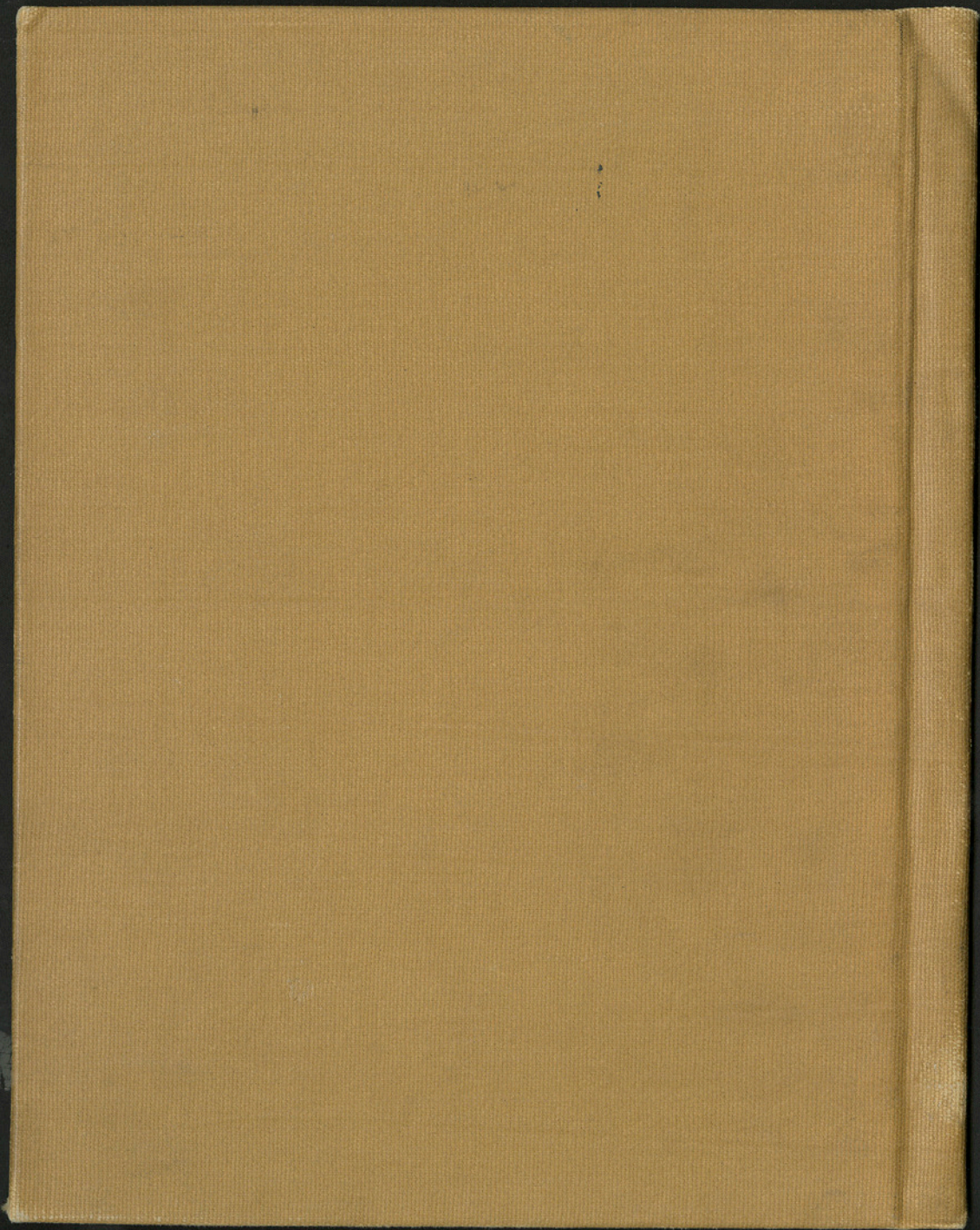
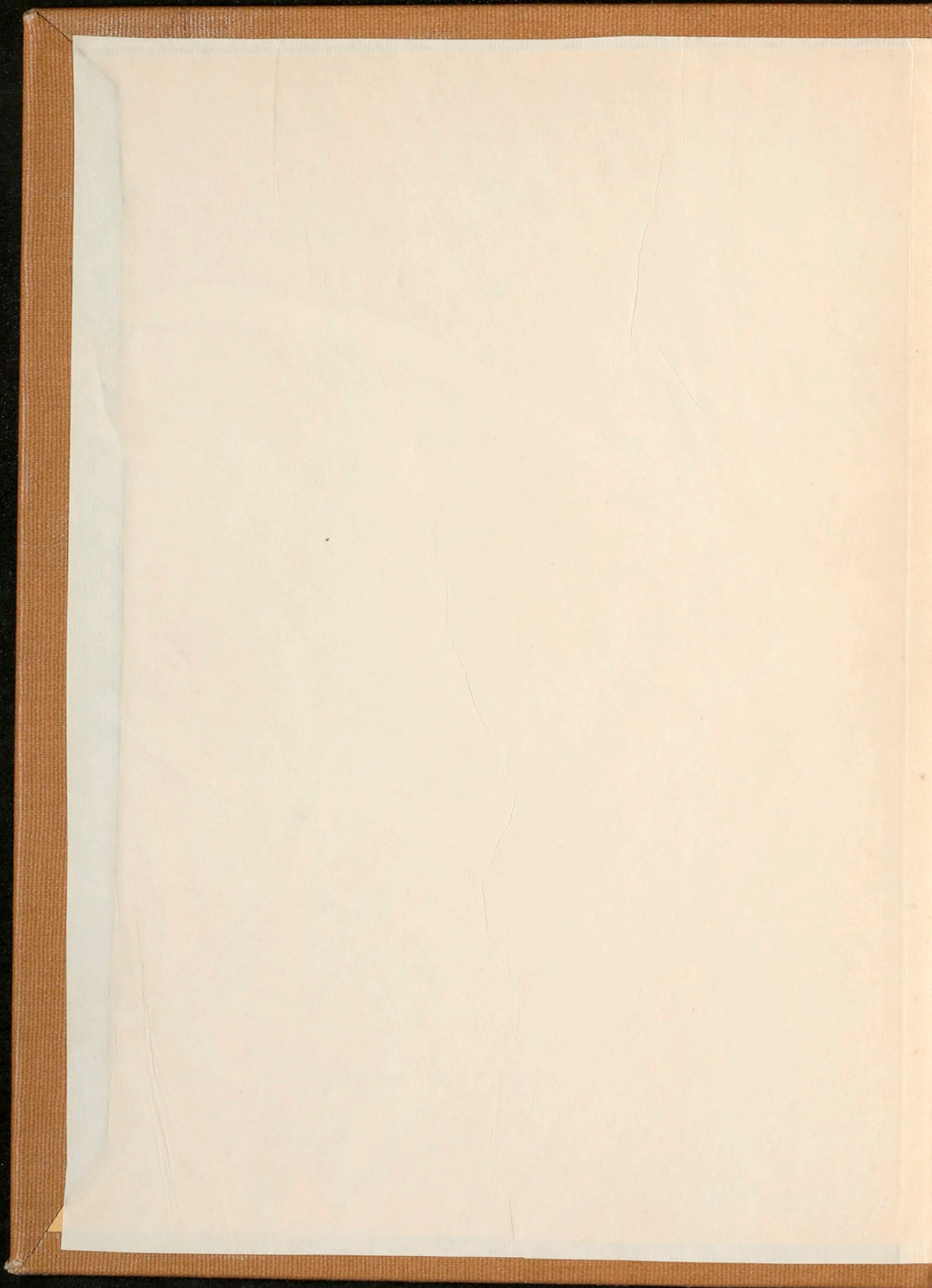


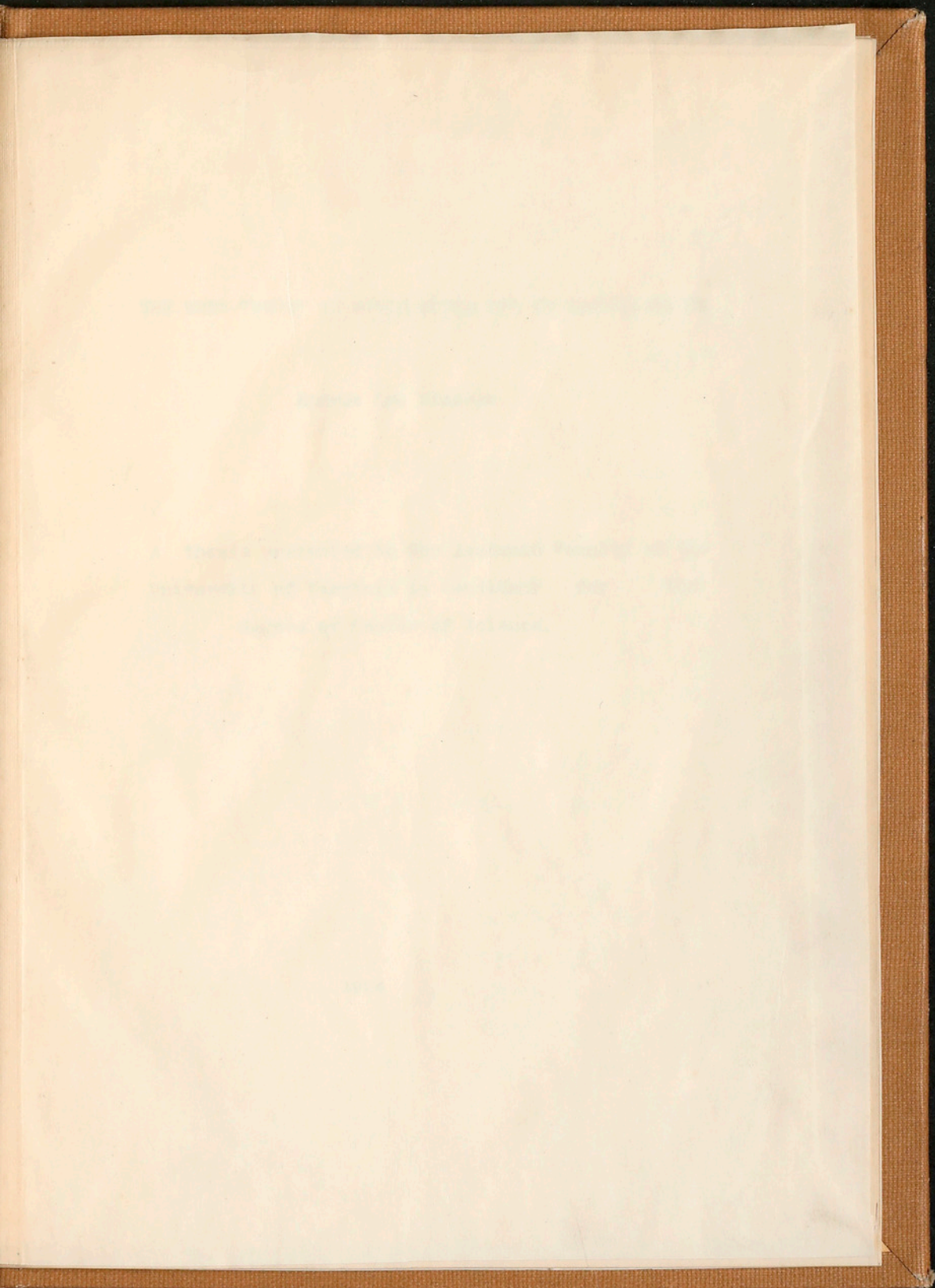


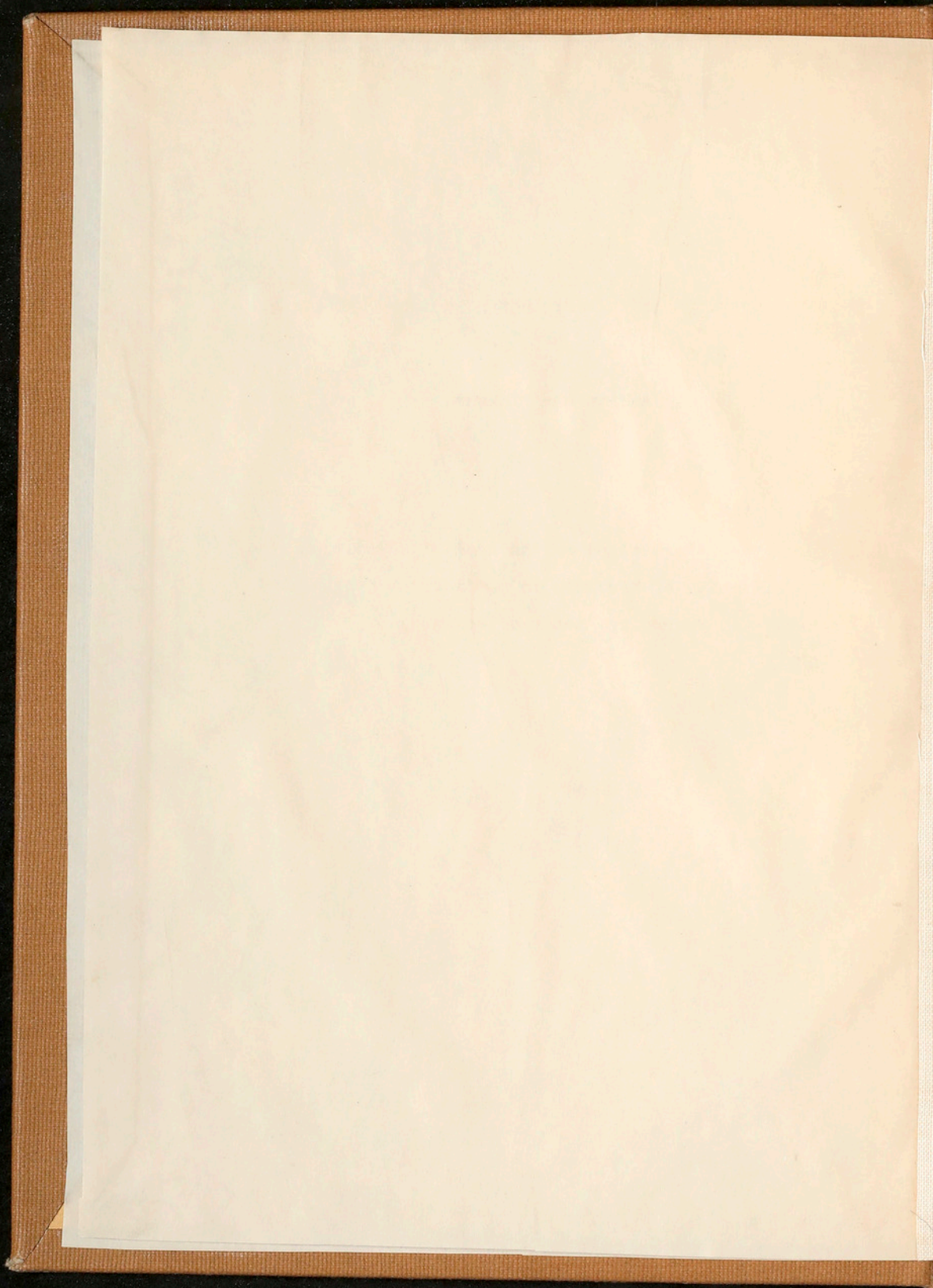
THE RUBY-THROAT AS MIMIC
MODEL AND CROSS-POLLINATOR
ANDREW LEE PICKENS











THE RUBY-THROAT AS MIMIC MODEL AND CROSS-POLLINATOR

Andrew Lee Pickens

A thesis presented to the Academic Faculty of the
University of Virginia in candidacy for the
degree of Master of Science.

1924

THE UNIVERSITY OF MICHIGAN LIBRARY

M. Va. Masters
Theses

74

519005

COPY 2

A thesis presented to the Academic Faculty of the
University of Michigan in candidacy for
the degree of Master of Science.

1974

THE RUBY-THROAT AS MIMIC MODEL AND CROSS-POLLINATOR

I. The Ruby-throat as a Mimic Model

The similarity of form between the hawk moths and the humming birds is noted by even casual observers, but is apparently taken for mere coincidental resemblance rather than for real mimicry. In most cases such explanation suffices, but one of the insects, the Clear-wing Thysbe, (*Haemorrhagia thysbe*), has elaborated and improved this coincidental resemblance to a remarkable degree.

Quite all the members of the hawk moth family resemble the humming birds in the possession of scimitar-like wings, heavy tapering bodies, and bright bird-like eyes. But to these the Thysbe adds a number of important features. The scales of the body are colored like the feathers of the ruby-throat, and are plume-like in form, giving the thorax and pendulous abdomen much the appearance of the bird's body, for not only do these scales quite cover the insect's body with a feathery sheen, but those at the tip of the abdomen are elongated and spread out fan-wise in a manner that strikingly simulates the tail of a bird. All these likenesses remarkable as they seem might be thwarted by wings opaque as those of most moths, if the transparency, not to say invisibility, of the whirring wings of the feeding ruby-throat is to be simulated. The outline of the humming bird's body when in the act of feeding, presents the appearance of a quite wingless form of green suspended in the air. How shall this feature be simulated? Like other hawk moths the Clear-wing thysbe begins its adult life with the wings opaque; soon, however, the

scales begin to drop from the central portion of each wing; not in a careless, irregular way as if rubbed off on the fingers of a mischievous boy, but in a symmetrical manner in the center of each wing, leaving a narrow margin of scales all about the clear spaces. These wings in motion have much of the invisibility of the whirring pinions of the ruby-throat, and the very movement of the bird is simulated in the way the insect approaches, probes, and backs off from a flower. So striking is the resemblance in fact that the layman's eye is often deceived, and well might a naturalist be struck with the resemblance. The insect seems to make good use of the deception, for while most of its cousins are crepuscular and even nocturnal, it ventures forth boldly to the feeding bowers in broad day thus escaping the nocturnal birds that gorge on the night-flying insects.

Yet another of the Lepidoptera, the long-tailed skipper, (*Eudamus proteus*), to a keen eye suggests rather than resembles a humming bird as it hovers before a flower. This suggestion comes partly from its hovering flight, partly from the pseudo-transparency of its wings, but largely from the long thick line of green presented by the body and a pair of swallow-tails on the rear portion of the hind wings. Such swallow-tail appendages are usually regarded by naturalists as false antennae, luring lizards and birds to grab at the wrong end of the intended victim thus affording a chance to break away and escape even if the insect does so with the loss of the appendage. However that be, I have noted but one night-flying moth, the Luna, with swallow-tails, and the inference is strong that such fine deceptive points are not noted by nocturnal birds as they are by diurnal relatives.

I believe that the wing-tails of the long-tailed skipper have been evolved under conditions different from those in connection with other such prolongations. Most tail-winged species have the extension on the fifth nerve from the inside of the rear wing as in *Grapta*, *Victoria*, *Hypanartia*, and others. (Fig. I, 1). Even the classic examples of swallow-tails, those of the *Papilios*, get no nearer the inner angle of the wing than the fourth nerve, (Fig. I, 2), and the hair-streaks and the tiny blues attach their mere pig-tails to the third nerve from the inside. The long-tailed skipper, however, is unique in prolonging on the second nerve, (Fig. I, 3), and at such an angle that the two tails lie almost parallel, even sometimes overlapping, and as Langstaff has pointed out, these extensions, even when the body proper of each wing is held vertical remain at a horizontal angle. Like the abdomen and the inner fold of the rear wing, they are covered with long, soft, plumey scales of a humming bird green. This of course gives an apparently greater length to the insect's body, while the anterior wings are spotted with squarish patches of silver that give an appearance of transparency to the otherwise somber-hued wings when the insect hovers before a flower and vibrates them rapidly. Now birds, according to J.R. Slonaker have a preponderance of color-seeing cones in their eyes while mammals have a preponderance of ray-seeing rods. Acute vision seems to depend on the presence of a fovea in the eye. Man has such: so has the sharp-sighted sparrow-hawk. The dog, uncertain of his own master's identity until tested with his nose has no fovea; the eyes of many birds show the same defect. To such an eye, a slender green body supported by seemingly transparent wings, might easily appear to be a humming bird. Though skippers are scattered thruout the world these long-tailed forms occur only in America the home of the humming birds, and the area where

I believe that the wing-falls of the long-tailed titmouse have been
noticed under conditions different from those in question with
other such species. Both tailfeathers extend over the edge of
on the right side from the inside of the wing as in figure
Historic, 1900, and others (1911) from the clouds
examples of similar-falls from the tailfeather, but no other
the inner angle of the wing than the fourth nerve (1911, 1912), and
the tail-feather and the third nerve which are similar to
the third nerve from the inside. The long-tailed titmouse, however,
is unique in projecting to the fourth nerve (1911, 1912) and as
such an angle that the two fall in a single vertical line, even
oscillating, and as indicated in the sketch and these extensions
even when the body moves of each side in a vertical plane at
a horizontal angle like the others and the inner side of the
wing which are covered with long, soft, downy scales of a
hanging bird's foot. This of course gives an apparently greater
length to the insect's body, while the anterior side are united
with special patches of clear skin which are continuous at
transversely to the dorsal surface of the body when the insect
moves before a lower and shorter form really, the body
according to A. S. Henshaw has a resemblance to other species
in this case while the female have a resemblance to the other
lefts which were in found in the region of the wing in the
has been noticed for the first time in the region of the wing
necessity of his own species' identity might be tested with the
has no doubt the way of my birds also the same defect. To
as yet, a similar group has been supported by scientific treatment
wing, right and left, to be a hanging bird. These distinct
are scattered through the world these long-tailed forms other
only in the case of the hanging bird, and the same thing

the long-tailed skippers abound both as species and as individuals corresponds closely to the area where humming birds are most numerous both as to species and as to individuals, for *Eudamus proteus* has a number of long-tailed relatives. It is the one type that is found in eastern parts of the United States, and strays as far north as New York, protected perhaps by its resemblance to the ruby-throat.

The advantages to be derived from mimicry of the humming bird is obvious. No bird, when we take size in consideration, is more pugnacious than this midget. The martin and the blue-bird hurry to their holes to escape its vicious jabs; the tufted tit attempting resistance from the perch is soon vanquished; the swift finds safety in its rapid wings, and even the bold king-bird is not immune from attack. Some moths mimic wasps and bees and unconsciously threaten their foes with a sting; some butterflies mimic inedible relatives and threaten their devourers with unpleasant tastes. How much more effective the threat that a humming bird's mimic makes! The foe may well desist from attack fearing the onslaught of a rapier beak in a battle that ends only in the aggressor's flight.

Wallace thought a mimic should occur in the same territory with its model, should be more defenceless, less numerous, differ from most of its relatives, and be only externally imitative. With quite all of these rules the Clear-wing *Thysbe* accords, and so does the long-tailed skipper, with the exception of the doubtful numerical requirement. Such resemblance after all may be mere examples of those remarkable phenomena of nature such as silhouettes a vine and its berries along the midrib of the otherwise plain leaf of the maranta, a tropical plant found in hot-houses, but many details point strongly toward natural selection of more suitable mimics.

II. The Ruby-throat as a Factor in Cross-pollination

Water, wind, insects, and birds have figured in the cross-fertilization of plants as they have risen from the primitive forms, and all these methods are in use today in the cross-pollination of flowers while the bees and the humming-birds are closely matched in the production of complex and efficient forms.

All humming bird forms of flowers have apparently descended from older insect-pollinated forms, mostly those of bees and moths, though sometimes to be sure a thrip-pollinated flower might be changed by the visits of the bird to such flowers in order to vary its nectar diet with some insect fare, for even the ruby-throat is to a large degree insectivorous, and small spiders and insects constitute much of its food. Most flowers visited by humming birds in the temperate zone are mere compromises. The flame azalea and its relatives are probably pollenized by both moths and humming birds; the fire-pink, or Virginia catch-fly is visited by both butterflies and ruby-throats; dozens of forms divide their time between the bees and the birds. The European columbine is blue that being it seems a favorite color with bees, no humming birds being found in the Old World. The American columbine, on the other hand, is red a favorite color with humming birds. In form the trumpet creeper blossom resembles the Paulownia of the Orient, but the former is arrayed in red, and the stamens have a more definite compact arrangement. Something of the same difference is seen between the honeysuckles of the Old World and those of the New, for these feathered midgets have influenced the form and color of many American flowers which manifest features not seen in similar forms from Europe, where the ancestors of the plant world have been absent from the humming bird influence. This influence appears to produce flowers of red and orange colors, cornucopia and tubular forms of

corollas, and compactly arranged stamens maturing later or earlier than the pistil. Some such forms would probably survive were all the humming birds exterminated, as this arrangement lends itself to pollination by bees, moths and butterflies. Still others have become so specialized that like the jewel weed when introduced into Europe, in the absence of humming birds they can do little more than produce cleistogamous seeds, a dangerous step because in the direction of degeneracy. Let us consider some of the more highly specialized flowers visited by the ruby-throats.

As a first example take the Cardinal flower, (*Lobelia cardinalis*), and contrast it with another member of the same genus, the Blue Cardinal flower, (*Lobelia siphilitica*). As might be expected the red caters to the humming bird, the blue to the bees. In the first the anthers are coalesced to form a tube about the pistil, all standing up in stiff military style and making a conspicuous erect column at the back of the flower. The pistil is completely covered at first, but when the bird has visited the blossom, and brushed the pollen from the end of the tube formed by the surrounding anthers we may be sure that the stigma will emerge from the end of this tube enough to receive the pollen from another flower during a later visit. (Fig. II, 1 a and b). This column is found in the bee-visited blue species, but is much more conspicuous in the red form, and one form has evidently been developed from the other, or both evolved from an ancestral form, common to both.

The scarlet salvia, (*Salvia splendens*), though developed by tropical humming birds is one of the interesting forms introduced into our gardens which show how the cross-fertilizing apparatus developed by bees readily lends itself to the visits of the bird. As it drops downward from the air to probe the flower, it touches first the stigma, which extends farther out from the flower, and is

...and naturally arranged elements existing later or earlier than the petals. Some such forms would probably survive were it not for the fact that the present birds are not adapted to this arrangement. In this arrangement insects are attracted to the flowers by their color and by the odor of the flowers. In the present case the insects are attracted to the flowers by their color and by the odor of the flowers. In the present case the insects are attracted to the flowers by their color and by the odor of the flowers.

As a first example take the Cardinal flower, *Lobelia cardinalis*, and compare it with another member of the same genus, the Red Cardinal flower, *Lobelia spicata*. As might be expected the red petals of the Cardinal flower are visited by the humming birds. In the case of the Red Cardinal flower the petals are not visited by the humming birds. In the case of the Red Cardinal flower the petals are not visited by the humming birds. In the case of the Red Cardinal flower the petals are not visited by the humming birds.

The result is that the Red Cardinal flower, though developed by the same process as the Cardinal flower, is not visited by the humming birds. In the case of the Red Cardinal flower the petals are not visited by the humming birds. In the case of the Red Cardinal flower the petals are not visited by the humming birds.

higher up than the anthers. (Fig. II, 2a). It leaves there a touch of pollen from the last flower visited, then dropping even lower, and probing farther into the flower, touches the anthers and gathers the magic dust for the next, or some later flower. (Fig. II, 2b). There are, let us note in passing, but two fertile stamens to the flower out of a probable original four. Glancing inside we see the reason. Two of the four stamens have been developed into elbowed arms that reach out from the walls of the flowers and hold the other two down out of the stigma's way, much in the same manner that a small boy's legs are held down by the arms of an older brother as he is carried in a sitting posture on the latter's shoulders with legs astride the neck.

The wild touch-me-not, or jewel weed, (*Impatiens biflora*), stores the nectar in a long curved tube to protect it from tongues other than long ones such as the ruby-throat has. In the exact upper middle of the entrance to the flower hangs the pistil, quite covered over by the basket formed by the united stamens and anthers. (Fig II, 3a). Probing for nectar the bird strikes off on its forehead the pollen, bearing it away to another flower. The stamens having served their purpose, dry at the point of attachment, and the entire basket drops from around the hitherto covered pistil, leaving it naked to receive the pollen from a younger flower when next the ruby-throat comes for nectar. Very similar in form is the cross-fertilizing device of the introduced *Impatiens sultani* of the same genus as the above. It improves its cousin's plan, however, by the use of a triple divergence at the end of the pistil making contact with the pollen-laden forehead trebly assured. Yet another exotic, the nasturtium, originally from Peru, makes use of the long anterior cornucopia to lock away the humming bird's sweets, but cleverly contrives to place its pollenizing stamens and pistil on the lower side of the

higher to than the surface (Fig. 11, 12). It leaves there a rough
rolled from the last flower stalk. This structure was found, and
and proper labels into the flower, between the surface and surface
the axis that the next, or some later flower. (Fig. 13, 14). There
was, but as noted in paragraph 1, but the fertile stem of the flower was
of a prothallial origin. It is found inside as was the case. The
the four stems have been developed into a single stem which
out from the axis of the flower and hold the other two down out of
the stem's way, such in the same manner that a small hole has
held down by the axis of an other flower as he is carried in a
line course on the lateral surface with less inside the root.
The will reach-out, or level with, (Fig. 15, 16) when
the matter in a long curved tube to protect it from further
than long ones such as the tube-throat has in the same way
middle of the entrance to the flower being the result of the
over by the basket formed by the united stems and surface. (Fig. 17,
18). Looking for matter for the first time off on the surface of
roll, bending it away to another flower. The stems having turned
their course, by at the point of attachment, and the entire
edge from around the surface covered with, leaving it open to
receive the pollen from a younger flower when next the tube-throat
comes for matter. Very similar in form to the cross-section
device of the introduced insect instead of the same as the
above. It however the central part, however, by the use of a single
thickness at the end of the prothallial matter instead of the
later formed lobes. Yet another example, the modification
originally from four, rather one of the long slender compound
look away the bearing that's made, but clearly confined to
place the pollination stems and stamens on the lower side of the

flower, so that the feathers of the throat are used in the act of cross-pollination. As most other flowers use the top of the head this is quite a business-like change and enables the flower to use an otherwise quite unexploited field.

More highly specialized flowers with reference to visits of the ruby-throat occur in the genus *Macranthera* growing along the Gulf Coast from Mississippi to Florida. Here they have so long a season that they can throw the discretion of the northern flowers to the wind, and snubbing the insects woo with a highly specialized ardor the autumnal hordes of ruby-throats fleeing south before the northern winds and collecting along the margin of the mainland. I have had opportunity to examine but one species of the genus, *Macranthera Lecontei*, which may grow as tall as six feet, with the tubular orange flowers standing up like candles in a candelabra, each candle bracket having a certain amount of resilient springiness. Let us consider the part played by the pistil, and that played by the stamens.

Hardly have the mere scallops of the corolla begun to spread apart before the style thrusts itself out and up beyond the flower, the stigma bending outward. (Fig. II, 4a). To this golden chalice comes a ruby-throat, its nape hoary with pollen from another flower. To get at the stiffly erect tube it must rise on wing, drop its bill on its breast and thrust it almost vertically downward. (Fig. II, 4b). It is an uncomfortable position and the bird resents it and pulls downward on the flower to bring it more nearly into a horizontal position. This act aids in the end to be accomplished, and the flower yields gracefully with its springy curved bracket. As it does so the style with its outward, now downward bending stigma almost with the canniness of intellect, comes down with the flower, and lightly touches the pollen-bearing nape, another spot the other

flower, so that the position of the lobes are used in the end of
a classification. In most other flowers the lobes of the petals
is quite a business-like shape and makes the flower to be an
obvious and recognized form.

Some highly specialized flowers with very small lobes of
the type found occur in the genus *Passiflora* growing along the
Gulf Coast from Mississippi to Florida. Here they have so long a
season that they are known the character of the northern flowers
to the west, and making the flowers very with a highly specialized
under the natural border of very-branches of long each before the
northern winds and collecting along the margin of the rainforest.
I have had opportunity to examine but one species of the genus,
Passiflora foetida, which may grow as tall as six feet, with the
tubular orange flowers standing up like candles in a candlestick, each
pedicel bearing a certain amount of reddish-orange, but
as another the next placed by the pedicel, and that placed by the
stamens.

Finally have the more common of the species known to extend
greatly before the style through the lobes and to beyond the flower,
the lobes being outward. (Plate II, fig. 1) In this golden color
comes a very-branch, the main body with golden from another flower.
To get at the staminal tube it must rise on which, keep the style
on the front and thrust it about vertically toward the style.
It is an uncomfortable position and the kind remains it and will
forward on the flower to point it more nearly into a horizontal
position. This not only in the way to be accomplished, but the
flower itself especially with the lobes curved forward, as it does
so the style with its lobes, not toward pedicel tubes almost
with the umbels of stamens, comes down with the flower, and
lightly touches the pedicel-bearing tube, another root the other

flowers have neglected, and there receives the magic of cross-fertilizing pollen. As the bird withdraws its beak the flower springs back to its upright position. (Fig. II, 4b and a).

Now the stamens come into play. They stand not around nor above the style but back of it like the four fingers of an upheld hand. Every anther is turned outward. One almost feels that military precision is endangering the symmetry of the flower. These anthers green and gummy at the bird's early visit, are hoary now with ripened pollen; then they were much shorter than the pistil, thus keeping out of the way of the magic spot on the ruby-throat's nape. Now they have grown equally as long as the pistil which has dried up and receded as if to get out of the way. (Compare II, 4a and c). The scallops of the corolla are blackening with approaching death, and one almost fears the complex machinery is in vain. But there is still honey in the nectary; there is a flash and whirr of wings; the returning ruby-throat thrusts its bill into the vertical flower and again bends it down. The dried style has receded, but the outward, now downward bending stamens come lower, and still lower, then the anthers on the lower side of the very ends of the stamens touch the bird's nape. Like the four fingers of an extended hand of blessing the stamen of the flower rest there a moment, but patriarchal as the act seems there is something of the patriarch Jacob in that touch, which forces the unwitting humming bird to return in transportation service the value of the nectar gleaned. That the arrangement is satisfactory, however, seems well attested by the twittering hordes of ruby-throats found about these flowers, and later in the fall by the thousands of fertile seeds borne in the capsules of the plants.

This flower, like the *Salvia* appears to have descended from an ~~ancestral bee-form being closely related to the bee-visited members~~

ancestral bee-form being closely related to the bee-visited members of the Figwort family in which are found such familiar forms as snap-dragons, toadflax, foxglove, and mullen. Highly specialized as it is it is not red, reputed to be the favorite color of the humming bird, but fairly shines in orange, just as the touch-me-not and several other specialized forms do. In fact I believe that observations in the southern states show that the ruby-throat's eye has as much if not more tendency toward orange flowers than toward red ones.

several specimens being almost entirely white, and the
 wings of the White family in which are found with lighter
 as dark-brown, chestnut, rufous, and other highly speckled
 as it is not red, reputed to be the specific color of the
 mourning bird, but which differs in orange, just as the form-
 and several other speckled forms do, in fact I believe that
 observations in the southern states show that the white-throat's eye
 has as much if not more tendency toward orange than toward
 red ones.

BIBLIOGRAPHY

- Audubon: Birds of America.
- Bingley: History of Birds.
- Blanchan: Nature's Garden.
- Comstock: Manual for the Study of Insects.
- Coleman: British Butterflies.
- Delage: L'Annee Biologique, Vols. 2-20.
- Holland: Butterfly Book; Moth Book
- Kellogg: American Insects.
- Lounsberry: Southern Trees and Wild Flowers.
- Packard: Guide to the Study of Insects.
- Sharp: Insects.
- Slonaker: Acute Vision in Vertebrates. Journal of Morphology. Vol. 13.
- Small: Flora of the Southeastern United States.
- Weed: Butterflies.
- Weissman: Evolutionary Theory.
- Weyssse: Synoptic Textbook of Zoology.

Note:- Valuable assistance was given by Dr. Harrison G. Dyar of the Smithsonian Institution, Mr. W. D. Niley of the British Museum, Mr. Geo. R. Koester of the Greenville (S.C.) Evening Piedmont, and Mrs. H. D. Garrison of Easley, S.C.

BIBLIOGRAPHY

- Anderson: Birds of America.
 Audubon: History of Birds.
 Bancroft: Bancroft's Edition.
 Cooper: Manual for the Study of Insects.
 Coquillett: British Butterflies.
 DeLong: James DeLong's, Vol. 2-3.
 Collins: Butterfly Book: with Book.
 Kellogg: American Insects.
 Linsley: Southern Insects on Wild Flowers.
 Packard: Guide to the Study of Insects.
 Sharp: Insects.
 Stål: Insects of the Southern United States.
 Wall: Birds of the Southern United States.
 West: Butterflies.
 Westwood: Entomology Theory.
 Young: Scientific Textbook of Zoology.
- Note: A special assistance was given by Dr. Garrison of the
 Smithsonian Institution, Mr. E. D. Miller of the British Museum,
 Mr. Geo. H. Mosher of the University (L.S.) Evening Museum, and
 Mr. E. D. Garrison of Cedar, S.C.

PLATE I

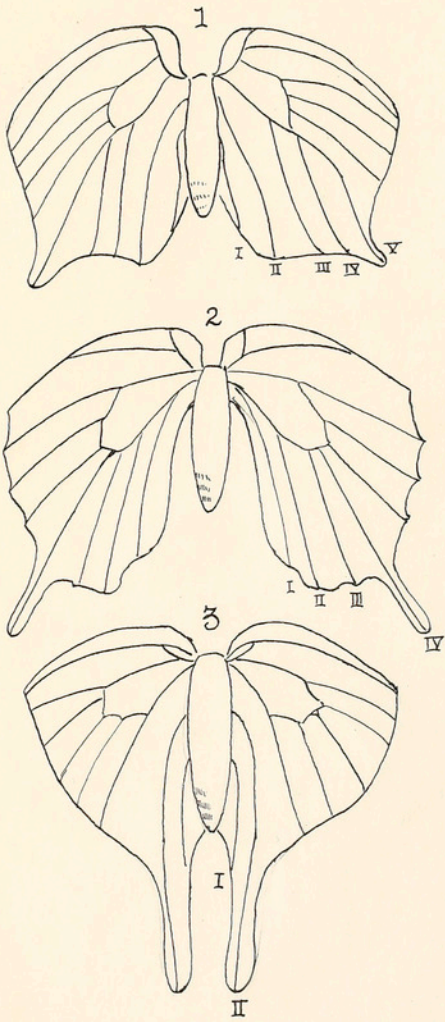
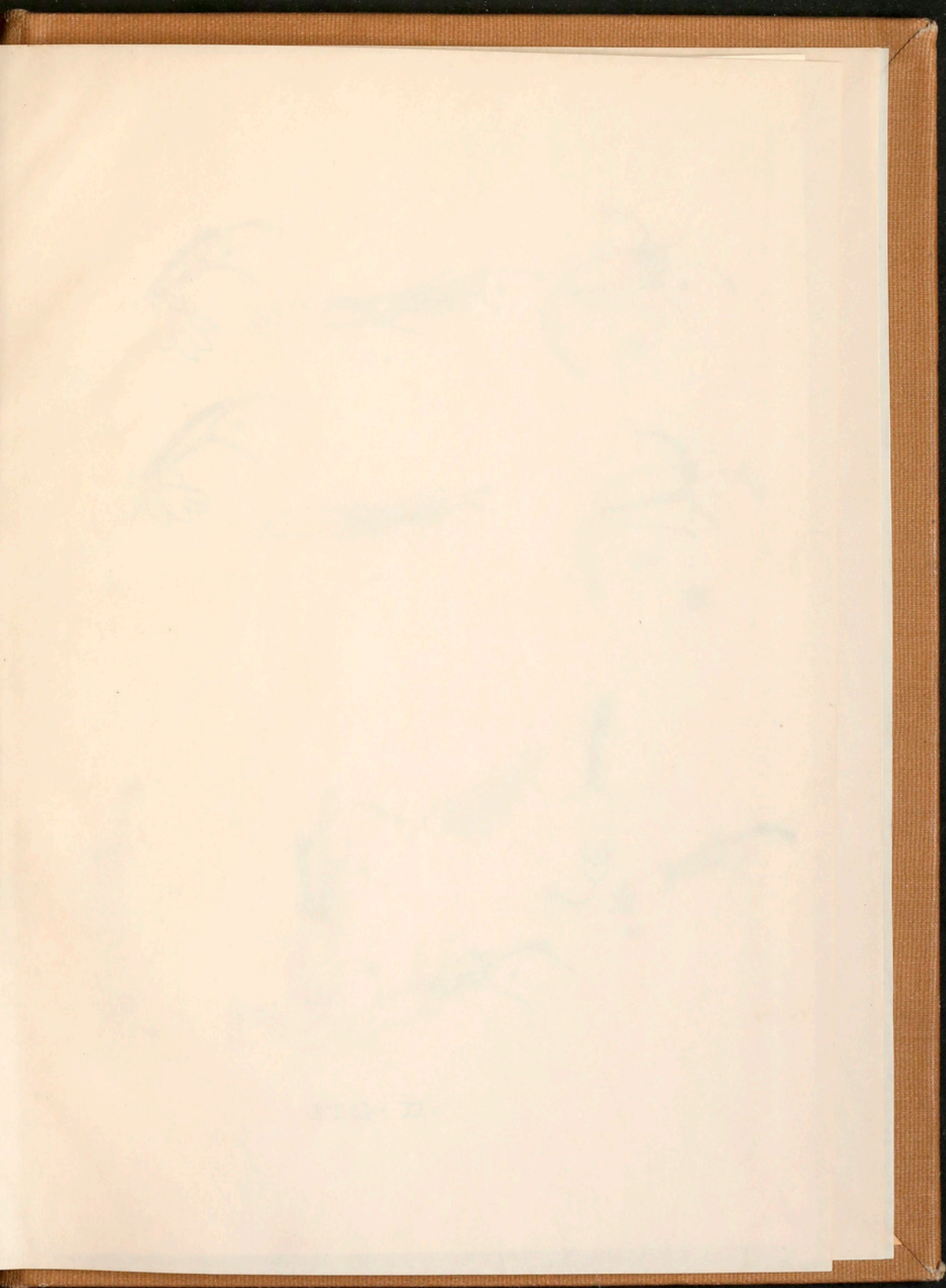
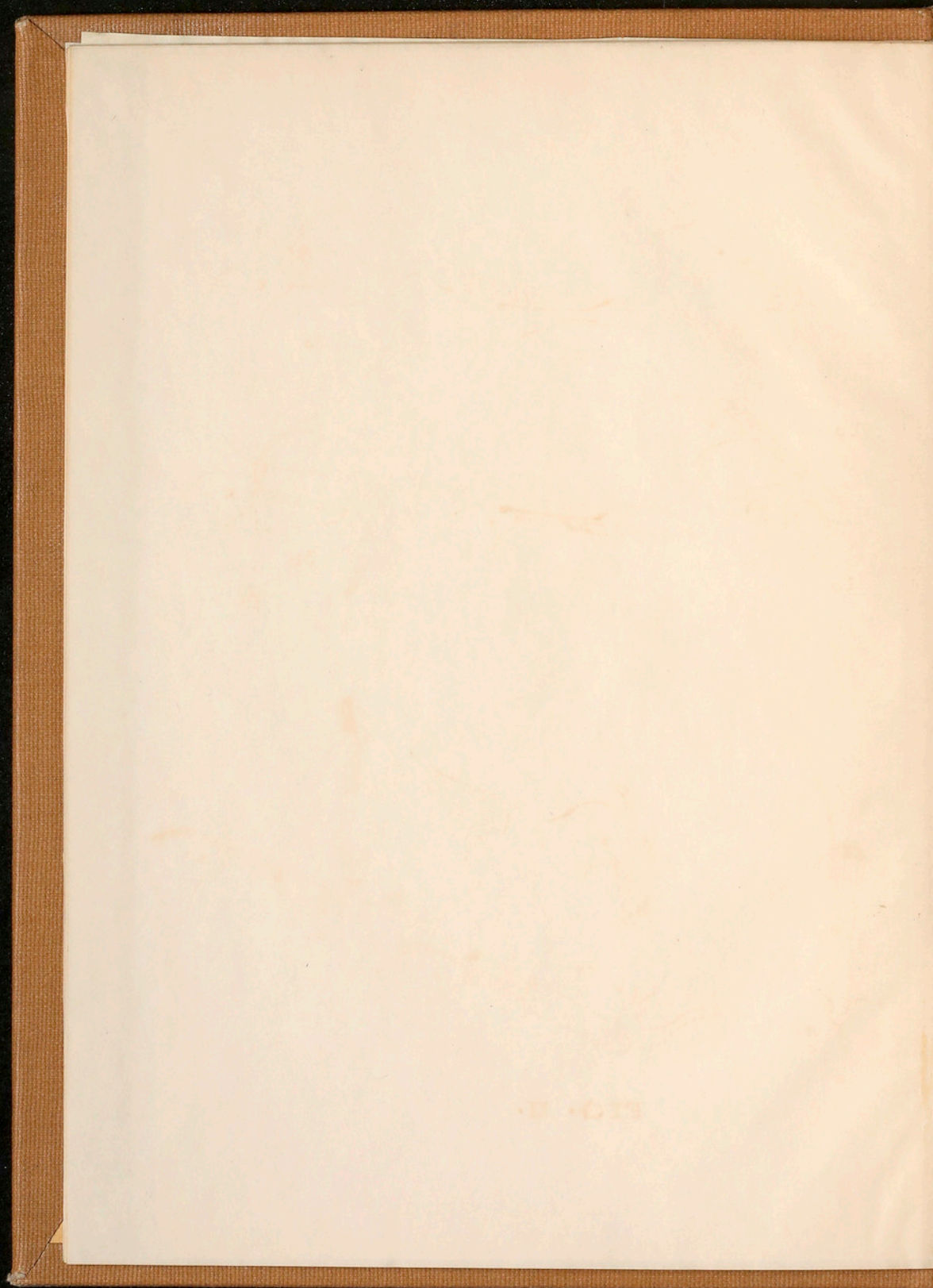


FIG. I.







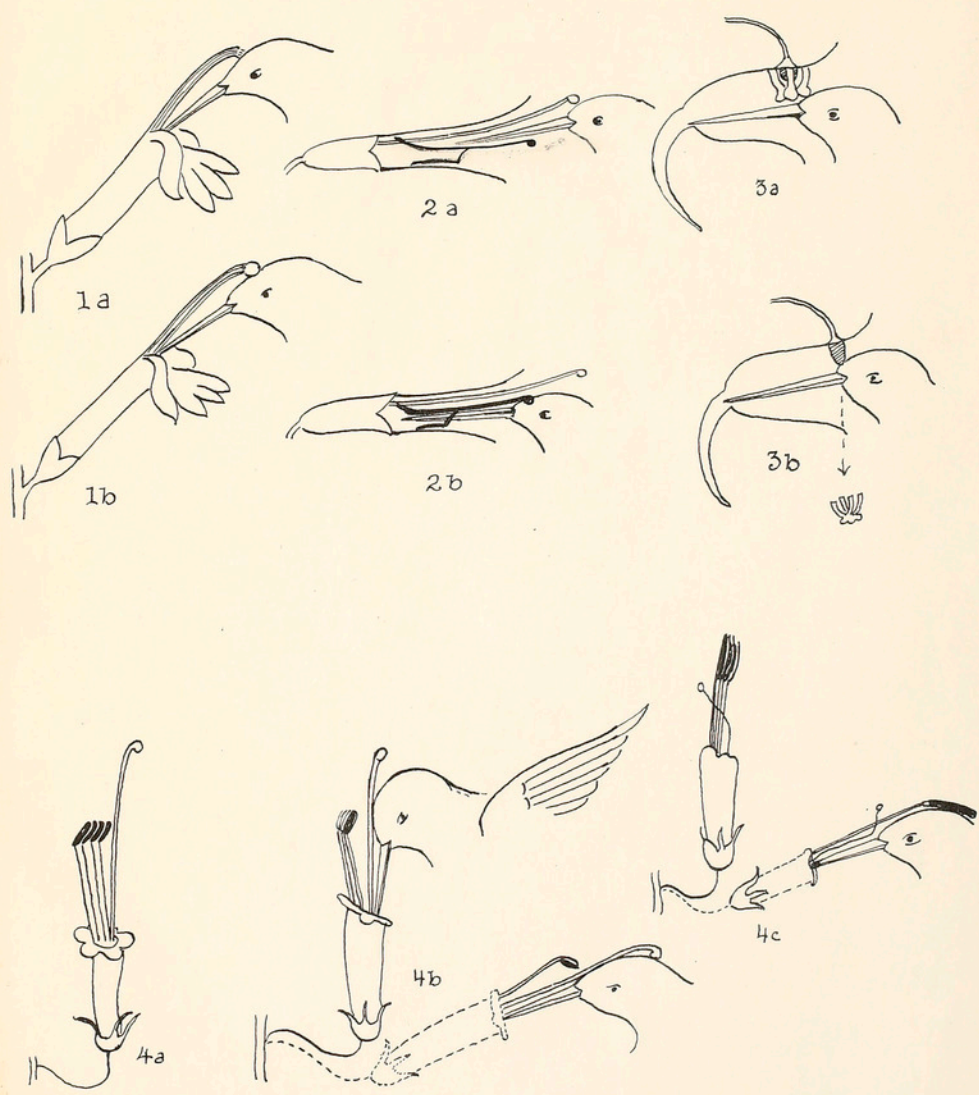


FIG. II.

