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MICROMORPHOLOGY OF BEETLE ELYTRA,
USING SIMPLE REPLICAS

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ABSTRACT

One of the simplest techniques in biology, an instant replica, utilized cellulose acetobutyratfolie and yielded transparent impressions that were examined directly and photographed by light microscopy. The resulting photographs were comparable to those of the scanning electron microscope at that magnification. Elytra of hundreds of species, belonging to various families of Coleoptera were examined. The microsculpture was somewhat different in almost every species possessing it. Taxonomists can routinely utilize this very simple method for a better understanding of the interrelationships between various taxa.

The stereoscope has been used routinely by entomologists for identification and classification. Coleopterists have used it to study the surface sculpture of beetles, especially that of elytra. Punctures, striae, sulci, setae, scales, etc., have been constantly compared in various taxa. However, there are finer micromorphological details that can be seen and utilized when resolution beyond that of the stereoscope is used.

Balfour-Browne (1940) attempted to study the surface sculpturing of the elytra of beetles. His method was the classical biological technique, including softening by boiling in caustic soda or potash, bleaching, dehydrating, clearing, and mounting in balsam. Balfour-Browne studied the sculpture only of the water beetles that belong to the suborder Adephaga. However,

his photographs did not have enough magnification to show useful detail, and the technique was an elaborate, time-consuming one. Perhaps for these reasons he did not make extensive use of it in the taxonomy of water beetles.

The replica technique of electronmicroscopy (2-stage replica) can serve as a useful tool in insect classification by revealing structural details that cannot be seen by light microscopy (Khalaf 1959). This method, in addition to requiring extensive training and expensive equipment, was too elaborate to be used in routine taxonomic work.

The scanning electron microscope has been used lately; however, many entomologists have no access to such an expensive instrument. In addition to this, before it becomes possible to examine the integument, the specimen is usually prepared for the SEM through a series of processes.

I realized that useful magnification can be secured when the replica is coupled with light microscopy (single-stage replica) in one of the simplest procedures in science. This is the method I utilized in the present investigation.

PREVIOUS FINDINGS ON THE INTEGUMENT MICROSCULPTURE

Balfour-Browne (1940) considered the polygonal pattern as the primitive pattern in beetles. He based his conclusion on its occurrence in all sections of the Dytiscidae and of the Gyrinidae, and also in the Amphizoidae and the Hygrobiidae.

Locke (1967) stated that the pattern was determined by: 1) the initial shape of the cell secreting the cuticulin (each polygon being formed from a single cell) and 2) the rate of deposition which implies differential cuticular deposition).

Hinton and Gibbs (1969a, 1971) also believed that the shapes and dimensions of the polygons probably correspond to the shapes and dimensions of the epidermal cells that secreted the cuticle. Hinton (1970a) published a scanning electron micrograph for the surface cells of the ovarian follicles, the cells that secreted the eggshell, stating that the distribution of these cells determined the pattern of the surface of the eggs.

Hinton (1970b) found that the most common kind of microsculpture on the outer surface of the cuticle of insects consisted of a pattern of polygons, 7-20 μm wide and frequently hexagonal. On this basis, he concluded that the pattern of polygons was the primitive pattern. Hinton added that on different parts of the body, the hexagonal pattern was sometimes modified, reflecting changes in the orientation and shape of the epidermal cells that occurred before the cuticle was secreted.

SIGNIFICANCE OF MICROSTRUCTURE OF ELYTRA

Since the primitive pattern of insects is presumed to be polygonal, and since such a pattern was widely represented in the elytra of the various groups of beetles, the most primitive pattern on the elytra probably is polygonal. Judging from its extreme modification, the elytron was not the most conservative structure in beetles. As a result, it was not surprising to find the archaic insect pattern often modified or even lost. The scutellum and the pronotum of beetles, on the other hand, often seem to be more conservative, exhibiting patterns which are sometimes lost in the elytron.

Among living beetles, the polygonal pattern is somewhat different in almost every species possessing it. Moreover, a quick look at the accompanying micrographs, will show the diversity of the elytral pattern. The pattern had been modified in various directions. The differences are in the shape, the arrangement, and the surface of polygons; the tendency of certain sides to become faint, disappear, or project, etc. It is suggested that these features be utilized in taxonomy, especially after now describing the simple method that brings them to light. Patterns constitute sound morphological features that can serve taxonomy. In related taxa, they sometimes reflect similarity; thus, they are phylogenetically important. On the other hand, like other anatomical features, many species develop a similar pattern independently, not found in their common ancestor (parallelism).

The need of new features in the classification of insects is constantly felt. In discussing the status of Coleoptera taxonomy, Arnett (1967) stated that more anatomical data and anatomical reviews are needed.

PRESENT METHOD OF INVESTIGATION

The impressions were made on the dull surface of triafol BN (cellulose acetobutyratefolie; Mobay Chemical Corporation, Plastic and Coatings Division, Pittsburgh, PA) rectangles, which were attached with tape on narrow sides onto microscope slides. The rectangles were ca. 1.5 X 1cm, and 0.1mm thick. A drop of acetone was placed on the center of the triafol, and the elytron was laid on the drop with the test surface towards the acetone. The system was allowed to dry; 15 min was usually sufficient. The elytron was then removed from the impression, which was transparent and then ready for examination and photography. The prepared slides can be filed and stored in conventional slide boxes for future studies.

The micrographs taken were of the surfaces of the replicas, in which an elevation represented a concavity or depression in the surface of the elytron. A pore of a tubule in the elytron will leave a projecting filament on the replica. On the contrary, what appeared in the replica to be a groove, depressed below the general level, represented a ridge above the surface of the actual cuticle. Hairs or scales also sometimes left their impressions on the replica or detached themselves from the cuticle and became attached to the replica, giving a more opaque outline.

The slides were examined and photographed under high magnification (X400). Under such magnification, patterns of parallel lines $1\mu\text{m}$ apart were resolved. Similarity between the refractive indices of oil and the triafol made the pattern indistinguishable when the replica was examined by oil immersion.

The present investigation was concerned only with the microsculpture or pattern of elytra. When the neighboring regions—such as the scutellum and pronotum—were compared with the elytra, the pattern might be different not only in type but also in its very existence.

This replica method can contribute valuable data to the field of macromorphology by disclosing details of the shape, surface, length, arrangement, and density of setae, hairs, scales, pits, and punctures (see Fig. 76-8 for example).

This study was based mainly on identified species that were part of

Tulane University collection, and made available to me through the courtesy of Dr. Harold A. Dundec.

RESULTS

Suborder Adephaga Cicindelidae

The 5 species examined had polygonal patterns.

Cicindela Linnaeus: *C. dorsalis* Say, *C. repanda* Dejean, and *C. sexguttata* Fabricius. The pattern was deep; the polygons were about 0.01mm wide and were often keeled. Sometimes, however, they possessed more prominent sides (Fig. 1). The metallic, green or blue specks were identifiable in the replica as depressed areas with a few differently oriented polygons. These polygons appeared closer; that is, separated by narrower grooves. Openings to microtubules were present. The pore canals that were investigated by Richards and Anderson (1942) and Scheie et al. (1968) were much finer structures than these microtubules. Furthermore, according to these authors, the canals extend to but not into the epicuticle. Their diameter averages 0.15 μm and their number per epidermal cell averages about 200. The microtubules seem to be more similar to the dermal ducts (ducts of dermal glands) described by these authors.

Megacephala Latreille: *M. carolina* (Linnaeus) and *M. virginica* (Linnaeus). The polygons were shallow.

Carabidae

Crowson (1955) stated that some characteristics in Caraboidea are polyphyletic. Their development seemed to have taken place independently along several separate or parallel lines.

After analyzing the elytral ultrastructure of about 50 species in this family, the following became clear: 1) the radiating modifications of the stem pattern, and 2) the acquisition of somewhat similar patterns, which seemed to have occurred more than 1 time.

In this family, a pattern was often present, sometimes a polygonal one. However, the basic pattern was usually modified. A common series of modifications was represented by the development of zigzag parallel lines and then by the close or spaced parallel lines (that were less than 2 μm and 3 or more μm apart respectively—see the genera *Bembidion* and *Loxandrus*).

Calosoma Weber: *C. calidum* Fab., *C. alternans sayi* Dejean, and *C. scrutator* Fab. A nearly regular polygonal pattern was encountered with microtubules (Fig. 2). A regular pattern is one with polygons which are equilateral and equiangular. The polygons were sometimes convex with less sharp angles.

Calosoma scrutator and several other species of this genus possessed defensive scent glands in both sexes (McCullough and Weinheimer 1966). Wheeler et al. (1970) reported similar findings in 4 species of the allied genus, *Scaphinotus*.

Scarites Fabricius: *S. subterraneus* Fab. and *S. substriatus* Haldeman. The pattern was shallow, with the polygon angles oriented in an antero-posterior direction. McCullough (1969) reported the production of defensive scent fluid by 2 species of the allied genus, *Pasimachus*.

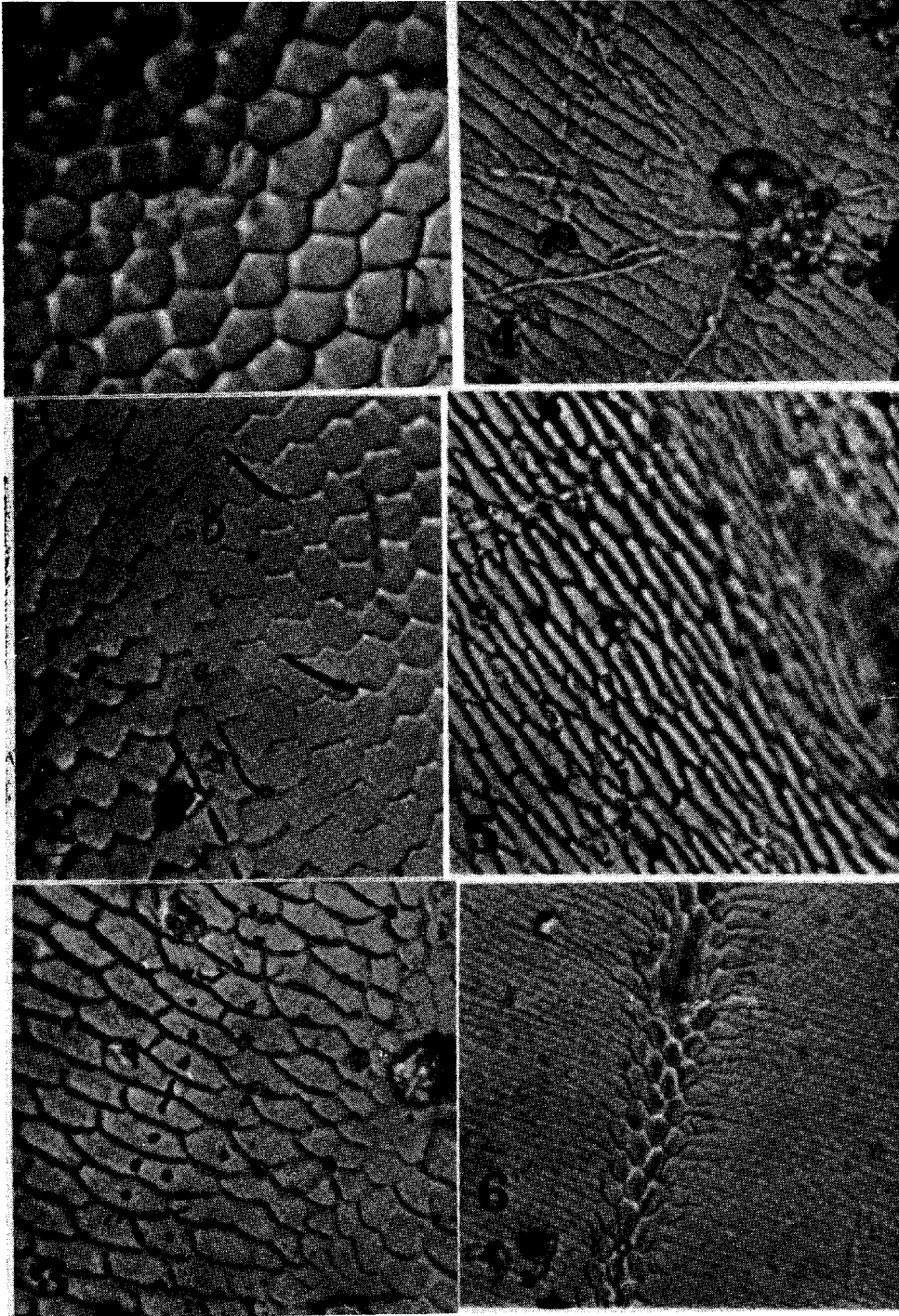


Fig. 1-6.—Light micrographs of replicas of elytra: 1, *Cicindela dorsalis* Say. 2, *Calosoma scrutator* Fab. 3, *Bembidion variegatum* Say. 4, *Bembidion fraternum* Leconte. 5, *Evarthrus americanus* (Dejean). 6, *Loxandrus* sp.

Bembidion Latreille: *B. americanum* Dejean, *B. fraternum* Leconte, and *B. variegatum* Say. In some species, there were microtubules and polygons which were less angular. In another species the pattern (here named pisciform) involved polygons that were widened, reflecting an overlapping appearance (Fig. 3). In another species this widening developed further, and the pattern superficially appeared as spaced parallel lines (Fig. 4). In the latter case, less modified polygons were still found in longitudinal lines, marked by rows of punctures.

Tachys Stephens: *T. proximus* (Say) and *T. scitulus* Leconte. They possessed a pattern of close parallel lines, ca. $1.5\mu\text{m}$ or less apart (see *Loxandrus*). In the tribe Bembidiini, the modifications of pattern seemed to have progressed further in *Tachys* than in *Bembidion*. The elytra of an additional species of *Tachys* seemed to lack a pattern, while the scutellum and pronotum had 1, indicating that they are more conservative than the elytra.

Morion Latreille: *M. monilicornis* Latreille had a polygonal pattern.

Evarthrus Leconte: *E. americanus* (Dejean). The pattern (Fig. 5) differed greatly from that of the rest of the Pterostichini. The polygons were elongate, narrow, and shaped like narrow rectangles or parallelograms. Microtubules were present.

Pterostichus Bonelli: *P. acutangulus* Chaudoir and *P. scrutator* Leconte. In the more primitive pattern, the polygons were present, but there was a tendency for the longitudinal lines to become faint, leaving zigzag parallel lines (see Fig. 11); further, the polygons appeared to extend laterally in parallel rows. In the other species of the genus, differentiation had gone further; and the pattern became close parallel lines, ca. $1\mu\text{m}$ apart, which were connected to the polygons in the striae. Scattered microtubules were present.

Loxandrus Leconte: *L. erraticus* (Dejean), *L. minor* Chaudoir, and *L. taeniatus* Leconte. They possessed a pattern of close parallel lines ca. $1\mu\text{m}$ apart (Fig. 6). This seems to be a case of descent from a common stem. The lines were interconnected in places and also connected to polygons in the striae, where rosettes of polygons surrounded micropunctures. These punctures appeared to represent glands. Scattered microtubules were present. Hinton and Gibbs (1969a) found transverse parallel ridges in many but not all species of this genus.

Agonum Bonelli: *A. decorum* Say and *A. punctiformum* Say. The polygonal pattern was present. However, in 1 species, there was a tendency for the longitudinal lines to become faint, leaving zigzag parallel lines. Scattered microtubules were present at some angles.

Amara Bonelli: *A. muscula* (Say). The polygons widened considerably; longitudinal lines became faint, giving rise to a pattern of widened parallelograms (Fig. 8). The polygonal pattern was present in the striae. Microtubules were also present. Compare with *Bembidion* (Fig. 4).

Harpalus Latreille: *H. pennsylvanicus* DeGeer. The polygons were keeled; one side appeared to be more projecting (Fig. 7). Microtubules and rosettes surrounding micropunctures were present.

Selenophorus Dejean: *S. pedicularius* Dejean, *S. subtinctus* Leconte, *S. stigmaticus* Germ., and *S. troglodytes* Dejean. Polygons were present in the striae. In the intervals, the patterns of the different species could be arranged in a series from 1 in which the polygons appear to run in parallel

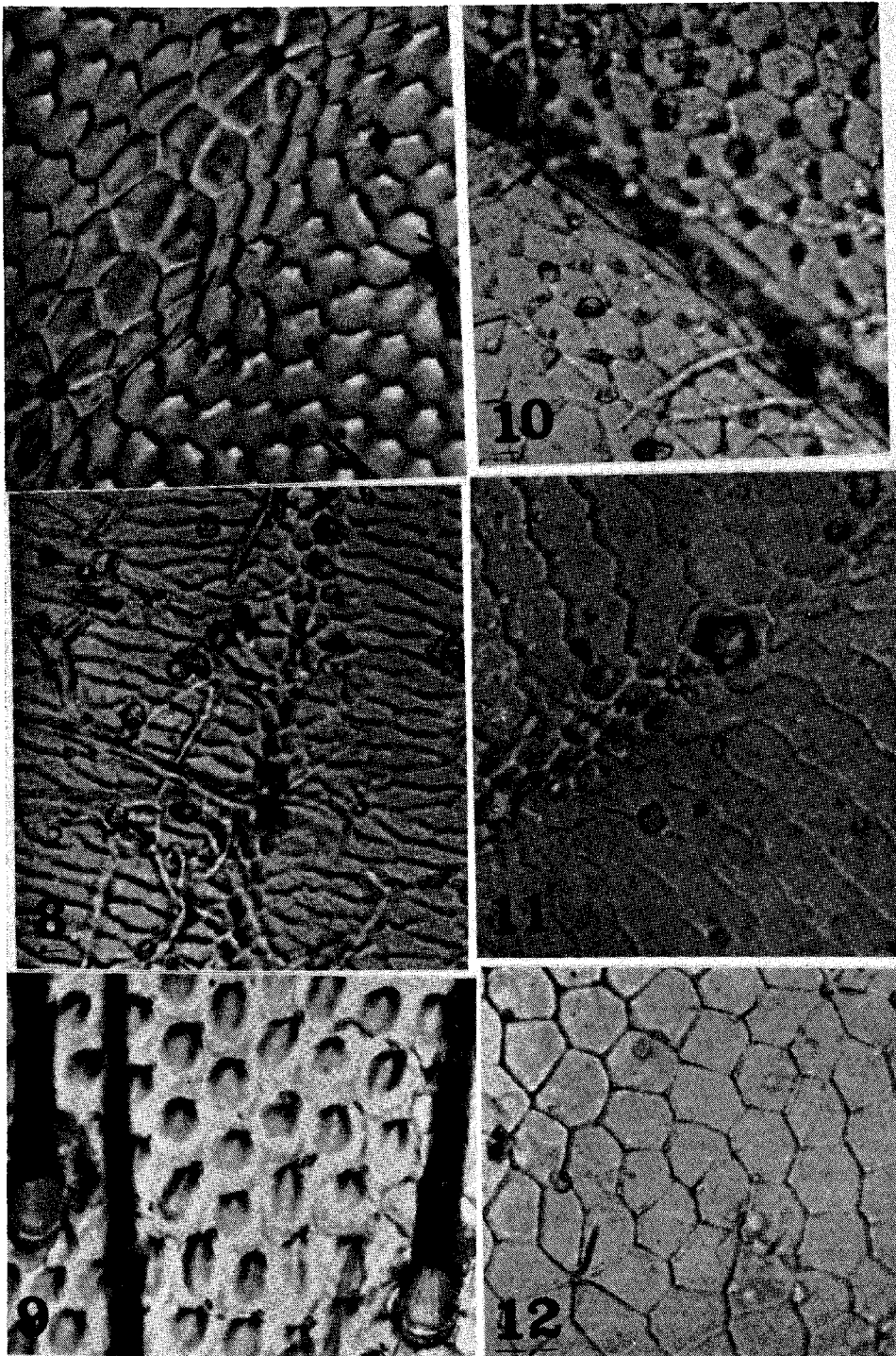


Fig. 7-12.—Light micrographs of replicas of elytra: 7, *Harpalus* sp. 8, *Selenophorus pedicularius* Dejean. 9, *Chlaenius* sp. 10, *Apenes sinuata* (Say). 11, *Pinacodera platicollis* (Say). 12, *Lebia marginicollis* Dejean.

rows (zigzag lines), to a pattern of widened parallelograms (Fig. 8), and finally to an evolved pattern of spaced, parallel lines, more than $1\mu\text{m}$ apart.

Stenolophus Dejean: *S. dissimilis* Dejean and *S. ochropezus* (Say). The diffraction gratings attained a climax in this genus. The gratings spacing was ca. $1\mu\text{m}$; polygons were still present in the striae. Hinton and Gibbs (1969a) found gratings spacing of about $1\mu\text{m}$ in the genus *Acupalpus*, which belongs also to Harpalini.

Badister Schellenberg: *B. ferrugineus* Dejean. The pattern of close parallel lines was present, with gratings spacing of $1\mu\text{m}$. Hinton (1970b) reported gratings spacing of $1.5\mu\text{m}$ in the elytra of *B. transversus* Casey.

McCullough (1967) reported the presence of a pair of defensive scent glands in 2 species of the allied genus, *Dicaelus*. One of the species had a metallic sheen as another defensive mechanism. Carabid beetles possess pygidial glands that they employ in escaping predators. It would be interesting to investigate the surfaces of their integuments and correlate the 2 defensive mechanisms with their nocturnal or diurnal lives.

Panagaeus Latreille: *P. cruciger* Say and *P. fasciatus* Say. A shallow polygonal pattern was present. In 1 of the species, the microtubules were prominent at the angles.

Chlaenius Bonelli: The polygons were keeled (Fig. 9).

Apenes Leconte: *A. sinuata* (Say). In the polygons, 1 angle was deeper (Fig. 10), very much like *Panagaeus*.

Calleida Latreille: *C. punctata* Leconte. The pattern, as in *Pinacodera* (Fig. 11) was formed of parallel rows of polygons, reflecting zigzag parallel lines. Rosettes were present in the striae.

Lebia Latreille: *L. marginicollis* Dejean, *L. ornata* Say, *L. scapularis* Dejean, *L. viridipennis* Dejean, and *L. viridis* Say. This genus had shallow irregular polygons. Rosettes and micropunctures were also present (Fig. 12).

Microlestes Schmidt: *M.* sp. The polygons widened and narrowed to about $4\mu\text{m}$ (Fig. 13), while in the scutellum they were still relatively unmodified. Hinton (1969) encountered even diffraction gratings in the same tribe in the genus *Eucaerus*.

Pseudaptinus Castelnau: *P. pygmaeus* Dejean. The polygons widened further, reflecting spaced parallel lines, $2-3\mu\text{m}$ apart, except at sutures where the lines were oriented longitudinally (Fig. 14).

ORIGIN AND FUNCTION OF DIFFRACTION GRATINGS

Hinton (1907b) stated that diffraction gratings have been independently evolved in more than 14 groups of beetles. He also reported that the number of grating lines, produced by each epidermal cell, varied between 2-12 in the different species. The present replicas, however, showed that the lines were boundaries between separate entities that have widened excessively. Hinton (1969, 1970b) reported that in Phalacridae alone many of the genera had elytra with diffraction gratings; but in each of these genera, there were some species without such structures. Purely on the basis of selective advantage, he concluded that the gratings have been independently evolved in each genus, rather than being present in the common ancestor of these genera and polyphyletically lost. In the present investigation, I have encountered a polygonal pattern in the elytron of a phalacrid, and the most

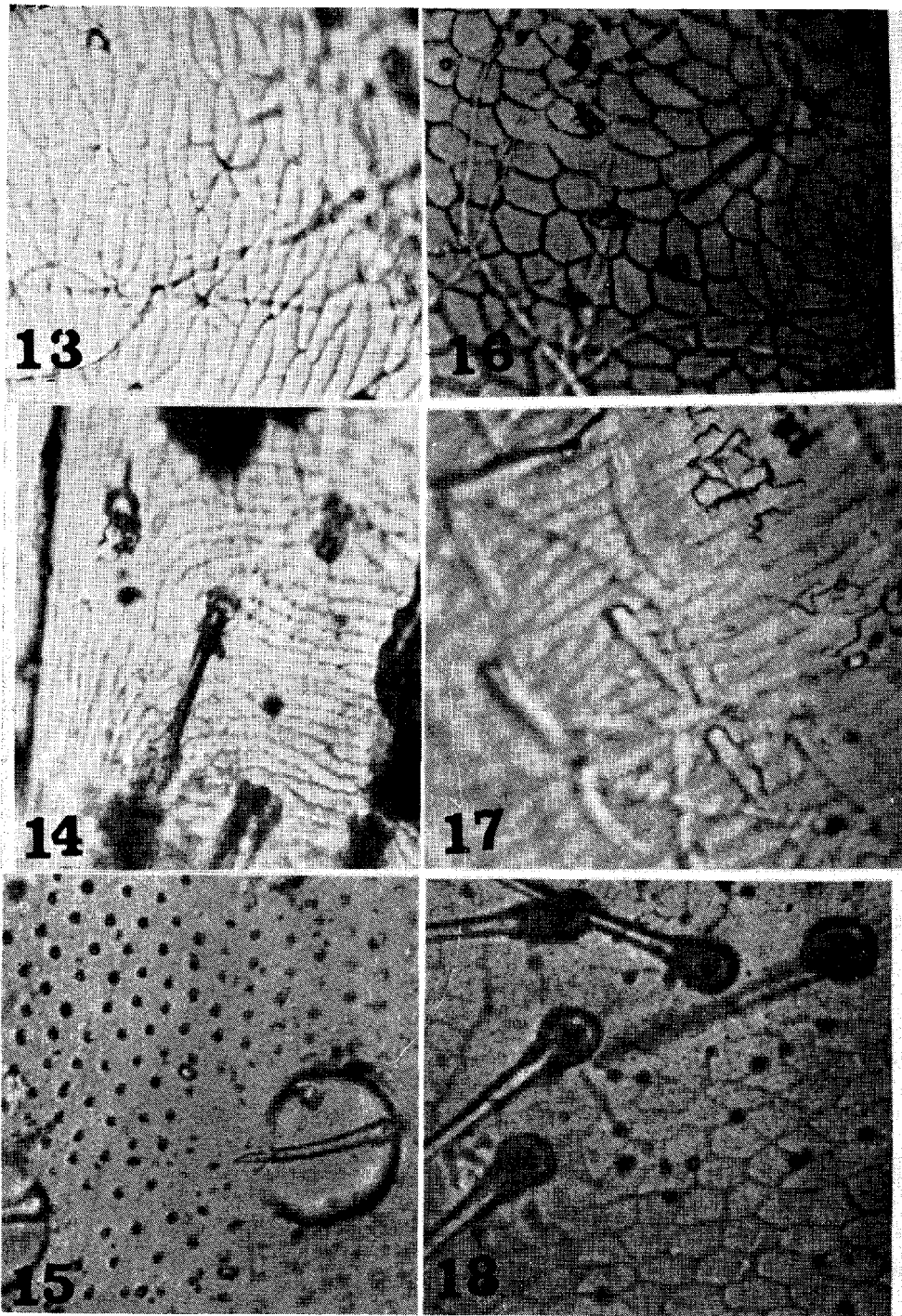


Fig. 13-18.—Light micrographs of replicas of elytra: 13, *Microlestes* sp. 14, *Pseudaptinus pygmaeus* Dejean. 15, *Haliplus connexus* Math. 16, *Celina grossula* Leconte. 17, *Bidessus affinis* (Say). 18, *Thermonectes basillaris* (Harris).

primitive phalacrid must have had elytra with the latter pattern (see discussion under Phalacridae).

As in Phalacridae, Hinton (1970b) advanced similar accounts for the presence of diffraction gratings in Carabidae and Scarabaeidae and described them as polyphyletic in origin. However, common ancestry seems also to have been a factor; the presence of similar patterns in some allied species must be the result of common descent.

Diffraction gratings normal to the long axis were found in numerous families of beetles. The gratings seem to have developed independently along several parallel lines; however, in the cases that I encountered, the primordial pattern seemed to have been a polygonal pattern. Intermediate forms had been shown. Moreover, some of the gratings in the species were still connected to polygons. In genera with gratings, the lack of sculpturing could have occurred polyphyletically. It can be due to the loss of the original, polygonal pattern (especially when the genus still contains forms possessing such a pattern) or the loss of gratings (especially when the polygonal pattern is not found in the genus).

Diffraction (reflection) gratings, with gratings spaced 1-2 μ m apart, were the cause of iridescent colors, which were thought to be warning colors. At the same time, according to Hinton (1969), as some light was specularly reflected, it would make it more difficult for a predator to estimate the distance away from and, therefore, the size of the insect.

Color which results from diffraction gratings is known as physical (or structural) color; pigments are not responsible. Sometimes, thin film interference is responsible for the structural color. In the latter case, as in some green scarabaeid beetles, the color results from multilayer interference. The color also changes with the direction of illumination.

Haliplidae

The species of this group are known to form a compact family which probably arose from Carabidae, independently of other aquatic beetles.

Haliplus Latreille: *H. cribrarius* Leconte, *H. punctatus* Aubé, *H. ruficollis* DeG., and *H. connexus* Math.

Peltodytes Regimbart: *P. duodecimpunctatus* (Say), *P. edentulus* (Leconte), and *P. muticus* (Leconte).

The surface patterns of the 7 species examined were quite similar but, they were extremely modified as compared to those of Carabidae. The polygonal pattern disappeared, leaving micropunctures that formed dense dotted patterns (Fig. 15).

Balfour-Browne (1940) studied this family and reported such a pattern as refractive spots from several species of *Haliplus* and *Brychius*. He considered the persistence of the "spots" as evidence that the family evolved from an ancestor that had a polygonal pattern.

Dytiscidae

Dytiscidae, according to Balfour-Browne (1940), is not a compact family. It showed great variations and evolved along several lines; it is perhaps polyphyletic. This diversity was not drastically evident from the microsculp-

ture of the elytra of the 15 species examined; the patterns exhibited a remarkable degree of uniformity.

Mydroporinae:

Hydrovatus Motschoulsky: *H. cuspidatus* (Kunze).

Hydroporus Clairville: *H. alpinus* (Payk.) and *H. sp.*

Celina Aubé: *C. grossula* Leconte.

Bidessus Sharp: *B. affinis* (Say).

Hydaticinae:

Hydaticus Leach: *H. bimarginatus* (Say.)

Acilius Leach: *A. fraternus* (Harris).

Thermonectus Dejean: *T. basillaris* (Harris).

Cybistrinae:

Cybister Curtis: *C. fimbriolatus* (Say).

Dytiscinae:

Dytiscus Linnaeus: *D. sp.*

Laccophilus Leach: *L. fasciatus* Aubé, *L. gentilis* Leconte, and *L. maculosus* (Germ.).

Colymbetinae:

Matus Aubé: *M. bicarinatus* (Say).

Coptotomus Say: *C. interrogatus* (Fab.).

The generalized pattern in this family was a shallow polygonal pattern with large polygons, and rosettes surrounding micropunctures. Such a pattern was present in all subfamilies that were studied and was present in *Hydrovatus* (where each rosette marked the location of a pit), *Hydaticus*, *Acilius*, *Thermonectus* (Fig. 18) (where groups of setae were found in rows), *Graphoderus* and the allied Eretini (Balfour-Browne 1940), *Cybister*, *Dytiscus* (Fig. 19) (where the micropunctures appeared to represent microtubules), *Matus*, and *Agabus* and *Copelatus* of related tribes (Balfour-Browne 1940).

In Hydroporinae, the polygons of the stem pattern tended to widen and to possess a round border (*Hydroporus*), or they were further modified to form a pisciform pattern (*Celina*, Fig. 16), or finally some showed a pattern of spaced parallel lines (*Bidessus*, Fig. 17). A pattern of transverse parallel lines was found also by Balfour-Browne (1940) in the subfamily Colymbetinae, in *Colymbetes fuscus* L.

Balfour-Browne (1940) described the surface pattern in many European species of *Hydroporus* and noted the variations from regular to widened polygons which became transverse. He found that the pattern, in the allied genus *Hygrotus*, might even disappear. He reported the loss of microsculpture also in *Acilius* (with the persistence of refractive spots). A similar condition occurred in the genus *Coptotomus* (Fig. 21) which lost all pattern except the micropunctures, giving a sparse, dotted pattern.

The pattern in *Laccophilus* (Fig. 20) was somewhat different from the generalized pattern in this family especially with regard to the micropunctures.

Noteridae

Colpius Leconte (Fig. 22): *C. inflatus* Leconte. Only the micropunctures remained from the pattern, somewhat as in the dytiscid genus *Coptotomus*.

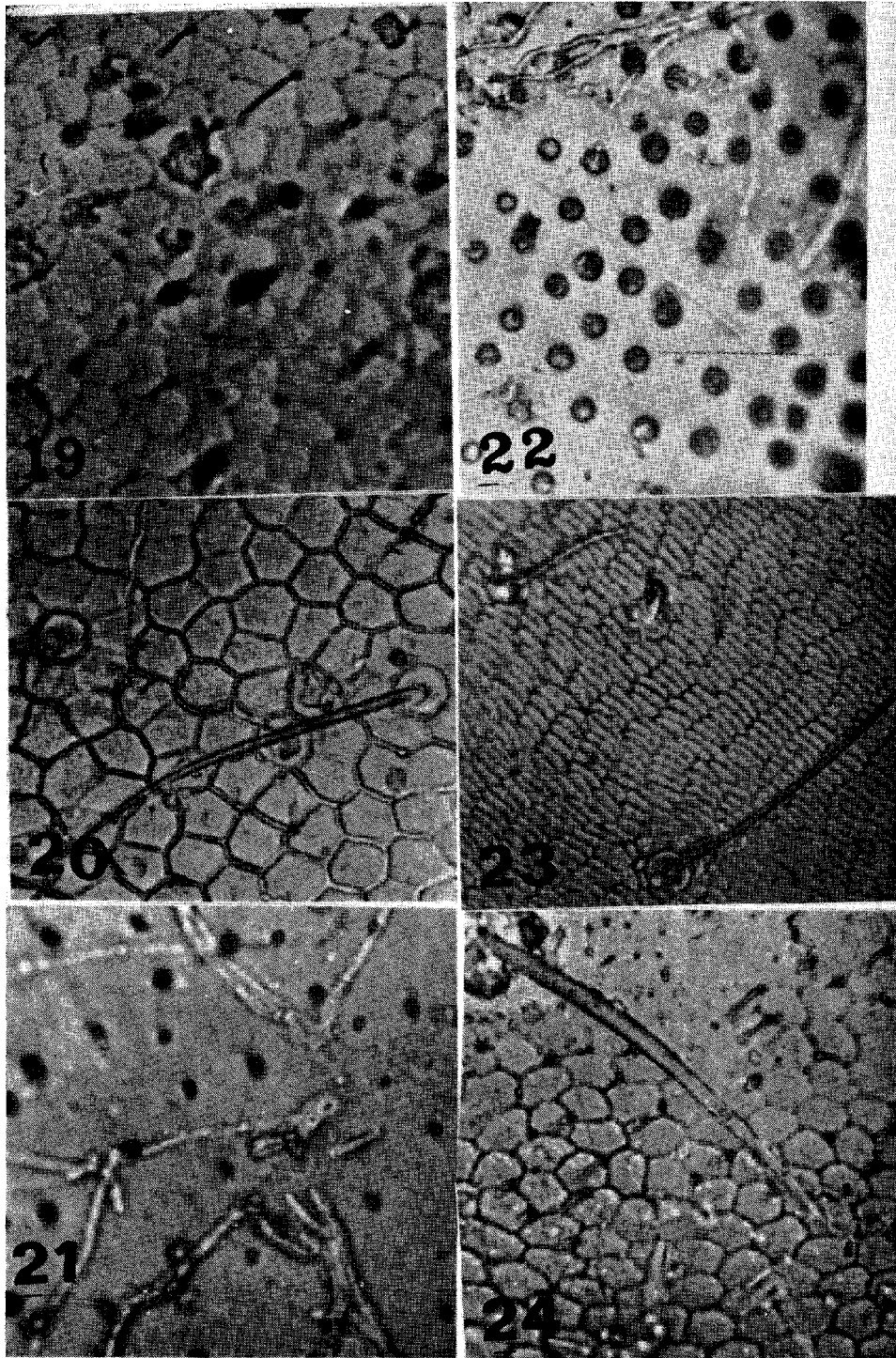


Fig. 19-24.—Light micrographs of replicas of elytra: 19, *Dytiscus* sp. 20, *Laccophilus fasciatus* Aubé. 21, *Coptotomus interrogatus* (Fab.). 22, *Colpius inflatus* Leconte. 23, *Hydrocanthus iricolor* (Say). 34, *Dineutus* sp.

Hydrocanthus Say (Fig. 23): *H. iricolor* Say. This species exhibited a pattern which was unique among beetles examined. It was composed of narrow rectangles, ca. 2 X 8 μ m. Rosettes and scattered micropunctures were present.

Gyrinidae

The family is allied to Dytiscidae as was evident from the pattern.

Dineutus Macleay (Fig. 24): *D. assimilis* Kirby, *D. carolinus* Leconte, *D. discolor* Aubé, *D. emarginatus* Say, *D. hornii* Roberts, and *D. vittatus* (Germ.). The polygonal pattern was very much like the generalized pattern of the Dytiscidae. The polygons were large, widened, and round, often giving the pisciform pattern. Microtubules were present.

Hinton and Gibbs (1971) encountered a polygonal pattern in *Gyretes*. These investigators also found grating lines, with grating spacing ca. 2 μ m, in this and 2 other genera that belong to the tribe Orectochilini; they considered the tribe as the most highly evolved in the family. They also stated that the gratings evolved independently in each genus.

Suborder Polyphaga

Hydrophiloidea

Hydrophilidae

Twenty-six species of this family were studied. Hydrophilinae seemed to be the most primitive subfamily.

Hydrophilus triangularis Say, *Hydrochara obtusata* (Say), *Dibolocelus ovatus* (Geminger and Harold) possessed, more or less, regular polygonal patterns with scattered micropunctures (Fig. 25).

Tropisternus Solier: *T. glaber* (Herbst), *T. l. nimbatus* (Say), *T. striolatus* (Leconte), *T. sublaevis* (Leconte). These and almost all species of the other 5 subfamilies studied had lost the polygonal pattern except for the micropunctures (Fig. 26). The surviving micropunctures gave a surface sculpture somewhat resembling that of some dytiscids and noterids. This particular similarity does not indicate phylogenetic relationship with the last 2 families since the archaic elytral pattern for all 3 families was a polygonal one. The appearance of a dotted pattern in these families, therefore, seemed to have developed independently in several parallel lines.

Hydrobiinae:

Helobata Bergroth: *H. larvalis* Horn. The micropunctures were densely represented (Fig. 28) where they seemed, as in *Enochrus* Thomson, to be leading to microtubules.

Cercyon Leach: *C. praetextatus* (Say) and *C.* sp. The micropunctures were slit-like and 5 μ m wide (Fig. 27).

Sphaeridiinae:

Dactylosternum Wollaston [*D. abdominale* (Fab.)] and *Megasternum Mulsant* (*M.* sp.): The scutellum possessed a pattern.

Berosinae:

Berosus Leach: *B. exiguus* (Say), *B. infuscatus* Leconte, and *B.* sp. They seemed to have scattered microtubules.

Staphylinoidea

Staphylinidae

Twenty-nine species of this family were examined. The stem pattern was polygonal.

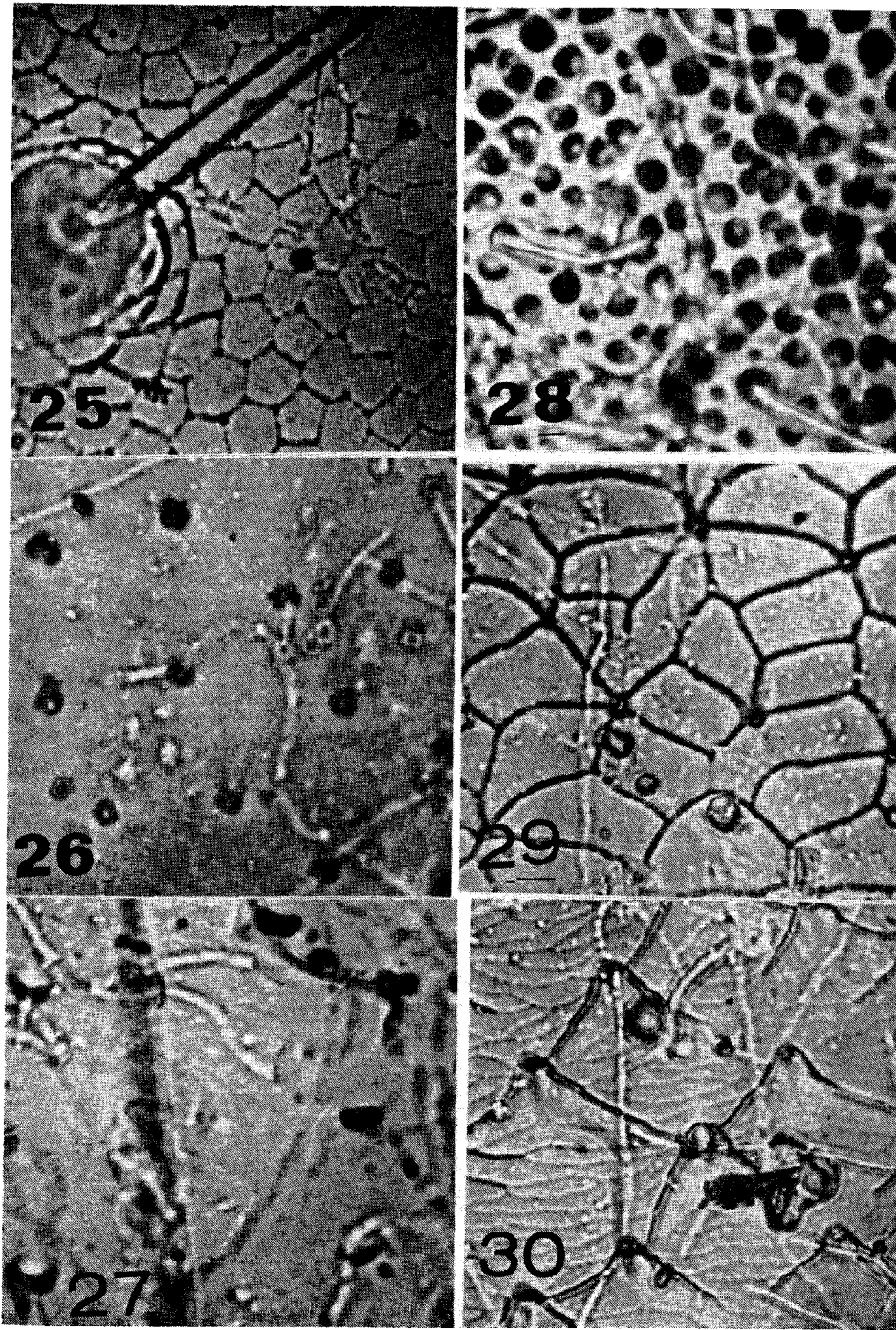


Fig. 25-30.—Light micrographs of replicas of elytra: 25, *Hydrochara obtusata* (Say). 26, *Dactylosternum abdominale* (Fab.). 27, *Cercyon* sp. 28, *Helobata larvalis* Horn. 29, *Tachinus* sp. A. 30, *Tachinus* sp. B.

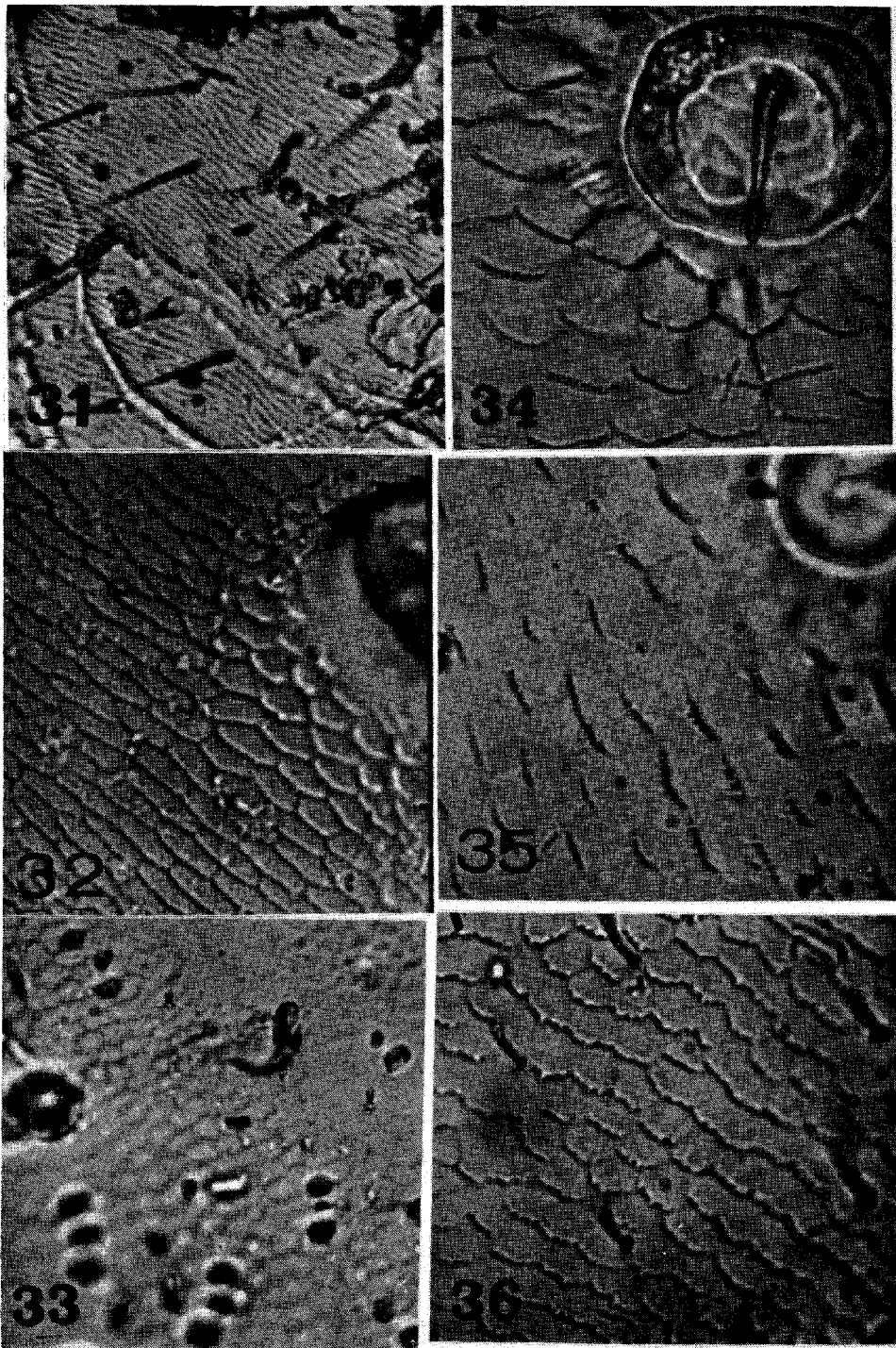


Fig. 31-36.—Light micrographs of replicas of elytra: 31, *Euaesthetus americanus* Er. 32, *Nicrophorus* sp. 33, Unidentified histerid sp. 34, *Phyllophaga congrua* (Lec.). 35, *Phyllophaga ephilida* (Say). 36, *Euphoria sepulchralis* (Fab.).

Thoracophorus Motschulsky: *T. costalis* Er. possessed a polygonal pattern. At the suture, the polygons were elongate.

Tachinus Gravenhorst: *T. basalis* Er. and *T. spp.* (Fig. 29, 30). The polygons were widened to various degrees, finally forming parallel lines.

Mycetoporus Mannerheim (*M. sp.*), and *Aleochara* Gravenhorst (*A. sp.*) had a pattern similar to *Euasthetus americanus* Er. (Fig. 31). A similar pattern was also reported by Hinton (1970b) from the elytra of a *Lordithon* which belongs to Tachyporinate. In the latter subfamily, which possessed various kinds of patterns, the genus *Coproporus* (*C. laevis* Leconte), like most other genera examined of this family, secondarily lost the sculpture.

Apocellus Erichson [*A. sphaericollis* (Say)], *Stenus* Latreille (*S. semicolon* Leconte and *S. sp.*): The pattern was still present in regions near the elytra, as on the scutellum. The subfamily Staphylininae and its allies, have already lost their patterns.

In the related family Scaphidiidae, no pattern was found on the elytra of *Toxidium* sp.

Pselaphidae

Like most members of the family Staphylinidae, there was no pattern on the elytra of the 4 species studied.

Decarthron Brendel: *D. exsectum* Bndl. This species possessed a pattern near the elytron.

No pattern was encountered also in a species of the related family Scydmaenidae.

Silphidae

Silpha L.: *S. americana* L., *S. inaequalis* Fab., *S. noveboracensis* Forster, and *S. surinamensis* Fab. They exhibited the more primitive polygonal pattern of elytra. In this genus, the pattern was modified later, and the polygons either became keeled or were widened and thus shaped as narrow trapezoids or rectangles with scattered microtubules (e.g. *Nicrophorus*, Fig. 32 with widened parallelograms). Hinton (1969) found that the elytra of several species of the latter genus were iridescent because of the presence of diffraction gratings. The grating spacing in 1 species was 3 μ m.

In the allied family, Leiodidae, a shallow polygonal pattern was found in *Leiodes globosa* (Leconte).

Histeroidea Histeridae

Only 1 unidentified histerid possessed a shallow polygonal pattern and curious triads of micropunctures (Fig. 33). Thirteen other species examined possessed no pattern; however, there were micropunctures in *Epiurus* and some species of *Hister*.

Scarabaeoidea

There was no pattern on the elytra of the lucanid, *Pseudolucanus capreolus* (L.), and the passalid, *Popilius disjunctus* Illiger.

Scarabaeidae

The primitive scarabaeid beetle undoubtedly possessed a polygonal pattern on the elytra, and the 4 subfamilies studied inherited such a pattern.

Melolonthinae:

Macroductylus Latreille: *M. subspinosus* (Fab.). This genus possessed polygons that were large and variable in shape.

Serica Macleay: *S. atricapilla* (Kirby). The pattern was that of the widened parallelogram type. Diffraction gratings were known in the latter genus (Anderson and Richards 1942) and some others in the same tribe (e.g., *Maladera* according to Hinton 1969). According to the latter author, iridescence due to diffraction was common in many genera of the tribes Sericini and Melolonthini.

Phyllophaga Harris: *P. congrua* (Leconte), *P. crassissima* (Blanchard), *P. crenulata* Froelich, *P. crinita* (Burm.), *P. profunda* (Blanchard), and *P. ephilida* (Say). There was a tendency for the polygons to widen and for the transverse lines to become faint or completely disappear (Fig. 34). Finally, the lines became discontinuous giving segmented parallel lines (Fig. 35), which were sometimes serrated. Microtubules were found in some of the species.

Rutelinae:

Pelidnota Macleay: *P. punctata* L. This possessed polygons that were arranged in parallel rows, reflecting zigzag parallel lines.

Anomala Samouelle [*A. flavipennis* Burmeister, *A. innuba* (Fab.), *A. nigropicta* Casey, and *A. sp.*] and *Popillia* Serville (*P. japonica* Newman): The pattern was that of the segmented, parallel lines with microtubules.

Dynastinae:

Dyscinetus Harold: *D. trachypygus* (Burm.). A polygonal pattern was present.

Cyclocephala Latreille: the polygons were arranged in parallel rows, reflecting zigzag parallel lines.

Bothynus Hope: *B. gibbosus* (DeGeer). The previous pattern gave way to one composed nearly of segmented, parallel lines. The pattern has disappeared in some genera as in some *Dynastes* and, according to Khalaf (1959), *Oryctes*.

Cetoniinae:

Euphoria Burmeister: *E. sepulchralis* (Fab.). The pattern was made of serrated parallel lines (Fig. 36). A related pattern was reported by Khalaf (1959) from the allied genus *Cetonia*.

Cotinis Burmeister: *C. nitida* (L.). The surface of polygons was uneven (Fig. 37). The dark center radiated towards the margin. It is possible that such patterns reduce specular reflection and reflect light diffusely, making the insect less conspicuous.

Trogidae

Trox: *T. aequalis* Say, *T. scabrosus* Beauvois, *T. terrestris* Say, and *T.*

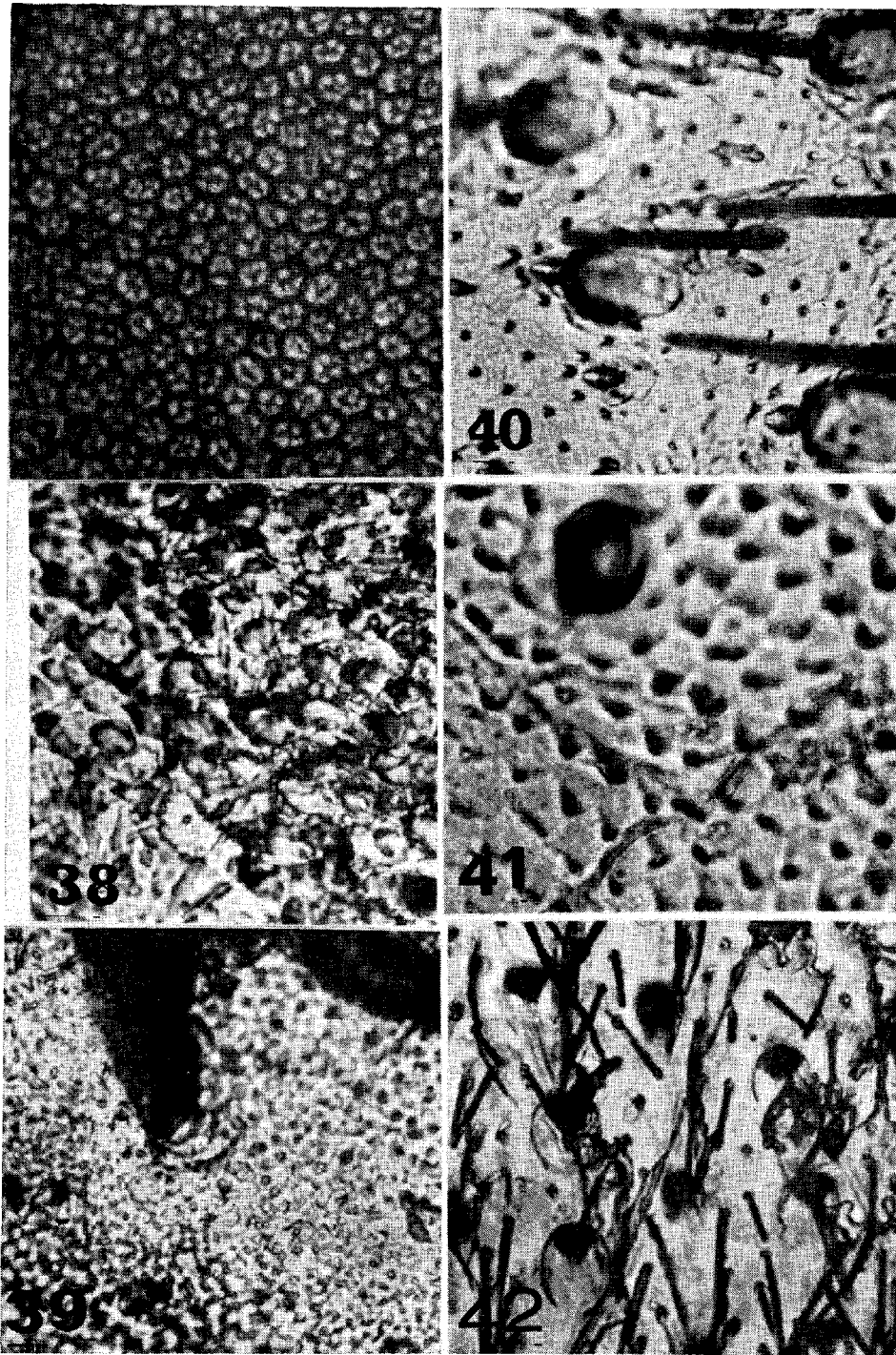


Fig. 37-42.—Light micrographs of replicas of elytra: 37, *Cotinis nitida* (L.). 38, *Trox scabrosus* Beauvois. 39, *Trox aequalis* Say. 40, *Helichus fastigiatus* (Say). 41, *Chrysobothris chrysoela* (Illiger). 42, *Trixagus* sp.

tuberculatus (DeGeer). The polygonal pattern of the 4 species studied was masked, and the surface appeared matte (Fig. 38, 39). Beyers and Hinks (1973) used the SEM to examine the surface of the integument of lepidopterous larvae, some of which possessed a cuticle surface which appeared matte. The matte effect was found to be caused by the presence of complexly shaped, closely spaced, and intertwined microtubercles, which masked the pattern. Small, closely spaced microtubercles serve to reduce specular (mirror like) reflection; thus, they reflected light diffusely, more or less equally in all directions. Such a matte surface seems to have an adaptive value, making the insect less conspicuous.

Dryopoidea

No pattern was seen in 6 species of Heteroceridae and Limnichidae.

Helichus Erickson: *H. fastigiatus* (Say). Only the micropunctures were left (Fig. 40).

Buprestoidea

Buprestidae

The polygonal pattern was shallow and with microtubules in Agrilinae. *Dicerca* Eschscholtz: *D. obscura* (Fab.). The pattern was semi-rhombic.

Buprestis L.: *B. rufipes* (Oliv.). The polygons were arranged in parallel rows, with the tendency for the cross lines to become faint, leaving zigzag parallel lines. Microtubules were present at angles.

Chrysobothris Eschscholtz: *C. chrysoela* (Illiger). Parallel angles of the polygons were deeper (Fig. 41).

Elateroidea

Elateridae

In 9 species examined, no pattern was encountered. Microtubules were present in *Alaus oculatus* (L.).

Throscidae

Trixagus Kugelann: *Trixagus* sp. There was no polygonal pattern (Fig. 42). Micropunctures were present, and the micrograph was somewhat similar to that of *Helichus* (Fig. 40).

No pattern was detected in the eucnemid, *Fornax* sp.

Cantharoidea

In many ways, this superfamily is the most primitive group among the living beetles (Arnett 1968). In Lampyridae, remains of a pattern were still present at the bases of setae (Fig. 43), while the pattern seemed to have completely disappeared in 4 species of Cantharidae and Lycidae.

Dermestoidea and Bostrychoidea

No pattern was observed in the general surface of 17 species, and only the micropunctures remained in *Nosodendron* (*N. unicolor* Say) (Fig. 44). Remains of a pattern were seen at the suture in *Sinoxylon* sp.

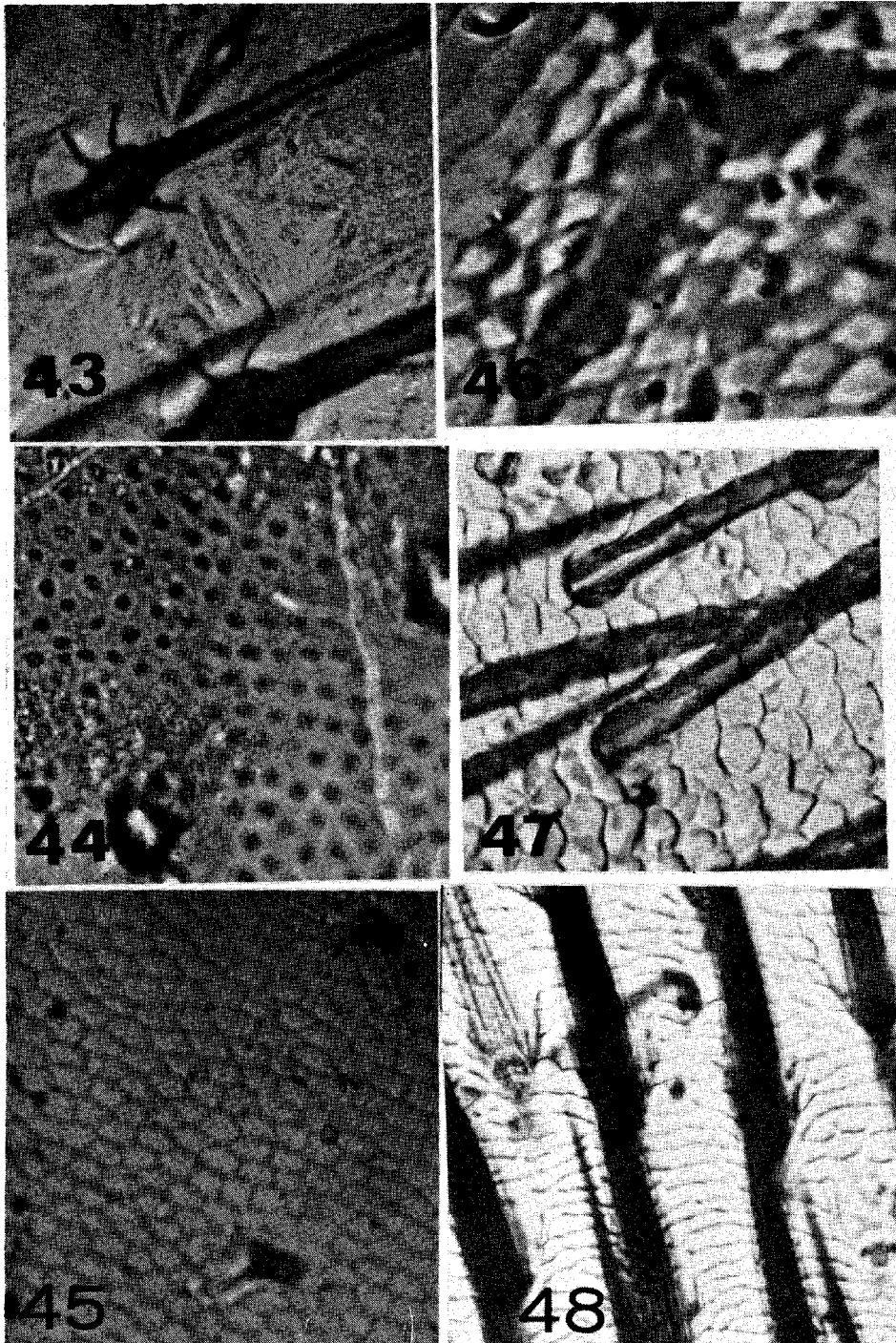


Fig. 43-48.—Light micrographs of replicas of elytra: 43, *Photuris pennsylvanica* (DeGeer). 44, *Nosodendron unicolor* Say. 45, *Tenebroides corticalis* (Melsheimer). 46, *Meloe angusticollis* Say. 47, *Epicauta cinerea* (Forst.). 48, *Hoshihananomia octopunctata* (Fab.).

Cleroidea

Tenebroides Piller and Mitterpacher: *T. castaneus* (Melsheimer), *T. corticalis* (Melsh.), *T. dubia* (Melsh.), *T. mauritanicus* (L.), and *T. nanus* (Melsh.). The pattern was shallow, and the polygons varied in shape (Fig. 45). They were trapezoids, semi-rhombic, or rectangles, oriented in line with the long axis of the elytron.

No pattern was found in *Temnochila* sp., *Airora* sp., and *Necrobia* sp. Microtubules were present in the first species.

Meloidea
Meloidea

Meloe Linnaeus: *M. angusticollis* Say and *M. impressus* Kby. The pattern was deep, and the polygons were large and variable in shape (Fig. 46). There were trapezoids and parallelograms but most of them appeared semi-rhombic, oriented parallel to the axis of the elytron. Microtubules were present, sometimes with large openings.

Epicauta Dejean: *E. cinerea* (Forst.) and *E. pennsylvanica* (DeGeer). The pattern was deep, and the polygons reflected an overlapping effect (Fig. 47).

Mordellidae

Hoshihananomia Kono: *H. octopunctata* (Fab.). The pattern was the type having spaced, parallel lines. (Fig. 48).

Sphalera Leconte: *S. melaena* (Germar) and *S. quadripunctata* (Say). The parallel lines were closer together (ca. 2 μ m apart).

On the basis of the study of wing venation (Khalaf 1970), *Hoshihananomia* was considered to be the most archaic in the family. The wing venation of *Sphalera* exhibited no appreciable difference from that of *Hoshihananomia*. The microsculpture of elytra also reflected the similarity between these 2 genera.

Mordellistena was considered to be the most highly evolved genus in the family. The microsculpture of elytra reflected that, too. The pattern has disappeared and only remains survived at the bases of the setae (Fig. 49). This situation can also be seen at the bases of setae in more primitive species (Fig. 48).

Tenebrionoidea
Tenebrionidae

Most of the examined species possessed a polygonal pattern.

Blapstinus Latreille (*B. pulverulentus* Mann.), *Platydema* Laporte and Brulle [*P. excavatum* (Say)], *Gnathocerus* Thymberg [*G. cornutus* (Fab.) and *G. maxillosus* (Fab.)], *Sitophagus* Mulsant (*S.* sp.), and *Coelocnemis* Mannerheim (*C. obesa* Leconte): These possessed the more generalized pattern in this family, which was widely represented, shallow, irregular and composed of polygons that were variable in shape (Fig. 51). In *Blapstinus* microtubules were present.

Alphitobius Stephens [*A. diaperinus* (Panz.) and *A. piceus* (Oliv.)], *Merinus* Leconte [*M. laevis* (Olivier)], and *Opatrinus* Latreille [*O. notus*

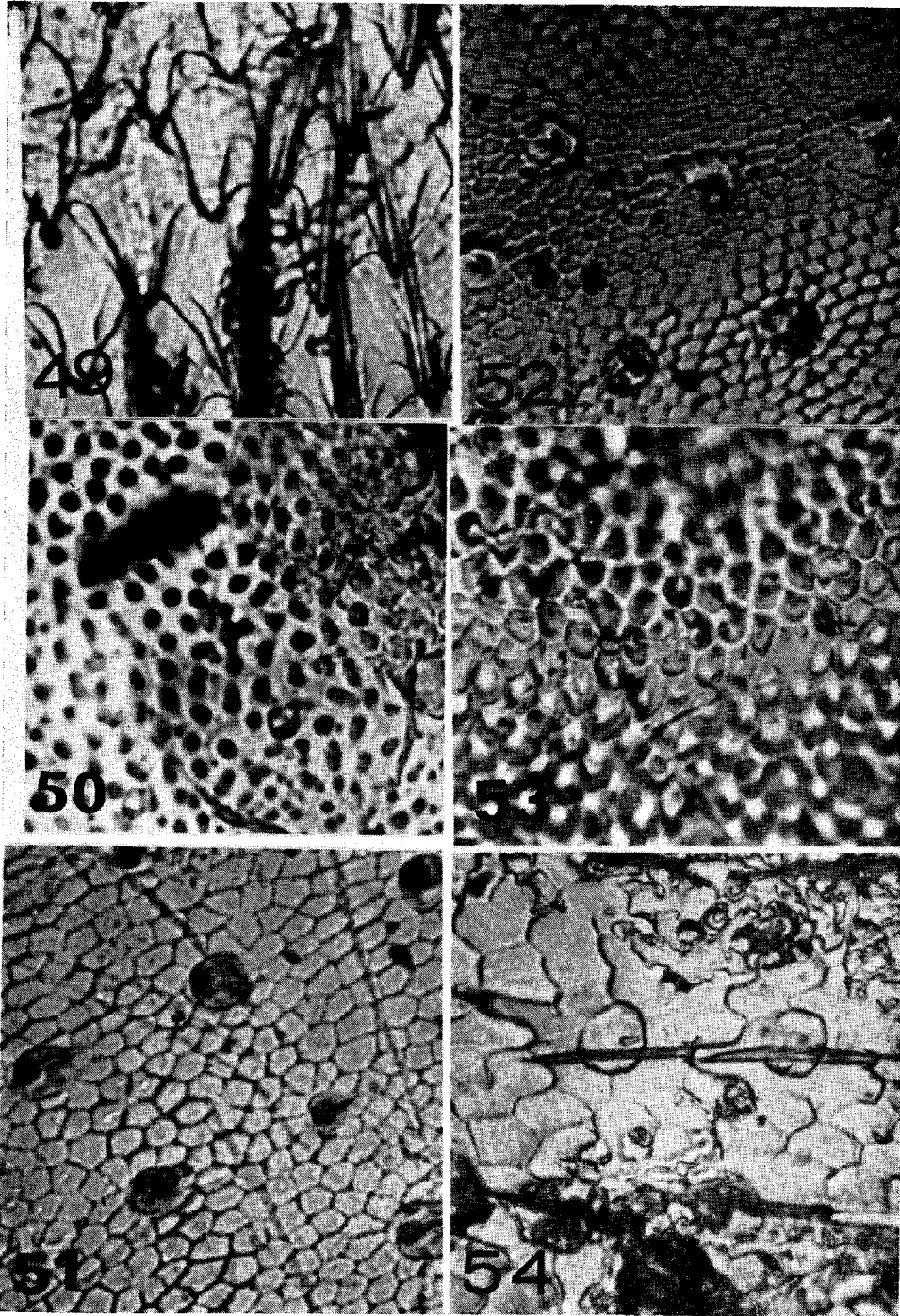


Fig. 49-54.—Light micrographs of replicas of elytra: 49, Unidentified mordellid species. 50, *Bolitotherus* sp. 51, *Gnathocerus maxillosus* (Fab.). 52, *Tribolium castaneum* (Herbst). 53, *Polypleurus perforatus* (Germ.). 54, *Conotelus obscurus* Erichson.

(Say)]: These taxa possessed another common pattern in this family, a regular polygonal pattern. In *Opatrinus* the surfaces of the polygons were concave.

More specialized microsculpture was found in a few other species.

Bolitotherus Candeze: *B.* sp. A tubercular pattern appeared in the replica (Fig. 50), where the polygons were represented as tubercles. In the elytron the surfaces, of course, would be concave.

Polypleurus Eschscholtz: *P. perforatus* (Germ.). The pattern was deep and the polygons were convex in the insect [concave in the replica (Fig. 53)]. Microtubules were present.

Tribolium Macleay: *T. castaneum* (Herbst) and *T. ferrugineum* (Fab.). The pattern was deep and composed of small polygons (Fig. 52).

Other tenebrionids, e.g. *Diaperis* sp., *Hoplocephala ferruginea* Leconte, and *Phaleria* sp., seemed to have secondarily lost the pattern.

Oedemeridae and Anthicidae

There was no special microsculpture in the 6 species studied.

Cucujoidea

Nitidulidae

Carpophilus Stephens: *C. antiquus* (Melsh.) and *C. hemipterus* (L.) showed the less modified pattern in this family. The pattern was made of large, somewhat elongate polygons.

Conotelus Erichson: *C. obscurus* Erich. The polygons reflected an overlapping effect like roof-shingles (Fig. 54). Here, a careful look at the bases of setae revealed special lines that were the boundaries between polygons. These were very similar to lines surviving at the bases of setae in elytra that have lost the rest of the pattern.

Epuraea Erichson: *E. labilis* Er. and *E. rufida* (Melsh.). In this genus the tendency for some of the lines to disappear has gone a step further and the pattern reflected parallel lines (Fig. 55).

Cryptarcha Shuckard: *C.* sp. The polygons appeared like bricks, arranged in parallel rows with some of the cross lines faint or absent (Fig. 56).

Cucujidae

Modification of the surface pattern seemed to have gone far in this family.

Catogenus Westwood: *C. rufus* (Fab.). The polygons were small, elongate, and variable in shape (Fig. 57). Some had the shape of rectangles, parallelograms, or even trapezoids. Furthermore, they were arranged in parallel longitudinal rows.

Laemophloeus Laporte: *L. biguttatus* Say, *L. modestus* Say, *L. punctatus* Leconte, and *L. testaceus* (Fab.). The pattern seemed to be essentially the same.

Silvanus Latreille: *S.* spp. Only remains of a pattern were left, in the form of rosettes at the bases of setae (Fig. 58). In addition, there were unique structures in the elytra of this genus represented as rows of smooth plates.

Telephanus sp.: All of the pattern was lost.

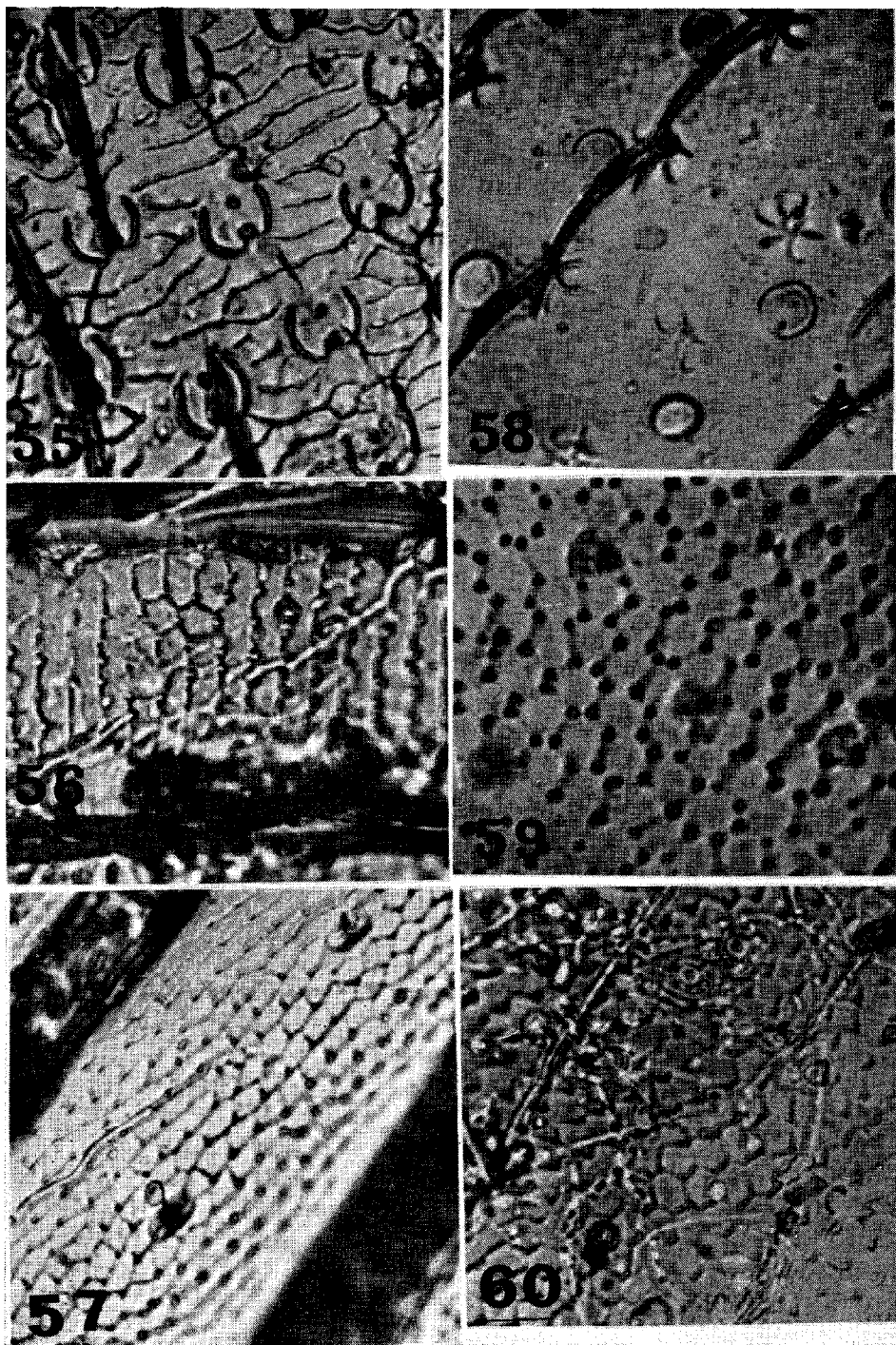


Fig. 55-60.—Light micrographs of replicas of elytra: 55, *Epuraea labilis* Er. 56, *Cryptarcha* sp. 57, *Catogenus rufus* (Fab.). 58, *Silvanus* sp. 59, *Hippodamia convergens* Guérin. 60, *Megalodacne fasciata* (Fab.).

Cryptophagidae, Languriidae, Endomychidae, Cisidae

The 6 species that were examined showed no pattern.

Languria Latreille: *L. angustata* (Beauvois) and *L. mozardi* Latreille. Microtubules and a pattern on the scutellum were present.

Coccinellidae

The primitive pattern in this family was polygonal.

Ceratomegilla Crotch: *C. maculata* DeG. had such a pattern with microtubules.

Hippodamia Dejean: *H. convergens* Guerin and *H. sp.* The pattern (dotted polygonal) was very shallow and was seen mainly by the microtubules at the angles (Fig. 59).

Coccinella Linnaeus: *C. trifasciata* L. and *Cycloneda* Crotch: *C. sanguinea* (L.). The dense microtubules were all that remained of the pattern.

In 5 other genera examined, there was no pattern. Scattered microtubules were present in *Scymnus* (*S. cinctus* Leconte and *S. spp.*), *Chilocorus* (*C. bivulnerus* Muls.), and *Epilachna* [*E. borealis* (Fab.)].

The pattern of the openings of microtubules on the elytra of *Hippodamia* (Fig. 59) resembled those published by Hinton (1970a) for the aeropyles which extended through the shell of certain moth eggs. The aeropyles were believed to mediate the transfer of gases between the egg and the atmosphere. However, the microtubules of beetle elytra seem to be vestigial structures; they probably act to reduce the weight of elytra.

Erotylidae

Ischyrus Lacordaire: *I. quadripunctatus* (Oliv.). The pattern was shallow.

Megalodacne Crotch: *M. fasciata* (Fab.). Parallel sides of the polygons were more projecting giving a pattern (Fig. 60) remarkably similar to that of *Chrysobothris* (Fig. 41).

Phalacridae

The pattern in the single species examined was shallow and composed of large, mostly square polygons. The elytra of at least some species of many genera in this family possessed diffraction gratings (Hinton 1969, Hinton and Gibbs (1969b)). However, the most primitive pattern is the polygonal one. Otherwise, its appearance in this family would represent reversion. The Dollo (or Meyrick) principle of irreversibility indicates that when a condition involves the loss of a complex or phylogenetically old characteristic, it is not usually reversible and not likely to be regained in the same form.

Lathridiidae

Lathridius Herbst: *L. sp.* The pattern was made of large polygons of various shapes (Fig. 61).

Colydiidae

Colydiini:

Colydium: *C. lineola* Say and *Aulonium sp.* The pattern was made of poly-

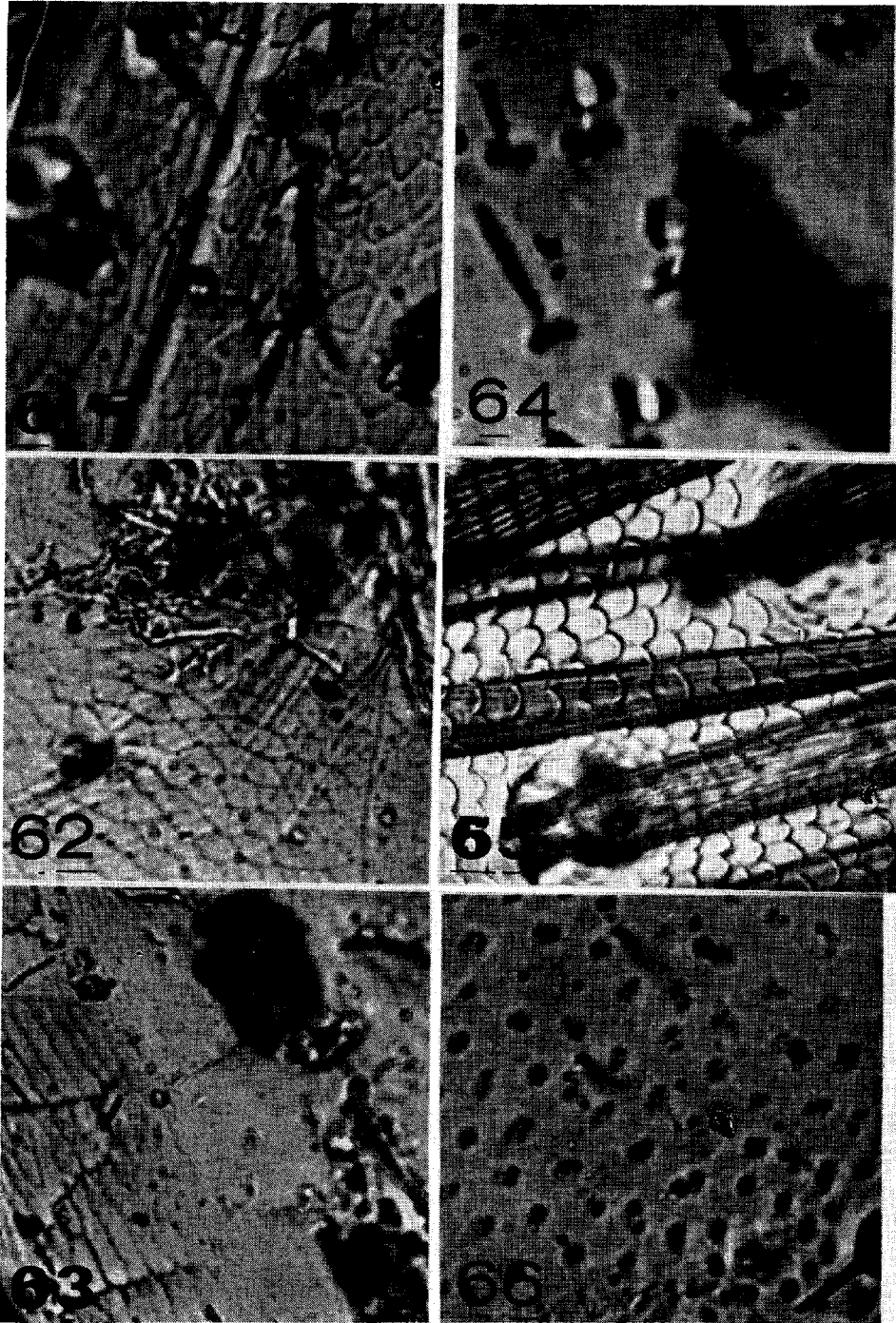


Fig. 61-66.—Light micrographs of replicas of elytra: 61, *Lathridius* sp. 62, *Aulonium* sp. 63, *Colydium lineola* Say. 64, *Typhaea fumata* L. 65, *Leptura emarginata* Fab. 66, *Stenodontes dasytomus* (Say).

gons that were mainly trapezoids or parallelograms (Fig. 62, 63), and the pattern appeared very much like that of *Tenebroides* (Fig. 45).

Pycnomerus Erichson: *P.* sp. The polygons were less modified.

Synchita Hellwig: *S.* sp. lost its pattern.

Mycetophagidae

No polygonal pattern was encountered in the 2 species examined.

Typhaea Curtis: *T. fumata* L. Possessed smooth plates near the bases of certain setae (Fig. 64). The Cucujidae is the only other family in which this peculiar feature was found.

Chrysomeloidea

Cerambycidae

Lepturinae:

Leptura: *L. emarginata* Fab.: The pattern was polygonal. The polygons, in some, had a round border and exhibited an overlapping effect (Fig. 65), giving a pisciform pattern. In *Desmocerus* Serville: *D. palliatus* (Forster). The pattern was shallow and was made of rather uniform polygons.

Prioninae:

Prionus Fabricius: *P. laticollis* (Drury) and *Stenodontes*: *S. dasytomus* (Say). A pattern of angular, rather uniform polygons was present in *Prionus*, together with microtubules. In other species, the polygons disappeared leaving a pattern of peculiar punctures, some of which seem to represent microtubules (Fig. 66). The microtubules of *Prionus* seem to be of the same nature.

Cerambycinae:

Purpuricenus Dejean: *P. humeralis* (Fab.). The polygons were indented (Fig. 67). *Eburia* sp. and *Elaphidion* sp. lost their patterns.

Lamiinae:

Tetraopes: *T.* sp.: No pattern was seen. Microtubules were present.

Chrysomelidae

Apparently, each of the studied subfamilies inherited the polygons.

Chrysomelinae:

Leptinotarsa Stal: *L. decimlineata* (Say).

Calligrapha Chevrolat: *C.* sp.

Gastrophysa Chevrolat: *G. cyanea* Melsheimer.

Plagiodera Redtenbacher: *P.* sp.

Chrysomela Linnaeus: *C. scripta* Fab.

The more primitive pattern of the elytra of this subfamily was found in the Doryphorini. It was a regular polygonal pattern with scattered microtubules. An example of such a pattern is that of *Leptinotarsa* which was described by Khalaf (1959). However, there was a tendency for some of the lines to disappear, and the pattern appeared open and fragmented (Fig. 68).

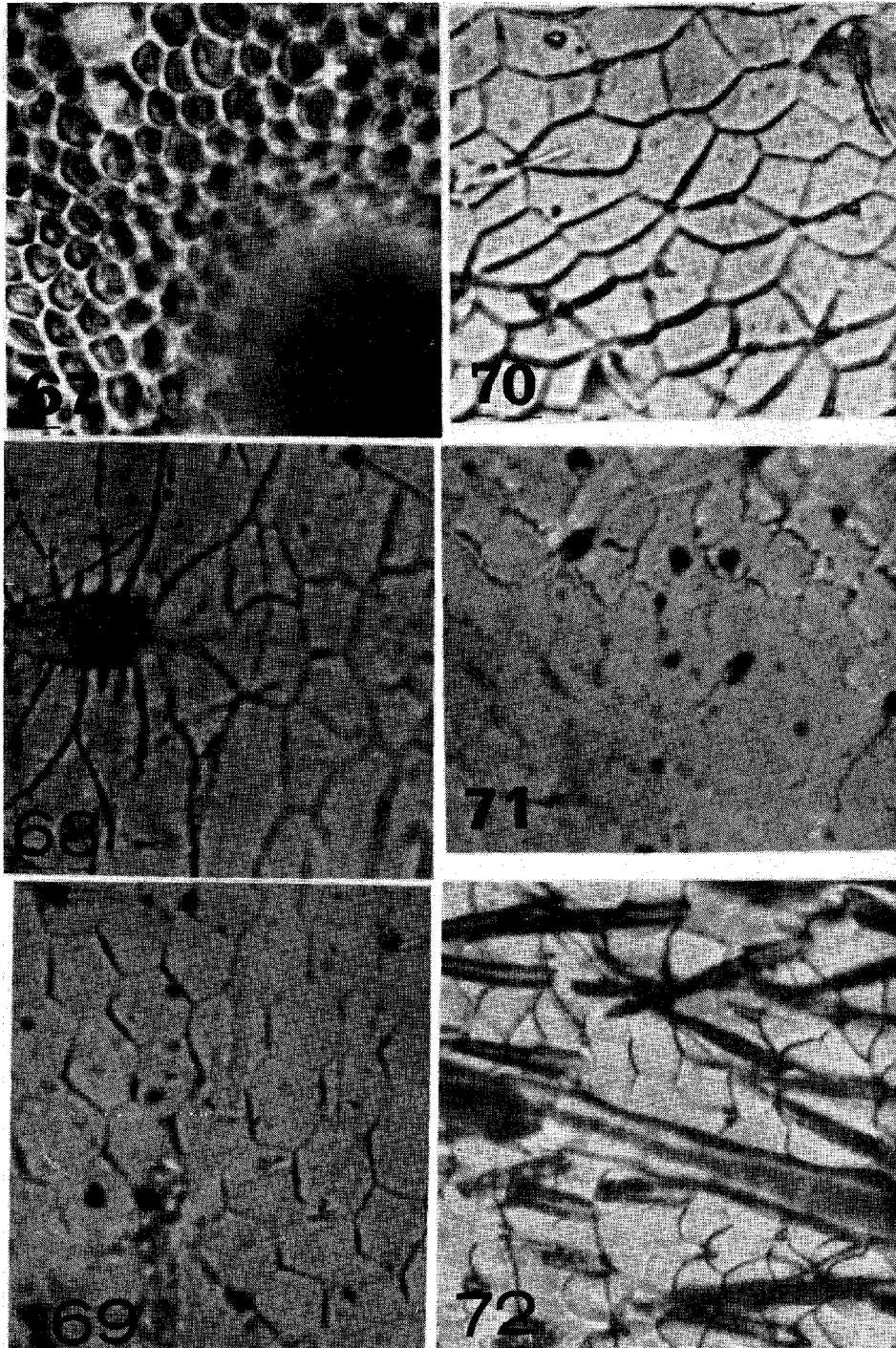


Fig. 67-72.—Light micrographs of replicas of elytra: 67, *Purpuricenus humeralis* (Fab.). 68, *Plagiodesa* sp. 69, *Diabrotica duodecimpunctata* (Fab.). 70, *Cerotoma trifurcata* (Forster). 71, *Longitarsus* sp. 72, *Bruchus hibisci* Oliv.

Finally, the lines completely disappeared leaving behind only the microtubules. On the other hand, in an unidentified member of this subfamily, there were pits at all angles of the polygons (dotted polygonal pattern) very much like *Hippodamia* (Fig. 59).

Criocerinae:

Crioceris Fabricius: *C. asparagi* (L.).

Lema Fabricius: *L. sexpunctata* Olivier, *L. solani* Fab., and *L. trilineata* (Olivier). This subfamily lost the microsculpture, and only scattered microtubules were left behind.

Cryptocephalinae:

Pachybrachis Chevrolat: *P. luridus* (Fab.) had a deep pattern of convex polygons that reflected an overlapping appearance.

Cryptocephalus Fab.: *C. leucomelas* Suffrian and *C. sp.* The pattern had disappeared, and only the microtubules were left behind.

Eumolpinae:

Nodonota Lafevre: *N. sp.*

Fidia Baly: *F. longipes* (Melsheimer).

Myochrous Erichson: *M. denticollis* (Say) and *M. sp.*

Paria Leconte: *P. quadriguttata* Leconte, *P. quadrinotata* (Say), and *P. sexnotata* (Say).

Primitively, as in *Nodonota*, this subfamily possessed a regular polygonal pattern which was later secondarily lost. *Paria* still had microtubules and a pattern on the scutellum and pronotum.

Galerucinae:

Diabrotica Chevrolat: *D. duodecimpunctata* (Fab.). The polygons had deeper parallel sides. These gave a pattern of zigzag parallel lines (Fig. 69) with scattered microtubules.

Cerotoma Chevrolat: *C. trifurcata* (Forster). The polygons were widened to 15 μ m or more and became very variable in shape and orientation (Fig. 70). Rosettes were present.

Alticinae:

Blepharida Chevrolat: *B. rhois* Forster and *Altica* Fourcroy: *A. chalybea* Illiger and *A. sp.* Both taxa possessed regular polygonal patterns.

Longitarsus Latreille: *L. sp.* The polygons became large and tended to resemble parallelograms (Fig. 71).

Phyllotreta Foudras: *P. vittata* (Fab.) and *P. sp.* Both species had lost their patterns. Microtubules were present.

Psylliodes Latreille: *P. sp.* This genus, as well as *Phyllotreta*, still had a pattern on the scutellum.

Cassidinae:

Hilarocassis Spaeth: *H. sp.* and *Cassida* Linnaeus: *C. sp.* The dotted polygonal pattern was marked by micropunctures (see Fig. 59), some of which at least represented microtubules.

Metriona Weise: *M. bicolor* (Fab.). This species had lost its pattern; however, microtubules were still present.

Bruchidae

Bruchus Linnaeus: *B. hibisci* Olivier, *B. rufimanus* Boh., *B. obsoletus* Say, and *B. sp.* In a few groups of beetles, a pattern was found which consisted of a few lines at the bases of setae. In this genus, various stages were represented which showed the possible origin of such a highly reduced pattern. Irregular polygonal pattern and the intermediate stage of reduction (Fig. 72) were present as well as the extreme condition where the pattern became highly reduced and represented by a few lines that survived at the bases of setae (Fig. 73).

Callosobruchus Pic: *C. maculatus* (Fab.). The pattern was like the last extreme state.

Spermophagus Schoenherr: *S. robiniae* Fab. This species possessed a pattern which was basically the irregular polygonal type (Fig. 74) with characteristic lines at the base of setae.

Curculionoidea Anthribidae

There was no polygonal pattern in the 5 species studied. The scales were densely represented; each was placed in a fossa that had a microtubule.

Brentidae

The polygonal pattern was present only in the striae (Fig. 75), and the intervals were without a pattern. Microtubules were present.

Curculionidae

The ancestral curculionid undoubtedly possessed a polygonal pattern. The most primitive pattern in the surviving forms seemed to be composed of polygons which appeared more like parallelograms (Fig. 79, 81). This pattern appeared similar to that of the scales of some reptiles (herpetiform).

Cylas Latreille: *C. formicarius elegantulus* (Summers). The polygons were highly elongate forming long parallelograms or trapezoids.

Hyllobius Germar: *H. confusus* Kirby and *H. sp.* A herpetiform pattern was present in grooves and at the bases of narrow scales. Microtubules were also present.

Anthonomus Germar: *A. eugenii* Cano, *A. grandis* Boheman (Fig. 78), and *A. musculus* Say. A pattern was present on the scutellum and pronotum.

Rhyssomatus Schoenherr: *R. lineaticollis* Say and *R. palmacollis* Say. The pattern was deep; and the polygons varied in size and shape and were often elongate (Fig. 80). Microtubules were present.

Tyloderma Say: *T. aerea* Say, *T. morbillosa* (Leconte), and *T. variegata* (Horn). There were micropunctures at angles (Fig. 81).

Sphenophorus Schoenherr: *S. melanocephalus* (Fab.), *S. cariosus* (Oliv.), *S. ochreus* Lec., *S. pertinax* (Oliv.), and *S. sayi* Gyllenhal. (Fig. 82-85). The polygonal pattern was present but was partly or completely masked and the

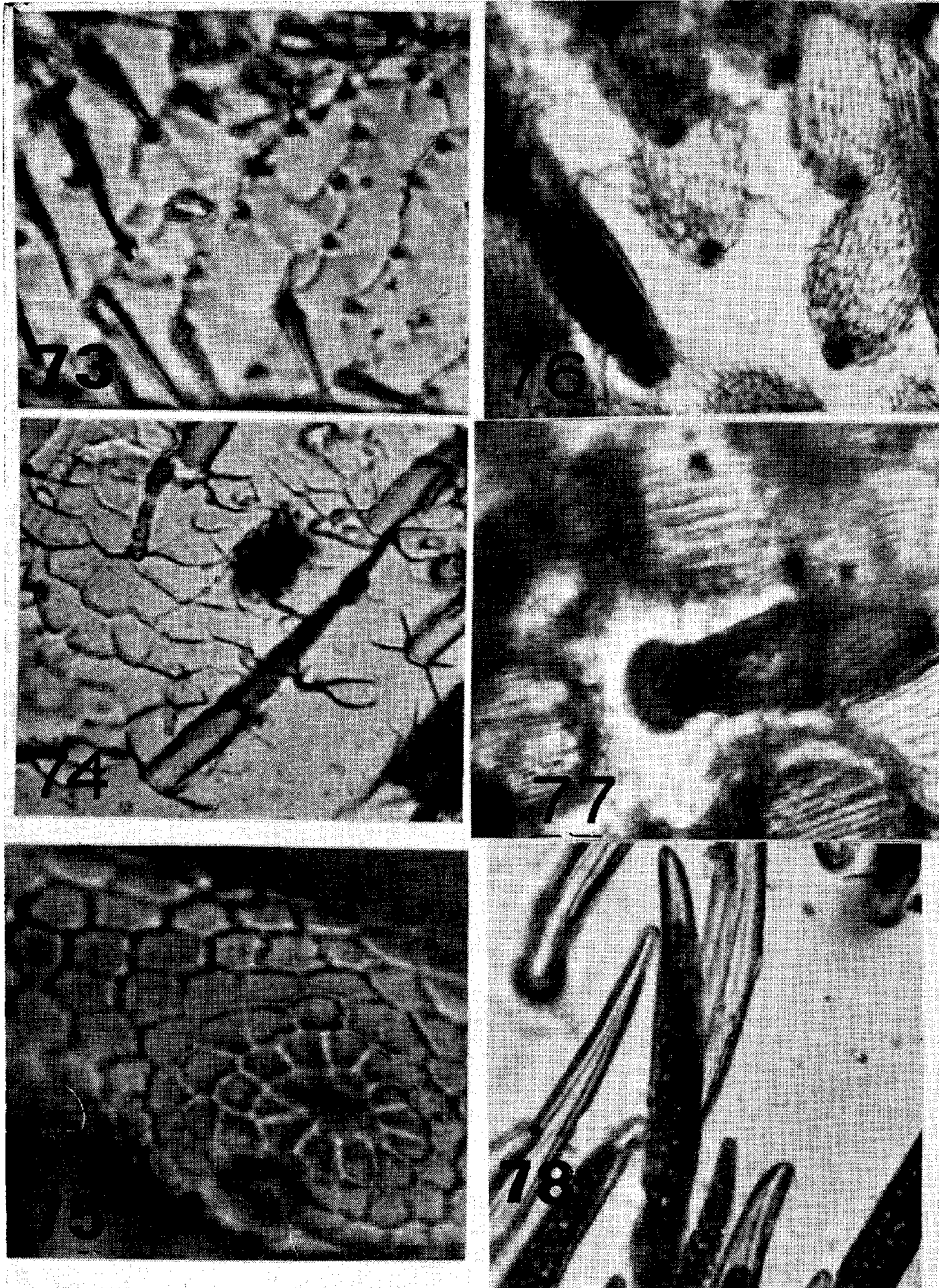


Fig. 73-78.—Light micrographs of replicas of elytra: 73, *Bruchus* sp. 74, *Spermophagus robiniae* Fab. 75, Unidentified brentid sp. 76, *Tanymecus* sp. 77, *Listronotus appendiculatus* (Boh.). 78, *Anthonomus grandis* Boheman.

surface appeared matte. This seems to be an adaptation that serves to reduce specular reflection and renders the beetle less conspicuous.

Sitophilus Schoenherr: *S. remotepunctata* Gyll., and *S.* sp. The pattern was herpetiform in which the polygons were moderately elongate and ap-

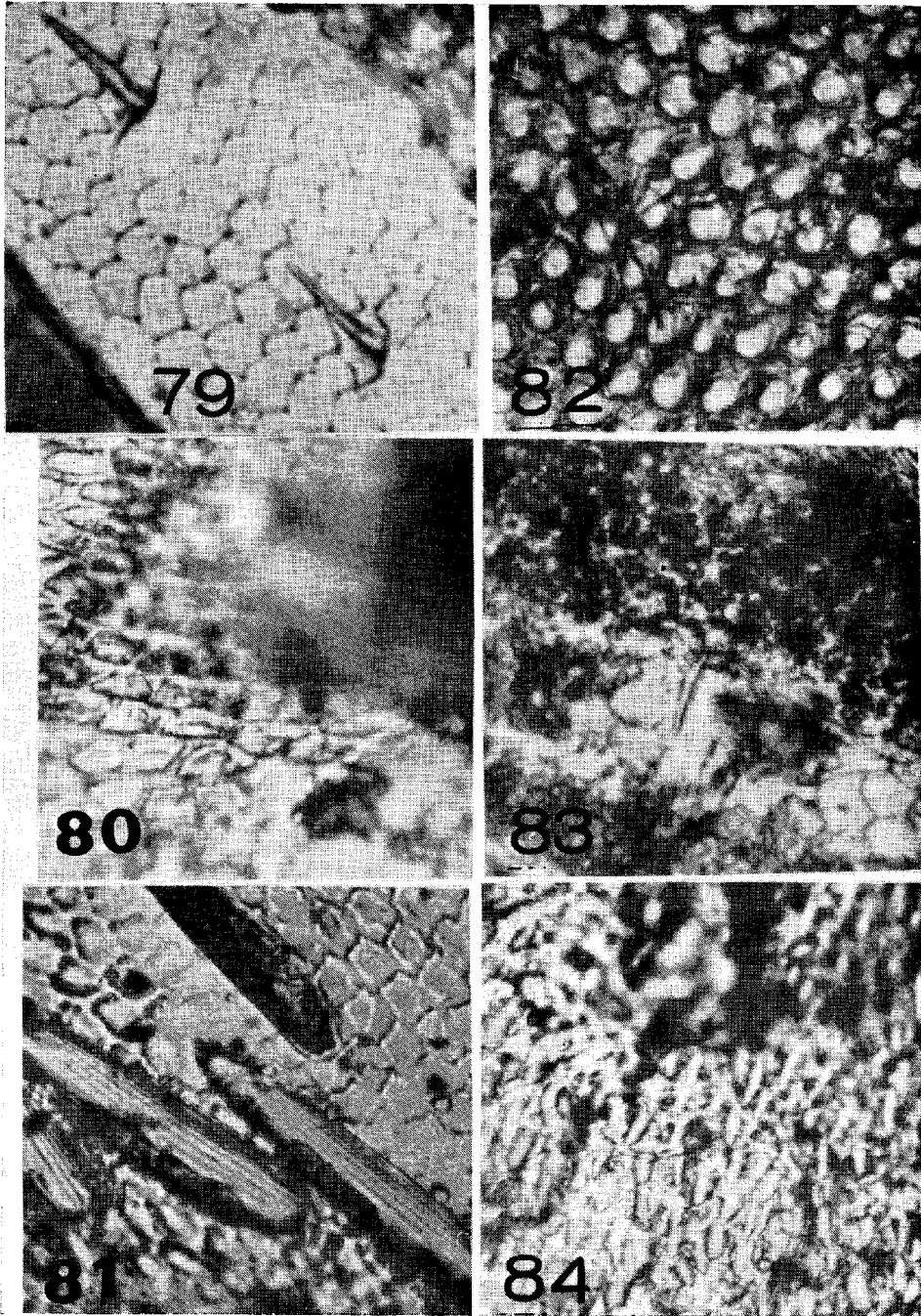


Fig. 79-84.—Light micrographs of replicas of elytra: 79, *Baris* sp. 80, *Rhyssomatus lineaticollis* (Say). 81, *Tyloderma morbillosa* (Lec.). 82, *Sphenophorus ochreus* Lec. 83, *Sphenophorus cariosus* (Oliv.). 84, *Sphenophorus melanocephalus* (Fab.).

peared rectangular (Fig. 86). However, these were less modified on the scutellum.

Several genera in Apioninae, Otorhynchinae, and Curculioninae have lost all microsculpture.

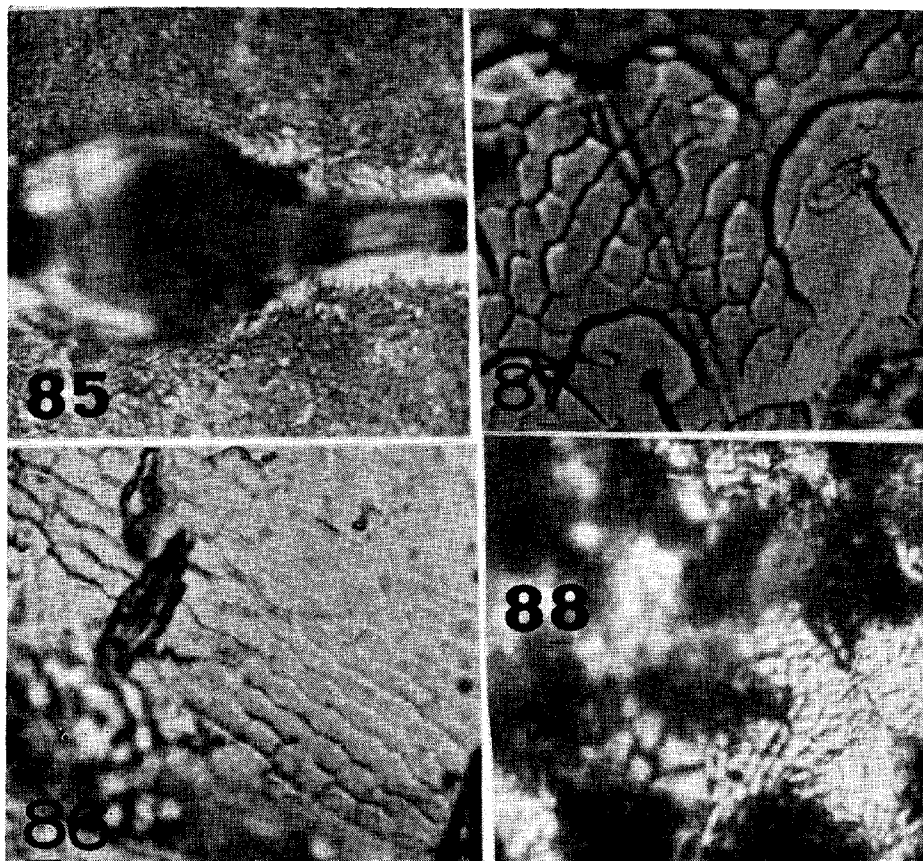


Fig. 85-88.—Light micrographs of replicas of elytra: 85, *Sphenophorus* sp. 86, *Sitophilus remotepunctata* Gyll. 87, *Platypus compositus* Say. 88, *Micracis* sp.

Platypodidae

Platypus Herbst: *P. quadridentatus* (Oliv.) and *P. compositus* Say. The polygons tended to run in parallel rows (Fig. 87). Microtubules were present.

Scolytidae

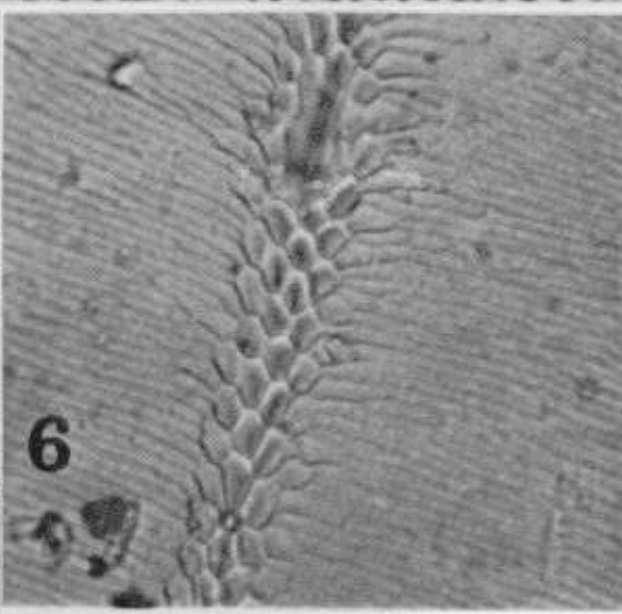
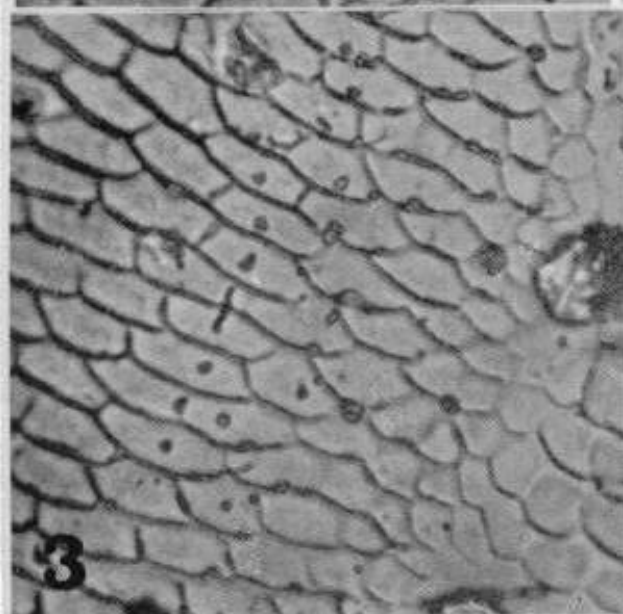
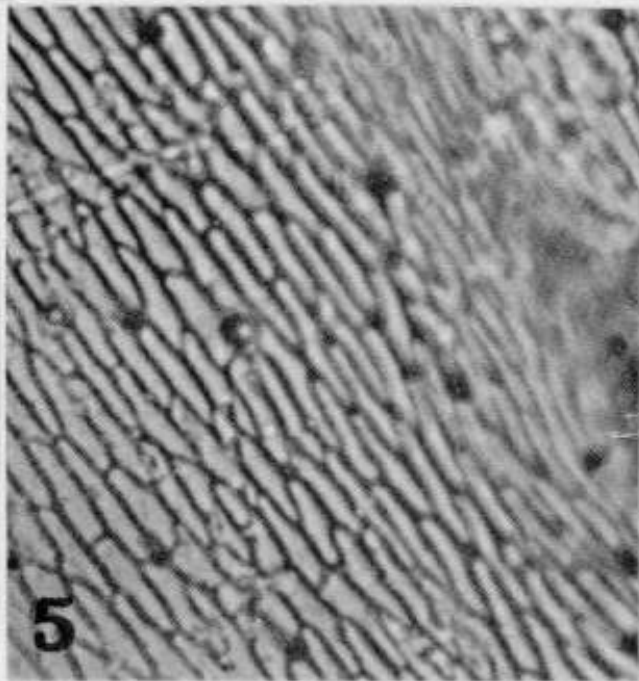
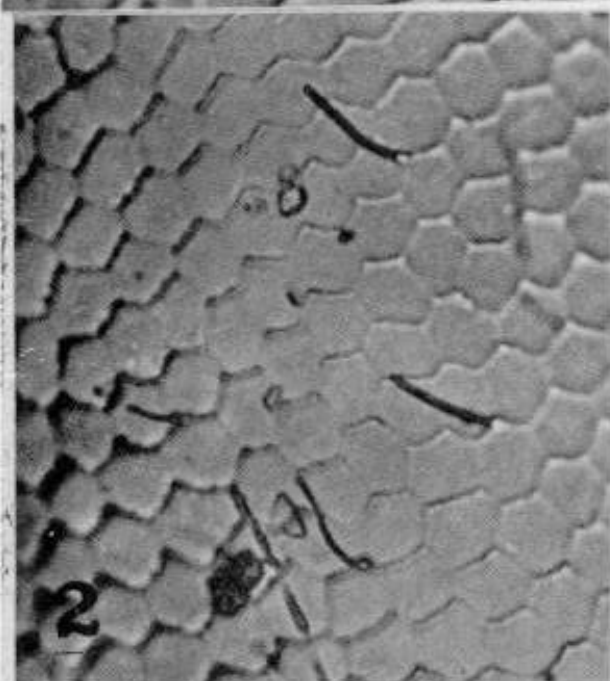
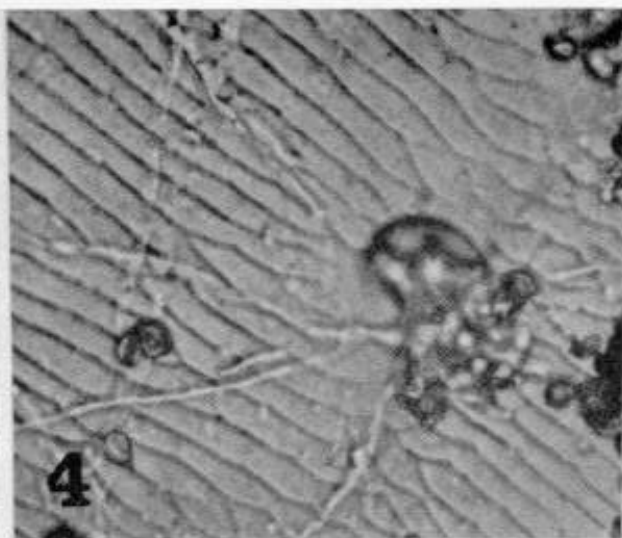
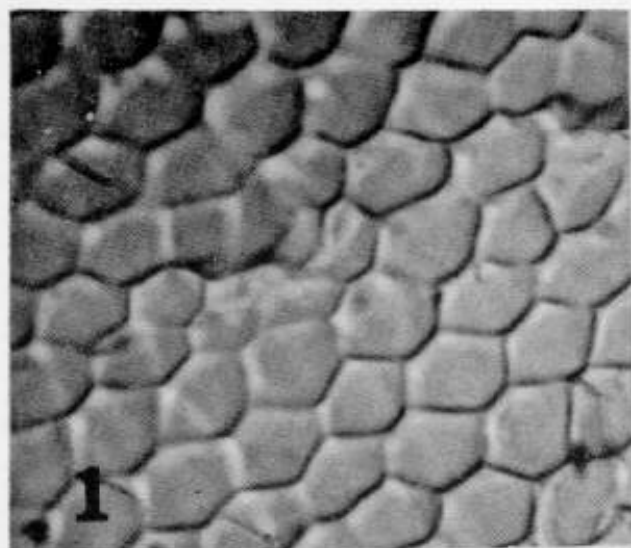
Leperisinus Reitter: *L. fasciatus* (Lec.). This had regular polygons. The pattern, however, was extremely modified in *Micracis* sp. (Fig. 88), where the polygons had uneven surfaces and were highly irregular in shape. No pattern was encountered in 2 other genera examined.

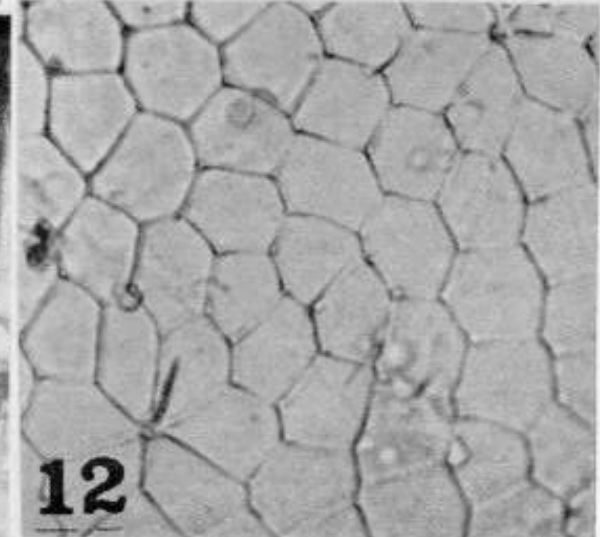
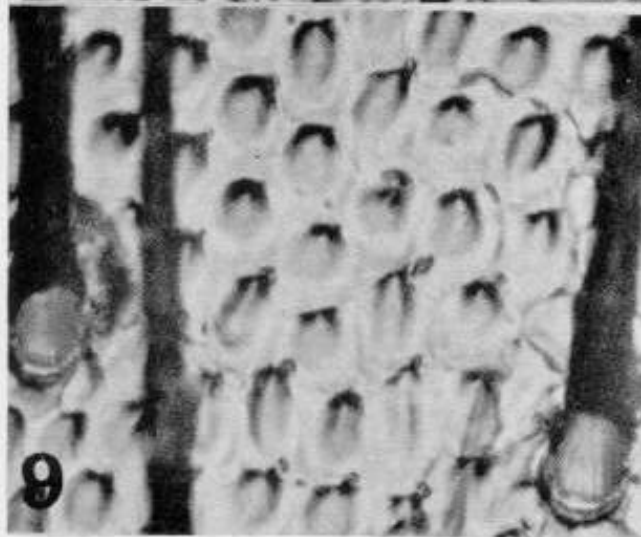
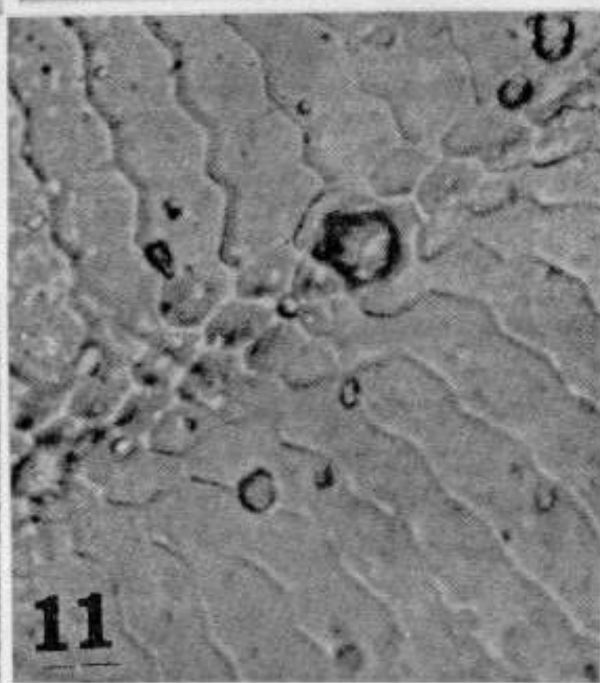
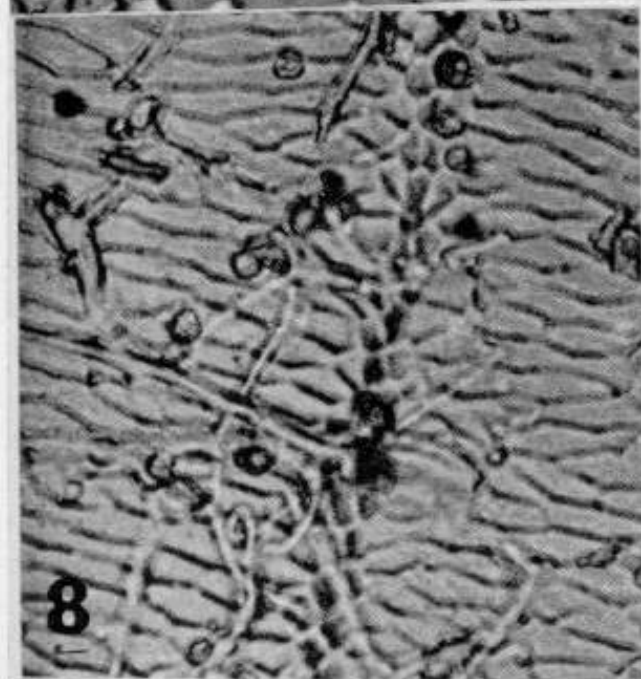
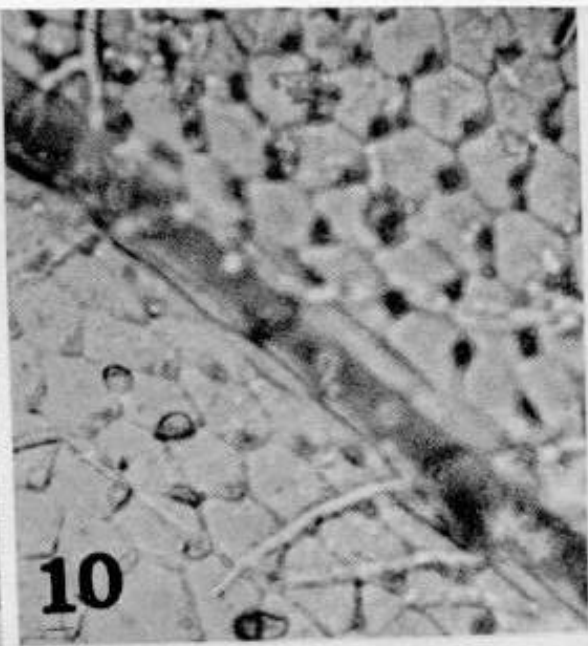
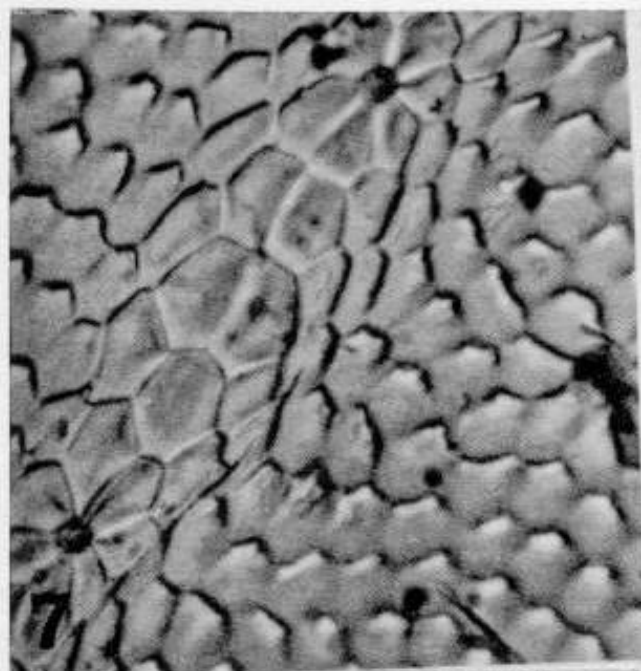
ACKNOWLEDGMENT

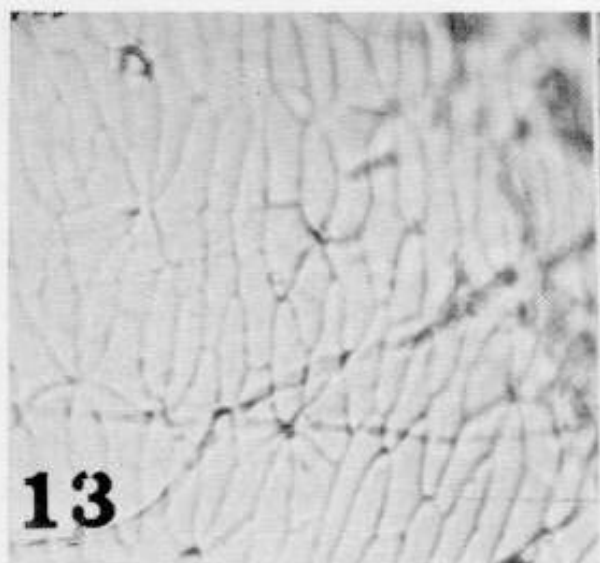
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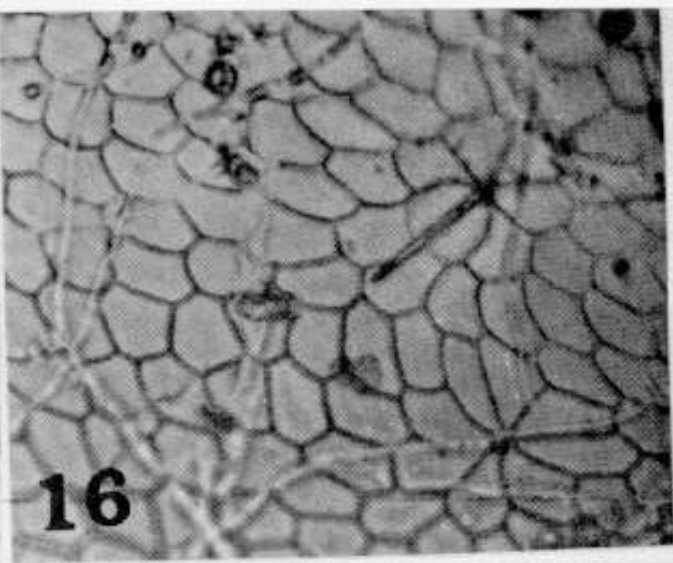
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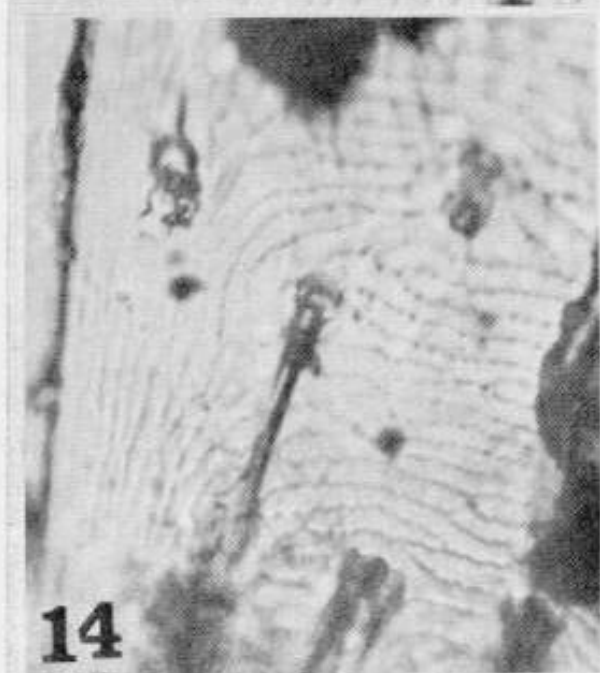




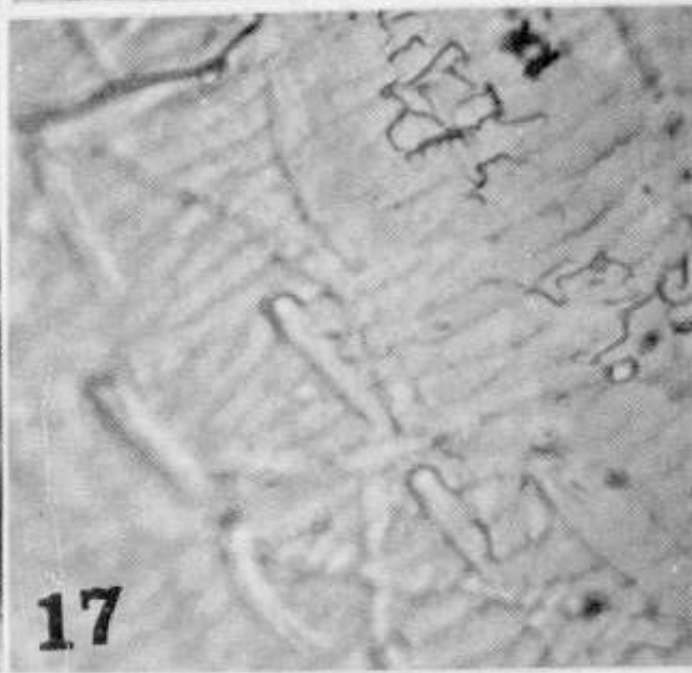
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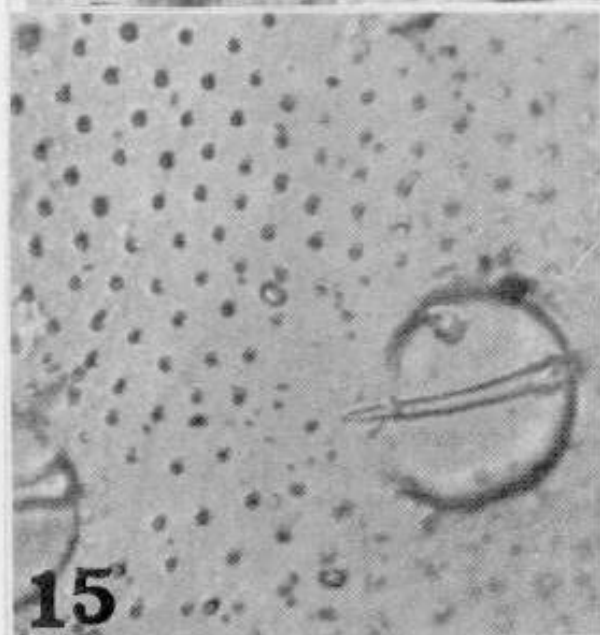
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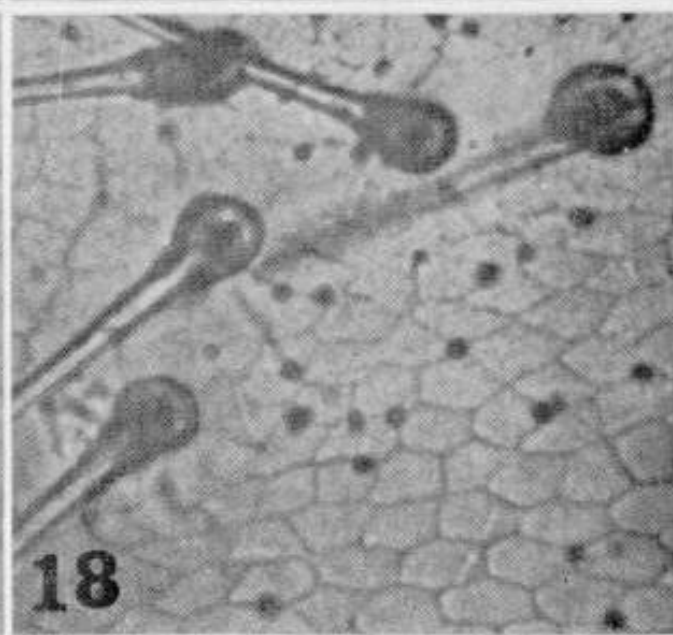
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