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CHARACTERISTICS AND EVOLUTION OF ELYTRAL SCULPTURE IN THE TRIBE
GALERITINI (COLEOPTERA: CARABIDAE)¹

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ABSTRACT

A reconstructed phylogeny, based primarily on structural features other than details of the elytral cuticle, provides the basis for inferring evolution of macrosculpture and microsculpture of the elytra of galeritine adults. Macrosculpture consists of a system of alternating linear depressions (interneurs) and elevations (intervals). A transformation series extends in the subtribe Galeritina from primary intervals that are broad and slightly convex (or flat) to costate to carinate, with or without development of secondary intervals. In the monobasic more plesiotypic subtribe Planetina, the elytra have developed carinate primary and secondary intervals independently of these features in the more highly evolved groups of subtribe Galeritina. Within some taxa of Galeritina, the secondary intervals (carinulae) have been reduced or lost. The microsculpture system of microlines and included sculpticells has undergone a complex series of changes in the Planetina and Galeritina. Independently, in both subtribes, the plesiotypic microlines have been lost, and sculpticells are represented by nodules, which are only parts of the original sculpticells. In the genus Eunostus Castelnau (subtribe Galeritina), the plesiotypic microlines are evident, and sculpticells are transverse and flat, but a few exhibit small nodules. Convergence is postulated between Planetina and Galeritina with independent development of the same type of macrosculpture and microsculpture, and also within the Galeritina, with independent reduction in different lineages of the system of carinae and carinulae. The patterns of macrosculpture and microsculpture are correlated to the extent that adults with carinate intervals exhibit elongate sculpticells with transversely aligned nodules. This relationship may be the result of: 1) selective forces acting similarly on different genes to produce a functional complex; or 2) there may be a developmental constraint, such that ontogenetic development of carinae somehow channels or influences development of the derived form of microsculpture. If alternative 1 is correct, the derived, correlated forms of macrosculpture and microsculpture may be accepted as discrete character states for evaluation of phylogenetic relationships; if alternative 2 is correct, the derived pattern of macrosculpture and microsculpture must be regarded as a single character state. The biological significance of these transformation series is unknown, though the transverse form of sculpticells is generally correlated in other carabids with life in tightly packed leaf litter. The system of longitudinal carinae and sculpticells is reminiscent of a corrugated iron roof, and may be especially effective for shedding water and debris. Because this latter form of sculpture is exhibited by related species that have strikingly different

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ecological requirements, the additional inference is made that sculpture is not responding to specific environmental factors, but rather to factors that are more general.

RÉSUMÉ

Une reconstruction de la phylogénie des Galeritins, établie principalement à partir de caractères structuraux autres que les détails de la cuticule élytrale, nous sert de base pour déduire les étapes évolutives de la macrosulpture et de la microsulpture des élytres chez les Galeritins adultes. La macrosulpture consiste en un ensemble de sillons (internes) alternant avec des élévations linéaires (intervalles). Dans la sous-tribu des Galeritina, il existe une série de transformations des intervalles primaires qui passent de larges et légèrement convexes (ou aplatis) à costés ou carénés, avec ou sans apparition d'intervalles secondaires. Dans la sous-tribu monogénérique des Planetina, qui constitue un groupe plus plésiotypique, les élytres ont développé des carènes primaires et des intervalles secondaires indépendamment de ceux qu'on retrouve dans les groupes plus évolués de la sous-tribu des Galeritina. Chez certains taxons des Galeritina, il y a réduction ou perte des intervalles secondaires (carénules). La microsulpture, comprenant un ensemble de microlignes et de «sculpticellules», a subi une série complexe de changements chez les Planetina et les Galeritina. Indépendamment dans les deux sous-tribus, les microlignes plésiotypiques ont disparu et les «sculpticellules» n'existent plus qu'à l'état de nodules qui correspondent à une partie des «sculpticellules» originelles. Chez le genre Eunostus Castelnau (de la sous-tribu des Galeritina), les microlignes plésiotypiques sont évidentes et les «sculpticellules» sont transverses et aplaties, mais certaines «sculpticellules» montrent de petits nodules. Nous postulons qu'il y a eu convergence, d'une part entre les Planetina et les Galeritina lors du développement d'un type semblable de macrosulpture et de microsulpture, et d'autre part parmi les Galeritina où il y a eu réduction du système de carènes et de carénules de façon indépendante dans les différentes lignées. Les motifs de macrosulpture sont corrélés avec ceux de microsulpture dans la mesure où les adultes ayant des intervalles carénés possèdent des «sculpticellules» allongées avec des nodules alignés transversalement. Cette relation peut être le résultat soit de forces sélectives agissant similairement sur des gènes différents pour produire un ensemble fonctionnel, soit de contraintes de développement qui font que, d'une certaine façon, l'ontogénèse des carènes canalise ou influence le développement du type dérivé de microsulpture. Si la première alternative est correcte, nous pouvons accepter les types dérivés et corrélés de macrosulpture et de microsulpture comme étant des états de caractères distincts pour l'évaluation des relations phylogénétiques; par contre, si la seconde alternative est correcte, le motif dérivé de macrosulpture et de microsulpture doit être considéré comme un seul état de caractère. La signification biologique de ces séries de transformations est inconnue, bien que la présence de «sculpticellules» transverses est généralement corrélée, chez d'autres Carabiques, avec un mode de vie dans la litière compacte. Le système de carènes et de «sculpticellules» longitudinales fait penser à un toit de tôle ondulée et peut être particulièrement efficace pour se débarrasser de l'eau et des débris. Étant donné que ce dernier type de sculpture se rencontre chez des espèces apparentées qui possèdent des exigences écologiques fort différentes, nous déduisons par surcroît que la sculpture n'est pas assujettie à des facteurs environnementaux spécifiques, mais plutôt à des facteurs plus globaux.

INTRODUCTION

Most of what is known about galeritine carabids is summarized in various comparatively recent taxonomic treatments: Basilevsky (1963), Afrotropical species, Reichardt (1965 and 1967), the Asian species of *Galerita*, and the species of Galeritini in the New World, respectively; Lindroth (1969: 1091), and Ball and Nimmo (1983), species of the predominantly Nearctic subgenus *Progaleritina*.

The tribe Galeritini is pan-tropical, with northern extensions into the Nearctic (northward to southern Ontario and Québec) and eastern Palaearctic (northward to the Japanese Archipelago and southern Korea) Regions. Habitats occupied range from waterside stations and the rain forest floor in the tropics to dry open forests and savannas. Most species live at low altitudes, but in the American tropics, a number of species are known from montane forest.

Adults and larvae of all species are probably predators on other arthropods, though this has been shown for only a few species. It seems reasonable to make the extrapolation, because of general similarity in body form and details of the mouthparts among all taxa. Females of *Galerita (Progaleritina) bicolor* Drury lay their eggs in mud balls which are then attached to the undersides of leaves. This behavior is correlated with a peculiarly modified ovipositor,

which is characteristic of the more highly evolved galeritines. By extrapolation, it seems likely that all such taxa have similar habits, and that those with more plesiotypic ovipositors have more plesiotypic habits, and probably lay eggs in cavities in the soil, as do most female carabids. Adults of many of the macropterous species are found at lights, at night, showing that they are nocturnal and that they fly. Little else is known about ecological aspects of galeritines.

Although knowledge of galeritines is markedly restricted, I was able to make a reconstructed phylogeny, using previously studied features of adults, and adding analyses of structure of the mandibles and ovipositor (Ball, in press). Macrosculpture of the elytra was used to reconstruct the phylogeny of *Galerita* (*sensu lato*), but microsculpture was not studied in detail. Subsequently, I realized that elytral sculpture exhibited some interesting complexity, so I asked if patterns of sculptural variation might be correlated with the reconstructed phylogeny that I had made. Results are presented below.

MATERIAL AND METHODS

Material

The adults studied were those on hand that had been collected by me, were in the Strickland Museum of my Department, or were borrowed from other institutions for the phylogenetic study of the Galeritini. In aggregate, they represented a reasonably diverse cross-section of the tribe, but not all species. Sculpture of the elytra was examined superficially using representatives of the following taxa: *Planetes bimaculatus* MacLeay, *P. ruficollis* Nietner, *P. pendleburyi* Andrewes, and *Planetes* species?; *Eunostus herrarensis* Alluaud, *E. vuilloti* Alluaud, *Eunostus* new species; *Ancystroglossus ovalipennis* Reichardt, *A. dimidiaticornis* Chaudoir, and *Ancystroglossus* new species; *Trichognathus marginipennis* Latreille; and all seven species of *Galerita*, subgenus *Progaleritina*. From subgenus *Galerita*, I examined specimens of *G. perrieri* Fairmaire, *G. sulcipennis* Reichardt, various members of eight New World sub-groups: *americana*, *carbonaria*, *costulata*, *gracilis*, *jelskii*, *occidentalis*, *striata*, and *unicolor*; and four species of the *G. africana* group.

Detailed examination of microsculpture was made for specimens of *Planetes bimaculatus*, *Eunostus herrarensis*, *Ancystroglossus ovalipennis*, *Trichognathus marginipennis*, *Galerita mexicana* Chaudoir, *G. sulcipennis*, *G. perrieri*, *G. ruficollis* Dejean, *G. boucardi* Chaudoir, *G. balli* Reichardt, *G. attelaboides* Fabricius, and *G. procera* Gerstaecker.

Methods

Preparation and study of specimens.--Elytra of specimens chosen for superficial study were cleaned initially with ammonia applied with a moistened bit of tissue paper held in forceps. These specimens were examined with a Wild M5 Stereo-binocular microscope, at 50X magnification. On the basis of such examination, major types of sculpture were identified and specimens representing each type were selected for detailed examination.

For such study, except for the specimen of *G. perrieri*, the left elytron was removed, cleaned in water using a sonicator, attached to a standard mount, and coated with gold using a sputter coater. Specimens were examined and photographed, using a Cambridge S-250 "Stereoscan" Scanning Electron Microscope. The specimen of the rare Madagascan *G. perrieri*, was examined with its elytra attached to the body, uncoated, at relatively low magnifications of the SEM.

Analytical procedures.— These concerned identification of ancestral features of sculpture for each of the branching points of a tree that represented the reconstructed phylogeny of the

suprageneric groups of Galeritini. The general method used was hypothesis of transformation series (Figs. 2 and 5) polarized with the premises that flat (or slightly convex) elytral intervals are plesiotypic features of macrosculpture, and an isodiametric pattern with flat, non-imbricate sculpticells is the plesiotypic condition of the microsulpture. The latter premise is based on conclusions reached by Hinton (1970: 41-42), and Lindroth (1974).

The sequence of stages proposed in evolution of macrosculpture and microsulpture follows from the reconstructed phylogeny of Galeritini (Fig. 1, from Ball [in press]). For each pair of sister groups, the sculpture pattern most like the proposed ancestral pattern was judged the more plesiotypic, and accepted as the ancestral pattern for that pair of sister taxa. Transformation series for macrosculpture and microsulpture were established separately. The separate analyses are presented together on diagrams representing the reconstructed phylogeny of Galeritini (Figs. 7 and 8).

SCULPTURE OF THE ELYTRA

For purposes of this presentation, the term "macrosculpture" refers to the alternating system of longitudinal convexities (intervals) and concavities (interneurs) on the surface of a typical elytron. Intervals mark the areas which are the courses of veins of the fore wing (Jeannel, 1941: 30-31). "Microsulpture" refers to the network of fine lines and microscopic sculpticells (Allen and Ball, 1980: 486) that cover the surface. This network, in its most plesiotypic form, reflects the form of the cellular network of the underlying epidermis (Hinton, 1970: 41-42). Types of macrosculpture are designated by Roman numerals and capital letters; microsulpture types are designated by Arabic numerals and capital letters.

Macrosculpture

Within the tribe Galeritini, intervals range in form from broad and flat (Fig. 2, Type I) to broad and convex (costate, Fig. 2, Type III), to narrow and convex (carinate, Fig. 2, types II-IV). An elytron exhibits a simple arrangement, with all intervals being equal in width and convexity, or a complex arrangement, with a pair of secondary intervals (carinulae) intercalated between adjacent broader, primary intervals (carinae, Fig. 2, Subtype IVA, and Fig. 3). The number of carinae is either nine (Fig. 2, Subtype IIa, and Type IV), or five (Subtype IIB).

Microsulpture

At magnifications of about 50X, the cuticle of most arthropods exhibits a mesh of fine lines, like the lines of a fish net (Lindroth, 1974: 252, and Allen and Ball, 1980: 485-486). Meshes are characterized as isodiametric, transverse, or longitudinal, depending upon their relative lengths and widths. "Sculpticells" (Allen and Ball, 1980: 486) between microlines range in form from flat to slightly or markedly convex, to carinate (Ball, 1975: Fig. 114).

Galeritines exhibit a variety of forms of microsulpture. At the base of an elytron, sculpticells are flat, slightly imbricate (Harris, 1979: 19 and 30, Fig. 40), and nearly isodiametric (Fig. 6), or transverse (Fig. 4). Most of the elytral surface is:

- a. covered with a network of transverse meshes (some sculpticells with posterior nodules, Fig. 5, Type 1); or
- b. with nodule-like swellings, either not arranged in a pattern (Subtypes 2A and B), or aligned transversely (Types 3 and 4).

RECONSTRUCTED PHYLOGENY OF TRIBE GALERITINI

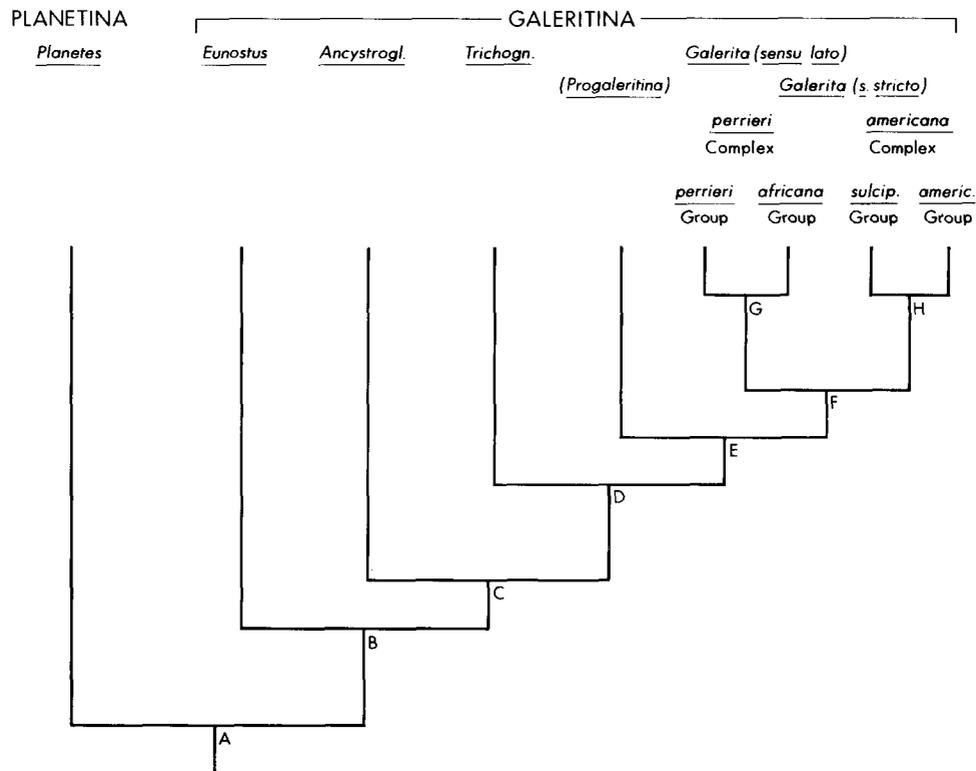


Fig. 1. Reconstructed phylogeny of Tribe Galeritini. Taxa are: Subtribe Planetina - *Planetes* MacLeay; Subtribe Galeritina - *Eunostus* Castelnau; *Ancystroglossus* Chaudoir; *Trichognathus* Latreille; *Galerita (sensu lato)* - subgenus *Progaleritina* Jeannel, and subgenus *Galerita* Fabricius, including the *G. perrieri* complex (with *G. perrieri* and *G. africana* groups), and the *G. americana* complex (with *G. sulcipennis* and *G. americana* groups).

The general term for sculpture of Types 2, 3, and 4 is nodulate (Harris, 1979: 15). As detailed below, each nodule is hypothesized as representing only part of an original sculpticell.

PHYLOGENETIC RELATIONSHIPS OF THE GALERITINI

A reconstructed phylogeny of the Galeritini (Fig. 1), based on features of adults (Ball, in press), provides a framework for an evolutionary analysis of sculpture patterns. Each node is designated by a capital letter (A-H), in alphabetical sequence, depending upon recency of common ancestry, except for the terminal two nodes. Aspects of elytral sculpture were used as a major feature to reconstruct the phylogeny of the supraspecific taxa of the genus *Galerita*, but

SUBTRIBE GALERITINA : TRANSFORMATION SERIES
IN MACROSCULPTURE OF ELYTRA

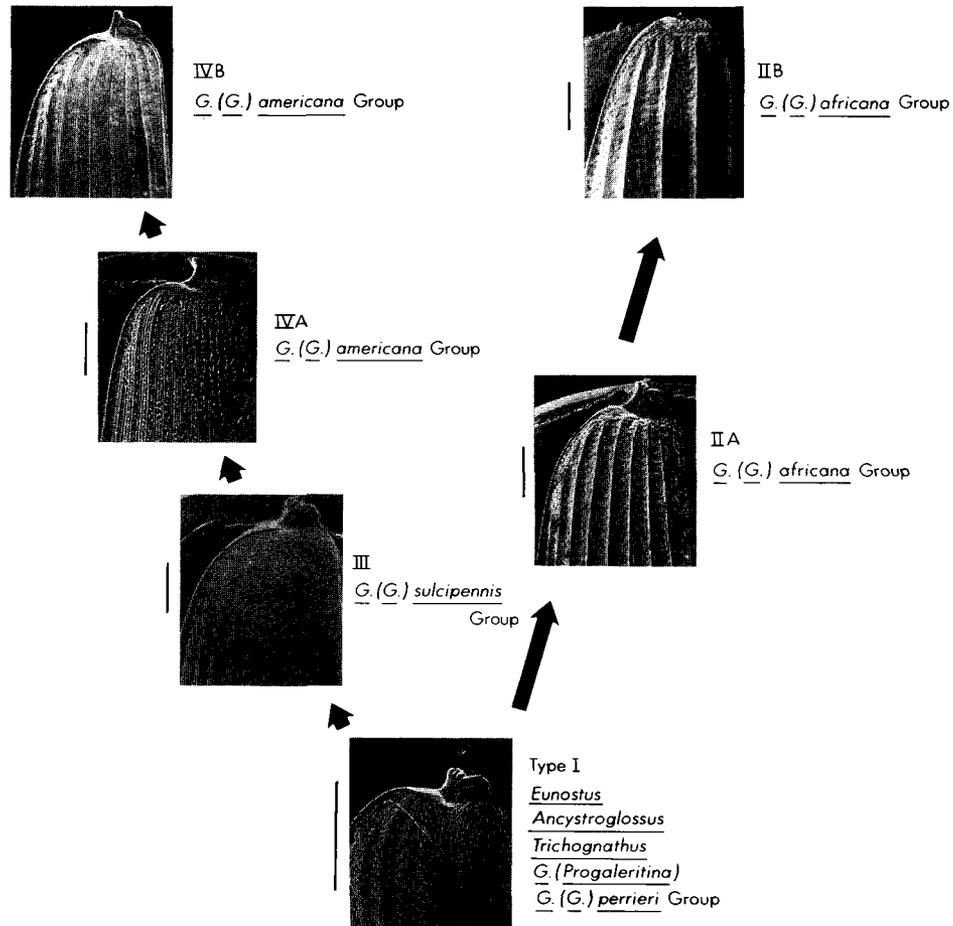


Fig. 2. Subtribe Galeritina: transformation series in macrosculpture of elytra. Types IIA-IVB represent approximately the basal one third, and Type I, the basal one quarter, of the left elytron. Species represented by illustrations are the following: Type I - *Eunostus herrarensis* Alluaud, *Ancystroglossus ovalipennis* Reichardt, *Trichognathus marginipennis* Latreille, *G. (Progaleritina) mexicana* Chaudoir, and *G. (Galerita) perrieri* Fairmaire; Subtype IIA - *G. (Galerita) attelaboides* Fabricius; Subtype IIB - *G. (Galerita) procera* Gerstaecker; Type III - *G. (Galerita) sulcipennis* Reichardt; Subtype IVA - *G. (Galerita) ruficollis* Dejean; and Subtype IVB - *G. (Galerita) balli* Reichardt. Scale bars represent 1.0 mm.

SUBTRIBE PLANETINA : Planetes
 MACROSCULPTURE - LEFT ELYTRON

BASAL PORTION

DISC

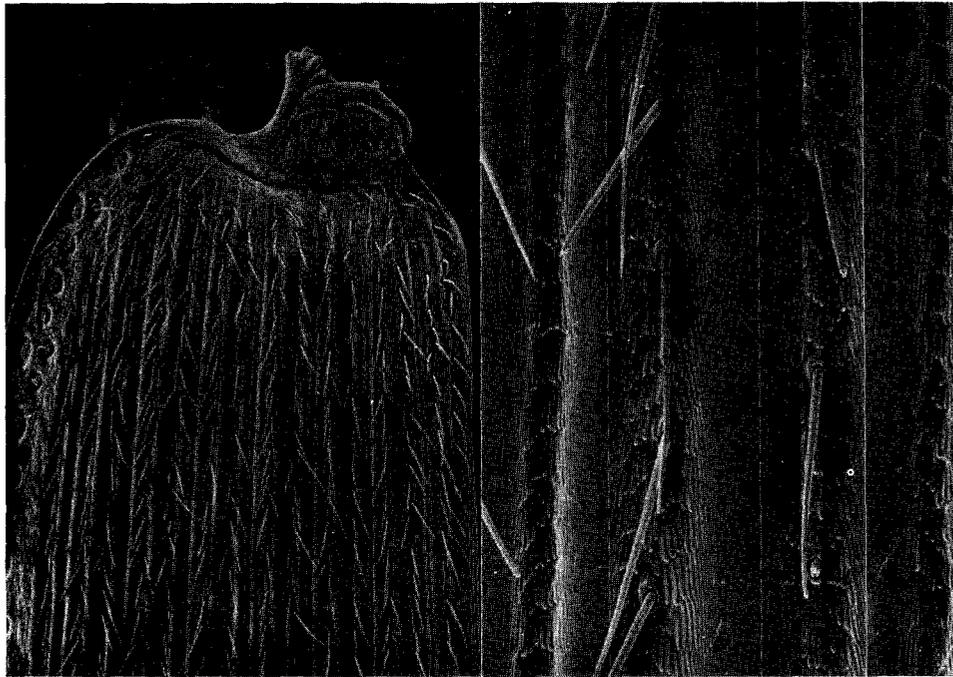


Fig. 3. Subtribe Planetina: macrosculpture of the left elytron of *Planetes bimaculatus* MacLeay. Scale bars represent 250 μm .

not to reconstruct the phylogeny of the other genera.

Overall, the system reflects important changes in structure of the mouthparts and ovipositor. There is also a striking increase in body size associated with node D, probably reflecting a change in habits from that of hunting concealed in the leaf litter to running on the surface of the forest floor, or in more open areas.

PATTERNS OF ELYTRAL SCULPTURE OF THE GALERITINI

Although the subtribe Planetina exhibits more plesiotypic features than does the Galeritina, outgroup comparison shows that planetine adults have highly derived sculpture. Thus, the subtribe Galeritina, with its greater range of sculpture types, is the focal group for elucidation

of evolution of these systems, and the following analyses begin with consideration of this subtribe.

Macrosculpture

Subtribe Galeritina.— Figure 2 illustrates the hypothesized trends in elytral macrosculpture. The figures also illustrate the reduced basal ridge that is characteristic of the adults of *Galeritina*. Four general types of macrosculpture are recognized, based on structural and phylogenetic considerations.

Type I includes elytra with broad intervals that are either flat or slightly convex. I did not formally distinguish between the slight difference involved. Type I is characteristic of three genera, and of one subgenus and one species group of *Galerita* (*sensu lato*).

Type II macrosculpture is characteristic of the *G. africana* group (*Galeritiola* Jeannel, of previous authors). It differs from Type I by having wider and deeper interneurs, and consequently narrower intervals, the latter being carinate. Two subtypes of macrosculpture are recognized: IIA, with nine carinae; IIB, with five carinae.

Type III macrosculpture is characteristic of the monobasic Middle American montane *G. sulcipennis* group. The elytral intervals are more elevated than in Type I, and are classified as costate. The figure, unfortunately, does not do justice to the difference between the two types of sculpture.

Type IV macrosculpture is characterized by carinae and readily seen carinulae (Subtype IVA), or if carinulae are not readily apparent, careful examination reveals vestiges of them (Subtype IVB). Subtype IVB looks very much like IIA, but the carinae of IVB are not as high, and the interneurs of IIA lack any indication of carinulae.

Subtribe Planetina.— Figure 3 illustrates macrosculpture for a specimen of *Planetes*. The pattern is Subtype IVA. Carinulae appear to be nearly as wide as the carinae, but in fact there is a substantial difference as the figure of a portion of the elytral disc, taken at higher magnification, indicates. At working magnifications (ca. 5X - 50X), however, the carinae and carinulae appear about equal, so that the elytra seem to have a densely packed system of carinae, and thus seem quite different from the Subtype IVA elytra of *Galerita*.

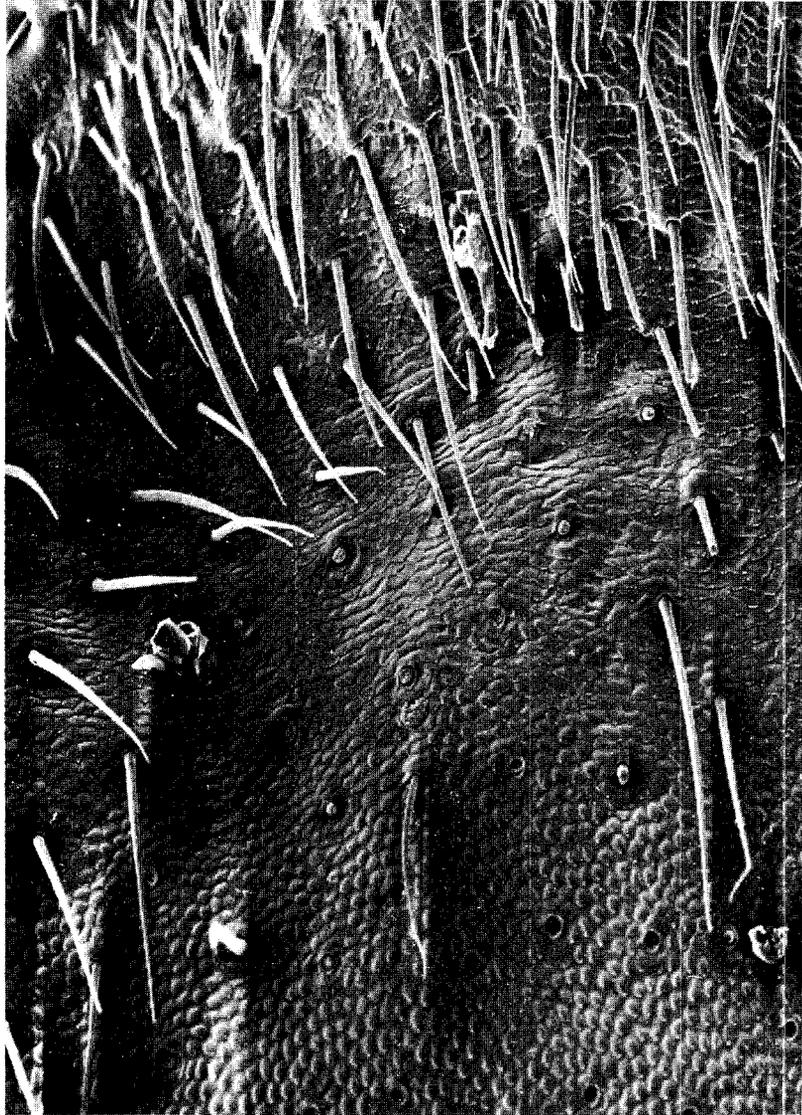
Microsculpture

Subtribe Galeritina.— Figure 4 illustrates two general types of microsculpture characteristic of galeritines: imbricate, which is confined to the basal area, principally basad of the basal ridge; and nodulate, which is more or less extensive on the disc. The sculpticells of the imbricate type are flat and broad, while the nodulate sculpticells are narrower and convex. Four types of microsculpture are recognized on the elytral disc in the *Galeritina*, and their proposed evolutionary trends are illustrated in Figure 5. Type I, which is characteristic of *Eunostus* the sister group of the other three galeritine genera, exhibits markedly transverse, flat sculpticells across most of the surface. Laterally, however, some sculpticells have small medio-apical nodules.

Types 2-4 are characterized by widespread nodulate microsculpture, without microlines. Type 2 exhibits a non-patterned arrangement of nodules, with Subtype 2A having fewer nodules than Subtype 2B. The former is characteristic of *Ancystroglossus*, the latter of *Trichognathus* and subgenus *Progaleritina*.

In Type 3 microsculpture, which is confined to the *G. perrieri* species complex, the nodules are in transverse rows: in 3A, exhibited by adults of the *G. perrieri* group, the nodules are short

MICROSCULPTURE AT BASE
OF LEFT ELYTRON



Trichognathus marginipennis

Fig. 4. Macrosculpture at base of left elytron of *Trichognathus marginipennis* Latreille. Scale bar represents 150 μ m.

SUBTRIBE GALERITINA : TRANSFORMATION SERIES
IN MICROSCULPTURE OF ELYTRA

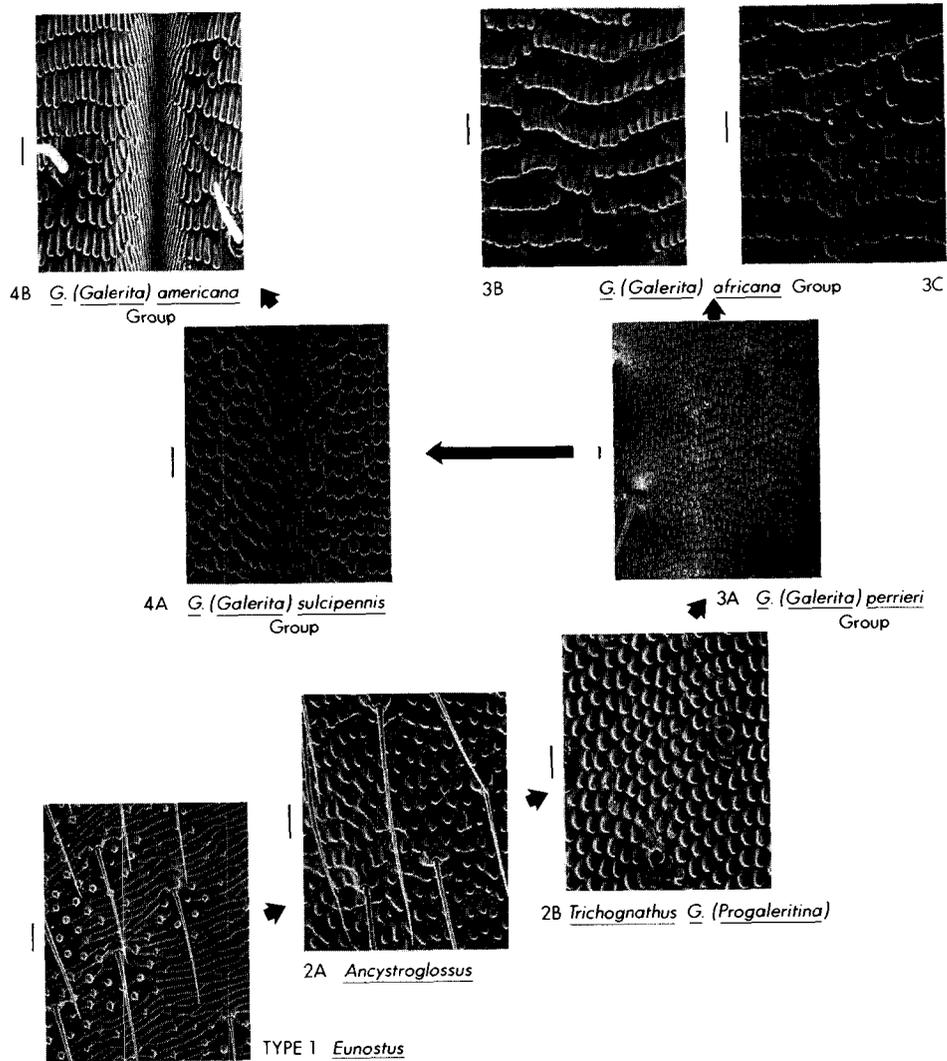


Fig. 5. Subtribe Galeritina: transformation series in microsculpture of elytra. Type I illustrates a portion of interneur 7 in the basal third of the left elytron. Subtypes 2A-4B illustrate portions of interneur 3 and/or 4, in the basal third of the left elytron. Species represented are: Type I - *Eunostus herrarensis* Alluaud; 2A, *Ancystroglossus ovalipennis* Reichardt; 2B, *Trichognathus marginipennis* Latreille, and *G. (Progaleritina) mexicana* Chaudoir; 3A, *G. (Galerita) perrieri* Fairmaire; 3B, *G. (Galerita) attelaboides* Fabricius; 3C, *G. (Galerita) procera* Gerstaecker; 4A, *G. (Galerita) sulcipennis* Reichardt; 4B, *G. (Galerita) ruficollis* Dejean. Scale bars represent 50 μm .

SUBTRIBE PLANETINA : Planetes
MICROSCULPTURE - LEFT ELYTRON

BASE

DISC



Fig. 6. Subtribe Planetina: microsculpture of the left elytron of *Planetes bimaculatus* MacLeay. The illustrations represent parts of the left elytron: the basal tenth, toward the sutural margin; and a portion of interneur 3 and adjacent carinulae. Scale bars represent 10 μ m.

and uniform across the elytral surface; for 3B and 3C, characteristic of the *G. africana* group, the nodules are longer than those of 3A, but *inter se* are relatively shorter (3B) or longer (3C), flattened basally, and in fairly well marked transverse rows, between carinae. On the tops of the carinae, the sculpticells are elongate and flat, and closely adpressed.

Type 4 microsculpture is exhibited by adults of the *G. americana* complex. Of the two Subtypes, 4A (*G. sulcipennis* group) is most like that of the *G. perrieri* group. The difference is seen in the elongate and flattened nodules on the top of the elytral costae. In Subtype 4B (exhibited by adults of the *G. americana* group), the nodules are longer and the transverse rows between adjacent carinae and carinulae are better defined. In those adults exhibiting Subtype IVB macrosulpture (*i.e.*, with carinae reduced), locations of atrophied carinulae are indicated

by the markedly elongate sculpticells that are a characteristic feature of the tops of carinae and carinulae.

Subtribe Planetina.— Figure 6 illustrates microsculpture characteristic of *Planetes* adults. The elytral base has imbricate, flat, and essentially isodiametric sculpticells. The disc exhibits long, keeled nodules arranged in transverse rows between adjacent carinae and carinulae. The sculpticells of the latter are very narrow and linear.

EVOLUTION OF ELYTRAL SCULPTURE OF THE GALERITINI

The Pattern

Figures 7 and 8 illustrate and summarize the hypothesis of evolution of sculpture. Figure 8 is a continuation of Fig. 7. For the labelled nodes except G, the hypothesized ancestral combination of sculptural features is illustrated, based on features of extant galeritines, macrosculpture above, microsculpture below. The ancestral states for node G are the same as for F. For each of the extant groups whose sculptural features differ from those of the ancestral stock, illustrations are also provided.

Features of the common ancestor.—These are inferred from the most plesiotypic sculptural features of extant adult galeritines. They are Type I macrosculpture, and imbricate-isodiametric microsculpture, the latter as seen on the elytral base of *Planetes* adults.

Macrosculpture.— The reconstructed phylogeny suggests that from Ancestor A to F or G in subtribe Galeritina, there were no significant changes in macrosculpture. From Ancestor G, with Type I macrosculpture, Type II developed, and further differentiated into two subtypes, in the *G. africana* group, with Subtype IIB losing four carinae. From Ancestor F, Type III sculpture emerged in Ancestor H, and from the latter, Type IV, which in turn differentiated into two subtypes, in the *G. americana* group.

To determine polarity of Type IV sculpture, I relied on correlation of characters, for this part of the transformation series is not ordained by the reconstructed phylogeny presented in Figure 1. Subtype IVB is associated with the derived features of brachyptery and life in montane environments, in the northern part of the Neotropical Region. Subtype IVA, on the other hand, is associated with the ancestral features of macroptery and life in lowland environments, over extensive areas of the tropics. Reichardt (1967: 158) postulated, and I agree, that the traces of carinulae are evidence of loss, associated with reduction of wings and loss of flight, rather than that the traces represent the precursors of fully developed carinulae.

Although there is no sign in Type III of developing carinulae, or widened interneurs to foreshadow development of Type IV sculpture, a costate condition (Type III) could be a reasonable step between nearly flat (Type I) and carinate (Type IV) conditions.

In the lineage that gave rise to the Planetina, macrosculpture Type IVA also arose. Although intermediate extant forms are unknown, it seems unlikely that the change from the postulated ancestral condition occurred without intermediate changes like those proposed for the Galeritina.

Microsculpture.— Although changes in macrosculpture came relatively late in the Galeritina lineage, the pattern for microsculpture suggests an early striking change, followed by less marked differentiation. I suggest that imbricate isodiametric sculpture of Ancestor A changed in Ancestor B to transverse sculpture, with some sculpticells exhibiting nodules. This was followed on the surface apicad of the basal ridge, by spread of the nodules over the disc, and disappearance of the plesiotypic lines that marked the sculpticells. The number of nodules increased, and took on an arrangement in rather irregular transverse rows (Ancestor F,

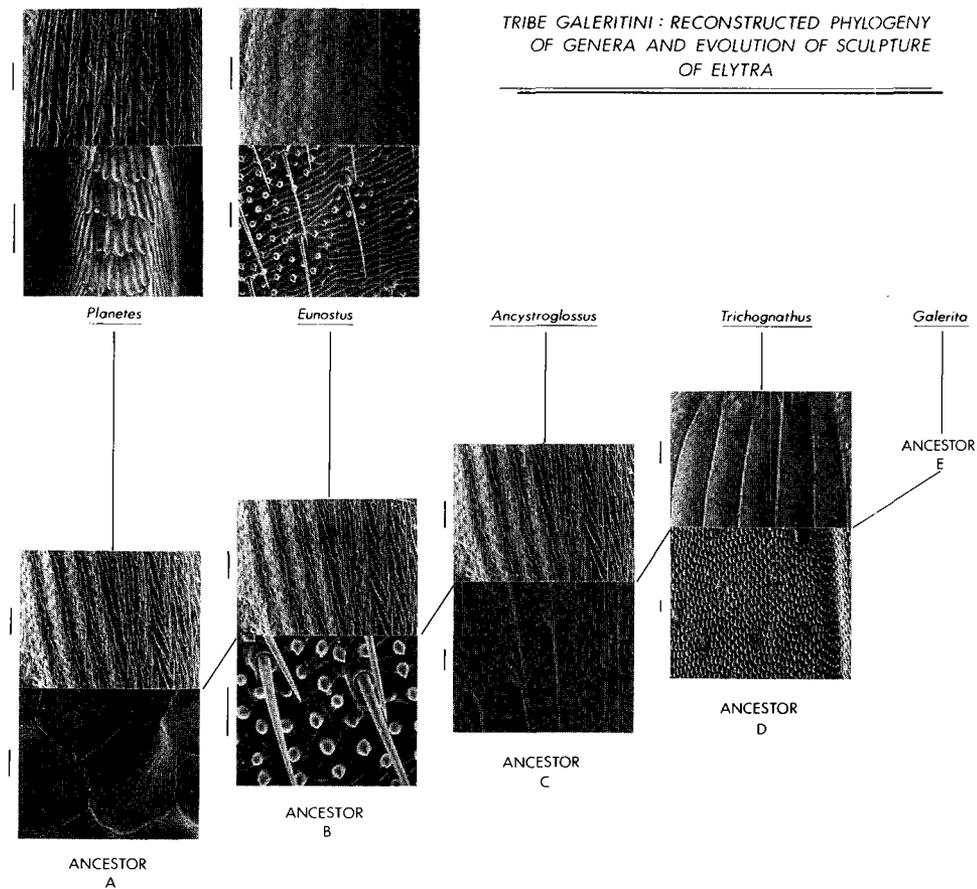


Fig. 7. Tribe Galeritini: reconstructed phylogeny of genera and evolution of sculpture of elytra. Sculpture of elytra of *Planetes*, *Eunostus*, and Ancestors A-D are each represented by a pair of figures, of which the lower is microsculpture, and the upper macrosculpture. The figure for Ancestor C also represents *Ancystroglossus*, and those for Ancestor D also represent *Trichognathus* and *Galerita*. The illustrations are of the left elytron, basal portion, as explained in captions for Fig. 2 (macrosculpture) and Fig. 5 (microsculpture). Specimens represented are: Ancestor A - microsculpture, *Planetes bimaculatus* MacLeay, and macrosculpture, *Ancystroglossus ovalipennis* Reichardt; *Planetes bimaculatus*; Ancestor B - microsculpture, *Eunostus herrarensis* Alluaud, and microsculpture, *A. ovalipennis*; *Eunostus herrarensis*; Ancestor C, *A. ovalipennis*; Ancestor D, *Trichognathus marginipennis* Latreille. Scale bars represent at low magnification, 500 μ m; at high magnification, 50 μ m.

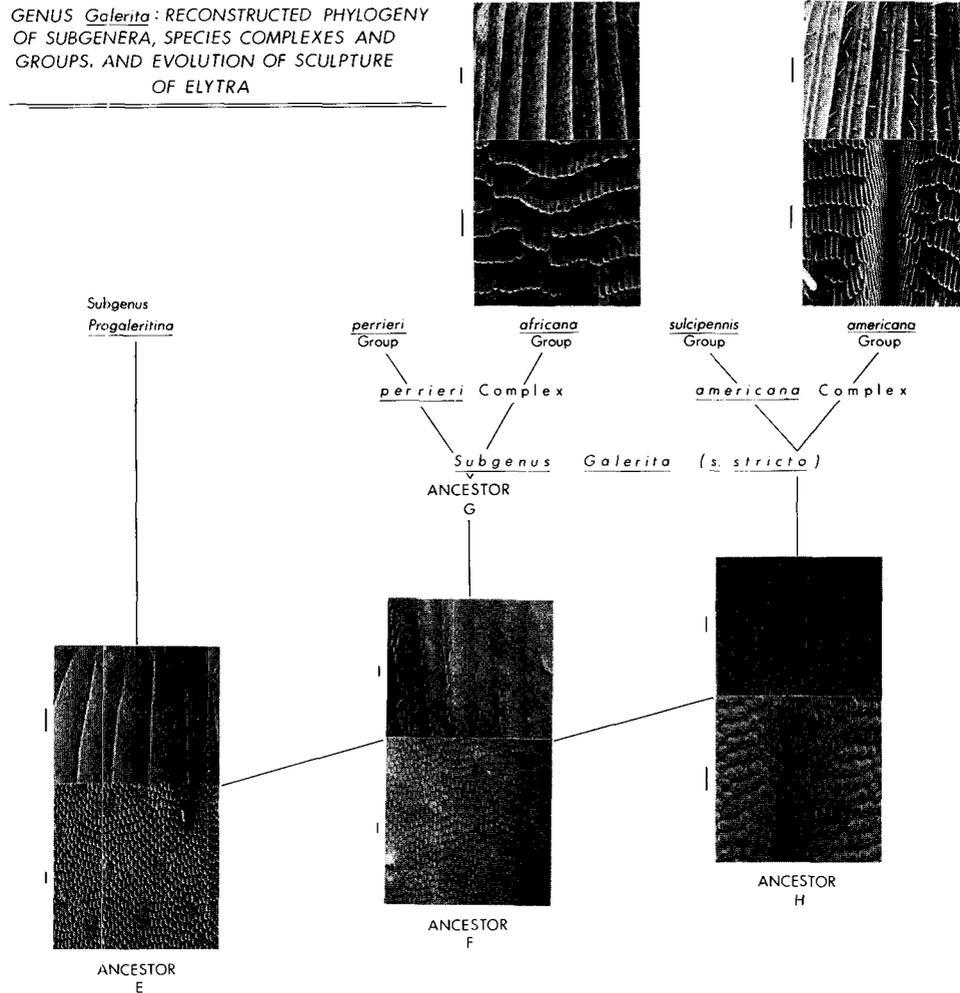


Fig. 8. Genus *Galerita*: reconstructed phylogeny of subgenera, species complexes and groups, and evolution of sculpture of the elytra. Sculpture of the elytra of Ancestor E, Ancestor F, the *G. africana* group, Ancestor H, and the *G. americana* group are each represented by a pair of figures, of which the lower is microsculpture and the upper macrosculpture. The figures for Ancestor E also represent subgenus *Progaleritina*; for Ancestor F, also Ancestor G and the *G. perrieri* group; for Ancestor H, also the *G. sulcipennis* group. The figures are of the left elytron, basal portion, as explained in the caption for Fig. 2 (macrosculpture) and Fig. 5 (microsculpture). Specimens represented are of these species: Ancestor E - *G. (Progaleritina) mexicana* Chaudoir; Ancestor F - *G. (Galerita) perrieri* Fairmaire; *G. africana* group - *G. (Galerita) attelabooides* Fabricius; Ancestor H - *G. (Galerita) sulcipennis* Reichardt; and *G. americana* group - *G. (Galerita) ruficollis* Dejean. Scale bars represent at low magnification, 500 μm ; at high magnification, 50 μm , and at very high magnification, 5 μm .

Subtype 3A). As a more complex macrosculpture evolved, the transverse rows of nodules were confined to the interneurs (Subtypes 3B, 3C, 4A, and 4B).

Subtype 3A microsculpture seems easily derived from Subtype 2B by development of a more orderly arrangement of nodules. Subtypes 3B and 3C are derived from 3A by a still more ordered arrangement of nodules, and possibly by fusion of pairs of nodules, in adjacent rows, to yield nodules that are fewer and longer. The transverse rows of nodules, confined to the interneurs (Subtypes 3B, 3C, 4A, and 4B), probably decreased in number by fusion of members of adjacent rows, and, consequently, the individual nodules became longer (Subtypes 3C and 4B). On the elytral base, transverse imbricate sculpture was retained. Transformation of 3A to 4A and the latter to 4B is virtually self-evident, parallelling the transformation of 3A to 3B, and to 3C.

It is important to note that the transverse sculpticells on the elytral disc of *Eunostus* adults are not imbricate. This change is interpreted as a loss, and a reversion to a state more plesiotypic than is exhibited by the sculpture of Ancestor A.

The planetine lineage adults evolved, on the elytral surface apicad of the basal ridge, nodulate microsculpture with long nodules, similar to that of Subtype 4B. As for the macrosculpture, intermediate steps are not known for evolution of the microsculpture, between the hypothetical ancestral condition and that of the extant species of *Planetes*. On the basal area of the elytra, the imbricate isodiametric sculpture was retained.

Microsculpture of the elytral base that is characteristic of *Planetes* seems the most plesiotypic pattern among extant Galeritini. The discal sculpture, on the other hand, is highly derived, with no known extant antecedants.

Convergence among taxa.— The same derived patterns of macrosculpture and microsculpture are represented in planetines and galeritines, and within distantly related members of the Galeritina. Adults of *Planetes* and of the *G. americana* group exhibit the complex type of elytral macrosculpture, with development of a system of alternating carinae and pairs of carinulae. Similarly, within the genus *Galerita*, a system of carinate intervals has evolved independently in different groups of the subgenus *Galerita*. Also, *Planetes*, and the *Galerita americana* and *africana* groups, have evolved independently a pattern of long, transversely aligned nodular microsculpture, and elongate sculpticells on the tops of the carinae.

Loss of carinae or carinulae has occurred independently in the *G. africana* group (carinae lost), and in the *G. americana* group (carinulae lost). Although these losses involve different structures, the end result in each lineage is similar.

Parallel development of macrosculpture and microsculpture.— As noted above, carinate macrosculpture has had correlated with it development of long narrow nodules, transversely arranged between intervals.

Significance of the Pattern

In order to highlight general implications of this study, brief comments are offered about historical, developmental, and functional significance of the evolutionary pattern of sculpture of the Galeritini. From an historical perspective, I suggest that the highly complex surface of the arthropod cuticle exhibits patterns of variation that are amenable to phylogenetic analysis. This study suggests that features of the cuticle are sufficiently stable that old patterns persist. For example, if the estimate of age of *Galerita* is correct (Ball, in press, based on vicariant distribution patterns of extant taxa), the subgenera of this genus pre-date the beginning of the

Tertiary Period, and the other genera likely originated still earlier. Therefore, the microsculpture patterns ought to be of a similar range of ages. Thus, seemingly minor and inconsequential details of surface structure have potentially as much value as have other, more obvious structural features for phylogenetic analysis and taxonomic use.

The examples of convergence are interesting, for they show that even rather complex and detailed similarities may arise independently. Thus, it is important to evaluate critically such similarities if one uses cuticular features in phylogenetic analysis.

Similarities between the patterns of evolution of macrosculpture and microsculpture exhibited among the species whose adults have carinate intervals may result from a functional relationship (see below) of genetically independent elements, or they may be the result of one system constraining the other. If these derived forms of sculpture were genetically independent of one another, then they would constitute separate character states for use in analysis of phylogenetic relationship. Perhaps, however, development of carinae somehow channels or influences development of the transverse pattern of and elongation of the nodules. If this is so, and if one wanted to use the characters as sources of evidence about evolutionary relationship, it would be necessary to determine the extent of the developmental relationship. If microsculpture type were totally dependent upon type of macrosculpture, then one would have but a single character, rather than two, with which to evaluate propinquity of relationship.

Previous authors (Hinton and Gibbs, 1969: 962; Lindroth, 1974: 261-263; Erwin, 1979: 547; Allen and Ball: 544; Goulet, 1983: 375; and Ball and Shpeley, 1983: 800) have considered the ecological role played by surface features of carabids, proposing that irregularities and dullness contribute to cryptic patterns, while brilliance caused by marked reflectivity or iridescence yields flash patterns which are confusing to potential predators. Alternatively (Erwin, 1979: 547), it has been proposed that since different patterns of sculpture are associated with different types of habitats, the patterns might function to protect an insect's body against unfavorable environmental influences. For example, a grated pattern (*i.e.*, diffraction grating) might be especially effective in shedding mud and water, and thus of value to insects living in wet, sticky environments. Using the analogy of a corrugated iron roof, the correlation of elytral carinae with longitudinally directed nodules looks like a run-off system for shedding unwanted material that comes in contact with the cuticle. Perhaps this system has therefore a similar function to that of a grated system of microsculpture, the different solutions being the result of selection for different types of environmental impediments.

More specifically, adults of *Eunostus* exhibit the transverse pattern of microsculpture. In other carabid taxa, this pattern is correlated with life in tightly-packed leaf litter, but I do not know if this is the type of habitat frequented by *Eunostus*. The nodular forms of microsculpture are characteristic of all other galeritine groups, whose range of habitats collectively extends from closed canopy rain forest to open woodland and riparian situations. So, the functional significance of the different types of microsculpture is not likely to be found by seeking correlates with different habitats. Correlation might be found at the level of microhabitats, when these have been determined for galeritines.

In spite of my inability to demonstrate its adaptive significance, since this evolutionary pattern has developed and has been maintained for an extended period of time, and since the features are exposed to environmental pressures including potential predators that rely on eyesight while hunting, it seems reasonable to infer that natural selection has influenced and is maintaining this structural system. Furthermore, in view of the rather small steps in at least portions of the transformation series, it seems reasonable to infer sustained directional

selection, perhaps associated with either changes in habitat, or with improved design for occupying the old habitats. (Ball, in press).

ANOTHER INTERPRETATION OF EVOLUTION OF ELYTRAL SCULPTURE IN THE GALERITINI

Reichardt (1967: 158) considered evolution of macrosculpture of the elytra of subgenus *Galerita*. Assuming that Subtype IVA sculpture was plesiotypic for this group, which he ranked as a genus, and to which he related *Planetes*, he proposed that Types I, II, and III and Subtype IVB were derived from the former Subtype: for II and IVB, by simple loss of carinulae; and for Types I and III, both by loss of the carinulae and reversion from carinate to costate or nearly flat intervals. In turn, this notion was based on two considerations: evident reduction of the carinulae in adults of highland species in Middle America, and association of this loss with brachyptery, an apotypic condition. However, he did not take account of the fact that associated with macrosculpture Types I and III is a plesiotypic form of microsculpture, nor that in the *G. africana* group (with Type II macrosculpture) there is no evidence that carinulae had ever been present.

Having taken account of these facts, and as well having shown elsewhere (Ball, in press) that the subgenus *Galerita* and *Planetes* are not closely related to one another, and consequently there is no need on the basis of out-group comparison to postulate that Subtype IVA macrosculpture is plesiotypic, I believe that Reichardt's hypothesis of the evolution of elytral macrosculpture in the Galeritini can be rejected.

CONCLUDING STATEMENT

In this paper, I have recognized and described the types of sculpture exhibited by representative galeritines, using both structural and phylogenetic considerations to do so. I have demonstrated a marked correlation between microsculpture pattern and the reconstructed phylogeny that I had made previously. Underlying the reconstructed phylogeny based on structural features, there ought to be a correlated series of ecological transformations. When the latter are found and analyzed, I believe we will have the basis for understanding in both functional and historical terms the patterns of evolution of elytral sculpture postulated here.

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