COCOON-SPINNING AND THE DEFENSIVE FUNCTION OF THE MEDIAN GLAND IN LARVAE OF ALEOCHARINAE (COLEOPTERA, STAPHYLINIDAE): A REVIEW[1]

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ABSTRACT

Ability of a Leptusa *prepupa to spin a silken cocoon was reported by Albert Fauvel in 1862. A median gland of abdominal segment VIII of a* Leptusa *larva was described in 1914 by Paul Brass who speculated that it might have a locomotory function, but more probably a defensive function. Knowledge was expanded in 1918 by Nils Alarik Kemner who found the gland in larvae of 12 aleocharine genera and contended it has a defensive function. He also suggested that cocoon-spinning may be a subfamilial characteristic of Aleocharinae and that the Malpighian tubules are the source of silk. Kemner's work has been largely overlooked and later authors attributed other functions to the gland. However, the literature yet contains no proof that Kemner was wrong even though some larvae lack the gland and even though circumstantial evidence points to another (perhaps peritrophic membrane) origin of the silk with clear evidence in some species that the Malpighian tubules are the source of a nitrogenous cement. The degree of development of the gland varies among tribes of Aleocharinae with a higher level of development occurring in what are now considered the most derived tribes. Developmental state of the median gland and the ability to spin a cocoon may help elucidate the phylogeny of Aleocharinae.*

RÉSUMÉ

La capacité de la pupe de Leptusa *à filer un cocon de soie a été rapportée par Albert Fauvel en 1862. En 1914, Paul Brass décrivit une glande médiane sur le huitième segment abdominal de la larve de* Leptusa *et il supposa qu'elle pouvait avoir une fonction locomotrice ou, plus probablement, une fonction défensive. Les connaissances sur cette glande ont été étendues en 1918 par Nils Alarik Kemner qui la trouva chez les larves de 12 genres d'Aléocharinés et qui soutint qu'elle avait une fonction défensive. Il suggéra également que la filature d'un cocon puisse être une caractéristique de la sous-famille des Aleocharinae et que les tubes de Malpighi soient la source de soie. Le travail de Kemner a été largement ignoré et les auteurs subséquents attribuèrent d'autres fonctions à la glande. Cependant la littérature ne contient aucune preuve indiquant que Kemner était dans l'erreur, bien que certaines larves n'aient pas de glandes, que des preuves indirectes indiquent une origine différente de la soie (peut-être la membrane péritrophique) et que des preuves nettes montrent que chez certaines espèces, les tubes de Malpighi sont la source d'un ciment azoté. Le degré de développement de la glande varie selon les tribus d'Aleocharinae, un niveau de développement plus élevé se rencontrant chez les tribus*

considérées comme les plus dérivées. L'état de développement de la glande médiane et la capacité à filer un cocon peuvent aider à élucider la phylogénie des Aleocharinae.

Arnett (1961) wrote that aleocharines were the most poorly known of all beetles. Unfortunately, that situation remains the same two decades later. If knowledge of the adults of this taxonomically difficult group is inadequate, knowledge of the immature stages lags so far behind that larvae collected in the field usually cannot be identified even to tribe. This is true even though many aleocharine larvae have been described; however, many descriptions of larvae identified only by association with adults (*ex societate imaginis*) are of doubtful validity. Since the current classification of the Aleocharinae is based solely on the structure of the adults, increased knowledge of the larvae, through thorough descriptions of reared larvae placed in the context of the existing literature to allow discrimination between tribal, generic and specific characters, should help provide a better understanding of the phylogeny of this huge group.

Because of the small size of aleocharine larvae, only the larger and more obvious structures have been described for many taxa. Among these is the median gland (sometimes called the dorsal gland) of abdominal segment VIII. When it is darkly pigmented and protuberant, the gland is readily visible, and in some larvae it even overhangs tergite IX. Another obvious character is the cocoon-spinning ability of the prepupa of many aleocharine genera.

What is the ecological, phylogenetic, and behavioral significance of cocoon-spinning? Where are the glands that produce the silk and what is their structure? What is the physiological manner of its production? What were the genetic and evolutionary pathways that led to cocoon-spinning? The presence of a median gland raises a similar group of questions. Unfortunately, even though both the median gland and cocoon-spinning have been known in the literature for more than a century, not one of those questions can be answered.

This paper is concerned principally with: 1) reviewing the literature as it pertains to the median gland and cocoon-spinning; 2) compiling the known distribution of these two characters among the tribes of the Aleocharinae; and, 3) assessing the potential of these characters toward elucidating phylogenetic relationships within the subfamily and between the Aleocharinae and the rest of the Staphylinidae. Cocoon-spinning and glands of other staphylinid larvae as well as the tergal gland of aleocharine adults are discussed insofar as they relate to the objectives.

THE MEDIAN GLAND OF ALEOCHARINE LARVAE

Perris (1853) mentioned and illustrated a protuberant dorsal structure of abdominal segment VIII, extending posteriorly over segment IX in larvae of *Phloeopora*. He did not attribute a function to this structure. Some other aleocharine larvae were found to have similar structures by Fauvel (1862, 1875) and Rey (1887) (Table 1).

Recognizing the glandular nature of the protuberance, Brass (1914) sectioned, described and illustrated a structure consisting of four groups of glands connected to a large reservoir opening at the apex of the protuberance. He placed an unidentified larva (attributed by Kemner (1918) and Verhoeff (1919) to *Leptusa*) between two narrowly separated glass plates for observation. Seeing a yellow, viscous secretion (which he found to be neutral or weakly acidic) produced from the gland, he proposed two alternative hypotheses about its function. First, he thought the secretion might enable the larva to obtain a grip with the anal pseudopod on the substrate, thus assisting locomotion. Second, and more likely because of its acidity, he thought the secretion might serve a defensive function against predators.

Apparently unaware of the work by Brass (1914), Wasmann (1915) sectioned larvae of *Lomechusoides* and discovered a median gland similar to that of *Leptusa* but lacking a posterior protuberance. He illustrated it and suggested an exudatory function but did not speculate on its purpose. However, this work was a stimulus for further studies on myrmecophilous and termitophilous Aleocharinae. Silvestri (1921) speculated that the substance produced by the median gland of *Termitoptochus* larvae probably is consumed by termites which in turn nourish the beetle larvae. Hölldobler (1967) working on *Lomechusa* and *Lomechusoides* larvae, and Hölldobler *et al.* (1982) working on *Pella* larvae, found circumstantial evidence to suggest that the secretion prompts adoption behavior in the host ants.

Kemner (1918) examined larvae of several aleocharine genera and reported three conditions of the gland. In larvae of *Leptusa, Bolitochara, Homalota, Anomognathus* and *Autalia*, the gland is well developed, protuberant and overhangs segment IX. In larvae of *Placusa* and *Haploglossa*, the gland is well developed but lacks the posterior protuberance. In larvae of *Thamiaraea, Atheta, Dinaraea, Falagria* and *Drusilla*, the gland is more feebly developed and lacks a reservoir. Kemner (1918) believed the gland to have a defensive function and discounted the possibility of a locomotory function Later, Kemner (1925a) described larvae of *Diglotta* and (1926) of *Aleochara* without reference to a median gland, seemingly implying its absence and (1925b) reported presence of a median gland in larvae of *Affinoptochus*. The Brass-Kemner hypothesis that the function of the median gland is defensive appears subsequently to have been ignored until Badgley and Fleschner (1956) suggested a defensive function for the gland of *Oligota* larvae, a suggestion reiterated by Moore *et al.* (1975) and Moore (1978).

Verhoeff (1919) was the third author to describe the median gland of *Leptusa* larvae, although he made no reference to the work by Kemner (1918). He presented a reasoned argument refuting the suggestion by Brass (1914) of a possible locomotory function of the gland. He did not mention Brass' preferred hypothesis of a defensive function but produced a wholly new hypothesis. Observing cocoon-spinning, he assumed the median gland was the source of the threads of silk. The hypothesis of the median gland as a sericigenic gland was adopted by subsequent authors including Paulian (1941) and Beaver (1967), whereas Chamberlin and Ferris (1929) seem to have arrived at the same hypothesis independently.

Presence of a protuberance of abdominal segment VIII has been noted in various other aleocharine larvae whose external structures have been described for purely taxonomic purposes (Table 1).

COCOON-SPINNING BY PREPUPAE OF ALEOCHARINAE

The first account of an aleocharine cocoon appears to have been an observation by Fauvel (1862) on *Leptusa*. Further records were added over the following decades (Table 2).

The definition of the material as silk does not imply that it is of the same chemical nature as in either the silkworm *Bombyx* or in spiders, but rather follows the broad definition used by Rudall and Kenchington (1971) of a fibrous material insoluble in water, whose predominant polymeric substance is proteinaceous, or polysaccharide or even hydrocarbon.

Verhoeff (1919) observed the process in a *Leptusa* prepupa. The production of silken threads was accompanied by to-and-fro movement of the abdominal apex, thus excluding the possibility of origin of the silk from modified salivary glands. Whereas Verhoeff (1919)

associated silk production with the median gland and hardening of the silk with a mucous secretion from the anus, Kemner (1926) mentioned the production of a silken cocoon by *Aleochara* prepupae of two species which seem to lack a median gland, thus substantiating his earlier (1918) hypothesis that silk issues from the anus. Badgley and Fleschner (1956) observed cocoon-spinning by an *Oligota* prepupa; since these authors had identified the median gland as a defensive gland, their implication of sericigenic glands "at the tip of the abdomen" excludes the median gland. Observations by Ashe (1982) on cocoon-spinning by *Gyrophaena* again point to silk production from the anus. Further, since dissections and histological sections of aleocharine larvae by Brass (1914), Wasmann (1915), Kemner (1918), Verhoeff (1919), Warren (1920) and Hölldobler (1967) produced no evidence of any other large abdominal glands apart from the median gland, then silk must issue from the anus and must be produced by some part of the digestive system.

Kemner's (1918) hypothesis that the Malpighian tubules are the site of silk production rests partly on his evidence of the swollen state of the Malpighian tubules in prepupal aleocharines he examined, and partly on his analogy of Malpighian tubules as the source of silk in Neuroptera and various other families of Coleoptera. There remains the possibility that the peritrophic membrane is the source of the silk as reported for prepupae of some other families of Coleoptera (e.g. Kenchington 1976), with the Malpighian tubules as source of a nitrogenous cement or hardening agent.

Many, if not all, *Aleochara* larvae are parasitoidal inside dipterous puparia. Whereas some of these larvae emerge from the host puparium to pupate and produce a silken cocoon, others pupate inside the host puparium and do not spin a cocoon (Kemner 1926, Fuldner 1960, Peschke and Fuldner 1977). At least some of the latter produce a nitrogenous cement in the Malpighian tubules, secreted into a widening of the hind gut, then smeared over the inner surface of the excavated host puparium to form a pupal cell (Fuldner 1960). This phenomenon could be expanded into a unifying hypothesis: Malpighian tubules being the source of the cement could explain their swollen state in the *Leptusa* prepupae observed by Kemner (1918) and the mucus secreted from the anus of *Leptusa* prepupae observed by Verhoeff (1919). The ability to spin a silken cocoon occurs in prepupae of some *Aleochara* but could have been lost from those *Aleochara* which pupate inside the host puparium as an adaptation to endoparasitoidal existence. The source of the silk in all cocoon-spining aleocharines could then be the peritrophic membrane.

All knowledge of aleocharine cocoons is based on observations of members of relatively more derived tribes. The need is now for studies of members of the less derived tribes Gymnusini, Deinopsini, Myllaenini and Pronomaeini. Such studies will determine whether cocoon-spinning is characteristic of all aleocharine prepupae or whether it evolved within various lineages of Aleocharinae. The Trichopseniinae have been considered a tribe of Aleocharinae by some authors but not others, so the question of ability of their prepupae to spin cocoons is pertinent.

COCOON-SPINNING BY PREPUPAE OF OTHER STAPHYLINIDS

Schlick (1894), Kryger (1915), Blair (1917), Welch (1965) and Weinreich (1968) observed that larvae, or more properly prepupae, of *Stenus* species spin a silken cocoon before pupation. Bro Larsen (1959) stated that most *Stenus* prepupae make a loosely woven cocoon, but some (e.g. *S. cicindeloides* (Schaller)) make a tightly woven one. Jenkins (1958) observed spinning behavior in *Dianous coerulescens* Gyllenhal and dissected larvae to locate the silk glands. He

used histological techniques to demonstrate the presence of silk in them. These glands are elongate and extend through five abdominal segments; their openings are on tergum IX and they form the twelfth of a series of paired openings (Fig. 1C) of which 1-11 are those of the segmental glands. It is highly likely that silk production in *Stenus* is of the same origin, despite a conflicting observation by Weinreich (1968) of silk issuing from the anus, so that this method of silk production is characteristic of the subfamily Steninae.

In the Paederinae, larvae of *Astenus procerus* (Gravenhorst) and of an unidentified *Astenus* were reported to build silken cocoons by Peyerimhoff (1899) and Kemner (1925b) respectively, but these authors did not investigate the origin of the silk. In dissections of alcohol-preserved *Astenus* larvae collected with the adults in Florida and whose generic identity was confirmed using keys by Kasule (1970), we found no trace of glands such as described for *Dianous* by Jenkins (1958). Silk production seems to have been reported in no other genus of Paederinae. If the above accounts are accurate and silk production is characteristic of *Astenus*, it seems not to be of the same origin as in stenine prepupae.

Ability to spin silk by aleocharine and stenine prepupae holds no implications for a close relationship of these two subfamilies for the silk is of different origin and the ability to spin is a convergence. However, possibly the origin of silk in prepupae of *Astenus* and of aleocharines may be the same; further, it may be that the origin of the nitrogenous cement used for hardening of the wall of earthen pupation cells of some staphylinines (e.g. Paulian 1941) is produced by the Malpighian tubules as in *Aleochara* prepupae. Study of silk production throws no more light on relationships of Steninae than did a recent study (Frank 1982) of host-parasite relationships. Silk production is yet unreported for prepupae of subfamilies of Staphylinidae other than those of Aleocharinae, Paederinae and Steninae.

GLANDS OF STAPHYLINID LARVAE AND ALEOCHARINE ADULTS

The openings of the silk glands of *Dianous* larvae appear to be the openings of the modified 12th pair of segmental glands (Jenkins 1958 and Fig. 1C). The function of the remaining pairs of glands, which are very small in relation to the silk glands, was suggested by Jenkins (1958) to be defensive. The segmental glands of staphylinines (Fig. 1A) and oxytelines (Fig. 1B) are not modified into silk glands.

Abdominal segment IX of aleocharines (Fig. 1D) lacks segmental glands and segment VIII contains segmental glands as well as the median gland (Hölldobler 1967). The median gland consists of two pairs of glands opening into a common reservoir. Are the two pairs of glands those of segment IX which migrated anteriorly to segment VIII? Since segment IX of some other staphylinids (Fig. 1A, B) contains two pairs of glands, one pair of which may have migrated from segment X, the question is not too far-fetched. Then, if Jenkins' (1958) suggestion of a defensive function of the segmental glands is correct, the median gland may retain its original function. If Kemner (1918) was correct that the median gland characteristic of *Thamiaraea*, *Atheta*, *Dinaraea*, *Falagria* and *Drusilla* lacks a reservoir but has a single dorsal opening, then the evolutionary process should have consisted of: 1) anterior migration of the four separate glands from segment IX; 2) their unification with a common duct; and 3) the development of an enlarged reservoir.

Unfortunately, the true function of the segmental glands is unclear. Georgevitsch (1898) likened them to the nephridial excretory system of annelids. Verhoeff (1919) named them "Gelenkdrüsen", thus imputing lubricative properties to their secretion in connection with

	head	thorax i	ii	iii	abdomen i	ii	iii	iv	v	vi	vii	viii	ix	x
A	O	O	O	O	O	O	O	O	O	O	O	O	O O	
	O	O	O	O	O	O	O	O	O	O	O	O	O O	
B				O	O	O	O	O	O	O	O	O	O O	
				O	O	O	O	O	O	O	O	O	O O	
C		O	O	O	O	O	O	O	O	O	O	O s		
		O	O	O	O	O	O	O	O	O	O	o s		
D	O	O	O	O	O	O	O	O	O	O	O	O m		
	O	O	O	O	O	O	O	O	O	O	O			

FIG. 1. Schematic diagrams of the distribution of exocrine glands in staphylinid larvae: A, *Ocypus* (after Georgevitsch, 1898); B, *Anotylus* (after Verhoeff 1919); C, *Dianous* (after Jenkins 1958); D, *Lomechusa* and *Lomechusoides* (after Hölldobler 1967). Roman numerals indicate body segments, O = segmental glands, M = median gland, S = sericigenic gland.

articulation of sclerites. Jenkins (1958) guessed they have a defensive function. Hölldobler (1967) reported that their secretion in the myrmecophilous genera *Lomechusa* and *Lomechusoides* caused ant hosts to groom the beetle larvae. None of these hypotheses can be discounted at present and new studies are desirable to attempt to arrive at a unifying hypothesis.

Glandular systems of adult aleocharines have been studied more thoroughly than those of larvae and show suggestive parallels between adult and larval systems. Secretion of mucoproteins to lubricate articulations between sclerites by the primary glandular system of adults (Pasteels 1968, Araujo 1978) lends support to Verhoeff's (1919) idea of the general function of segmental glands of larvae. There is also a possibility that some of the secretions have anti-fungal properties (Frank 1982, Lawrence and Newton 1982). Adults possess a large tergal gland having paired gland clusters in abdominal segment VII but a reservoir in segment VI and with proven defensive function (Pasteels 1968). This is extraordinarily analogous to the median gland of larvae in both structure and function. The tergal gland was reported by Jordan (1913) and Pasteels (1968) to occur in adults of all aleocharine genera examined, belonging to free-living as well as myrmecophilous and termitophilous aleocharines of the tribes Oxypodini, Callicerini, Aleocharini, Falagriini, Myrmedoniini, Bolitocharini, Phytosini, Autaliini and Oligotini. It occurs in adults of Corotocini, Termitonannini and Termitohospitini (Pasteels 1969). It is present in some pygostenine adults, but is reduced or modified in, or lost from other members of this tribe and in termitophilous members of several tribes (Pasteels 1969, Shower and Kistner 1977, Kistner 1979). The earlier findings led Pasteels (1968) to conclude that it probably is present in all aleocharine adults. Unfortunately, no members of the plesiomorphic tribes Gymnusini, Deinopsini, Myllaenini and Pronomaeini had been included in these surveys. Therefore the state of phylogenetic knowledge rests on little better inclusiveness than that of

the tribal distribution of the larval median gland (Table 2) or cocoon-spinning (Table 1). Further, trichopseniine adults were reported to lack the tergal gland (Pasteels and Kistner 1971) just as their larvae lack the median gland (Kistner and Howard 1980).

Finally, it is apparent that the tergal gland of adults of different tribes, genera and species produces different chemicals (e.g., Brand et al. 1973, Peschke and Metzler 1982), so there is no conflict in the assumptions that what may be entirely or mainly defensive secretions in free-living species may have special functions in myrmecophilous and termitophilous species. It is not unreasonable to suggest that the secretions of the median gland of larvae act similarly, as defensive secretions in some species and with special functions in myrmecophilous and termitophilous species.

CLASSIFICATION OF ALEOCHARINAE

Tribal classification of Aleocharinae is unsettled. Hammond's (1975) suspicion that the subfamily may contain as many as 100,000 species makes a satisfactory higher classification a matter of some urgency. The traditional arrangement is exemplified by Lohse (1974). Hypocyphtinae are treated as a subfamily separate from Aleocharinae, and the tribes of Aleocharinae arranged in linear order from Deinopsini, Gymnusini and Myllaenini through Bolitocharini to Oxypodini and Aleocharini.

Hammond (1975) pointed out a number of plesiomorphic character states of Deinopsini and Gymnusini and included Hypocyphtini and Trichopseniini within Aleocharinae. Seevers (1978): 1) considered the members of Hypocyphtini to belong to Aleocharinae, but included them in Oligotini; 2) maintained the distinction between Trichopseniinae and Aleocharinae mainly because the hind coxae are fused to the metasternum in adults of the former; 3) recognized that adults of Deinopsini-Gymnusini-Myllaenini are generalized in structure, but nevertheless placed them near the end of his linear arrangement; 4) critized the traditional arrangement of tribes, pointing out its artificiality in placing the generalized Oxypodini and Aleocharini near the end of the list, and called for reversion to a more natural classification similar to that by Ganglbauer (1895). This arrangement began with Oxypodini and progressed through Aleocharini and Myrmedoniini, with Bolitocharini, Phytosini and Oligotini near its end (Seevers 1978).

Investigation of phylogeny in Aleocharini will be aided by the identification of derived character states common to groups of tribes. To date, structures of aleocharine larvae seem not to have been used for this purpose despite numerous descriptions scattered in the literature.

Characterization of the Aleocharinae in terms of presence of a tergal gland in the adult, cocoon-spinning ability of the prepupa, and occurrence and condition of a median gland in the larva is hampered by lack of knowledge of the tribes Gymnusini, Deinopsini, Myllaenini and Pronomaeini. Hammond (1975) considered Gymnusini-Deinopsini as a sister taxon to all remaining tribes of Aleocharinae. Klimaszewski (1982) considered Gymnusini-Deinopsini-Myllaenini a monophyletic group. Seevers (1978) also included Pronomaeini in this group.

Seevers (1978) considered Aleocharini and Hoplandriini distinct tribes forming a single phyletic line. Adults of both tribes have a tergal gland. The prepupa of some species has the ability to spin a cocoon and it is conceivable that some species have lost the ability in adaptation to an endoparasitoidal existence. Neither Kemner (1918, 1926) nor subsequent authors have reported median glands in *Aleochara* larvae. Whether lack of the median gland in Aleocharini is a plesiomorphic character state must yet be considered uncertain.

Diglottini have been considered by some authors (e.g., Seevers 1978, Klimaszewski 1982) as possibly related to Phytosini (see below), yet Kemner (1925a) made no mention of a median gland or cocoon-spinning in *Diglotta* prepupae nor has a tergal gland in the adult been revealed. Since members of Phytosini (see below) possess all 3 characteristics, the relationships of Diglottini still remain obscure.

Falagriini and Callicerini are reported to possess a tergal gland in the adult, silk-spinning ability in the prepupa, and a feebly developed median gland without reservoir in the larva. However, in larvae questionably attributed to *Alianta* (Callicerini), the median gland has been reported to be protuberant. These two tribes seem to exhibit a plesiomorphic condition of the median gland which, in the tribes mentioned below, is either better developed or there is reason to believe its reduction is an adaptation to a specialized way of life.

Oxypodini and Myrmedoniini, both *sensu* Seevers (1978), have a tergal gland in the adult, silk-spinning ability in the prepupa, and a median gland with large reservoir in the larva. These characteristics are shared with those corotocines and drepanoxenines in which the tergal gland has not been modified or lost secondarily. Unlike its condition in the tribes mentioned below, the median gland is not protuberant. The two known exceptions to these generalizations bear consideration. *Phloeopora* larvae (Oxypodini) have a protuberant gland. Since adult *Phloeopora* possess widely separated mesocoxae although the tribe is characterized as having narrowly separated mesocoxae (Seevers 1978), *Phloeopora* may be misplaced in the Oxypodini. *Drusilla* larvae (Myrmedoniini) seem to lack a median gland reservoir; if so, it could be a secondary loss in this myrmecophilous genus just as the tergal gland in some myrmecophilous and termitophilous species has been reduced, modified or lost.

Bolitocharini, Autaliini, Phytosini, Oligotini and Hypocyphtini were considered by Seevers (1978) to form a related group of tribes. The adult has a tergal gland (not known for Hypocyphtini), the prepupa has the ability to spin a silken cocoon (not known for Autaliini and Hypocyphtini), and the median gland of the larva is prominent and protuberant. This group of tribes has the most highly developed median gland structure; in *Oligota* larvae the gland has been reported to be operculate (Badgley and Fleschner 1956, Moore *et al.* 1975) and this may represent a further structural development. The only known exception is *Placusa* (Bolitocharini) whose larvae seem to lack the glandular protuberance; if so it could represent a secondary loss or the genus is incorrectly assigned.

It is difficult to determine the relationships of Trichopseniinae to any of the above groups of tribes. The adults lack a tergal gland (Pasteels and Kistner 1971) but this could be a secondary loss as in other termitophilous aleocharines; a lamellar process of the metacoxa is more highly developed than in oligotines and hypocyphtines (Seevers 1978). The mandible of the larva has a more pronounced median tooth (Kistner and Howard 1980) than is known in other aleocharines. The abdomen has a structure resembling the protuberant median gland of larvae of the Bolitocharini-Autaliini-Phytosini-Oligotini-Hypocyphtini, but no orifice has been discovered (Kistner and Howard 1980) so the homologies of this structure are unclear.

CONCLUSION

Present knowledge suggests that cocoon-spinning ability of prepupae and presence of a tergal gland in adults are characteristic of Aleocharinae except in those groups where the attributes have been lost secondarily. It is not known whether the possibly monophyletic and probably generalized Gymnusini-Deinopsini-Myllaenini-Pronomaeini possess these attributes,

so examination of members of these tribes will elucidate phylogeny.

The median gland of aleocharine larvae is most highly developed within the more-derived tribes Bolitocharini-Autaliini-Phytosini-Oligotini-Hypocyphtini. Its less developed condition within the less derived tribes suggests the gland evolved within Aleocharinae, shows a phyletic sequence of development among tribes, and may not be present within all tribes. Its condition is unknown for larvae of the less derived tribes Gymnusini-Deinopsini-Myllaenini-Pronomaeini. The median gland is feebly developed within larvae of Falagriini-Callicerini and better developed within larvae of Oxypodini-Corotocini-Drepanoxenini-Myrmedoniini. Aleocharini, in whose larvae the gland has not yet been revealed, may be less derived than Oxypodini. A detailed histological survey of this structure within larvae of Aleocharinae should yield a wealth of phylogenetic information.

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Table 1. Four conditions of the median gland in aleocharine larvae as interpreted from the following sources: 1: Perris (1853), 2: Fauvel (1862), 3: Fauvel (1875), 4: Rey (1887), 5: Wasmann (1915), 6: Kemner (1918), 7: Falcoz (1919), 8: Verhoeff (1919), 9: Warren (1920), 10: Silvestri (1921), 11: Kemner (1925a), 12: Kemner (1925b), 13: Kemner (1926), 14: Beier and Strouhal (1928), 15: Chamberlin and Ferris (1929), 16: Bøving and Craighead (1931), 17: Paulian (1941), 18: Paulian (1948), 19: Cerruti (1952), 20: Badgley and Fleschner (1956), 21: Moore (1956), 22: Scheerpeltz (1958), 23: Dajoz (1960), 24: Fuldner (1960), 25: Steel (1964), 26: Kasule (1966), 27: Beaver (1967), 28: Hölldobler (1967), 29: Topp (1971), 30: Kistner and Watson (1972), 31: Watson and Kistner (1972), 32: Topp (1973), 33: Watson (1973), 34: Topp (1975a), 35: Topp (1975b), 36: Kistner (1976), 37: Moore (1977), 38: White (1977), 39: Topp (1978), 40: Moore (1979), 41: Watson (1979), 42: Kistner and Howard (1980), 43: Ashe (1981), 44: Topp (in litt.), 45: Hölldobler *et al.* (1982), 46: newly reported observation.

A. MEDIAN GLAND NOT REPORTED, HERE PRESUMED ABSENT
    ALEOCHARINI: *Aleochara* 13, 24, 32, 39; DIGLOTTINI: *Diglotta* 11.
B. MEDIAN GLAND NOT REPORTED EXCEPT BY AUTHORS WHO EXAMINED INTERNAL STRUCTURE AND THEN GLAND FOUND TO BE POORLY DEVELOPED AND WITHOUT RESERVOIR
    FALAGRIINI: *Cordalia* 44, *Falagria* 6, 44; CALLICERINI: *Aloconota* 35, *Atheta* 1, 6, 8, 17, 22, 25, 34, 35, 39, *Dinaraea* 6, 35, *Geostiba* 35, *Nehemitropia* 28, 35, *Pachnida* 35, *Thamiaraea* 6 (exception: *Alianta* 17, described as having a protuberant median gland as in condition D, but identified *ex societate imaginis*).
C. MEDIAN GLAND NOT REPORTED EXCEPT BY AUTHORS WHO EXAMINED INTERNAL STRUCTURE AND THEN GLAND FOUND TO HAVE LARGE RESERVOIR
    OXYPODINI: *Colle* 25, *Haploglossa* 6, 7, 17, *Ocalea* 17, *Ocyusa* 39, *Oxypoda* 14, 39, *Platyola* 4, *Tachyusa* 39 (exception: *Phloeopora* 1, 17, 46, has a protuberant median gland as in condition D); COROTOCINI: *Affinoptochus* 12, *Paracorotoca* 9, *Termitoptochus* 10, *Termitoptocinus* 10; DREPANOXENINI: *Drepanoxenus* 30, 31, 33, 41; MYRMEDONIINI: *Creodonia* 19, *Goniusa* 36, *Lomechusa* 28, *Lomechusoides* 5, 17, 28, *Pella* 45, *Smectonia* 19, *Zyras* 18, 39 (exception: *Drusilla* 6, 17, 39, seems to lack reservoir).
D. MEDIAN GLAND REPORTED AS PROMINENT AND PROTUBERANT, AS WELL (BY AUTHORS WHO EXAMINED INTERNAL STRUCTURE) AS HAVING A LARGE RESERVOIR
    BOLITOCHARINI: *Anomognathus* 6, 17, *Bolitochara* 6, 17, 26, 27, 32, *Cyphea* 3, *Gyrophaena* 4, 16, 17, 38, *Homalota* 6, 46, *Leptusa* 2, 6, 8, 23, 39, *Phanerota* 43 (exception: *Placusa* 1, 6, lacks the protuberance); AUTALIINI: *Autalia* 6; PHYTOSINI: *Amblopusa* 15, *Baeostethus* 25, *Bryothinusa* 40, *Diaulota* 21, *Halmaeusa* 17, 25, *Liparocephalus* 15, 21, *Phytosus* 2, *Rothium* 37; OLIGOTINI: *Oligota* 4, 17, 20, 46; HYPOCYPHTINI: *Hypocyphtus* 26. ˙
INCERTAE SEDIS
    TRICHOPSENIINAE: *Trichopsenius* and *Xenistusa* 41 have a structure which resembles the protuberant condition D of the median gland but no orifice has been observed and the internal structure has not yet been examined.

Table 2. Aleocharine prepupae with cocoon-spinning ability according to: 1: Fauvel (1862), 2: Wasmann (1890), 3: Coquillett (1891), 4: Wasmann (1894), 5: Peyerimhoff (1899), 6: Schlick (1899), 7: Joy (1906), 8: Wasmann (1915), 9: Kemner (1918), 10: Verhoeff (1919), 11: Kemner (1925b), 12: Kemner (1926), 13: Chamberlin and Ferris (1929), 14: Cottier (1932), 15: de Balsac (1938), 16: Kryger and Sønderup (1940), 17: Paulian (1941), 18: Nuorteva (1956), 19: Badgley and Fleschner (1956), 20: Dobson (1961), 21 Azab *et al.* (1963), 22: White and Legner (1966), 23: Beaver (1967), 24: Topp (1971), 25: Topp (1973), 26: Tawfik *et al.* (1976), 27: Peschke and Fuldner (1977), 28: Ashe (1981), 29: Ashe (1982), 30: newly reported observation.

OXYPODINI: *Haploglossa pulla* (Gyllenhal) 7, 15; *Ocalea picata* (Stephens) 30

COROTOCINI: *Affinoptochus exclusus* Kemner 11.

CALLICERINI: *Atheta pseudocoriaria* Bernhauer 14, *Nehemitropia sordida* (Marsham) 24; *Thamiaraea cinnamomea* (Gravenhorst) 9.

ALEOCHARINI: *Aleochara curtula* (Goeze), *A. laevigata* Gyllenhal, *A. intricata* Mannerheim 12; *A. valida* LeConte 3; *A. inconspicua* Aubé 20; *A. moesta* Gravenhorst 21, 26; *A. taeniata* Erichson 22; *A. lata* Gravenhorst, *A. ripicola* Mulsant and Rey, *A. brevipennis* Gravenhorst, *A. puberula* Klug 27.

FALAGRIINI: *Cordalia* sp. 17.

MYRMEDONIINI: *Lomechusa emarginata* (Paykull), *Lomechusoides strumosa* (Fabricius) 2, 4, 8; *Zyras cognatus* (Märkel) 6.

BOLITOCHARINI: *Bolitochara obliqua* Erichson 23; *B. pulchra* (Gravenhorst) 25; *Euryusa sinuata* Erichson 16; *Gyrophaena nana* Paykull 29; *Homalota ? lepidula* Casey 30; *Leptusa fumida* (Erichson) 1; *L. pulchella* (Mannerheim) 10; *Phanerota fasciata* Say 28; *Placusa* spp. 18.

PHYTOSINI: *Amblopusa brevipes* Casey, *Liparocephalus brevipennis* Mäklin 13.

OLIGOTINI: *Oligota flavicornis* (Boisduval and Lacordaire) 5; *O. oviformis* (Casey) 19; *O. minuta* Cameron 30.

Appendix 1. Synonymies. Names of some genera and species as used in the text differ from names as used by some authors cited. Synonyms are given in regular print and names used in the text are in italics.

Antarctophytosus Enderlein, 1909 = *Halmaeusa* Kiesenwetter, 1877
Astenus filiformis (Latreille) = *Astenus procerus* (Gravenhorst)
Astilbus Dillwyn, 1829 = *Drusilla* Samouelle, 1819
Atemeles Dillwyn, 1829 = *Lomechusa* Gravenhorst, 1806
Atheta sordida (Marsham) = *Nehemitropia sordida* (Marsham)
Bolitochara lunulata (Paykull) = *Bolitochara pulchra* (Gravenhorst)
Cardiola Mulsant & Rey, 1875 = *Cordalia* Jacobs, 1925
Creodonia Wasmann has been raised to generic status
Diaulota brevipes (Casey) = *Amblopusa brevipes* Casey
Homalota celata Erichson = *Atheta celata* (Erichson)
Leptusa angusta Aubé = *Leptusa pulchella* (Mannerheim)
Lomechusa strumosa (Fabricius) = *Lomechusoides strumosa* (Fabricius)
Microglossa Stein, 1868 = *Haploglossa* Kraatz, 1856
Microglotta Kraatz, 1862 = *Haploglossa* Kraatz, 1856
Myrmedonia cognata Märkel = *Zyras cognatus* (Märkel)
Oxypoda moesta ERROR = *Aleochara moesta* Gravenhorst
Oxytelus tetracarinatus (Block) = *Anotylus tetracarinatus* (Block)
Sipalia circellaris (Gravenhorst) = *Geostiba circellaris* (Gravenhorst)
Sunius Erichson, 1839, nec Stephens, 1833 = *Astenus* Dejean, 1833
Thectura Thomson, 1859 = *Anomognathus* Solier, 1819