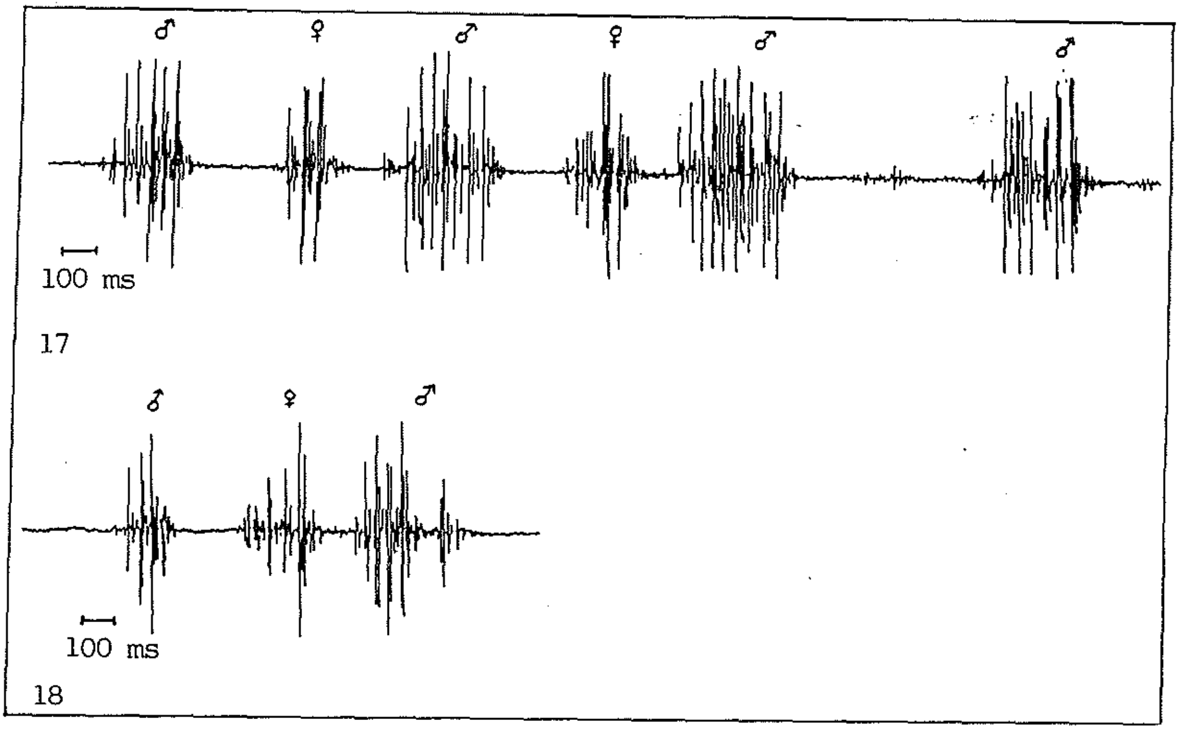
The male signals of the Øvre Heimdalen population (loc. no. 12) consisted of a slow first part of 3 - 17 beats followed by a much more rapid part consisting of an average of 14.9 ± 7.5 beats with a frequency of 102.9 ± 28.4 beats/sec. The three series contained an average of 5.0 ± 1.0 signals/series, each signal lasting 0.17 ± 0.10 sec. The interval between signals in a series was 0.25 ± 0.08 sec. The females of this population answered with one beat between each signal in a series. The single female beat followed the male signal by an average of 0.08 ± 0.03 sec. Recording temperatures ranged from 21 - 24 ° C. Drumming signals of Isoperla grammatica are shown in Figures 13 and 14. Further details of the drumming signals are listed in Table 5.

3. Isoperla obscura. The male signals consist of simple monophasic tapping. They consisted of an average of 9.2 ± 2.2 beats and lasted 2.01 ± 0.55 sec. The frequency of the signals was 4.67 ± 0.34 beats/sec. Recording temperatures were 21 - 24° C. Details of the drumming signals

are shown in Table 6. See also Figures 15 and 16.

Family Perlidae

4. Dinocras cephalotes. The individual signals of both the males and females of this species consist of simple monophasic tapping. The drumming exchange between the male and female is interspersed, either of the type male-female-male, or male-female-male-female-male, the male always completing the exchange. The male signals contained an average of 5.2 ± 1.7 beats and were of a duration of 0.18 ± 0.08 sec. The average frequency of the male signals was 31.5 ± 4.6 beats/sec. The female signal followed the male signals by on average 0.28 ± 0.05 sec. The interval between a female signal and the following male signal was 0.20 ± 0.05 sec. The average frequency of the female signal was 27.0 ± 2.4 beats/sec. Recording temperatures were 21° C. Table 7 lists further details of the drumming signals. Drumming signals of Dinocras cephalotes are shown in Figures 17 and 18.



Figs. 17 and 18. Two male-female exchanges of Dinocras cephalotes from Neselven at Osen.

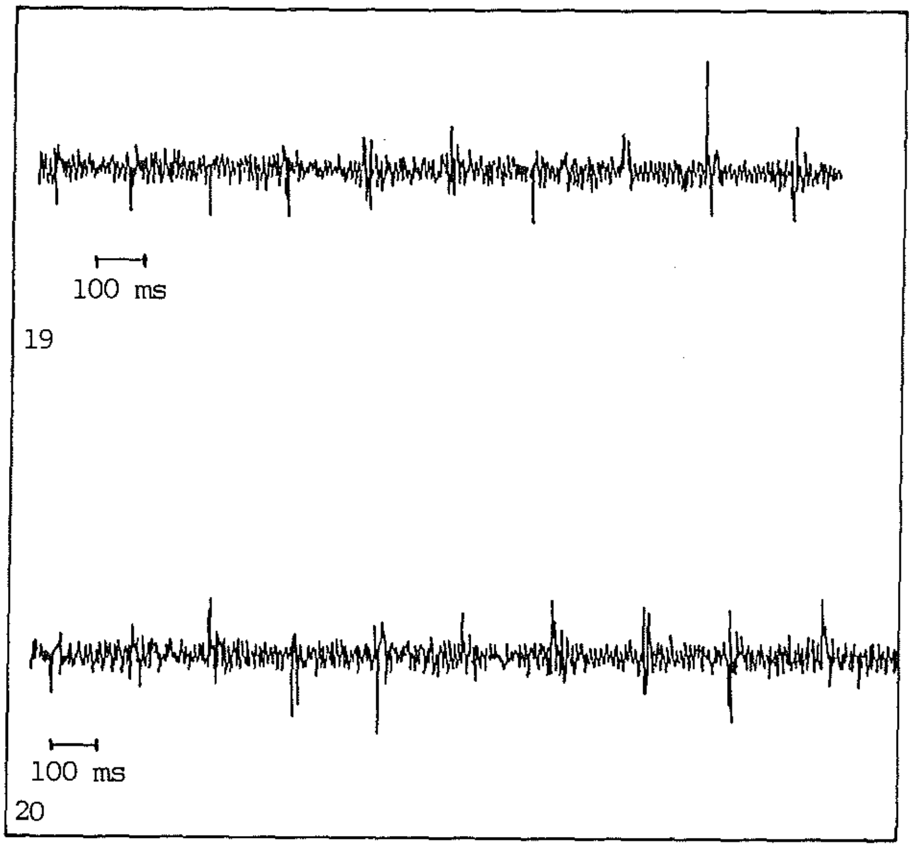
Family Chloroperlidae

5. Siphonoperla burmeisteri. Numerous efforts were made to record drumming from these insects at temperatures from 22 - 25° C. Attempts were made at various times of the day over several days. Nonetheless, no signals were obtained and no behavior similar to that of drumming behavior was observed.

Group Euholognatha

Family Taeniopterygidae

6. Taeniopteryx nebulosa. The male signals consist of simple monophasic tapping of on average 10.1 ± 0.8 beats and a duration of 1.7 ± 0.2 sec. The average frequency of the signals was 5.9 ± 0.7 beats/sec. Signals were recorded at 20° C. Further details of the drumming signals are listed in Table 8. See also Figures 19 and 20.



Figs. 19 and 20. Two male drumming signals of Taeniopteryx nebulosa from Lomma.

Family Nemouridae

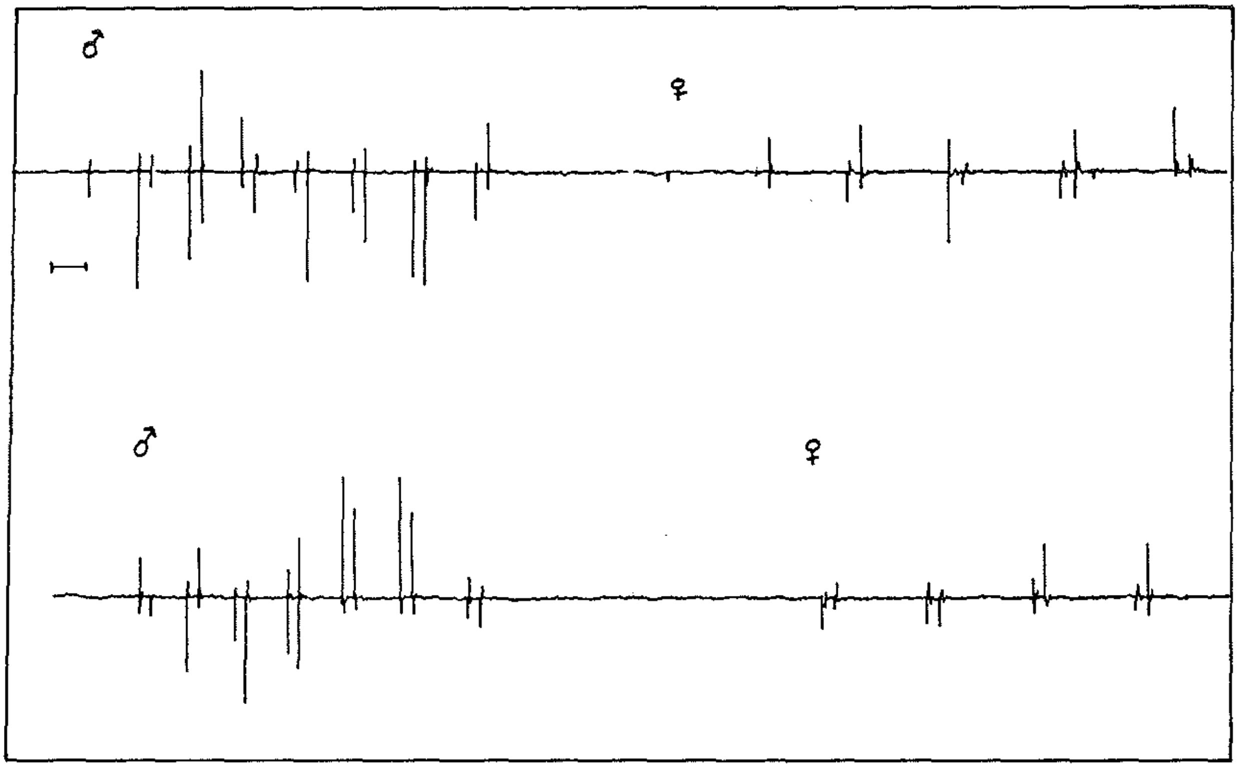
7. Nemoura avicularis. Attempts to record drumming over a six day period at temperatures ranging from 15 - 24° C. were made. No signals were obtained.

8. Nemurella pictetii. Ten signals were obtained from 2 males at 24° C. The signals were so weak that further analysis on the oscilloscope was impossible. The signals were very similar, however, to those signals described by Gnatzy and Rupprecht (1972) for Nemurella pictetii.

9. Protonemura meyeri. Two signals were recorded from 1 male, but, unfortunately, like the signals of Nemurella pictetii, the signals were too weak for further analysis. The signal seemed to consist of 4 or 5 taps, and the first time the male drummed this was repeated twice, the second time only once. Recording temperatures were 20° C.

Family Capniidae

10. Capnia atra. The drumming signal is a grouped bi-beat signal, consisting of a series of closely spaced double knocks (bi-beats). The male call of the Øvre Heimdalen population (loc. no. 11) consisted of an average of 7.8 ± 0.9 bi-beats lasting 1.6 ± 0.3 sec. The interval between the male call and the female answer was on average 0.7 ± 0.3 sec. The female signals contained 4.5 ± 0.8 bi-beats and lasted 1.2 ± 0.3 sec.



Figs. 21 and 22. Two examples of a male call followed by a female answer of Capnia atra from Heimdalen. The male call in fig. 22 shows an example of aliasing distortion (see text).

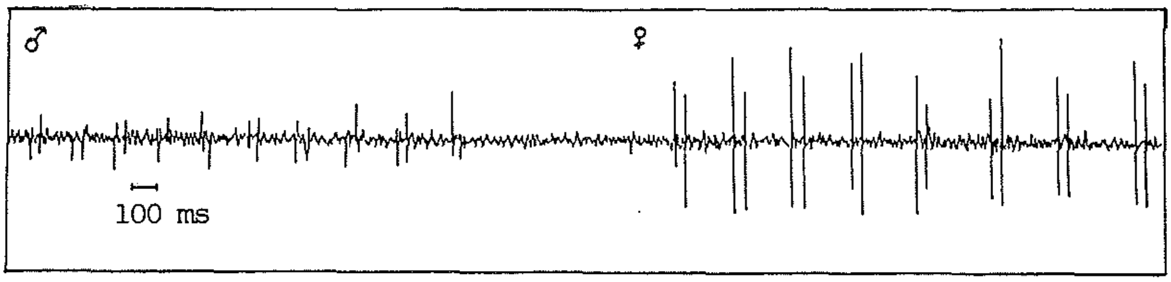
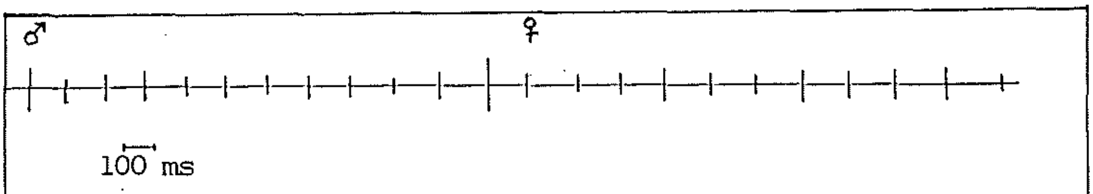


Fig. 23. Male call and female answer of Capnia atra from Grindalen.

The male signals of the Grindalen population (loc. no. 6) consisted of 8.0 ± 1.3 bi-beats lasting 1.5 ± 0.3 sec., and the interval between the male call and the female answer was 0.9 ± 0.4 sec. The female signals consisted of 5.7 ± 1.9 bi-beats lasting 1.6 ± 0.5 sec. Recording temperatures ranged from 18 - 21° C. Drumming signals of Capnia atra are shown in Figures 21 - 23, and further details of the drumming signals are listed in Table 9.

11. Capnia bifrons. Both males and females drum with a monophasic tapping signal. The male signal from the Tjøme population (loc. no. 1) contained on average 7.8 ± 1.7 beats and lasted 0.9 ± 0.3 sec. The frequency of the signals was 9.0 ± 1.7 beats/sec. and the interval between the male signal and the female answer was 0.5 ± 0.1 sec. Females drummed with 9.2 ± 2.5 beats and a signal duration of 1.2 ± 0.4 sec. The frequency of the female signals was 7.8 ± 1.5 beats/sec.



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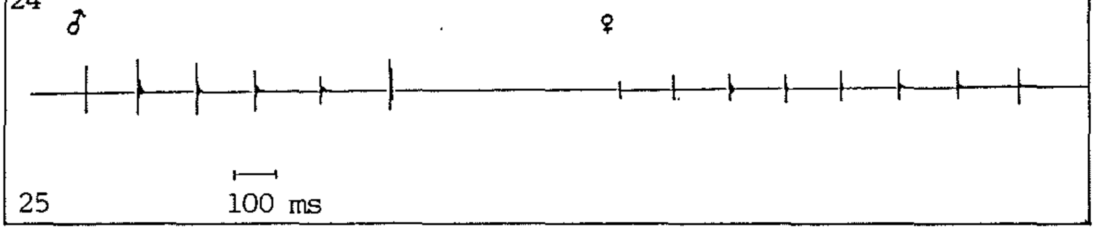

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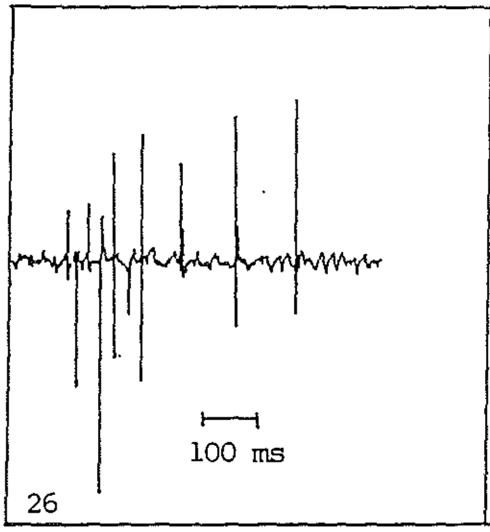
Fig. 24. Male call and female answer of Capnia bifrons from Tjøme.
Fig. 25. Male call and female answer of Capnia bifrons from Heimdalen.



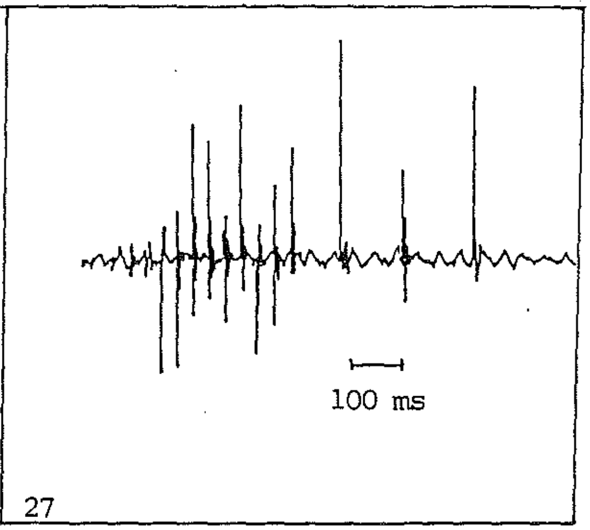
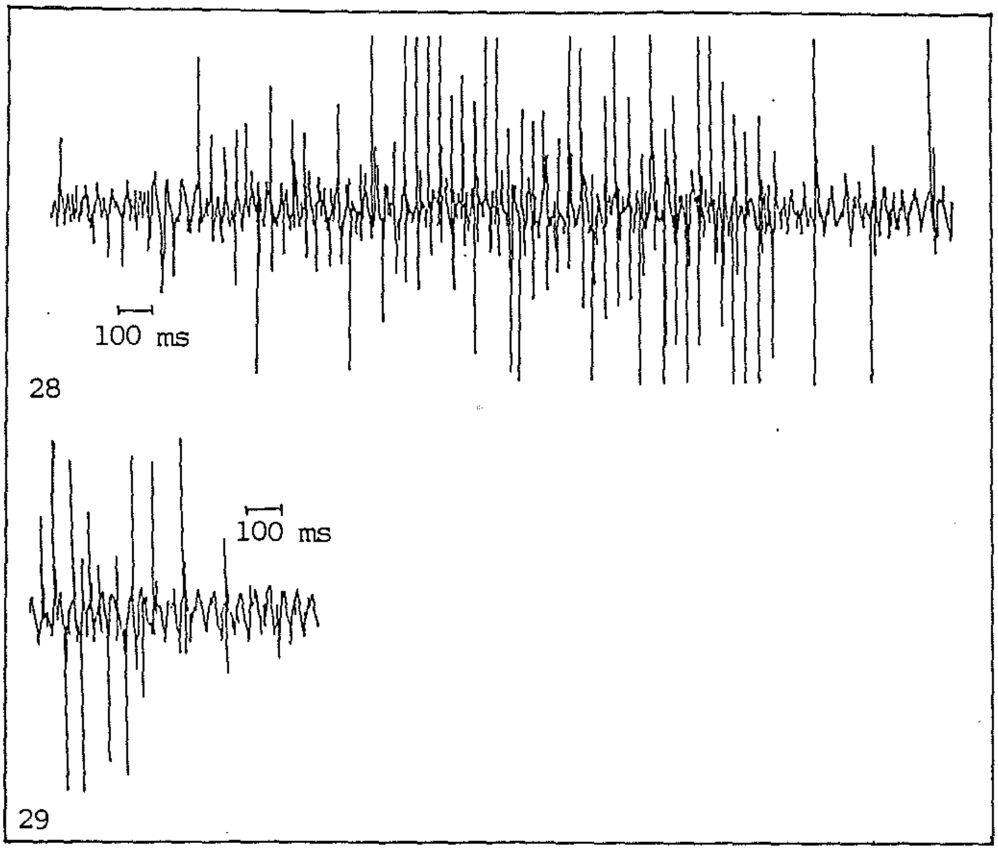


Fig. **26** Male drumming signal of Leuctra hippopus from Lake Istern.
Fig. 27 Male drumming signal of Leuctra hippopus from Suldal.



Figs. 28 and 29. Two drumming signals of male Leuctra hippopus from Nøklevann, showing the great variation in number of beats in the first part of the signal, even within one population.

Males from the Heimdalen population (loc. no. 13) drummed with, on average, 10.2 ± 2.8 beats lasting 1.2 ± 0.3 sec. The frequency of these signals was 8.6 ± 1.1 beats/sec. The interval between the male call and female answer was 0.5 ± 0.2 sec. The female signals from this population consisted of 9.4 ± 0.9 beats lasting 1.3 ± 0.2 sec. The frequency of the female signals was 7.6 ± 0.8 beats/sec. All recording temperatures were 22° C. Further details of the drumming signals of both populations are listed in Table 10. Drumming signals of *Capnia bifrons* are shown in Figures 24 and 25.

Family Leuctridae

12. *Leuctra fusca*. No signals were obtained at temperatures of 23 - 24° C, though attempts were made over several days.

13. *Leuctra hippopus*. A qualitative description of the drumming of this species was given by Ørmen (1991). Using the tapes he made of the drumming signals a further quantitative analysis was done for this study. Ørmen (1991) recorded drumming from 5 populations. Analyses of the signals of 3 of these populations are included here. The drumming signals are diphasic consisting of a rapid first part followed by 2 - 4 single beats. The first part of the signal consisted of 18.5 ± 11.3 beats and lasted 0.59 ± 0.40. The frequency of the first part was 33.2 ± 4.5 beats/sec. A great deal of variation existed in the number of beats in the first part. This was true for all three populations. Figures 28 and 29 illustrate this with two signals from the Nøklevann population (loc. no. 3) differing greatly in the number of beats in the first part. The signals from the three populations were analyzed separately and together, and the details of the drumming signals of each population are listed in Table 11. The number listed here are for the three populations as a whole. One signal from the Suldal population (loc. no. 2) deviated significantly. It consisted of the usual rapid first part with 23 beats lasting 0.8 sec. and having a frequency of 29.0 beats/sec. The second part, instead of containing 2 - 4 simple beats, was made up of 4 bi-beat knocks! This type of signal occurred only once and from only one male. Further illustrations of the drumming signals of *Leuctra hippopus* are shown in Figures 26 and 27.

14. *Leuctra nigra*. In spite of hard efforts, no drumming was obtained at temperatures of 21 - 22° C.

Table 4. Details of the drumming signals of *Diura bicaudata* from Heimdalen and Valdresflya, 16-21°C

Population No. of signals / No. of ind.	Groups/ signal $\bar{X}$ ± SD	Beats/ group $\bar{X}$ ± SD	Signal length in sec $\bar{X}$ ± SD	Interval between groups in a signal in sec* $\bar{X}$ ± SD						Frequency of groups in beats/sec $\bar{X}$ ± SD
Heimdalen: 5/2♂	5.2 ±0.5	2.65 ±0.63	1.11 ±0.24	0.221 ±0.050	0.252 ±0.027	0.259 ±0.032	0.277 ±0.027	0.322 (n=1)		39.7 ±4.3 beats/sec
Valdresflya: 17/6♂	5.7 ±1.5	3.02 ±0.71	1.56 ±0.60	0.280 ±0.043	0.302 ±0.023	0.303 ±0.02	0.315 ±0.027	0.314 ±0.127	0.459 ±0.011	38.2 ±6.9 beats/sec

*Measured from first beat in a group to first beat in the following group.
For intragroup beat intervals see Appendix A.

Table 5* Details of the drumming signals of _Isoperla_ _grammatica_ from Leirelven and Heimdalen, 19-24°C

Population No. of series / No. of signals / No. of ind.	Signals/series $\bar{X} \pm SD$	Signal length in sec $\bar{X} \pm SD$	Interval between signals in a series, in sec $\bar{X} \pm SD$	Interval between ♂ and ♀ signals in sec $\bar{X} \pm SD$	Frequency in beats/sec $\bar{X} \pm SD$ 2nd part
Leirelven:					
4/52/2♂	13.0 ±4.8	0.34 ±0.10	0.27 ±0.04	-	62.2 ±16.8
Heimdalen:					
3/15/2♂	5.0 ±1.0	0.17 ±0.10	0.25 ±0.08	-	102.9 ±28.4
2/8/2♀	one knock			0.08 ±0.03	

* Table 5 is continued on the next page.

Table 5. (cont.)

Population No. of series / No. of signals / No. of ind.	Beat intervals in sec $\bar{X}$ ± SD 1st part															
Leirelven:																
4/52/2♂	0.105 ±0.021	0.088 ±0.018	0.063 ±0.027	0.063 ±0.033	0.1 (n=1)											
Heimdalen:																
3/15/2♂	0.109 ±0.049	0.092 ±0.025	0.077 ±0.021	0.073 ±0.017	0.067 ±0.020	0.059 ±0.017	0.058 ±0.018	0.052 ±0.015	0.045 ±0.013	0.042 ±0.022	0.037 ±0.016	0.040 ±0.028	0.041 ±0.028	0.038 ±0.030	0.035 ±0.024	0.025 ±0.012

Table 6. Details of the drumming signals of *Isoperla obscura* from Heimdalen, 21-24°C

No. of signals / No. of ind.	Beats/ signal $\bar{X} \pm SD$	Signal length in sec $\bar{X} \pm SD$	Beat intervals in sec $\bar{X} \pm SD$											Frequency in beats/sec $\bar{X} \pm SD$
8/2♂	9.2 ±2.2	2.01 ±0.55	0.242 ±0.015	0.235 ±0.012	0.232 ±0.008	0.234 ±0.009	0.236 ±0.014	0.308 ±0.190	0.236 ±0.009	0.232 ±0.012	0.234 ±0.009	0.239 ±0.011	0.242 ±0.009	4.67 ±0.34

Table 7. Details of the drumming signals of Dinocras cephalotes from Neselven near Osen, 21°C

No. of signals / No. of ind.	Beats/ signal X̄ ± SD	Signal length in sec X̄ ± SD	Interval between ♂ and ♀ signals in sec X̄ ± SD	Frequency in beats/sec X̄ ± SD	Beat intervals in sec X̄ ± SD							
29/6♂	5.2 ±1.7	0.18 ±0.08	0.28 ±0.05	31.5 ±4.6	0.040 ±0.006	0.040 ±0.003	0.041 ±0.005	0.042 ±0.009	0.048 ±0.028	0.046 ±0.004	0.046 ±0.004	0.047 ±0.001
			Interval between ♀ and ♂ signals in sec X̄ ± SD									
7/1♀	5.3 ±1.1	0.20 ±0.05	0.20 ±0.05	27.0 ±2.4	0.040 ±0.007	0.050 ±0.018	0.046 ±0.005	0.050 ±0.005	0.050 ±0.003			

Table 8. Details of the drumming signals of *Taeniopteryx nebulosa* from Lomma, 20°C

No. of signals / No. of ind.	Beats/ signal $\bar{X}$ ± SD	Signal/ length $\bar{X}$ ± SD	Frequency in beats/sec $\bar{X}$ ± SD	Beat intervals in sec $\bar{X}$ ± SD									
15/1♂	10.1 ±0.8	1.7 ±0.2	5.9 ±0.7	0.163 ±0.026	0.173 ±0.015	0.178 ±0.022	0.192 ±0.022	0.192 ±0.029	0.206 ±0.035	0.207 ±0.034	0.209 ±0.036	0.208 ±0.043	0.189 ±0.029

Table 9. Details of the drumming signals of <u>Capnia</u> <u>atra</u> from Heimdalen and Grindalen, 18-21°C

Population No. of signals / No. of ind.	Bi-beats/ signal $\bar{X}$ ± SD	Signal length in sec $\bar{X}$ ± SD	Interval between ♂ and ♀ signals in sec $\bar{X}$ ± SD	Interbibeat intervals* in sec $\bar{X}$ ± SD								
Heimdalen:												
12/4 ♂	7.8 ±0.9	1.6 ±0.3	0.7 ±0.3	0.205 ±0.034	0.204 ±0.030	0.210 ±0.031	0.220 ±0.030	0.220 ±0.030	0.240 ±0.020	0.260 ±0.047	0.270 ±0.006	
6/2 ♀	4.5 ±0.8	1.2 ±0.3	-	0.319 ±0.036	0.325 ±0.030	0.360 ±0.050	0.366 ±0.023	0.356 (n=1)				
Grindalen:												
12/4 ♂	8.0 ±1.3	1.5 ±0.3	0.9 ±0.4	0.199 ±0.013	0.187 ±0.017	0.194 ±0.010	0.199 ±0.010	0.213 ±0.022	0.226 ±0.042	0.220 ±0.033	0.240 ±0.039	0.234 ±0.002
11/3 ♀	5.7 ±1.9	1.6 ±0.5	-	0.296 ±0.045	0.305 ±0.047	0.333 ±0.057	0.353 ±0.071	0.340 ±0.060	0.297 ±0.028	0.300 ±0.030	0.294 ±0.124	0.241 ±0.007

*Measured from first beat in a bi-beat to first beat in the following bi-beat.
for intrabibeat intervals see Appendix B.

Table 10. Details of the drumming signals of Capnia bifrons from Tjøme and Heimdalen, 22°C

Population No. of signals / No. of ind.	Beats/ signal $\bar{X}$ ± SD	Signal length in sec $\bar{X}$ ± SD	Interval between ♂ and ♀ signals in sec $\bar{X}$ ± SD	Frequency in beats/sec $\bar{X}$ ± SD	Beat intervals in sec $\bar{X}$ ± SD											
Tjøme:																
18/9 ♂	7.8 ±1.7	0.9 ±0.3	0.5 ±0.1	9.0 ±1.7	0.12 ±0.03	0.12 ±0.03	0.12 ±0.02	0.12 ±0.02	0.13 ±0.02	0.15 ±0.04	0.18 ±0.13	0.13 ±0.04	0.15 ±0.03	0.15 (n=1)	0.15 (n=1)	
6/3 ♀	9.2 ±2.5	1.2 ±0.4	-	7.8 ±1.5	0.13 ±0.04	0.15 ±0.03	0.14 ±0.03	0.14 ±0.02	0.15 ±0.04	0.14 ±0.02	0.14 ±0.02	0.17 ±0.04	0.17 ±0.01	0.19 ±0.01	0.19 ±0.08	
Heimdalen:																
12/7 ♂	10.2 ±2.8	1.2 ±0.3	0.5 ±0.2	8.6 ±1.1	0.12 ±0.03	0.11 ±0.03	0.11 ±0.03	0.11 ±0.03	0.12 ±0.03	0.12 ±0.03	0.13 ±0.03	0.15 ±0.03	0.18 ±0.11	0.14 ±0.03	0.16 ±0.03	0.16 ±0.02
5/3 ♀	9.4 ±0.9	1.3 ±0.2	-	7.6 ±0.8	0.12 ±0.04	0.11 ±0.03	0.11 ±0.04	0.12 ±0.03	0.12 ±0.03	0.13 ±0.03	0.15 ±0.08	0.14 ±0.05	0.22 ±0.17			

Table 11. Details of the drumming signals of *Leuctra hippopus* from L. Istern, Suldal, and Nøklevann, 15-25°C

Population No. of signals / No. of ind.	Beats/signal $\overline{X}$ ± SD		Signal length in sec, $\overline{X}$ ± SD		Frequency beats/sec $\overline{X}$ ± SD	Beat intervals in sec $\overline{X}$ ± SD
	1st phase	total	1st phase	total	1st phase	2nd phase
L. Istern:						
11/5 ♂	14.9 ±11.2	18.2 ±11.4	0.455 ±0.39	0.90 ±0.48	35.8 ±7.1	0.108 0.144 0.170 ±0.020 ±0.030 ±0.034
Suldal:						
19/8 ♂	18.1 ±9.0	21.2 ±8.9	0.558 ±0.31	0.97 ±0.29	33.1 ±2.9	0.105 0.134 0.152 0.204 ±0.02 ±0.02 ±0.02 ±0.04
Nøklevann:						
17/8 ♂	21.3 ±13.4	24.8 ±13.3	0.70 ±0.49	1.20 ±0.47	31.6 ±3.3	0.115 0.147 0.163 0.190 ±0.030 ±0.020 ±0.020 ±0.020
Total (three populations):						
47/21 ♂	18.5 ±11.3	21.8 ±11.3	0.59 ±0.40	1.0 ±0.4	33.2 ±4.5	0.109 0.141 0.160 0.194 ±0.020 ±0.020 ±0.020 ±0.020

IX. Discussion.

The descriptions of the drumming signals of *Isoperla obscura*, *Protonemura meyeri*, and *Capnia atra* are first descriptions. To date, the drumming signals of only two species, *Nemurella pictetii* and *Amphinemura sulcicollis*, of the family Nemouridae have been described (Gnatzy and Rupprecht 1972, Rupprecht 1982). Rupprecht (1982) found that in spite of hard efforts only one out of twelve males of *Amphinemura sulcicollis* drummed and then with only seven signals. As shown in this thesis, not one out of ten males of *Nemoura avicularis* tested drummed under the given laboratory conditions. This, together with the small number of the Nemouridae whose drumming has been described, might lead one to think that the Nemouridae do not drum, or that drumming in this species has lost its significance. If the latter is the case, it is particularly interesting that *Protonemura meyeri* has been shown to drum, because even if drumming has lost its significance for some or all of the Nemouridae in their natural environment, the fact that their drumming signals may be studied could greatly add to our understanding of their phylogenetic status. The signals of both *Nemurella pictetii* and *Amphinemura sulcicollis* are derived, two part signals. This opens the possibility that at least some of the Nemouridae may have evolved complex derived signals only to then evolve non-drumming as a secondary characteristic. Stewart and Maketon (1991) propose that the capacity to drum " . . . was presumably acquired in ancestral Euholognatha, in conjunction with the appearance of vesicles, specialized tactile hairs or special innervation of abdominal sterna." If this is correct, one would expect the Nemouridae at one time to have evolved drumming behavior, all the Fennoscandian species having well developed vesicles. Subsequently, the ability to drum or the significance of drumming may have been lost, while the vesicles were retained. The situation may be similar for the European *Leuctra* species, as will be discussed below. It is, of course, too early to say whether drumming has any significance for this group of insects in their natural environment or not, but the fact that another Nemouridae has been shown to drum indicates that research into the significance of this drumming and descriptions of the drumming of other species in this family are interesting and relevant fields for further research.

So far, only three species have been known to drum with a grouped bi-beat signal (Stewart and Maketon 1991). These authors characterize this type of call as highly specialized and have tested the necessity of the bi-beat characteristic for female response in *Kogotus modestus* (Stewart and Maketon 1990). By playing back computer-simulated calls of males of *K. modestus* to females, they found that females only answered bi-beat groups and that the intrabibeat intervals were of secondary importance (Stewart and Maketon 1990). Only the male call consists of bi-beat groups, the females answering with a simple monophasic tapping call. The drumming signals of *Capnia atra* have been shown to be grouped bi-beat signals. It is important to note that both the males and the females have grouped bi-beat signals. As Maketon and Stewart (1991) have pointed out, complex drumming signals are unecessary for females, as they need only provide an answer to a complex male call or remain silent. The males initiate the calling and the male call contains enough complexity or differs enough from that of other related or sympatric species as to exclude answers from females of other species. This is the case in the European Isoperla, the males of *Isoperla goertzi*, *I. grammatica*, and *I. rivulorum* having some form of derived call, whereas the females answer only with a single tap (Rupprecht 1969). The situation is different for *C. atra*.

Stewart and Maketon (1991) state that, "North American and European Capniidae, Leuctridae, and *Taeniopteryx* that have retained vesicles, have also retained ancestral drumming." Until the description of the drumming of *Capnia atra*, all Capniidae species known to drum have had ancestral, simple, monophasic tapping signals (Rupprecht 1968, 1982, Stewart and Maketon 1991). *Capnia atra* does not have a vesicle. If *Capnia atra* have secondarily lost their vesicles, this may have been concurrent with the development of their highly specialized signals. Maketon and Stewart (1988) have assigned the character "non-grouped call" to the family Capniidae (as opposed to grouped call), on the basis of the described non-grouped signals of three species, no species of the Capniidae at that time being known to have a grouped signal. The results obtained for *Capnia atra* and the possibility of further complex signals being discovered in the future may alter this picture.

Rupprecht (1968, 1982) has described the drumming of *Capnia bifrons* from the Taunus mountains of central Germany and from Denmark.

The signals of the German population are of a frequency of 80 ± 6 beats/sec. for the males and 68 ± 6 beats/sec. for the females, whereas the same frequencies for the Danish population were 6.1 ± 0.56 beats/sec. and 5.8 ± 0.94 beats/sec. respectively (Rupprecht 1982). These values were for temperatures of 22° C. As shown in Table 10, the signals of Capnia bifrons at 22° C from Heimdalen and Tjøme, are very close to the Danish population in frequency, though slightly higher. The number of beats/signal are not significantly different for the Norwegian and Danish population, whereas the duration of the signals and the interval between the male signal and the female answer are slightly lower for the Norwegian population. The variation present between the drumming of the Norwegian and the Danish populations is not of any great significance, whereas the differences between the drumming of Fennoscandian and central European C. bifrons are very great considering them both to be simple monophasic signals. The fact that the Danish drumming is more similar to the Norwegian drumming than the German, though Norway and Denmark are separated by a large body of water, is interesting. During the last ice-age, the glaciation covered all of present day Fennoscandia and stretched into northern Germany (Kurtén 1969). If the drumming of the British Capnia bifrons is similar to that of the Fennoscandian populations it would be notable that the border between the two types of drumming would approximately follow the limits of the glaciation of the last ice-age. Surely this would be more than coincidental. It therefore seems that further studies of the geographical variations of the drumming of Capnia bifrons may yield important and interesting results concerning the evolution, phylogeny and zoogeography of the species and, indeed, the genus, as well as shedding light on the systematic status of present day Capnia bifrons. Whether the Capnia bifrons of central Europe and the C. bifrons of Fennoscandia are the same species must certainly be called into question.

The drumming signals of the males of Leuctra hippopus are derived diphasic calls. North American representatives of the family Leuctridae which are known to drum, all from the genus Zealeuctra, drum with monophasic tapping signals (Zeigler and Stewart 1977, Maketon and Stewart 1991). The signal of the European Leuctra pseudosignifera is more complex, consisting of a two part signal (Rupprecht 1977). The first part consists of a succession of bi- or tri-beats, the second part of tapping at a frequency of 14 beats/sec (Rupprecht 1977). In their hypothesis of stonefly drumming evolution, Maketon and Stewart (1988) list four species of the family Leuctridae, all of which have ancestral states for all seven drumming characters considered. Maketon and Stewart do not make explicit which four species have been considered and do not refer to Rupprecht's (1977) description of the drumming of Leuctra pseudosignifera. Nonetheless, L. pseudosignifera must be the fourth of these species, the three first being Zealeuctra arnoldi, Z. claaseni, and Z. hitei (Zeigler and Stewart 1977, Stewart and Maketon 1991). From the description given by Rupprecht (1977) of the drumming of Leuctra pseudosignifera, it seems clear that this drumming must be considered to be derived for at least one character in that the signal is diphasic. The description of the drumming of Leuctra hippopus means that 2 of 5 species of the family Leuctridae whose drumming is known, have evolved derived complex drumming patterns. Maketon and Stewart (1988) state that it is " . . . probable that non-drumming has also been retained by some groups of Arctoperlaria, since it has never been observed in southern hemisphere Notonemouridae, or in many species or genera of Capniidae, Leuctridae, Nemouridae, Taeniopterygidae and Chloroperlidae, either naturally or experimentally." As mentioned earlier, it is difficult to ascertain whether lack of an observation of drumming actually means that a species is a non-drummer. But one possibility which Maketon and Stewart (1988) do not consider is that non-drumming may have evolved secondarily. All four Leuctra species found in Norway have vesicles, and though three of these species have been tested only one of these, Leuctra hippopus has been shown to drum. In light of the relatively complex signals of Leuctra pseudosignifera (Rupprecht 1977) and Leuctra hippopus (Ørmen 1991), it seems possible that complex drumming diversity has evolved in the Leuctridae, possibly in conjunction with the vesicle, and that some species have later lost the ability or the necessity to drum, while retaining their vesicles. If some species can secondarily lose their vesicles, but retain their ability to drum, such as Capnia atra, certainly other species could, in theory, secondarily lose their ability to drum but retain their vesicles. It is, for instance, uncertain what function the drumming of Leuctra hippopus might serve if laboratory observations accurately reflect the natural state of the species' pre-mating behavior. The females of Leuctra hippopus are not known to drum, though Ørmen (1991) observed that females reacted to drumming imitations. It may be that only the males drum and then only to notify the females of their presence, female responses then not being necessary (Maketon and Stewart 1988, Ørmen 1991). Another possibility is that the drumming of the male has remained as a relic, the drumming of the females having been lost (and possibly the drumming of other *Leuctra* species such as *L. fusca* and *L. nigra* also). This might explain Ørmen's (1991) observation that few males drummed spontaneously, most drumming only after stimulation by artificial signals.

The monophasic tapping signals of *Isoperla obscura* are reminiscent of the signals of North American *Isoperla* species, all but two known species also drumming with simple monophasic tapping (Szczytko and Stewart 1979, Maketon and Stewart 1984, Stewart, Szczytko and Maketon 1988, and Stewart and Maketon 1991). The signals of the European *Isoperla grammatica*, *I. goertzi*, *I. oxylepsis*, and *I. rivulorum* consist of complex series or sequences of signals (Rupprecht 1969, 1982). This may at first indicate a closer relationship between *Isoperla obscura* and the North American *Isoperla* species. Illies (1952) has hypothesized the existence of four species groups of European *Isoperla*, each group corresponding to an ancestral species existing at the beginning of the last ice age. The first group is the grammatica group consisting only of *I. grammatica*. The second is the rivulorum group consisting of among others *I. goertzi*, *I. oxylepsis*, and *I. rivulorum*. The third species group is the obscura group containing only *I. obscura*, and the fourth the difformis group with only *I. difformis*. Comparing the drumming signals of the four European Isoperla species mentioned above, one finds that the signals of *I. goertzi*, *I. oxylepsis*, and *I. rivulorum* may be seen as succesive shortenings of the signals of *I. grammatica*. Indeed, Rupprecht (1969) seems aware of this fact and comments on the similarity of the signals. If we subtract some of the first knocks from the signals of *I. grammatica* we get a signal very similar to that of *I. goertzi*, and so on with the signals of *I. oxylepsis* and *I. rivulorum*. The signals of *I. rivulorum* consists of series of just 2 - 3 knocks, and one can imagine arriving at the signals of *I. obscura* by subtracting one or two knocks from each signal in the series of *I. rivulorum*.

This view of *Isoperla* drumming would seem to support the species groupings of Illies (1952), *I. obscura* apparently maintaining the most primitive form of drumming, the other species evolving successively more complex derived drumming. From this view we need no longer assume a close relationship between *Isoperla obscura* and nearctic *Isoperla* species.

The signals of Isoperla grammatica recorded from the Heimdalen population are similar in form to those obtained by Rupprecht (1968) for a population in the Taunus mountains of central Germany. However, the signals are of a much shorter duration. Rupprecht (1982) described the signals of a Danish population of I. grammatica with important drumming signal deviations from the population in central Germany, the most important being the shorter duration of the Danish signals and the frequency of the beginning of the signal. The duration of the Danish signal was 0.55 ± 0.08 sec (Rupprecht 1982). The duration of the Heimdalen signals was 0.17 ± 0.10 sec, at comparable temperatures. The time between signals in a series and the number of signals in a series seem comparable for the Heimdalen and the German population. Nonetheless, a shorter signal duration with other parameters about the same must lead to shorter beat intervals for the Heimdalen population and this is a decisive signal parameter for several species (Stewart and Maketon 1990). Zeigler and Stewart (1986) show that females of both Perlinella drymo and P. badia have a wide "window of recognition" for signal duration. At any rate the drumming of the Heimdalen population represents a variation of both the German and the Danish signals.

The Leirelven population of I. grammatica drums so differently from all these populations that the drumming must be considered a dialect. Whereas the drumming signals of both the German and the Heimdalen populations consist of ca. 30 - 35 beats altogether, the Leirelven signals consist of only 6 - 12 beats, the first part of the signal often containing only two beats. The second rapid part is of a lower frequency and contains very few beats compared to the other two populations (see Table 5). There is also a much greater distinction between the two parts of the signal for the Leirelven population. The transition from the first to the second parts of the Heimdalen signals is much more gradual. The drumming of Isoperla grammatica seems to be highly variable over geographic areas and it is clear that further studies need to be made of other populations.

Rupprecht (1972) described dialects between two populations of Diura bicaudata, one in Germany and one in northern Sweden. The main difference between the two populations was in frequency, the males of the German population drumming with a frequency of 34 ± 2 beats/sec, and the males of the Swedish population with a frequency of 25 ± 2 beats/sec (Rupprecht 1972). The frequency of the drumming signals of Diura bicaudata from Heimdalen and Valdresflya was slightly higher than the German signals, but was significantly different from that of the Swedish population (see Table 4). Rupprecht (1972) mentions that the individual groups of the signals of the German population contained 2 - 4 beats and those of the Swedish population 2 - 3 beats. The groups of the signals of the Heimdalen population contained 1 - 3 beats (seldom 1, most often 3), whereas those of the Valdresflya population consisted of 1 - 4 beats (often 4). Whereas the bi-beat character was of great importance for the signal integrity of Kogotus modestus as mentioned above (Stewart and Maketon 1990), the number of beats/group seems to be much more variable in the signals of Diura bicaudata. Though the signals of the Heimdalen population never included 4 beats in a group the difference in the mean number of beats/group in the Heimdalen and Valdresflya population is not statistically significant (2.65 ± 0.63 and 3.02 ± 0.71 for Heimdalen and Valdresflya respectively). The fact that four beats in a group never occurred in the Heimdalen signals, make it interesting to investigate whether statistical and biological significance coincide in this case or not. The data from the Heimdalen population is, however, based on only two males. It would also be of great interest to test the necessity of the presence of 3 or 4 beats for the response of females of both populations using computer-simulated signals like those used by Stewart and Maketon (1990).

The drumming of Dinocras cephalotes from Neselven near Osen is the same in frequency as that of the species in Germany (Rupprecht 1968, 1969). The German population drums with a frequency of 29.8 ± 6 beats/sec for males and 27.8 ± 6 beats/sec for females (Rupprecht 1968). The comparable numbers for the Norwegian population are 31.5 ± 4.6 beats/sec for the males and 27.0 ± 2.4 beats/sec for the females (see Table 7). The Norwegian signals are of a longer duration, the duration of the German signals being 0.14 sec for the males and 0.15 sec for the females. The number of beats/signal and the interval between the male and female signals is not significantly different from the German population (Rupprecht 1968).

All five species of Taeniopteryx whose drumming has been described have had ancestral monophasic tapping signals (Rupprecht 1982, Stewart and Maketon 1991). The drumming of Taeniopteryx nebulosa was first described for a Danish population by Rupprecht (1982). The signals of the one male tested from the river Lomma near Oslo were not significantly different from the signals of the Danish population for any parameters.

Though 16 individuals of *Siphonoperla burmeisteri* were tested for drumming, no such behavior was observed. This would support the assertion of Maketon and Stewart (1988) that many species or genera of among other families the Chloroperlidae, may prove to be non-drummers. Rupprecht (1981), however, has found that in two species of *Siphonoperla* the insects drum by tremulation. No such behavior was observed in *S. burmeisteri*.

X. Conclusion

Fourteen species of Norwegian stoneflies were studied in an attempt to determine whether or not they use drumming as a means of mate localization, as part of their pre-mating behavior. The signals obtained were analyzed for species specificity, dialects and/or geographic variation. Of the species studied, ten of them drummed under the given laboratory conditions. The descriptions of the drumming of Capnia atra, Isoperla obscura, and Protonemura meyeri are first descriptions. Five of the species studied were collected from more than one locality. For Diura bicaudata there were variations in the drumming of the two populations studied, but the question if this is of any biological significance must for the time being remain open. For Isoperla grammatica the differences between the two populations studied were so great that the drumming of the Leirelven population must be considered a dialect. The drumming of both the Norwegian populations of Capnia bifrons investigated were similar to the drumming of a Danish population described by Rupprecht (1982). The drumming of all of these populations is so different from that of the central European representative of the species, that the systematic status of the species Capnia bifrons must be called into question. Even where only one Norwegian population of a species was investigated, variations in one or more drumming parameter were found when the signals were compared to those described in the literature for the species from other countries. The exception to this was Taeniopteryx nebulosa. The drumming of the one individual described was not significantly different from previous descriptions of the drumming of this species for any parameters.

Quantitative analyses were also made of the drumming of Leuctra hippopus using the tapes recorded by Ørmen (1991). The signals were derived diphasic signals. These results, along with those obtained for Capnia atra, and other descriptions of the drumming of Euholognathan stonefly species (Gnatzy and Rupprecht 1972, Rupprecht 1977, 1982), show that several species from three families have evolved derived, complex signal forms. This indicates that complex derived drumming may be more prevalent in the Euholognatha than previously supposed. The reason

Euholognathan species have been thought to drum primarily with simple ancestral signals, or not at all, is in part due to the small number of species of the Euholognatha whose drumming has been described. There are also strong arguments in favor of viewing non-drumming as a secondary derived characteristic in some groups, notably the Nemouridae and the Leuctridae, though great difficulties remain in finding proof for such a view. It seems that a thorough study of the drumming of Euholognathan stoneflies would fill vital gaps in our knowledge of stonefly drumming, and be necessary to clarify the status of the hypothesis of stonefly drumming evolution proposed by Maketon and Stewart (1988).

Drumming has been shown to be of such importance to the study of the life cycle, ecology, and evolution of stoneflies, that it will surely continue to be one of the major areas of stonefly research in the future.

References

Andersson, K. G. 1986. Bäcksländornas kärleksliv, en beteendeekologisk studie. - *Fauna Flora, Upps.*, *81:* 207-214.

Brink, P. 1949. Studies on Swedish stoneflies. - *Opusc. Ent. Suppl.*, *11:* 1-250.

Brittain, J. E. 1978. Semivoltinism in mountain populations of *Nemurella pictetii* (Plecoptera). - *Oikos*, *30:* 1-6.

Brodskiy, A. K. 1982. Evolution of the wing apparatus in stoneflies (Plecoptera). IV. Kinematics of the wings and general conclusions. - *Entomol. Obozr.*, *61:* 491-500.

Elliott, J. M. 1987. Life cycle and growth of *Leuctra geniculata* (Stephens) (Plecoptera: Leuctridae) in the river Leven. - *Entomologist's Gaz.*, *38:* 129-134.

Frison, H. 1935. The stoneflies, or Plecoptera, of Illinois. - *Illinois Nat. Hist. Surv. Bull.*, *20:* 281-471.

Gnatzy, W. and Rupprecht, R. 1972. Die Bauchblase von *Nemurella pictetii* Klapálek (Insecta, Plecoptera). - *Z. Morph. Tiere*., *73:* 325-342.

Graham, E. A. 1982. Drumming communication and pre-mating behavior of fourteen eastern Nearctic stonefly species (Plecoptera). - M.S. Thesis Univ. of Wisconsin at Stevens Point. 79 pp.

Hassage, R. L., Stewart, K. W., and Zeigler D. D. 1988. Female response to computer-simulated male drumming call variations in *Pteronarcella badia* (Plecoptera: Pteronarcyidae). - *Ann. entomol. Soc. Am.*, *81:* 528-531.

Hennig, W. 1966. Phylogenetic Systematics. Univ. of Illinois press, Urbana. 263 pp.

Huru, H. 1987. Occurence and life cycle of *Dinocras cephalotes* (Curtis, 1827) (Plec. Perlidae) in North Norway. - *Fauna Norv. Ser. B.*, *34:* 14-18.

Illies, J. 1952. Die europäischen Arten der Plecopteren gattung *Isoperla* Banks (= Chloroperla Pictet). - *Beitr. Ent.*, *2:* 369-424.

- 1960. Archiperlaria, eine neue Unterordnung der Plecopteren (Revision der Familien Eusthenidae und Diamphipnoidae) (Plecoptera). - *Beitr. Ent.*, *10:* 661-697.

- 1961. Phylogenie und Verbreitungsgeschichte der Ordnung Plecoptera (Verhandl. Deut. Zool. Ges. Bonn). - *Zool. Anz. Suppl.*, *25:* 384-394.

- 1965. Phylogeny and zoogeography of the Plecoptera. - *Ann. Rev. Entomol.*, *10:* 117-146.

- 1966. Katalog der rezenten Plecoptera. - Das Tierreich, Berlin, 82: I-XXX; 1-632.

Kurtén, B. 1969. Istiden., Forum Forlag, Stockholm. 179 pp.

Lillehammer, A. 1987. Diapause and quiescence in eggs of Systellognathan stonefly species (Plecoptera) occuring in alpine areas of Norway. - *Annls Limnol.*, *23:* 179-184.

- 1988. Stoneflies (Plecoptera) of Fennoscandia and Denmark. - Fauna ent. scand., 21: 1-165.

Lillehammer, A., Brittain, J. E., Saltveit, S. J., and Nielsen, P. S. 1989. Egg development, nymphal growth and life cycle stategies in Plecoptera. - Holarct. Ecol., 12: 173-186.

Maketon, M., and Stewart, K. W. 1984a. Drumming behavior in four North American Perlodidae (Plecoptera) species. - Ann. entomol. Soc. Am., 77: 621-626.

- 1984b. Further studies of the drumming behavior of North American Perlidae (Plecoptera). - Ann. entomol. Soc. Am., 77: 770-778.
- 1988. Patterns and evolution of drumming behavior in the stonefly families Perlidae and Peltoperlidae. - Aquat. Ins., 10: 77-98.

McNamara, C. 1926. The drumming of stoneflies (Plecoptera). - Can. Ent., 58: 53-54.

Nelson, C. H. 1984. Numerical cladistic analysis of phylogenetic relationships in Plecoptera. - Ann. entomol. Soc. Am., 77: 466-473.

Newport, G. 1851. On the anatomy and affinities of Pteronarcys regalis. - Trans. Linn. Soc. London., 20: 425-452.

Ricker, W. E. 1950. Some evolutionary trends in PLecoptera. - Proc. Indiana Acad. Sci., 59: 197-209.

- 1952. Systematic studies in Plecoptera. - Indiana Univ. Publ. Sci. Ser., 18: 1-200

Romoser, W. S. 1981. The Science of Entomolgy. Macmillan Publ. Co., Inc., New York. 575 pp.

Rupprecht, R. 1968. Das Trommeln der Plecopteren. - Z. vergl. Physiol., 59: 38-71.

- 1969. Artsspezificität der Trommelsignale der Plecopteren (Insecta). - Oikos, 20: 26-33.
- 1972. Dialektbildung bei den Trommelsignalen von Diura (Plecoptera)., - Oikos, 23: 410-412.
- 1976. Struktur und Funktion der Bauchblase und des Hammers von Plecopteren. - Zool. Jahrb. (Anat.), 95: 9-80.
- 1977. Nachweis von Trommelsignalen bei einem europäischen Vertreter der Steinfliegen-Familie Leuctridae (Plecoptera). - Entomol. Germ., 3: 333-336.
- 1981. A new system of communication within Plecoptera and a signal with a new significance. In: Kawai, T. (ed.) Proc. 7th int. sympos. Plecoptera. - Biol. Inl. Wat., 2: 30-35.
- 1982. Drumming signals of Danish Plecoptera. - Aquat. Ins., 4: 93-103.

Rupprecht, R. and Gnatzy, W. 1974. Die Feinstruktur der Sinneshaare auf der Bauchblase von Leuctra hippopus und Nemoura cinerea (Plecoptera). - Cytobiologie, 9: 422-431.

Snellen, R. K. and Stewart, K. W. 1979. The life cycle and drumming behavior of *Zealeuctra claaseni* (Frison) and *Zealeuctra hitei* Ricker and Ross (Plecoptera: Leuctridae) in Texas, USA. - *Aquat. Ins.*, *1:* 49-61.

Stewart, K. W., Atmar, G. L., and Solon, B. M. 1969. Reproductive morphology and mating behavior of *Perlesta placida* (Plecoptera: Perlidae). - *Ann. entomol. Soc. Am.*, *62:* 1433-1438.

Stewart, K. W. and Maketon, M. 1990. Intraspecific variation and information content of drumming in three Plecoptera species. In: Campbell, Ian C. (ed.) Mayflies and stoneflies, life histories and biology, Proc. 5th int. Ephemeroptera Conf. and 9th int. Plecoptera Conf. - *Ser. Ent.*, *44:* 259-268.

- 1991. Structures used by Nearctic stoneflies (Plecoptera) for drumming, and their relationship to behavioral pattern diversity. - *Aquat. Ins.* *13:* 33-53.

Stewart, K. W., Szczytko, S. W., and Maketon, M. 1988. Drumming as a behavioral line of evidence for delineating species in the genera *Isoperla*, *Pteronarcys*, and *Taeniopteryx* (Plecoptera). - *Ann. entomol. Soc. Am.*, *81:* 689-699.

Stewart, K. W., Szczytko, S. W., and Stark, B. P. 1982. Drumming behavior of four species of North American Pteronarcyidae (Plecoptera): Dialects in Colorado and Alaska *Pteronarcella badia*. - *Ann. entomol. Soc. Am.*, *75:* 530-533.

Stewart, K. W., Szczytko, S. W., Stark, B. P., and Zeigler, D. D. 1982. Drumming behavior of six North American Perlidae (Plecoptera) species. - *Ann. entomol. Soc. Am.*, *75:* 549-554.

Stewart, K. W. and Zeigler, D. D. 1984a. The use of larval morphology and drumming in Plecoptera systematics, and further studies of drumming behavior. - *Annls Limnol.*, *20:* 105-114.

- 1984b. Drumming behavior of twelve North American stonefly (Plecoptera) species: First descriptions in Peltoperlidae, Taeniopterygidae, and Chloroperlidae. - *Aquat. Ins.*, *6:* 49-61.

Szczytko, S. W. and Stewart, K. W. 1979. Drumming behavior of four western Nearctic Isoperla (Plecoptera) species. - *Ann. Entomol. Soc. Am.*, *77:* 781-786.

Tillyard, R. J. 1921. A new classification of the order Perlaria. - *Can. Ent.*, *53:* 35-43.

Ulfstrand, S. 1968. Life cycles of benthic insects in Lapland streams (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Simuliidae). - *Oikos*, *19:* 167-190.

Watrous, L. E. and Wheeler, Q. D. 1981. The out-group comparison method of character analysis. - *Syst. Zool.*, *30:* 1-11.

Zeigler, D. D. 1989. Drumming behavior of three Pennsylvania stonefly (Plecoptera) species. - Proc. entomol. Soc. Wash., 91: 583-587.

Zeigler, D. D. and Stewart, K. W. 1977. Drumming behavior of eleven Nearctic stonefly (Plecoptera) species. - Ann. entomol. Soc. Am., 70: 495-505.

- 1985. Drumming behavior of five stonefly (Plecoptera) species from central and western North America. - Ann. entomol. Soc. Am., 78: 717-722.

- 1986. Female response thresholds of two stonefly (Plecoptera) species to computer-simulated and modified male drumming calls. - Anim. Behav., 34: 929-931.

- 1987. Behavioral characters with systematic potential in stoneflies (Plecoptera). - Proc. entomol. Soc. Wash., 89: 794-802.

Zwick, P. 1969. Das Phylogenetische System der Plecopteren als Ergebnis vergleichend-anatomischer Untersuchungen. Dissertation Univ. Kiel. (291 pp.; Kurzfassung 4 pp.).

- 1973. Insecta: Plecoptera. Phylogenetisches System und Katalog. - Das Tierreich, 94.

- 1974. Das Phylogenetisches System der Plecoptera. - Entomol. Germ., 1: 50-57.

- 1980. Plecoptera (Steinfliegen). - Handb. Zool., 4: 1-115.

- 1981. Addendum: Plecoptera (stoneflies), pp. In: Hennig, W. (ed.), The Phylogeny of Insects. J. Wiley and Sons, Chichester.

Ørmen, T. 1991. Leuctra hippopus Kempny, 1899 (Plecoptera: Leuctridae): Studies on a species problem, with notes on related species. Unpubl. thesis. Univ. of Oslo, Zoological Museum.

Appendix A

This appendix gives additional information on the drumming signals of Diura bicaudata. The drumming signals consist of several groups of 2 - 4 beats. The interval between the first and second beat in a group is the first intragroup interval. The interval between the second and third beat in a group is the second intragroup interval, and so on. These values are listed as means and standard deviations for each group in a signal.

Population	Group	First intragroup interval	Second intragroup interval	Third intragroup interval
Heimdalen:	1	0.037 ±0.014	0.032 (n=1)	
	2	0.041 ±0.005	0.037 ±0.004	
	3	0.043 ±0.007	0.035 ±0.002	
	4	0.042 ±0.007	0.037 ±0.003	
	5	0.042 ±0.005	0.038 ±0.008	
Valdresflya:	1	0.041 ±0.008	0.036 ±0.006	
	2	0.042 ±0.008	0.037 ±0.006	0.034 ±0.005
	3	0.046 ±0.015	0.036 ±0.005	0.034 ±0.004
	4	0.045 ±0.010	0.037 ±0.005	0.037 ±0.007
	5	0.043 ±0.005	0.035 ±0.004	0.035 ±0.001
	6	0.045 ±0.005	0.042 ±0.008	0.048 ±0.004
	7	0.046 (n=1)	0.041 (n=1)	0.041 (n=1)

Appendix B

This appendix gives additional information on the drumming signals of Capnia atra. The signals consist of 5 - 8 bi-beat knocks. The interval between two knocks in a bi-beat is the intrabibeat interval. These values are listed for both males and females as means and standard deviations, and are measured in seconds.

Population	Bi-beat number	Intrabibeat interval	Intrabibeat interval
Heimdalen:	1	0.036 ± 0.004	0.044 ± 0.004
	2	0.041 ± 0.004	0.043 ± 0.002
	3	0.042 ± 0.003	0.046 ± 0.003
	4	0.041 ± 0.005	0.041 ± 0.003
	5	0.043 ± 0.004	0.045 ± 0.002
	6	0.044 ± 0.005	0.042 (n=1)
	7	0.043 ± 0.006	-
	8	0.046 ± 0.005	-
	9	0.047 ± 0.002	
Grindalen:	1	0.036 ± 0.003	0.045 ± 0.005
	2	0.04 ± 0.03	0.045 ± 0.005
	3	0.042 ± 0.037	0.043 ± 0.007
	4	0.043 ± 0.004	0.045 ± 0.003
	5	0.042 ± 0.004	0.044 ± 0.002
	6	0.044 ± 0.008	0.045 ± 0.001
	7	0.041 ± 0.006	0.044 ± 0.003
	8	0.043 ± 0.004	0.042 ± 0.006
	9	0.044 ± 0.004	0.11 ± 0.1
	10	0.033 ± 0.003	0.04 ± 0.01