THE EVOLUTION OF STRIDULATORY COMMUNICATION IN ANTS

Hubert Markl, Fachbereich Biologie, Technische Hochschule Darmstadt, FRG

While it is possible to track the evolution of social bees or wasps by comparing the behaviour of living species with varying degrees of sociality, we lack that opportunity in the Formicidae, since all living ants are highly social. In order to shed light on the evolution of this family we will therefore have to use all available sources of information. This paper, the summary of a comprehensive investigation into the evolution of stridulatory organs (SO) in ants, which will be published in detail with the full list of references elsewhere (Markl, in prep.) tries to provide new evidence for that purpose. The main argument is based on a study of the function of sound-communication in leaf-cutter ants (Markl 1967, 1968, 1970), which gave the following results. All castes of Atta can emit trains of clicks by pulling a cuticular file on the first tergite of the gaster forward, beneath the posterior edge of the postpetiolar tergite. The click-repetition rate is 700 to 1000 sec^{-1}; "trains" contain about 30 to 40 clicks and last 40 to 50 msec; their repetition-rate is 4 to 7 sec^{-1}. A leaf-cutter will produce sound when it is prevented from moving freely. Under natural conditions this can happen most easily when ants nesting deep in the soil are buried by a "cave-in". Buried ants stridulate violently and attract nest-mates by the vibrations produced on the ground surface. These nest-mates finally dig out the entrapped ants. Airborne signals cannot elicit these reactions. Thus stridulation in Attines serves as an alarm in underground emergency. The substrate-borne vibration signals can only be used in substrates which conduct vibrations well. Since there is no selective advantage in making the signals species-specific, we are not surprised to find them rarely specific even on the genus level. The main importance of this alarm system may be to rescue the queen, if she has been entrapped, the importance of which is evident in an ant society with a monogynous colony-foundation.

The question arises, whether this function of the SO is confined to attines or whether it is a primary function in ants. Though it cannot be denied that stridulation may serve other or additional functions (see below), the following considerations assume that stridulation in many groups of ants serves as an underground distress alarm of terrestrially nesting ants. This follows from a correlative study of nesting ecology, mode of colony foundation and occurrence of a SO in ants of all subfamilies. This was studied in 1354 species belonging to 205 genera of ants, out of a total number of 267 genera recognised by Brown (1973). This sample includes 85% of all genera of those subfamilies in which a SO is found (Ponerinae, Pseudomyrmecinae, Myrmicinae).1) Only

---

1) This study would not have been possible without the generous help of Drs. E.O. Wilson, W.L. Brown jr. and H.E. Evans and the excellent myrmecological collection of the Museum of Comparative Zoology, Harvard University. This is gratefully acknowledged.

Sharp (1893), Raignier (1933) and Haskins & Enzmann (1938) have previously surveyed the distribution of the SO in ants, though in much too small samples. The presence or absence of a SO is always a species characteristic, valid for all members of all castes of a species. However, within one genus there may be species with or without the SO. If there is a SO, it is always to be found between the 3rd and 4th abdominal segment.

Table 1 summarizes the results. No SO is found in the fossil Sphecomyrminae, in Myrmeciinae, Dolichoderinae, Formicinae, Ecitoninae, Leptanillinae, and Dorylinae, while it is present in all Pseudomyrmecinae, in 83% of the Myrmicinae species and 48% of the Ponerinae species checked. The latter subfamilies warrant closer inspection:

Ponerinae: 27 (58%) of 47 genera checked lack the SO. In 14 (30%) of the genera all species studied have the SO, while in 6 (12%) some do and others don't, the relation on the species level being 245 (+) to 89 (-). In these 6 genera we find 334 (50%) of 661 species studied, mostly in the large genera Rhytidoponera, Pachycondyla (new, see Brown 1973), Leptogenys and Odontomachus (tribes Ectatommini and Ponerini). All genera of the tribes Amblyoponini, Typhlomyrmecini, Cerapachyini and Acanthostichini lack the SO.

Myrmicinae: 100 (93.5%) out of 107 genera studied possess the SO in all 419 species. Only 5 (4.5%) genera with together 61 species lack the SO entirely, while in 2 (ca. 2%) (Pristomyrmex, Myrmicaria) some species (3) have the organ and others (25) lack it. Thus, Myrmicines are almost completely "stridulatory", the more important exceptions being all or most Cataulacini, Myrmicariini and Cephalotini.

Fig. 1 presents a phylogenetic diagramm following Brown (1954, 1973) and Wilson et al. (1967), but modifying their proposals according to the data on the distribution of the SO. This affects most notably the position of the Pseudomyrecinae, which was included by Brown among the "Myrmecioid Complex". Since we find that all other groups of this complex lack a SO, while the Pseudomyrmecinae possess it without exception, it is proposed to reconsider their relationship and maybe also the dichotomous scheme of formicid evolution, which should also bear on the open question of mono- or diphyletic origin of ants (see Gotwald 1969, Wilson 1971). Fig. 1 shows that the SO occurs neither randomly nor independent of phyletic relations, since it is often characteristic of a genus, tribe or even subfamily. Major features of this enigmatic pattern of distribution can be explained by applying our knowledge of the function of stridulation in the leaf-cutter ants.

1. The myrmecioid complex (excluding the Pseudomyrmecinae) does not contain species with a SO. It may have been absent in the common ancestor, since the cretaceous Sphecomyrma, which is regarded as being close to myrmecoids (Wilson et al. 1967) shows no trace of the organ.
2. It is most probable that the ancestral forms of the poneroid complex nested in the soil, since the more primitive genera of both ponerines and myrmicines nest that way. In them, accordingly, stridulation could have served, as in the attines, as an underground alarm signal in cave-in

emergencies. It is important that the attines can be derived in direct line from exclusively terrestrially nesting myrmicines and those from soil-dwelling ponerine ancestors (Wheeler 1907, Wilson 1971). Consequently we should expect that all ants of the poneroid complex, which nest in the soil and stem in continuous line from ground-nesting ancestors, possess the SO. This is indeed the case in many ponerine genera (e.g. Ectatomma, Paraponera, Harpegnathus, Dinoponera, Streblognathus, Megaponera, Odontoponera) and most myrmicine tribes (e.g. Myrmicini, Pheidolini, Pheidologetini, Leptothoracini, Tetramoriini, Solenopsidini, Attini and most Myrmecinini).

3. On the other hand, in ants which gave up inhabiting permanent nests in the ground, the SO could be lost without disadvantage. We should therefore expect to find loss of the SO most often in ants of the poneroid complex which a) nest arboreally; b) nest in substrates like rotting leaf-litter, which conduct vibration poorly and where there is no danger of being interred; or, c) gave up permanent nests. For all three cases there is supporting evidence.

ad a) The arboricolous Cataulacini and most of the arboreal Cephalotini lack the SO. The same is true for the arboreal Rhopalomastix and for most Myrmicariini, which have strong tendencies to arboreal life.

ad b) The ponerines include numerous groups of ants, mostly of small body size, which nest in rotting plant materials on the soil surface. Many of these cryptobiotic ants lack the SO (e.g. Typhlomyrmex, Gnamptogenys, Proceratium, Discothyrea, Probolomyrmex, Cryptopone). Many Amblyoponini might be counted here also, though it seems conceivable that this most primitive ponerine tribe lacks the SO primarily and not due to secondary loss. In genera which contain soil-dwelling species as well as others nesting in rotting material, development of the SO is extremely variable (e.g. Rhytidoponera, Platythyrea, Pachycondyla, Leptogenys, Odontomachus). In Leptogenys there is also the tendency to nomadic life in some species, (Wilson 1958).

ad c) Nomadic ants as a rule possess no permanent terrestrial nests and almost all of them lack the SO: Ecitoninae, Leptanillinae, Dorylinae, Cerapachyini, Acanthostichini, Simopelta, Onychomyrmex.

It therefore seems that a hypothesis which correlates the evolution of sound production with nesting ecology in ants, can explain major features of the pattern of distribution of the SO within the family and help clarify phylogenetic relationships. However, there remain many exceptions which do not fit that picture. Of course there is no reason to expect that every cryptobiotic or arboreal group has lost the SO, since there is no selection pressure in that direction. Nor can one overlook the possibility that in some groups, e.g. of ponerines, which have a long evolutionary history, nesting in the soil was taken up again after a loss of the SO had already occurred in a different nesting milieu (change of

Fig. 1

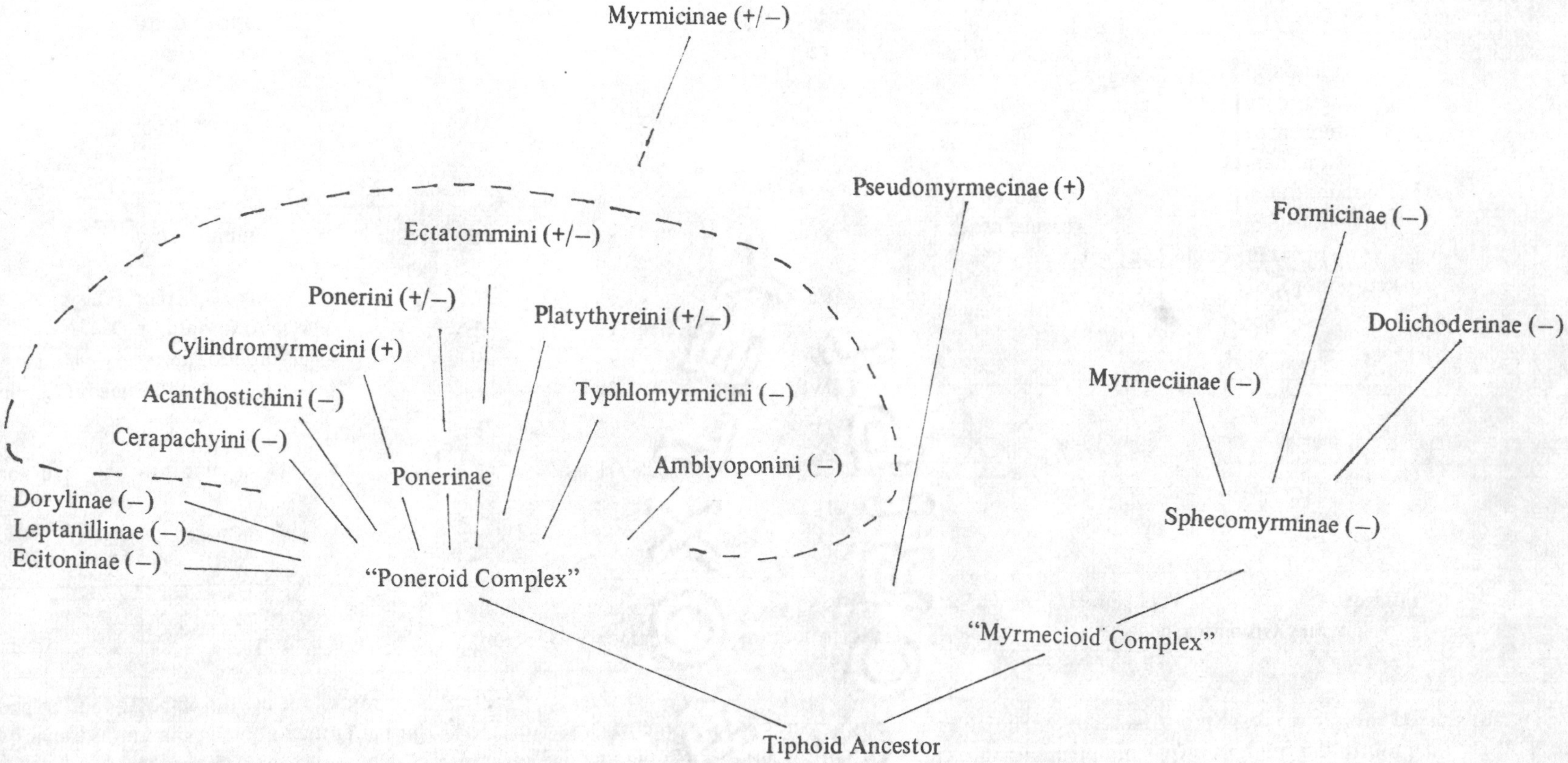
Myrmicinae (+/–)
Pseudomyrmecinae (+)
Formicinae (–)
Ectatommini (+/–)
Ponerini (+/–)
Platythyreini (+/–)
Dolichoderinae (–)
Cylindromyrmecini (+)
Myrmeciinae (–)
Acanthostichini (–)
Typhlomyrmicini (–)
Cerapachyini (–)
Amblyoponini (–)
Ponerinae
Dorylinae (–)
Leptanillinae (–)
Ecitoninae (–)
Sphecomyrminae (–)
"Poneroid Complex"
"Myrmecioid Complex"
Tiphoid Ancestor

Table 1: The occurrence of a stridulatory organ (SO) in 205 genera (1354 species) of Formicidae. In those subfamilies or tribes, in which all genera possess or lack a SO, only the total numbers of genera (according to Brown 1973), and the numbers of genera and species checked are given. When the SO is present in some genera of a tribe and absent in others, the names of these genera are listed in the + or – columns. When there are within one genus species with and species without the SO, the numbers of species with (+) or without (–) the SO are given besides the name of that genus. The arrangement of ponerine tribes follows W.L. Brown (in litt., 1972). In the Myrmicinae the tribal arrangement is not finally settled for genera belonging to the former tribes Myrmicini, Pheidolini, Myrmecinini, Leptothoracini, Tetramoriini, Solenopsidini and Pheidologetini (W.L. Brown, in litt.; Ettershank 1966). Since all the genera belonging there with only two exceptions possess the SO, they are lumped in one "tribe-group" in the table.

Subfamily	Tribe	Number of Genera		Number of Species	Stridulatory Organ	
		Total	Checked	Checked	Present (+)	Absent (–)
Sphecomyrminae		1	1	1		–
Myrmeciinae		2	1	51		–
Dolichoderinae (incl. "Aneuretinae")		22	10	22		–
Formicinae		44	25	41		–
Ponerinae (incl. "Cerapachyinae")		49	47	661	+/–	
	Amblyoponini	6	6	60		–
	Typhlomyrmecini	1	1	2		–
	Platythyreini	2	2	23		Probolomyrmex (18+) Platythyrea (4–)
	Ectatommini	9	8	132	Paraponera Ectatomma	Acanthoponera Heteroponera Gnamptogenys Proceratium Discothyrea (48+) Rhytidoponera (1–)
	Cerapachyini	3	3	74		–
	Acanthostichini	1	1	5		–
	Cylindromyrmecini	1	1	5	+	
	Ponerini	26	25	370	Thaumatomyrmex Harpegnathus Dinoponera Streblognathus Megaponera Odontoponera Ophthalmopone Belonopelta Ponera Hypoponera Prionogenys	Diacamma Centromyrmex Paltothyreus Hagensia Crypotpone Simopelta Emeryopone Plectroctena Psalidomyrmex Asphinctopone (67+) Pachycondyla (55–)

Table 1 continued

Subfamily	Tribe	Number of Genera Total	Number of Genera Checked	Number of Species Checked	Stridulatory Organ Present (+)	Stridulatory Organ Absent (–)
Ponerinae contd.	Ponerini contd.				(5+) Brachyponera	(6–)
					(69+) Leptogenys	(5–)
					(38+) Odontomachus	(18–)
Ecitoninae		6	6	13		–
Leptanillinae		5	3	7		–
Dorylinae		4	3	14		–
Pseudomyrmecinae		2	2	36	+	
Myrmicinae		132	107	508		+/–
	"Tribe-Group 1"	71	63	288	+ with exception of:	
					(2+) Pristomyrmex	(12–)
						Carebarella (1–)
	Meranoplini	5	5	28	Prodicroaspis	Meranoplus
					Promeranoplus	
					Calyptomyrmex	
					Mayriella	
	Metaponini	1	1	4	+	
	Melissotarsini	2	2	2	Melissotarsus	Rhopalomastix
	Stereomyrmecini	1	1	1	+	
	Ocymyrmecini	1	1	2	+	
	Myrmicariini	1	1	14	(1+) Myrmicaria	(13–)
	Cardiocondylini	1	1	8	+	
	Ochetomyrmecini	3	2	8	+	
	Crematogastrini	1	1	25	+	
	Stegomyrmecini	1	0	0		?
	Agroecomyrmecini	1	0	0		?
	Basicerotini	6	3	6	+	
	Cataulacini	1	1	12		–
	Dacetini	23	12	34	+	
	Cephalotini	2	2	41	Procryptocerus	Cephalotes
	Attini	11	11	35	+	
Formicidae		267	205	1354		+/–

arboreal to terrestrial nesting and vice-versa is well-known from several dolichoderine and formicine groups). It might be that causes like these are responsible for some of the odd presences or absences of the SO among the Ponerini (e.g. the terrestrial Paltothyreus, Hagensia, Plectroctena or Psalidomyrmex lack the SO; some of the arboreal Pachycondyla - formerly Neoponera - have it). In addition, however, there are a few well-defined groups, which have many or all species living arboreally and nevertheless have and use[2] a well-developed SO. This is most evident in the Pseudomyrmecinae and in the Crematogastrini. So far, we have no satisfactory explanation for this. However, they have a remarkable trait in common: they seem not to have taken up arboreal life through a stage of nesting on the soil-surface in decaying material, but through soil-dwelling forms which entered living trees through or along roots and bark, thus they never left a substrate which conducts mechanical vibrations excellently. They may therefore never have stopped using vibrational signals, though, of course, one has to postulate a change in their function, which remains, however, to be discovered. It must be mentioned, that some tree-dwelling dolichoderines and formicines (e.g. Dolichoderus, Hypoclinea, Polyrrhachis, Camponotus; Markl unpubl. experiments, Markl & Fuchs 1972) also use vibrational communication by drumming on the substrate with hard body-parts.

As is true for many evolutionary hypotheses which have to be based on plausible correlation rather than crucial experimental proof, these considerations on the evolution of stridulation in ants should be regarded as a working hypothesis for focussing the interest on groups, the study of which might answer key-questions for further corroboration or refutation of the model (e.g. Leptogenys, Pseudomyrmex or Crematogaster).

---

[2] Many cryptobiotic genera of ponerines and myrmicines, which nest in rotting plant material, though having a stridulatory organ, cannot be induced to use it when restrained, as all typical soil-dwellers do (e.g. many Ponera and Hypoponera, as well as many Basicerotini and Dacetini; Markl, unpubl. experiments).

REFERENCES

(A comprehensive list of references will be provided in Markl, in preparation)

BROWN, W.L., jr. (1954) Insectes soc. 1, 21-31

BROWN, W.L., jr. (1973) p. 161-185 in "Tropical Forest Ecosystems in Africa and South America: A comparative Review". Smithsonian Institution Press, Washington

ETTERSHANK, G. (1966) Aust. J. Zool. 14, 73-171

GOTWALD, W.H. (1969) Cornell University Agriculture Experimental Station Memoir No. 408

HASKINS, C.P. AND ENZMANN, E.V. (1938) Ann. N.Y. Acad. Sci. 37, 97-162

MARKL, H. (1967) Z. vergl. Physiol. 57, 299-330

MARKL, H. (1968) Z. vergl. Physiol. 60, 103-150

MARKL, H. (1970) Z. vergl. Physiol. 69, 6-37

MARKL, H. Stridulationsvermögen und Evolution der Ameisen (in preparation)

MARKL, H. AND FUCHS, S. (1972) Z. vergl. Physiol. 76, 204-225

RAIGNIER, A. (1933) Brotéria 2, 51-82

SHARP, D. (1893) Trans. R. ent. Soc. Lond. p. 144-213

WHEELER, W.M. (1907) Bull. Am. Mus. nat. Hist. 23, 669-807

WILSON, E.O. (1958) Evolution Lancaster, Pa. 12, 24-31

WILSON, E.O. (1971) The Insect Societies. (Belknap Press Cambridge)

WILSON, E.O., CARPENTER, F.M. AND BROWN, W.L., jr. (1967) Psyche, Camb. 74, 1-19