# WING VENATION AND PHYLOGENETIC RELATIONSHIPS IN MORDELLIDAE (COLEOPTERA: HETEROMERA)

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ABSTRACT

The hind wings of 7 species of Mordellidae, belonging to 6 genera, are described and their venation compared. Of these, the wing of *Hoshihananomia* Kono seems to be the most archaic. The wing of *Sphalera* Leconte exhibits no appreciable difference from that of the previous genus. *Conalia* Mulsant and Rey is moderately advanced and probably had a common descent with *Glipodes* Leconte, though they have apparently long since diverged from each other. The genus *Tolidomordella* Ermisch is moderately specialized, and there seem to be no grounds for including it in the same tribe with *Hoshihananomia* and *Sphalera*. *Mordellistena* Costa seems to be more highly evolved than the other genera studied, exhibiting closer ties to *Tolidomordella*.

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In the higher taxa of many winged insects, taxonomy depends regularly on wing venation. This is not the case in many Coleoptera groups in spite of the work of Forbes (1922) and Crowson (1955).

In his plates of the wings of Coleoptera, Kempers (1923) included the wings of 2 species of Mordellidae. Unfortunately, the veins in Kempers' figures were unlabeled, and the plates were not accompanied by descriptions.

The hind wings of this family remained undescribed in spite of the difficulties which existed in defining the taxa. There is a good deal of controversy about the validity of some genera and uncertainty in reaching correct species identification. The inclusion of hind wings in species description and the analysis of wing venation will have appreciable diagnostic value and might prove useful in checking the status of some genera.

In this family, as in many other insect groups, wing venation is relatively constant, disclosing affinities which may not be otherwise recognized. A comprehensive comparative study of the wing venation will contribute to a better understanding of their phylogenetic relationships. In order to attain a sound classification for Mordellidae, a family revision utilizing wing venation, in addition to other basic structures (e.g. genitalia and legs), is urgently needed.

## MATERIAL AND METHODS

The wings of 7 species (Table 1) belonging to 6 genera were studied and their venation compared. The study of North American Mordellidae has lately been neglected: Liljeblad's monograph (1945) was put in its final form in 1929, and Ray did his work on the U.S. fauna before 1947. Since then some genera have been split by Old World investigators, with the generic names of only a few North American species remaining unchanged (Table 1).

The following procedure was used to unfold the wings and maintain them in that position. The specimen was soaked in 75% alcohol, the elytra were raised, and any air trapped within the folds was removed. It was

TABLE 1.—THE SPECIES OF MORDELLIDAE WHOSE WINGS ARE PRESENTLY BEING STUDIED.

| Current Status | Name in Liljeblad's Monograph (1945) |
|---|---|
| *Hoshihananomia octopunctata* (Fabricius) | *Glipa octopunctata* (Fabricius) |
| *Sphalera quadripunctata* (Say) | *Mordella quadripunctata* (Say) |
| *S. melaena* (Germar) | *M. melaena* Germar |
| *Glipodes sericans* (Melsheimer) | *Glipodes sericans* (Melsheimer) |
| *Conalia helva* (Leconte) | *Conalia helva* (Leconte) |
| *Tolidomordella discoidea flaviventris* (Smith) | *Tomoxia discoidea flaviventris* (Smith) |
| *Mordellistena ancilla* Leconte | *Mordellistena ancilla* Leconte |

transferred to a drop or two of polyvinyl alcohol (medium viscosity) in the cavity of a depression slide. The elytron was clipped, and the wing cut for unfolding, using minuten nadelins (with tip bent at an angle) mounted on wooden applicators, or standard insect pins. Pinned specimens were easier to process, since the pin itself served to stabilize the specimen during clipping. The viscosity of polyvinyl alcohol was important since the small, thin wing tends to fold back in thin medium, and may be torn on unfolding in thick medium. Polyvinyl alcohol has the advantage of delayed setting over some other mounting media (e.g., Canada balsam).

## HIND WING VENATION

The wing venation in Mordellidae (Fig. 1) is somewhat allied to that of other Heteromera. The nomenclature adopted is that of Forbes (1922) as modified in the anal field by Crowson (1955).

The subcosta is distinct at the base of the wing. Distally it is closely associated with the radius to a distance that varies with the taxon.

The radius closely parallels Sc. The surviving branches are mostly heavy. $R_1$ is prominent, while Rs is missing near the base and cross-vein r connects the 2 veins, closing a radial cell proximally. The principal folds of the wing interrupt the distal branches of vein Rs and, to a lesser degree, vein M, causing distortion in their path.

The media, like Rs, is obsolescent near the base. Distally, it is strong, curving toward the heavy cubitus, and joining the latter to form the M-Cu loop. Vein $M_4$+Cu runs from the apex of the loop toward the posterior wing margin. The veins near the bottom of this loop carry a few small fine setae or their sockets. Crossvein r-m connects Rs and M.

There are 4 anal veins, besides the jugal (axillary) vein. They are weak and often poorly indicated. The common stem of the first 2 anal veins is united, somewhat indistinctly, with base of cubitus.

Several thickened areas (flecks), which seem to represent aberrant veins, are present: anterior, intermediate, posterior, medial, one located on

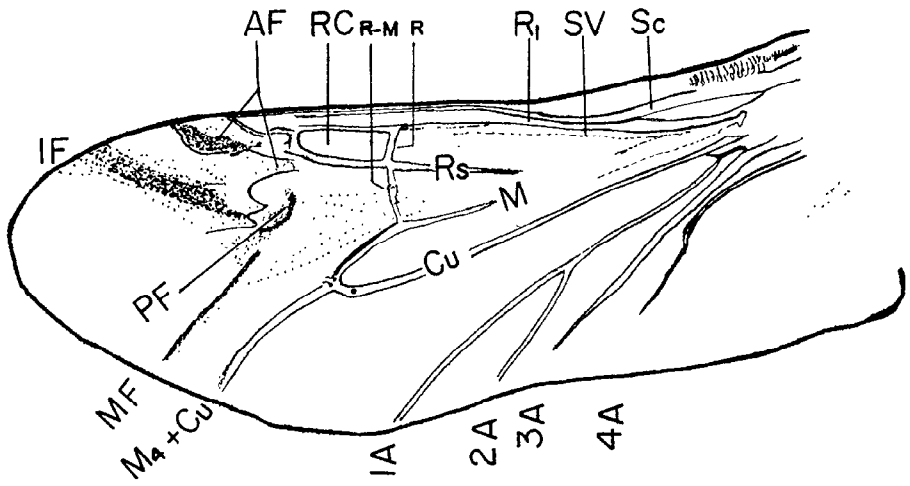


Fig. 1: Wing venation of *Sphalera quadripunctata*. AF, IF, MF, PF, anterior, intermediate, medial, and posterior flecks respectively; RC, radial cell; SV, spurious vein.

crossvein r-m, and a spurious one occasionally present behind base of vein $R_1$. A fleck strip behind fleck r-m sometimes joins M to the front of the medial fleck. The anterior fleck, which is derived from the radius behind vein $R_1$, includes $R_2$ and seems to be compound. It is continuous through a "bridge" with the intermediate fleck. A homologue of the latter is present in allied families and probably represents vein $R_3$ (Forbes 1922). The posterior fleck, which presumably represents the posterior branch of the radius, is usually well sclerotized. The medial fleck is nearly in line with the posterior one and seems to represent a detached branch of the media.

Two descriptive terms are introduced: 1) the "radial cell ratio", which represents the ratio between the maximal inside length and width of that cell; and 2) the "loop ratio", which is the ratio of the depth of M-Cu loop (inside measurement from the level of the basal end of vein M) to the length of cross-vein r-m. This ratio represents one way of expressing the relative length of the curved vein M.

### Wing of *Hoshihananomia* Kono (Fig. 2)

Vestiges of Rs and M present at base of wing. Four distinct anal veins noted. Faint spurious vein present behind $R_1$. Radial cell very long, radial cell ratio 5:1.

Loop ratio slightly more than 3:1. Medial fleck long, reaching posterior wing margin. Distal segment of anterior fleck widened towards costal margin of wing. Bridge with a proximal peg.

### Wing of *Sphalera* Leconte (Fig. 1, 3)

Spurious vein parallel to and behind $R_1$. Four anal veins present. Remnants of base of Rs and M present. Radial cell long, radial cell ratio 3:1. Vein M long, loop ratio 3:1. Medial fleck reaching posterior wing margin.

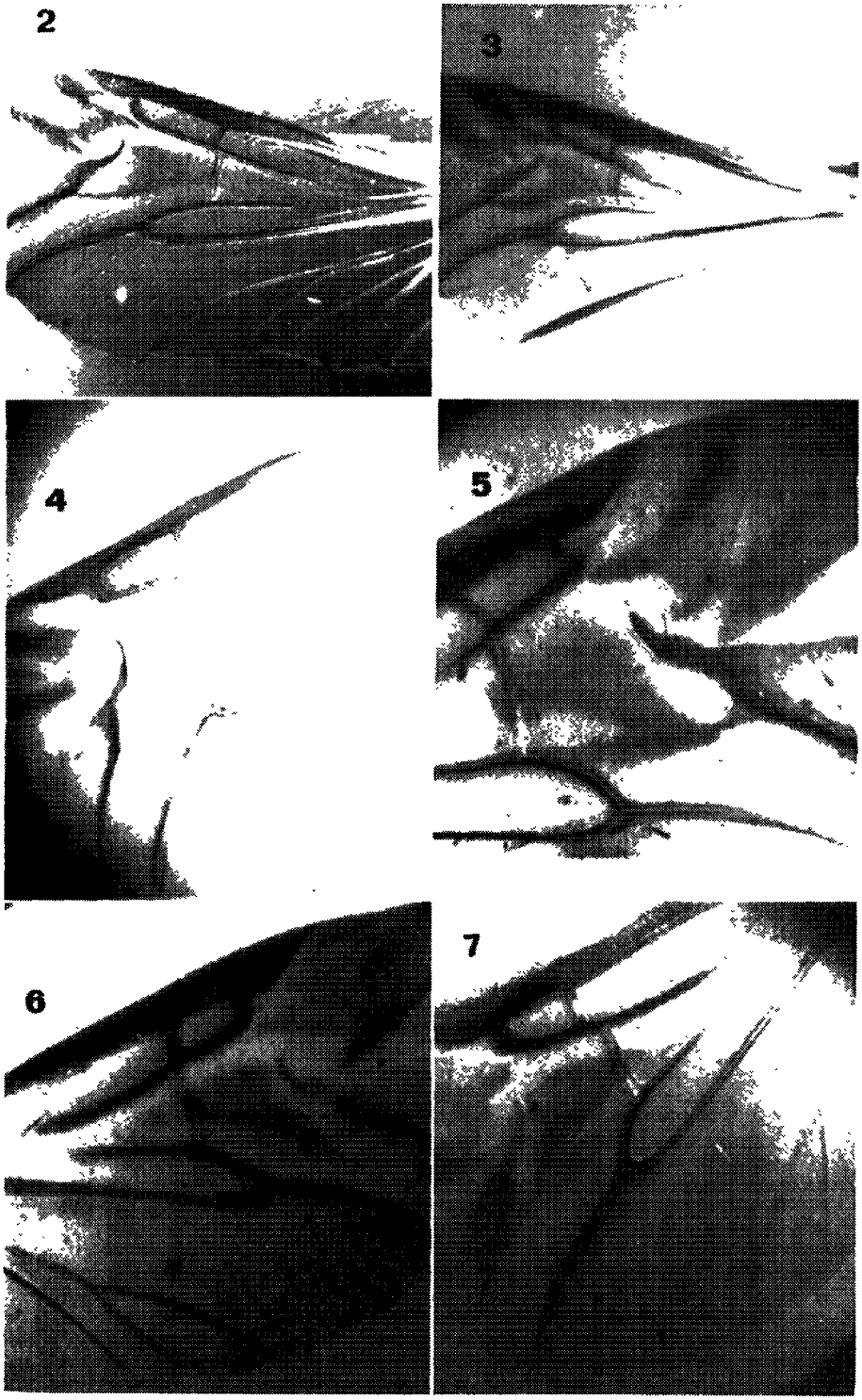


Fig. 2-7: Wings of Mordellidae. 2, *Hoshihananomia octopunctata*; 3, *Sphalera melaena*; 4, *Glipodes sericans*; 5, *Conalia helva*; 6, *Tolidomordella discoidea flaviventris*; 7, *Mordellistena ancilla*.

Bridge with a proximal peg. Distal segment of anterior fleck wide, broadly touching costal margin. In *S. quadripunctata* (Fig. 1), this fleck is compound in structure and apparently represents the more primitive condition in the genera examined. Proximally it still exhibits a vein origin in two separate locations, the anterior one apposing a similar vestige issuing from the radial cell.

### Wing of *Glipodes* Leconte (Fig. 4)

Four anal veins present. Remnant of crossvein still attached to stem of first 2 anal veins. Crossveins r and r-m unaligned. Radial cell ratio hardly more than 2:1. M long, loop ratio 3:1. Spurious fleck present at base of cell $R_1$. Distal segment of anterior fleck wide; distal border round, not reaching costal margin. Bridge with only a vestige of proximal peg. Medial fleck nearly reaching posterior wing margin. Fleck strip behind fleck r-m joining M to front of medial fleck.

### Wing of *Conalia* Mulsant and Rey (Fig. 5)

Rs extremely reduced, shorter than length of radial cell, and not extending as far basally as M. Fourth anal vein present, although faint. Radial cell ratio 2:1. Loop ratio 17:10. Medial fleck well separated from posterior wing margin. Posterior fleck more primitive i.e. less reduced, and extending postero-apically. Bridge with a proximal peg. As in *Glipodes*, the distal segment of anterior fleck wide, not reaching costal margin of wing, and fleck strip behind fleck r-m joining vein M to front of medial fleck.

### Wing of *Tolidomordella* Ermisch (Fig. 6)

Fourth anal vein degenerate, almost absent. Other 3 veins distinct, although fading out proximally. Dark spot present on crossvein r-m. Radial cell short, radial cell ratio slightly more than 2:1. Loop ratio 2:1. Extremely fine crease facing the basal end of Rs diagonally. A faint spurious fleck present at base of cell $R_1$. Anterior fleck faint, although appearing to extend almost to costal margin. Medial fleck separated by less than its length from posterior wing margin. Remnant of the fleck strip present although connection to M lost.

### Wing of *Mordellistena* Costa (Fig. 7)

Anal veins, especially the fourth, exceedingly faint. Crossvein r vestigial, appearing on way to disappearance. Radial cell short, radial cell ratio nearly 2:1. Loop ratio slightly more than 2:1. Distal segment of anterior fleck completely absent leaving anterior to "bridge", basal segment only. Medial fleck abbreviated, separated by more than its length from posterior wing margin. Fleck strip ill defined and connection to M usually lost.

PHYLOGENETIC RELATIONSHIPS

In some genera, e.g. *Hoshihananomia* (Fig. 2), the medial fleck extends to the wing margin, somewhat as in an unreduced vein. In others, e.g. *Mordellistena* (Fig. 7), it is considerably shortened. Based on evidence derived from morphological features other than the wings, the *Mordellistena* is considered the most highly evolved of the family (Crowson 1955). Results from the present comparative study of wing venation agree with Crowson's conclusion. A reduced vein does not represent the more primitive condition. The presence of the long fleck of *Hoshihananomia* would imply restoration of full vein after reduction, a sequence highly improbable in the processes of evolution. The wing with the minimum relative morphological specialization seems to be one possessing the following: a long radial cell; Rs and M long, with vestiges of their bases still distinguishable; a spurious vein behind and parallel to vein $R_1$; 4 well represented anal veins; an unreduced, veinlike medial fleck, reaching the posterior wing margin; an anterior fleck of a distinct compound nature, widely touching the costal margin; a bridge with a proximal peg. These generalized characters are well exemplified in *Hoshihananomia* (Fig. 2), which seems to be the most archaic of the genera studied.

The wing of *Sphalera* (Fig. 3) has a somewhat shorter radial cell; it otherwise exhibits no essential difference from that of *Hoshihananomia*. Both genera have the following characteristics: hind tibiae with short preapical (subapical) comb; tiny, isolated spurs irregularly arranged dorsolaterally on the tibia and the first (or first and second) tarsal segment of hind legs; no dorsal ridge or lateral combs on hind tibiae and hind tarsal segments; penultimate segment of front and middle tarsi emarginate; glabrous (glossy) eyes, finely granulated; antennae serrate. Some authors attempted to separate the 2 genera on the basis of the relation of the eye to the occiput (the extension of the temporal region behind the eyes). Presumably, the eyes reach the occiput in *Sphalera* and do not in *Hoshihananomia*. There seems to be no such universal distinction among species of the 2 genera. These 2 genera are so closely allied that their separate identity becomes questionable.

In the genus *Glipodes* (Fig. 4), the medial fleck is still rather well developed. The radial cell is somewhat shortened, with the anterior fleck not reaching the costa, and the peg on the bridge reduced.

The genus *Conalia* is considered one of the more primitive genera in imaginal structure (Crowson 1955). The wing (Fig. 5) still preserves primitive features like the peg on the bridge, the somewhat expanded anterior fleck, and the more primitive posterior fleck. However, the wing shows that the genus is moderately advanced. Rs is extremely reduced. The genus resembles *Glipodes* in having a long, oblique, lateral, preapical comb on outer surface of hind tibia, in addition to the fine dorsal ridge. There are no other lateral combs on the tibia, although such combs may be present on one or more of the hind tarsal segments. In both genera, a fleck strip behind fleck r-m joins M to the front of the medial fleck. *Conalia* probably had a common descent with *Glipodes* but they have apparently long since split from their common stalk. As these 2 genera diverged

from each other, each acquired significant specialized characters: in *Glipodes* appeared the large, coarsely granulated eyes, transverse suture in the metasternal plates (Franciscolo 1962), and the spurious fleck; while in *Conalia* evolved the finely granulated eyes, the reduced Rs, and the absence of the dorsal ridge on the hind tarsus.

The genus *Tolidomordella* had been placed with *Hoshihananomia* and *Sphalera* in the tribe Mordellini because of the similarity in the antennae, the penultimate segment of the front and middle tarsi, the short, preapical comb on hind tibiae, and the absence of lateral combs on hind tibiae and tarsi. Such hind legs seem to be quite archaic. However, examination of wing venation (Fig. 6) shows that *Tolidomordella* is far remote from the ancestral form, and is moderately specialized. The distal segment of the anterior fleck is exceedingly faint, the peg on the bridge no longer visible, the medial fleck and radial cell distinctly shortened, and the fourth anal vein almost absent. A remnant of the fleck strip is present. A generically unique diagonal crease faces the basal end of Rs. Other progressive changes which accompanied the specialization of *Tolidomordella* are also reflected in its differences from both *Hoshihananomia* and *Sphalera*. These differences include the presence of a dorsal ridge on the tibia and the first tarsal segment of hind legs (this ridge seems to be of an older origin than the lateral combs); pubescent eyes; hammer-shaped, terminal segment of male maxillary palp. There appear to be no grounds for including this genus in the same tribe with *Hoshihananomia* and *Sphalera*.

*Mordellistena*.—This genus is cosmopolitan and one of the larger genera of the family. It is rightfully recognized (Crowson 1955) as the most highly evolved genus of the family. In spite of the differences between the larva of this genus and that of *Tomoxia*-group, Crowson believes that the stem-boring larva found in *Mordellistena* has been derived from such types as the *Tomoxia*-group which bores in decaying wood. The genus *Mordellistena* is more allied to *Tolidomordella* than to any other genus studied. The wing (Fig. 7) is highly specialized, and the radial cell is reduced. The crossvein r tends to disappear, and the anterior and medial flecks are highly reduced. The fleck strip is faint and incomplete. The loop is shortened, and the anal veins are disappearing. The hind tibiae and tarsi possess lateral combs which seem to be of a rather late development in this family. Franciscolo (1967) considered *Mordellistena* as the origin of some other "unspecialized genera". This view conflicts with Crowson's (1955) and the results of the present investigation, both of which consider the genus quite advanced.

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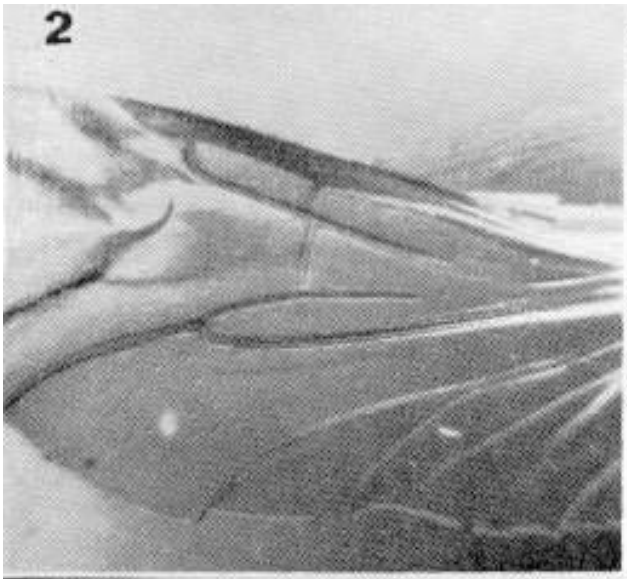
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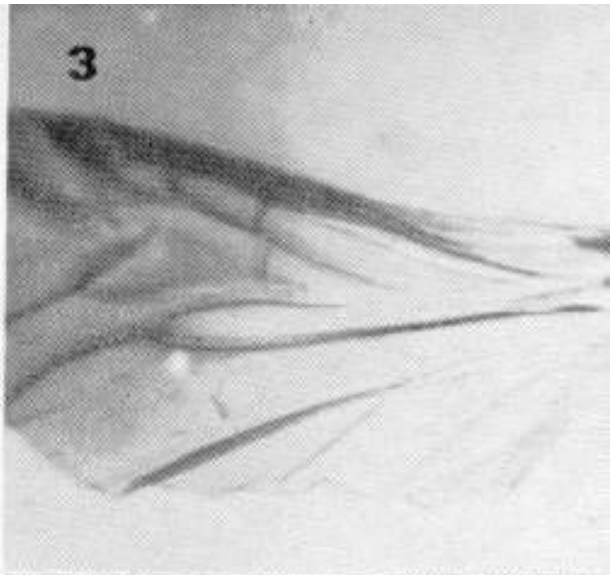
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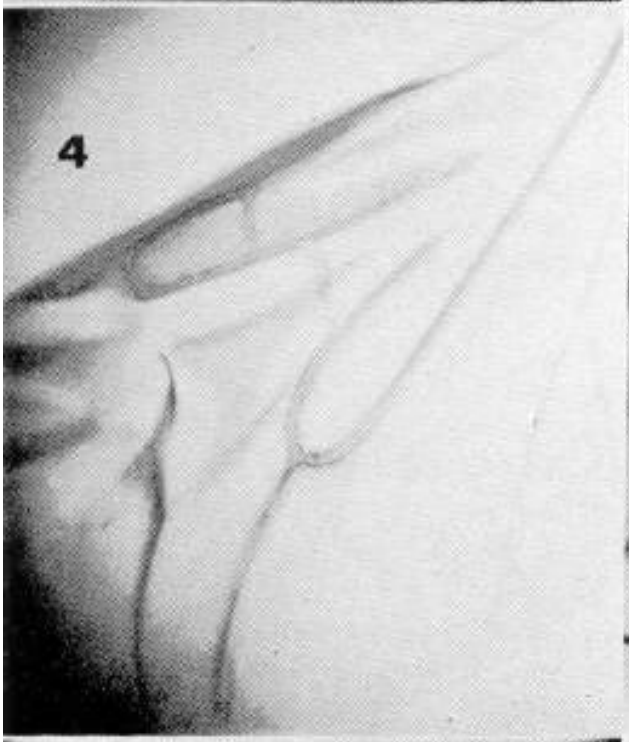
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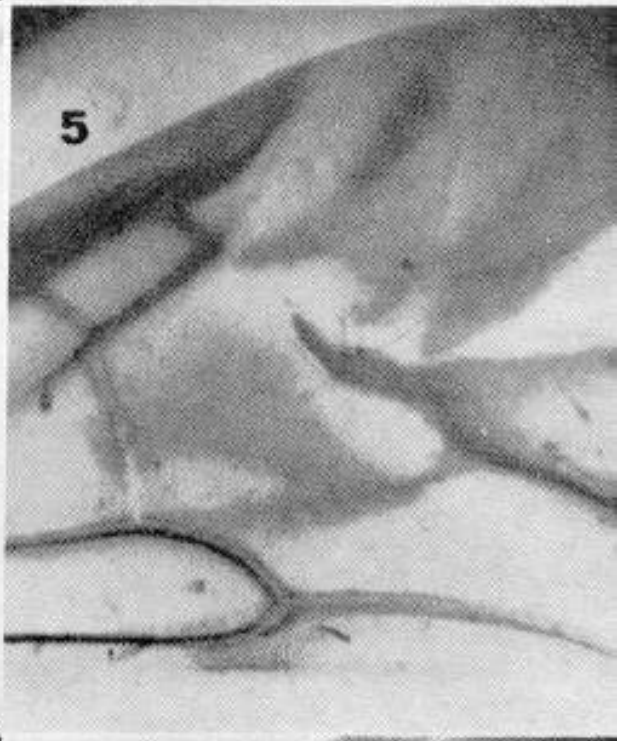
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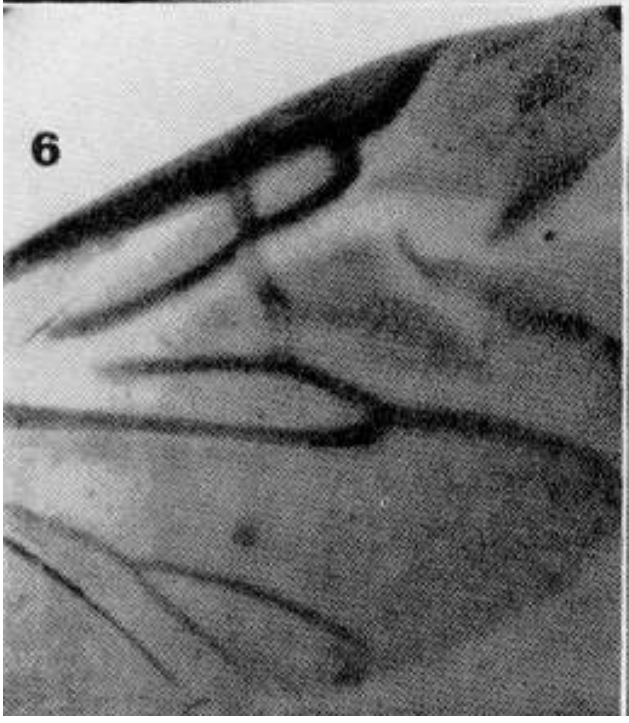
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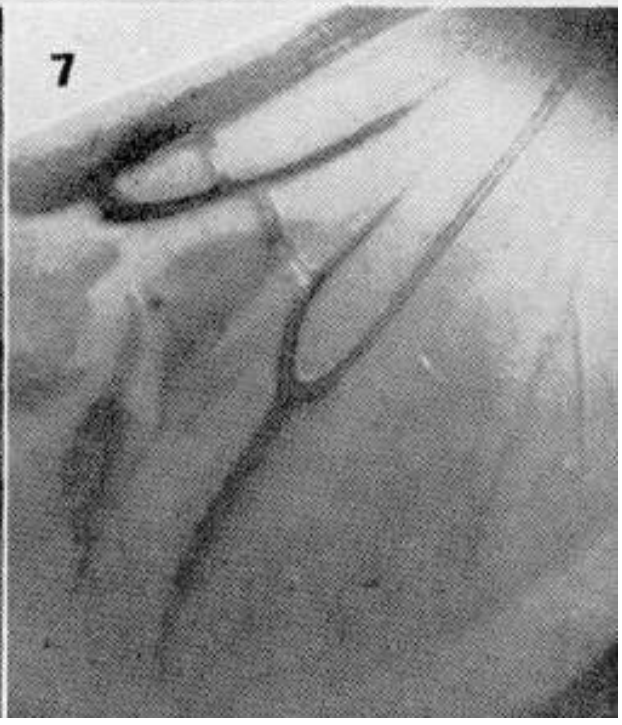
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