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Structure of the "preoral comb" in larvae of European Agabini (Coleoptera, Dytiscidae)

INTRODUCTION

The presence of a singular, comb-like head organ, located to the pumping-chamber floor in the third-instar larvae of *Agabus bipustulatus* (L.) and *Ilybius fuliginosus* (Fabr.), was made known some years ago (DE MARZO, 1979).

This comb is composed of a number of differently shaped spinulae, which are arranged in a row just anterior to the border between the cibarial floor and the pharynx, inside the pumping-chamber (DE MARZO, l.c., fig. 31). The function of the comb has not been established. Out from its transverse position in the stream of the meal fluids, the function is evidently connected with the feeding, and three different hypotheses have been suggested (DE MARZO, 1983): (1) the comb is a filtering apparatus which prevents large food particles from entering the pharynx; (2) the comb contributes to the closing of the alimentary canal during the peristaltic motions that both sucking and digestion require; (3) the comb is useful in removing the secretion which is probably produced by the dorsal surface of the cibarium in front of it.

Both the number and shape of comb spinulae show a pronounced interspecific variation. Within each species, variation is sometimes large between the three different larval instars.

In order to collect new data for the systematic knowledge of the tribe Agabini, we have esteemed useful to search for presence and structure of this comb in several species by tradition placed in the subf. Colymbetinae.

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MATERIAL AND METHODS

39 species of the agabine genera *Platambus* Thomson, *Agabus* Leach and *Ilybius* Erichson, and 12 species in 8 genera of the tribes Copelatini, Colymbetini, Coptotomini and Matini were examined. Also studied was *Agabetes acuductus* (Harris) that previously was placed with the Copelatini, but now transferred to the subf. Laccophilinae (NILSSON, 1989).

Most larvae were collected in the field and identified either by comparing them with reared specimens or with published descriptions (GALEWSKI, 1966; 1980). Further, larvae were obtained *ex ovo*. The geographical origin of the specimens of the tribe Agabini is given for each species in table 3. Specimens of *Copelatus glyphicus* (Say), *Coptotomus interrogatus* (Fabr.), *Matus bicarinatus* (Say) and *Agabetes acuductus* (Harris) were courteously provided by Dr. H.J. Spangler (Smithsonian Inst., Washington).

In most species, only 1 or 2 specimens were examined. Several specimens from different localities in Central and South Italy were studied of *Agabus bipustulatus* (L.), *A. conspersus* (Marsh.) and *A. didymus* (Ol.). Usually, only third-instar larvae were examined, but all three instars have been studied of *Agabus biguttatus* (Ol.), *A. nebulosus* (Forst.), *A. melanocornis* Zimm. and of the three above-mentioned species of *Agabus*.

Heads of specimens preserved in fluid (formalin 5% or ethanol 70%) were freed from soft tissues by hot treatment in 0.5% solution of Potassium hydroxide; then, they were briefly boiled in an equal-part mixture of glycerol and acetic acid, before mounted in glycerol.

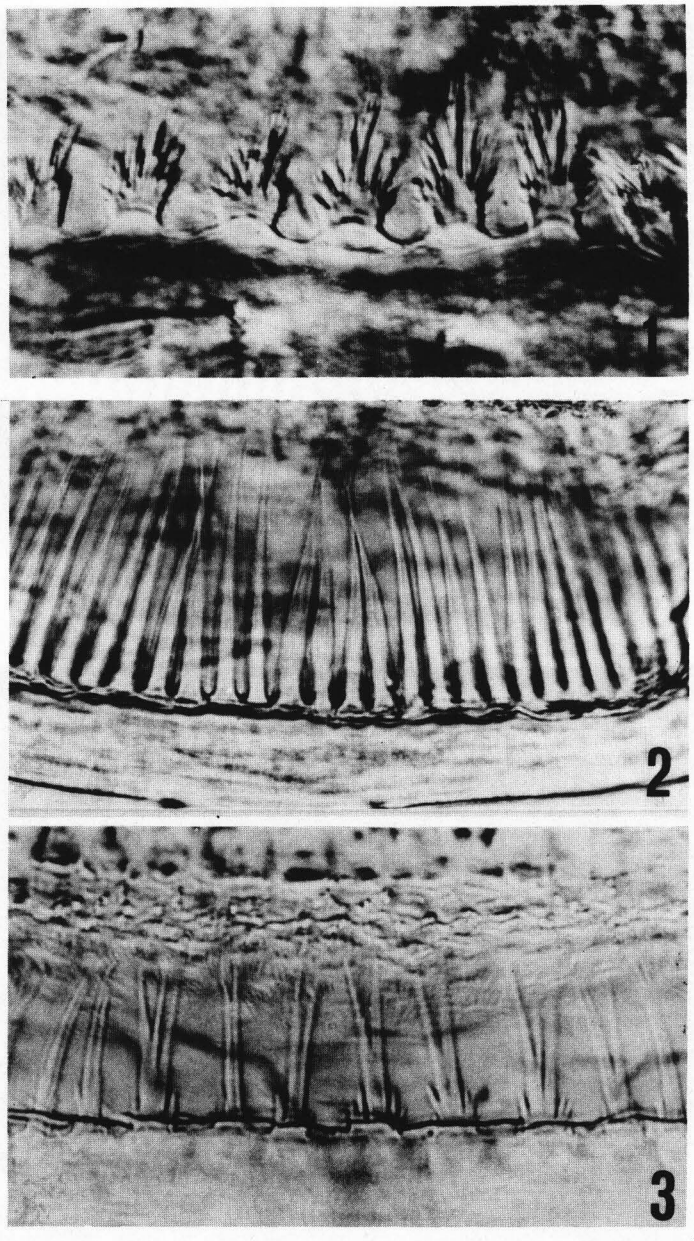
Photos by SEM were taken from samples dissected, washed and dried up by ethanol, and plated by gold-palladium sputter.

RESULTS

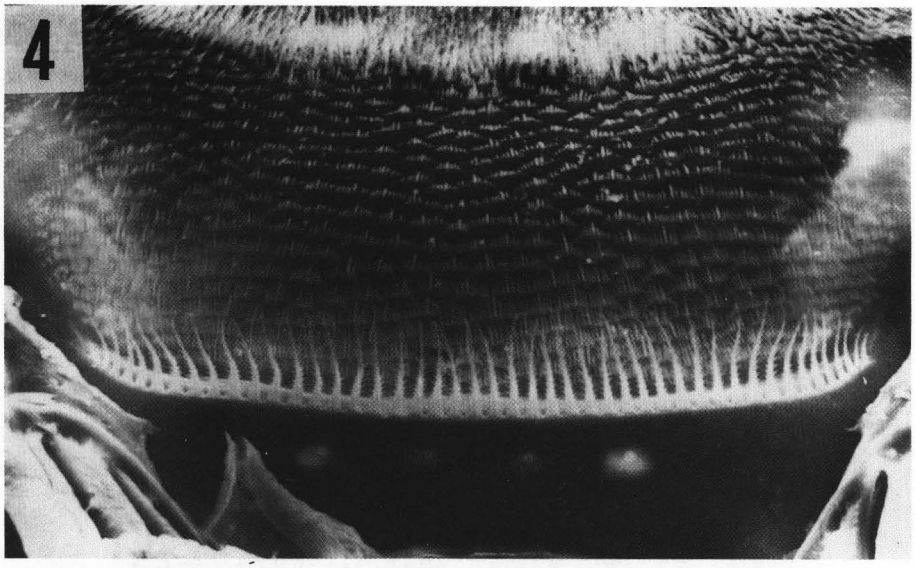
Presence of the comb in the subf. Colymbetinae

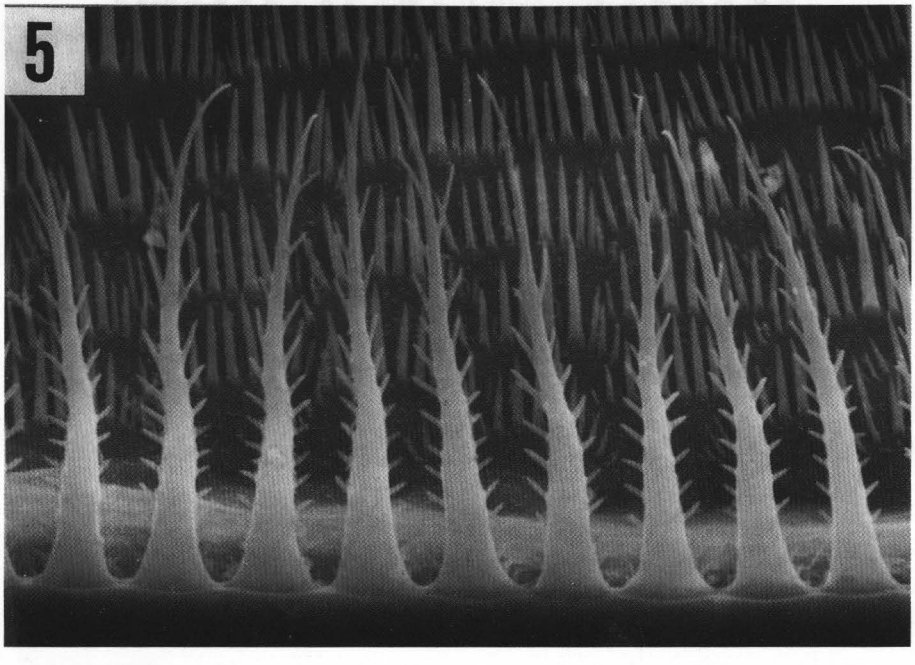
All species examined of the tribe Agabini, except *Ilybius similis*, exhibit the comb (table 3). This organ is absent in the following non-agabine members of the subfamily:

— tr. Copelatini: *Copelatus haemorrhoidalis* (Fabr.), *C. glyphicus* (Say);
— tr. Colymbetini: *Rhantus bistriatus* (Bergstr.), *R. exsoletus* (Forst.), *R. suturalis* (Macl.), *Nartus grapii* (Gyll.), *Melanodytes pustulatus* (Rossi), *Colymbetes fuscus* (L.), *C. dolabratus* (Payk.), *Meladema coriacea* Cast.;
— tr. Coptotomini: *Coptotomus interrogatus* (Fabr.);



Figs 1-3 - Preoral comb in third-instar larvae of: 1, *Platambus maculatus*; 2, *Agabus arcticus*; 3, *A. serricornis*.

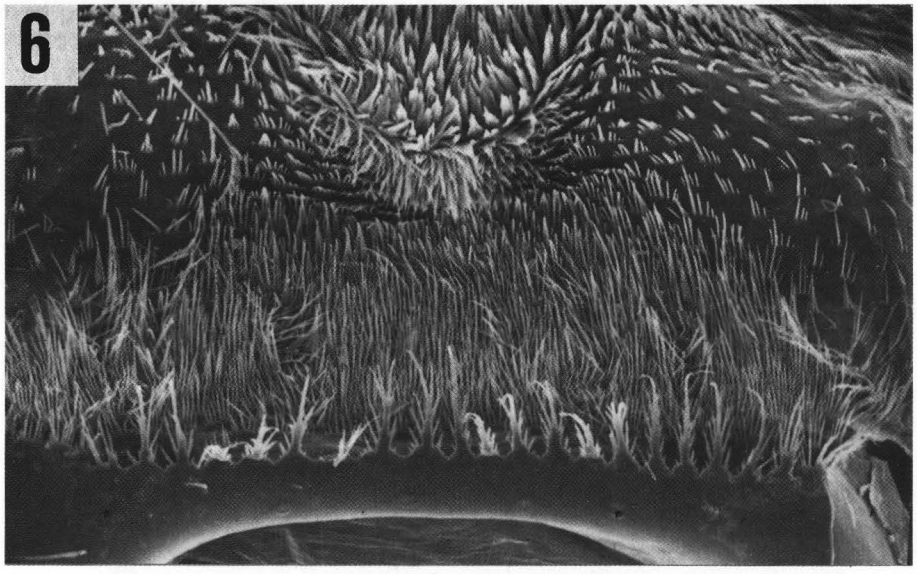


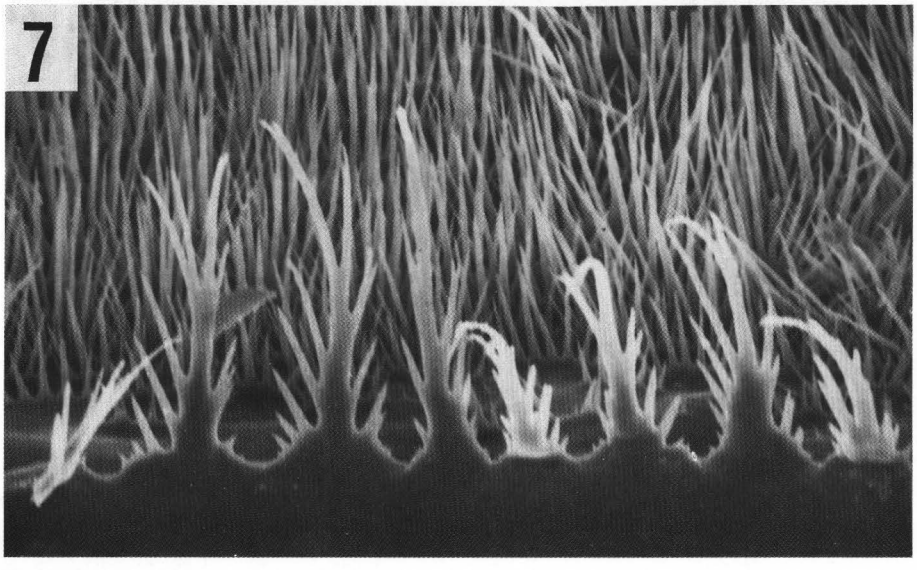


Figs 4-5 - Preoral comb in a third-instar larva of *Agabus bipustulatus*.

— tr. Matini: *Matus bicarinatus* (Say).

Agabetes acuductus (Harris), traditionally placed with the Copelatini, does not possess a typical comb, but it bears a number of short spinulae, which are not arranged in a row, scattered on its cibarial floor (fig. 16).

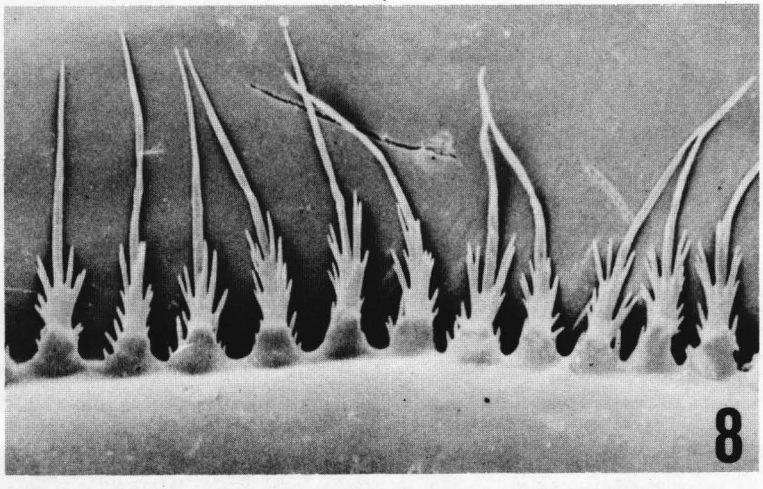




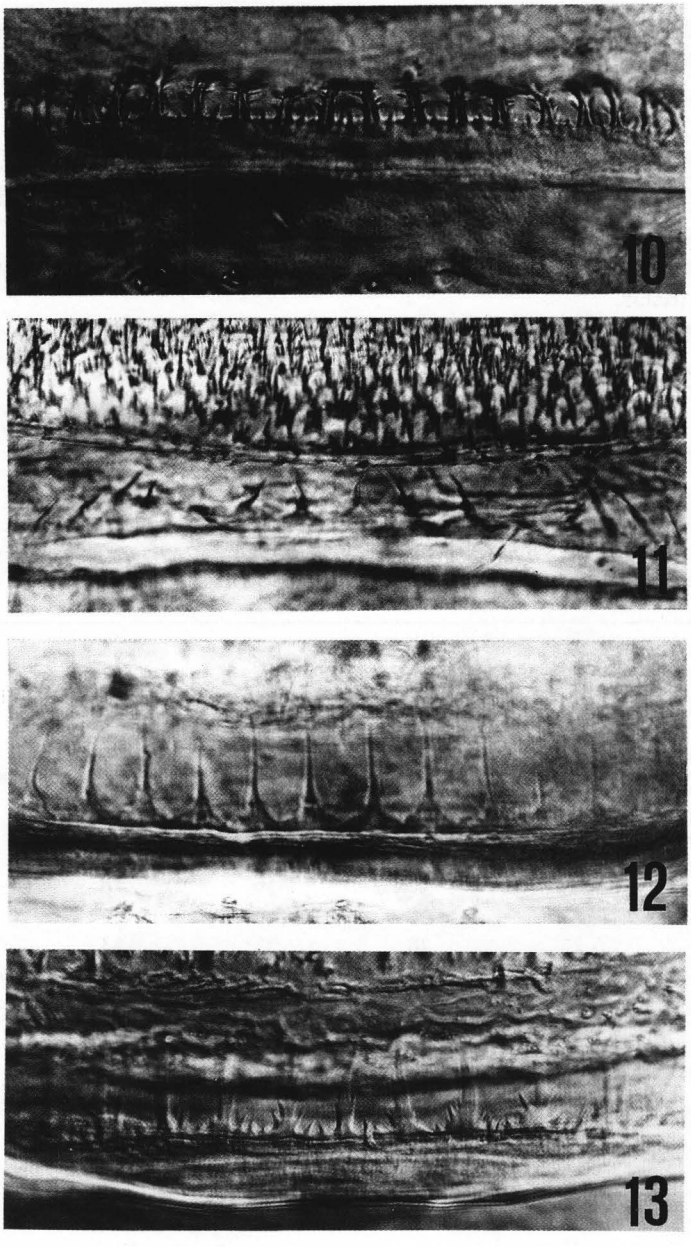
Figs 6-7 - Preoral comb in a third-instar larva of *Agabus affinis*.

Intraspecific variation: number of spinulae

In conspecific third-instar larvae, variation in the number of spinulae was studied in three species (table 1), including comb-types with moderate (*A. conspersus*, *A. didymus*) and high (*A. bipustulatus*) numbers of spinulae. Five specimens, choosen at random, were examined per each of three different localities. Results show that most values fall in the range ± 10% of the mean value, but individuals with either markedly lower or markedly higher values do occur as well.



Figs 8-9 - Very different forms of preoral comb in third-instar larvae of *Agabus conspersus* (8) and *A. nebulosus* (9).



Figs 10-13 - Preoral comb in third-instar larvae of *Ilybius*: 10, *I. crassus*; 11, *I. guttiger*; 12, *I. quadriguttatus*; 13, *I. aenescens*.

No geographical basis for such deviations is obviously recognizable.

In conspecific larvae of different instars, the number of spinulae was found either similar or different (table 2) in agreement with the following rules:

I) in species with a low or moderate number (*A. conspersus, A. melanocornis, A. didymus*), this is similar in the first and second instar, but nearly redoubles in the third;

II) in species with a high number (*A. bipustulatus*), this is similar between each instar;

III) in species with a very high number (*A. nebulosus*), this increases stepwise in both moultings.

TABLE 1 - Number of spinulae in conspecific third-instar larvae from three different localities. The mean values and the values exceeding ± 10% of the mean value are given. Five randomly selected specimens from each locality were examined.

Agabus conspersus					
loc. A	26	26	27	28	35
loc. B	25	25	26	27	28
loc. C	24	26	26	27	27
			mean value: 27	extreme values: 24 and 35	
Agabus didymus					
loc. D	25	27	29	30	32
loc. E	27	27	29	32	34
loc. F	27	28	33	33	34
			mean value: 30	extreme values: 25 and 34	
Agabus bipustulatus					
loc. G	51	52	53	54	54
loc. H	39	44	45	46	51
loc. I	46	49	49	52	63
			mean value: 50	extreme values: 39 and 63	

Legend of localities (all in Italy): A) Apulia, prov. Taranto, Sava; B) Apulia, prov. Foggia, Zapponeta; C) Calabria, prov. Cosenza, Sibari; D) Basilicata, prov. Potenza, Vaglio; E) Umbria, prov. Perugia, Assisi; F) Apulia, prov. Taranto, Laterza; G) Apulia, prov. Bari, Modugno; H) Apulia, prov. Taranto, Palagianello; I) Apulia, prov. Taranto, Manduria.

TABLE 2 - Number of spinulae in different instars (I, II, III) in single individuals (named A, B, C, etc.).

Agabus conspersus			
ind. A	I: 15	II: 17	III: 31
ind. B	I: 14	II: 15	III: 28
Agabus melanocornis			
ind. C	I: 11	II: 12	
Agabus didymus			
ind. D		II: 16	III: 29
Agabus bipustulatus			
ind. E	I: 41	II: 43	
ind. F	I: 50	II: 50	
ind. G		II: 52	III: 49
Agabus nebulosus			
ind. H	I: 60	II: 70	III: 80
ind. I	I: 68	II: 78	
ind. J		II: 67	III: 92

TABLE 3 - Number and shape of comb spinulae in the third-instar larvae of the examined species of Agabini. The geographical origin of the specimens is also reported: I = Italy, N = Norway, P = Poland, S = Sweden.

Species	Geogr. origin	No. of Spinulae	Addit. Spinulae	Shape of Spinulae			
				slender-simple	slender-branched	short-simple	short-branched
Platambus							
maculatus (L.)	P	10					*
Agabus Gaurodytes							
affinis (Payk.)	S	26	*				*
striolatus (Gyll.)	S	67			*		
melanarius Aubé	S	52			*		
bipustulatus (L.)	I	39-63			*		
guttatus (Payk.)	S	20			*		
biguttatus (Ol.)	I	24					*
paludosus (Fabr.)	I	24					*
conspersus (Marsh.)	I	24-35					*
nebulosus (Forst.)	I	90-100		*			
sturmii (Gyll.)	S	16			*		
arcticus (Payk.)	S	21			*		
elongatus (Gyll.)	S	19			*		
congener (Thunb.)/							
lapponicus (Thoms.)	S	18			*		
levanderi Hellén	S	35			*		
zetterstedti Thoms.	S	30			*		
confinis (Gyll.)	S	34			*		
fuscipennis (Payk.)	S	35			*		
melanocornis Zimm.	I	24					*
wasastjernae (Sahlb.)	S	23					*
opacus Aubé	S	18					*
subtilis Er.	S	32					*
erichsoni Gemm. & Harold	S	35			*		
brunneus (Fabr.)	I	18					*
didymus (Ol.)	I	25-34		*			
Agabus Eriglenus							
labiatus (Brahm)	S	100		*			
undulatus (Schrank)	N	25					*
Agabus s.str.							
serricornis (Payk.)	S	46		*			
Ilybius							
vittiger (Gyll.)	S	22			*		
angustior (Gyll.)/*picipes* (Kby.)	S	25			*		
crassus Thoms.	S	25			*		
subaeneus Er.	S	28			*		
ater (DeG.)	I	31			*		
guttiger (Gyll.)	S	15				*	
quadriguttatus (Lac.)	I	15				*	
similis Thoms.	S	0					
aenescens Thoms.	S	11					*
fuliginosus (Fabr.)	I	20-21			*		
fenestratus (Fabr.)	P	30	*				*

Intraspecific variation: shape of spinulae

In conspecific larvae of the same instar, no marked variation was found in this character.

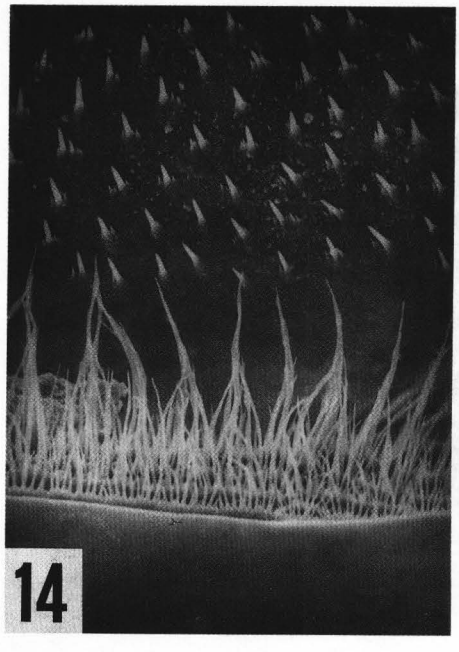
In larvae of different instars, the spinulae of the third-instar larvae were usually more slightly slender than those of the previous instars. Exceptionally, in *A. didymus*, the spinulae are branched in the first and second instar, but not branched in the third.

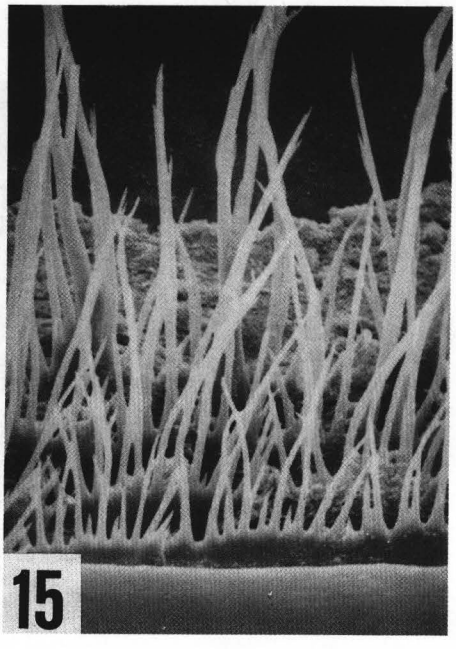
Interspecific variability: number and shape of spinulae in third-instar larvae

On this subject, table 3 gives data as follows:

I) relation between number of spinulae and number of species:

nought	1 sp. (*Ilybius*)
low (10-11)	2 spp. (1 *Platambus*, 1 *Ilybius*)
moderate (15-35)	30 spp. (21 *Agabus*, 9 *Ilybius*)
high (39-67)	4 spp. (*Agabus*)
very high (90-100)	2 spp. (*Agabus*)





Figs 14-15 - Preoral comb in a third-instar larva of *Ilybius fenestratus*.

II) relation between shape of spinulae and number of species:

slender-simple	4 spp. (*Agabus*)
slender-branched	19 spp. (13 *Agabus*, 6 *Ilybius*)
short-simple	2 spp. (*Ilybius*)
short-branched	13 spp. (1 *Platambus*, 10 *Agabus*, 2 *Ilybius*)

Particular forms of comb occur in both *A. affinis* (figs 6-7) and *I. fenestratus* (figs 14-15), which bear a great number of long additional spinulae besides the main row.

Intergeneric variation

The number of spinulae in *Agabus* is moderate to very high (16-100). In *Ilybius* the range is from 0 to 31 spinulae, i.e. generally lower values but with a marked overlap with *Agabus*. In both genera the most frequent shape of spinulae is slender-branched. The slender-simple spinulae were found only in *Agabus*, mainly in species with high or very high numbers of spinulae. The short-simple kind of spinulae was only found in *Ilybius*.

The single *Platambus* species has a low number of short-branched spinulae.

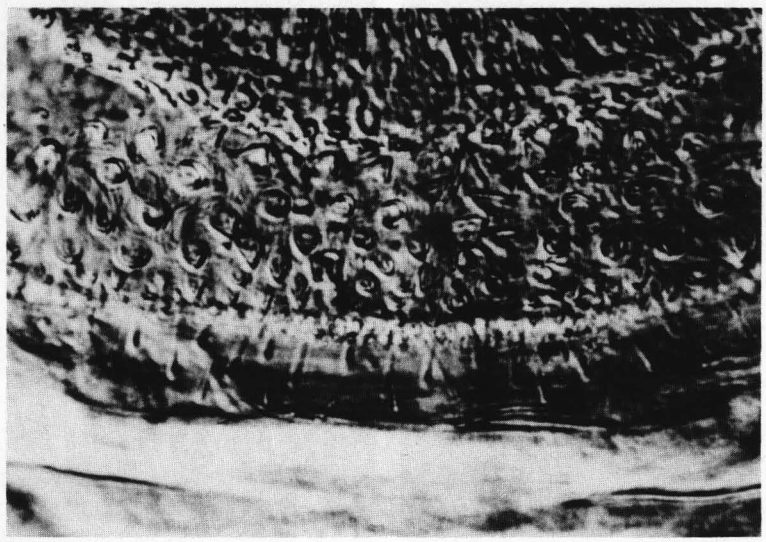


Fig. 16 - Supposed ancestral form of the preoral comb (scattered spinulae) in a third-instar larva of *Agabetes acuductus* (subf. Laccophilinae).

DISCUSSION

From an evolutionary point of view, our data suggest that the comb has evolved in agreement with two main trends.

The first trend involved a numerical increase of spinulae. We can realize this from the observation of both conspecific individuals in their different instars and larvae of different species. In most instances, the main row becomes richer in spinulae; otherwise, the addition of secondary rows is achieved. This evolution of the comb is in agreement with all three functional hypotheses (see Introduction).

Because most species have combs with 15-35 spinulae, we suggest that the primitive number of spinulae is found within this range. Consequently, we must hypothesize that the comb evolved from a number of scattered spinulae, which then assembled in a row. Such scattered spinulae were only observed in the third-instar larva of *Agabetes acuductus* (fig. 16), which actually exhibits some thirty scattered spinulae on its cibarial floor instead of a typical comb. However, this species is seemingly not a member of the subf. Colymbetinae (NILSSON, 1989). It is also possible that the presence of additional spinulae in *A. affinis* represents a primitive condition, in which the comb has evolved but the other spinulae have not yet been reduced.

The second trend involved degeneration of the comb in both number and shape of its spinulae, up to a total obliteration of the organ. As both a residual comb and an absence of comb have been observed in larvae with very slender mandibles (*Ilybius guttiger, I. quadriguttatus* and *I. similis*), we must relate this evolution to that of the mandibles. This view is in agreement with the hypothesis of a filtering function of the comb, as a thin mandibular canal can prevent the entering of large food particles into the cibarial chamber. In this way the comb looses its function.

From a taxonomical point of view, the inclusion of *Ilybius* into the tribe Agabini, together with *Platambus* and *Agabus*, is validated by the common presence of the comb, so that we do not realize the need of the separate "tribe Ilybiini" proposed by GALEWSKI (1971).

Because the intraspecific variation of the comb has not been minutely studied, the use of the comb as source of characters for a key to species is not suitable at present. However, the examination of the comb can be useful in certain instances. For example, we have found two very different forms of comb in *Agabus conspersus* and *A. nebulosus* (figs 8-9), species which are difficult to separate on the basis of their external characters. On the contrary, their identification on the basis of the comb structure lacks uncertainty.

In conclusion, the study of the preoral comb seems to provide useful data for the systematics of Agabini. A more extensive analysis of intra- and interspecific variation will be undoubtfully important for solving certain questions about both its evolution and taxonomical importance.

RIASSUNTO

STRUTTURA DEL "PETTINE PREORALE" NELLE LARVE DEGLI AGABINI EUROPEI (COLEOPT. - DYTISCIDAE)

Viene analizzata la variabilità strutturale (intra- e interspecifica e intergenerica) del pettine preorale delle larve degli Agabini, con particolare attenzione alle differenze fra larve mature, che vengono esaminate in 39 specie dei tre generi, *Platambus, Agabus* e *Ilybius*.

Per quanto riguarda la forma delle spinule - che è quasi sempre uguale nei tre stadi larvali di una stessa specie -, si sono individuate quattro categorie strutturali: allungate-semplici, allungate-ramificate, brevi-semplici e brevi-ramificate, delle quali è più comune la seconda. In due specie sono presenti anche spinule supplementari.

Per quanto riguarda il numero delle spinule, almeno nelle larve mature la sua variabilità è tendenzialmente contenuta nell'intervallo di ±10% del valore medio; ma anche valori nettamente maggiori e nettamente minori sono stati trovati nell'ambito di una stessa popolazione.

Nell'ontogenesi, il numero delle spinule può comportarsi in diversa maniera: (1) è all'incirca uguale nel primo e secondo stadio, ma è circa il doppio nel terzo; (2) è all'incirca uguale in tutti e tre gli stadi; (3) cresce gradatamente dal primo al terzo stadio. Il diverso comportamento è in relazione con il numero finale (basso, moderato, alto, molto alto) delle setole del pettine stesso.

Considerando l'insieme delle specie esaminate, si riscontrano differenze intergeneriche fra *Agabus* e *Ilybius* soprattutto nel numero delle spinule. Negli *Agabus* si son trovati esclusivamente valori da moderati a molto alti, mentre negli *Ilybius* si son trovati solo valori bassi e moderati. Inoltre, il genere *Ilybius* contiene l'unica specie nota della tribù Agabini che manca del pettine.

L'esame di specie di altre tribù (Copelatini, Colymbetini, Coptotomini e Matini) indica che la presenza del pettine è strettamente caratteristica degli Agabini, nell'ambito della subf. Colymbetinae. In una specie inquadrata di recente nella subf. Laccophilinae, *Agabetes acuductus*, si osserva, al posto del tipico pettine, un insieme disordinato di una trentina di spinule, che può essere riguardato quale esempio di modello ancestrale del pettine stesso.

Si avanza l'ipotesi che il pettine si sia evoluto in accordo con due tendenze principali: (1) aumento numerico delle spinule, a potenziamento della sua funzionalità; (2) riduzione progressiva fino all'obliterazione, legata alla perdita della sua funzione filtrante.

L'uso in tassonomia del pettine quale fonte di caratteri discriminativi delle specie è improponibile senza un più esteso esame della sua variabilità intraspecifica. Tuttavia, va fermata l'attenzione sul fatto che due tipi profondamente differenti di pettine si riscontrano rispettivamente in due specie, *Agabus conspersus* e *A. nebulosus*, che per altri caratteri morfologici sono difficilmente distinguibili.

SUMMARY

Data are presented on intra- and interspecific variations of the preoral comb of larvae of European Agabini, along with data on its distribution within the subf. Colymbetinae.

Evolutionary and taxonomic remarks are also given.

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Errata corridges da inserire nel volume XXII -1987 di "Entomologica".

E. SYLVÈN - SOLINAS M. - Structural and systematic review of *Gephyraulus* Rübsaamen (Diptera, Cecidomyiidae, Oligotrophini) with description of *G. moricandiae* sp. n. from Tunisia.

		ERRATA	CORRIGE
pag. 15, 18 th	line	Description	Descriptive
" 16, 11 th	"	inticating	indicating
" 17, 2 th	"	Faure'a	Faure's
" 17, 9 th	"	Medeira	Madeira
" 18, 23 th	"	Higer	Higher
" 19, 19 th	"	(Fig. 6, c)	(Fig. 7, c)
" 19, 34 th	"	Oligoytrophini	Oligotrophini
" 19, 35 th	"	furnisched	furnished
" 19, 35 th	"	setae	setae (Fig. 6)
" 22, 15 th	"	*moricandae*	*moricandiae*
" 27, 3 th	"	later	lateral
" 32, 5 th	"	costitutes	constitutes
" 33, 14 th	"	Poomyni	Poomyini
" 33, 23 th	"	pretarsal	tarsal
" 33, 30 th	"	7 - 9	6 - 9
" 34, 3 th	"	Cecidoymiidae	Cecidomyiidae
" 34, 15 th	"	Phytoceciden	Phytocecidien