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Musculature of the pre-genital abdominal segments of Bruchidae and Chrysomelidae (Coleoptera), and its systematic and phylogenetic significance

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Summary

We investigated the musculature of adult abdominal segments 1-7 in 5 species representing 5 genera of Bruchidae, and 76 species representing 14 subfamilies of Chrysomelidae (Coleoptera). By out group comparisons (hampered by the lack of a comparable study in Cerambycidae) and by internal correlations, we were able to establish a probable basic pattern in these muscles for Chrysomelidae. In Bruchidae, Caryedon came nearest to this basic pattern, showing particular resemblances to the Sagrinae and Donaciinae. Within Chrysomelidae, Orsodacne probably preserves the most primitive pattern among the forms studied; Sagrinae, Donaciinae and Criocerinae have apparent relations with each other, and to a less degree with Orsodacne and Megalopodinae. The close relations of Hispinae to Cassidinae, and of Halticinae to Galerucinae, were confirmed, while rather less marked similarities were noted between Eumolpinae and Chrysomelinae. The absence of intersegmental tergosternal muscles served to separate the Galerucinae from Halticinae in the species studied, and may provide a useful distinction between these 2 closely allied groups. Camptosomata showed a distinctive muscular pattern, not clearly related to any others.

It was found that the presence of long oblique sternolateral muscles was correlated with strong transverse curvature of the corresponding sternites, and that lack of sternolateral muscles generally correlated with very flat sternites. Sternal muscles were absent in sternites connate with the next posterior one. Correlations of muscular patterns with types of aedeagus or ovipositor were not very evident in our data.

Introduction

Previous published studies of abdominal musculature in Coleoptera (Ford, 1923; Snodgrass, 1935; Saxena, 1953; Evans, 1961; Hieke, 1966; Erber, 1968; Kasap and Crowson, 1975, 1976, 1977; Crowson, 1981) have revealed differences of systematic and functional significance. The present study aims to reveal the extent of similarities and differences in the musculature of abdominal segment 1-7 in adults of Chrysomelidae and Bruchidae, and reveal possible evidences of functions and phylogenetic relations.

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Material and Methods

Most of the British species studied were collected in southern Scotland. Other species were collected in Turkey by H. Kasap or in Australia by R. A. Crowson. A number of species were studied from dried specimens in the collections of the Zoology department, Glasgow, University. Both freshly-killed or alcohol-preserved specimens were used. Abdominal tergites were carefully detached at their lateral edges and lifted off to display to dorsal longitudinal and alary muscles, and then the main contents of the abdominal haemocoele were removed to show the sternal longitudinal muscles. Specimens were also divided sagitally with a sharp blade and each half was dissected to show the tergosternal and pleural muscles. Dried specimens were first soaked for some time in a cold weak solution of KOH, then transferred to water, dissected and stained with borax carmine, and then dehydrated and mounted in Canada Balsam.

Nomenclature of Muscles

It was found possible to homologise all the abdominal muscles in Chrysomelidae with the basic patterns found in Elateriformia and Curculionoidea (Kasap and Crowson, 1975, 1977), and we have used here the same terminology, and the same system of abbreviations in the figures, as were used in those papers.

Results

1. Sternal Muscles

In all species studied, there were a pair of posteriorly diverging sternal extrinsic muscles extending from the metendo-sternite to insert on the base of the abdomen above the hind-coxae, and a pair of posteriorly converging full-length sternal longitudinal muscles in sternite 7 (ventrite 5) inserting on abdominal sternite 8; these muscles will not be discussed further. Muscles of sternites 3-6 differ among the species studied; we distinguish 6 main types.

In Type I, sternites 3-6 all have sternomedian longitudinal and sternolateral longitudinal muscles, the sternolateral ones being short and evenly spaced between the sternomedian ones and the lateral edges of the sternites. There may be a median division of the sternomedian muscles into 2 bundles, as in sternites 3-4 of Caryedon and 3-6 of Orsodacne. The sternomedian muscles may be full length in sternites 3-5, as in Acanthoscelides, Callosobruchus (Fig. 1), Euspermophagus, Sphondylia, Zeugophora, Luperus and Sermylassa, or short in sternite 3 as in Caryedon (Fig. 24), Longitarsus (Fig. 2), Aphthona, Phyllotreta and Sphaeroderma. In Orsodacne (Fig. 3) sternomedian muscles are short in sternites 3-4 but long in 5-6.

In Type II, the sternolateral muscles are reduced to narrow muscle bands and rather widely separeted from sternomedian ones, as seen in some Halticinae (Derocrepis (Fig. 4), Crepidodera, Psylliodes, Haltica) and some Galerucinae (Galerucella, Lochmaea); in these Galerucinae, the sternolateral muscles extend to the side margins of the sternites. In Lochmaea, there may be sex dimorphism in the sternolateral muscles, those of males being longer and more fan-shaped than those of females.

Type III sternal muscles were found in species of Sagrinae, Donaciinae and Criocerinae studied (Figs. 5, 6); they have the short sternolateral divergent muscles widely separated from sternomedian ones, close to the side margins of the sternites, and the sternomedian ones are short in sternite 3 only (Sagrinae, Donaciinae) or sternites 3-6 (Criocerinae).

Type IV is distinguished by the absence of sternolateral muscles, while showing some variety in the sternomedian ones, which are present in sternites 3-6. This type is prevalent in Chrysomelinae (all species studied, except Plagiodera) and Eumolpinae (all species studied, except Spilopyra and Macrolema) and occurs also in many Halticinae (Podagrica, Mantura, Chalcoides, Epithrix, Batophila, Apteropeda, and Mniophila) and in Phylobrotica (Fig. 7) among Galerucinae. In all Chrysomelinae (Fig. 8), the muscles are short in sternite 3; they may be long in sternites 4-6 (most species), short in 3-5 (Chrysolina polita) or short in 4-6 (Chrysolina americana, Gastroidea, Timarcha). Sternal musculature in primitive Camptosomata (Lamprosomatinae, Sphaerocharini) resembles this type too.

The main mass of Camptosomata is distinguished by Type V muscles, differing from type IV by the lack of muscles in sternite 6, as seen in species of Chlamisinae, Cryptocephalinae and Clytrinae (Fig. 10) studied. The longitudinal muscles of sternite 3 are short Cryptocephalus but long in other types studied.

Type VI sternal muscles differ from type IV in the absence of longitudinal muscles in sternite 3; it was seen in all species of Hispinae and Cassidinae studied (Fig. 11), in Chaetocnema (Fig. 9) among Halticinae, Plagiodera in Chrysomelinae, Spilopyra and Macrelema among Eumolpinae. In Chaetocnema, longitudinal muscles are short in sternite 4, full-length in sternites 5 and 6; in the others they are short in sternites 4-6.

2. Tergal Muscles

In all species studied, the tergal longitudinal muscles of the abdomen were divided in the middle in the position occupied by the heart. In Eumolpinae, except for Spilopyra, tergal muscles of segment 1 comprised tergomedian longitudinal, tergolateral extrinsic convergent, and tergolateral extrinsic divergent muscles (Figs. 16, 21, 30), the convergent and divergent tergolateral extrinsic ones crossing over each other. In Cassida, tergite 1 has tergomedian and tergolateral extrinsic divergent muscles (Fig. 22), in Criocerinae it has only tergomedian longitudinal muscles, while in other species studied there were tergomedian and tergolateral extrinsic convergent muscles. In all species studied, we found a single band of full-length tergomedian longitudinal muscles on each side of tergite 7. Four types were distinguished in the arrangement of tergal muscles of segments 2-6.

In Type I, there are tergomedian longitudinal, tergolateral longitudinal, and tergal oblique upper muscles, as in the bruchid Caryedon, all Donaciinae, Clytrinae and Chrysomelidae studied, most of the Halticinae and some of the Eumolpinae, also in Sagra. In Caryedon, Sagra, Donacia, and Plateumaris, the tergomedian muscles are in 2 bundles on each side (Figs. 12, 14). In Donacia, tergolateral longitudinal and tergal oblique upper muscles were lacking in tergite 3; in Sagra, the tergomedian muscles are shortened in tergited 3-6.

In Clytrinae, tergolateral longitudinal muscles of tergites 5 and 6 are in their normal positions, but in tergites 1-4 their posterior insertions are displaced, as are the corresponding spiracles, to the paratergites in Coptocephala (Fig. 26) and to the pleural membrane in Clytra (Fig. 13). In Labidostomis, these muscles appear to be homologous with the normally inserted tergolateral muscles of segment 1-4, so we treat them as tergal rather than pleural; these muscles are abbreviated in tergite 6 of Clytra and Labidostomis.

In Chrysomelinae, the flightless Timarcha (Fig. 28) has membranous tergites; in it, as in the winged Phaedon, Prasocuris, Hydrothassa, Phytodecta, Gastroidea and Phyllocharis, tergomedian and tergolateral muscles are shortened in tergites 2-6, while in Entomoscelis (Fig. 15), Zygogramma, Chrysolina, Phyllodecta and Plagiodera they are full-length. Division of the tergolateral muscles into 2 bundles was seen in tergites 4-6 of Entomoscelis and 2-5 of Zygogramma.

All Galerucinae studied have Type I tergal musculature, as do Psylliodes, Longitarsus, Aphthona, Phyllotreta, Podagrica and Haltica in Halticinae; in Psylliodes chrysocephala tergomedian and tergolateral muscles were shortened, whereas in P. cuprea and the rest they were full-length.

Of the Eumolpinae studied, Spilopyra, Geloptera, Chrysochus and Tricliona have Type I tergal muscles; in Spilopyra the tergomedian and tergolateral muscles are shortened in tergites 3-6 (Fig. 14), and they are shortened in 2-6 of Geloptera (Fig. 30) and Tricliona, while Chrysochus has full length ones in all segments.

Type II includes species with only tergal longitudinal and tergal oblique upper muscles, as seen in Zeugophora (Fig. 25), the Eumolpinae Abirus (Fig. 16), and in males only of Phyllodecta vulgatissima and Lochmaea suturalis. Tergal longitudinal muscles are full length, or shortened in segments 3-6 of Abirus.

In our Type III, tergites 2-6 have only one bundle of tergal longitudinal muscles on each side (Figs. 17-22), as seen in Callosobruchus (Fig. 17), all Criocerinae (Fig. 18), Sphondylia and the Eumolpinae Pagria, Scelodonta, Pseudopiomera (Fig. 21), and Nodina, the Cryptocephalinae studied (Fig. 27), the Halticinae Apteropoda (Fig. 20) and Mniophila, the Lamprosomatinae Oomorphus (Fig. 19) and Cassida; the muscles are shortened in all segments in the Cryptocephalinae, Lamprosomatinae and Halticinae named, and segments 4-6 in Cassida (Fig. 22).

Our Type IV groups species which combine type I features in some segments, with type II or III ones in others, as can be seen in some Bruchidae, Halticinae, and Hispinae. In Acanthoscelides, tergite 2, and in Euspermophagus tergites 2-3 have tergomedian and tergolateral muscles, while other segments have only tergolateral muscles. In Derocrepis (Fig. 29), Crepidodera, Sphaeroderma and Longitarsus jacobeae, tergites 2-5 have tergal oblique upper muscles, full-length tergomedian and tergolateral muscles, while tergite 6 has only the upper oblique and tergal longitudinal ones; in Chaetocnema (Fig. 23), Epithrix and Manutura tergite 2 has Type I and tergites 3-6 have Type II muscles. In Aproida and Hispa tergite 2 has full-length tergomedian and tergolateral muscles, while tergites 3-6 have upper oblique muscles together with short tergomedian and tergolateral muscles.

3. Tergosternal Muscles (Figs. 24-31)

The most widespread, and probably primitive, pattern has segmental tergosternal muscles in segments 2-7 and intersegmental tergosternal muscles in segments 3-7. Intersegmental tergosternal muscles were not found in any Criocerinae studied, and the same was true of Galerucinae. In some groups, the segmental tergosternal muscles of segment 7 attach ventrally to the lateral parts of the antecosta rather than to the edges of the sternite, as in _Callosobruchus_, _Sagra_, _Zeugophora_ (Fig. 25), _Coptocephala_ (Fig. 26), _Cryptocephalus_ (Fig. 27), _Timarcha_ (Fig. 28), _Apteropeda_, _Sphaeroderma_ and _Geloptera_ (Fig. 30).

In Criocerinae, there are 2 segmental tergosternal muscles, one arising from the lateral part of the tergits, the other from the adjacent paratergite (Fig. 18). In _Zeugophora_ (Fig. 25), segments 2-6 have 2 segmental and intersegmental tergosternal muscles on each side, and anterior segmental and intersegmental tergosternal muscles are closely associated while segment 7 has a single band of segmental ones. In Clytrinae the pattern shows some resemblance to that of _Zeugophora_ but is more complex (Fig. 13, 26); in addition to segmental tergosternal muscles, there are 3 muscle bands running between the membrane just outside the edges of the tergites, and the edges of the sternites, the anterior one appears to be intersegmental, the other 2 segmental. We have treated these muscles as tergosternal rather than pleurosternal. It is possible however that these muscles are homologous with pleural ones in other groups, and that _Zeugophora_ and Clytrinae lack true intersegmental tergosternal muscles.

In Galerucinae, intersegmental tergosternal muscles were lacking in species studied; segments 2-6 have a single large tergosternal muscle on each side, while there are 2 pairs in segment 7.

4. Pleural Muscles (Figs. 24-31)

These were observed in some of the species studied by us, however they are often difficult to distinguish and may have been overlooked in some instances. At the base of the abdomen, there may be tergopleural extrinsic muscles, running from the pleural ridge of the metathorax to insert on abdominal tergite 1 and tergite 2. The extrinsic muscles of tergite 2 were lacking in the Bruchidae _Caryedon_ (Fig. 24) and _Callosobruchus_ (Fig. 17). In other segments there may be tergopleural and sternopleural muscles.

In all species here studied, we found a muscle arising from the pleural membrane, close to the 1st pair of abdominal spiracles, and inserting on the anterior margin of the metacoxal sheaths, which is here designated as the sternopleural muscle of segment 1. It may be homologous to muscles in Elateriformia, which arise from the lateral ends of the posterior phragma of the metathorax and insert similarly on the metacoxal sheaths, and were interpreted by us (Kasap and Crowson, 1975) as tergosternal muscles of the 1st abdominal segment. We found differences in the sternopleural muscles of segments 2-6—there was a single such muscle in each segment in _Callosobruchus_, _Sagra_, _Zeugophora_ (Fig. 25), _Donacia_, _Zygogramma_, _Apteropeda_, _Mniophila_, _Phyllotreta_, _Chalcoides_, _Derocrepis_ (Fig. 29), _Sphaeroderma_, _Psylliodes_, _Podagrica_, _Haltica_ and _Pseudopiomera_ (Fig. 21), but 2 pairs, 1 small and 1 large in _Caryedon_ (Fig. 24), _Oulema_, _Cryptocephalus_ (Fig. 27), _Chrysolina_, _Phyllodecta_, _Phaedon_, _Apthona_, Chaetocnema (Fig. 23), Sermylassa, Luperus, Phyllobrotica, Lochmaea, Galerucella, Cassida (Fig. 22) and Hispa. In Callosobruchus, Zeugophora (Fig. 25), Cryptocephalus (Fig. 27), and Cassida (Figs. 22, 31) these muscles arise from paratergites rather than from the pleural membrane as in the other genera mentioned. A tergopleural muscle, linking the lateral edge of the tergite with an area of membrane near the spiracle, was detected in segments 2-6 of most species studied; Timarcha (Fig. 28) we found a single tergopleural muscle in segments 1 and 2, but 3 on each side in segments 3-6, the anterior one of them being intersegmental.

Spiracular muscles, presumably present in all species, were studied by us only in Donacia, Oulema and Timarcha. The extend from the lateral ends of the sternites to the closing bar of the corresponding spiracle. They were seen in segments 1-7 of Donacia and Timarcha (Fig. 28), and 1-6 of Oulema (Fig. 18).

5. Alary Muscles

As in the Elateriformia (Kasap and Crowson, 1975) alary muscles in Bruchidae and Chrysomelidae generally occur in segments 2-7, in each segment arising from close behind the antecosta of the tergite to attach close to the corresponding chambers of the heart (Figs. 13, 21). In Timarcha and Chrysolina, the alary muscles of each segment are divided towards their insertions into anterior and posterior bundles. In some species the heart chambers appeared to be as in Timarcha, Chrysolina, Apteropeda and Pseudopiomera (Fig. 21), in others to be within individual segments, as in Cryptocephalus and Clytra (Fig. 13).

Phylogenetic and Functional Conclusions

In musculature, evolutionary changes seem mainly to involve splitting or fusion of adjacent muscle-bands, shifts of origins or insertions and losses of particular muscles. Losses of particular muscles apeear rarely but most other changes have to be regarded as reversible.

Orsodacne is a particularly primitive genus of Chrysomelidae, and the muscle-pattern we have observed in O. cerasi seems likely to be near the primitive type of the family. Type III of sternal musculature was found only in all species studied of Sagrinae, Donaciinae and Cricerinae, indicating a relationship. Type V of sternal muscles, found only in all Camptosomata (except the more derived Oomorphus) emphasises the isolation of Camptosomata. The complete absence of intersegmental tergosternal muscles in Cricorinae and Galerucinae studied may be diphyletic derived state. Type II sternal muscles, found only in some species of Galerucinae and Halticinae support their close relationship. Type VI sternal muscles probably represent a basic apomorphism of the Hispinae-Cassidinae line, but independently developed in the Chrysomelinae Plagiodera and elsewhere in Chrysomelidae. The combination of type IV sternal muscles and Type I tergal ones seems to characterise Chrysomelinae, but also recurs in some Eumolpinae.

The most obvious functional correlation is between the absence of sternal musculature in a particular segment and the connation of its ventrite with the following one, as in all species of Hispinae and Cassidinae, in Plagiodera, Chaetocnema, Spilopyra and Macrolema for sternite 3, and in Camptosomata for sternite 6 (ventrite 4).

Özet

Bruchidae ve Chrysomelidae (Coleoptera)'nin pre-genital abdomen segmentlerinin kas yapısı ve bunun sistematik ve filogenetik önemi

Bruchidae'nin 5 cinsinden birer türde ve Chrysomelidae'nin 14 cinsinden 76 türde, erginlerin 1.-7. abdomen segmentlerinin kas yapısı incelendi. Grup dışı karşılaştırmalar ve grup içi korelasyonla Chrysomelidae içinde benzer kaslara ait temel bir yapı planı saptamak mümkün oldu. Bruchidae'den Caryedon, Sagrinae ve Donaciinae'ye gösterdiği özel benzerliklerden dolayı bu temel yapıya çok yaklaşmaktadır. İncelenen Chrysomelidae formları içinde Orsodacne muhtemelen en ilkel temel kas yapısını korumaktadır; Sagrinae, Donaciinae ve Criocerinae birbirleriyle daha çok, Orsodacne ve Megalopodinae ile kısmen daha az belirgin bir akrabalığa sahiptir. Eumolpinae ile Chrysomelinae arasındaki benzerliklerin oldukça az olduğu görülmüş fakat Hispinae ile Cassidinae ve Halticinae ile Galerucinae arasındaki yakın akrabalıklar doğrulanmıştır. İntersegmental tergosternal kasların olmayışı ile Galerucinae türleri Halticinae türlerinden ayrılabilmiştir; bu özellik çok yakın akraba olan iki altfamilya arasında iyi bir ayrım olabilir. Camptosomata kendine özgü bir kas yapısına sahiptir.

Uzun ve oblik sternolateral kasların özellikle çukur sternitlerde bulunduğu çok düz sternitlerde ise genellikle sternolateral kasların olmadığı, kendinden sonra gelen ile kaynaşmış olan bir sternitte ise sternal kasların kaybolduğu gözlenmiştir. Bizim verilerimizle ovipozitor ve aedeagus ile abdominal kasların ilişkisi yeterince belirlenememiştir.

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Explanation of figure of lettering

Structures - cx: metacoxal sheath, em: epipleuron, ls: latero-sternite, pm: pleural membrane, pn: metapostnotum, pr: pleural ridge, ps: parasternite, pt: paratergite, s: sternite, sp: spiracle, t: tergite.

Muscles: its: intersegmental tergosternal, se: sternal extrinsic, sld: sternolateral divergent, sllg: sternolateral longitudinal, smlg: sternomedian longitudinal, sol: sternopleural, spm: spiracular, tlec: tergolateral extrinsic convergent, tled: tergolateral extrinsic divergent, tlg: tergal longitudinal, tmlg: tergomedian longitudinal, tllg: tergolateral longitudinal, tpe: tergopleural extrinsic.

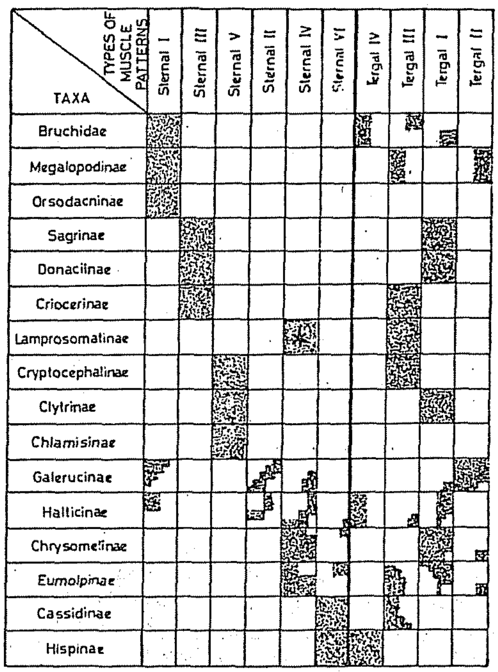
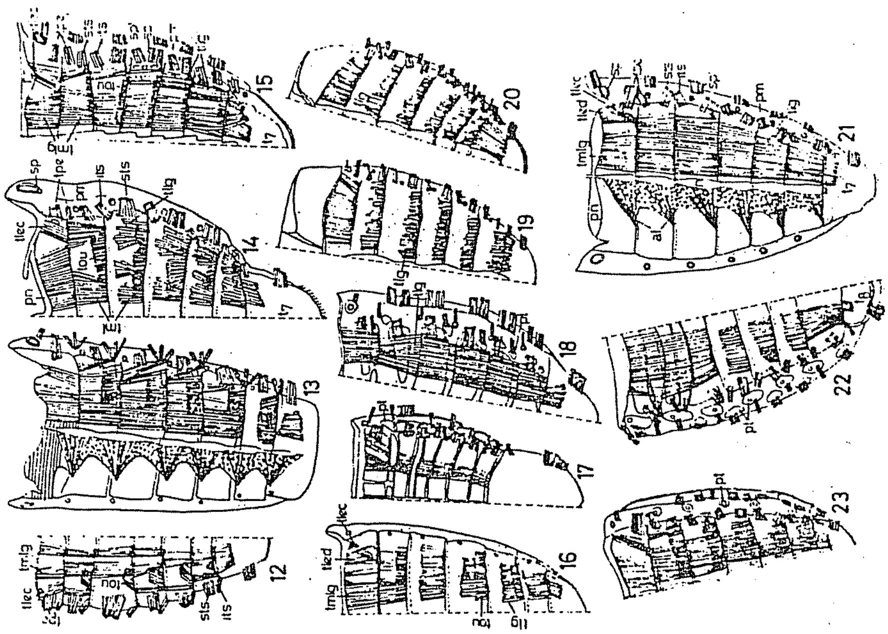
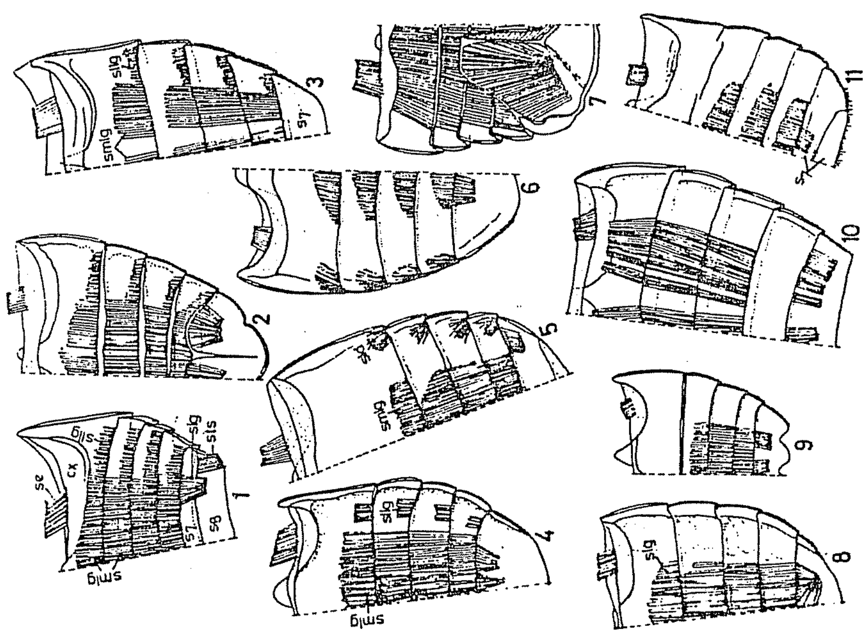
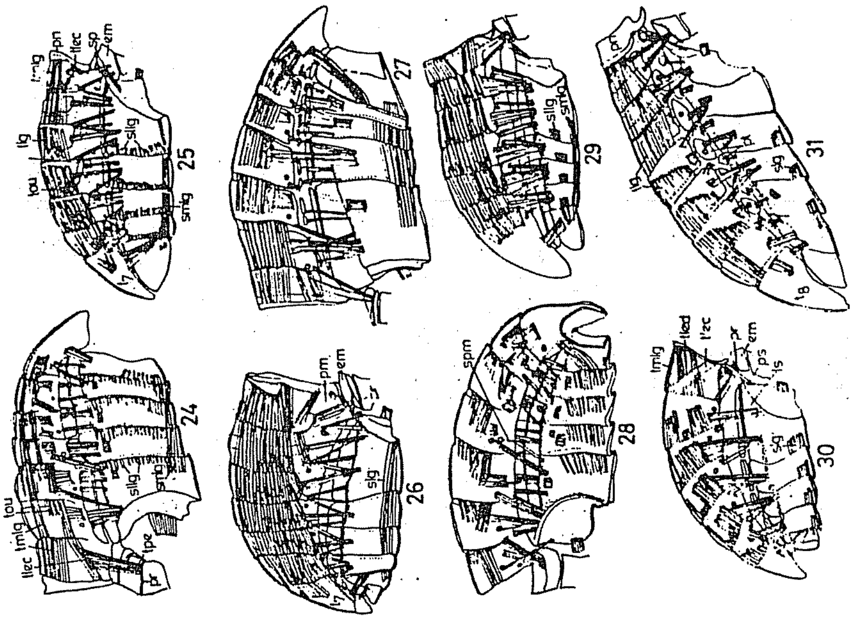


Figure 32: Distribution of abdominal musculature patterns in Bruchidae and subfamilies of Chrysomelidae. The hatched portion of a square represents the relative proportion of species of the respective taxon (✱) Oomorphus has no sternal muscles but Lamprosoma itself and also Sphaerocarinae have sternal type IV (Kasap and Crowson, 1976).



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